

# Systematic and biogeographic review of the Staphylinini rove beetles of Lord Howe Island with description of new species and taxonomic changes (Coleoptera, Staphylinidae)

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## Abstract

Lord Howe is an oceanic and relatively young island situated in an area of complex geological and therefore biogeographical processes. The island boasts a large number of endemic species, including many beetles, however, few groups are in an adequate state of systematic knowledge for biogeographic investigation. Recent advances in the systematics of the hyper-diverse rove beetle tribe Staphylinini on a global scale enable us to implement taxonomic changes for species from Lord Howe Island. With the improved systematics we are able to make more accurate biogeographic conclusions and set a framework for further more in-depth exploration of this unique island using rove beetles. Two new species are described: *Cheilocolpus olliffi* **sp. n.** and *Quediopsis howensis* **sp. n.** Taxonomic changes for the tribe are implemented resulting in the following new combinations: *Cheilocolpus castaneus* (Lea, 1925), **comb. n.**, *Cheilocolpus kentiae* (Lea, 1925), **comb. n.**, *Ctenandropus mirus* (Lea, 1925), **comb. n.**, and *Hesperus dolichoderes* (Lea, 1925), **comb. n.** With the updated state of knowledge, the Staphylinini fauna of Lord Howe Island appears to be mainly derived from lineages on mainland Australia.

**Keywords**

Staphylininae, Staphylinini, systematics, biogeography

**Introduction**

Lord Howe Island (LHI) is the eroded remains of a 6.9-million-year old shield volcano situated about 600 km East of Australia (McDougall et al. 1981). At 11 km in length and 2.8 km wide at its widest point, the island is characterised by two peaks, Mount Gower (875 m) and Mount Lidgbird (777 m) (Woodroffe et al. 1995), which are both located in the southern half of the island. Given the islands' volcanic origins, geographic position along the western edge of the Lord Howe Rise (a major component of the Melanesian Rift) and its exposure to environmental factors such as winds typically dominated by seasonal prevailing westerly winds and year-round south to southwesterly trade winds (Woodroffe et al. 1995), LHI presents an ideal opportunity to investigate island colonization and biogeography.

LHI exhibits an impressive level of endemism across many taxonomic groups. For example, almost half of invertebrates on LHI are endemic (Cassis et al. 2003). The island was declared a UNESCO World Heritage Site in 1982 partly because of its insular biota and significant proportion of endemic species. Despite these figures, it is apparent that much biodiversity from the island remains to be described. It is also important that proper sister-group relationships and respective taxonomic placement is established for many described but systematically poorly understood species.

As a big and diverse insect order, beetles (Coleoptera) are one of the best groups to investigate evolutionary forces and resulting biogeographic patterns on LHI. According to Cassis et al. (2003) 60% of LHI beetles are endemic. Cassis et al. (2003) also suggested at least ten species of beetles to be extinct on LHI due to predation by introduced rodents.

Staphylinidae (rove beetles) is the biggest family of beetles, with around 60,000 species so far described (Solodovnikov et al. 2013). About 45 species of rove beetles are known from the LHI, plus a number of morphospecies identified to genus level (unpublished checklist maintained by C. Reid). Many rove beetles are generalised predators or saprophages and therefore they are not dependent on any particular environmental factor such as host plants for phytophagous beetles. Therefore, staphylinids are a particularly suitable model for studying evolution and biogeography of LHI. The poor state of taxonomic and phylogenetic knowledge of rove beetles, especially in Australasia, acts as an impediment for their use for biogeographic studies, and the rove beetle fauna of the LHI is no exception. Despite this, the rove beetle tribe Staphylinini, comprising over 5500 species globally (Brunke et al. 2016), have become much better understood phylogenetically and can now be used for biogeographic purposes as

well, including studies focussing on the Australo-Pacific region (e.g. Solodovnikov and Brunke 2016).

Here, we review Staphylinini of LHI in the context of biogeography. Prior to our study, knowledge about Staphylinini of the LHI was very limited. Therefore, we fill this knowledge gap by critically reviewing taxonomy of all described species of Staphylinini of the LHI, and studying some newly collected material, especially for the subtribe Amblyopinina Seevers, 1944 which is a predominant lineage of that tribe in the Australo-Pacific region. This led to the discovery of new species and proper generic placements of some hitherto described species presented in this paper.

## Materials and methods

Material was examined as either traditionally point-mounted specimens or as disarticulated wet preparations in small petri dishes containing glycerin. Specimens were studied using a Leica MZ APO stereomicroscope. Genitalia are stored in glycerin in capsules under their respective specimens. Photographs were taken using a Leica MZ 16 A dissection microscope with a Leica DFC450C camera or a Canon EOS 7D combined with a Visionary Digital Imaging System and stacked using the Zerene Stacker Software. Photos were edited in Adobe Photoshop CS6. Drawings were digitally inked from photos in Adobe Illustrator CS6. The following measurements were taken using an ocular micrometer and are given in millimetres (mm). **HL** – Head Length (from apex of frons to neck constriction), **HW** – Head Width (maximal, including eyes), **PL** – Pronotum Length (along midline), **PW** – Pronotum Width (maximal), **EL** – Elytral Length (from acute humerus to most distal apical margin (best taken in lateral view), **EW** – combined Width of both Elytra (maximal, with elytra closed along suture). Total body length was taken from the apex of the frons to apex of abdomen. Data labels on holotype and paratype specimens are repeated verbatim; label data from additional material is standardized (not verbatim). A forward slash (/) indicates separation of labels and a semi-colon (;) indicates separation of specimens in the ‘Material examined’ sections. To both new species we attach our ‘holotype’ (red) and ‘paratype’ (yellow) labels with all necessary information.

Specimens in the present study are deposited in the following collections:

- AMS** Australian Museum, Sydney (C. Reid)
- ANIC** Australian National Insect Collection, Canberra (C. Lemann)
- BMNH** Natural History Museum, London (R. Booth, M. Barclay)
- FMNH** Field Museum of Natural History, Chicago (A. Newton, M. Thayer, C. Maier)
- SAM** South Australian Museum, Adelaide (P. Hudson)
- QM** Queensland Museum, South Brisbane (G. Monteith, G. Thompson)
- ZMUN** Zoological Museum, University of Oslo, Oslo (V. Gusarov)

## Results

### Taxonomy

#### Subtribe Amblyopinina Seevers, 1944

#### Genus *Cheilocolpus* Solier, 1849

#### *Cheilocolpus kentiae* (Lea, 1925), comb. n.

Figures 1, 2C

*Heterothops kentiae* Lea, 1925

**Material examined. Type material. Paratypes:** All 20 paratypes kept in three institutions are mounted on 9 cards (pins) in groups from 1 to 5 specimens, with each pin having the same label printed on green or plain paper: ‘On Kentia. Lord Howe I. A.M. Lea’. Additionally, respective groups of specimens on each pin have the following labels: 2 females, ‘*Heterothops kentiae* Lea. Lea, Co-type [preprinted label with Lea’s handwriting] / Cotypes / Paratype [blue printed label] / K 188918 [printed white label]’; 2 females, ‘Co-type [printed label] / Paratype [pale blue printed label] / K56145 / Paratype [dark blue printed label] / K 188917 [printed white label]’; 1 male [mounted on its back] and 1 female, ‘*Heterothops kentiae* Lea. H288 Lea, Co-type [preprinted label with Lea’s handwriting] / Paratype [pale blue printed label] / A.H. Elston Collection [printed label] / K 188916’ (all six specimens on three pins from AMS); 1 male, 1 female, ‘*Heterothops kentiae*. Lea, Co-type [preprinted label with Lea’s handwriting] / Department of Zoology. Natural History Museum. University of Oslo. (ZMUN) [printed label] / Syntype. V.I. Gusarov rev. 2005 [two red printed labels]’ (ZMUN); 3 males, 2 females, ‘Summit of Mt. Gover, L.H.I. A.M. Lea / *Heterothops kentiae* Lea, Co-type [preprinted label with Lea’s handwriting] / Cotypus, Lea don. A. Lea [purple label in M. Bernhauer’s handwriting] / Chicago NHMus M. Bernhauer Collection [printed label]’; 1 male, 2 females, ‘*Heterothops kentiae* Lea, Co-type [preprinted label with Lea’s handwriting] / Cotypus, Lea don. A. Lea [purple label in M. Bernhauer’s handwriting] / Chicago NHMus M. Bernhauer Collection [printed label]’ (FMNH); 2 males on the same card, ‘c/3079 / *Heterothops kentiae* Lea, Co-type [preprinted label with Lea’s handwriting]’; 2 specimens mounted on two separate cards but on the same pin, ‘Lord Howe I., A.M. Lea / C 3199 / *Heterothops kentiae* Lea, Co-type’ (QM).

**Additional material, all from Lord Howe Island, Australia.** 5 specimens: Stevens Reserve, rotted log and bark litter with fungi, 23.v.1980, S. + J. Peck; 2 specimens, Intermediate Hill, Big Creek, malaise trap through tall forest, 18-30.v.1980, S. + J. Peck; 1 specimen, Intermediate Hill, Big Creek, litter under carrion baits, 30.x.1980, S. + J. Peck; 7 specimens, Far Flats, thatch palm litter with nuts, 21.v.1989, S. + J. Peck (ANIC); 9 specimens: Mount Gower, 650–882 m [various collection dates] (AMS); 1 specimen: Mount Lidgbird, leaf litter of Bird’s Nest Fern *Asplenium goudeyi* 1.5 m off ground, 21.x.2001, Ian Hutton (AMS).

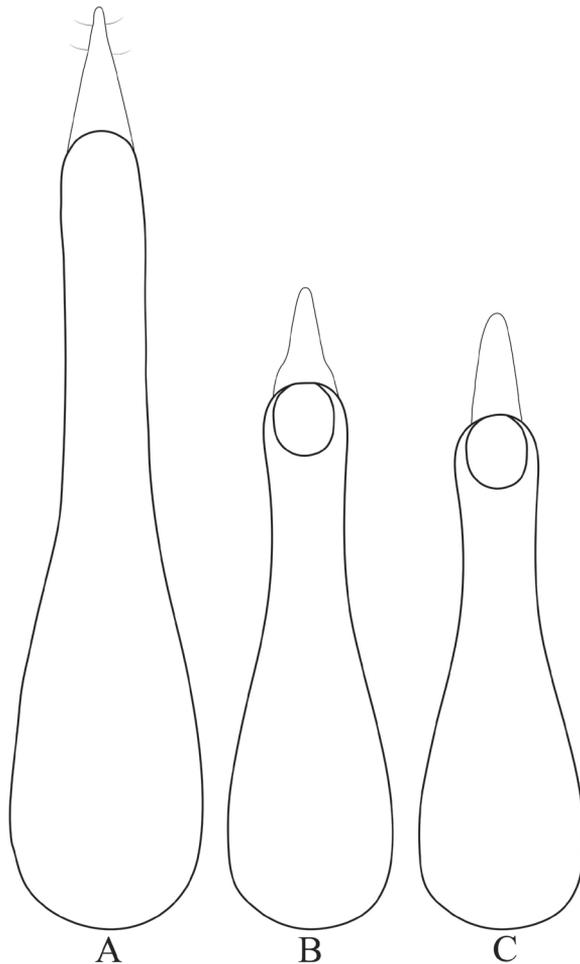


**Figure 1.** Habitus of *Cheilocolpus kentiae* (Lea, 1925).

**Diagnosis.** Habitus as in Figure 1. Head as wide as, or wider than pronotum, black to dark brown with distinct microsculpture; infraorbital ridges short, far not reaching base of mandibles; postmandibular ridges well developed, extending towards gular sutures but not reaching them; postgena with scattered shallow punctures; eyes about a third of the size of the side of the head; antennomeres 1–3 yellow, 4–11 dark brown; distal antennomeres transverse; apical segment of labial and maxillary palpi aciculate. Pronotum dark brown with two punctures in each dorsal series and distinct microsculpture, hypomera without post-coxal process; elytra dark yellow, each elytron generally with posterior two thirds darkened; fully winged; legs yellow, tarsi with very long setae ventrally, protarsi with a few long white adhesive setae ventrally. Tergites III to V with anterior and posterior basal carinae; male sternite VIII without apical incision (unusual for most of Staphylininae); aedeagus with paramere; closely attached to, and apically protruding over, but median lobe and paramere still two distinctly separate entities, paramere apically rounded with several setae (Figure 2C).

**Taxon discussion.** The original placement of *Cheilocolpus kentiae* in the genus *Heterothops* Stephens, 1829, like many other species of Australian Amblyopinina, was based on the aciculate last segment of maxillary palpi and resemblance in habitus. With such poorly justified generic identifications, *Heterothops* Stephens, 1829 was inflated to a genus of about 150 species from all over the world (Coiffait 1978; Smetana 1971, 1988; Herman 2001; Solodovnikov and Schomann 2009). *Heterothops* is based on the European species *H. binotatus* (Gravenhorst, 1802) and its generic limits when including better known Holarctic species only (Smetana 1971; Coiffait 1978) are more clear. Holarctic *Heterothops* can be defined by the following character combination: long infraorbital ridges extending to base of mandibles; aciculate last segment of maxillary palps; pronotal hypomera without translucent post-coxal process; anterior tarsi dilated in both sexes; abdominal segments III–V with posterior basal carina connecting spiracles; and aedeagus with paramere entirely fused to median lobe so that both structures appear as one entity. Earlier this fusion was correctly recognized by Coiffait (1978) but misinterpreted as the complete loss of parameres by Smetana (1988).

With poorly studied global species diversity of ‘*Heterothops*’, it is not clear how far this character combination holds when Neotropical or Oriental species are considered (*Heterothops* is represented by one species in the Afrotropical region according to Solodovnikov and Schomann 2009). But, as far as the native Australian ‘*Heterothops*’ are concerned, it is clear that they are not congeneric with the Holarctic ones. Although the Australian and Holarctic species share some characters from the above mentioned diagnostic combination, the former do not have extended infraorbital ridges and their aedeagi have very distinct median lobe and paramere. At the same time, Australian ‘*Heterothops*’ share the same diagnostic character combination with the Chilean genus *Cheilocolpus* Solier, 1849, namely: infraorbital ridges poorly developed, short, never reaching the base of mandibles; apical segment of labial and maxillary palps aciculate, at base distinctly more narrow than apex of penultimate segment; pronotal hypomera without translucent post-coxal process; abdominal tergites III–V (or at least III) with anterior and posterior basal



**Figure 2.** Aedeagi of Lord Howe Island *Cheilocolpus* (anti-parameral view). **A** *Cheilocolpus olliffi* sp. n. **B** *C. castaneus* (Lea, 1925) **C** *C. kentiae* (Lea, 1925).

carinae, the latter connecting spiracles; paramere not fused with median lobe, distinct. Also, *Cheilocolpus* differ from *Heterothops* in habitus: the former (in dorsal view) have elongate more or less parallel-sided pronotum, while the latter have pronotum with sides narrowing anteriorly.

The genus *Cheilocolpus* is based on *C. pyrostoma* (Solier, 1849) and, compared to other free living south temperate Amblyopinina, is relatively well monographed in a series of papers (Coiffait and Sáiz 1966; Sáiz 1971). Its limits with other related Neotropical genera such as *Rolla* Blackwelder, 1952 or *Philonthellus* Bernhauer, 1939 are not clear and must be investigated more elaborately. However, the listed shared character states and remarkable habitus similarity between the Australian '*Heterothops*'

species and smaller members of *Cheilocolpus* such as *C. angustatus* (Solier, 1849) from Chile, make it plausible to consider them congeneric. Such affinity is also biogeographically plausible in view of Gondwana-derived transantarctic connections between Australia and South America (e.g. Boger 2011). Even though we plan to move the main bulk of species of the Australian ‘*Heterothops*’ to *Cheilocolpus* in the course of a phylogeny-based generic revision of Amblyopinina (Jenkins Shaw & Solodovnikov, in prep.), here we already do so for *Heterothops kentiae* (and one other species, see below). Nomenclatural priority of the generic name *Cheilocolpus* over *Rolla* or *Philonthellus* also encourages this transfer now even though a separate genus status of these genera with respect to each other may be reconsidered in the future.

**Note on the type material.** In the original description of *Heterothops kentiae*, Lea (1925) mentioned that he and his wife collected multiple specimens at Mt. Gower on fallen fronds and on wet parts of the *Kentia canterburyana* palm trees. He also indicated a specimen with the number ‘I.12690’ as a ‘type’. Based on the information in the original description, all specimens examined here are paratypes, many of which were apparently distributed by Lea among colleagues. Even though we did not examine the holotype (specimen with ‘I.12690’) that apparently is kept in Lea’s collection at the South Australian Museum in Adelaide, identity of the paratypes is unambiguous.

***Cheilocolpus castaneus* (Lea, 1925), comb. n.**

Figure 2B

*Heterothops castaneus* Lea, 1925

**Material examined. Type material. Holotype (male) and two paratypes (male and female), all from Lord Howe Island, Australia.** All three specimens mounted on the same card (1 pin). Holotype is far right male marked by Lea with letters ‘TY’ written on the card next to the specimen [here dissected with apical abdominal segments and aedeagus placed in the microvial with glycerin pinned under]. ‘I. 12691 *Heterothops castaneus* Lea. Lord Howe I. also slide [Lea’s handwritten label with the word ‘TYPE’ written in red ink along right margin] / *castaneus*. Lea, type. Lord Howe [small preprinted label with handwriting] / SAMA database No. 25-036194’ / Holotype (male, TY) and 2 Paratypes *Heterothops castaneus* Lea Jenkins Shaw & Solodovnikov rev. 2016 [red printed label] (SAM)’.

**Additional material, all from Mt. Gower summit at 850 m of elevation, Lord Howe Island, Australia.** 1 female, 850m, 27.ix.1978, T. Kingston, mossy forest; 1 male, 9.xi.1979, G. B. Monteith / Q.M. BERLESATE No. 135. Volcanic soil, sieved litter. / Voucher Specimen 81-42 (QM)

**Diagnosis.** Head about as wide as pronotum, brown, depigmented; infraorbital ridges short, far not reaching base of mandibles; postmandibular ridges well developed, extending towards gular sutures but not reaching them; postgena with several shallow punctures; eyes about a quarter or the size of the side of the head; antennomeres 1-3

slightly paler than 4-11; antennomeres 1-6 elongate; apical segment of labial and maxillary palpi aciculate. Pronotum brown, concolourous with head, with two punctures in each dorsal series and faint microsculpture, hypomera without post-coxal process; elytra brown, concolourous with head and pronotum; legs brown, concolourous with rest of body. Tergites III to V with anterior and posterior basal carinae; male sternite VIII without apical incision; aedeagus with paramere closely attached to, and apically protruding over, but paramere still distinct as structure separate from median lobe, apex of paramere rounded but more acute than *C. kentiae* (Figure 2B).

**Taxon discussion.** *Heterothops castaneus* Lea, 1925 was described from Lord Howe Island where specimens were collected from leaf litter. Lea (1925) suggested its resemblance to species of *Calodera* (Aleocharinae) but also noted that it may be close to *H. xantholinoidea* MacLeay (1873) (= *H. fauveli* Bernhauer & Schubert, 1916), a species from Australia which will also be transferred to the genus *Cheilocolpus* in due time (Jenkins Shaw & Solodovnikov, in prep). Here we transfer *H. castaneus* to the genus *Cheilocolpus* for the same reasons as presented in 'Taxon discussion' for *C. kentiae*. Cassis et al. (2003) classified *C. castaneus* (there as *Heterothops castaneus*) as 'Threatened Vulnerable' and 'Uncommon'.

**Note on the type material.** In the original description of *Heterothops castaneus*, Lea (1925) mentions 6 specimens collected from fallen leaves. He also indicated a specimen with the number 'I. 12691' as the 'type'. Here we examined three specimens from Lea's collection in SAM, all mounted on the same card on one pin. Based on the information from the original description, among them a male marked by Lea with the letters 'TY' (for details see Material examined) is the holotype. All three specimens mounted on the same pin bear a handwritten label by Lea stating 'I. 12691' which reassures our correct interpretation of a holotype. The other two beetles (male and female) on the same card as the holotype are paratypes.

***Cheilocolpus olliffi* Jenkins Shaw & Solodovnikov, sp. n.**

<http://zoobank.org/CA56ADED-8397-4190-9A8D-F5169ACB35DD>

Figures 2A, 3

**Material examined. Type material. Holotype:** Male, point-mounted with apical abdominal segments in glycerin in capsule under specimen, with labels 'AUSTRALIA: N.S.W., Lord Howe Island, 17-31.v.1980, S. + J. Peck / Intermediate Hill, Big Creek, 50'-200', malaise trough, tall forest, 18-30.v.80 / Holotype *Cheilocolpus olliffi* Jenkins Shaw and Solodovnikov des. 2016' (ANIC). **Paratypes** [all supplied with the labels 'Paratype *Cheilocolpus olliffi* Jenkins Shaw and Solodovnikov des. 2016': 3 males with locality labels same as holotype specimen. 5 paratypes with labels 'AUSTRALIA: N.S.W., Lord Howe Island, 17-31.v.1980, S. + J. Peck / Intermediate Hill, 50' pan traps, 19-30.v.1989' (ANIC); 1 male with labels 'NSW: Lord Howe Is., Mt Gower summit, c870m, 31°35'23"S. 159°04'21"E, 05Dec2000, C. Reid, Visitors book, mossy floor / K 188898 / H. sp2' (AMS).



**Figure 3.** Habitus of *Cheilocolpus olliffi* Jenkins Shaw & Solodovnikov, sp. n.

**Description.** Measurements: HL 0.5–0.7; HW 0.5–0.6; PL 0.7–0.8; PW 0.5–0.7; EL 0.8–1; EW 0.8–1.1. Total body length 3.6–5.

Small, black to dark brown beetles. Habitus as in Figure 3.

Head capsule elongate more or less parallel-sided. Head surface with transverse microsculpture, on vertex with additional pair of punctures between anterior frontal punctures (sensu Smetana 1971), on temples sparsely pubescent. Length of eyes about one third of the side of the head. Nuchal ridge complete. Infraorbital ridge present but very short, far not reaching base of mandibles. Maxillary and labial palpi yellow, their apical segment aciculate. Labrum transverse, somewhat bilobed. Mandibles strongly produced. Dorsal mandibular ridge developed posteriorly. Gular sutures converging posteriad but not joining. Postmandibular ridge developed, directed towards gular sutures. All antennomeres elongate; first slightly paler than 2-11; 1-3 setose; 4-11 setose and with tomentose pubescence.

Surface of pronotum with transverse microsculpture and three pairs of punctures in dorsal series. Hypomeron strongly inflexed, and thus not visible in lateral view. Post-coxal process absent. Basisternum with pair of macrosetae.

Scutellum with only anterior scutellar ridge. Light brown, covered in setiferous punctures. Fully winged species, veins CuA and MP4 fused in one vein and vein MP3 present.

Legs yellow to orange with femora slightly darker than tibia and tarsi. Tarsal formula 5-5-5. Tarsi with sparsely distributed long setae ventrally.

Abdominal tergites III to V with anterior and posterior basal carinae the latter connecting spiracles.

Male. Sternite VIII without apical incision. Aedeagus with paramere closely attached to, and apically protruding over median lobe, but both still distinctly seen as two separate structures. Paramere apically acutely pointed with several small setae. In lateral view apical portion of paramere somewhat expanded. Apical tip of median lobe with narrow notch. Aedeagus of *C. olliffi* noticeably more elongated and about twice the length of the aedeagus of *C. kentiae* or *C. castaneus* (Figure 2A).

**Diagnosis.** *Cheilocolpus olliffi* can be distinguished from other species of the genus from Australia based on the three pairs of punctures in the dorsal series of the pronotum and the pair of punctures on the frons between the eyes. Compared to the other LHI species, *C. kentiae* and *C. castaneus* with respective antennomeres transverse, *C. olliffi* has antennomeres 6-11 elongate. All three LHI *Cheilocolpus* species have very distinctive habitus and aedeagi (Figure 2).

**Etymology.** *Cheilocolpus olliffi* is named in recognition of Arthur Sidney Olliff (1865–1895), an English-born entomologist and taxonomist who made significant contributions to the understanding of LHI's insect fauna, including recognising its affiliation with the mainland Australia. The species epithet is a noun in the genitive singular.

**Taxon discussion.** The species is placed in the genus *Cheilocolpus* because it fully matches the diagnosis of the genus given in the Taxon discussion section under *C. kentiae*.

## Genus *Ctenandropus* Cameron, 1926

### *Ctenandropus mirus* (Lea, 1925), comb. n.

*Heterothops mirus* Lea, 1925

**Material examined. Type material. Holotype:** male [mounted on the same card with two female paratypes but marked with letters ‘TY’ by Lea], ‘mirus Lea, Type, Lord Howe I. / I.12703 *Heterothops mirus* Lea Lord Howe, also slide [Lea’s handwritten label]/SAMA Database No. 25-036156 (SAM); **Paratypes:** 2 females [mounted on the same card with the holotype], same labels as in holotype; 1 male, 2 females [mounted on the same card], ‘On *Kentia* Lord Howe I. A.M. Lea / co-type / *Heterothops mirus* Lea co-type, Lord Howe I.’ (SAM).

**Taxon discussion.** *Heterothops mirus* Lea, 1925 was originally described from Lord Howe Island, based on specimens collected on *Kentia* palms. Lea (1925) noted its affiliation with *Heterothops magniceps* Bernhauer, 1920, in particular because of the unusually wide neck and extremely small eyes. The genus *Ctenandropus* was described by Cameron (1926) for a single species *C. nigriceps* Cameron, 1926 that is presumably broadly distributed in Australia and Indonesia. Smetana (1988) complemented the detailed original description of *Ctenandropus* by additional diagnostic notes, redescribed *C. nigriceps* and transferred *Heterothops magniceps* Lea, 1925 to that genus. *Ctenandropus* is one of the most easily recognizable genera of Amblyopinina due to its rather flat, small yellowish to brown body with very broad head having no neck constriction, and black combs in both sexes on the first mesotarsomere. The genus has wide distribution in the Oriental and Australo-Pacific regions and its species need revision which is not within the scope of this paper. Based on the study of type material of *H. mirus* kept at the South Australian Museum which fully matches the diagnosis of *Ctenandropus*, we propose the new combination *Ctenandropus mirus* (Lea, 1925). Species level identification of the *Ctenandropus* from LHI must be further verified, as stated above.

## Genus *Quediopsis* Fauvel, 1878

### *Quediopsis howensis* Jenkins Shaw & Solodovnikov, sp. n.

<http://zoobank.org/FE627261-1BA0-4057-9DCD-4BA77515CB5F>

Figures 4–7

**Material examined. Type material. Holotype:** Male, point-mounted with apical abdominal segments in glycerin in capsule under specimen, with labels ‘Lord Howe Is: Mt Gower tk, 159°04'59"E 31°35'2"S, 730m N Velez 1-14 Nov 2004, Site G29 litter Zygonium, Dracophyllum forest / Australian Museum K403172’/ Holotype *Quediopsis howensis* Jenkins Shaw and Solodovnikov des. 2016’ (AMS). **Paratypes** [all supplied with the labels ‘Paratype *Quediopsis howensis* Jenkins Shaw and Solodovnikov des. 2016’: 1 female, ‘Lord Howe Is: Mt Gower tk, 159°04'49"E 31°35'9"S, 800m

N Velez 1-12 Nov 2005, Site G32 litter Zygygy/Dracophyllum forest / Australian Museum, K403175'; 1 male, 'Lord Howe Is: Mt Gower tk, 159°05'1"E 31°35'00"S, 690m N Velez, 10-17 May 2004, Site G27 litter, Hedy. canterburyana forest / Australian Museum K403173'; 1 female, 'Lord Howe Is: Mt Lidgeb tk, 159°05'26"E 31°33'39"S, 360m N Velez, 1-14 April 2006, Site L11 litter, Drypetes/Cryptocarya / Australian Museum K403177'; 1 male, 'NSW; On Soldiers Ck at NW junction, Lord Howe Is; -31:34:55; 159:5:9; 12/12/2003 to 22/12/2003; L. Meades, S. Lassau, G. Brown; RATSF6-4P (pit / Australian Museum K403169'; 1 female, 'NSW; Mt Gower, Lord Howe Island – Midway down ridge N of igloo; -31:35:5; 159:4:35; 18-Jan-2002 to 31-Jan-2002; I. Hutton; ca. 819m; MG005 (pit trap) / K 188885 / Loan No. 1947, Australian Museum'; 1 male, 'Lord Howe Is: Mt Gower tk, 159°05'10"E 31°34'50"S, 490m N Velez, 1-12 Nov 2004, Site G19 litter Dracophyllum/Metrosideros nervulosa scrub / Australian Museum K403174'; 1 female, 'NSW; "Razorback", Mt. Gower, Lord Howe Is; -31:35:30; 159:4:18; 28-Nov-2000; CBCR, Australian Museum; LHIS056L leaf litter ex Broad Close Sclerophyll Forest – Hedyscepe habitat / K188888 / Australian Museum, Loan No. 1947'; 1 female, 'NSW; 1<sup>st</sup> sites reached, next to Soldiers Ck, Lord Howe Is; -31:34:55; 159:5:9; 20-Apr-2004; L. Meades, S. Lassau, G. Brown; RATSCNF5-1L leaf litter ex: Lowland Mixed Forest litter / Australian Museum K403171'; 1 female, 'Lord Howe Is: Mt Lidgbird tk 159°05'25"E 31°33'33"S, 260m N Velez 1-14 April 2006, Site L8 litter, Syzigium fullagarii forest / Australian Museum K403176'; 1 female, 'NSW; Walking trail to Mt. Gower, at base of Scaly Bark Ridge, Lord Howe Is.; -31:34:47; 159:4:40; 02-Dec-2000 to 12-Dec-2000; CBCR Australian Museum; LHIS047/01 (pit trap) / K188882 / Loan No. 1947, Australian Museum'; 1 male, 'NSW; Closest to 2<sup>nd</sup> Tree, besides Golf Course, Lord Howe Is; -31:33:11; 159:5:1; 12/12/2003 to 22/12/2003; L. Meades, S. Lassau, G. Brown; RATGCFC4-2P (pit trap) / Australian Museum K402170'; 1 female, 1 male, 'NSW; "Get Up Place", trail to Mt. Gower, Lord Howe Is.; -31:34:58; 159:4:52; 02-Dec-2000; CBCR, Australian Museum; LHIS048L leaf litter ex Broad Closed Sclerophyll Scrub – Dracophyllum/Metrosideros habitat / K188883 / Loan No. 1947, Australian Museum'; 1 male, 'NSW; 100m E from Soldiers Ck, closer to trail, Lord Howe Is; -31:34:55; 159:5:9; 12-Dec-2003; L. Meades, S. Lassau, G. Brown; RATSCFC8-3L leaf litter ex: Lowland Mixed forest Litter / Loan No. 1947, Australian Museum'; 1 male, 'NSW; Western edge Golf Course, Lord Howe Is – Left side of clearing; -31:33:11; 159:5:1; 12/12/2003 to 22/12/2003; L. Meades, S. Lassau, G. Brown; RATGCNF1-2P (pit trap) / Loan No. 1947, Australian Museum'; 1 female, 'NSW; Mt Gower, Lord Howe Island – Bottom of gully near igloo; -31:35:4; 159:4:31; 20/11/2001; I. Hutton, P. Flemons, C. Reid; MG003L leaf litter ex Bubbia – Dracophyllum / K188887 / Loan No. 1947, Australian Museum'; 1 female, 'NSW; Mt Gower, Lord Howe Island – Midway down gully near igloo; -31:35:6; 159:4:32; 20/11/2011; I. Hutton, P. Flemons, C. Reid; MG002L leaf litter ex Bubbia – Dracophyllum / K188881 / Loan No. 1947, Australian Museum' (AMS); 1 female, 'AUSTRALIA: N.S.W. Lord Howe Island, 17-31.v.1980, S. + J. Peck / Mt. Gower, 850m, 26.v.80, rot wood w/fungi & moss, 12 L Ber'; 1 male, 'AUSTRALIA: N.S.W. Lord



**Figure 4.** Habitus of *Quediopsis howensis* Jenkins Shaw & Solodovnikov, sp. n.

Howe Island, 17–31.v.1980, S. + J. Peck / Stevens Reserve, 10', 24.v.80, moist litter in limestone sink, 16 L Ber'; 1 male, 'AUSTRALIA: N.S.W. Lord Howe Island, 17-31.v.1980, S. + J. Peck / Intermediate Hill, 300', 18.v.1980, rotted bark w/fungi, tall forest, Ber 19 L / *Quediopsis* sp det. A.F. Newton 1987' (ANIC); 1 male, 'LORD



**Figure 5.** Lateroventral view of head of *Quediopsis howensis* Jenkins Shaw & Solodovnikov, sp. n. IONR = Infraorbital extension of nuchal ridge.

HOWE ISLAND, Goat House Track, 11 Nov 1979, G.B. Monteith / Q.M. BERLESATE No. 138, Volcanic Soil, 250m, Pickard VegL Hb, Sieved litter'; 1 female, 'LORD HOWE ISLAND, Mt Gower summit (NE), 9 Nov 1979, G.B. Monteith / Q.M. BERLESATE No. 134, Volcanic Soil, 850m, Pickard Veg: GMF, Sieved litter'; 1 female, 'LORD HOWE ISLAND, Erskine Valley, north side, 22 Nov 1979, G.B. Monteith / Q.M. BERLESATE No. 160, Volcanic soil, 150m, Pickard Veg:CfLq, Sieved litter / VOUCHER SPECIMEN 81-40' (QM).

**Description.** Measurements: HL 0.7–0.9; HW 0.8–1.1; PL 1–1.2; PW 1.1–1.4; EL 0.8–1.1; EW 0.9–1.3. Total body length 5.9–7.6.

Medium sized, dark to light brown beetles. Habitus as in Figure 4.

Head brown-black in colour. Eyes about a third of the length of the head. Nuchal ridge continuing as 'infraorbital extension' to base of mandibles (Figure 5). Labrum transverse and bilobed. Mandibles with dorsal mandibular ridge indistinct. Mentum with alpha seta present (sensu Brunke and Solodovnikov 2013). Gula with weakly defined suture projecting posteriorly in the middle; gular sutures slightly narrowing medially. Labial palpi: apical segment securiform (expanded; or triangular in shape, Figure 6), covered in short setae; penultimate segment with long macrosetae extending over apical segment.



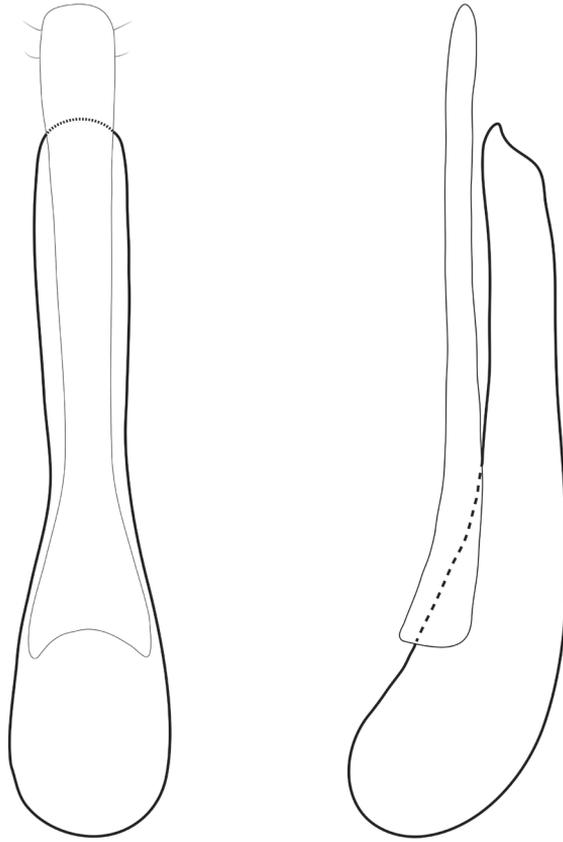
**Figure 6.** Labial palpi of *Quediopsis howensis* Jenkins Shaw & Solodovnikov, sp. n.

Antennomeres elongate, all of same colour. First antennomere slightly expanded apically, about as long as second and third combined.

Pronotum widest behind its middle at ca. posterior 2/3 of its length, slightly narrowed towards front angles; usually lighter than head in colour. Dorsal area with linear microsculpture and micropunctures visible at 40× magnification. Pronotal disk with two punctures in dorsal row: one very close to anterior margin of pronotum, and one on disc of pronotum before middle. Hypomeron inflexed and therefore not visible in lateral view, without post-coxal process. Basisternum with pair of black macrosetae and sometimes with other macrosetae positioned anterior to them.

Elytra usually the same colour as head, brown, sometimes with area around suture and scutellum rufous. Scutellum with only anterior scutellar ridge, setiferous in apical area. Sub-basal ridge present, not reaching humeral angles. Humeral angles with randomly positioned spine-like setae. Wings reduced, much shorter than elytra.

Legs concolourous. Tarsal formula 5-5-5. Both sexes with protarsi dilated and bearing dense white adhesive setae ventrally. Each tarsus with pair of empodial setae. Metacoxae almost parallel-sided along their entire length.



**Figure 7.** Aedeagus of *Quediopsis howensis* Jenkins Shaw & Solodovnikov, sp. n. Parameral view (left), lateral view (right). P = parameres, ML = median lobe.

Abdomen usually the same colour as the pronotum. Tergites III and IV with anterior and posterior basal carinae, the latter connecting spiracles; tergite VII without apical seam of palisade fringe. Sternite III with basal transverse carina medially sharply pointed and forming an acute angle. Lateral tergal sclerites IX somewhat cylindrical, slightly flattened.

Male. Sternite VIII with apical emargination. Sternite IX with basal portion asymmetrical. Apical area of paramere somewhat spatulate with several short setae (Figure 7).

Female. Sternite VIII without emargination.

**Diagnosis.** Among the described and all hitherto undescribed species of *Quediopsis* that we know from the material from throughout Australia, *Quediopsis howensis* may be separated based on the following combination of characters: apical segment of labial palpi extremely securiform; antennal segments concolourous; eyes slightly reduced; tergites III and IV with posterior basal carina connecting spiracles; apical margin of tergite VIII evenly rounded. Additionally, *Q. howensis* is the only species in the genus with characteristic microphthalmous and poorly pigmented (brownish) body.

**Etymology.** The species name refers to the fact that *Q. howensis* seems to be a unique endemic representative of the genus on Lord Howe Island. It is an adjective derived from the latter part of the islands' name.

**Distribution.** The species is only known from Lord Howe Island and is probably endemic to the island.

**Biology.** Nothing is known of the biology of the species, however label data associated with specimens indicates that it was collected in leaf litter of a variety of bush and tree species. The somewhat smaller eyes, distinctly depigmented body and fully reduced wings indicate that *Q. howensis* may be adapted to life in deep layers of leaf litter.

**Taxon discussion.** The genus *Quediopsis* Fauvel, 1878 was originally erected for two species from mainland Australia: *Quediopsis lugubris* Fauvel, 1878 and *Quediopsis abdominalis* Fauvel, 1878. Both species are very characteristic among all other Amblyopinina and share the following combination of characters that form the core of the diagnosis of the genus: apical segment of labial palpi securiform or wider than penultimate segment (Figure 6), covered in short setae; penultimate segment of labial palpi with long macro setae extending over apical segment; tergites III and IV and occasionally V with posterior basal carina in addition to anterior carina; nuchal ridge usually extending to base of mandibles (Figure 5). Subsequently, in the online database for Austral Staphylinioidea, Newton and Thayer (2005) proposed the transfer of *Quedius rubricollis* Fauvel, 1878 to *Quediopsis* (albeit without explanation). Even though the genus-level systematics of free living Amblyopinina is not developed and difficult as we have recently stated (Solodovnikov and Jenkins Shaw 2016), *Quediopsis* is a very clear cut and easy to recognise genus. Until now, no more species have been described in the genus, but based on the study of extensive material we estimate at least 6 new species of *Quediopsis* which still need to be described from mainland Australia. The genus seems to also be present in Tasmania, New Zealand and New Caledonia but this will be investigated further in our forthcoming generic revision of the subtribe. The weakly defined sinuate suture on the gula characteristic for the new species from LHI is also found in at least two undescribed species of *Quediopsis* from mainland Australia.

### Subtribe Philonthina, Kirby 1837

#### Genus *Cafius* Stephens, 1829

##### '*Cafius*' *gigas* Lea, 1929

*Cafius gigas* Lea, 1929

**Taxon discussion.** This large, wingless rove beetle is only known from the type series collected from Mount Lidgbird. Although the exact location on Mt. Lidgbird or the habitat where specimens were collected is unknown, Lea (1929) states that they were 'not taken from sea beaches'. *Cafius gigas* is now presumed to be extinct from Lord

Howe Island due to predation by introduced rats early in the 20th century (Cassis et al. 2003; Priddel et al. 2003). The species is only represented by a handful of earlier collected specimens which are 130 years old. Based on our examination of morphology, *C. gigas* does not belong to *Cafius*, or even the broader ‘*Cafius*-complex’ sensu Jeon et al (2012). It seems to be a member of the Australian *Hesperus-Actinus-Leucitus* lineage of *Philonthina* where it may be sister or closely related to *Hesperus dolichoderes* (Lea, 1925), a peculiar species also endemic for Lord Howe Island (see below). The fact that *C. gigas* was collected from a non-coastal location (while all true *Cafius* are known exclusively from the sea shores) supports the morphology-based suggestion regarding its misplacement in that genus. A phylogenetic study where we are also attempting to extract DNA from *C. gigas*, and where the formal transfer of that species to the proper genus will be implemented is currently in preparation.

### ***Cafius nauticus* (Fairmaire, 1849)**

*Philonthus nauticus* Fairmaire, 1849

**Taxon discussion.** *Cafius nauticus* was originally described in the genus *Philonthus* from Tahiti (Fairmaire 1849) and was later moved to *Cafius* by Fauvel (1874). *Cafius nauticus* was first reported from Australia by Fauvel (1903) and later Lea (1925), somewhat unclearly, suggested that *C. nauticus* was introduced to Lord Howe Island. In the phylogeny of Jeon et al. (2012), *Cafius nauticus* was based on a specimen from Australia and it was resolved as a sister group to the genus *Phucobius*, with *C. vestitus* Sharp, 1874 sister to the clade (*C. nauticus* + *Phucobius*). Undoubtedly *Cafius nauticus* belongs to the ‘*Cafius*-complex’ sensu Jeon et al. (2012) where, however, it was not assigned to any of the species groups but classified as *incertae sedis*. It is a wide-spread species known from Hawaii, Japan, China, Taiwan, Society Islands, Austral Islands, Samoa, Fiji, New Caledonia, Australia, Indonesia, Singapore, Sri Lanka, Madagascar, Seychelles, Mascarene Islands, Yemen, Eritrea, Djibouti, Somalia, Mauritius, Reunion, Rodriguez and, as an introduction, from Greece (Newton and Thayer 2005).

### ***Cafius sabulosus* Fauvel 1877**

**Taxon discussion.** *Cafius sabulosus* was originally described from Sydney, Australia. In the phylogeny of Jeon et al. (2012), *Cafius sabulosus* was based on a specimen from Australia and formed a monophyletic group with *Cafius algophilus* Broun, 1894 from New Zealand. Similarly with *C. nauticus* (see above), in the revised classification of Jeon et al. (2012) *C. sabulosus* and *C. algophilus* were placed as *incertae sedis* within the ‘*Cafius*-complex’. According to Newton and Thayer (2005) *C. sabulosus* is also

recorded from Queensland, New South Wales, Victoria, Tasmania, South Australia and Lord Howe Island.

### Genus *Philonthus* Stephens, 1829

#### *Philonthus antipodum* Fauvel, 1877

**Taxon discussion.** *Philonthus antipodum* was originally described from Victoria and Queensland in Australia. Subsequently, Lea (1925) reported the species from New South Wales, South Australia, West Australia and Lord Howe Island. Without a comprehensive global phylogenetic study of the genus *Philonthus*, which according to Chani-Posse (2013) and Chani-Posse et al. (in press) is not monophyletic, currently it is impossible to assess sister-group relationships of this species. Preliminary study of the photos of a syntype in the BMNH suggests *P. antipodum* may be closely related to or most likely a synonym of *Philonthus umbratilis* (Gravenhorst, 1802), a European species which is already known as adventive in New Zealand (Solodovnikov and Brunke 2016). Without examination of the rest of the type material of *P. antipodum* at Fauvel's collection in Brussels here we refrain from implementing a new synonymy. Also, material of that species from mainland Australia and Lord Howe Island, even though it superficially looks conspecific, remains to be carefully compared including genitalia dissections.

### Genus *Hesperus* Fauvel, 1874

#### *Hesperus dolichoderes* (Lea, 1925), comb. n.

*Philonthus dolichoderes* Lea, 1925

**Taxon discussion.** This species was originally described in the genus *Philonthus* (Lea 1925) where it was still listed in the printed catalogue by Herman (2001). Recently Newton and Thayer (2005) proposed the new combination *Hesperus dolichoderes* (Lea, 1925) in their online database. They are credited for the taxonomic change that we here confirm and formally implement in printed publication. Despite *Philonthus* and *Hesperus* not being monophyletic (Chani-Posse 2013; Chani-Posse et al. in press), *Hesperus dolichoderes* is clearly a part of the *Hesperus-Actinus-Leucitus-Peucoglyphus* lineage of the Asian and Australo-Pacific region. Like many taxa in that lineage, *H. dolichoderes* has a characteristically tube-like aedeagus with highly reduced paramere, a feature not characteristic to any lineage of a polyphyletic *Philonthus*. Until large scale revisions of both *Philonthus* and *Hesperus* complexes are carried out, *Philonthus dolichoderes* is moved to *Hesperus* even though this species is rather characteristic with unusually de-

pigmented brownish body, brachyptery and smaller eyes presumably adaptations to island inhabitation. Usually *Hesperus* and related listed genera of that complex are well pigmented and often brightly coloured species with well developed eyes and hind wings. In spite of the peculiar habitus of *H. dolichoderes*, its overall morphology does not conflict with the current broad and loose definition of *Hesperus*. As mentioned above, *H. dolichoderes* and '*Cafius*' *gigas* Lea, 1929 seem to be sister or at least closely related taxa, and both species will be treated in detail in a separate paper that is in preparation. The majority of *H. dolichoderes* specimens studied by us were collected from Mount Gower by pitfalls traps. The species is endemic to LHI.

### ***Hesperus pacificus* Olliff, 1887**

**Taxon discussion.** *Hesperus pacificus* Olliff, 1887 was originally described from LHI where it is endemic. In contrast to the above mentioned LHI endemic *Hesperus dolichoderes* and presumably closely related '*Cafius*' *gigas*, *Hesperus pacificus* looks like a more typical species of the genus, i.e. more brightly coloured, with well developed wings.

### **Subtribe Staphylinina Latreille, 1802**

#### **Genus *Creophilus* Leach, 1819**

#### ***Creophilus erythrocephalus* (Fabricius, 1775)**

**Taxon discussion.** *Creophilus erythrocephalus* is recorded from New Guinea, Australia, Lord Howe Island, New Caledonia, Tonga, Society Islands (French Polynesia), Hawaii, Easter Island, and finally Chile, where it is apparently introduced (Fauvel 1903; Clarke 2011). The species is found in open or disturbed habitats, often on dung and carrion; also can be attracted by light (Clarke 2011). It was first reported from LHI by Olliff (1889).

## **Discussion**

According to the most recent phylogeny of Staphylinini (Brunke et al. 2016), early evolution of this tribe displays a distinct biogeographic pattern. One of the most notable clades of Staphylinini that must have branched off early, the subtribe Amblyopinina, exhibits remarkable diversity in the temperate areas of the Southern Hemisphere and notable absence in their Northern Hemisphere temperate counterparts. In contrast, its sister clade that includes almost all other subtribes, is predominant in the temperate zone of the Northern Hemisphere and world (sub)tropics. This distinct biogeographic pattern was associated with early divergence within Staphylinini triggered by the break-

up of Pangea into Laurasia and Gondwana (Brunke and Solodovnikov 2013; Brunke et al. 2016). Diversification of the predominately south temperate Amblyopinina took place on Gondwana-derived lands in isolation from the Laurasian landmasses where the majority of other Staphylinini have evolved. With continents gradually changing shape and forming connections, as well as through trans-oceanic or island hopping dispersal of some species, lineages of the southern and northern origin moved around to form modern complex mixed faunas on larger continents or island archipelagoes. Compared to large continents or island groups of complex history, more and continuously isolated landmasses like Australia, New Zealand or some smaller islands may display clearer biogeographic patterns that can be very useful in deciphering world biogeography. For example, a recent biogeographic review of Staphylinini from New Zealand revealed that 66% of New Zealand's Staphylinini fauna are paleoendemic Gondwana-derived species of the subtribe Amblyopinina, while the rest of the fauna are either neoendemics or adventive species from the subtribes Staphylinina and Philonthina which (or their ancestors) reached New Zealand across sea gaps from the Laurasia-derived landmasses (Solodovnikov and Brunke 2016). That study of an insular New Zealand fauna in the context of recent phylogenetic hypotheses for Staphylinini went along with implementing some necessary taxonomic changes. Very poor taxonomic knowledge of the subtribe Amblyopinina, predominant in the Southern Hemisphere, remains a big obstacle on the way to more detailed biogeographic studies of New Zealand and other southern landmasses. The only recent species-level treatments of Amblyopinina concern the small genera *Mimosticus* (Brunke and Solodovnikov 2014) and *Myotyphlus* (Solodovnikov and Jenkins Shaw 2016).

The very limited fauna of Staphylinini on Lord Howe Island (LHI) with a number of unrevised or undescribed species of Amblyopinina seemed as an affordable next model to implement a biogeographic assessment similar to Solodovnikov and Brunke (2016). Besides, such an attempt was triggered by an extremely interesting biogeography and biology of the island (e.g. Buckley et al. 2009; Papadopulos et al. 2011). Prior to our taxonomic study of Staphylinini from LHI, it consisted of three endemic species of the globally distributed, poorly understood genus *Heterothops*, one endemic and two widely distributed species of *Cafius*, one Australian species of *Philonthus*, two endemic species of *Hesperus* and one species of *Creophilus* wide-spread in Australasian region.

Our study significantly changed the taxonomic and thus biogeographic composition of the LHI Staphylinini. About 40% of them are species of the Gondwana-derived subtribe Amblyopinina that are endemic on LHI: one species belonging to the Australo-Asian genus *Ctenandropus*; three (of which one is new to science) to the south temperate disjunctly distributed genus *Cheilocolpus*; and one to the mainly Australian genus *Quediopsis*. Based on our on-going study the most likely sister species to *Cheilocolpus* on LHI are to be found among unrevised species on the Australian mainland that are still placed in the genus *Heterothops*, such as *Heterothops ubiquitosus* Lea, 1925, *Heterothops nigrofrater* Lea, 1925 and *Heterothops laticeps* Fauvel, 1878. It is noteworthy that the *Sphingoquedius-Quedimimus* amblyopinine lineage which exhibits high diversity in Australia and New Zealand and also occurs on New

Caledonia and Norfolk Island (example species: *Quedius luridipennis* MacLeay, 1871 and *Quediomimus hybridus* (Erichson, 1840)) is apparently absent from Lord Howe Island. The remaining 60% of Staphylinini on LHI are part of the Laurasia-derived so called ‘Staphylinini propria clade’ (Brunke et al. 2016). Of them, four species (*Cafius nauticus*, *C. sabulosus*, *Philonthus antipodum* and *Creophilus erythrocephalus*) are more or less wide-spread, associated with sea-shore based (*Cafius*) or broader decaying substrates (*Philonthus* and *Creophilus*) and presumably colonised LHI from nearby Australia. Three species, *Hesperus pacificus*, *H. dolichoderes* and the closely related species currently wrongly assigned to *Cafius*, *C. gigas*, are more interesting. Presumably a less specialized *Hesperus pacificus* colonised LHI in the same way as other species from the *Hesperus*-complex (Chani-Posse et al. in press) colonized Australia. The origin of highly derived *H. dolichoderes* and ‘*Cafius*’ *gigas* maybe more complex and will be considered in a separate study.

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# Taxonomic notes on the genus *Bellenden* Chandler (Coleoptera, Staphylinidae, Pselaphinae)

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## Abstract

The monotypic genus *Buobellenden* Yin & Nomura, 2009 is placed as a junior synonym of *Bellenden* Chandler, 2001. This act results in *Bellenden jingyuanensis* (Yin & Nomura), **comb. n.** (from *Buobellenden*). A new species, *Bellenden siguniang* Yin & Jang, **sp. n.**, collected from the alpine area in Sichuan, SW China, is described, illustrated, and distinguished from all congeners. A new illustration of the aedeagus of *B. jingyuanensis* is given.

## Keywords

Pselaphini, new synonym, new combination, new species, China, Sichuan

## Introduction

The genus *Bellenden* Chandler of the pselaphine tribe Pselaphini contains four species with a highly disjunct distribution: *B. monteithi* Chandler (type species) occurs in Queensland, NE Australia, while *B. belousovi* Kurbatov, *B. botellarius* Kurbatov, and *B. nubigena* Kurbatov are distributed in alpine regions in SW and NW China (Chandler 2001; Kurbatov 2006). Within Pselaphini, *Bellenden* shares with many genera the

elongate maxillary palpomeres II and IV, but its palpomere IV is broadening throughout the entire length, rather than lengthily pedunculate or distinctly narrowed at the base. In Yin et al. (2009), a new genus *Buobellenden* Yin & Nomura was established from a single species collected in Ningxia, NW China, and was separated from *Bellenden* solely based on the aedeagal structures. Otherwise these two genera are morphologically similar. In this paper *Buobellenden* is placed as a junior synonym of *Bellenden*, and a new species of the genus is described from Sichuan, SW China.

## Material and methods

The type material of the new species is housed in the Insect Collection of Shanghai Normal University, Shanghai, China (SNUC).

The collecting data of the material are quoted verbatim. The Chinese translation of each locality is included in parentheses at the first appearance in the text. Each type specimen bears the following label: 'HOLOTYPE (red) (or PARATYPE (yellow)), ♂ (or ♀), *Bellenden siguniang* sp. n., det. Yin & Jiang, 2016, SNUC'.

## Taxonomy

### *Bellenden* Chandler, 2001

*Bellenden* Chandler, 2001: 504; Kurbatov 2006: 361 (revision).

Type species. *Bellenden monteithi* Chandler.

*Buobellenden* Yin & Nomura, 2009 (in: Yin et al. 2009: 65); **syn. n.**

Type species. *Buobellenden jingyuanensis* Yin & Nomura.

**Comments.** *Buobellenden* was described from a single male collected from the north-western Chinese province of Ningxia (Yin et al. 2009). The authors compared the type species *B. jingyuanensis* with the Australian *B. monteithi*, and separated these two genera based on the aedeagal characters. However, the earlier published revision of *Bellenden* by Kurbatov (2006) was not cited, in which three new *Bellenden* species were described from the alpine regions in central China. Kurbatov in his work specifically discussed the morphological differences between the *Bellenden* species from China and Australia, and concluded that creation of a new generic taxon for the Chinese *Bellenden* species is unjustified. After a re-examination of the type material of *Buobellenden*, we agree with Kurbatov's opinion, and here place *Buobellenden* as a junior synonym of *Bellenden*.

***Bellenden jingyuanensis* (Yin & Nomura), comb. n.**

Fig. 1D

*Buobellenden jingyuanensis* Yin & Nomura, 2009 (in: Yin et al. 2009: 66).

**Type locality.** Dongshanpo, Liupanshan National Nature Reserve, Jingyuan County, northwestern China.

**Type material examined.** Holotype ♂, labeled 'China: Ningxia A. R., Jingyuan Coun. (泾源县), (Liupanshan National Nature Reserve (六盘山自然保护区)), Dongshanpo (东山坡), alt. 2,200 m, 23.vi.2008, (Berlese Funnels), Yun Bu leg.' (SNUC).

**Comments.** This species can be separated from all congeners by the following combination of characters: 1) relative small body size (1.89 mm), 2) lateral margins of the frontal rostrum narrowing anteriorly, and roundly dilating laterally at the antennal bases, 3) unmodified protrochanter and metaventrite, and 4) unique structures of the aedeagal endophallus (Fig. 1D).

***Bellenden siguniang* Yin & Jiang, sp. n.**

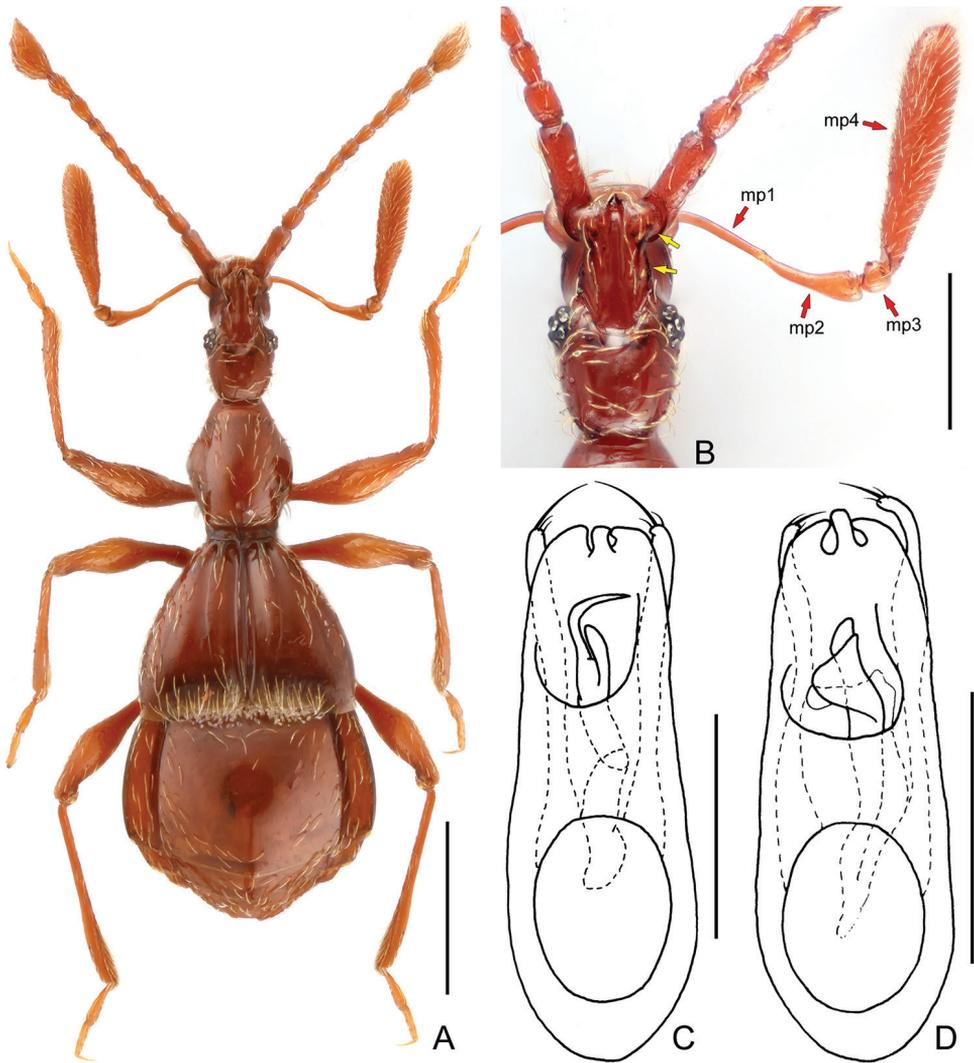
<http://zoobank.org/AAB5A9CF-5316-4CEE-AF71-911C5EB4ED50>

Fig. 1A–C

**Type material** (1 ♂, 5 ♀♀). **Holotype: CHINA:** ♂, labeled 'China: Sichuan, Xiaojin County (小金县), Siguniang Shan (四姑娘山), Haizigou (海子沟), 30°59'57"N, 102°50'51"E, leaf litter, sifted, 3,340 m, 17.vii.2015, J(iang), P(eng), T(u), Z(hou) leg.' (SNUC). **Paratypes: CHINA:** 5 ♀♀, same collecting data as the holotype (SNUC).

**Diagnosis.** Lateral margins of frontal rostrum before eyes sloping anteriorly, roundly dilating laterally at level of antennal bases; maxillary palpomere I only slightly shorter than II; male lacking ventral protuberance at ventral margin of the protrochanter, metaventrite unmodified; impressed area of sternite IV longer than wide and almost reaching posterior margin of the segment.

**Description.** Male (Fig. 1A), length 2.35 mm (combined length of head, pronotum, elytra and abdomen), body uniformly reddish-brown, pubescence recumbent and sparse. Head longer than wide, length from anterior clypeal margin to occipital constriction 0.47 mm, width across eyes 0.27 mm (Fig. 1B), frontal rostrum conspicuously narrowing anteriorly in front of anterior margin of eyes and dilating at level of antennal bases (Fig. 1B); anterior margin of frons with small triangular projection at middle, frontal sulcus without dense apical pubescence, narrow and deep anteriorly and somewhat dilating and gradually disappearing posteriorly; each eye with nine small facets; maxillary palpus (Fig. 1C) elongate, palpomere II longer than palpomere I; length of palpomere 1.05 mm, palpomere I 0.2 mm, II 0.27 mm, III 0.07 mm, IV 0.51 mm. Length of antenna 1.3 mm; antennomere I subcylindrical, more than three times as long as wide, slightly wider than antennomere II; antennomere II



**Figure 1.** *Bellenden siguniang* (A–C) and *B. jingyuanensis* (D). **A** male habitus **B** head and right maxillary palpus (yellow arrows indicate anterolateral margin of the frontal rostrum; red arrows indicate segmentation of the maxillary palpus) **C–D** aedeagus, in dorsal view. Abbreviation: mp1–4 = maxillary palpomeres I–IV. Scales bars **A** 0.5 mm; **B** 0.3 mm; **C–D** 0.2 mm.

about 1.5 times as long as wide; antennomeres III–VIII of subequal width, slightly narrower than antennomere II, antennomeres III–VII approximately twice as long as wide, antennomere VIII slightly shorter, and antennomere IX considerably wider than preceding segments, approximately as wide as antennomere II, but much longer, approximately twice as long as wide; antennomere X somewhat slightly wider than antennomere IX, antennomere XI shorter than antennomeres IX and X together, but

considerably wider than them, widest slightly before middle. Pronotum widest near middle, length along midline 0.48 mm, maximum width 0.38 mm; antebasal fovea small, puncture-like, lateral foveae larger. Elytra wider than long, length along suture 0.58 mm, maximum width 0.78 mm, covered with relatively dense long hairs along posterior margin; sutural and discal striae narrowed at base; sutural stria conspicuously deeper at base than discal stria; discal stria extending posteriorly to 3/4 elytral length. First tergite largest, widest near middle. Length of dorsally visible part of abdomen (posterior to elytra) along midline 0.82 mm, maximum width 0.92 mm; sternite IV (second visible sternite) slightly impressed medially. Aedeagus (Fig. 1C) slightly asymmetric dorso-ventrally, length 0.48 mm.

Female, similar to male in general appearance; each eye composed of nine small facets. Measurements of body parts: body length 2.24 mm, length of head 0.44–0.46 mm, width of head 0.27–0.29 mm, length of antenna 1.19–1.20 mm, length of pronotum 0.43–0.44 mm, width of pronotum 0.38 mm, length of elytra 0.59–0.61 mm, width of elytra 0.77–0.80 mm, length of abdomen 0.75–0.76 mm, width of abdomen 0.87 mm.

**Comparative notes.** *Bellenden siguniang* is similar to *B. bottellarius* and *B. jingyuanensis* by sharing unmodified male prothrochanter and metaventrite. The new species can be separated from *B. bottellarius* by the lateral margins of the frontal rostrum before eyes gradually sloping anteriorly and then roundly dilating at antennal bases, and from *B. jingyuanensis* by the much large body size. The lateral margins of the frontal rostrum in *Bellenden bottellarius* are parallel-sided and barely dilated at antennal bases, and the body length of *B. jingyuanensis* measures only 1.89 mm. *Bellenden jingyuanensis* similarly has the lateral margins of the frontal rostrum narrowing anteriorly, when combined with the structures of the aedeagal endophallus, it can be readily distinguished from *B. bottellarius*. The other three species, *B. monteithi*, *B. belousovi* and *B. nubigena*, all have spinose/protuberant prothrochanter in the male, thus are easily separable from *B. siguniang*. Moreover, the aedeagal endophallus of *B. siguniang* has a pointed and curved apex, which alone can be used to discriminate the new species from all other congeners.

**Distribution.** Southwestern China: Sichuan.

**Etymology.** The specific epithet is taken from the type locality of the new species, *i.e.*, Siguniang Mountain.

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# A preliminary molecular phylogeny of the genus *Scobura*, with a synonym of *Scobura masutaroi* (Lepidoptera, HesperIIDae)

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## Abstract

A molecular phylogeny of the genus *Scobura* based on the mitochondrial COI and the nuclear EF-1 $\alpha$  genes using maximum likelihood and Bayesian inference is proposed. The analyses include 19 specimens from nine ingroup species. The monophyly of *Scobura* is not strongly supported, but two strongly supported monophyletic groups within the genus are recognized: the *S. coniata* group and the *S. woolletti* group. Judging from combination of the molecular evidence and morphological features, the former consists of six species, including *S. masutaroi*, while four species belong to the latter. *S. mouchai* Krajcik, 2013 is confirmed to be a **syn. n.** of *S. masutaroi* Sugiyama, 1996. The key to the species of the genus *Scobura* is modified to reflect these results.

## Keywords

COI, EF-1 $\alpha$ , *Scobura masutaroi*, *Scobura mouchai*

\* These authors contributed equally to this work and should be considered co-first authors.

## Introduction

The skipper genus *Scobura* Elwes & Edwards, 1897 was recently revised by Fan et al. (2010), who recognized 14 species. The genus *Scobura*, however, includes another species, *S. masutaroi*, Sugiyama 1996. Fan et al. (2010) overlooked the existence of this taxon and did not include it in their revisional work, which resulted in Krajcik (2013) proposing a new taxon, *S. mouchai*, from Shaanxi.

Although a comprehensive morphological revision of the genus has been completed, no phylogenetic analysis has been performed to infer relationships within the genus. In the present study, we present a preliminary phylogeny of *Scobura*, based on molecular evidence. By comparing molecular and morphological evidence, we examine whether *S. mouchai* is a synonym of *S. masutaroi*.

## Methods

### Morphological examination

See Fan et al. (2010) for materials for the morphological study. In order to examine the wing venation, wings were removed from thorax, cleaned with 95% ethanol, and dyed red with acetocarmine (Wang et al. 2011).

### Taxon sampling

Twenty-three specimens including nine of the 15 valid species of *Scobura* and four out-group species were included in the phylogenetic reconstruction. Detailed information on the specimens is provided in Table 1. Specimens used in this study were mainly deposited in the Insect Collection, Department of Entomology, South China Agriculture University (SCAU), except for some specimens in Kyushu University museum (KU) and Mr. Hiroaki Onodera's private collection.

### Laboratory protocols

Genomic DNA was extracted from the thorax of specimens preserved in ethanol, or from legs of dried specimens, using Magen's Blood/cell/tissue DNA extraction kit. One mitochondrial gene *cytochrome c oxidase I* (COI) and one nuclear gene *elongation factor 1- $\alpha$*  (EF-1 $\alpha$ ) were used as molecular phylogenetic markers. The following primers were used for amplification and sequencing in this study: for COI – primers LCO1490 and HCO2198 (Folmer et al. 1994); for EF-1 $\alpha$  – primers ef44 and efrcM4 (Monteiro and Pierce 2001). Polymerase Chain Reaction (PCR) were performed in 20  $\mu$ l volumes containing 1  $\mu$ l

**Table 1.** Voucher information and GenBank accession numbers for the specimens in this study.

Species	Locality	Latitude	Longitude	Voucher Number	COI	EF-1 $\alpha$
<i>Scobura cephaloides kinka</i> Evans, 1949	China: Hainan	19.02N	109.53E	SCAU He102	KY049936	KY049958
<i>Scobura cephaloides kinka</i> Evans, 1949	Laos: Luang Prabang	19.93N	102.07E	Onodera He553	KY049937	KY049959
<i>Scobura coniata</i> Hering, 1918	China: Guangdong	24.91N	113.04E	SCAU He073	KY049938	KY049960
<i>Scobura coniata</i> Hering, 1918	China: Guangdong	24.87N	113.03E	SCAU He472	KY049939	KY049961
<i>Scobura hainana</i> (Gu & Wang, 1997)	China: Guangdong	24.87N	113.04E	SCAU He471	KY049940	KY049962
<i>Scobura hainana</i> (Gu & Wang, 1997)	China: Guangdong	24.87N	113.04E	SCAU He487	KY049941	KY049963
<i>Scobura hainana</i> (Gu & Wang, 1997)	China: Guangdong	24.87N	113.04E	SCAU He488	KY049942	KY049964
<i>Scobura isota</i> (Swinhoe, 1893)	Thailand: Kanchanaburi	14.08N	99.36E	SCAU He538	KY049943	KY049965
<i>Scobura isota</i> (Swinhoe, 1893)	Thailand: Mae Hong Son	19.35N	98.14E	SCAU He468	KY049944	KY049966
<i>Scobura lyso</i> (Evans, 1939)	China: Zhejiang	30.15N	119.25E	SCAU He465	KY049945	—
<i>Scobura lyso</i> (Evans, 1939)	China: Zhejiang	30.15N	119.25E	SCAU He475	KY049946	—
<i>Scobura masutaroi</i> Sugiyama, 1996	China: Sichuan	29.94N	102.48E	SCAU He300	KY049947	KY049967
<i>Scobura masutaroi</i> Sugiyama, 1996	China: Sichuan	29.94N	102.48E	SCAU He301	KY049948	KY049968
<i>Scobura masutaroi</i> Sugiyama, 1996 (= <i>mouchai</i> )	China: Shaanxi	31.91N	106.34E	SCAU He303	KY049949	KY049969
<i>Scobura parawoolletti</i> Fan et al., 2010	China: Hainan	19.03N	109.53E	SCAU He116	KY049950	KY049970
<i>Scobura stellata</i> Fan et al., 2010	China: Guangdong	24.92N	113.01E	SCAU He036	KY049951	KY049971
<i>Scobura woolletti</i> (Riley, 1923)	Indonesia: Kabandungan	6.77 S	106.60E	KU He535	KY049952	KY049972
<i>Scobura woolletti</i> (Riley, 1923)	Indonesia: Kabandungan	6.77 S	106.60E	KU He536	KY049953	KY049973
<i>Scobura woolletti</i> (Riley, 1923)	Indonesia: Kabandungan	6.77 S	106.60E	KU He537	KY049954	KY049974
<i>Suastus gremius</i> (Fabricius, 1798)	China: Guangdong	23.15N	113.34E	SCAU He157	KY049955	KY049975
<i>Suada swerga</i> (deNicéville, 1884)	Thailand: Chiang Mai	18.80N	98.92E	SCAU He495	KY049956	KY049976
<i>Hyarotis quinquepunctatus</i> Fan & Chiba, 2008	China: Hainan	19.03N	109.54E	SCAU He114	—	KY049977
<i>Zographetus satwa</i> (deNicéville, 1884)	China: Guangdong	24.88N	113.03E	SCAU He442	KY049957	KY049978

template DNA, 2  $\mu$ l 10 $\times$  buffer, 1.6  $\mu$ l dNTPs (containing 2.5 mM of each dNTP), 0.8  $\mu$ l of each primer (10  $\mu$ M), 0.2  $\mu$ l Taq Polymerase (2 U/ $\mu$ l), and 13.6  $\mu$ l ddH<sub>2</sub>O. The PCR Products were amplified using initial denaturation at 94 °C for 4 min, 35 cycles of denaturation at 94 °C for 30 s, annealing at 47 °C (COI) for 45 s, 55 °C (EF-1 $\alpha$ ) for 1 min, elongation at 72 °C for 1.5 min, and final elongation at 72 °C for 5 min.

Amplified DNA products were purified using an Agarose Gel Extraction kit (Magen Biotech), and directly sequenced, or cloned with pMD18-T vector (Takara Inc), and then sequenced. Sequencing was performed using the ABI 3730 automated sequencer. All sequences were submitted to the Genbank database (accession numbers are given in Table1).

### **Phylogenetic analyses**

Alignment of the DNA sequences were performed in Clustal X (Thompson et al. 1997) and edited manually in MEGA 6.0 (Tamura et al. 2013). All base frequencies and molecular character statistics were calculated in MEGA 6.0. Phylogenetic trees were constructed under maximum Likelihood (ML) and Bayesian inference (BI) criteria. For ML analysis, RAxML version 8 (Stamatakis et al. 2014) was used on a concatenated data set of two genes, with 1000 rapid bootstrap replicates using GTR+G substitution model on the CIPRES Science Gateway (Miller et al. 2010). BI was carried out using Markov Chain Monte Carlo (MCMC) randomization in MrBayes v3.2.3 (Ronquist et al. 2012). We used reversible-jump MCMC to allow for sampling across the entire substitution rate models. Four Markov chains (three heated chains, one cold) were run for 500, 000 generations, with the first 25% of sampled trees discarded as burn-in. The two independent runs were considered to have converged when the standard deviation of split frequencies value was <0.01. The convergence of the analysis was determined in Tracer v1.6 (Rambaut et al. 2014). Bayesian posterior probabilities (PP) and ML bootstrap values (BP) were used to evaluate branch support.

## **Results**

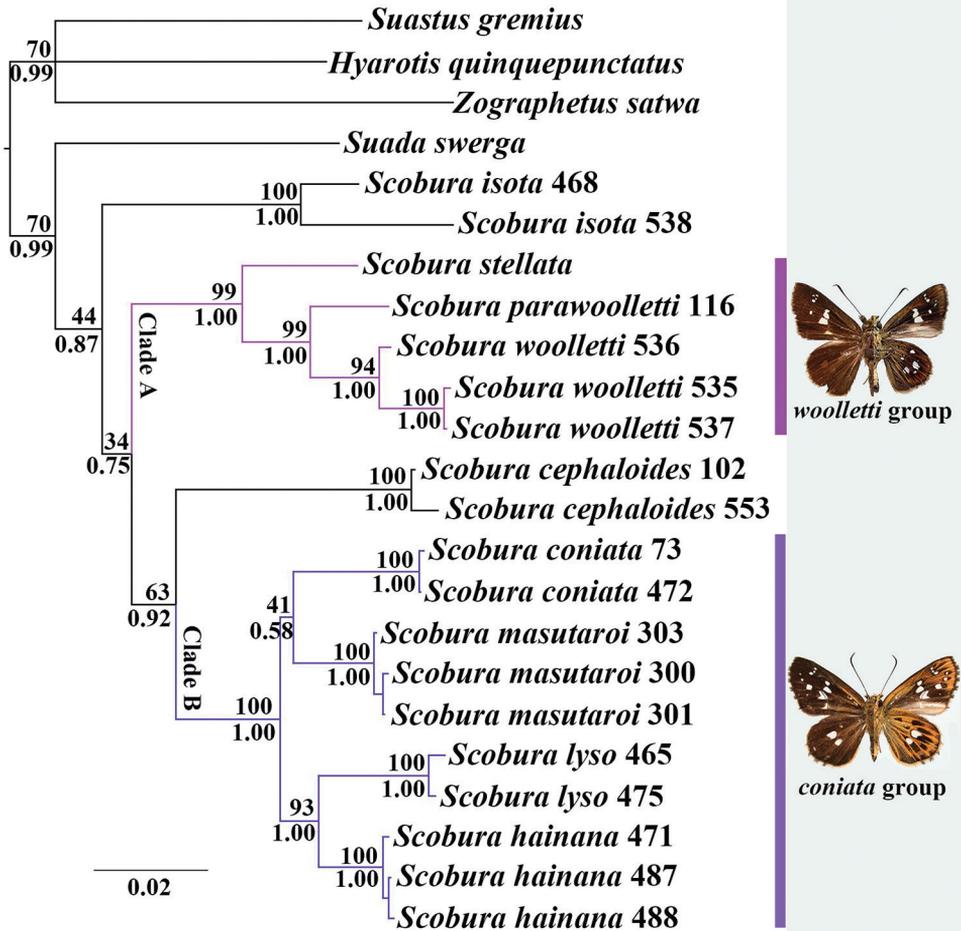
### **Sequence data**

From a total of 23 samples, 22 sequences for COI and 21 for EF-1 $\alpha$  were obtained. The alignment of the combined sequences consisted of a total of 1724 bp (658 bp of COI and 1066 bp of EF-1 $\alpha$  genes, respectively), including 277 variable and 200 informative sites.

The pairwise P2K distances among the sequences were variable between genes. The ranges of sequence divergences for two loci and ingroup taxa are: COI (0–12.4%), EF-1 $\alpha$  (0–5.0%). For COI, sequence divergence between conspecific individuals ranged from 0 to 0.6%; inter-specific genetic distances ranged from 3.6% to 12.4% with divergences among species averaging 7.9% (Table 2).

**Table 2.** Uncorrected pairwise genetic distances (Kimura 2-parameter) for the COI sequences of the genus *Scobura* species.

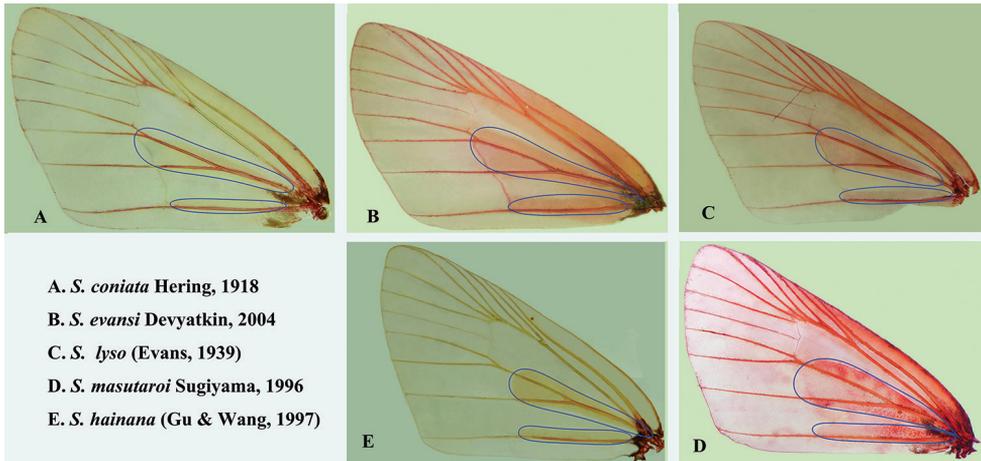
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 <i>S. cephaloides</i> 102																		
2 <i>S. cephaloides</i> 553	<b>0.003</b>																	
3 <i>S. coniata</i> 73	0.096	0.098																
4 <i>S. coniata</i> 472	0.096	0.098	<b>0.000</b>															
5 <i>S. hainana</i> 471	0.084	0.085	0.059	0.059														
6 <i>S. hainana</i> 487	0.084	0.085	0.059	0.059	<b>0.000</b>													
7 <i>S. hainana</i> 488	0.084	0.085	0.061	0.061	<b>0.002</b>	<b>0.002</b>												
8 <i>S. isota</i> 468	0.115	0.117	0.122	0.122	0.099	0.099	0.099											
9 <i>S. isota</i> 538	0.113	0.115	0.118	0.118	0.096	0.096	<b>0.006</b>	<b>0.006</b>										
10 <i>S. lyso</i> 465	0.087	0.089	0.061	0.061	0.039	0.039	0.039	0.105	0.101									
11 <i>S. lyso</i> 475	0.085	0.087	0.061	0.061	0.036	0.036	0.036	0.101	0.098	<b>0.003</b>								
12 <i>S. masutarovi</i> 300	0.092	0.096	0.059	0.059	0.056	0.056	0.056	0.107	0.103	0.052	0.052							
13 <i>S. masutarovi</i> 301	0.092	0.096	0.059	0.059	0.056	0.056	0.056	0.107	0.103	0.052	0.052	<b>0.000</b>						
14 <i>S. masutarovi</i> 303	0.092	0.096	0.059	0.059	0.056	0.056	0.056	0.109	0.105	0.052	0.052	<b>0.002</b>	<b>0.002</b>					
15 <i>S. parauwoolletti</i> 116	0.094	0.097	0.089	0.089	0.087	0.087	0.087	0.112	0.108	0.084	0.084	0.084	0.084	0.084				
16 <i>S. stellata</i> 36	0.101	0.104	0.104	0.104	0.101	0.101	0.101	0.108	0.105	0.099	0.099	0.092	0.092	0.094	0.070			
17 <i>S. woolletti</i> 535	0.094	0.097	0.096	0.096	0.085	0.085	0.085	0.124	0.121	0.092	0.092	0.099	0.099	0.099	0.039	0.074		
18 <i>S. woolletti</i> 536	0.092	0.096	0.094	0.094	0.084	0.084	0.084	0.123	0.119	0.090	0.090	0.097	0.097	0.098	0.038	0.072	<b>0.002</b>	
19 <i>S. woolletti</i> 537	0.094	0.097	0.096	0.096	0.085	0.085	0.085	0.124	0.121	0.092	0.092	0.099	0.099	0.099	0.039	0.074	<b>0.000</b>	<b>0.002</b>



**Figure 1.** Majority-rule consensus tree from the Bayesian analysis (BI) of the concatenated COI and EF-1 $\alpha$  sequences. Values at nodes represent the bootstrap support (BS) values of the maximum likelihood (ML) and the posterior probabilities (PP) of BI analyses, respectively (BP/PP).

## Phylogenetic analyses

The two model-based analyses (BI and ML) revealed nearly identical topologies, differing mainly in branch support (Fig. 1). In both analyses, the monophyly of the genus *Scobura* is weakly supported (BP = 44, PP = 0.87). Within the genus, although support for the basal clades was low, the *Scobura* species included here are clearly distinguished from each other, and formed four clades: the *S. isota* clade (which only included two representative specimens), Clade A, the *S. cephaloides* clade (only with two representative specimens), and Clade B. Clade A is comprised by *S. stellata* + (*S. parawoolletti* + *S. woolletti*) and receive high bootstrap support and posterior probability (BP = 99, PP = 1.00). We hereafter called the clade *S. woolletti* group.



**Figure 2.** Male band of scent scales in the *S. coniata* group species.

Clade B is comprised by *S. masutaroi* and the representatives of *S. coniata* group (Devyatkin 2004): *S. coniata*, *S. lyso* and *S. hainana*, and the latter two are sister species with strong support (BP = 93, PP = 1.00). The monophyly of *S. coniata* group including *S. masutaroi* is strongly supported (BP = 100, PP = 1.00).

In all the analyses, *S. cephaloides* is sister to Clade B, with moderate support (BP = 63, PP = 0.92), whereas the relationships between *S. isota* and the other clades (Clade A, *S. cephaloides* and Clade B) remain unresolved.

## Discussion

Although our phylogenetic analyses do not strongly support the monophyly of the genus *Scobura*, two strongly supported monophyletic groups within the genus are recognized: the *S. coniata* group and the *S. woolletti* group. The members of the *coniata* group share the following four morphological characters: 1) male band of scent scales on both sides of veins  $CuA_1$  and  $CuA_2$  and above 2A on the forewing (Fig. 2); 2) juxta U-shaped with two spine bearing arms, flat at base; 3) tegumen without socius; and 4) uncus thin and long. *S. masutaroi* is nested within this group. In our present analyses, two individuals (He 300, 301) of *masutaroi* from Nibashan, Sichuan (close to Dujiangyan, Sichuan, the type locality of *S. masutaroi*) and an individual (He303) from Jialingjiang, Fengxian, Shaanxi (the type locality of *S. mouchai*) are clearly grouped together with strong support values (BP = 100, PP = 1.00). Moreover, the pairwise P2K distances in COI between the species in the *S. coniata* group range from 3.3% to 6.1% with divergences between species averaging 4.5%, while divergence between individuals of *S. masutaroi* from Sichuan and Shaanxi province was 0.2%.

Based on the original description, distribution data, and the illustrations provided by Krajcik (2013), as well as our phylogenetic inferences, we conclude that *S. mouchai*

is identical to *S. masutaroi* and should be considered a junior synonym. The male genitalia are illustrated herein, and the female genitalia are described for the first time. On the basis of morphological study (Devyatkin, 2004), two other species, *S. phuongi* and *S. evani*, which are not included in the present study, likely also belong to this group.

A well-support clade comprised by *S. stellata*, *S. parawoolletti* and *S. woolletti* was recovered in all analyses. These species share the following three characters: 1) hindwing with white spots on underside but not on upperside; 2) socius slender and pointed at tip; and 3) juxta funnel-like, thin and long basally. The generic name *Mimambrix* Riley, 1923 was proposed with *Mimambrix woolletti* as the type species, but later synonymized by Evans (1949). We follow Evans’ treatment and consider this clade as a species group within the genus *Scobura*. Based on morphological characters, the group also includes *S. tytleri* (Evans, 1914).

### Taxonomic account

The key given by Fan et al. (2010) is modified to include *S. masutaroi*. The couplets leading to *S. masutaroi* only are included here. Couplets beyond 11 in the original increase their number by one.

- 3 Forewing upper side without spots in spaces  $M_3$  or  $M_1$  and  $M_2$ .....4
- Forewing upper side with spots in spaces  $M_1$ ,  $M_2$  and  $M_3$ .....6
- 4 Forewing upper side without spots in spaces  $M_1$  and  $M_3$ , hindwing under side: basal half yellow, distally ferruginous, with five small spots .....***S. cephaloides***
- Forewing upper side without spot in space  $M_3$ .....5
- 5 Hindwing under side with a conspicuous rectangular white spot in space  $CuA_2$ .....***S. cephalo***
- Hindwing under side without a conspicuous rectangular white spot in space  $CuA_2$ ..... ***S. isota***
- 6 Hindwing upper side without spot in space  $CuA_1$ , under side with small white spots in spaces  $Sc+R_1$ ,  $M_{1,2}$ ,  $M_3$  and cell .....***S. eximia***
- Hindwing upper side with the spot in space  $CuA_1$  .....7
- 7 Forewing cell spots conjoined, subequal.....8
- Forewing cell spots separated, if conjoined, the lower spot much larger .....9
- 8 Hindwing upper side hyaline spots white.....***S.evansi***
- Hindwing upper side hyaline spots yellow ..... ***S.masutaroi***
- 9 Forewing upper side the spot in space  $CuA_2$  triangular, and with a linear stigma crossing the spots in spaces  $CuA_1$  and  $CuA_2$ .....***S. conciata***
- Forewing upper side the spot in space  $CuA_2$  not as above ..... 10
- 10 Forewing upper side the spot in space  $CuA_1$  narrow, hindwing upper side without spot in space ..... ***S. lyso***
- Forewing upper side the spot in space  $CuA_1$  broad ..... 11

- 11 Hindwing upper side spot in space  $M_3$  tiny dot, forewing upper side cell spots cell spots conjoined..... *S. hainana*  
 – Hindwing upper side spot in space  $M_3$  significant, forewing upper side cell spots cell spots separated..... *S. phuongi*

***Scobura masutaroi* Sugiyama, 1996**

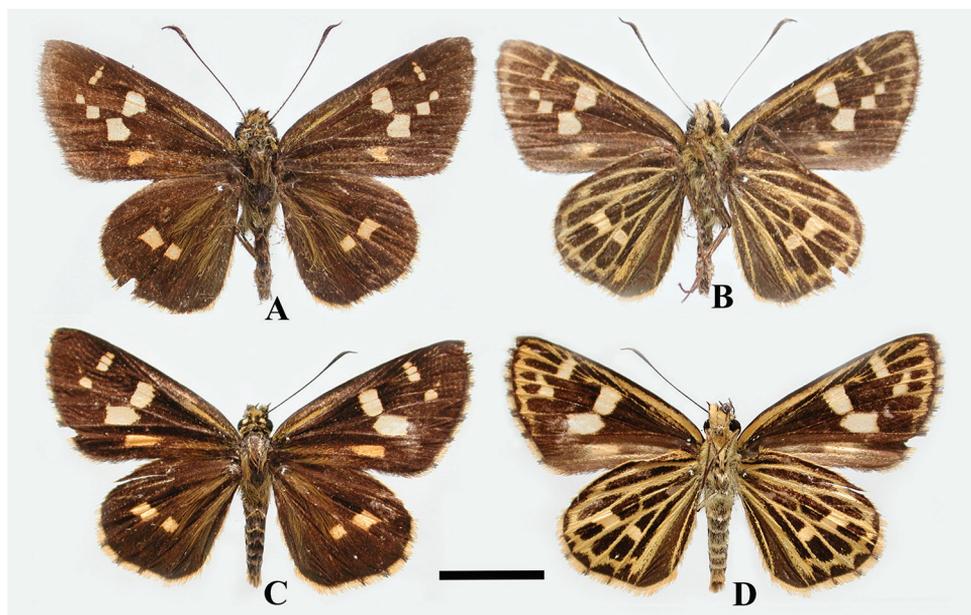
Fig. 3

*Scobura masutaroi* Sugiyama, 1996: 9 (Type locality: Dujiangyan, Sichuan, China)

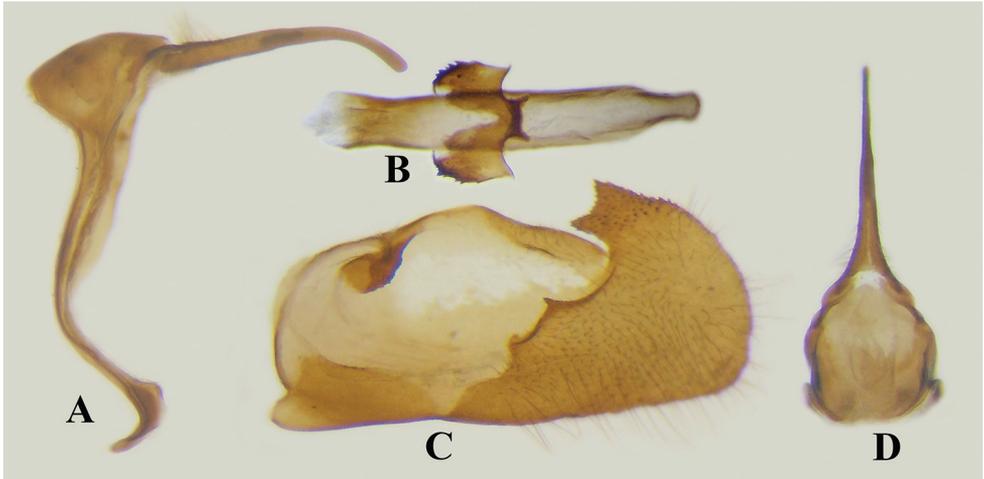
*Scobura mouchai* Krajcik, 2013: 2, **syn. n.** (Type locality: Fengxian, Shaanxi, China)

**Material examined.** 1♂, 1♀, Nibashan, Rongjing, Sichuan, 26.VII.2009, Min Wang; 1♂, Jialingjiang, Fengxian, Shaanxi, 15.VII.2010, Min Wang.

**Diagnosis.** Forewing length 17–18 mm. This species is different from other species of *S. coniata* group in the appearance of the wing upper side: forewing with yellow streak in subcosta space basally, a big cell spots solid across cell, the spot in space  $CuA_2$  yellow; hindwing with spots in spaces  $CuA_1$  and  $M_1$ – $M_2$  yellow. Wing under side: forewing costal and submarginal spots yellow; hindwing all veins and submarginal spots from spaces  $Sc+R_1$  to  $CuA_2$  yellow; and all yellow submarginal spots conjoined both forewing and hindwing.



**Figure 3.** *Scobura masutaroi* Sugiyama, 1996 (Sichuan): **A, B** male **C, D** female; scale bar 10 mm.



**Figure 4.** Male genitalia of *Scobura masutaroi* Sugiyama, 1996. (Sichuan). **A** Genitalia ring, lateral view; **B** aedeagus and juxta. **C** valva, inner view; **D** tegument, dorsal view.



**Figure 5.** Female genitalia of *Scobura masutaroi* Sugiyama, 1996 (Sichuan)

**Description.** Male genitalia (Fig. 4): Tegumen without socius, weakly rounded from lateral view; uncus slender and much longer than tegumen; valva with transtilla rounded and sclerotized with small spines, ventro-distal process irregularly shaped with outer edge rounded, inner edge uneven, and distal part rectangular with densely small spines; saccus short and broad; gnathos absent; juxta U-shaped with two arms with densely spines.

Female genitalia (Fig. 5): Papillae anales rectangular, covered with setae; anterior lamella U-shaped with sclerotization; posterior lamella triangular with upper margin arched; ductus bursae membranous and short; copulatrix bursa elongate, membranous.

**Distribution.** China (Sichuan, Shaanxi).

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# Two new deep-reef basslets (Teleostei, Grammatidae, *Lipogramma*), with comments on the eco-evolutionary relationships of the genus

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<http://zoobank.org/B8ADA2DB-F7DF-41F7-977D-9EB79DDDC34A>

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## Abstract

The banded basslet, *Lipogramma evides* Robins & Colin, 1979, is shown to comprise two species: *L. evides*, which inhabits depths of 133–302 m, and a new species described here as *Lipogramma levinsoni*, which inhabits depths of 108–154 m and previously was considered to represent the juvenile of *L. evides*. A second new species of banded basslet, described here as *Lipogramma haberi*, inhabits depths of 152–233 m and was previously not reported in the literature. Morphologically, the three species differ in color patterns and modal numbers of gill rakers, whereas various other morphological features distinguish *L. levinsoni* from *L. evides* and *L. haberi*. DNA barcode data and multilocus, coalescent-based, species-delimitation analysis support the recognition of the three species. Phylogenetic analysis of mitochondrial and nuclear genetic data supports a sister-group relationship between the two deepest-living of the three species, *L. evides* and *L. haberi*, and suggests that the shallower *L. levinsoni* is more closely related to *L. anabantoides* Böhlke 1960, which inhabits depths < 120 m. Evolutionary relationships within *Lipogramma* thus appear to be correlated with species depth ranges, an eco-evolutionary pattern that has been observed in other Caribbean marine teleosts and that warrants further investigation. The new species represent the eleventh and twelfth new fish species described in recent years from exploratory submersible diving in the Caribbean in the globally poorly studied depth zone of 50–300 m. This study suggests that there are at least two additional cryptic species of *Lipogramma*, which are being analyzed in ongoing investigations of Caribbean deep-reef ecosystems.

## Keywords

Manned submersible, cryptic species, integrative taxonomy, phylogeny, ocean exploration, Smithsonian Deep Reef Observation Project (DROP)

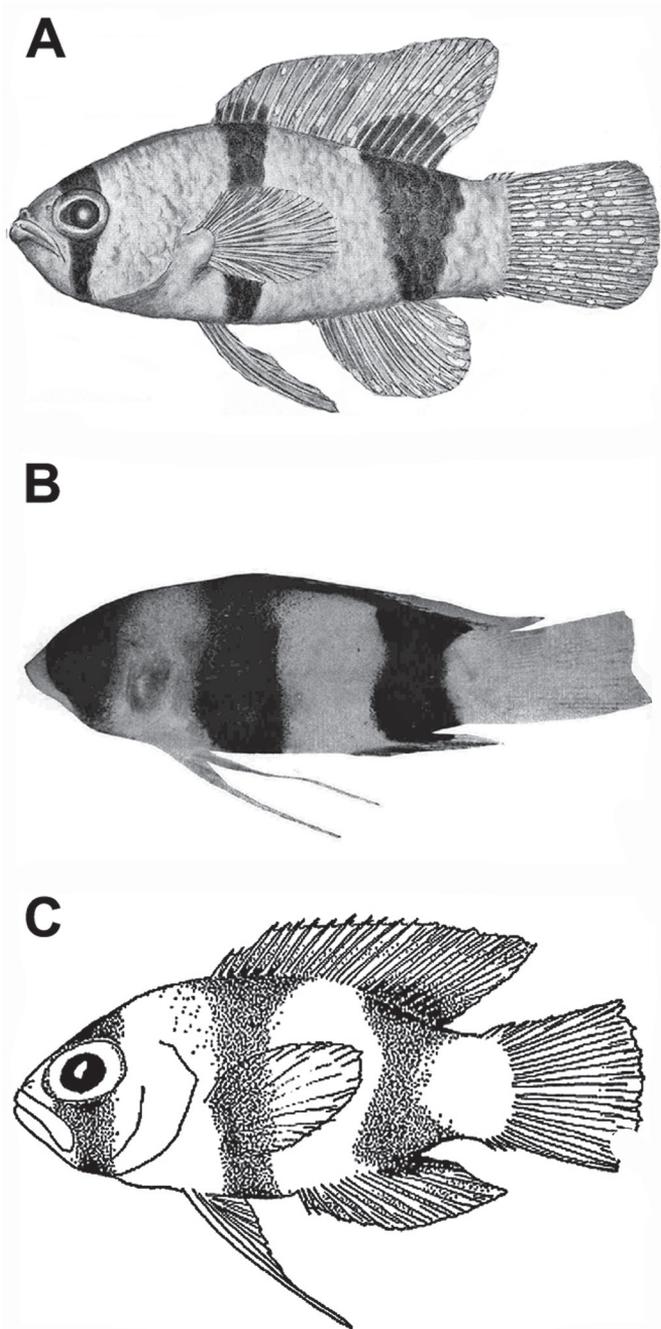
## Introduction

The western Atlantic family Grammatidae comprises small, usually brightly colored fishes in two genera, *Gramma* with four species and *Lipogramma* with eight (Robertson and Van Tassell 2015). Among other characters, the two genera are distinguished by the absence of a lateral line and presence of thickened, spinous, outer procurrent rays in *Lipogramma* (Mooi & Gill, 2002). The Banded Basslet, *Lipogramma evides* Robins & Colin, 1979, was described based on six specimens collected from Barbuda, Jamaica, Mexico, and Nicaragua. The original description also included observations of the species from Belize by Colin (1974). Subsequently, six additional specimens from the Bahamas were reported by Gilmore and Jones (1988). Robins and Colin (1979) noted differences in pigment pattern between adults and what they thought was a juvenile *L. evides* (Fig. 1A, B), in particular the presence of broader and more intense dark bands on the juvenile that completely encircle the body. Gilmore and Jones (1988) further commented on the presumed color differentiation between ontogenetic stages and noted that heavily banded “juveniles” (Fig. 1C) inhabit shallower waters (< 200 m) than adults (as deep as 250 m).

Exploratory submersible diving to 300 m in the southern and eastern Caribbean over the past several years by the Smithsonian Institution’s Deep Reef Observation Project (DROP) has resulted in the collection of over 50 specimens of “banded basslets” assignable to *Lipogramma* based on the absence of a lateral line and presence of spinous procurrent caudal-fin rays. That material includes individuals with both pigment patterns observed by previous authors and a third pigment pattern not previously described. Genetic and morphological analyses of individuals with those three pigment patterns suggested three distinct species and show that the heavily banded pattern is not an ontogenetic feature but diagnostic of a separate species. That species reaches a smaller maximum size than *L. evides* and has a shallower depth range. The other new species is similar in size and depth of occurrence to *L. evides*. Here we describe those two new species of *Lipogramma*, morphologically and genetically compare them with *L. evides*, and discuss depth distributions and evolutionary relationships of species of the genus.

## Methods and materials

**Collecting and morphology.** Basslets were collected using Substation Curaçao’s manned submersible *Curasub* (<http://www.substation-curaçao.com>). The sub has two flexible, hydraulic arms, one of which is equipped with a quinaldine/ethanol-ejection



**Figure 1.** Previously published images of **A** *Lipogramma evides*, 34.4 mm SL, ANSP 134329, holotype, from Robins and Colin (1979: fig. 1) **B** *Lipogramma levinsoni* sp. n., 12.6 mm SL, ANSP 134332, as juvenile paratype of *L. evides* in Robins and Colin (1979: fig. 2) **C** *Lipogramma levinsoni* sp. n., 14.1 mm SL, IRCZM 107: 07660, as juvenile of *L. evides* in Gilmore and Jones (1988: fig. 3). Images reproduced with permission from Bulletin of Marine Science.

system and the other with a suction hose. Anesthetized fish specimens were captured with the suction hose, which empties into a vented plexiglass cylinder attached to the outside of the sub. At the surface, the specimens were photographed, tissue sampled, and fixed in 10% formalin. Measurements were made weeks to months after fixation and subsequent preservation in 75% ethanol and were taken to the nearest 0.1 mm with dial calipers or an ocular micrometer fitted into a Wild stereomicroscope. Selected preserved specimens were later photographed to document preserved pigment pattern and X-rayed with a digital radiography system. Images of supraorbital pores and tooth-like structures on gill rakers were made using a Zeiss Axiocam on a Zeiss Discovery V12 SteREO microscope. Counts and measurements follow Hubbs and Lagler (1947). Specimens were cleared and stained following the protocol of Dingerkus and Uhler (1977). Symbolism for configuration of supraneural bones, anterior neural spines, and anterior dorsal pterygiophores follows Ahlstrom et al. (1976). USNM = Smithsonian Institution, National Museum of Natural History; ANSP = Academy of Natural Sciences, Philadelphia; IRCZM = Indian River Coastal Zone Museum, Harbor Branch Foundation, Fort Pierce, Florida; UF = University of Florida, Gainesville.

**Molecular analyses.** Tissue samples for 97 specimens assignable to eight species of *Lipogramma* were used for molecular analyses (Appendix 1). Tissues of *L. rosea* Gilbert, 1979 (in Robins and Colin 1979), *L. regia* Robins & Colin, 1979, and *L. flavescens* Gilmore & Jones, 1988 were not available. Tissues were stored in saturated salt-DMSO (dimethyl sulfoxide) buffer (Seutin et al. 1991). DNA extraction and cytochrome *c* oxidase subunit I (COI) DNA barcoding were performed for 96 specimens (i.e., for all available specimens except one *L. anabantoides* – Appendix 1) as outlined by Weigt et al. (2012). Four nuclear markers were amplified and sequenced—TMO-4C4, Rag1, Rhodopsin, and Histone H3—for 18 specimens of *Lipogramma*, and one or more of those genes was sequenced for an additional three specimens (Appendix 1). Primers and PCR conditions for the nuclear markers followed Lin and Hastings (2011, 2013). Sequences were assembled and aligned using *Geneious v. 9* (Biomatters, Ltd., Auckland). A neighbor-joining (NJ) network was generated for the COI data using the K2P substitution model (Kimura 1980) in the tree-builder application in *Geneious*. Mean within- and between-species K2P genetic distances were calculated from the COI data in *MEGA v. 7* (Kumar et al. 2015). Genetic distances were considered as corroborating morphology-based species delineation if the distances between species were ten or more times the intraspecific differences (Hebert et al. 2004). The alignments of COI and nuclear genes were concatenated and phylogeny was inferred using Bayesian Inference (BI) and Maximum Likelihood (ML), partitioning by gene. For the Bayesian analysis, substitution models and partitioning scheme were chosen using PartitionFinder (Lanfear et al. 2012) according to Bayesian Information Criterion scores. The chosen scheme had the following partitions and models: COI, HKY+I+G; Histone H3 plus Rhodopsin, HKY+G; TMO-4C4, K80+G; Rag1,

K80+G. All partitions in the ML analysis received a GTR-GAMMA substitution model. The BI phylogeny was inferred in the program *MrBayes v. 3.2* (Ronquist et al. 2012) using two Metropolis-coupled Markov Chain Monte Carlo (MCMC) runs, each with four chains. The analysis ran for 10 million generations sampling trees and parameters every 1000 generations. Burn-in, convergence and mixing were assessed using Tracer (Rambaut and Drummond 2007) and by visually inspecting consensus trees from both runs. The ML analysis was done in the program RAxML v.8.2.9 (Stamatakis, 2014), using 20 initial random searches, and topological support was assessed using 1000 bootstrap replicates. Outgroups for the phylogenetic analysis included two species of *Gramma* and several other genera from the *Ovalentaria sensu* Wainwright et al. (2012): *Acanthemblemaria* (Labrisomidae), *Helcogramma* (Tripterygiidae), *Blenniella* (Blenniidae), and *Tomicodon* (Gobiesocidae).

To corroborate the morphologically diagnosed species using our molecular data, we conducted a coalescent-based, Bayesian species-delimitation analysis (Yang and Rannala 2010, 2014). We used the computer program BP&P ver. 3.2 (Bayesian Phylogenetics and Phylogeography – Yang and Rannala [2010], Yang [2015]), which analyzes multi-locus DNA sequence alignments under the multispecies coalescent model (Rannala and Yang 2003). We used the five DNA alignments for the 21 *Lipogramma* specimens in BP&P, with each sequence in the alignments being assigned to one of eight groups *a priori*, based on the diagnostic morphological and coloration characters discussed in the ‘Morphological Comparisons’ section below. BP&P was then used to jointly infer a species tree and calculate posterior probabilities of different species-delimitation models containing either eight species, fewer than eight species (i.e. lumping multiple ‘morphological species’), or more than eight species (i.e. splitting ‘morphological species’ into multiple cryptic species).

**Depth distributions.** To evaluate depth distributions we searched FishNet2 ([www.fishnet2.net](http://www.fishnet2.net)) for all *Lipogramma* specimens that were identified to species and that included data on the depth of capture. For some specimens, capture depth was given as a range of possible depths, and in instances where this range was 50 m or narrower, we took the mean depth as a proxy for a point estimate of the exact depth of capture. Broader depth ranges of capture were excluded. Depth records for *L. evides* were only included for specimens whose identifications we confirmed to avoid possible confusion with one of the two new species described here. When combined with depth data from specimens from DROP collections, this search resulted in depth records for 278 identified specimens of *Lipogramma*. We also included depth records from 83 visual observations from DROP submersible dives, excluding those observations where there was uncertainty regarding identification of the three morphologically similar species (*L. evides* and the two species described here).

**Accession numbers.** GenSeq nomenclature (Chakrabarty et al. 2013) and GenBank accession numbers for DNA sequences derived in this study are presented along with museum catalog numbers for voucher specimens in Appendix 1.

## Taxonomy

### Hourglass Basslet

#### *Lipogramma levinsoni* Baldwin, Nonaka & Robertson, sp. n.

<http://zoobank.org/C12172C1-B3BF-48B8-B267-61D845EDCC63>

Figure 2

*Lipogramma evides* Robins & Colin, 1979: 43, fig. 2, table 1, ANSP 134332, paratype from Jamaica (photograph, counts, measurements).

*Lipogramma evides* Robins & Colin, 1979, fig. 3 in Gilmore and Jones (1988: 441), IRCZM 107:07660 from San Salvador, Bahama Islands (illustration, habitat information).

**Type locality.** Curaçao, southern Caribbean.

**Holotype.** USNM 406139, 28.3 mm SL, tissue no. CUR11139, Curasub submersible, sta. CURASUB11-02, Curaçao, off Substation Curaçao, 12.083197 N, 68.899058 W, 137–146 m depth, 23 May 2011, C. Baldwin, D. Robertson & B. Van Bebber.

**Paratypes.** **BONAIRE:** USNM 426784, 24.2 mm SL, tissue no. CUR13183, Curasub submersible, Bonaire, Bonaire City Dock, Kralendijk, Dive 2, 12.15 N, 68.2829 W, 121–137 m depth, 30 May 2013, B. Van Bebber, A. Schrier, C. Baldwin, T. Christiaan; **CURAÇAO:** ANSP 201863, 24.0 mm SL, Curasub submersible, Curaçao, off Substation Curaçao, 12.083197 N, 68.899058 W, no depth data available; UF 238589, 25.0 mm SL, tissue no. CUR11018, Curasub submersible, sta. CURASUB11-22, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 27 February 2011, C. Baldwin & L. Weigt; USNM 406393, 25.7 mm SL, tissue no. CUR11393, Curasub submersible, sta. CURASUB11-06, Curaçao, 132 m depth, 31 May 2011, C. Baldwin, A. Driskell, A. Schrier & B. Van Bebber; USNM 414877, 25.3 mm SL, cleared and stained, tissue no. CUR12159, Curasub submersible, sta. CURASUB12-15, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, 128 m depth, 10 August 2012, A. Schrier, B. Brandt, C. Baldwin, A. Driskell & P. Mace; USNM 440229, 12.7 mm SL, Curasub submersible, sta. CURASUB14-07, Curaçao, in between Porto Marie and Daaibooi beaches, 12.202842 N, 69.089507 W, 123 m depth, 21 March 2014, C. Baldwin et al.; USNM 440230, 13.4 mm SL, Curasub submersible, sta. CUR13-18, Curaçao, Playa Forti, Westpoint, 12.3679 N, 69.1553 W, 127 m, 15 August 2013, C. Baldwin, B. Brandt, A. Schrier, K. Johnson & C. DeForest; USNM 406140, 19.5 mm SL, tissue no. CUR11140, Curasub submersible, sta. CURASUB11-02, Curaçao, 137–146 m depth, 23 May 2011, C. Baldwin, D. Robertson & B. Van Bebber. **DOMINICA:** USNM 440231, 17.0 mm SL, tissue no. DOM16229, Curasub submersible, off northwest Dominica, no specific collection data available, March 2016, R/V Chapman Crew.

**Non-type specimens.** **BONAIRE:** USNM 426754, 21.2 mm SL, tissue no. CUR13184, Curasub submersible, Bonaire, Bonaire City Dock, Kralendijk, Dive 2,



**Figure 2.** *Lipogramma levinsoni* sp. n. **A** USNM 406139, holotype, 28.3 mm SL, photographed prior to preservation, photo by D. R. Robertson and C. C. Baldwin **B** USNM 406394, 22.2 mm SL, photographed prior to preservation, photo by D. R. Robertson and C. C. Baldwin **C** and **D** Aquarium photos, Curaçao Sea Aquarium, photos by D. Ross Robertson.

12.15 N, 68.2829 W, 121–137 m depth, 30 May 2013, B. Van Bebber, A. Schrier, C. Baldwin, T. Christiaan; USNM 426802, 9.4 and 18.3 mm SL, Curasub submersible, Bonaire, Bonaire City Dock, Kralendijk, 12.15 N, 68.2829 W, 114–137 m depth, 30 May 2013, B. Van Bebber, A. Schrier, C. Baldwin, T. Christiaan. **CURAÇAO:** USNM 426774, 17.6 mm SL, tissue no. CUR13267, Curasub submersible, sta. CURASUB13-18, Curaçao, Playa Forti, Westpoint, 12.3679 N, 69.1553 W, 118 m depth, 15 August 2013, C. Baldwin, B. Brandt, A. Schrier, K. Johnson & C. DeForest; USNM 426730, 12.3 mm SL, tissue no. CUR13268, Curasub submersible, sta. CURASUB13-18, Curaçao, Playa Forti, Westpoint, 12.3679 N, 69.1553 W, 118 m depth, 15 August 2013, C. Baldwin, B. Brandt, A. Schrier, K. Johnson & C. DeForest; USNM 406011, 20.9 mm SL, tissue no. CUR11011, Curasub submersible, sta. CURASUB11-22, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 27 February 2011, C. Baldwin & L. Weigt; USNM 406012, 18.0 mm SL, tissue no. CUR11012, Curasub submersible, sta. CURASUB11-22, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 27 February 2011, C. Baldwin & L. Weigt; USNM 406019, 14.0 mm SL, tissue no. CUR11019, Curasub submersible, sta. CURASUB11-22, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data avail-

able, 27 February 2011, C. Baldwin & L. Weigt; USNM 406394, 22.2 mm SL, tissue no. CUR11394, Curasub submersible, sta. CURASUB11-06, Curaçao, 132 m depth, 31 May 2011, C. Baldwin, A. Driskell, A. Schrier & B. Van Bebber. **DOMINICA:** USNM 438703, 19.0 mm SL, tissue no. DOM16052, Curasub submersible, sta. CURASUB16-07, Toucari Bay, Toucari, Dominica, NW corner of island, 15.608047 N, 61.471788 W, no depth data available, 2 March 2016, A. Schrier, R. Bakmeijer, B. Van Bebber & F. van der Hoeven; **JAMAICA:** ANSP 134332, 12.6 mm SL, Nekton Gamma dive 141, collection 151-2, Jamaica, Discovery Bay, 145 m depth, 15 August 1972, L. Land & S. Hastings.

**Diagnosis.** A species of *Lipogramma* distinguishable from congeners by the following combination of characters: pectoral-fin rays 16–18 (modally 17), gill rakers 17–20 (modally 19); three supraorbital pores present along dorsal margin of orbit, no pore present between pore at mid orbit and one at posterodorsal corner of orbit; caudal fin truncate, tips of lobes rounded; body with three broad blackish bars (one on head, two on trunk) on white background, width of bar on head sufficient to encompass entire eye, width just ventral to eye averaging 26.4% head length; trunk bars sometimes hourglass shaped, with narrower and less intensely colored central regions; anterior trunk bar covering pectoral-fin base; posterior trunk bar extending onto dorsal and anal fins as large oval blotches bordered in part by white or blue pigment to form partial ocelli; dorsal and anal fins with thin orange sub-marginal stripe. The new species is further differentiated from congeners for which molecular data are available in mitochondrial COI and nuclear Histone 3, Rhodopsin, TMO-4C4, and RAG1.

**Description.** Counts and measurements of type specimens given in Table 1. Frequency distributions of pectoral-fin rays and gill rakers on the first arch are given in Table 2. Twenty specimens examined, 9.4 to 28.3 mm SL. Dorsal-fin rays XII, 9 (last ray composite); anal-fin rays III, 8 (last ray composite); pectoral-fin rays 16–18, modally 17, 17 on both sides in holotype; pelvic-fin rays I,5; total caudal-fin rays 25 (13 + 12), principal rays 17 (9 + 8), spinous procurrent rays 6 (III + III), and 2 additional rays (i + i) between principal and procurrent rays that are neither spinous nor typically segmented; vertebrae 25 (10 + 15); pattern of supraneural bones, anterior dorsal-fin pterygiophores and dorsal-fin spines 0/0/0+2/1+1/1/; ribs on vertebrae 3–10; epineural bones present on vertebrae 1–16 in holotype and cleared and stained paratype (difficult to assess in radiographs of most other specimens); gill rakers on first arch 17–20 (5-6 + 12–14), modally 19 (6 + 13), 19 (6 + 13) in holotype; uppermost four and lowermost one or two rakers very small or present only as nubs, all other gill rakers elongate and slender with tooth-like secondary rakers as in *L. evides* (Fig. 3); pseudobranchial filaments 5–7 (7 in holotype), filaments fat and fluffy; branchiostegals 6.

Spinous and soft dorsal fins confluent, several soft rays at rear of fin forming elevated lobe that extends posteriorly beyond base of caudal fin. Pelvic fin, when depressed, extending posteriorly to point between anterior base of anal fin and beyond base of caudal fin, elongate first pelvic-fin ray broken in most preserved specimens. Dorsal profile from snout to origin of dorsal fin convex. Diameter of eye of holotype

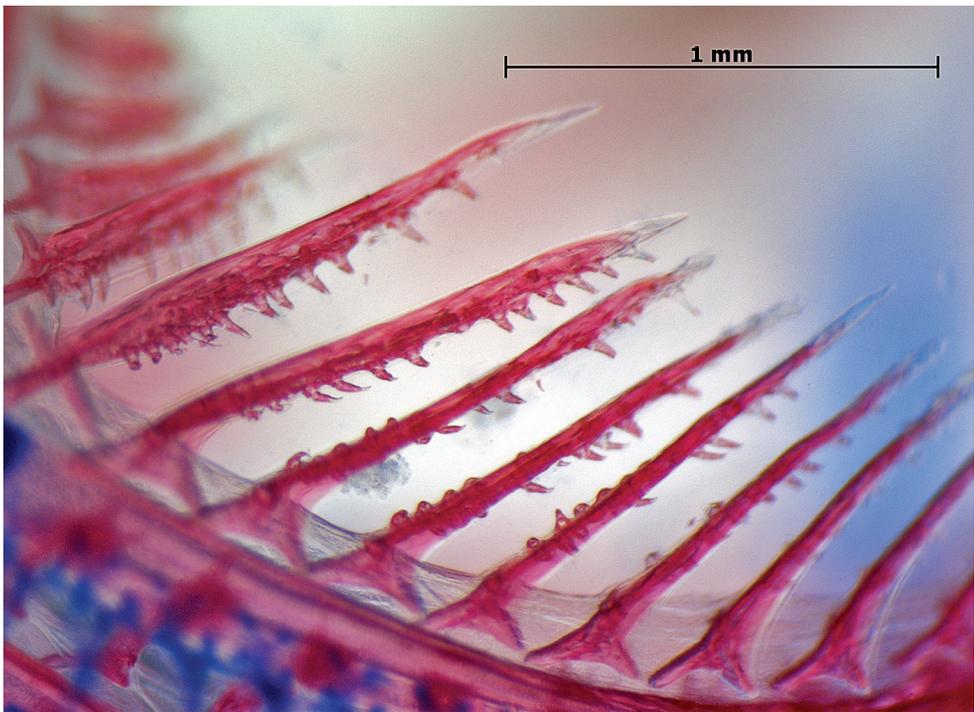
**Table 1.** Counts and measurements of type specimens of *Lipogramma levinsoni* sp. n.. Measurements are in percent SL except width of bar ventral to eye, which is in percent head length. C&S = cleared and stained; CP = caudal peduncle; PFO = pelvic-fin origin; P1 = pectoral fin; P2 = pelvic fin; DXII = twelfth dorsal-fin spine. "Other Caudal" rays include "i" – a slender, flexible, non-spinous, and typically non-segmented ray and "T" – a spinous procurent ray.

	USNM	USNM	USNM	USNM	USNM	USNM	USNM	USNM	USNM	USNM	USNM	ANSP	UF
	406139	406393	406140	414877	426784	440230	440229	440231	440231	201863	238589	201863	238589
	Holotype	Paratype	Paratype	Paratype (C&S)	Paratype								
SL	28.3	25.7	19.5	25.3	24.2	13.4	26.3	17.0	17.0	24.0	25.0	24.0	25.0
Dorsal-fin rays	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9	XII, 9
Anal-fin rays	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8	III, 8
Principal caudal	9+8	9+8	9+8	9+8	9+8	9+8	9+8	Broken	Broken	9+8	9+8	9+8	9+8
Other caudal	IIIi+III	IIIi+III	IIIi+III	IIIi+III	IIIi+III	IIIi+III	IIIi+III	Broken	Broken	IIIi+III	IIIi+III	IIIi+III	IIIi+III
Pectoral-fin rays	17, 17	17, 16	17, 17	17, 17	17*, 17	17, 17	17, 18	16, -	16, -	17, 17	17, 17	17, 17	17, 17
Gill rakers	19	20	19	19	19	19	18	18	18	19	18	19	18
Head length	33.2	36.2	35.4	-	38.0	37.3	34.6	39.4	39.4	35.8	37.0	35.8	37.0
Eye diameter	12.0	12.1	14.9	-	11.6	15.7	11.4	13.5	13.5	12.1	13.0	12.1	13.0
Snout length	7.1	7.4	6.2	-	7.4	6.7	5.7	5.9	5.9	7.1	5.5	7.1	5.5
Depth at CP	20.1	18.7	17.4	-	19.8	18.7	16.3	17.6	17.6	17.1	17.2	17.1	17.2
Depth at PFO	33.9	36.6	34.4	-	35.5	35.1	35.4	31.2	31.2	40.0	33.6	40.0	33.6
Length P1	25.8	24.5	23.1	-	21.9	26.1	24.7	22.4	22.4	28.8	25.6	28.8	25.6
Length P2	72.4	45.5	Broken	-	47.1	42.5	62.7	Broken	Broken	83.3	Broken	83.3	Broken
Length DXII	18.7	20.2	20.5	-	16.5	17.2	19.0	15.9	15.9	22.2	21.0	22.2	21.0
Width of bar ventral to eye	25.5	28.0	21.5	-	26.1	26.0	23.1	25.4	25.4	25.6	28.4	25.6	28.4

\*6<sup>th</sup> and 7<sup>th</sup> rays (counting from dorsalmost ray) separate proximally but joined distally within same sheath and appearing as a single fat ray.

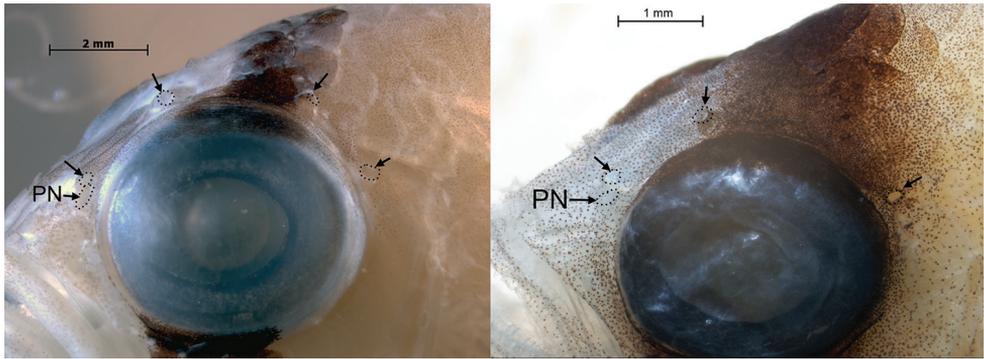
**Table 2.** Frequency distributions of gill rakers on first arch and left and right pectoral-fin rays in *Lipogramma levinsoni* sp. n., *L. evides*, and *L. haberi* sp. n. Counts for the holotype and three paratypes of *L. evides* are included from Robins and Colins (1979). Counts of gill rakers and pectoral-fin rays for a fourth paratype of *L. evides*, ANSP 134330, were not given in the original description. The fifth and smallest paratype, ANSP 134332, is a specimen of *L. levinsoni*, and counts of that specimen made in this study are included. An asterisk indicates count of gill rakers or left pectoral-fin rays in holotype.

	Gill Rakers								Pectoral-fin Rays				
	15	16	17	18	19	20	21	22	15	16	17	18	19
<i>L. levinsoni</i>			1	5	9*	1				5	26*	3	
<i>L. evides</i>					3	14*	11	1	1	45*	9		
<i>L. haberi</i>	1*	2							1	5*			



**Figure 3.** Tooth-like, secondary rakers on the first gill arch in *Lipogramma evides*, USNM 34771, cleared and stained paratype. Photo by L. Tornabene.

contained 2.8 times in head length. Pupil slightly tear shaped, with small aphakic space anteriorly. Scales extending anteriorly onto posterior portion of head, ending short of coronal pore. Scales present on cheeks, opercle, preopercle, interopercle, and isthmus. Scales lacking on top of head, snout, jaws, and branchiostegals. Scales large and deciduous, too many scales missing in most specimens to make accurate scale counts. In holotype, approximately 23 lateral scales between shoulder and base of caudal fin, approximately 4 scale rows on cheek, and approximately 9 scale rows across body above



**Figure 4.** Supraorbital pore patterns in *Lipogramma evides*, UF 238591, 34.5 mm SL (left) and *L. levinsoni* sp. n., UF 238589, 25.0 mm SL (right). Arrows point to pores, which have been outlined with tiny dots for emphasis. PN – posterior nostril.

anal-fin origin. Scales on head and nape without cteni, scales on rest of body ctenoid. Fins naked except small scales present at bases of soft dorsal and anal fins.

Margins of bones of opercular series smooth, opercle without spines. Single row of teeth on premaxilla posteriorly, broadening to 2-3 rows anteriorly, teeth in innermost row smallest, some teeth in outer row enlarged into small canines. Dentary similar, holotype with 3 enlarged teeth in outer row near symphysis. Vomer with chevron-shaped patch of teeth, palatine with long series of small teeth. Several canals and pores visible on head, but most pores inconspicuous. Conspicuous pores present in infraorbital canal (2 pores) and portion of supraorbital canal bordering dorsal portion of orbit (3); less conspicuous pores present on top of head (1 median coronal pore), preopercle (7), and lateral-line canal in the posttemporal region (3). Antermost of the 3 supraorbital pores situated at anterodorsal corner of orbit, middle supraorbital pore situated above mid orbit, and posteriormost supraorbital pore situated at posterodorsal corner of orbit (Fig. 4). This pore with fleshy rim in holotype, and mid-orbit supraorbital pore with smaller fleshy rim. Posterior nostril situated just ventral to anteriormost supraorbital pore, nostril a single large opening with ventral portion of rim slightly elevated. Anterior nostril in tube with anterior flap and situated just posterior to upper lip. No lateral line present on body.

Coloration: In life (Fig. 2), ground color of head and trunk white to tan dorsally grading to white below. **Head:** dark brown to black bar encompassing orbit and extending ventrally to ventral midline; above orbit, bar narrowing across dorsal midline; eye with dark brown outer ring, yellowish to bluish iris. **Trunk:** two broad, dark brown to blackish bars present beneath dorsal fin, bars sometimes hourglass shaped, with narrower and less intensely colored central regions (central regions losing almost all dark color in some freshly dead specimens); anterior bar extending ventrally from anterior third of spinous dorsal fin to ventral midline, its anterior border extending forward to encompass base of pectoral fin; posterior bar extending ventrally from base of soft dorsal fin to posterior half of anal fin. **Dorsal fin:** dark trunk bars extending onto base of fin

as two blotches, anterior blotch short, low, less conspicuous (than posterior blotch) and sometimes with faint orange upper border. Posterior blotch an intense, dark, longitudinal oval spanning lower half of soft dorsal and bordered posteriorly by white to bluish-white pigment. Base of fin between trunk bars whitish, central portion of fin brown to grey, and distal third of fin with bluish tint and thin, orange, submarginal stripe; this stripe breaking into spots along the rear third of fin. **Anal fin:** posterior trunk bar extending onto proximal portion of posterior half of fin as a strong, horizontally elongate, black blotch edged distally with bluish white line; base of fin with thin, white stripe, fin color grading into blackish to bluish-black distally. A thin, orange, sub-marginal stripe breaks into spots along posterior portion of fin. **Caudal fin:** basal half translucent pale orange, grading into translucent bluish distally, sometimes with indistinct, very narrow, submarginal orange band around entire edge. **Pectoral fins:** base blackish, fin translucent, rays translucent or tinted with orange. **Pelvic fins:** translucent white to bluish white, with orange tint medially on basal half of fin. In preservative (Fig. 5A), barred color pattern retained, but orange, yellow, and bluish pigments absent.

**Distribution.** Known from specimens collected from the Bahamas, Bonaire, Curaçao, Dominica, and Jamaica. This species was also clearly observed in October 2016 by DRR and LT from the mini-submarine “Idabel” at 140 m depth adjacent to Half Moon Bay, Roatan, Honduras.

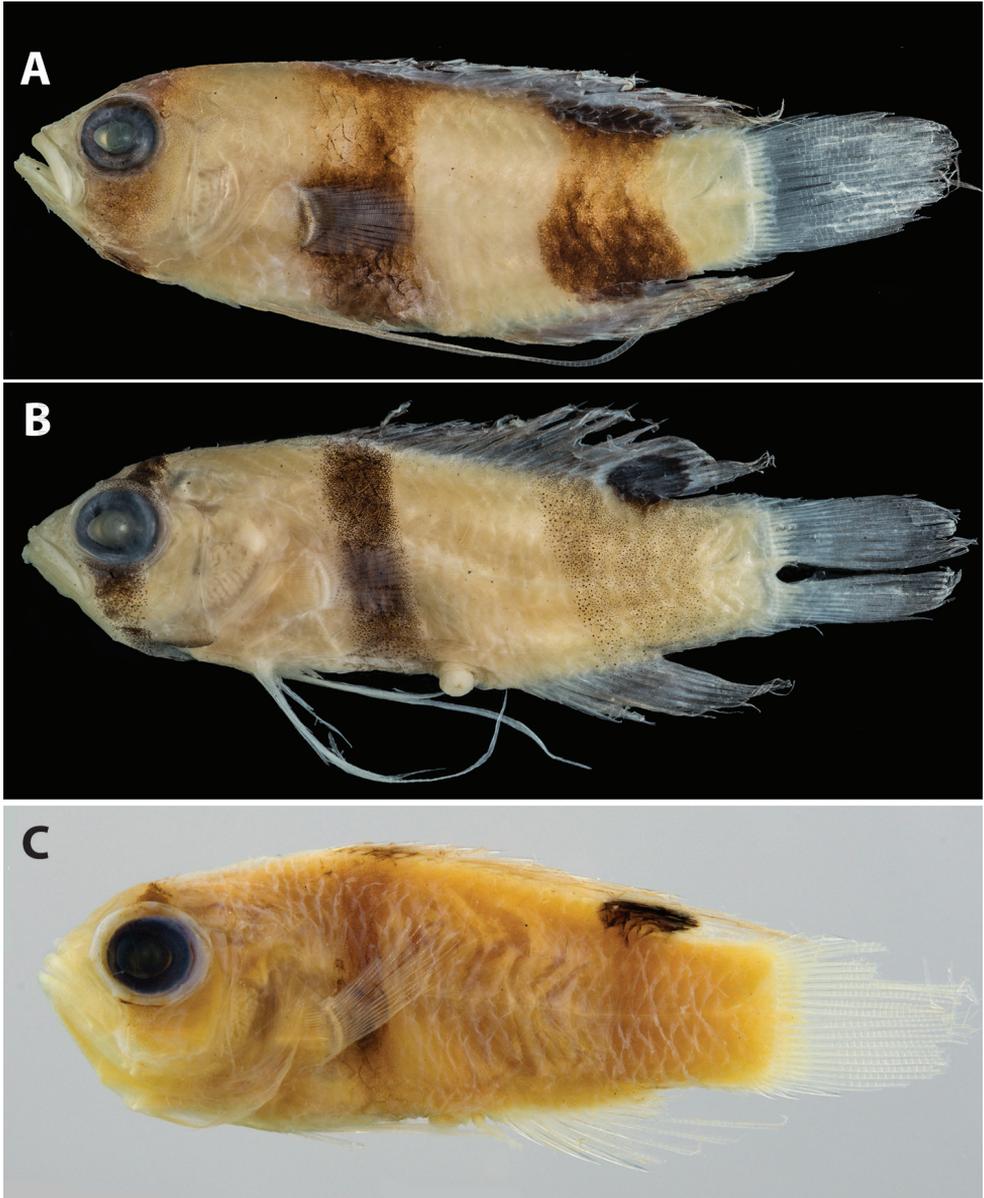
**Habitat.** Lives in or hovers above small rocky rubble on gradual slopes at depths of 108–154 m. When approached by the submersible, *L. levinsoni* disappears into the rubble. We observed them often in pairs.

**Etymology.** Named *Lipogramma levinsoni* in recognition of the generous, continuing support of research on neotropical biology at the Smithsonian Tropical Research Institute (Panamá) made by Frank Levinson.

**Common name.** We propose “Hourglass basslet” (Cabrilleta hierba-horaria as the Spanish equivalent) to differentiate this species from the Banded Basslet, *Lipogramma evides*, and the Yellow-banded Basslet, *L. haberi* (see description below), both of which have narrower, straight-sided bars on the trunk.

**Genetic comparisons.** Table 3 shows average inter- and intraspecific divergences in COI among species of *Lipogramma* analyzed genetically in this study. With the exception of a single substitution in one specimen, the 15 specimens of *Lipogramma levinsoni* exhibit no intraspecific genetic variation at this locus and differ from other *Lipogramma* species by 15.4–26.0%. *Lipogramma levinsoni* differs from *L. evides* by 17.1% and *L. haberi* by 19.0%.

**Comments.** The smallest paratype of *L. evides*, ANSP 134332 (Fig. 1B), 12.6 mm SL, is a specimen of *L. levinsoni*. Although Robins and Colin (1979) indicated 15 pectoral-fin rays on both sides of this specimen, we count 17 on the right and find the left side too bent to make an accurate count. *Lipogramma levinsoni* typically has 17–18 pectoral-fin rays, modally 17. The gill-raker count of 19 given by Robins and Colin (1979) was confirmed by our examination, and is the typical count for *L. levinsoni*. Counts of pectoral-fin rays (15–16, usually 16) and gill rakers on the first arch (19–21, usually 20 or 21) given by Robins and Colin (1979) for the remaining paratypes of *L. evides*



**Figure 5.** Preserved specimens of **A** *Lipogramma levinsoni* sp. n., holotype, USNM 406139, 28.3 mm SL **B** *Lipogramma haberi* sp. n., holotype, USNM 422679, 40.1 mm SL **C** *L. evides*, paratype, ANSP 134330, 30.5 mm SL Photos **A** and **B** by Sandra Raredon, **C** by Mark Sabaj.

support their identification as specimens of *L. evides*. As noted, previous authors have mistakenly identified the broad-banded *L. levinsoni* as the juvenile form of the more narrow-banded *L. evides*. Our material includes juvenile specimens of both *L. levinsoni* and *L. evides*, which in each case have the adult configuration of dark bands (Fig. 6).



**Figure 6.** Comparison of juveniles of **A** *Lipogramma levinsoni* sp. n., USNM 440230, paratype, 13.4 mm SL and **B** *L. evides*, USNM 431410, 12.7 mm SL.

**Table 3.** Average Kimura two-parameter distance summary for species of *Lipogramma* based on cytochrome c oxidase I (COI) sequences analyzed in this study. Intraspecific averages are in bold.

	"robinsi1"	"robinsi2"	levinsoni	haberi	anabantoides	trilineata	klayi	evides
"robinsi1" (n=6)	<b>0.003</b>							
"robinsi2" (n=7)	0.119	<b>0.002</b>						
levinsoni (n=15)	0.162	0.169	<b>0</b>					
haberi (n=3)	0.111	0.132	0.19	<b>0.002</b>				
anabantoides (n=2)	0.195	0.184	0.154	0.202	<b>0.005</b>			
trilineata (n=12)	0.217	0.251	0.227	0.236	0.258	<b>0.005</b>		
klayi (n=21)	0.266	0.259	0.26	0.279	0.246	0.242	<b>0.003</b>	
evides (n=30)	0.103	0.128	0.171	0.11	0.22	0.249	0.263	<b>0.001</b>

## Yellow-banded Basslet

### *Lipogramma haberi* Baldwin, Nonaka & Robertson, sp. n.

<http://zoobank.org/4A8447E9-205C-4639-9209-428D8DCDAC1F>

Figure 7

**Type locality.** Curaçao, southern Caribbean

**Holotype.** USNM 422679, 40.1 mm SL, tissue no. CUR13171, Curasub submersible, sta. CURASUB13-09, Curaçao, southwest tip of Klein Curaçao, 11.975783 N, 68.646192 W, 152 m depth, 27 May 2013, M. Harasewych, L. Weigt, B. Van Bebber & A. Schrier.

**Paratypes.** USNM 434772, 26.4 mm SL, tissue no. CUR15092, Curasub submersible, sta. CURASUB15-12, northwest corner of Klein Curaçao, 11.998453 N, 68.651308 W, 187 m depth, 27 August 2015, B. Brandt, A. Schrier, S. Haber & T. Haber; USNM 422670, 23.0 mm SL, tissue no. CUR13158, Curasub submersible, sta. CURASUB13-08, Curaçao, southwest tip of Klein Curaçao, 11.975783 N, 68.646192 W, 233 m depth, 27 May 2013, C. Baldwin, D. Robertson, B. Brandt, A. Schrier & L. Weigt.

**Diagnosis.** A species of *Lipogramma* distinguishable from congeners by the following combination of characters: pectoral-fin rays 15–16 (modally 16), gill rakers 15–16 (modally 16); four supraorbital pores along dorsal portion of orbit, a pore present between pore at mid orbit and one at posterodorsal corner of orbit; caudal fin truncate, tips of lobes rounded; body with three dusky bars (one on head, two on trunk) on yellow/white background; width of bar on head sufficient to encompass pupil but not entire eye, width just ventral to eye averaging 17.6% head length; anterior trunk bar narrow and not extending forward to cover pectoral-fin base, bar lighter and less conspicuous ventrally; posterior trunk bar a broad, yellow/tan triangle that is wider dorsally than ventrally; this triangle extending onto soft dorsal fin as large, round, well-defined ocellus; posterior trunk bar not extending onto anal fin; dorsal fin with thin yellow sub-marginal stripe; no yellow submarginal stripe on anal fin; dorsal, anal, and caudal fins with numerous yellow spots. The new species is further differentiated from congeners for which molecular data are available in COI and RAG1.

**Description.** Counts and measurements of type specimens given in Table 4. Frequency distributions of pectoral-fin rays and gill rakers on the first arch are given in Table 2. Three specimens examined, 23.0–40.1 mm SL. Dorsal-fin rays XII, 9 (last ray composite); anal-fin rays III, 8 (last ray composite); pectoral-fin rays 15–16, modally 16, 16 on both sides in holotype; pelvic-fin rays I, 5; total caudal-fin rays 25 (13 + 12), principal rays 17 (9 + 8), spinous procurrent rays 6 (III + III), and 2 additional rays (i + i) between principal and procurrent rays that are neither spinous nor typically segmented; vertebrae 25 (10 + 15); pattern of supraneural bones, anterior dorsal-fin pterygiophores and dorsal-fin spines 0/0/0+2/1+1/1/; ribs on vertebrae 3–10; epineural bones present on vertebrae 1–15 in one paratype, difficult to assess in other specimens; gill rakers on first arch 15–16 (4+5 + 11), 15 (4 + 11) in holotype, both paratypes with



**Figure 7.** *Lipogramma haberi* sp. n., USNM 422679, holotype, 40.1 mm SL, photographed prior to preservation against white (top) and black (bottom) backgrounds. Photos by D. R. Robertson and C. C. Baldwin.

16 (5 + 11); lowermost two rakers very small, all other gill rakers elongate and slender with tooth-like secondary rakers as in *L. evides* (Fig. 3); pseudobranchial filaments 6, filaments fat and fluffy; branchiostegals 6.

**Table 4.** Counts and measurements of type specimens of *Lipogramma haberi* sp. n. Measurements are in percent SL except width of bar ventral to eye, which is in percent head length. CP = caudal peduncle; PFO = pelvic-fin origin; P1 = pectoral fin; P2 = pelvic fin; DXII = twelfth dorsal-fin spine. "Other Caudal" rays include "i" – a slender, flexible, non-spinous, and typically non-segmented ray and "I" – a spinous procurent ray.

	USNM 422679	USNM 434772	USNM 422670
	Holotype	Paratype	Paratype
SL	40.1	26.4	23.0
Dorsal-fin Rays	XII, 9	XII, 9	XII, 9
Anal-fin Rays	III, 8	III, 8	III, 8
Principal Caudal	9+8	9+8	Broken
Other Caudal	IIIi+iIII	IIIi+iIII	Broken
Pectoral-fin Rays	16, 16	16, 15	16, 16
Gill Rakers	15	16	16
Head Length	35.2	39.0	34.8
Eye Diameter	11.2	14.0	13.0
Snout Length	6.7	5.7	6.1
Depth at CP	18.7	20.1	17.8
Depth at PFO	32.4	34.1	27.0
Length P1 Fin	22.2	27.7	24.3
Length P2 Fin	62.3	54.5	46.1
Length DXII	22.4	23.1	17.4
Width of Bar Ventral to Eye	14.9	20.4	17.5

Spinous and soft dorsal fins confluent, several soft rays in posterior portion of fin forming elevated lobe that extends posteriorly beyond base of caudal fin. Pelvic fin extending posteriorly to anterior third of caudal peduncle in holotype when depressed, longest pelvic-fin rays broken in preserved specimens. Dorsal profile from snout to origin of dorsal fin convex. Diameter of eye of holotype contained 2.7 times in head length. Pupil slightly tear shaped, with small aphakic space anteriorly. Scales extending anteriorly onto top of head, ending short of coronal pore. Scales present on cheeks, opercle, preopercle, interopercle, and isthmus. Scales lacking on frontal region, snout, jaws, and branchiostegals. Scales large and deciduous, too many missing in paratypes to make counts, holotype with approximately 24 lateral scales between shoulder and base of caudal fin, 5 cheek rows, and 11 rows across body above anal-fin origin. Scales on head and nape without cteni, scales on rest of body ctenoid. Fins naked except small scales present at bases of soft dorsal and anal fins.

Margins of bones of opercular series smooth, opercle without spines. Premaxilla with band of small conical teeth, band widest at symphysis, outer row with largest teeth, 3 or 4 near symphysis enlarged into canines. Dentary similar except 4-6 anterior teeth enlarged into canines. Vomer with chevron-shaped patch of teeth, palatine with long series of small teeth. Several canals and pores visible on head, but most pores inconspicuous. Conspicuous pores present in infraorbital canal (2) and in supraorbital

canal bordering dorsal portion of orbit (4); less conspicuous pores present on top of head (1 median coronal pore), preopercle (8), and lateral-line canal in posttemporal region (3). An additional 4 tiny pores present beneath orbit in holotype in infraorbital canal. Supraorbital pore pattern as in *L. evides* (Fig. 4): anteriormost of 4 supraorbital pores situated at anterodorsal corner of orbit, second supraorbital pore situated above mid orbit, and posteriormost supraorbital pore situated at posterodorsal corner of orbit. Between second and posteriormost supraorbital pores, another pore present and situated closer to latter. Posterior nostril situated just ventral to anteriormost supraorbital pore, nostril a single large opening with ventral portion of rim slightly elevated. Anterior nostril in tube with anterior flap and situated just posterior to upper lip. No lateral line present on body.

**Coloration:** In life, ground color of head and trunk pale yellow to tan dorsally, white ventrally. **Head:** mostly pale yellow-tan with white blotch on operculum; a brown to black C-shaped bar with yellow-brown edges originating on top of head, widening ventrally above orbit to width of pupil and passing over orbit at that width, then narrowing ventrally and continuing as dark line along lower edge of operculum; iris dark brown above and below where bar passes through, yellowish-white anteriorly and posteriorly, a thin gold ring circling pupil. **Trunk:** two dark bars beneath dorsal fin, anterior one brown to blackish (edged with yellow-brown) originating below anterior dorsal spines and descending obliquely behind pectoral-fin base to ventral midline; bar fading below pectoral-fin base; posterior bar much broader than anterior bar but paler and less conspicuous, bar spanning dorsal and ventral body margins and covering anterior half of caudal peduncle; bar narrowing ventrally. **Dorsal fin:** grey with a bluish tint (when photographed against black background – Fig. 7, bottom), with thin, submarginal yellow stripe; spinous dorsal fin with row of round to oblong yellow spots along base, 1–2 rows of obliquely oriented, oval, yellow spots above that; soft dorsal with large, conspicuous, circular, black ocellus covering lower half of fin and extending onto dorsal portion of trunk; thin, white, outer ring surrounding ocellus on both fin and trunk complete in holotype (Fig. 7), absent along underside of ocellus in both paratypes; above ocellus, soft dorsal fin with approximately three rows of rounded yellow spots; grey spaces between yellow spots appearing as well-defined grey to blue spots posteriorly. **Anal fin:** grey with bluish tint (when photographed against black background), each ray with 3–6 elongate yellow spots from base to fin edge; grey spaces between yellow spots appearing as well-defined grey to blue spots posteriorly. **Caudal fin:** base of fin mostly yellow, remainder of fin with rows of yellow spots along fin rays; grey spaces between yellow spots appearing as well-defined grey or blue spots. **Pectoral fins:** base yellowish with black dots, fin translucent. **Pelvic fins:** bright white, inner 2–3 rays with series of small yellow-brown dots. In preservative (Fig. 5B), barred color pattern retained, posterior trunk bar faint, and yellow and bluish pigments absent.

**Distribution.** Known only from Klein Curaçao, a 1.7 km<sup>2</sup> island 11 km southeast of Curaçao.

**Habitat.** No specific habitat information recorded.

**Etymology.** Named in honor of Spencer and Tomoko Haber, who funded and participated in a submersible dive by the Smithsonian's Deep Reef Observation Project (DROP) that resulted in the collection of USNM 434772, a paratype of the new species.

**Common name.** We propose "Yellow Banded Basslet" ("Cabrillela cinta-amarilla" as the Spanish equivalent) to distinguish *L. haberi* from *L. evides* and *L. levinsoni*. Although *L. evides* has a submarginal yellow stripe along the dorsal and anal fins, it lacks the overall yellow body color of *L. haberi*.

**Genetic comparisons.** Table 3 shows average inter- and intraspecific divergences in COI among species of *Lipogramma* analyzed genetically in this study. *Lipogramma haberi* exhibits 0.2% intraspecific genetic variation and 11.0–27.9% divergence from other *Lipogramma* species. It differs from *L. evides* by 11.0% and from *levinsoni* by 19.0%.

**Comments.** Relative to *L. levinsoni* and *L. evides*, which are known from multiple localities within the Caribbean Sea, *L. haberi* is an uncommon species on deep reefs and may have a more restricted geographic distribution. Although both *L. levinsoni* and *L. evides* are frequently observed and collected off the southern coast of Curaçao, in more than one hundred submersible dives there we have not collected *L. haberi*. Rather, we have only collected *L. haberi* on infrequent trips to Klein Curaçao, a small island, as noted above, 11 km southeast of Curaçao.

## Discussion

**Comments on *Lipogramma evides*.** The type series of *L. evides* includes the holotype and five paratypes (Robins and Colin 1979). We examined specimens or photographs of specimens of the type series from ANSP and FMNH and conclude that all except one, ANSP 134332, 12.6 mm SL, represent *L. evides*. We also examined 31 specimens of *Lipogramma evides* that we recently collected at Curaçao and that range in size from 12.7–45.4 mm SL. Frequency distributions of pectoral-fin rays and gill rakers on the first arch are given in Table 2, an illustration of the holotype that was included in the original description of the species is shown in Fig. 1A, color patterns of live and recently deceased individuals are shown in Fig. 8, a photograph of a preserved paratype (ANSP 134330) is provided in Fig. 5C, secondary spines on gill rakers of the first arch are shown in Fig. 3, supraorbital pore pattern is shown in Fig. 4, and a photograph of a preserved juvenile is featured in Fig. 6.

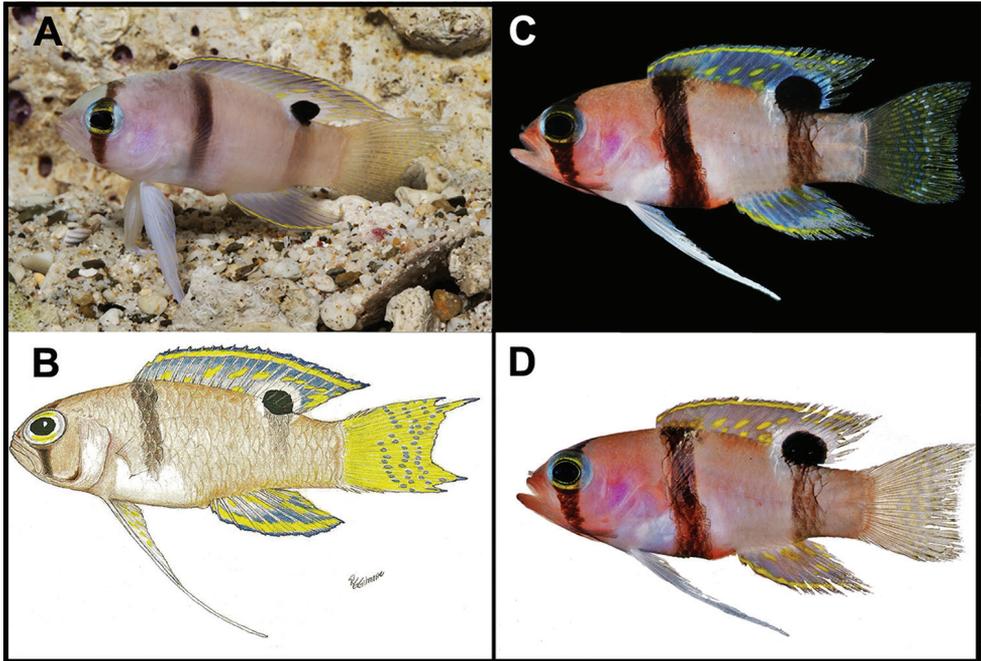
The illustration of the holotype (Fig. 1A) shows a triangular-shaped bar on the posterior portion of the trunk that more closely resembles the shape of that bar in *L. haberi* (Fig. 7) than *L. evides* (Fig. 8). The pigment is too faded in the preserved holotype now to determine the shape of that bar, but we note that in specimens or photographs of the four paratypes of the type series that are actually specimens of *L. evides*, the posterior trunk bar is narrow (e.g., Fig. 5C). This suggests that the shape of the posterior trunk bar illustrated in the holotype of *L. evides* is either incorrectly drawn or represents an anomaly for the species. *Lipogramma evides* and *L. haberi* are easily distinguished by numbers of gill rakers on the first arch—15 or 16 in *L. haberi*,

19–22 (modally 20) in *L. evides* (Table 2). Our examination of the holotype confirms the count by Robins and Colin (1979) of 20 gill rakers in the holotype of *L. evides*. Furthermore, the triangular-shaped posterior trunk bar in *L. haberi* is very pale relative to the anterior trunk and head bars. Robins and Colin's (1979) illustration of the holotype shows three body bars of equal intensity.

Colin's (1974) observation of "*Lipogramma sp.*" at Glover's Reef, Belize, was cited as *L. evides* by Robins and Colin (1979), and based on the recorded depths of observations, 165–180 m, we tentatively agree with this identification, as Belize is between Arrowsmith Bank and Nicaragua, where *L. evides* does occur. *Lipogramma evides* inhabits depths of 133–302 m, whereas *L. levinsoni* occurs from 103 to 154 m. However, Colin's (1974) observed fish could have been *L. haberi*, which occurs from 152–233 m. Polanco et al. (2012) recorded several specimens of *L. evides* from the Coralinos Archipelago off Colombia, and based on the stated counts of 15–16 pectoral-fin rays and 20–21 gill rakers, those specimens are correctly identified. In addition to Colombia and the tentative Belize location, *L. evides* is known definitively from the type locality of Arrowsmith Bank in the Yucatan Peninsula, Nicaragua, southeast of Barbuda, and Curaçao (including Klein Curaçao). It was also observed but not collected in October 2016 by DRR and LT from the mini-submarine "Idabel" at 232–250 m depth adjacent to Half Moon Bay, Roatan, Honduras. It was not collected or observed on DROP submersible dives at Bonaire or Dominica. A list of *L. evides* material examined in this study is given in Appendix 2.

**Morphological comparisons.** *Lipogramma levinsoni*, *L. evides*, and *L. haberi* can be readily distinguished from all congeners in having three dark bars (one on the head, two on the trunk) on a white background vs. a brown body with a reddish head in *L. anabantoides*; a yellow body with one black bar on the head in *L. flavescens*; a purple head and yellow trunk in *L. klayi* Randall, 1963; a brown body with one broad white bar and multiple narrow orange bars in *L. regia*; a brownish body with about 12 thin dark bars in *L. robinsi* Gilmore, 1997; a pink head and trunk with a yellow stripe along the dorsal profile of the head in *L. rosea*; and a yellow head and trunk with three long iridescent blue stripes on the head in *L. trilineata* Randall, 1963. The major differences among *L. levinsoni*, *L. evides*, and *L. haberi* are summarized in Table 5. *Lipogramma evides* and *L. haberi* are morphologically similar and reach a similar maximum size (45.5 and 40.1 in our material, respectively). They are easy to distinguish from one another on the basis of number of gill rakers on the first arch (usually 20–21 in *L. evides*, 15–16 in *L. haberi* – Table 2) and by live and preserved color pattern (Figs 5, 7, 8). In life, *L. haberi* has a considerable amount of yellow as ground color and associated with the dark bars, whereas the ground color of *L. evides* is mostly white. In fresh and preserved specimens, the posterior trunk bar in *L. haberi* is broad and much wider at the top than the bottom, whereas in *L. evides* it is narrower and of uniform width. There is also a difference in the shape of the caudal fin of the two species, with *L. haberi* having a truncate fin with rounded lobe tips and *L. evides* having a slightly emarginate fin with pointed lobe tips.

*Lipogramma levinsoni* reaches a smaller maximum size than *L. haberi* and *L. evides* (largest specimen examined 28.3 mm SL) and differs in modal numbers of gill rakers



**Figure 8.** *Lipogramma evides* **A** Aquarium photograph by Barry Brown, Substation Curacao **B** USNM 276560, 45.3 mm SL, illustration by Grant Gilmore in Gilmore and Jones (1988: fig. 1) **C** and **D** USNM 414885, 24.4 mm SL, photos by D. R. Robertson and C. C. Baldwin against black (**C**) and white (**D**) backgrounds.

on first arch and pectoral-fin rays (Table 2), supraorbital pore pattern (Fig. 4), and numerous aspects of color pattern (Figs 2, 5, 7, 8). In life, *L. levinsoni* is easily distinguished from *L. haberi* and *L. evides* by having an orange submarginal stripe on the dorsal fin (vs. yellow) and an orange submarginal stripe on the anal fin (vs. no stripe in *L. haberi*, a yellow submarginal stripe in *L. evides*). In preservative, *L. levinsoni* is easily distinguished from *L. haberi* and *L. evides* by the shape, size, and configuration of the dark body bars (Table 5).

**Species delimitation and phylogeny.** The neighbor-joining network (Suppl. material 1) shows eight distinct genetic lineages with an average within-lineage genetic distance of 0.002 substitutions/site and an average between-lineage genetic distance of 0.20 substitutions/site (Table 3). Considering between-lineage distances that are 10 or more times greater than within-lineage distances as indicative of distinct species (Hebert et al. 2014), genetic distances corroborate the recognition of the *L. levinsoni* and *L. haberi* lineages as species. Average between-lineage divergence for *L. levinsoni* is 19% (18% between *L. levinsoni* and the other two banded basslets, *L. haberi* and *L. evides*), whereas average within-lineage divergence is 0%. For *L. haberi*, average between-lineage divergence is 18% (11% between *L. haberi* and *L. levinsoni*/*L. evides*), whereas average within-lineage divergence is 0.2%.

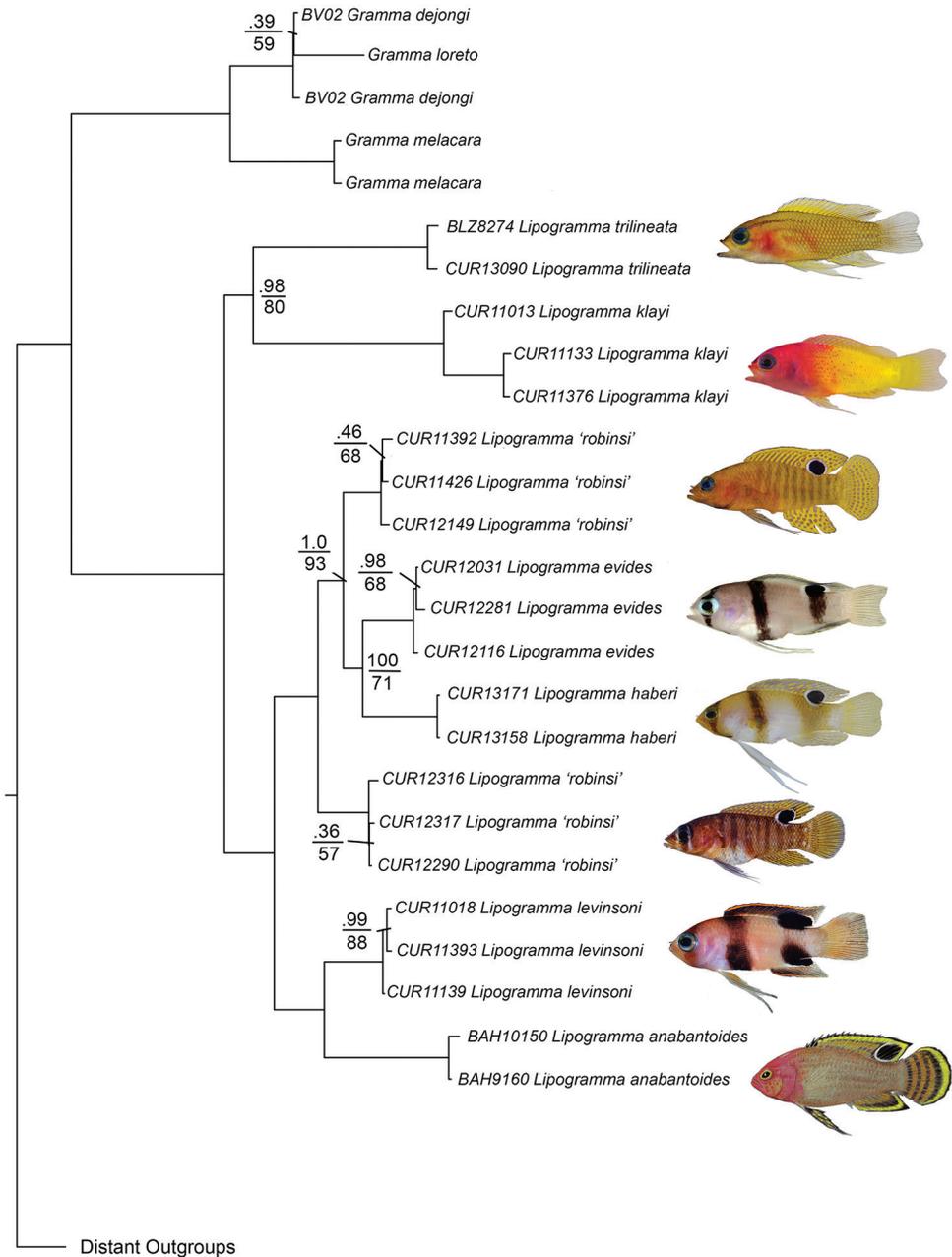
**Table 5.** Comparisons among *Lipogramma levinsoni* sp. n., *L. haberi* sp. n., and *L. evides*.

	<i>L. levinsoni</i>	<i>L. haberi</i>	<i>L. evides</i>
Standard length (mm)	9.4–28.3	23.0–40.1	13.7–45.5
Gill rakers on 1 <sup>st</sup> arch	Usually 19	15–16	Usually 20–21
Pectoral-fin rays	Usually 17	Usually 16	Usually 16
Supraorbital pores/pore present between pore at mid orbit and one at posterodorsal corner of orbit (Fig. 4)	3/Absent	4/Present	4/Present
Ground color	White, grey on nape & snout	Yellow above, white below	White
Dark bar on head	Black; relatively wide, widens to encompasses entire eye No rearward extension along lower edge of opercle	Brown, edged with yellow; relatively narrow, widens to encompass pupil Narrow rearward extension along lower edge of opercle	Black; relatively narrow, widens to encompass pupil Narrow rearward extension along lower edge of opercle
Width of dark bar on head (measured immediately ventral to eye) in % HL)	21.5–34.8 ( $\bar{x}$ = 26.4)	14.9–20.4 ( $\bar{x}$ = 17.6)	8.7–19.4 ( $\bar{x}$ = 14.7)
Anterior trunk bar	Black, wide, vertical, center often narrower & paler Covers pectoral base Extension onto dorsal fin large, intense	Brown, edged with yellow; narrow, slightly oblique, uniform width, paler on belly Behind pectoral base No extension onto dorsal fin	Black; narrow, slightly oblique, uniform width, paler on belly Behind pectoral base Extension onto dorsal fin small, weak
Posterior trunk bar	Same form and color as anterior bar Extension onto dorsal fin = oval partial ocellus Extension onto anal fin = elongate, partial ocellus	Yellow-brown; broad dorsally, thinning ventrally, triangular in shape Extension onto dorsal fin = round, well defined ocellus No extension onto anal fin	Same form and color as anterior bar but usually paler than anterior bar Extension onto dorsal fin = round, well defined ocellus Extension onto anal fin absent or a small, weak smudge
Dorsal-fin pigment	Submarginal stripe orange Remainder of fin without pale spots	Submarginal stripe yellow Remainder of fin with 2–3 rows of yellow spots	Submarginal stripe yellow Remainder of fin with 1–2 rows of yellow spots
Anal-fin pigment	Submarginal stripe orange No pale spots on remainder of fin	No pale submarginal stripe Remainder of fin with 1–6 rows of yellow spots	Submarginal stripe yellow Remainder of fin with 1–3 rows of yellow spots near base
Caudal-fin shape	Truncate, lobe tips rounded	Truncate, lobe tips rounded	Slightly emarginate, lobe tips pointed
Depth range (m)	108–154	152–233	133–302
Geographical distribution	Bahamas, Bonaire, Curaçao, Dominica, and Jamaica	Klein Curaçao	Barbuda, Belize(?), Colombia, Curaçao, Klein Curaçao, Mexico (Caribbean), and Nicaragua

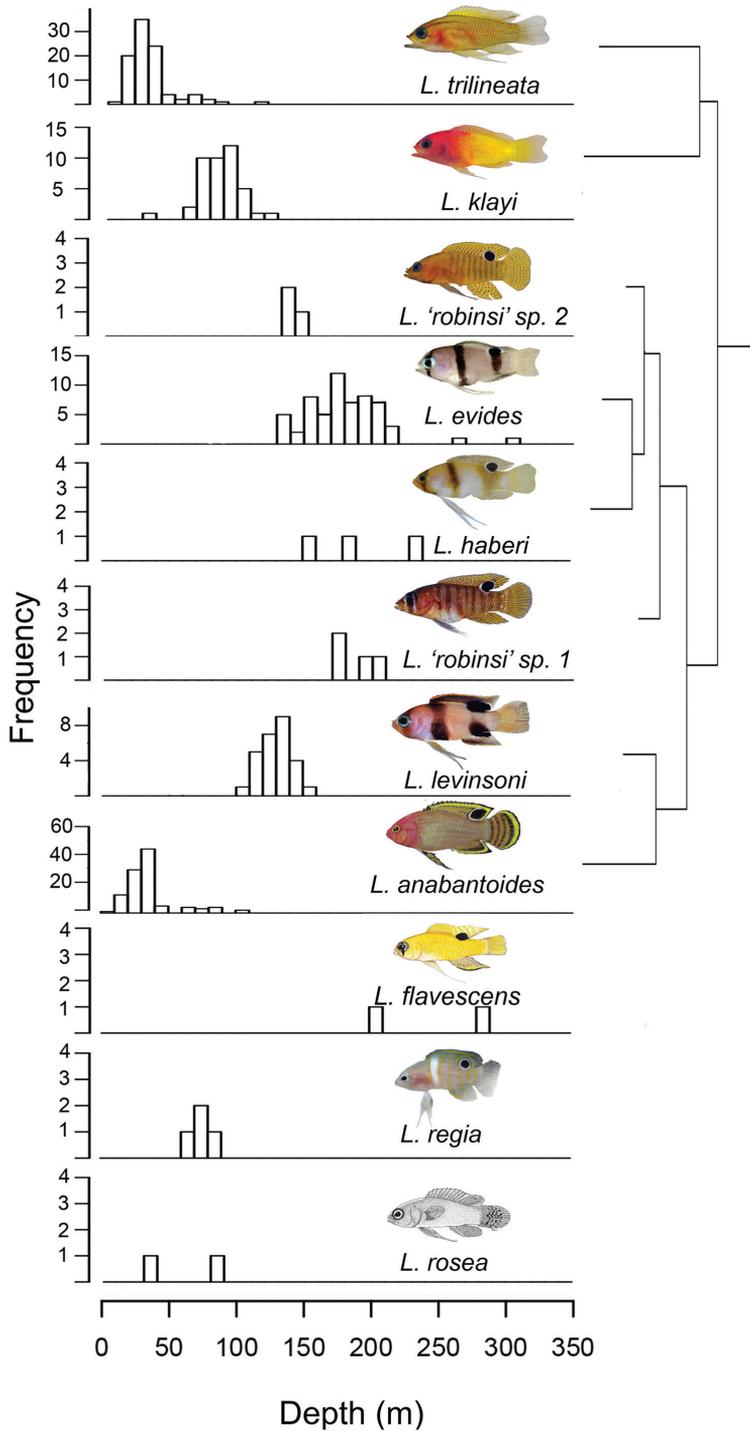
The ML and BI analyses resulted in identical topologies, with most relationships supported by 1.0 posterior probability and 100% bootstrap support (Fig. 9). The BP&P analysis inferred a coalescent-based species-tree that was identical in topology to the ML and BI trees. In addition, the BP&P analysis provided overwhelming support for the presence of eight species of *Lipogramma* in our phylogeny (posterior probability 0.99981), including three distinct species of banded basslets (*L. evides*, *L. haberi* and *L. levinsoni*), indicating perfect congruence between molecular and morphology-based species delimitation criteria. *Lipogramma trilineata* and *L. klayi*, which have two of the shallowest depth ranges among *Lipogramma* species (Fig. 10), were recovered as sister species. This pair is sister to a larger clade comprising *L. anabantoides* + *L. levinsoni* (as sister species) and *L. evides* + *L. haberi* + two putative new species superficially resembling *L. robinsi*. Not surprising given their morphological similarity, *L. evides*, and *L. haberi* resolve as sister species. There is strong support for a clade comprising the four deepest-known species in our phylogeny—*L. evides*, *L. haberi*, and the two “*L. robinsi*” species (Figs 9, 10). Baldwin and Robertson (2014) found a similar evolutionary grouping of deep-water species in the serranid genus *Liopropoma*, and Tornabene et al. (2016a) found repeated invasions of deep-reef depths in the family Gobiidae with subsequent species radiations entirely within the deep-reef zone. *Lipogramma flavescens*, which also inhabits deep water (200–300 m, Fig. 10), may be part of this clade. A dark ocellus on the base of the soft dorsal fin appears to be a synapomorphy of the clade comprising *L. anabantoides*, *L. levinsoni*, *L. evides*, *L. haberi*, and the two “*L. robinsi*” species. Presence of this ocellus in *L. flavescens* and *L. regia* suggests that they may also belong to this group, but genetic samples of both are needed for phylogenetic analysis. *Lipogramma flavescens* may be closely related to *L. haberi*, as they share a narrow dark bar through the eye, yellow coloration, and low gill-raker count (15–16), and they inhabit similar deep-reef depths (152–233 m for *L. haberi*, 200–300 m for *L. flavescens*). If the evolutionary relationships of *Lipogramma* species are correlated with depth as our data suggest, and if *Lipogramma regia*, which is known only from depths < 100 m is a member of the clade diagnosed by a dark ocellus on the soft dorsal fin, it may be most closely related to *L. anabantoides* and *L. levinsoni*, which are known only from depths < 120 m (*L. anabantoides*) and < 154 m (*L. levinsoni*). Those three are the only known *Lipogramma* species with a modal pectoral-fin count of 17 (Gilmore and Jones 1988: Table 2, this study). We note that the addition to our molecular phylogeny of the four known species of *Lipogramma* that are currently unavailable for analysis (*L. flavescens*, *L. regia*, *L. rosea*, and *L. robinsi*) could change our hypotheses of relationships within the genus.

The two “*L. robinsi*” included here (Table 3, Figs 9, 10) are genetically distinct and superficially different from one another and from *L. robinsi* Gilmore, 1997. A more thorough investigation of those three taxa is in progress, after which a key to all *Lipogramma* species will be constructed.

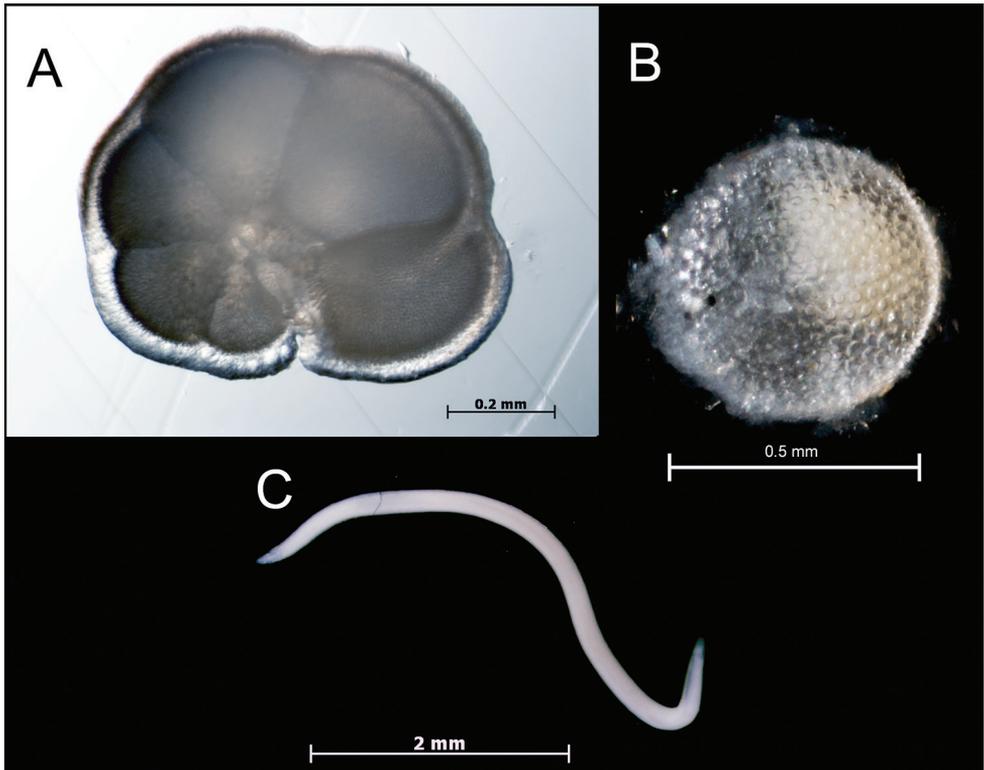
*Lipogramma* is currently classified along with *Gramma* in the family Grammatidae based on a single synapomorphy in the arrangement of cheek musculature (Gill and Mooi 1993). Molecular data have failed to corroborate the monophyly of the Grammatidae (Betancur-R et al. 2013, Mirande 2016); rather, those data suggest that *Lipogramma* and



**Figure 9.** Bayesian Inference molecular phylogeny of *Lipogramma* based on combined mitochondrial and nuclear genes. Numbers of individuals analyzed for each species are given in Appendix 1, along with the genes sequenced for each individual. Topology is identical to that from Maximum Likelihood analysis. Support values are Bayesian posterior probabilities (above) and bootstrap values (below). Nodes without labels have 1.0 posterior probability and 100 bootstrap values. Photos or illustrations by C. C. Baldwin, D. R. Robertson, R. G. Gilmore, and C. R. Robins.



**Figure 10.** Depth distributions for species of *Lipogramma*. Photos or illustrations by C. C. Baldwin, D. R. Robertson, R. G. Gilmore, and Mooi and Gill (2002: fig. 9).



**Figure 11.** Items from stomachs of deep-reef *Lipogramma*: **A** Planktonic foraminiferan, possibly *Globorotalia manardii*, from *L. evides*, USNM 434771, collected at 174 m **B** Diatom, possibly *Coscinodiscus eccentricus*, from *L. levinsoni* sp. n., USNM 406140, collected between 137 and 146 m **C** Parasitic Nematoda from same specimen as **B**. Photos by A. Nonaka and L. Tornabene.

*Gramma* are each related to different taxa within the diverse Ovalentaria. Relationships within the Ovalentaria have proven difficult to resolve with traditional molecular markers (Betancur-R et al. 2013), molecular markers plus some morphological characters (Mirande 2016), and phylogenomic data (Eytan et al. 2015). Potential close relatives of *Lipogramma* based on molecular data include blennioids, cichlids, plesiopids, pseudochromids, and *Pholidichthys*. Some of these groups have been previously linked to either *Lipogramma*, *Gramma*, or both, based on shared morphological characters, but the homologies of many of these characters have been questioned (Gill and Mooi 1993). At present, the phylogenetic position of *Lipogramma* is unresolved.

**Ecology and life history.** Little is known about community structure on deep reefs, including food networks. Although an analysis of the diet of banded basslets based on stomach contents is beyond the scope of this study, the gastrointestinal tract of the cleared and stained *L. evides* (USNM 434771) contained numerous individuals of a planktonic foraminiferan that was tentatively identified by Smithsonian Curator of Planktic Fo-

raminifera Brian Huber as *Globorotalia manardii* (d'Orbigny) – Fig. 11A. Two items found in the gastrointestinal tract of *L. levinsoni* (USNM 406140) appear to be a diatom (possibly *Coscinodiscus eccentricus* Ehrenberg, Huber pers. comm, Fig. 11B) and a parasitic nematode (identification by Smithsonian Curator of Invertebrate Zoology Jon Norenberg and Assistant Professor of Biology at Virginia Military Institute Ashleigh Smythe, Fig. 11C). Future investigations of diets of deep-reef fish species are planned.

The broad Caribbean distributions of *L. levinsoni* and *L. evides* (Table 5) suggest a pelagic larval stage capable of dispersal, so it is perplexing that there are no records of *Lipogramma* or *Gramma* larvae from plankton tows (Asoh and Yoshikawa 1996, Hardy 2006). Thresher (1980) noted that *L. trilineata* constructs nests within algae in aquaria settings, and Asoh and Yoshikawa (1996) described similar nesting behavior in *Gramma loreto* Poey, 1868. The apparent restricted geographic distribution of *L. haberi* (Table 5) could indicate that some species have limited dispersal capabilities; however, the paucity of faunal investigations of deep-reef ecosystems may mask a larger geographic distribution for that species. Interestingly, Leis et al. (2012) calculated swimming speed for reared *G. loreto* larvae and found that the actual and relative critical speed (Ucrit) were so low that for most of the pelagic larval duration their ability to influence their dispersal by horizontal swimming would be much less than that of many other tropical fish species. Further study of the early life history of *Lipogramma* is needed, including exploring the possibility that planktonic dispersal in the genus may be limited.

## Conclusions

Adults and juveniles of the banded basslet, *L. evides*, were previously recognized as different ontogenetic color patterns of a single species. This study shows that the juvenile color pattern belongs to a cryptic species, described here as *L. levinsoni*. This study also documents the first known juveniles of *L. evides*, which share the color pattern of adults. A second new species that is morphologically similar to *L. evides*, *L. haberi*, is also described. These three basslet species are confined to deep-reef depths, but they stratify such that *L. levinsoni* occurs at shallower depths than *L. evides* and *L. haberi*. A molecular analysis of evolutionary relationships among available *Lipogramma* species reveals correlations between depth of occurrence and phylogeny, an eco-evolutionary pattern observed in other deep-reef Caribbean fishes that warrants further investigation. The two new basslets represent the eleventh and twelfth new fish species described in recent years from exploratory submersible diving by the Smithsonian's Deep Reef Observation Project (DROP) to Caribbean depths of 300 m (Baldwin and Robertson 2013, 2014, 2015; Baldwin and Johnson 2014; Baldwin et al. 2016; Tornabene et al. 2016b, 2016c). Numerous other new fish and invertebrate species discovered by DROP await description, including the two putative new species identified in this study as morphologically similar to but distinct from *L. robinsi*. Considerably more effort is needed to adequately explore tropical deep reefs, diverse but largely overlooked global ecosystems.

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## Appendix I.

Links between DNA voucher specimens, GenBank accession numbers, and DNA sequences of *Lipogramma* derived for use in this study.

Catalog number	Tissue number	Species	GenBank COI	GenBank H3	GenBank TMO-4C4	GenBank RagI	GenBank Rhodopsin	GenSeq designation
Photo Voucher Only	BAH10150	<i>Lipogramma anabantoides</i>	KX713732	KX713823	KX713880	KX713842	KX713862	genseq-5
USNM 413759	BAH9160	<i>Lipogramma anabantoides</i>		KX713824	KX713881	KX713843	KX713863	genseq-4
USNM 420334	BLZ5340	<i>Lipogramma anabantoides</i>	KX713733					genseq-4
USNM 414886	CUR12013	<i>Lipogramma euides</i>	KX713750					genseq-4
USNM 414889	CUR12031	<i>Lipogramma euides</i>	KX713751	KX713834	KX713891	KX713852	KX713872	genseq-4
USNM 414883	CUR12044	<i>Lipogramma euides</i>	KX713752					genseq-4
USNM 414884	CUR12050	<i>Lipogramma euides</i>	KX713753					genseq-4
USNM 414887	CUR12078	<i>Lipogramma euides</i>	KX713754					genseq-4
USNM 414890	CUR12084	<i>Lipogramma euides</i>	KX713755					genseq-4
USNM 414888	CUR12116	<i>Lipogramma euides</i>	KX713757	KX713835	KX713892	KX713853	KX713873	genseq-4
USNM 414882	CUR12118	<i>Lipogramma euides</i>	KX713758					genseq-4
USNM 414878	CUR12276	<i>Lipogramma euides</i>	KX713760					genseq-4
USNM 414881	CUR12280	<i>Lipogramma euides</i>	KX713761					genseq-4
USNM 414885	CUR12281	<i>Lipogramma euides</i>	KX713762	KX713837	KX713894	KX713855	KX713875	genseq-4
USNM 414879	CUR12288	<i>Lipogramma euides</i>	KX713763					genseq-4
USNM 414876	CUR12353	<i>Lipogramma euides</i>	KX713767					genseq-4
USNM 421602	CUR13100	<i>Lipogramma euides</i>	KX713771					genseq-4
USNM 426769	CUR13233	<i>Lipogramma euides</i>	KX713779					genseq-4
USNM 426770	CUR13234	<i>Lipogramma euides</i>	KX713780					genseq-4
USNM 426771	CUR13265	<i>Lipogramma euides</i>	KX713781					genseq-4
USNM 426737	CUR13266	<i>Lipogramma euides</i>	KX713782					genseq-4
USNM 426746	CUR13279	<i>Lipogramma euides</i>	KX713785					genseq-4
USNM 426709	CUR13286	<i>Lipogramma euides</i>	KX713786					genseq-4
USNM 426722	CUR13294	<i>Lipogramma euides</i>	KX713787					genseq-4
Photo Voucher Only	CUR15032	<i>Lipogramma euides</i>	KX713793					genseq-5

Catalog number	Tissue number	Species	GenBank COI	GenBank H3	GenBank TMO-4C4	GenBank Ragl	GenBank Rhodopsin	GenSeq designation
Photo Voucher Only	CUR15055	<i>Lipogramma evides</i>	KX713795	-	-	-	-	genseq-5
Photo Voucher Only	CUR15057	<i>Lipogramma evides</i>	KX713796	-	-	-	-	genseq-5
Photo Voucher Only	CUR15060	<i>Lipogramma evides</i>	KX713798	-	-	-	-	genseq-5
Photo Voucher Only	CUR15061	<i>Lipogramma evides</i>	KX713799	-	-	-	-	genseq-5
USNM 434771	CUR15091	<i>Lipogramma evides</i>	KX713811	-	-	-	-	genseq-4
USNM 434783	CUR15103	<i>Lipogramma evides</i>	KX713813	-	-	-	-	genseq-4
USNM 434784	CUR15104	<i>Lipogramma evides</i>	KX713814	-	-	-	-	genseq-4
USNM 431313	TIK003	<i>Lipogramma evides</i>	KX713822	-	-	-	-	genseq-4
USNM 422670, paratype	CUR13158	<i>Lipogramma haberi</i>	KX713775	-	-	KX713860	-	genseq-2
USNM 422679, holotype	CUR13171	<i>Lipogramma haberi</i>	KX713776	-	-	KX713861	-	genseq-1
USNM 434772, paratype	CUR15092	<i>Lipogramma haberi</i>	KX713812	-	-	-	-	genseq-2
USNM 406013	CUR11013	<i>Lipogramma klayi</i>	KX713737	KX713826	KX713883	KX713845	KX713865	genseq-3
USNM 406133	CUR11133	<i>Lipogramma klayi</i>	KX713740	KX713828	KX713885	KX713847	KX713867	genseq-3
USNM 406134	CUR11134	<i>Lipogramma klayi</i>	KX713741	-	-	-	-	genseq-3
USNM 406375	CUR11375	<i>Lipogramma klayi</i>	KX713744	-	-	-	-	genseq-3
USNM 406376	CUR11376	<i>Lipogramma klayi</i>	KX713745	KX713830	KX713887	KX713849	KX713869	genseq-3
USNM 422669	CUR13112	<i>Lipogramma klayi</i>	KX713772	-	-	-	-	genseq-3
USNM 422676	CUR13113	<i>Lipogramma klayi</i>	KX713773	-	-	-	-	genseq-3
USNM 422690	CUR13114	<i>Lipogramma klayi</i>	KX713774	-	-	-	-	genseq-3
Photo Voucher Only	CUR15064	<i>Lipogramma klayi</i>	KX713800	-	-	-	-	genseq-5
Photo Voucher Only	CUR15066	<i>Lipogramma klayi</i>	KX713801	-	-	-	-	genseq-5
Photo Voucher Only	CUR15068	<i>Lipogramma klayi</i>	KX713802	-	-	-	-	genseq-5
Photo Voucher Only	CUR15069	<i>Lipogramma klayi</i>	KX713803	-	-	-	-	genseq-5
Photo Voucher Only	CUR15070	<i>Lipogramma klayi</i>	KX713804	-	-	-	-	genseq-5
Photo Voucher Only	CUR15075	<i>Lipogramma klayi</i>	KX713805	-	-	-	-	genseq-5
Photo Voucher Only	CUR15076	<i>Lipogramma klayi</i>	KX713806	-	-	-	-	genseq-5
Photo Voucher Only	CUR15077	<i>Lipogramma klayi</i>	KX713807	-	-	-	-	genseq-5
Photo Voucher Only	CUR15084	<i>Lipogramma klayi</i>	KX713810	-	-	-	-	genseq-5
USNM 438687	DOM16036	<i>Lipogramma klayi</i>	KX713817	-	-	-	-	genseq-4

Catalog number	Tissue number	Species	GenBank COI	GenBank H3	GenBank TMO-4C4	GenBank Rag1	GenBank Rhodopsin	GenSeq designation
USNM 438741	DOM16090	<i>Lipogramma klaji</i>	KX713819	–	–	–	–	genseq-4
USNM 438742	DOM16091	<i>Lipogramma klaji</i>	KX713820	–	–	–	–	genseq-4
USNM 438803	DOM16152	<i>Lipogramma klaji</i>	KX713821	–	–	–	–	genseq-4
USNM 406011	CUR11011	<i>Lipogramma levinsoni</i>	KX713735	–	–	–	–	genseq-3
USNM 406012	CUR11012	<i>Lipogramma levinsoni</i>	KX713736	–	–	–	–	genseq-3
USNM 406018, paratype	CUR11018	<i>Lipogramma levinsoni</i>	KX713738	KX713827	KX713884	KX713846	KX713866	genseq-2
USNM 406019	CUR11019	<i>Lipogramma levinsoni</i>	KX713739	–	–	–	–	genseq-3
USNM 406139, holotype	CUR11139	<i>Lipogramma levinsoni</i>	KX713742	KX713829	KX713886	KX713848	KX713868	genseq-1
USNM 406140, paratype	CUR11140	<i>Lipogramma levinsoni</i>	KX713743	–	–	–	–	genseq-2
USNM 406393, paratype	CUR11393	<i>Lipogramma levinsoni</i>	KX713747	KX713832	KX713889	KX713851	KX713871	genseq-2
USNM 406394	CUR11394	<i>Lipogramma levinsoni</i>	KX713748	–	–	–	–	genseq-3
USNM 426784, paratype	CUR13183	<i>Lipogramma levinsoni</i>	KX713777	–	–	–	–	genseq-2
USNM 426754	CUR13184	<i>Lipogramma levinsoni</i>	KX713778	–	–	–	–	genseq-3
USNM 426774	CUR13267	<i>Lipogramma levinsoni</i>	KX713783	–	–	–	–	genseq-3
USNM 426730	CUR13268	<i>Lipogramma levinsoni</i>	KX713784	–	–	–	–	genseq-3
Photo Voucher Only	CUR15031	<i>Lipogramma levinsoni</i>	KX713792	–	–	–	–	genseq-5
Photo Voucher Only	CUR15058	<i>Lipogramma levinsoni</i>	KX713797	–	–	–	–	genseq-5
USNM 438703	DOM16052	<i>Lipogramma levinsoni</i>	KX713818	–	–	–	–	genseq-4
USNM 406392	CUR11392	<i>Lipogramma "robinsi"</i>	KX713746	KX713831	KX713888	KX713850	KX713870	genseq-4
USNM 406426	CUR11426	<i>Lipogramma "robinsi"</i>	KX713749	KX713833	KX713890	–	–	genseq-4
USNM 414913	CUR12101	<i>Lipogramma "robinsi"</i>	KX713756	–	–	–	–	genseq-4
USNM 414914	CUR12149	<i>Lipogramma "robinsi"</i>	KX713759	KX713836	KX713893	KX713854	KX713874	genseq-4
USNM 413864	CUR12290	<i>Lipogramma "robinsi"</i>	KX713764	KX713838	KX713895	KX713856	KX713876	genseq-4
USNM 414911	CUR12316	<i>Lipogramma "robinsi"</i>	KX713765	KX713839	KX713896	KX713857	KX713877	genseq-4
USNM 414912	CUR12317	<i>Lipogramma "robinsi"</i>	KX713766	KX713840	KX713897	KX713858	KX713878	genseq-4
USNM 430035	CUR13329	<i>Lipogramma "robinsi"</i>	KX713788	–	–	–	–	genseq-4
USNM 431687	CUR14079	<i>Lipogramma "robinsi"</i>	KX713789	–	–	–	–	genseq-4
USNM 431722	CUR14114	<i>Lipogramma "robinsi"</i>	KX713790	–	–	–	–	genseq-4
USNM 435299	CUR15012	<i>Lipogramma "robinsi"</i>	KX713791	–	–	–	–	genseq-4

Catalog number	Tissue number	Species	GenBank COI	GenBank H3	GenBank TMO-4C4	GenBank Ragl	GenBank Rhodopsin	GenSeq designation
USNM 436460	CUR15125	<i>Lipogramma "robini"</i>	KX713815	-	-	-	-	genseq-4
USNM 436474	CUR15139	<i>Lipogramma "robini"</i>	KX713816	-	-	-	-	genseq-4
Photo Voucher Only	BLZ8127	<i>Lipogramma trilineata</i>	JQ841643	-	-	-	-	genseq-5
Photo Voucher Only	BLZ8128	<i>Lipogramma trilineata</i>	JQ841642	-	-	-	-	genseq-5
USNM 415245	BLZ8168	<i>Lipogramma trilineata</i>	JQ841645	-	-	-	-	genseq-4
USNM 415298	BLZ8274	<i>Lipogramma trilineata</i>	JQ841646	KX713825	KX713882	KX713844	KX713864	genseq-4
Photo Voucher Only	BLZ8343	<i>Lipogramma trilineata</i>	JQ841644	-	-	-	-	genseq-5
USNM 404204	BLZWF204	<i>Lipogramma trilineata</i>	KX713734	-	-	-	-	genseq-4
USNM 414989	CUR13082	<i>Lipogramma trilineata</i>	KX713768	-	-	-	-	genseq-3
USNM 414990	CUR13089	<i>Lipogramma trilineata</i>	KX713769	-	-	-	-	genseq-3
USNM 414991	CUR13090	<i>Lipogramma trilineata</i>	KX713770	KX713841	KX713898	KX713859	KX713879	genseq-3
Photo Voucher Only	CUR15034	<i>Lipogramma trilineata</i>	KX713794	-	-	-	-	genseq-5
Photo Voucher Only	CUR15078	<i>Lipogramma trilineata</i>	KX713808	-	-	-	-	genseq-5
Photo Voucher Only	CUR15079	<i>Lipogramma trilineata</i>	KX713809	-	-	-	-	genseq-5

## Appendix 2.

### Specimens of *Lipogramma evides* examined in this study.

ANSP 134329, holotype, 34.4 mm SL, R/V Pillsbury Sta. 581, Mexico, Arrowsmith Bank, 21°05'N, 86°23'W, 146–265 m depth, 22 May 1967; ANSP 134330, n=2, paratypes, 28.0–32.0 mm SL, R/V Pillsbury Sta. 581, Mexico, Arrowsmith Bank, 21 05'N, 86 23'W, 146–265 m depth, 22 May 1967; ANSP 134331, paratype, 17.2 mm SL, R/V Pillsbury Sta. 969, southeast of Barbuda, 17°27.8'N, 61°41.1'W, 68–216 m depth, 20 July 1969; FMNH 82583, paratype, 34.5 mm SL, Nicaragua, 12°32'N, 82°25 ' W, 155 m depth, 23 May 1692; USNM 426801 25.1 mm SL, Curasub submersible, sta. CURASUB13-18, Curaçao, Playa Forti, Westpoint, 12.3679 N, 69.1553 W, no depth data, 15 August 2013, C. Baldwin, B. Brandt, A. Schrier, K. Johnson & C. DeForest; USNM 431410, 12.7 mm SL, Curasub submersible, sta. CURASUB14-07, Curaçao, in between Porto Marie and Daaibooi beaches, 12.202842 N, 69.089507 W, 123 m depth, 21 March 2014, C. Baldwin et al.; USNM 426746, 45.4 mm SL, tissue no. CUR13279, Curasub submersible, sta. CURASUB13-19, Curaçao, Playa Forti, Westpoint, 12.3679 N, 69.1553 W, 179 m depth, 15 August 2013, B. Van Bebber, N. Knowlton, A. Schrier & R. Sant; USNM 431408, 35.5 mm SL, Curasub submersible, sta. CURASUB14-02, Curaçao, off Substation Curaçao downline., 12.083197 N, 68.899058 W, no depth data available, 17 March 2014, B. Brooks et al.; USNM 410992, 43.0 mm SL, Curasub submersible, sta. CURASUB13-33, Caracas Baii and back to Substation Curaçao downline, 12.068 N, 68.873367 W, 215 m depth, 5 November 2013, C. Baldwin, B. Brandt, A. Schrier & C. Castillo; UF 238591, 34.5 mm SL, Curasub submersible, sta. CURASUB15-13, Northwest corner of Klein Curaçao, 11.998453 N, 68.651308 W, 182 m depth, 28 August 2015, C. Baldwin & B. Van Bebber; USNM 434771, 33.3 mm SL, cleared and stained, tissue no. CUR15091, Curasub submersible, sta. CURASUB15-12, northwest corner of Klein Curaçao, 11.998453 N, 68.651308 W, 174 m depth, 27 August 2015, B. Brandt & A. Schrier; USNM 434783, 17.9 mm SL, tissue no. CUR15103, Curasub submersible, sta. CURASUB15-13, Northwest corner of Klein Curaçao, 11.998453 N, 68.651308 W, 171 m depth, 28 August 2015, C. Baldwin & B. Van Bebber; UF 238590, 27.7 mm SL, tissue no. CUR15104, Curasub submersible, sta. CURASUB15-13, Northwest corner of Klein Curaçao, 11.998453 N, 68.651308 W, 172 m depth, 28 August 2015, C. Baldwin & B. Van Bebber; USNM 431313, 39.2 mm SL, tissue no. T1K003, Curasub submersible, sta. CURASUB14-03, Curaçao, west of Substation Curaçao downline, 12.083197 N, 68.899058 W, 177 m depth, 18 March 2014, C. Baldwin et al.; USNM 414886, 24.9 mm SL, tissue no. CUR12013, Curasub submersible, sta. CURASUB12-01, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, 171 m depth, 21 May 2012, C. Baldwin, A. Schrier & B. Brandt; USNM 414889, 31.3 mm SL, tissue no. CUR12031, Curasub submersible, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 21 May 2012, C. Baldwin et al.; USNM 414883, 40.0 mm SL, tissue CUR12044, Curasub

submersible, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 21 May 2012, C. Baldwin et al.; USNM 414884, 32.0 mm SL, tissue no. CUR12050, Curasub submersible, sta. CURASUB12-11, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, 164 m depth, 6 August 2012, B. Brandt, C. Baldwin, A. Schrier & A. Driskell; USNM 414887, 31.3 mm SL, tissue CUR12078, Curasub submersible, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 21 May 2012, C. Baldwin et al.; USNM 414890, 40.3 mm SL, tissue no. CUR12084, Curasub submersible, Curaçao, off of Substation Curaçao downline, 12.083197 N, 68.899058 W, no depth data available, 21 May 2012, C. Baldwin et al.; USNM 414888, 39.8 mm SL, tissue no. CUR12116, Curasub submersible, sta. CURASUB12-14, Curaçao, east of downline off Substation dock, 12.083197 N, 68.899058 W, 133 m depth, 9 August 2012, A. Schrier, B. Brandt, C. Castillo, A. Driskell & D. Robertson; USNM 414880, 29.0 mm SL, tissue no. CUR12117, Curasub submersible, sta. CURASUB12-14, Curaçao, east of downline off Substation dock, 12.083197 N, 68.899058 W, 134 m depth, 9 August 2012, A. Schrier, B. Brandt, C. Castillo, A. Driskell & D. Robertson; USNM 414882, 20.1 mm SL, tissue CUR12118, Curasub submersible, sta. CURASUB12-14, Curaçao, east of downline off Substation dock, 12.083197 N, 68.899058 W, 134 m depth, 9 August 2012, A. Schrier, B. Brandt, C. Castillo, A. Driskell & D. Robertson; USNM 414878, 24.1 mm SL, tissue no. CUR12276, Curasub submersible, sta. CURASUB12-16, Curaçao, west to Stella Maris and down, 154 m depth, 13 August 2012, A. Schrier, C. Baldwin & B. Van Bebber; USNM 414881, 21.1 mm SL, tissue no. CUR12280, 21.2 mm SL, Curasub submersible, sta. CURASUB12-17, Curaçao, East of downline off Substation Curaçao dock, 12.083197 N, 68.899058 W, 161 m depth, 13 August 2012, A. Schrier, B. Brandt, C. Castillo & D. Robertson; USNM 414885, 24.4 mm SL, tissue no. CUR12281, Curasub submersible, sta. CURASUB12-17, Curaçao, East of downline off Substation Curaçao dock, 12.083197 N, 68.899058 W, 161 m depth, 13 August 2012, A. Schrier, B. Brandt, C. Castillo & D. Robertson; USNM 414879, 25.0 mm SL, tissue no. CUR12288, Curasub submersible, sta. CURASUB12-16, Curaçao, west to Stella Maris and down, 154 m depth, 13 August 2012, A. Schrier, C. Baldwin & B. Van Bebber; USNM 414876, 41.7 mm SL, tissue no. CUR12353, Curasub submersible, no station data, off Substation Curaçao dock, 12.083197 N, 68.899058 W, no depth data available, 2012, Substation Curaçao crew; USNM 421602, 43.6 mm SL, tissue CUR13100, Curasub submersible, Curaçao, off Substation Curaçao, 12.083197 N, 68.899058 W, no depth data available; USNM 426769, 19.0 mm SL, tissue CUR13233, Curasub submersible, sta. CURASUB13-12, Curaçao, off downline at Substation Curaçao, 12.083197 N, 68.899058 W, 137–173 m depth, 7 August 2013, C. Baldwin, D. Robertson, C. Castillo & B. Van Bebber; USNM 426770, 13.7 mm SL, tissue no. CUR13234, Curasub submersible, sta. CURASUB13-12, Curaçao, off downline at Substation Curaçao, 12.083197 N, 68.899058 W, 137–173 m depth, 7 August 2013, C. Baldwin, D. Robertson, C. Castillo & B. Van Bebber; USNM 426771, 24.9 mm SL, tissue CUR13265, Curasub submersible, sta. CURASUB13-18, Curaçao, Playa Forti,

westpoint, 12.3679 N, 69.1553 W, 137–164 m depth, 15 August 2013, C. Baldwin, B. Brandt, A. Schrier, K. Johnson & C. DeForest; USNM 426737, 19.3 mm SL, tissue CUR13266, Curasub submersible, sta. CURASUB13-18, Curaçao, Playa Forti, westpoint, 12.3679 N, 69.1553 W, 137–173 m depth, 15 August 2013, C. Baldwin, B. Brandt, A. Schrier, K. Johnson & C. DeForest; USNM 426709, 40.2 mm SL, tissue no. CUR13286, Curasub submersible, sta. CURASUB13-21, Curaçao, off Substation Curaçao downline, 12.083197 N, 68.899058 W, 171–201 m depth, 17 August 2013, C. Baldwin, A. Schrier, B. Brandt & A. Driskell; USNM 426722, 32.5 mm SL, tissue no. CUR13294, Curasub submersible, sta. CURASUB13-21, Curaçao, off Substation Curaçao downline, 12.083197 N, 68.899058 W, 171–201 m depth, 17 August 2013, C. Baldwin, A. Schrier, B. Brandt & A. Driskell.

## Supplementary material I

### Figure S1

Authors: Carole C. Baldwin, D. Ross Robertson, Ai Nonaka, Luke Tornabene

Data type: Tif image file

Explanation note: Neighbor-joining network based on COI sequences of *Lipogramma* species investigated in this study. Scale-bar units are substitutions per site.

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# The ichthyofauna of limnic systems in Quaternary deposits of extreme southern Brazil

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## Abstract

The Quaternary in the state of Rio Grande do Sul (RS), southern Brazil, is geologically represented by the coastal plain and was originated by successive events of Pleistocene-Holocene marine transgressions and the occurrence of alluvial deposits. This paper aimed to characterize the fish assemblage occurring in a swampy Quaternary area adjacent to Lagoa Pequena, a lacustrine system connected to the west margin of the Laguna dos Patos estuary. A checklist is also provided of the ichthyofauna so far recorded in limnic systems of Quaternary deposits in the state of Rio Grande do Sul. A total of 42 species was recorded, distributed in nine orders, 18 families and 31 genera. Characidae and Cichlidae were the most representative families, comprising 15 and 4 species respectively. A bibliographic revision associated to our sample data revealed the occurrence of 156 species in limnic systems inserted in RS Quaternary deposits (114 limnic, 15 marine/estuarine/limnic, ten marine/estuarine, nine estuarine/limnic and eight marine). Characiformes and Siluriformes are the most diverse orders, corroborating the Neotropical pattern. Seven species can be considered endemic to RS Quaternary deposits.

## Keywords

Biogeography, Cenozoic, coastal plain, endemism, fishes

## Introduction

The Quaternary in the state of Rio Grande do Sul (RS), southern Brazil, is geologically characterized by a sequence of four depositional events resulting from marine transgressions that occurred around 400,000 and 5,000 years ago, in addition to the occurrence of extensive alluvial systems (Tomazelli and Villwock 2000; Villwock and Tomazelli 2007). These Quaternary deposits are hydrographically heterogeneous and can be found in swamps, extensive floodplains (*várzeas*), coastal lagoons, coastal streams and lower stretches of fluvial systems originated from older geological formations in RS (Vieira 1984). Depositional events that occurred in RS during the Quaternary period also shaped the Patos-Mirim lagunar complex and resulted in the formation of the Patos Lagoon, the largest choked coastal lagoon worldwide (Kjerfve 1986; Möller and Fernandes 2010).

In relation to the ichthyofauna, limnic systems enclosed in RS Quaternary deposits home characteristically limnic, estuarine and coastal marine species, the last two due to temporary or permanent connections with estuarine and oceanic environments that allowed specimens to migrate (Tagliani 1994; Loebmann and Vieira 2005; Malabarba et al. 2013; Bastos et al. 2013). Sampling efforts on these limnic systems, especially on greater water bodies located in the coastal peninsular deposits (*restingas*), which include the Taim wetlands (Buckup and Malabarba 1983; Reis 1983; Grosser et al. 1994; Garcia et al. 2006), Lagoa Mangueira (Artoli et al. 2009), Lagoa do Peixe (Loebmann and Vieira 2005) and the northern complex of coastal lagoons (Schifino et al. 2004; Malabarba and Isaia 1992; Malabarba et al. 2013), provided consistent data on the species composition in these areas. However, information on fish assemblages present in limnic systems of Quaternary deposits located at the west margin of the Patos-Mirim complex is scarce. Data available on this segment is restricted to investigations by Becker et al. (2007) on the *Butiazais* region of the Tapes and the recent inventories produced by Volcan et al. (2012) and Burns et al. (2015) on the lower courses of the Corrientes and Turuçu streams, respectively. On such account, this study aimed to characterize the ichthyofauna in a swampy area adjacent to Lagoa Pequena, a lacustrine system under estuarine influence located at the west margin of the Patos Lagoon. We compare the assemblage found in the study area to other assemblages recorded in RS Quaternary deposits. A checklist is also presented of species recorded in limnic systems thus far in this geological formation, along with a brief discussion on distribution patterns of the species.

## Material and methods

### Study area

The west margin of the Patos Lagoon is characterized by the presence of Pleistocene-Holocene sedimentary deposits, with the predominance of silty-clayey sand (Tomazelli

and Villwock 2000; CPRM 2007). The swamps we studied are located around Lagoa Pequena, a lacustrine system with an area of approximately 4,000 km<sup>2</sup>, in the boundaries of the Pelotas and Turuçu municipalities (Fig. 1). Lagoa Pequena is connected to the Patos Lagoon estuary on its west margin and is subject to estuarine physical-chemical and biological influence (Alves et al. 2009).

Fishes were sampled in four marginal swamps: swamp 1 (S1) -31°56'96"S, 52°11'78"W – emergent vegetation (*Juncus* sp. L.), with higher incidence of floating species (*Azolla* sp. Lam.) during warm periods; swamp 2 (S2) -31°56'90"S, 52°12'02"W – predominance of floating macrophytes (*Azolla* sp., *Pistia stratiotes* L., *Salvinia* sp. Ség.); swamp 3 (S3) -31°56'50"S, 52°13'10"W – margins sparsely covered by *Juncus* sp. and higher concentration of floating species (*Salvinia* sp.) during warm periods; swamp 4 (S4) -31°56'80"S, 52°13'82"W – predominance of *Nymphoides indica* (L.) Kuntze. Distances between the swamps and Lagoa Pequena are respectively 101 m, 395 m, 1,386 m and 2,229 m.

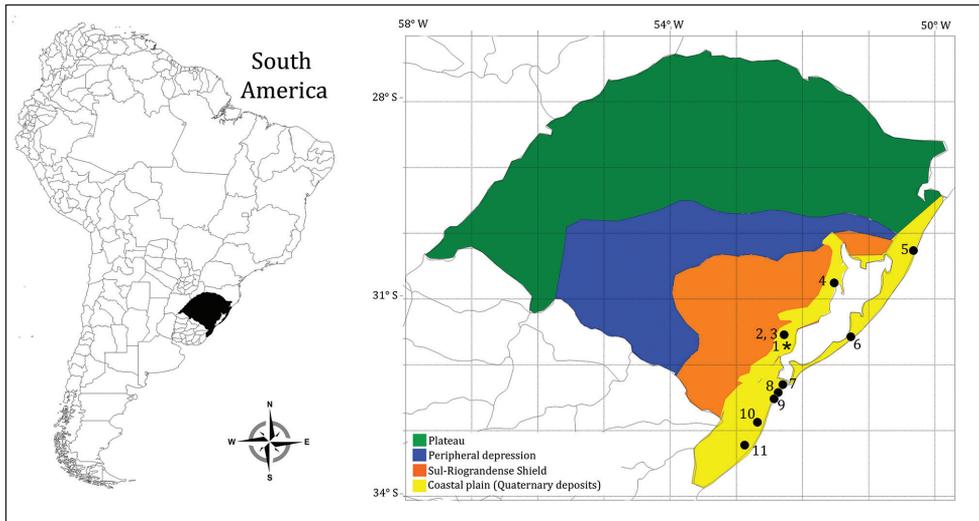
## Sampling

The ichthyofauna of the study area was sampled seasonally during the year of 2010 with the use of a 5 m long, 2 m high seine net with a 5 mm mesh between adjacent nodes. We applied an effort of three seines by seasonal sampling campaign in each swamp, totalizing an effort of 48 seines. Captured individuals were euthanized in clove oil solution, fixed in 10% formalin, preserved in 70% ethanol and housed in the Fish Reference Collection of the Instituto de Ciências Biológicas at the Universidade Federal do Rio Grande (CIFURG) (Appendix 1).

## Data analysis

Aiming to evaluate similarities on species composition between the study area assemblage and other fish assemblages recorded in RS Quaternary deposits (Tagliani 1995; Schifino et al. 2004; Loebmann and Vieira 2005; Garcia et al. 2006; Becker et al. 2007; Quintela et al. 2007; Artioli et al. 2009; Volcan et al. 2012 [partial: P12-P15]; Burns et al. 2015 [partial: potamon zone]), we calculated the Dice Similarity Index (DSI) based on a matrix of species presence/absence, using 1,000 *bootstrap* resampling. Obtained values were submitted to a cluster analysis based on the Unweighted Pair Group Method with Arithmetic Means (UPGMA) and similarity relationships were expressed in the form of a dendrogram. Grouping significance was tested through an Analysis of Similarity (ANOSIM). Analyses were performed in PAST version 1.79 (Hammer et al. 2001).

Finally, we compiled data regarding fish species recorded in limnic systems of RS Quaternary deposits from the list of the binary matrix used in the similarity analysis and from the literature, including information on additional species contained in



**Figure 1.** Four main geological formations from the state of Rio Grande do Sul, Southern Brazil. The study area (Quaternary deposits) as well as previous studies used in Dice Similarity Index analysis is entirely inserted in Coastal Plain. Key: **1** present study **2** Turuçu River basin; Burns et al. 2015 **3** Corrientes Stream; Volcan et al. 2012 **4** Tapes *Butiazais*; Becker et al. 2007 **5** Fortaleza lagoon; Schifino et al. 2004 **6** Lagoa do Peixe; Loebmann and Vieira 2005 **7** Peat forest; Quintela et al. 2007 **8** Rio Grande coastal streams; Tagliani 1995 **9** Cassino coastal streams; Bastos et al. 2013 **10** Taim wetland; Garcia et al. 2006 **11** Lagoa Mangueira; Artioli et al. 2009.

punctual records, references on type material and references on comparative systematic/taxonomic studies (Malabarba and Isaia 1992; Buckup and Reis 1997; Costa and Cheffe 2001 2002 2005; Costa 2002 2006; Giora et al. 2008; Malabarba and Dyer 2002; Lucinda 2005 2008; Costa and Lanés 2009; Claudino et al. 2010; Volcan et al. 2010; Corrêa et al. 2011; Carvalho and Reis 2011; Malabarba et al. 2013; Lanés et al. 2015; Giora and Malabarba 2016).

## Results

A total of 4,206 individuals was captured in the four marginal-lacustrine swamps sampled. They were distributed in nine orders, 18 families, 31 genera and 42 species. Characidae and Cichlidae were the most representative families, comprising 15 and four species respectively. All other families were represented by two or one single species (Table 1).

DSI values (Table 2) showed that the assemblage found in marginal swamps is most similar to the assemblages found in the lower course of the Corrientes Stream (Volcan et al. 2012) and the Lagoa do Peixe National Park (DSI = 0.674; Table 2), while the most dissimilar assemblages included a set of three coastal streams sampled

**Table 1.** Checklist of fish species recorded in limnic systems of Quaternary deposits in Rio Grande do Sul State. References: 1) Malabarba and Isaia (1992), 2) Tagliani (1994), 3) Buckup and Reis (1997), 4) Costa and Cheffe (2001), 5) Costa (2002), 6) Costa and Cheffe (2002), 7) Malabarba and Dyer (2002), 8) Schifino et al. (2004), 9) Costa and Cheffe (2005), 10) Loebmann and Vieira (2005), 11) Lucinda (2005), 12) (Costa (2006), 13) Garcia et al. (2006), 14) Becker et al. (2007), 15) Quintela et al. (2007), 16) Giora et al. (2008), 17) Lucinda (2008), 18) Artioli et al. (2009), 19) Costa and Lanés (2009), 20) Claudino et al. (2010), 21) Volcan et al. (2010), 22) Correa et al. (2011), 23) Carvalho and Reis (2011), 24) Volcan et al. (2012), 25) Bastos et al. (2013), 26) Malabarba et al. (2013), 27) Lanés et al. (2015), 28) Burns et al. (2015), 29) Giora and Malabarba (2016); PS = present study, M (marine), E (estuarine), L (limnic).

Taxon	Habit	References
Clupeiformes		
Clupeidae		
	<i>Brevoortia pectinata</i> (Jenyns, 1842)	M,E 10, 28
	<i>Harengula clupeola</i> (Cuvier, 1829)	M 10
	<i>Platanichthys platana</i> (Regan,1917)	E, L 8, 10, 13, 14, 18, 25, 26, 28, PS
	<i>Sardinella aurita</i> Valenciennes, 1847	M, E 10
Elopiformes		
Elopidae		
	<i>Elops saurus</i> Linnaeus, 1766	M, E 10
Albuliformes		
Albulidae		
	<i>Albula nemoptera</i> Fowler, 1911	E,L 10
Gadiformes		
Phycidae		
	<i>Urophycis brasiliensis</i> (Kaup, 1858)	M 10
Mugiliformes		
Mugilidae		
	<i>Mugil curema</i> Valenciennes, 1836	M,E,L 10, 25
	<i>Mugil brevisrostris</i> (Ribeiro, 1915)	M,E,L 10, 25
	<i>Mugil liza</i> Valenciennes, 1836	M,E,L 10, 25, 28, PS
Engraulidae		
	<i>Anchoa marinii</i> Hildebrand, 1943	M 10
	<i>Lycengraulis grossidens</i> (Agassiz, 1829)	M,E 8, 10, 24, 25, PS
Characiformes		
Acestrorhynchidae		
	<i>Acestrorhynchus pantaneiro</i> Menezes, 1992	L 26
Characidae		
	<i>Aphyocharax anisitsi</i> Eigenmann & Kennedy, 1903	L 13, 14, 18, 24, 26
	<i>Astyanax</i> aff. <i>fasciatus</i> (Cuvier, 1819)	L 1, 8, 10, 13, 14, 15, 18, 24, 26, PS
	<i>Astyanax eigenmanniorum</i> (Cope, 1894)	L 1, 2, 8, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
	<i>Astyanax henseli</i> Melo & Buckup, 2006	L 21, PS
	<i>Astyanax lacustris</i> (Lütken, 1875)	L 1, 8, 10, 13, 14, 18, 25, 28, PS
	<i>Astyanax laticeps</i> (Cope, 1894)	L 21
	<i>Astyanax stenohalinus</i> Messner, 1962	L 28

Taxon	Habit	References
<i>Bryconamericus iberingii</i> (Boulenger, 1887)	L	13, 14, 18, 28
<i>Charax stenopterus</i> (Cope, 1894)	L	1, 8, 13, 14, 18, 24, 26, 28, PS
<i>Cheirodon ibicuhiensis</i> Eigenmann, 1915	L	1, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
<i>Cheirodon interruptus</i> (Jenyns, 1842)	L	1, 2, 10, 14, 15, 18, 24, 25, 26, 28, PS
<i>Diapoma alburnus</i> (Hensel, 1870)	L	1, 10, 13, 14, 15, 18, 24, 26, 28, PS
<i>Diapoma speculiferum</i> Cope, 1894	L	24, 28
<i>Hyphessobrycon boulengeri</i> (Eigenmann, 1907)	L	1, 2, 10, 13, 14, 15, 24, 25, 26, 28, PS
<i>Hyphessobrycon igneus</i> Miquelarena, Menni, López & Casciotta, 1980	L	1, 2, 10, 13, 14, 18, 24, 25, 26, 28, PS
<i>Hyphessobrycon luetkenii</i> (Boulenger, 1887)	L	2, 8, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
<i>Hyphessobrycon meridionalis</i> Ringuelet, Miquelarena & Menni, 1978	L	1, 2, 10, 13, 14, 18, 24, 25, 26, 28, PS
<i>Hyphessobrycon togoi</i> Miquelarena & López, 2006	L	26, PS
<i>Macropsobrycon uruguayanae</i> Eigenmann, 1915	L	13, 18, 28
<i>Mimagoniates inequalis</i> (Eigenmann, 1911)	L	10, 24, 25, 26, 28
<i>Mimagoniates microlepis</i> (Steindachner, 1877)	L	1, 26
<i>Oligosarcus jenynsii</i> (Günther, 1864)	L	1, 2, 8, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
<i>Oligosarcus robustus</i> Menezes, 1969	L	1, 2, 8, 10, 13, 14, 18, 25, 26, 28, PS
<i>Pseudocorynopoma doriae</i> Perugia, 1891	L	1, 10, 13, 14, 24, 26, 28, PS
<i>Serrapinnus calliurus</i> (Boulenger, 1900)	L	14
Crenuchidae		
<i>Characidium aff. zebra</i> Eigenmann, 1909	L	14, 26
<i>Characidium orientale</i> Backup & Reis, 1997	L	3, 24, 23, 28, PS
<i>Characidium rachovii</i> (Regan, 1913)	L	3, 10, 13, 14, 18, 23, 24, 28, PS
<i>Characidium pterostictum</i> Gomes, 1947	L	28
<i>Characidium tenue</i> (Cope, 1894)	L	14, 18, 28
Curimatidae		
<i>Cyphocharax saladensis</i> (Meinken, 1933)	L	1, 10, 14, 24, 26, 28
<i>Cyphocharax voga</i> (Hensel, 1870)	L	1, 2, 8, 10, 13, 14, 18, 24, 26, 28, PS
<i>Steindachnerina biornata</i> (Braga & Azpelicueta, 1987)	L	1, 24, 26, 28, PS
Erythrinidae		
<i>Hoplias malabaricus</i> (Bloch, 1794)	L	1, 2, 8, 10, 13, 14, 18, 24, 25, 26, 28, PS
Lebiasinidae		
<i>Pyrrhulina australis</i> (Eigenmann & Kennedy, 1903)	L	1, 14, 26
Siluriformes		
Ariidae		
<i>Genidens genidens</i> (Cuvier, 1829)	M,E	10, 28
Aspredinidae		
<i>Bunocephalus erondinae</i> Cardoso, 2010	L	28

Taxon		Habit	References
	<i>Pseudobunocephalus iberlingii</i> (Boulenger, 1891)	L	13, 14, 28
Auchenipteridae			
	<i>Glanidium</i> cf. <i>catharinensis</i> Miranda Ribeiro, 1962	L	26
	<i>Trachehyopterus lucenai</i> Bertolotti, Silva & Pereira, 1995	L	8, 13, 14, 18, 24, 26
Callichthyidae			
	<i>Callichthys callichthys</i> (Linnaeus, 1758)	L	1, 10, 13, 24, 25, 26, 28
	<i>Corydoras paleatus</i> (Jenyns, 1842)	L	1, 2, 8, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
	<i>Corydoras undulatus</i> (Regan, 1912)	L	1, 26
	<i>Hoplosternum littorale</i> (Hancock, 1828)	L	1, 10, 13, 14, 18, 24, 25, 26, 28, PS
	<i>Lepthoplosternum tordilho</i> Reis, 1997	L	14
Heptapteridae			
	<i>Heptapterus sympterygium</i> Buckup, 1988	L	1, 2, 13, 24, 25, 26, 28
	<i>Heptapterus mustelinus</i> (Valenciennes, 1835)	L	28
	<i>Rhamdella</i> sp.	L	26
	<i>Pimelodella australis</i> Eigenmann, 1917	L	1, 2, 10, 13, 14, 18, 24, 26, PS
	<i>Rhamdella eriarcha</i> (Eigenmann & Eigenmann, 1888)	L	1, 28
	<i>Rhamdia</i> aff. <i>quelen</i> (Quoy & Gaimard, 1824)	L	1, 2, 8, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
Loricariidae			
	<i>Ancistrus brevipinnis</i> (Regan, 1904)	L	14, 28
	<i>Hisonotus laevior</i> Cope, 1894	L	28, PS
	<i>Hisonotus leucofrenatus</i> (Ribeiro, 1908)	L	26
	<i>Hisonotus nigricauda</i> (Boulenger, 1891)	L	23, 24, 28
	<i>Hisonotus armatus</i> Carvalho, Lehmann, Pereira & Reis, 2008	L	28
	<i>Hisonotus taimensis</i> (Buckup, 1981)	L	2, 13, 18, 24
	<i>Hypostomus aspilogaster</i> (Cope, 1894)	L	28
	<i>Hypostomus commersoni</i> (Valenciennes, 1836)	L	1, 13, 14, 18, 26, 28
	<i>Loricariichthys anus</i> (Valenciennes, 1836)	L	1, 8, 13, 14, 18, 24, 26, 28
	<i>Otothyris rostrata</i> (Garavello, Britski & Schaefer, 1998)	L	26, 28
	<i>Otocinclus flexilis</i> Cope, 1894	L	28
	<i>Rineloricaria cadeae</i> (Hensel, 1868)	L	13, 14, 18, 24, 28
	<i>Rineloricaria longicauda</i> Reis, 1983	L	1, 13, 18, 28
	<i>Rineloricaria quadrensensis</i> Reis, 1983	L	1, 8, 26
	<i>Rineloricaria microlepidogaster</i> (Regan, 1904)	L	28
	<i>Rineloricaria strigilata</i> (Hensel, 1868)	L	14, 18, 28
Pimelodidae			
	<i>Parapimelodus nigribarbis</i> (Boulenger, 1889)	L	13, 18, 28
	<i>Pimelodus pintado</i> Azpelicueta, Lundberg & Loureiro, 2008	L	13, 14, 18, 28
Pseudopimelodidae			
	<i>Microglanis cibela</i> Malabarba & Mahler, 1998	L	26
	<i>Microglanis cottoides</i> (Boulenger, 1891)	L	2, 13, 14, 18, 28
Trichomycteridae			
	<i>Scleronema</i> sp. aff. <i>S. operculatum</i> Eigenmann, 1917	L	28

Taxon		Habit	References
	<i>Homodiaetus anisitsi</i> Eigenmann & Ward, 1907	L	1, 13, 14, 18, 24, 28
Gymnotiformes			
Gymnotidae			
	<i>Gymnotus omarorum</i> Richer-de-Forges, Crampton & Albert, 2009	L	28
	<i>Gymnotus refugio</i> Giora & Malabarba, 2016	L	29
	<i>Gymnotus</i> aff. <i>carapo</i> Linnaeus, 1758	L	1, 13, 14
Hypopomidae			
	<i>Brachyhypopomus bombilla</i> Loureiro & Ana Silva, 2006	L	24, 28
	<i>Brachyhypopomus draco</i> Giora, Malabarba & Crampton, 2008	L	16, 20, 26, PS
	<i>Brachyhypopomus gauderio</i> Giora & Malabarba, 2009	L	22, 24, 26, 28, PS
Sternopygidae			
	<i>Eigenmannia trilineata</i> López & Castello, 1966	L	1, 2, 10, 13, 14, 24, 26, 28
Cyprinodontiformes			
Anablepidae			
	<i>Jenynsia multidentata</i> (Jenyns, 1842)	E,L	2, 10, 13, 14, 15, 18, 24, 25, 26, 28, PS
Poeciliidae			
	<i>Cnesterodon decemmaculatus</i> (Jenyns, 1842)	E,L	2, 10, 13, 15, 18, 26, 28
	<i>Phalloceros caudimaculatus</i> (Hensel, 1868)	E,L	1, 2, 13, 14, 15, 18, 24, 25, 26, 28, PS
	<i>Phalloceros spiloura</i> Lucinda, 2008	L	17
	<i>Phalloptychus iheringi</i> (Boulenger, 1889)	L	10, 11, 26, PS
	<i>Poecilia vivipara</i> Bloch & Schneider, 1801	E,L	1, 26
Cynolebiidae			
	<i>Atlantirivulus riograndensis</i> (Costa & Lanés, 2009)	L	19, 26
	<i>Austrolebias adloffii</i> (Ahl, 1922)	L	12, 14
	<i>Austrolebias charrua</i> Costa & Cheffe, 2001	L	4, 12, 21
	<i>Austrolebias jaegari</i> Costa & Cheffe, 2002	L	6, 12
	<i>Austrolebias luteoflammulatus</i> (Vaz-Ferreira, Sierra de Soriano & Scaglia de Paulete, 1965)	L	12, 21
	<i>Austrolebias minuano</i> Costa & Cheffe, 2001	L	4, 12, 15, 24
	<i>Austrolebias natchtigalli</i> Costa, 2006	L	12
	<i>Austrolebias nigrofasciatus</i> Costa & Cheffe, 2001	L	4, 12
	<i>Austrolebias prognathus</i> (Amato, 1986)	L	21
	<i>Austrolebias univentripinnis</i> Costa & Cheffe, 2005	L	9
	<i>Austrolebias wolterstorffi</i> (Ahl, 1924)	L	12, 15, 27
	<i>Cynopoecilus fulgens</i> Costa, 2002	L	5, 27
	<i>Cynopoecilus melanotaenia</i> (Regan, 1912)	L	2, 5, 13, 15, 21, 28, PS
	<i>Cynopoecilus multipapillatus</i> Costa, 2002	L	5, 27
	<i>Cynopoecilus nigrovittatus</i> Costa, 2002	L	14
Atheriniformes			
Atherinopsidae			
	<i>Atherinella brasiliensis</i> (Quoy & Gaimard, 1825)	M,E	10, 24, 26, PS
	<i>Odontesthes</i> aff. <i>perugia</i> Evermann & Kendall, 1906	L	13, 18
	<i>Odontesthes argentinensis</i> (Valenciennes, 1835)	M,E,L	10, 26, PS
	<i>Odontesthes bicudo</i> Malabarba & Dyer, 2002	L	7, 26

Taxon	Habit	References
	<i>Odontesthes bonariensis</i> (Valenciennes, 1835)	M,E,L 13, 18, 26
	<i>Odontesthes humensis</i> de Buen, 1953	L 13, 18
	<i>Odontesthes ledae</i> Malabarba & Dyer, 2002	E,L 7, 8, 26
	<i>Odontesthes mirinensis</i> Bemvenuti, 1995	L 13, 18
	<i>Odontesthes piquava</i> Malabarba & Dyer, 2002	L 7, 26
	<i>Odontesthes retropinnis</i> de Buen, 1953	L 18
Perciformes		
Carangidae		
	<i>Selene vomer</i> (Linnaeus, 1758)	M,E 10
	<i>Trachinotus carolinus</i> (Linnaeus, 1766)	M,E 10
	<i>Trachinotus marginatus</i> Cuvier, 1832	M 10, 25
	<i>Uraspis secunda</i> (Poey, 1860)	M 10
Centropomidae		
	<i>Centropomus parallelus</i> Poey, 1860	M,E,L 10
Gerreidae		
	<i>Eucinostomus argenteus</i> Baird & Girard, 1855	M,E,L 10
	<i>Eucinostomus melanopterus</i> (Bleeker, 1863)	M,E,L 25
Lutjanidae		
	<i>Lutjanus cyanopterus</i> (Cuvier, 1828)	M,E 25
Pomatomidae		
	<i>Pomatomus saltatrix</i> Linnaeus, 1776	M,E 10
Sciaenidae		
	<i>Micropogonias furnieri</i> (Desmarest, 1823)	M,E 10, 25
	<i>Pachyurus bonariensis</i> Steindachner, 1879	L 14
	<i>Pogonias cromis</i> Linnaeus, 1766	M,E 10
	<i>Stellifer brasiliensis</i> (Schultz, 1945)	M 10
Epinephelidae		
	<i>Epinephelus marginatus</i> Lowe, 1834	M 10
	<i>Mycteroperca acutirostris</i> (Valenciennes, 1828)	M 10
Labriformes		
Cichlidae		
	<i>Australoheros acaroides</i> (Hensel, 1870)	L 1, 2, 10, 13, 14, 18, 24, 25, 28, PS
	<i>Cichlasoma portalegrense</i> (Hensel, 1870)	L 10, 13, 14, 18, 24, 25, 26, 28, PS
	<i>Crenicichla lepidota</i> Heckel, 1840	L 1, 2, 8, 10, 13, 14, 18, 24, 25, 26, 28, PS
	<i>Crenicichla maculata</i> Kullander & Lucena, 2006	L 26
	<i>Crenicichla punctata</i> Hensel, 1870	L 8, 13, 18, 28
	<i>Geophagus bnasiensis</i> (Quoy & Gaimard, 1824)	L 1, 2, 8, 10, 13, 14, 18, 24, 25, 26, 28, PS
	<i>Gymnogeophagus gymnogens</i> (Hensel, 1870)	L 1, 13, 14, 18, 26, 28
	<i>Gymnogeophagus lacustris</i> Reis & Malabarba, 1988	L 1, 26
	<i>Gymnogeophagus rhabdotus</i> (Hensel, 1870)	L 1, 13, 14, 18, 24, 26, 28
Gobiiformes		
Eleotridae		
	<i>Dormitator maculatus</i> (Bloch, 1792)	M,E,L 10, 25
	<i>Eleotris pisonis</i> (Gmelin, 1789)	M,E,L 10, 25

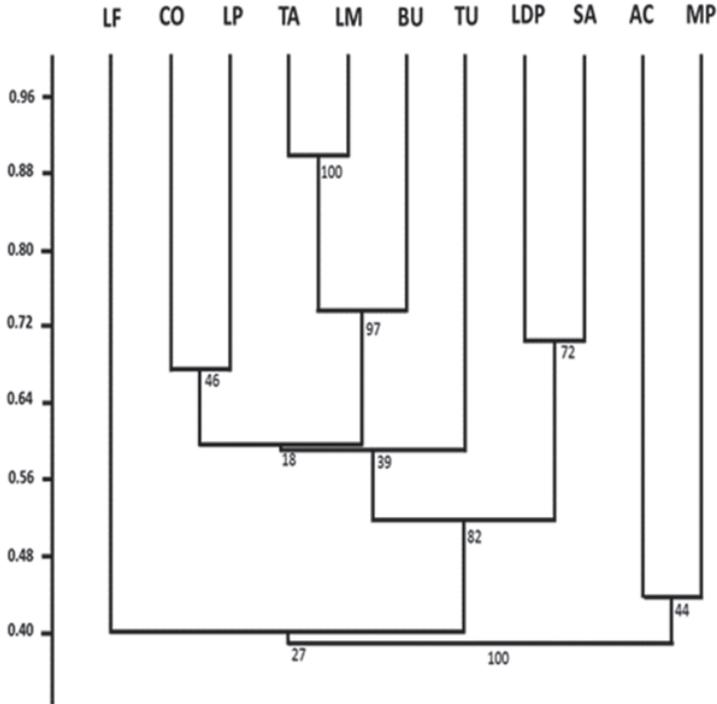
Taxon	Habit	References
Gobiidae		
	<i>Awaous tajasica</i> (Lichtenstein, 1822)	E,L 10
	<i>Ctenogobius shufeldti</i> (Jordan & Eigenmann, 1887)	E,L 10, 13, 18, 24, 25, 26, PS
	<i>Gobionellus oceanicus</i> (Pallas, 1770)	M,E,L 10
Pleuronectiformes		
Paralichthyidae		
	<i>Citharichthys spilopterus</i> Günther, 1862	M,E,L 10
	<i>Paralichthys orbignyana</i> (Valenciennes, 1839)	M,E 10, 24
Synbranchiformes		
Synbranchidae		
	<i>Synbranchus marmoratus</i> Bloch, 1795	L 1, 2, 13, 14, 15, 24, 25, 26, 28, PS

**Table 2.** Values of Dice Similarity Index (DSI) between ichthyocenoses recorded in limnic systems of Rio Grande do Sul Quaternary deposits. Legend: AC (Rio Grande coastal streams; Tagliani [1995]), BU (Tapes *Butiazais*; Becker et al. [2007]), CO (Corrientes Stream; Volcan et al. [2012]), LDP (Lagoa do Peixe; Loebmann and Vieira [2005]), LF (Lagoa Fortaleza; Schiffino et al. [2004]), LM (Lagoa Mangureira; Artioli et al. [2009]), LP (Lagoa Pequena marginal marshes; present study), MP (peat forest; Quintela et al. [2007]), SA (Cassino coastal streams; Bastos et al. [2013]), TA (Taim wetland; Garcia et al. [2006]), TU (Turuçu River basin; Burns et al. [2015]).

	BU	TA	LDP	SA	AC	LM	LP	MP	LF	CO	TU
BU	1	0.745	0.524	0.484	0.390	0.729	0.586	0.432	0.421	0.641	0.574
TA	0.745	1	0.544	0.547	0.463	0.897	0.566	0.405	0.447	0.660	0.620
LDP	0.524	0.544	1	0.705	0.427	0.52	0.674	0.388	0.406	0.542	0.475
AS	0.484	0.547	0.705	1	0.418	0.522	0.548	0.475	0.328	0.477	0.368
AC	0.390	0.463	0.427	0.418	1	0.405	0.394	0.435	0.375	0.373	0.297
LM	0.729	0.897	0.520	0.522	0.405	1	0.542	0.394	0.466	0.580	0.571
LP	0.586	0.566	0.674	0.548	0.394	0.542	1	0.444	0.462	0.674	0.542
MP	0.432	0.405	0.388	0.475	0.435	0.394	0.444	1	0.350	0.328	0.258
LF	0.421	0.447	0.406	0.328	0.375	0.466	0.462	0.350	1	0.348	0.316
CO	0.641	0.660	0.542	0.477	0.373	0.580	0.674	0.328	0.348	1	0.639
TU	0.574	0.620	0.475	0.368	0.297	0.571	0.542	0.258	0.316	0.639	1

by Tagliani (1995) in the Rio Grande municipality (DSI = 0.394; Table 2). Values for other comparisons are shown in Table 2.

The dendrogram obtained from DSI values (Fig. 2) showed the formation of four clusters. The cluster with higher support (*bootstrap* = 97) gathers the assemblages of Taim (Garcia et al. 2006), Lagoa Mangureira (Artioli et al. 2009) and the *Butiazais* region of Tapes (Becker et al. 2007). Another cluster (*bootstrap* = 72) was formed by the assemblages of Lagoa do Peixe (Loebmann and Vieira 2005) and three coastal streams sampled by Bastos et al. (2013) in Cassino beach. The assemblage from our study area clustered with the ichthyocenose from the Corrientes stream’s lower course (Volcan et al. 2012), with low support (*bootstrap* = 46). The assemblages of a peat for-



**Figure 2.** Dendrogram generated from the values of DSI between ichthyocenoses recorded in limnic systems of Rio Grande do Sul Quaternary deposits. Key: AC (Rio Grande coastal streams; Tagliani [1995]), BU (Tapes *Butiazais*; Becker et al. [2007]), CO (Corrientes Stream; Volcan et al. [2012]), LDP (Lagoa do Peixe; Loebmann and Vieira [2005]), LF (Lagoa Fortaleza; Schifino et al. [2004]), LM (Lagoa Mangueira; Artioli et al. [2009]), LP (Lagoa Pequena marginal marshes; present study), MP (Peat forest; Quintela et al. [2007]), SA (Cassino coastal streams; Bastos et al. [2013]), TA (Taim wetland; Garcia et al. [2006]), TU (Turuçu River basin; Burns et al. [2015]).

est fragment (Quintela et al. 2007) and a set of coastal streams in Rio Grande (Tagliani 1995) grouped with low support (*bootstrap* = 44). The assemblages of Lagoa Fortaleza (Schifino et al. 2004) and Turuçu River (Burns et al. 2015) remained isolated. The ANOSIM indicated significant differences between the clusters ( $p = 0.0003$ ;  $R = 0.98$ ).

## Discussion

### Marginal-lacustrine swamps

The marginal-lacustrine swamps sampled in the present study host a considerable ichthyofaunistic diversity, showing a species richness within the range observed in limnic systems of RS Quaternary deposits. For example, Garcia et al. (2006) recorded 57 species in lagoons of the Taim Ecological Station in the Rio Grande *restinga*, while Artioli et al. (2009)

sampled 52 species in Lagoa Mangueira. Smaller systems in this *restinga* have shown lower richness, such as 31 species in a set of three coastal streams (Tagliani 1995) and 18 species in a peat forest fragment (Quintela et al. 2007). Loebmann and Vieira (2005) recorded 67 species (among limnic, estuarine and marine forms) in Lagoa do Peixe at the *restinga* of São José do Norte, while Schifino et al. (2004) listed 22 species in Lagoa Fortaleza, at the Tramandaí River basin. Becker et al. (2007) recorded 55 species in alluvial deposits of swamps, ponds and streams on the west margin of the Patos-Mirim complex, at the *Butiazais* region in Tapes, while Volcan et al. (2012) found 49 species in the Corrientes Stream's lower course. Such a high species richness registered for characids, which represent 34% of the species recorded in the study area, corroborates with the pattern found in other fish assemblages previously investigated in RS Quaternary deposits (e.g. Tagliani 1995; Schifino et al. 2004; Loebmann and Vieira 2005; Garcia et al. 2006; Becker et al. 2007; Quintela et al. 2007; Artioli et al. 2009; Volcan et al. 2012; Bastos et al. 2013).

Regarding system comparisons, the assemblage of marginal-lacustrine swamps is more similar on its species composition to the assemblage of the lower course of the Corrientes Stream (Volcan et al. 2012), followed by the ichthyocenose of the Lagoa do Peixe National Park (Loebmann and Vieira 2005). The Corrientes Stream, however, is closest to the study area when compared to the other systems, distancing from 50 m up to 590 m from the marginal swamps. Thirty-four of the forty-two species (81%) recorded in the marginal swamps were also found by Volcan et al. (2012) in the Corrientes Stream's lower course and the following species were found exclusively in the swamps: *Odontesthes argentinensis*, *Platanichthys platana*, *Mugil liza*, *Astyanax* aff. *fasciatus*, *Hyphessobrycon togoi*, *Brachyhypopomus draco*, *Hisonotus laevior* and *Phalloptychus iheringi*. Such similarity may be related to the proximity and possible connection between the stream and marshes during rainfall periods, leading to an exchange of species. The second most similar assemblage of the Lagoa do Peixe National Park (Loebmann and Vieira 2005), on the other hand, is located in deposits at the eastern margin of the Patos Lagoon. The fact that higher similarity is found between assemblages from the study area and Lagoa do Peixe is remarkable, considering that other systems such as the Turuçu basin (Burns et al. 2015) and the systems of Rio Grande (Tagliani et al. 1995; Quintela et al. 2007; Bastos et al. 2013), are closer to the study area. These results suggest that environmental factors may exert greater influence on the species composition in these systems compared to the effect of geographic distances.

With the exception of *Characidium orientale*, all other species found in the study area have been recorded in limnic systems of the coastal *restingas* of Rio Grande and São José do Norte (Malabarba and Isaia 1992; Tagliani 1995; Loebmann and Vieira 2005; Garcia et al. 2006; Quintela et al. 2007; Artioli et al. 2009; Bastos et al. 2013; Malabarba et al. 2013). *Characidium orientale* was described among specimens collected in Arroio Chasqueiro and the type series includes specimens from several localities in the RS Shield (Precambrian) and the Central Depression (Permian-Triassic) (Buckup and Reis 1997). Posteriorly, the species was recorded by Volcan et al. (2012) in the Corrientes Stream and by Burns et al. (2015) in the Turuçu River basin. Therefore, this species' distribution in the RS Quaternary may be restricted to alluvial deposits of the west margin of the Patos-Mirim complex.

## Ichthyofauna of limnic systems in the Quaternary deposits of Rio Grande do Sul

The compilation of bibliographic information associated to our sample data revealed a total of 156 species (114 limnic, 15 marine/estuarine/limnic, ten marine/estuarine, nine estuarine/limnic and eight marine) occurring in limnic systems inserted in RS Quaternary deposits (Table 1). Comparatively, 160 species (including undescribed forms) can be found in the Patos Lagoon basin (Malabarba et al. 2009), which includes rivers and streams originated from distinct geological formations in RS such as the Shield and the Paraná Basin (Central Depression and Meridional Plateau), located beyond the Patos Lagoon itself, which in turn, covers an area of approximately 10,360 km<sup>2</sup> (Vieira 1984). Approximately 100 species were recorded in the Tramandaí River basin, which is formed by rivers and streams of the Serra Geral slopes (eastern Meridional Plateau) and several lakes and channels of the northern coastal plain (Malabarba et al. 2013). Therefore, limnic systems in the RS Quaternary host relevant ichthyofaunistic diversity, compassing approximately 27% of the freshwater ichthyofauna recorded in RS (Bertaco et al. 2016). Furthermore, this study recorded a low percentage (around 8%) of the marine species usually found in the RS coastal zone (Seeliger et al. 1998).

The Siluriformes and Characiformes orders, which comprise respectively 38 and 36 species, were the most speciose orders in RS Quaternary deposits, corroborating with the pattern already found for the Neotropical region (Lowe-McConnell 1987; Reis et al. 2003a). With the exception of *Acestrorhynchus pantaneiro*, a species typical for the Paraná, Uruguay, Paraguay and Mamoré River basins (Menezes 2003), and *Pachyurus bonariensis*, native from the Paraná, Uruguay and Paraguay River basins (Casatti, 2003), all other recorded species are characteristic of Atlantic basins in RS, which include the Patos-Mirim basin and Tramandaí and Mampituba rivers (Buckup and Reis 1997; Melo and Buckup 2006; Malabarba 2008; Malabarba et al. 2013). *Acestrorhynchus pantaneiro* was recorded for the first time in RS Atlantic basins by Saccol-Pereira et al. (2006), who reported the capture of three individuals in the Parque Estadual Delta do Jacuí during the years of 2004 and 2005. Posteriorly, Artioli et al. (2013) reported the capture of three more individuals during the year of 2008 in lagoons in Fortaleza and Malvas and in the Tramandaí basin. Recently, Einhardt et al. (2014) registered the species in the Chasqueiro Stream micro-basin, an integrant of the Mirim Lagoon sub-basin. Before these records, the occurrence of *A. pantaneiro* in RS was known only for the Uruguay River basin, where it is considered a native species (Menezes 2003). Thus, this phenomenon represents a case of recent invasion and dispersion of an aloctone species in RS Atlantic basins, which according to Artioli et al. (2013), could have been favored by the geomorphology of the coastal plain, associated to connectivity between systems during flooding periods and the opening of artificial channels used for drainage and irrigation.

An analysis of the geographic distribution of species occurring in RS Quaternary deposits reveals distinct patterns. One group of “subtropical” species is distributed mainly in the Pampa biome, although some species also spread out to peripheral systems of subtropical Atlantic Forest and to other contacting biomes (e.g. *Astyanax ei-*

*genmanniorum*, *Cheirodon interruptus*, *Hyphessobrycon meridionalis*, *H. igneus*, *H. togoi*, *Oligosarcus jenynsii*, *Cyphocarax voga*, *Loricariichthys anus*, *Odontesthes bonariensis*, *Phalloceros caudimaculatus*). These species are typical for the Tramandaí, Patos-Mirim, Uruguay and lower Paraná basins (Malabarba 1998; Dyer 2003; Ferraris 2003; Lima et al. 2003; Lucinda 2008; Malabarba et al. 2013). Most of them are widely distributed in the RS Quaternary, occurring in systems from all segments of the coastal *restingas* and also in alluvial plains at west of the Patos-Mirim complex (Loebmann and Vieira 2005; Artioli et al. 2009; Volcan et al. 2012; Malabarba et al. 2013; present study). One sub-group of “subtropical” species (e.g. *Australoheros acaroides*, *Cichasoma portalegrense*, *Gymnogeophagus gymnogenys*, *Oligosarcus robustus*, *Heptapterus sympterygium*) is restricted to Atlantic discharge basins in RS (Reis and Malabarba 1988; Schindler et al. 2010; Malabarba et al. 2013) and is also widespread in RS Quaternary deposits (Artioli et al. 2009; Bastos et al. 2013; Malabarba et al. 2013; as well as the present study). Meanwhile, another sub-group is restricted to specific segments of the RS Quaternary deposits. For example, *Rineloricaria quadrensis*, *Microglanis cibela* and *Pachyurus bonariensis*, natives from the Paraná, Uruguay and Paraguay basins (Casatti, 2003), occur exclusively in lagoons and channels of the northern coastal plain and rivers of the Tramandaí basin (Malabarba et al. 2013); the second also occurring in the Mampituba basin (Malabarba and Mahler 1998).

The RS Quaternary deposits are also marked by endemism. *Odontesthes ledae*, *O. piquava*, *O. bicudo*, *Gymnogeophagus lacustris* and *Gymnotus refugio* occur only in systems of the Tramandaí basin (Reis and Malabarba 1988; Malabarba and Dyer 2002) and consequently represent endemic species of the northern coastal plain. Two other cases of endemism in the central and southern segments of coastal *restingas* are known: *Cynopoecilus fulgens* is known only in its typical locality (municipality of São José do Norte) (Costa 2002) and in the Lagoa do Peixe National Park (municipalities of Tavares and Mostardas) (Keppeler et al. 2015; Lanés et al. 2014, 2015), therefore occupying a restrict portion of the central coastal plain; *Austrolebias minuano* was described among specimens collected in the Rio Grande municipality (Costa and Cheffe 2001). Posteriorly, this same species was recorded in new areas of Rio Grande (Porciuncula et al. 2006), in a *restinga* of São José do Norte, in the municipalities of Tavares and São José do Norte (Costa 2006), and in the Lagoa do Peixe National Park (Corrêa et al. 2009; Keppeler et al. 2015; Lanés et al. 2014, 2015).

In contrast, there is one group of species that is widely distributed in Brazil and in the Neotropical region and is also well distributed in the RS Quaternary, occurring both in coastal *restingas* and alluvial plains at the Patos-Mirim west margin. The callichthyids *Hoplosternum littorale* and *Callichthys callichthys* occur in a great portion of the cis-Adean South America (Reis 2003). The gobiid *Ctenogobius shufeldti* is spread from North Carolina (EUA) to southern Brazil (Malabarba et al. 2013). Among cichlids, *Crenicichla lepidota* occurs from the Guaporé River (Amazon basin) up to the Uruguay and Paraná basins, while *Geophagus brasiliensis* is distributed along eastern Brazilian coastal basins and Uruguayan systems (Kullander 2003). Other species that inhabit coastal basins of southeastern and southern Brazil are the characid *Hyphessobry-*

*con boulengeri* and the anablepid *Jenynsia multidentata*, both also occurring in Uruguay and Argentina (Malabarba et al. 2013). However, some widespread taxa are currently recognized as a species complex, including *Astyanax* “*fasciatus*”, *Characidium* “*zebra*”, *Hoplias* “*malabaricus*”, *Gymnotus* “*carapo*”, *Rhamdia* “*quelen*” and *Synbranchus* “*marmoratus*” (Malabarba et al. 2013). Therefore, these forms lack an integrative systematic analysis and appropriate taxonomic definitions.

Biogeographic hypotheses on South American ichthyofauna date back to the early twentieth century (Ribeiro et al. 2013) and point to sea level oscillations and orogenic effects as the main factors that shape distribution patterns (Malabarba and Isaia 1992; Ribeiro 2006; Ribeiro et al. 2013). The fact that few species from genera that are usually well represented in “inland basins” occur in condition of endemism in the coastal basin (e.g. *Crenicichla* and *Gymnogeophagus*) suggests the occurrence of vicariance events followed by cladogenesis. Indeed, speciation by vicariance involving the genera *Gymnogeophagus* (Reis and Malabarba 1988; Malabarba and Isaia 1992), *Mimagoniates* (Menezes and Weitzman 1990) and *Odontesthes* (Malabarba and Dyer 2002) is suggested as one of the evolutionary processes that occurred in the Tramandaí River basin. Molecular data (Beheregaray et al. 2001) revealed that three endemic *Odontesthes* species in the Tramandaí basin (*O. bicudo*, *O. ledae* and *O. piquava*) have probably diverged after the Pleistocene-Holocene marine regressions that shaped the complex of lagoons where these species occur almost allopatrically. The “Pattern C” proposed by Ribeiro (2006), which suggests the occurrence of recent intraspecific vicariance events between “inland basins of the Brazilian Shield” and “coastal basins”, is corroborated by the presence of species whose distribution is restricted to the Atlantic drainage basins in RS (Patos and Tramandaí) and the “adjacent inland basin” of the Uruguay River - those species being *Astyanax* aff. *fasciatus*, *Gymnogeophagus rhabdotus* and *Mimagoniates inequalis*. Therefore, the extant ichthyofaunistic composition of limnic systems in RS Quaternary deposits seems to be the result of both internal processes and evolutionary events triggered in older adjacent geological formations.

In conclusion, limnic systems of Quaternary RS deposits host a diversified ichthyofauna, including endemic species and species with restricted distribution (to the RS state). These systems are home to 15 endangered species at state level (State Decree 51.797/2014), which include 13 killifishes (Rivulidae), *Odonthestes bicudo* and *Gymnotus refugio*. Rivulids, as well as other representatives of the ichthyofauna, are affected by the destruction and alteration of aquatic environments. In RS, interferences caused by rice cultivation, livestock, silviculture and urbanization are the main threats to the freshwater ichthyofauna (Reis et al. 2003b; Volcan et al. 2010). Moreover, only two integral protection conservation units host populations of endangered rivulids along the entire domain of the RS Quaternary deposits: the Banhado do Maçarico Biological Reserve (Costa 2006) and the Lagoa do Peixe National Park (Corrêa et al. 2009; Lanés et al. 2015). Thus, most of the threatened killifish populations, as well as populations of *Odonthestes bicudo* and *Gymnotus refugio*, remain unprotected. In this context, conserving these and other species, as pointed out by Reis et al. (2003b) and Volcan et al. (2012), implies the creation of public and private conservation units.

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## Appendix I

List of vouchers housed in the Fish Reference Collection of FURG (CIFURG), Instituto de Ciências Biológicas, Universidade Federal do Rio Grande, Rio Grande do Sul, Brazil.

*Astyanax eigenmanniorum*: CIFURG 22, 24, 39, 51, 65, 82, 101, 107, 113, 117, 126, 148, 159, 169, 179, 196; *Astyanax fasciatus*: CIFURG 23, 96, 125, 197; *Astyanax henseli*: CIFURG 25, 62, 67, 173, 180; *Astyanax lacustris*: CIFURG 50, 70, 90, 146, 162, 167, 175; *Atherinella brasiliensis*: CIFURG 78, 109; *Australoheros acaroides*: CIFURG 35, 58, 85, 99, 145, 153, 191; *Brachyhypopomus draco*: CIFURG 57, 123; *Brachyhypopomus gauderio*: CIFURG 15, 110, 124, 143; *Characidium orientale*: CIFURG 171; *Characidium rachovii*: CIFURG 54, 119, 139, 151, 185; *Charax stenopterus*: CIFURG 41, 98, 130, 158, 181, 187; *Cheiridon ibicubiensis*: CIFURG 16, 32, 45, 52, 63, 89, 127, 155, 172, 177, 198; *Cheirodon interruptus*: CIFURG 53, 72, 102, 144, 168; *Cichlasoma portoalegrense*: CIFURG 21, 73, 100, 140, 165, 186; *Corydoras paleatus*: CIFURG 164, 188; *Crenicichla lepidota*: CIFURG 33, 91; *Ctenogobius shufeldti*: CIFURG 93, 104; *Cyanocharax alburnus*: CIFURG 44; *Cynopocilus melano-*

*taenia*: CIFURG 112, 121; *Cyphocharax voga*: CIFURG 13, 27, 43, 60, 71, 81, 92, 129, 135, 154, 163, 176, 195; *Geophagus brasiliensis*: CIFURG 84, 103; *Gymnogeophagus* sp.: CIFURG 46; *Hisonotus laevis*: CIFURG 105; *Hoplias malabaricus*: CIFURG 34, 59, 122, 138, 157, 189; *Hoplosternum littorale*: CIFURG 17; *Hyphessobrycon boulengeri*: CIFURG 48, 114, 118; *Hyphessobrycon igneus*: CIFURG 10, 31, 38, 56, 66, 87, 94, 115, 116, 134, 142, 156, 182; *Hyphessobrycon luetkenii*: CIFURG 14, 26, 40, 61, 64, 88, 95, 128, 147, 160, 174, 178, 199; *Hyphessobrycon togoi*: CIFURG 106; *Jenynsia multidentata*: CIFURG 75; *Lycengraulis grossidens*: CIFURG 76; *Mugil Liza*: CIFURG 80; *Odontesthes argentinensis*: CIFURG 108; *Oligosarcus jenynsii*: CIFURG 12, 28, 42, 69, 77, 131, 149, 183, 194; *Oligosarcus robustus*: CIFURG 29, 47, 55, 68, 79, 97, 132, 137, 150, 170, 184, 193; *Phalloceros caudimaculatus*: CIFURG 11, 30, 36, 49, 83, 111, 120, 133, 152, 192; *Phalloptychus iheringii*: CIFURG 37; *Pimelodella australis*: CIFURG 18, 190; *Platanichthys platana*: CIFURG 74; *Pseudocorynopoma doriae*: CIFURG 19; *Rhamdia quelen*: CIFURG 20, 86, 136, 166; *Steindachnerina biornata*: CIFURG 161; *Synbranchus marmoratus*: CIFURG 141.

# A contribution to mayfly studies of Western Mongolia (Insecta, Ephemeroptera)

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## Abstract

Streams in the Mongolian Altai Mountains are mostly fed from glaciers and are extreme conditions for mayflies because of high elevation, low temperatures and low annual precipitation. Previous information about mayflies of Western Mongolia is scarce, but with this study a total of 38 species belonging to 26 genera and subgenera and 8 families of mayflies has been recorded in the Mongolian Altai region. Study material was entirely imagos and collected from 78 sites during expeditions led by the Mongolian Aquatic Insect Survey in 2008, 2009 and 2010. *Raptobaetopus tenellus*, *Caenis luctuosa* and *C. rivulorum* are recorded as new to the fauna of Mongolia, and there are new distribution records for *Ameletus montanus*, *Baetis (Acentrella) lapponica*, *Baetis sibiricus*, *Baetis (Labiobaetis) atrebatinus*, *Centroptilum luteolum*, *Proclleon pennulatum*, *Ephemerella aurivillii*, *Serratella setigera*, *Ephemera sachalinensis*, *Ecdyonurus (Afronurus) abracadabrus*, *Cinygmula kurenzovi*, *Ecdyonurus (Afghanurus) vicinus* and *Epeorus (Belovius) pellucidus* from the Mongolian Altai region. *Baetis vernus* and *Ephemerella aurivillii* are the most frequently encountered species in this region.

## Keywords

*Raptobaetopus tenellus*, *Caenis luctuosa*, *C. rivulorum*, Biodiversity, Altai Mountain Range, Aquatic Insects

## Introduction

Early studies of the mayfly fauna from the Mongolian region date to 1940 by Kinji Imanishi (Landa and Soldán 1983), although the major focus of this work consisted of exploring Inner Mongolia, a province of China, and to a lesser extent, the modern state of Mongolia (Bae et al. 2000). A decade later, Tshernova (1952) was the first to thoroughly describe the Mongolian (i.e., from the current Mongolian State) mayfly fauna with a paper including describing a new species, *Baetis mongolicus* (later, redescribed as a synonym of *Baetis (Labiobaetis) tricolor* by Kluge (2012)), from Khalkh gol, Eastern Mongolia. Most recently, Soldán et al. (2009), published a review of the Mongolian mayfly fauna and listed a total of 96 species belonging to 34 genera and 14 families. Of these, 28 species were recorded from Western Mongolia (defined as Uvs, Khovd and Bayan-Olgii provinces of Mongolia).

Most of the area of Western Mongolia is highly elevated, mostly dominated by the Mongolian Altai Mountains, which have permanent glacial snow at the highest points. The average altitude of the Mongolian Altai Mountains is about 3200–3500 m a.s.l. The air temperature of the warmest month in Mongolian Altai Mountains is 12.3 °C in the higher areas and 21.1 °C in the lower areas of the region (Altantsetseg et al. 2008). Thus, for the region sampled for this study, we consider this area of high elevation and relatively cold summers as extreme conditions for mayflies.

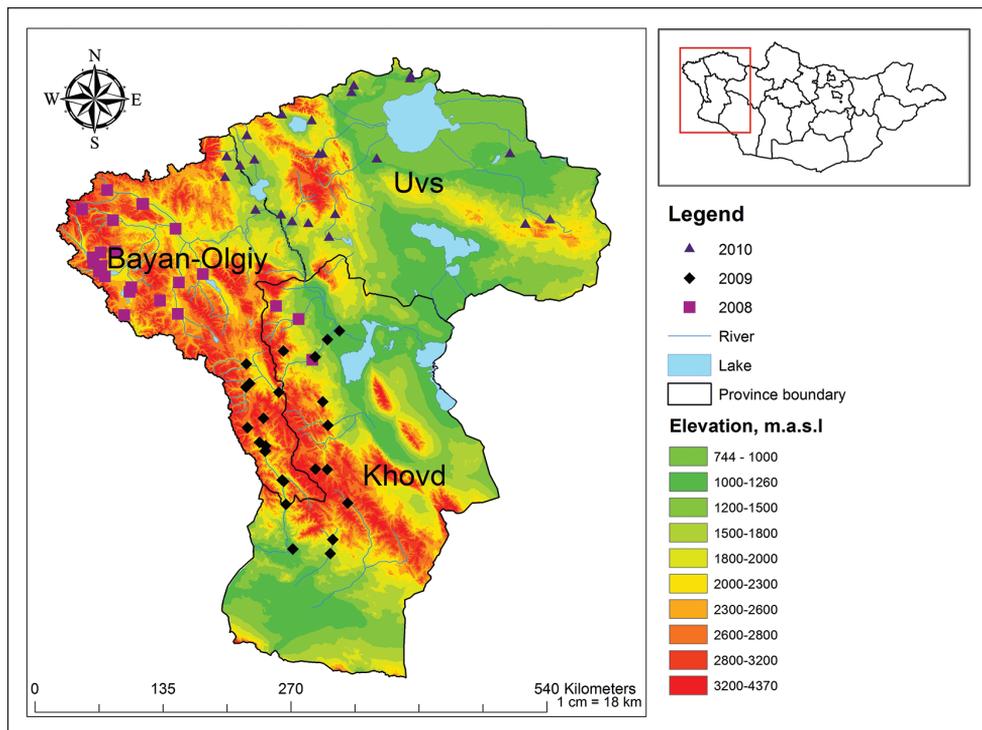
Mayflies occur in variety of lotic and lentic environments and these habitats, including rivers, streams, springs and lakes, occur in Western Mongolia. The entire region of Western Mongolia is included within the Central Asian Internal Watershed (CAIW) (“Internal” from, Kelderman and Batima 2006; Maasri and Gelhaus 2012) which is one of the three major basins of Mongolia (Tsegmid 1969). The CAIW is an endorheic basin but equivalent to the size of the Arctic and Pacific Ocean basins of Mongolia (Dulmaa 1979). In this watershed, streams originating from glacial melt are common, in addition to lakes that originated from tectonic and glacial processes. The largest river by its discharge is Khovd gol (“gol” refers to stream or river in Mongolian) flowing for 516 km with a drainage area of 58000 km<sup>2</sup> (Tsegmid 1969). The second largest river is Bulgan gol, which is 268 km long, and with a drainage area of about 9180 km<sup>2</sup>. The Bulgan gol originates from south of the Mongol Altai Mountains and flows west into the Urungu River of China. Bodonch gol and Uyench gol are the next largest rivers after Bulgan gol (Myagmarjav and Davaa 1999). Three out of the five largest lakes in Mongolia (as measured by surface area) occur in the CAIW specifically Uvs, Khyargas and Khar-Uls lakes (the first two listed are salt water lakes, the last one is a freshwater lake). Uvs nuur (“nuur” refers to lake in Mongolian) is the largest lake in Mongolia, with a drainage basin of 70712 km<sup>2</sup>. In addition to these there are several smaller freshwater (Khoton nuur, Khorgon nuur, Dayan nuur and Achit nuur) and saltwater lakes (Uureg nuur) in the basin (Myagmarjav and Davaa 1999).

In this paper, we provide data on the species composition of mayflies in Western Mongolia and the Altai Mountains in order to contribute to the inventory of aquatic insect biodiversity in this relatively unexplored area of Mongolia and the larger Central Asian region. This study has the specificity to include a wide range of aquatic habitat types distributed along a wide latitudinal gradient.

## Materials and methods

### Study area

Mayfly samples were collected throughout the three provinces (aimags) of Western Mongolia, namely Khovd, Bayan-Olgii and Uvs. We collected a total of 2180 adult specimens from 78 sites (Figure 1) in the Mongolian Altai mountain region, along streams, rivers, springs and several large lakes. Sampling sites included a wide range of elevation between 923 to 2798 m a.s.l, and a majority of streams and rivers (Figures 2 to 7, and Appendix 1).



**Figure 1.** Sampling sites in the Mongolian Altai Mountain range (2008–2010).



**Figure 2.** Khovd gol (site # 4).



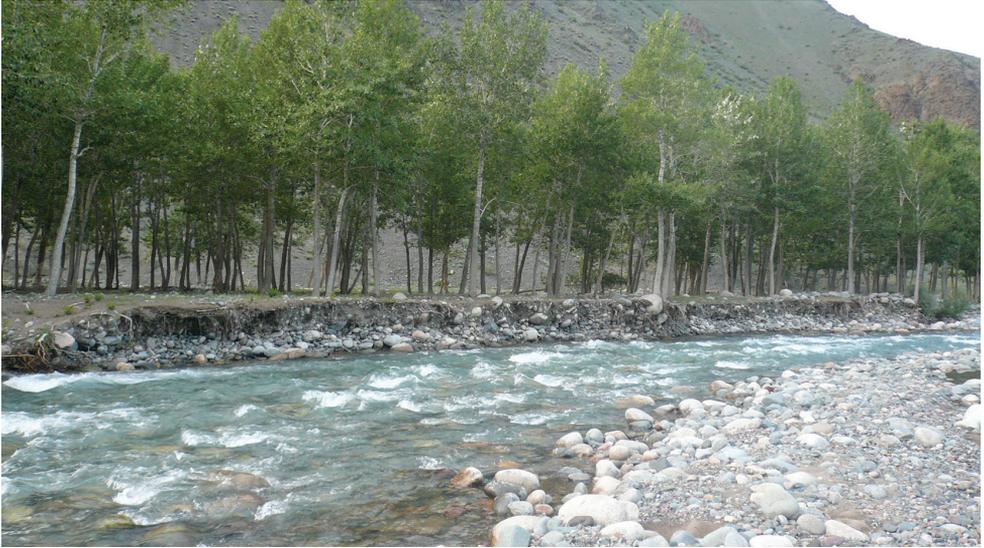
**Figure 3.** Khoton nuur (site # 13).



**Figure 4.** Uyench gol (site # 45).



**Figure 5.** Bortiin gol (site # 49).



**Figure 6.** Turgen gol (site # 73).



**Figure 7.** Baruunturuun gol (site # 77).

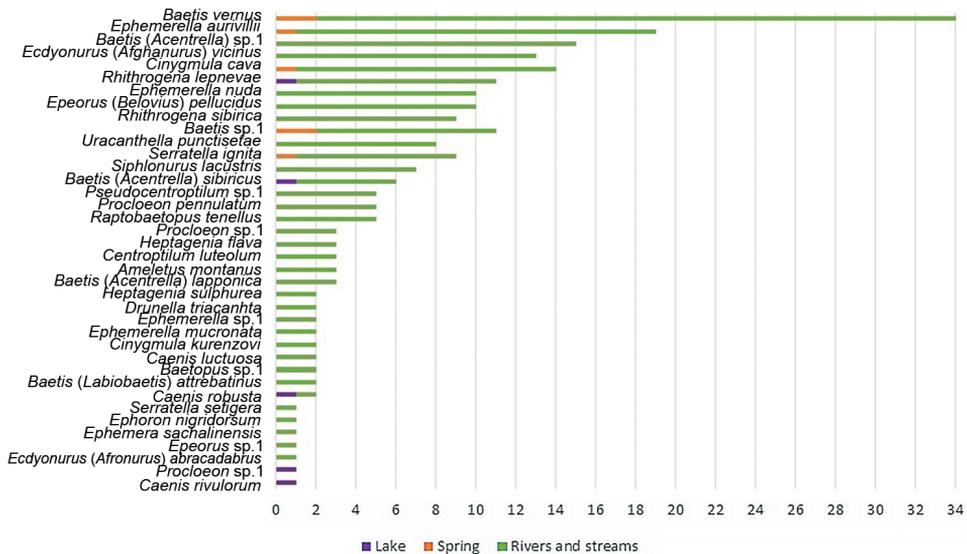
### Sampling

Imago samples were collected in the framework of the Mongolian Aquatic Insect Survey (see Gelhaus 2012; Phillips-Iverson and Gelhaus 2010) in July of each year between 2008 and 2010. At each sampling site, sweep net and Malaise traps were used to collect mayfly imagos and occasionally white and black light traps were used to complement the collection. Two Malaise traps were set overnight directly along the stream channel with the head end of the trap adjacent to the stream bank. After collection, all specimens were preserved in the field in 80% ethanol solution. If subimagos were captured alive, they were kept in a dry place until the imago emerged.

Specimens were identified in the laboratory using a Leica EZ4 dissecting microscope and identification keys (Bajkova 1972; 1974; Kluge 1980; 1987; Tshernova 1952; 1964; Tshernova and Belov 1982). All specimens are preserved at the Institute of Meteorology, Hydrology and Environment, Ulaanbaatar, Mongolia.

### Results

A total of 38 species, belonging to 26 genera and subgenera and 8 families of mayflies, are recorded in this study area (Figure 8). Among these, *Raptobaetopus tenellus* Albadra, 1878, *Caenis luctuosa* (Burmeister, 1839) and *C. rivulorum* Eaton, 1884 are new to the fauna of Mongolia, and there are new distribution records in Western Mongolia for 13 species: *Ameletus montanus* Imanishi, 1930, *Baetis (Acentrella) lapponica* Bengtsson, 1912,



**Figure 8.** Species of mayflies recorded in Western Mongolia (ordered by the number of site occurrences). The different colors on the bar for each species represent the three main habitats and the length represents the number of occurrences for each type.

*Baetis (Acentrella) sibiricus* Kazlauskas, 1963, *Baetis (Labiobaetis) attrebatinus* Eaton, 1870, *Centroptilum luteolum* (Müller, 1776), *Procloeon pennulatum* (Eaton, 1870), *Ephemerella aurivillii* Bengtsson, 1909, *Serratella setigera* (Bajkova, 1965), *Ephemerella sachalinensis* Matsumura, 1911, *Ecdyonurus (Afronurus) abracadabrus* (Kluge, 1983), *Cinygmula kurenzovi* (Bajkova, 1965), *Ecdyonurus (Afghanurus) vicinus* Demoulin, 1964, and *Epeorus (Belovius) pellucidus* (Brodsky, 1930). The following species list gives the specific localities where a species was found as site number (#), and Figure 8 ranks the species by number of sites where each species occurred. In the species list, preceding the species name, (\*) refers to a new record for the Western Mongolia and (\*\*) refers to a new record for the country.

### Ameletidae

-\* *Ameletus montanus* Imanishi, 1930 - # 22, 26, 31

### Baetidae

- \* *Baetis (Acentrella) lapponica* Bengtsson, 1912 - # 31, 51, 59
- *Baetis (Acentrella)* sp. 1 - # 1, 2, 4, 24, 27, 31, 33, 43, 47, 53, 56, 63, 65, 72, 77
- \* *Baetis (Acentrella) sibiricus* Kazlauskas, 1963 - # 3, 16, 34, 35, 49, 50
- \* *Baetis (Labiobaetis) attrebatinus* Eaton, 1870 - # 47, 70
- *Baetis vernus* Curtis, 1834 - # 2, 3, 7, 8, 9, 10, 12, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24, 25, 29, 32, 35, 37, 38, 40, 45, 51, 52, 53, 56, 59, 61, 62, 63, 71
- *Baetis* sp. 1 - # 1, 3, 15, 18, 24, 41, 60, 62, 65, 66, 68
- *Baetopus* sp. 1 - # 60, 64
- \* *Centroptilum luteolum* (Müller, 1776) - # 31, 37, 39
- \* *Procloeon pennulatum* (Eaton, 1870) - # 59, 60, 61, 64, 66
- *Procloeon* sp. 1 - # 13
- *Pseudocentroptilum* sp. 1 - # 3, 22, 43, 48, 57
- *Pseudocloeon* sp. 1 - # 8, 16, 17
- \*\* *Raptobaetopus tenellus* Albadra, 1878 - # 57, 61, 63, 67, 71

### Caenidae

- \*\* *Caenis luctuosa* (Burmeister, 1839) - # 16, 53
- \*\* *Caenis rivulorum* Eaton, 1884 - # 13
- *Caenis robusta* Eaton, 1884 - # 53, 58

### Ephemerellidae

- *Drunella triacantha* (Tshernova, 1949) - # 23, 41
- \* *Ephemerella aurivillii* Bengtsson, 1909 - # 5, 6, 16, 19, 28, 31, 33, 35, 36, 37, 38, 41, 65, 67, 68, 70, 71, 73, 75
- *Ephemerella mucronata* (Bengtsson, 1909) - # 3, 38
- *Ephemerella nuda* Tshernova, 1949 - # 1, 3, 10, 11, 29, 30, 40, 53, 65, 66
- *Ephemerella* sp. 1 - # 30, 60
- *Serratella ignita* (Poda, 1761) - # 24, 43, 45, 54, 59, 61, 63, 66, 76
- \* *Serratella setigera* (Bajkova, 1965) - # 43
- *Uracanthella punctisetae* Matsumura, 1931 - # 33, 37, 38, 39, 40, 41, 42, 43

### Ephemeridae

- \* *Ephemerella sachalinensis* Matsumura, 1911 - # 43

### Heptageniidae

- *Cinygmula cava* (Ulmer, 1927) - # 6, 17, 18, 19, 23, 31, 36, 65, 68, 69, 70, 73, 74, 75
- \* *Cinygmula kurenzovi* (Bajkova, 1965) - # 4, 63
- \* *Ecdyonurus (Africanurus) vicinus* Demoulin, 1964 - # 18, 20, 22, 24, 45, 46, 47, 61, 65, 66, 72, 77, 78
- \* *Ecdyonurus (Africanurus) abracadabrus* (Kluge, 1983) - # 43
- \* *Epeorus (Belovius) pellucidus* (Brodsky, 1930) - # 3, 33, 36, 39, 40, 41, 42, 43, 47, 61
- *Epeorus* sp. 1 - # 19
- *Heptagenia flava* Rostock, 1878 - # 53, 54, 60
- *Heptagenia sulphurea* (Müller, 1776) - # 3, 53
- *Rhithrogena lepnevae* Brodsky, 1930 - # 2, 3, 24, 39, 40, 41, 42, 43, 44, 60, 78
- *Rhithrogena sibirica* Brodsky, 1930 - # 4, 19, 31, 32, 38, 55, 64, 67, 73

### Polymitarcyidae

- *Ephoron nigradorsum* (Tshernova, 1934) - # 53

### Siphonuridae

- *Siphonurus lacustris* Eaton, 1970 - # 12, 14, 56, 57, 71, 75, 78

Of the 38 species recorded as adults, 36 occurred along streams and rivers. Three species, *Caenis robusta*, *Baetis (Acentrella) sibiricus* and *Rhithrogena lepnevae*, were found along both lotic and lentic habitats. Only two species, *Proclleon* sp. and *Caenis rivulorum*, were recorded from a lake (# 13- Khoton nuur). Five species were taken around cold springs although none was found exclusively along this habitat.

The most frequently encountered species was *Baetis vernus*, which was recorded from 34 of the 78 sites (Figure 8). *Ephemerella aurivillii*, *Baetis (Acentrella)* sp. 1 and *Cinygmula cava* were found at 19, 15, and 14 different sites, respectively. In contrast, seven species were recorded as adults only at one site: *Serratella setigera* (site # 43), *Ephoron nigradorsum* (site # 53), *Ephemera sachalinensis* (site # 43), *Epeorus* sp. 1 (site # 19), *Ecdyonurus (Africanurus) abracadabrus* (site # 43), *Proclleon* sp. 1 (site # 13), and *Caenis rivulorum* (site # 13). The remaining species occurred at between two to 13 sites.

Taxa richness at rivers and lakes varied between one and 16 (Figure 9). The highest taxa richness was found along Bulgan gol (16 species) with 15 and 11 species along the rivers Khovd and Sagsai, respectively. The lowest species richness (one species) was observed at 18 rivers (e.g. Bodonch gol, Bortiin gol, Buural gol etc.).

### Discussion

Our study shows that the Ephemeroptera fauna of Western Mongolia comprise more than one-third of the total species recorded for the country. In addition, three new species were recorded for Mongolia for the first time, *Raptobaetopus tenellus*, *Caenis luctuosa* and *C. rivulorum*. *Raptobaetopus tenellus* is a Transpalearctic (also referred as Entire Palearctica, Beketov (2009)) species (Bauernfeind and Soldán 2012). Distribution of this species is known from west Palearctic (Iberian Peninsula through Europe to the



ously recorded in lakes with stony substrate as well as rivers at variable elevations between 200–500 m a.s.l. in Europe (Bauernfeind and Soldán 2012). However, the elevation of Lake Khoton is 2086 m a.s.l. making this site the highest elevation record for the species.

*Baetis vernus* was the most commonly encountered taxon in Western Mongolia and occurred in 45% of the sampled sites. This species was found at a variety of lotic habitats including streams and springs. The elevation range of this species in Western Mongolia extended from 1172 to 2798 m a.s.l. The wide occurrence of this species among our sampled sites is most likely due to its very broad ecological range (Bauernfeind and Soldán 2012).

*Serratella setigera*, *Proclleon* sp. 1, *Ephoron nigridorsum*, *Ephemera sachalinensis*, *Epeorus* sp. 1, *Ecdyonurus (Afronurus) abracadabrus*, and *Caenis rivulorum* were found only at a single sampling site. *Ephoron nigridorsum* and *Ephemera sachalinensis* are both burrowing mayflies preferring larger and lowland rivers (Bauernfeind and Soldán 2012) and were recorded at Bulgan or Khovd River, the only suitable river habitat within the sampling area. For *Serratella setigera* and *Ecdyonurus (Afronurus) abracadabrus*, both found only at Bulgan Gol (Appendix 1, site # 43), this study adds significant habitat information to what little is known on the distribution of these two species (Bauernfeind and Soldán 2012).

## Conclusion

In this study a total of 38 species was recorded in Western Mongolia (Uvs, Khovd and Bayan-Olgii provinces). Soldán et al. (2009) listed 28 species that have been recorded from the Khovd, Uvs and Bayan-Olgii provinces, with more than half of these not collected in our sampling expeditions. Therefore, despite the valuable information taxonomic and geographical distribution of mayflies of Western Mongolia, this study does not constitute an inclusive checklist of the total mayfly fauna of Western Mongolia. This discrepancy could be related to a number of reasons due to sampling and current taxonomy. First, our sampling effort was restricted to July, a favorable period for emergence of aquatic insects in Mongolia, but nevertheless did not cover the complete ice-free period in Western Mongolia. Second, the sampling duration and number of samples at the different aquatic habitats was variable. Some rivers and streams were sampled thoroughly at different sites (e.g. Bulgan and Khovd River), others were only sampled overnight and in few sites was sampling occurring at the right timing during the day to encompass adult swarming. Therefore, our sampling might have been affected by different emergence patterns. Third, there were difficulties to identify some adult mayflies at the species level because of the lack of reliable identification keys for the Mongolia fauna and also having subimagos in the samples. Maasri and Gelhaus (2012) previously listed mayfly species based on larval identification and recorded 21 genera for the CAIW. However, Maasri and Gelhaus (2012) included sites throughout the whole CAIW, covering a wider geographical range. Erdenee (2011) in her previous study recorded 17 genera all included in this study. In addition to Soldán et al. (2009), Beketov (2005) in a survey of the Northeastern Altai Mountains recorded 25 species with 20 of these included in Western Mongolia. Therefore, our results and the avail-

able literature on Western Mongolia support the statement of an estimated number of mayfly species for this geographical area to be above 65 species.

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## Appendix I

Study area and localities sampled for mayfly imagos in Western Mongolia. Soum refers to an administrative subunit of the aimag (or province). Dates are provided in day-month-year format.

Site number (#)	Site code in the MAIS database	GPS	Elevation, m.a.s.l	Site name	Province	Soum	Collection date	Habitat type
1	MAIS2008070301	48°19.26'N 91°18.53'E	1474	Shurag gol	Khovd	Erdenetburen	3.07.2008	Stream
2	MAIS2008070302	48°25.30'N 90°58.40'E	1805	Hongor-Uulun gol	Khovd	Erdenetburen	3–4.07.2008	Stream
3	MAIS2008070502	48°38.89'N 89°53.03'E	2065	Sagsai gol	Bayan-Olgii	Sagsai	4–6.07.2008	River
4	MAIS2008070602	49°02.51'N 89°25.00'E	1775	Khovd gol	Bayan-Olgii	Ulaankhus	6.07.2008	River
5	MAIS2008070701	49°14.28'N 88°54.43'E	2108	Sogoog gol	Bayan-Olgii	Ulaankhus	7.07.2008	River
6	MAIS2008070702	49°14.09'N 88°54.01'E	2101	Segoog gol	Bayan-Olgii	Ulaankhus	7–8.07.2008	River
7	MAIS2008070802	49°19.11'N 88°21.98'E	2394	Ulastrai gol	Bayan-Olgii	Ulaankhus	8.07.2008	Stream
8	MAIS2008071001	49°06.27'N 88°02.91'E	2798	Sul Uuliin gol	Bayan-Olgii	Tsengel	10.07.2008	Stream
9	MAIS2008071302	49°02.71'N 88°30.53'E	2382	Khatuugin gol	Bayan-Olgii	Tsengel	13.07.2008	River
10	MAIS2008071304	48°45.53'N 88°36.06'E	2146	Unnamed tributary of Mogoitiin gol	Bayan-Olgii	Tsengel	13–14.07.2008	Stream
11	MAIS2008071305	48°45.35'N 88°36.26'E	2142	Mogoitiin gol	Bayan-Olgii	Tsengel	13–14.07.2008	Stream
12	MAIS2008071401	48°43.59'N 88°24.06'E	2431	Urt Khuimii gol	Bayan-Olgii	Tsengel	14.07.2008	River

Site number (#)	Site code in the MAIS database	GPS	Elevation, m.a.s.l	Site name	Province	Soum	Collection date	Habitat type
13	MAIS2008071402	48°40.03'N 88°17.96'E	2086	Khoton nuur	Bayan-Olgii	Tsengel	14–15.07.2008	Lake
14	MAIS2008071503	48°32.64'N 88°24.89'E	2147	Ikh Turgenuii gol	Bayan-Olgii	Tsengel	15–16.07.2008	Stream
15	MAIS2008071602	48°37.04'N 88°19.25'E	2115	Parrizanii bulag	Bayan-Olgii	Tsengel	16.07.2008	Spring
16	MAIS2008071603	48°35.92'N 88°26.21'E	2087	Syrgali gol	Bayan-Olgii	Tsengel	16.07.2008	River
17	MAIS2008071604	48°30.38'N 88°30.57'E	2133	Sumdairag ol	Bayan-Olgii	Tsengel	16–17.07.2008	Stream
18	MAIS2008071702	48°26.21'N 88°54.06'E	2232	Godon gol	Bayan-Olgii	Sagsai	17.07.2008	River
19	MAIS2008071703	48°10.03'N 88°51.25'E	2065	Yamaatnin gol	Bayan-Olgii	Sagsai	17–18.07.2008	Stream
20	MAIS2008071802	48°23.53'N 88°53.02'E	2184	Ikh Khanajashiin gol	Bayan-Olgii	Sagsai	18.07.2008	Stream
21	MAIS2008071803	48°20.71'N 89°19.57'E	2422	Khoit Bardat gol	Bayan-Olgii	Altai	18–19.07.2008	Stream
22	MAIS2008071901	48°14.47'N 89°36.10'E	2137	Sagsai gol	Bayan-Olgii	Altai	19.07.2008	River
23	MAIS2008071902	48°32.48'N 89°33.60'E	2029	Kholtsootiin gol	Bayan-Olgii	Buyant	19.07.2008	Stream
24	MAIS2008072002	47°56.87'N 91°33.48'E	1444	Buyant gol	Khovd	Khovd	20–21.07.2008	River
25	MAIS2009070101	47°58.59'N 91°35.48'E	1428	Buyant gol	Khovd	Khovd	01–03.07.2009	River
26	MAIS2009070201	48°00.19'N 91°08.46'E	2120	Unnamed tributary of Buyant gol	Khovd	Bayanbulag	2.07.2009	Stream

Site number (#)	Site code in the MAIS database	GPS	Elevation, m.a.s.l	Site name	Province	Soum	Collection date	Habitat type
27	MAIS2009070403	47°34.87'N 91°10.23'E	2049	Buyant gol	Bayan-Olgii Olgi	Deluun	03.07.2009	Stream
28	MAIS2009070404	47°36.55'N 91°08.14'E	1947	Buyant gol	Bayan-Olgii	Deluun	04.07.2009	River
29	MAIS2009070405	47°50.64'N 90°38.56'E	2165	Chigerrei gol	Bayan-Olgii	Deluun	04–05.07.2009	River
30	MAIS2009070501	47°37.47'N 90°40.32'E	2241	Gantsmodnii gol	Bayan-Olgii	Deluun	05.07.2009	Stream
31	MAIS2009070502	47°39.84'N 90°43.10'E	2196	Gantsmodnii gol	Bayan-Olgii	Deluun	05–06.07.2009	River
32	MAIS2009070602	47°20.80'N 90°57.61'E	2519	Confluence of “Dood Asgat Ulul gol” and “Ulaagchiny Davaa gol” (two unnamed stream)	Bayan-Olgii	Bulgan	06.07.2009	Stream
33	MAIS2009070604	47°05.32'N 91°01.61'E	2056	Bulgan gol	Bayan-Olgii	Bulgan	06–07.07.2009	River
34	MAIS2009070703	47°14.48'N 90°45.19'E	2563	Khar nuur	Bayan-Olgii	Bulgan	07.07.2009	Lake
35	MAIS2009070704	47°14.62'N 90°45.15'E	2560	Outfall stream from Khar nuur	Bayan-Olgii	Bulgan	07.07.2009	Stream
36	MAIS2009070801	47°06.93'N 90°56.48'E	2122	Bulgan gol and roadside pools	Bayan-Olgii	Bulgan	08.07.2009	Stream
37	MAIS2009070802	47°02.28'N 91°01.76'E	2016	“Elstrin Davaa” gol (unnamed stream)	Bayan-Olgii	Bulgan	08–09.07.2009	Stream
38	MAIS2009070803	47°02.37'N 91°02.07'E	2010	Bulgan gol	Bayan-Olgii	Bulgan	08–09.07.2009	River
39	MAIS2009070901	46°46.80'N 91°18.24'E	1801	Bulgan gol	Bayan-Olgii	Bulgan	09.07.2009	River
40	MAIS2009070902	46°46.20'N 91°19.40'E	1792	Bulgan gol	Bayan-Olgii	Bulgan	09–10.06.2009	River

Site number (#)	Site code in the MAIS database	GPS	Elevation, m.a.s.l	Site name	Province	Soum	Collection date	Habitat type
41	MAIS2009070903	46°46.17'N 91°19.66'E	1788	Tsonkhogol/Turgen gol (tributary of Bulgan gol)	Bayan-Olgii	Bulgan	09–10.06.2009	Stream
42	MAIS2009071002	46°33.19'N 91°23.31'E	1509	Deed Nariin gol	Border of Bayan-Olgii and Hovd	Bulgan	10.07.2009	Stream
43	MAIS2009071003	46°08.07'N 91°32.50'E	1200	Bulgan gol	Khovd	Bulgan	10–12.07.2009	River
44	MAIS2009071101	46°08.29'N 91°32.46'E	1210	Oxbow of Bulgan gol	Khovd	Bulgan	12.07.2009	Lake
45	MAIS2009071202	46°07.47'N 92°03.25'E	1470	Uyench gol	Khovd	Uyench	12–13-.07.2009	Stream
46	MAIS2009071301	46°15.63'N 92°04.37'E	1683	Urd Jargalant gol	Khovd	Uyench	13.07.2009	Stream
47	MAIS2009071302	46°15.66'N 92°04.36'E	1677	Uyench gol	Khovd	Uyench	13.07.2009	Stream
48	MAIS2009071401	46°37.21'N 92°13.84'E	2544	Bodonch gol	Khovd	Must	14.07.2009	Stream
49	MAIS2009071501	46°55.28'N 91°54.65'E	2311	Bortiin gol	Khovd	Munkhkhairkhan	15.07.2009	Stream
50	MAIS2009071503	46°54.89'N 91°44.83'E	2708	Tributary of Bortiin gol	Khovd	Munkhkhairkhan	15–16.07.2009	Stream
51	MAIS2009071701	47°20.40'N 91°51.79'E	1762	Khoi Tsenkher gol	Khovd	Duut	17–18.07.2009	Stream
52	MAIS2009071801	47°33.56'N 91°45.66'E	1865	Tsagaan Burgasniit gol	Khovd	Duut	18–19.07.2009	Spring
53	MAIS2009072002	48°14.74'N 91°54.09'E	1172	Khovd gol	Khovd	Khovd	20.07.2009	River
54	MAIS2009072003	48°09.20'N 91°44.58'E	1269	Buyant gol	Khovd	Khovd	20–21.07.2009	Stream

Site number (#)	Site code in the MAIS database	GPS	Elevation, m.a.s.l	Site name	Province	Soum	Collection date	Habitat type
55	MAIS2009072101	47°58.56'N 91°35.80'E	1420	Buyant gol	Khovd	Buyant	21.07.2009	Stream
56	MAIS2010070402	49°20.40'N 91°40.90'E	1876	Orlogiin gol	Uvs	Umnugovi	04.07.2010	River
57	MAIS2010070403	49°07.10'N 91°37.51'E	1593	Orlogiin gol	Uvs	Umnugovi	04.07.2010	River
58	MAIS2010070502	49°13.70'N 91°18.64'E	1701	Shaazgai nuur	Uvs	Khovd	05.07.2010	Lake
59	MAIS2010070603	49°13.82'N 91°04.38'E	1475	Braid of Shiver gol	Uvs	Khovd	06.07.2010	Stream
60	MAIS2010070702	49°17.00'N 90°54.18'E	1405	Khovd gol bridge	Uvs	Khovd	07.07.2010	River
61	MAIS2010070802	49°18.12'N 90°31.78'E	1467	Braid of Khovd gol	Bayan-Olgii	Nogoonnuur	08.07.2010	River
62	MAIS2010070803	49°34.66'N 90°02.10'E	1764	Zakhiin-Us gol	Bayan-Olgii	Nogoonnuur	08–09.07.2010	Stream
63	MAIS2010070902	49°46.40'N 90°01.36'E	1694	Baga Khatuugiin gol	Bayan-Olgii	Nogoonnuur	09–10.07.2010	River
64	MAIS2010071002	49°42.23'N 90°13.82'E	1526	Bokhmoron/Tavan salaa gol	Uvs	Bukhmurun soum	10.07.2010	River
65	MAIS2010071003	49°59.81'N 90°16.73'E	1763	Altan gadas gol	Uvs	Bukhmurun soum	10–11.07.2010	River
66	MAIS2010071101	49°46.55'N 90°25.87'E	1504	Altan gadas gol	Uvs	Bukhmurun soum	11.07.2010	River
67	MAIS2010071102	50°13.86'N 90°45.39'E	1552	Khoig gol	Uvs	Sagil	11.07.2010	River
68	MAIS2010071302	50°12.34'N 91°12.12'E	1637	Omno Bij bulag	Uvs	Sagil	13.07.2010	Spring

Site number (#)	Site code in the MAIS database	GPS	Elevation, m.a.s.l	Site name	Province	Soum	Collection date	Habitat type
69	MAIS2010071402	50°43.04'N 92°35.96'E	1043	Tokhilog gol	Uvs	Davst	14.07.2010	River
70	MAIS2010071403	50°41.50'N 92°35.57'E	1003	Braid of Tokhilog gol	Uvs	Davst	14–15.07.2010	River
71	MAIS2010071502	50°34.57'N 91°46.22'E	1281	Borshoo gol	Uvs	Sagil	15–16.07.2010	Stream
72	MAIS2010071601	50°30.69'N 91°44.70'E	1229	Unnamed spring brook	Uvs	Sagil	17.07.2010	Stream
73	MAIS2010071602	49°53.54'N 91°21.14'E	1849	Confluence of Javartuin gol and Turgun gol	Uvs	Turgun	16–17.07.2010	River
74	MAIS2010071605	49°54.23'N 91°24.66'E	1812	Buural gol	Uvs	Turgun	17.07.2010	Stream
75	MAIS2010071701	49°54.24'N 92°12.51'E	955	Tedliin gol	Uvs	Tarialan	17–18.07.2010	River
76	MAIS2010071802	50°03.15'N 94°09.25'E	923	Nariin gol	Uvs	Zuungovi	18–19.07.2010	Spring
77	MAIS2010071902	49°26.76'N 94°47.76'E	1688	Baruun Turuun gol	Uvs	Undurkhangai	19–20.07.2010	River
78	MAIS2010072001	49°23.31'N 94°26.57'E	1832	Unknown stream	Uvs	Tsagaankhairkhan	20–21.07.2010	Stream



# *Epimeria abyssalis* sp. n. from the Kuril-Kamchatka Trench (Crustacea, Amphipoda, Epimeriidae)

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## Abstract

A new deep-sea epimeriid, *Epimeria abyssalis* is described from the Kuril-Kamchatka Trench, in the north-western Pacific. This species differs from its congeners in having a short rostrum and a telson with deep and narrow Y-shaped excavation. *Epimeria abyssalis* is the deepest recorded *Epimeria* species. A key to the north Pacific species of *Epimeria* is provided.

## Keywords

*Epimeria*, Epimeriidae, Kuril-Kamchatka Trench

## Introduction

*Epimeria* Costa, 1851, is the largest genus of the family Epimeriidae Boeck, 1871 and includes 54 species (WoRMS 2016), which it is nearly cosmopolitan and was previously recorded between 0 and 3710 m depth. Among these, seven species have to date been reported from the North Pacific: *E. cora* J. L. Barnard, 1971 at 2086 m, off Oregon (Barnard 1971), *E. morronei* Winfield et al., 2012 at 1395–2093 m, Gulf of California and off the west coast of Baja, Mexico (Winfield et al. 2012; Hendrickx et al. 2014), *E. ortizi* Varela & García-Gómez, 2015 at 198–1224 m, Gulf of Mexico (Varela and García-Gómez 2015), *E. pacifica* Gurjanova, 1955 at 1430–1450 m, the

Japan Trench (Gurjanova 1955), *E. pelagica* Birstein & Vinogradov, 1958, caught in a plankton net sampling at 0–8000 m, the Kuril-Kamchatka Trench and the Japan Trench (Birstein and Vinogradov 1958; Nagata 1963), *E. subcarinata* Nagata, 1963 at 2230 m, off Onagawa, the northwestern Pacific (Nagata 1963), and *E. yaquinae* McCain, 1971 at 2800–2862 m, off Oregon (McCain 1971).

This deep-sea survey yielded an undescribed species *Epimeria* from an abyssal zone of the Kuril-Kamchatka Trench, the northwestern Pacific, which is described and illustrated in this work.

## Materials and methods

Amphipod specimens were collected during a survey of deep-sea benthic fauna of northern Japan by the R/V “Hakuho-Maru” of the Ocean Research Institute, University of Tokyo in 2001 (now the ship belongs to Japan Agency for Marine-Earth Science and Technology), from station KH-01-02-XR-8 and XR-12. The gear used for the collection was an ORE beam trawl of 4 m span (mesh size approx. 5 mm). Samples were elutriated on board through a 0.5 mm mesh sieve. The specimens retained were fixed and preserved in 70 % ethanol. Appendages of each individual were dissected and observed using a compound and stereo microscopes. Total length was measured from the tip of the head to the end of the telson. Terminology follows Coleman (2007). The type specimens are deposited in the Kitakyushu Museum of Natural History and Human History, Japan (KMNH).

## Systematics

### *Epimeria* Costa in Hope, 1851

**Type-species.** *Epimeria tricristata* Costa in Hope, 1851 (= *Gammarus corniger* Fabricius, 1779)

### *Epimeria abyssalis* sp. n.

<http://zoobank.org/1A3E4D57-208C-40F9-8B63-484F2304A8B2>

Figures 1–11

**Material examined. Holotype.** Ovigerous ♀ (53 mm) (KMNH IvR 500905), with 5 eggs, Sta. KH-01-02-XR-12, 41°37.67N, 146°54.19E–41°26.20N, 146°23.03E, 5473–5484 m depth, muddy bottom, Kuril–Kamchatka Trench, 22–23 September 2001, 4 m ORE beam trawl, towed by R/V “Hakuho-Maru”.

**Paratypes.** 1 ovigerous ♀ (47 mm) (KMNH IvR 500906), 1 juvenile ♀ (22 mm) (KMNH IvR 500907), Sta. KH-01-02-XR-8, 41°50.08 N 145°37.85E–41°49.70N

145°35.18E, 5695–5664 m depth, muddy bottom, Kuril–Kamchatka Trench, 19 September 2001, 4 m ORE beam trawl, towed by R/V “Hakuho-Maru”.

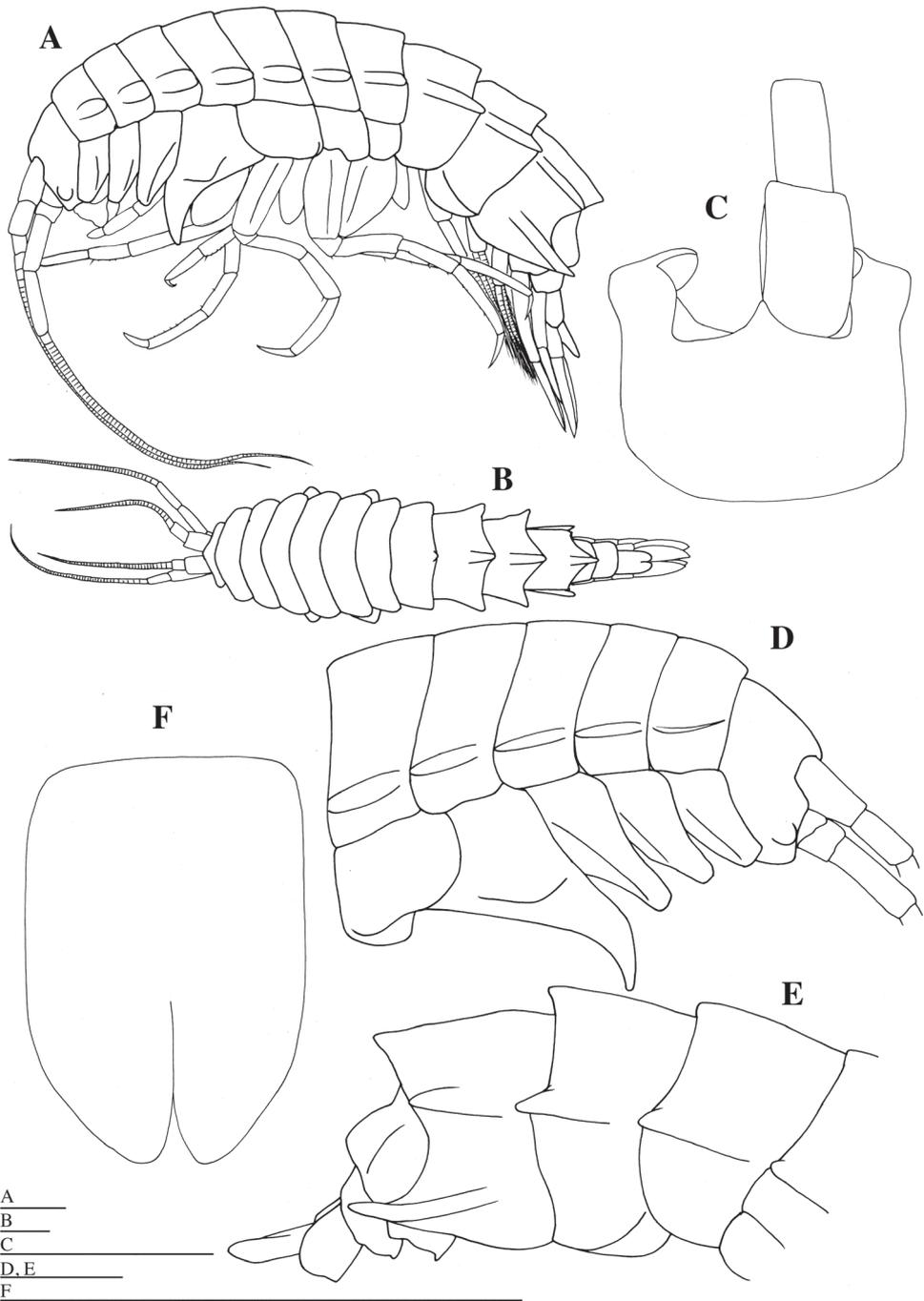
**Description of the holotype.** Rostrum (Fig. 1A, D, C) short, 0.2 times as long as head, not reaching one third of first article of antenna 1. Head (Fig. 1D) ventral lobe blunt. No eye pigments but swelling present in expected eye position. Pereonites 1–7 (Fig. 1A, B, D) without dorsal carinae: pereonite 1 0.8 times as long as head (excluding rostrum); pereonite 2 0.9 times as long as pereonite 1; pereonites 1–7 each with short dorsolateral processes, lacking mid-dorsal processes; pereonite 7 with short dorsolateral and mid-dorsal process. Pleonites 1–3 (Fig. 1A, B, E) with dorsal carinae and posterolateral processes: dorsal carinae of pleonites 1 and 2 not reaching apex of posterolateral processes; dorsal carina of pleonite 3 reaching apex of posterolateral processes. Epimeral plate 1 (Fig. 1A, E) with rounded posteroventral angle; epimeral plate 2 (Fig. 1A, E) with less rounded posteroventral angle; epimeral plate 3 (Fig. 1A, E) with posteroventral angle produced into a large tooth, reaching apex of dorsal carina of pleonite 3.

*Urosomites* 1–3 (Fig. 1A, E) without dorsal processes, extremely low rounded lobe on urosomite 1: urosomite 1 longest; urosomite 2 shortest, 0.4 times as long as urosomite 1; urosomite 3 1.7 times as long as urosomite 2.

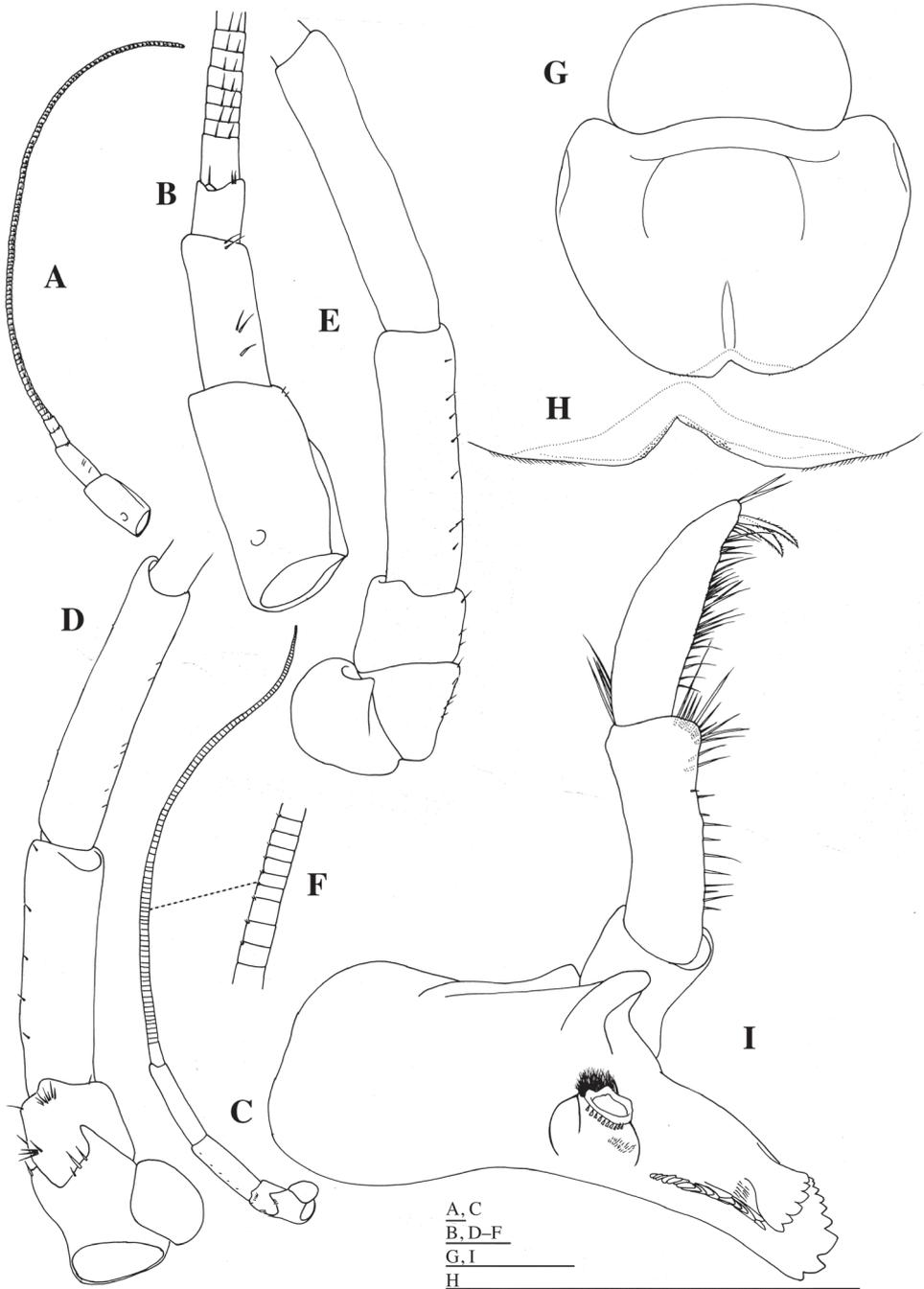
*Antenna 1* (Fig. 2A, B) peduncle without teeth, length of articles 1:2:3 approximately 5:3:1; article 1 twice as long as width; accessory flagellum 1-articulate, scale-like; primary flagellum of 102 articles. *Antenna 2* (Fig. 2C–F): article 1 mediolaterally projected; article 2 distolaterally projected; article 3 bluntly projected distolaterally; article 4 0.8 times as long as article 5; article 5 longest; flagellum of 104 articles.

*Labrum* (= upper lip) (Fig. 2G, H) with shallow notch distally; epistome broadly rounded. *Mandible* (Figs 2I, 3A–E): incisor and lacinia mobilis strongly dentate, left incisor and lacinia mobilis 9- and 6-dentate, respectively; molar produced and triturative, densely setose medially, with acute teeth distally; mandibular palp (Figs 2I, 3D) long; article 1 shortest; article 2 as long as article 3, sparsely setose medially; article 3 with some simple setae medially, two setulate and two simple long setae apically. *Maxilla 1* (Fig. 4A–E): inner plate ovate, with ten stout plumose setae distally; outer plate distal margin oblique, with ten weakly serrate or unarmed robust setae; palp exceeding outer plate; palp article 1 short; palp article 2 2.9 times as long as article 1, with two simple setae laterally, and with stout setae distally and medially. *Maxilla 2* (Fig. 4F–I): inner plate with stout plumose setae distally, and with short simple setae medially and laterally; outer plate stout with simple short setae laterally, and with simple and crenulate setae distally. *Maxilliped* (Fig. 5A–F): inner plate moderately narrow, with long plumose setae medially and short plumose setae distally; outer plate broadly rounded distally, reaching two thirds the length of second article of maxillipedal palp; palp articles 1 and 2 with plumose setae distolaterally and medially; article 3 with row of short, stout setae medially and short claw apically. *Lower lip* (= labium) (Fig. 4J, K) with stout setae distomedially, fine setae medially and distolaterally; broad hypopharyngeal lobes; lateral processes narrow; inner lobe absent.

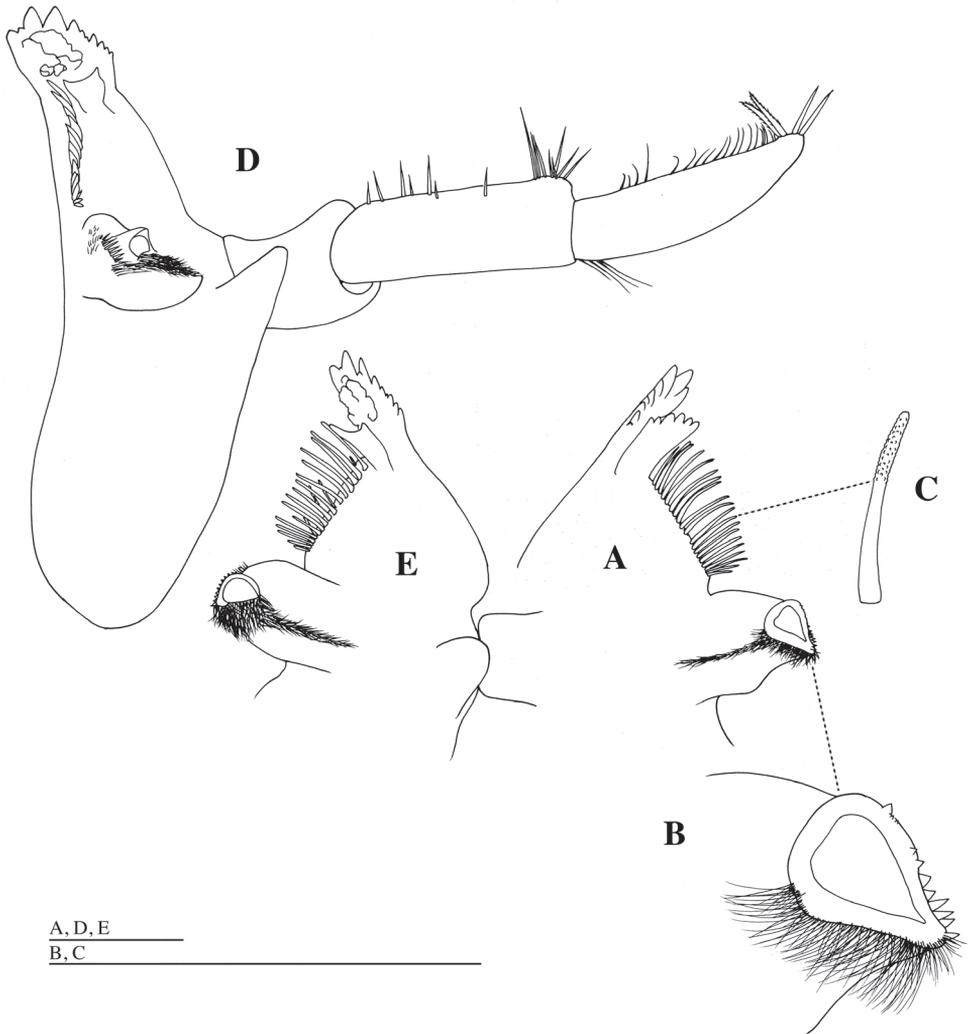
*Gnathopod 1* (Figs. 1A, D, 6A, B): coxa slender, with blunt apex; anterior margin of coxa slightly concave; basis longest, with numerous fine setae anteriorly and poste-



**Figure 1.** *Epimeria abyssalis* sp. n., holotype female: **A** habitus, lateral **B** habitus, dorsal **C** head and articles 1 and 2 of right antenna 1, dorsal **D** anterior part of body, lateral **E** posterior part of body, lateral **F** telson, dorsal. Scale bars: 5 mm.

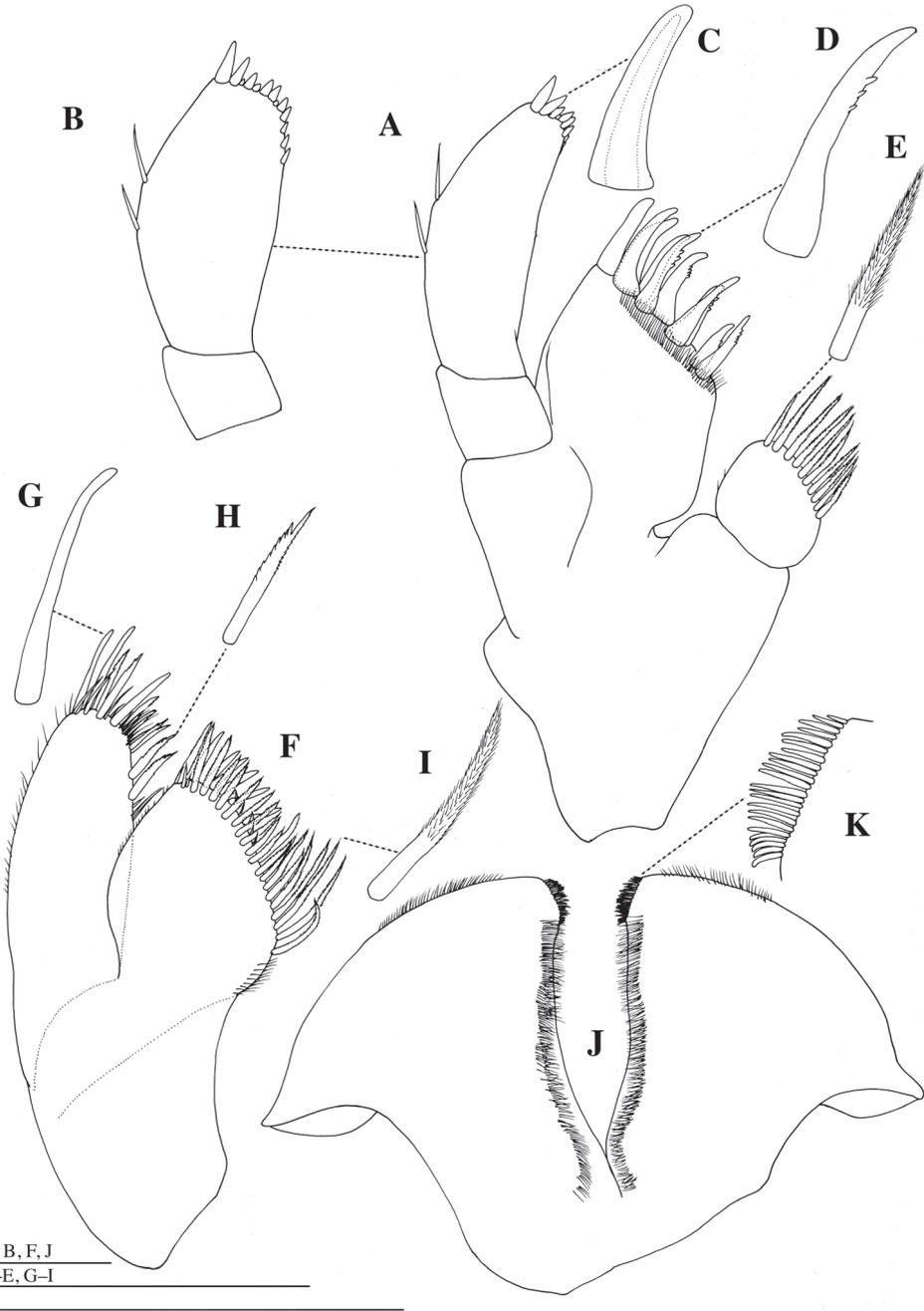


**Figure 2.** *Epimeria abyssalis* sp. n., holotype female: **A** left antenna 1, medial **B** basal part of left antenna 1, medial **C** left antenna 2, medial **D** basal part of left antenna 2, medial **E** basal part of left antenna 2, lateral **F** flagella of left antenna 2, medial **G** labium, dorsal **H** anterior part of labium, dorsal **I** left mandible, medial. Scale bars: 1 mm.

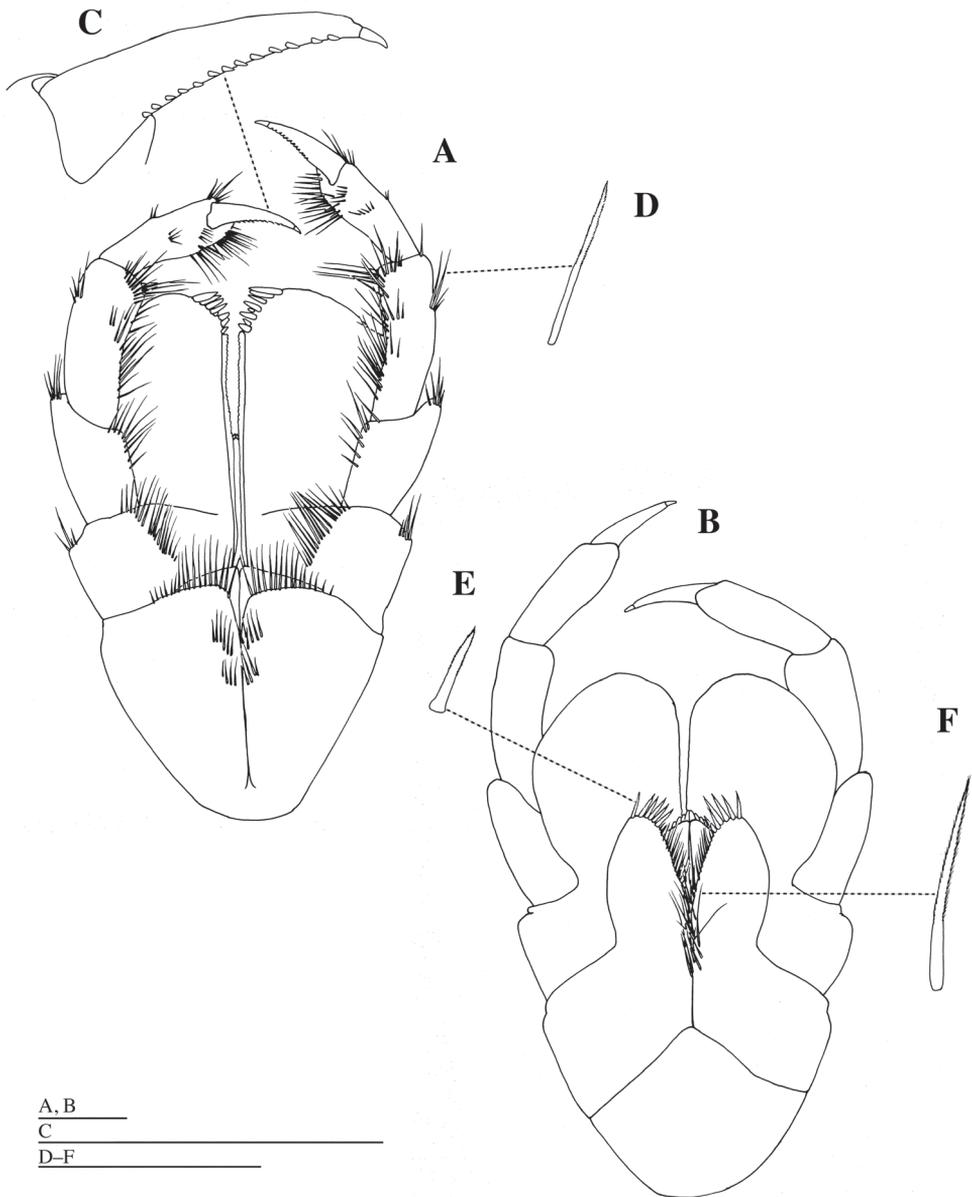


**Figure 3.** *Epimeria abyssalis* sp. n., holotype female: **A** molar process, incisor, lacinia mobilis and setal row of left mandible, dorsal **B** molar process of left mandible, dorsal **C** seta of setal row of left mandible, dorsal **D** right mandible, medial **E** molar process, incisor and setal row of right mandible, dorsal. Scale bars: 1 mm.

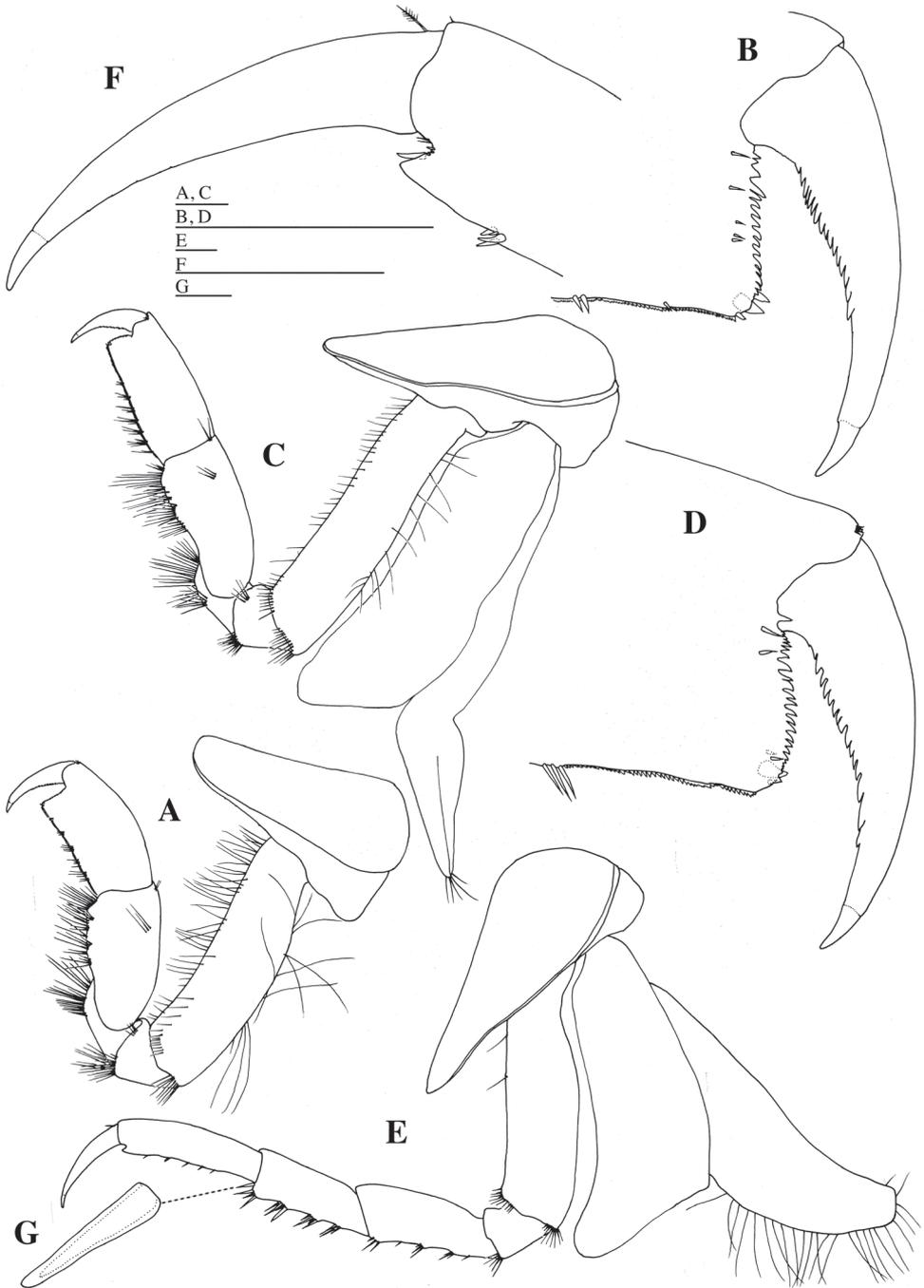
riorly, and with groups of setae anterodistally and posterodistally; ischium triangular, with many long setae distally; merus slightly longer than ischium, with many long setae distally; carpus 0.6 times as long as basis, with groups of long setae posteriorly; propodus stout, as long as carpus, crenulate posteriorly, with groups of short setae on posterior border, and with two robust and some slender setae distally; posterodistal angle squared; palmar margin transverse strongly serrate; dactylus slender, slightly curved, serrate posteriorly, with acute unguis apically.



**Figure 4.** *Epimeria abyssalis* sp. n., holotype female: **A** left maxilla 1, dorsal **B** articles 1 and 2 of palp of left maxilla 1, dorsal **C** seta on article 2 of palp of left maxilla 1, dorsal **D** seta on outer plate of left maxilla 1, dorsal **E** seta on inner plate of left maxilla 1, dorsal **F** left maxilla 2, dorsal **G** seta on outer plate of left maxilla 2, dorsal **H** seta on outer plate of left maxilla 2, dorsal **I** seta on inner plate of left maxilla 2, dorsal **J** lower lip, dorsal. Scale bars: 1 mm.



**Figure 5.** *Epimeria abyssalis* sp. n., holotype female: **A** left maxilliped, ventral **B** left maxilliped, dorsal (omitted setae excluding setae on inner plates), dorsal **C** article 4 of left maxillipedal palp, ventral **D** seta on article 2 of left maxillipedal palp, ventral **E** seta on inner plate of left maxilliped, dorsal **F** seta on inner plate of left maxilliped, dorsal. Scale bars: 1 mm.



**Figure 6.** *Epimeria abyssalis* sp. n., holotype female: **A** left pereopod 1, lateral **B** distal part of propodus and dactylus of left pereopod 1, lateral **C** left pereopod 2, medial **D** distal part of propodus and dactylus of left pereopod 2, lateral **E** left pereopod 3, medial **F** distal part of left pereopod 3, lateral **G** seta on carpus of left pereopod 3, lateral. Scale bars: 1 mm.

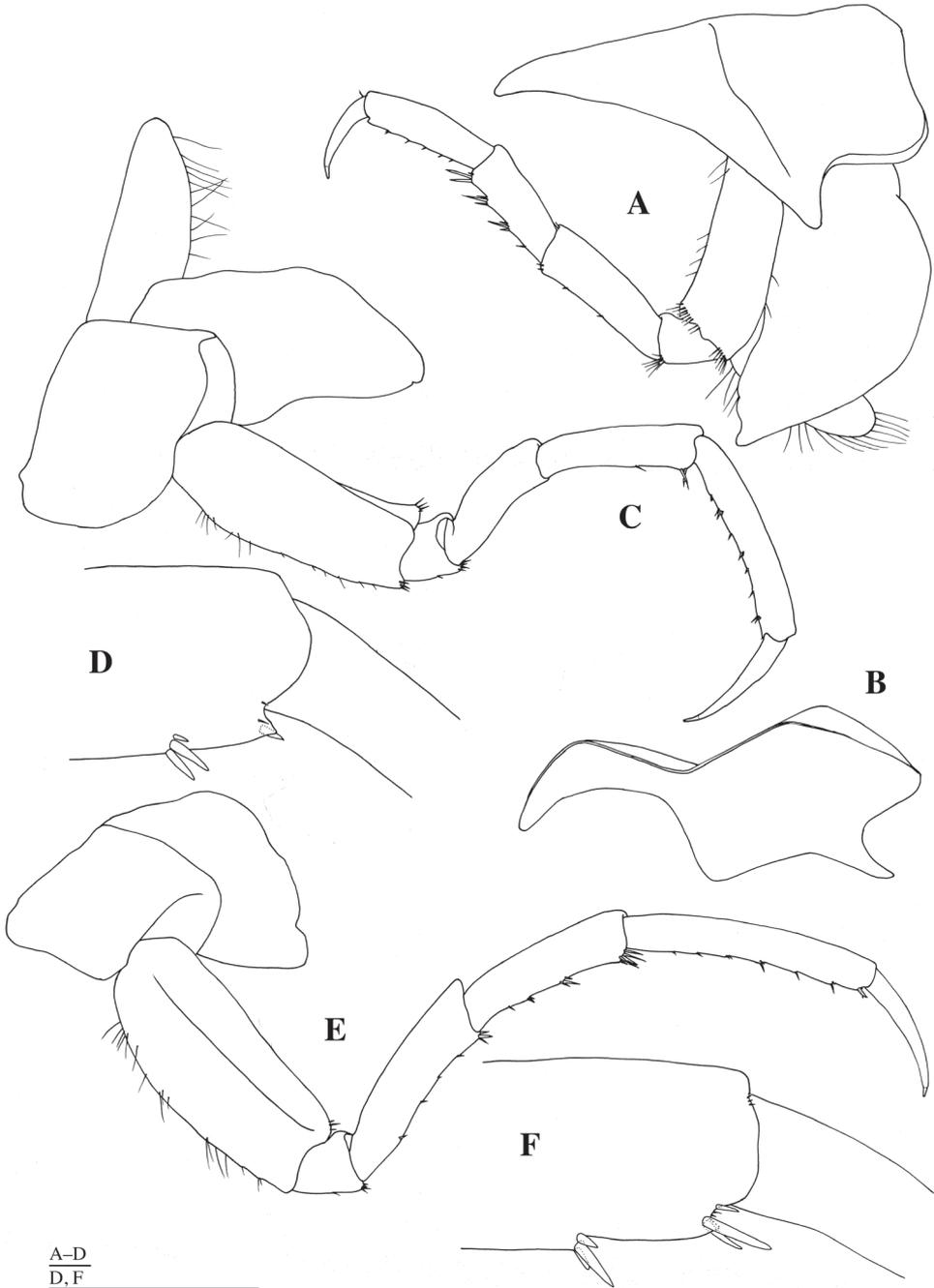
*Gnathopod 2* (Figs 1A, D, 6C, D): coxa as wide as coxa 1, with blunt apex; anterior margin of coxa slightly concave; basis longest, slender than basis of gnathopod 1, with numerous fine setae anteriorly and posteriorly, and with groups of setae anterodistally and posterodistally; ischium trapezoidal, with many long setae distally; merus slightly longer than ischium, with many long setae distally; carpus half as long as basis, with groups of long setae posteriorly; propodus stout, slightly narrower than propodus of gnathopod 1, 0.9 times as long as carpus, crenulate posteriorly, with groups of short setae posteriorly, and with 1 robust and some slender setae distally; posterodistal angle squared; palmar margin transverse, strongly serrate; dactylus slender, slightly curved, serrate posteriorly, with acute unguis apically.

*Pereopod 3* (Figs 1A, D, 6E, G): coxa as wide as coxa 2, with blunt apex; anterior margin of coxa slightly concave; basis 0.9 times as long as basis of gnathopod 2, sparsely setose anteriorly, and with groups of setae anterodistally and posterodistally; ischium trapezoidal, with some setae distally; merus 2.9 times as long as width, 2.8 times as long as ischium, with groups of setae posteriorly; carpus 0.9 times as long as merus, with groups of setae posteriorly; propodus 1.3 times as long as carpus, acutely projected posterodistally, with groups of short setae posteriorly; dactylus slender, slightly curved, 0.7 times as long as propodus, lacking serration, with acute unguis apically.

*Pereopod 4* (Figs 1A, D, 7A, B): coxa 1.9 times as wide as coxa 3, produced into posterodistal cusp directed posterodistally, laterally projected at mid part; anterior margin of coxa slightly concave; basis as long as basis of pereopod 3, sparsely setose anteriorly and posteriorly, and with groups of setae anterodistally and posterodistally; ischium trapezoidal, with some setae distally; merus 3.6 times as long as width, 2.8 times as long as ischium, sparsely setose posteriorly; carpus 0.7 times as long as merus, with groups of long setae posteriorly; propodus 1.2 times as long as carpus, acutely projected posterodistally, with groups of short setae posteriorly; dactylus slender, slightly curved, 0.7 times as long as propodus, lacking serration, with acute unguis apically.

*Pereopod 5* (Figs 1A, D, 7C, D): coxa as wide as coxa 4, subrectangular, without anterodistal and posterodistal projections; anterior margin of coxa broadly rounded; basis as long as basis of pereopod 4, 1.5 times as wide as basis of pereopod 4, setose anteriorly, and with groups of setae anterodistally and posterodistally; ischium trapezoidal, with some setae distally; merus 3.3 times as long as width, 2.9 times as long as ischium; carpus 1.3 times as long as merus, sparsely setose anteriorly; propodus 1.4 times as long as carpus, acutely projected posterodistally, with groups of short setae anteriorly; dactylus very long, slender, slightly curved, 0.6 times as long as propodus, lacking serration, with acute unguis apically.

*Pereopod 6* (Figs 1A, 7E, F): coxa 0.6 times as wide as coxa 5, subrectangular, ventrally concave, without anterodistal and posterodistal projections; anterior margin of coxa nearly straight; basis ventrally convex, nearly straight dorsally, with longitudinal keel laterally, as long as basis of pereopod 5, 1.4 times as wide as basis of pereopod 5, setose anteriorly, and with groups of setae posterodistally; ischium trapezoidal, with some setae distally; merus 3.8 times as long as width, 3.6 times as long as ischium, with groups of short setae anteriorly; carpus 0.8 times as long as merus, with groups of setae



**Figure 7.** *Epimeria abyssalis* sp. n., holotype female: **A** left pereopod 4, lateral **B** coxa of left pereopod 4, dorsal **C** left pereopod 5, lateral **D** distal part of propodus of left pereopod 5, lateral **E** left pereopod 6, lateral **F** distal part of propodus of left pereopod 6, lateral. Scale bars: 1 mm.

anteriorly and anterodistally; propodus 1.4 times as long as carpus, without projection posterodistally, with groups of short setae anteriorly; dactylus very long, slender, slightly curved, 0.5 times as long as propodus, lacking serration, with acute unguis apically.

*Pereopod 7* (Figs 1A, 8A, B): coxa 0.6 times as wide as coxa 5, subquadrate, ventrally convex, without anterodistal and posterodistal projections; anterior margin of coxa nearly straight; posteroventral corner of coxa very broadly rounded; basis broadest, convex ventrally and dorsally, 1.4 times as long as width, as long as basis of pereopod 6, 1.6 times as wide as basis of pereopod 6, setose anteriorly, and with groups of setae posterodistally; ischium trapezoidal, with some setae distally; merus 3.4 times as long as width, 2.8 times as long as ischium, with groups of short setae anteriorly; carpus as long as merus, with groups of setae anteriorly and anterodistally; propodus 1.3 times as long as carpus, without projection posterodistally, with groups of short setae anteriorly; dactylus very long, slender, slightly curved, half as long as propodus, lacking serration, with acute unguis apically.

*Coxal gills* on gnathopod 2 and pereopods 3–7 (Figs 6C, E, 7A, B, D, 8A). *Oostegites* (= brood plates) (Figs 6C, E, 7A, B) with numerous marginal setae; oostegites of gnathopod 2 and pereopod 3 longer than bases and coxal gills; oostegites of pereopod 4 longer than basis and shorter than coxal gill; oostegite of pereopod 5 as long as basis and shorter than gill.

*Pleopods 1–3* (Fig. 8C–H) similar in shape, decreasing in length posteriorly: peduncle broad, subrectangular, with many setae laterally, three plumose setae mediodistally and two coupling hooks (= retinacula); inner ramus as long as outer ramus; rami articulated with many plumose setae medially and laterally.

*Uropod 1* (Fig. 9A): peduncle subequal in length to inner ramus, with five short robust setae medially and five short robust setae laterally; inner ramus slightly curved medially, acutely pointed, with many short robust setae on margin; outer ramus as long as inner ramus, acutely pointed, with many short robust setae on margin.

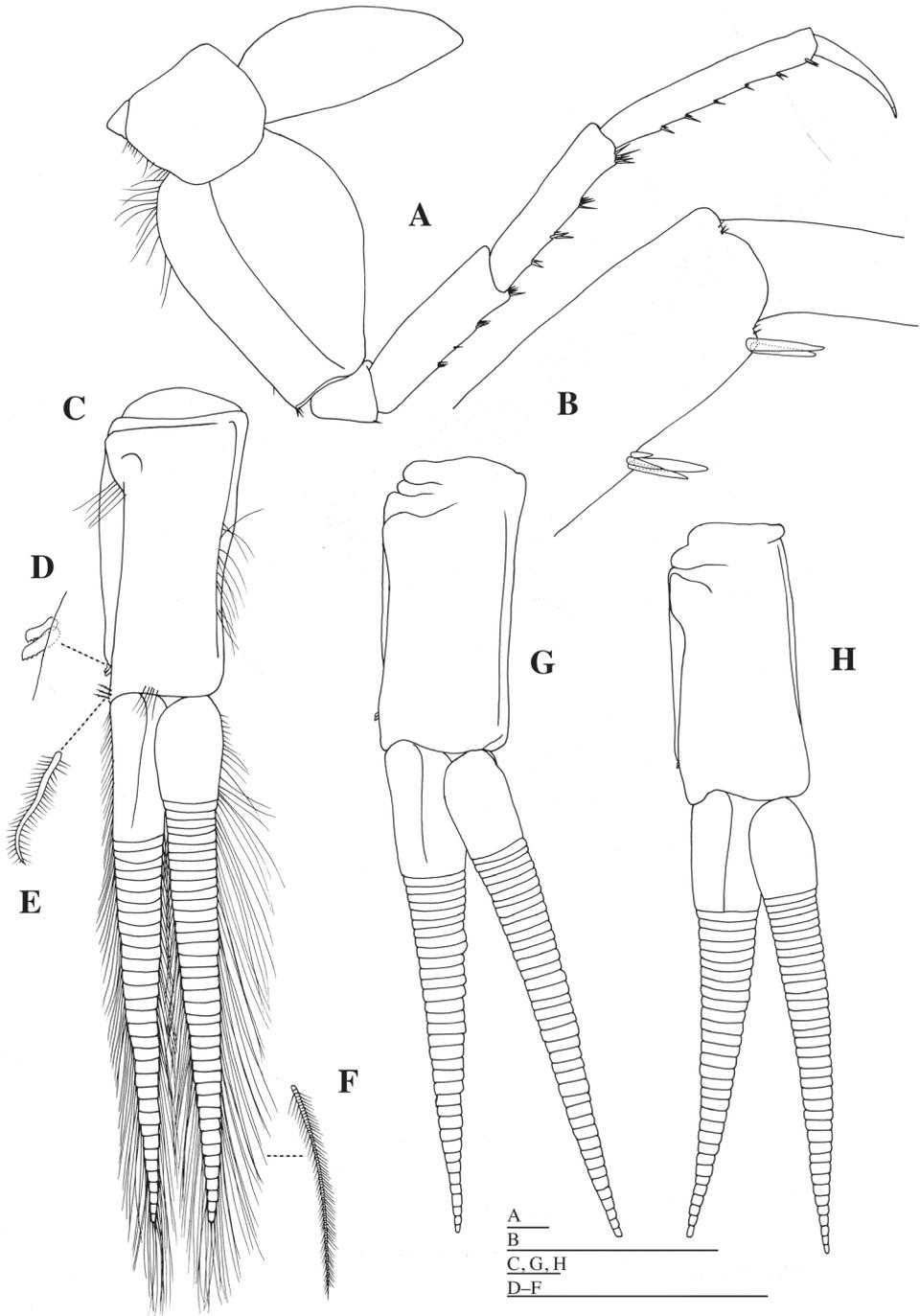
*Uropod 2* (Fig. 9B) 0.8 times as long as uropod 1; peduncle subequal in length to inner ramus, increasing in width distally, with two short robust setae laterally; inner ramus acutely pointed, with many short robust setae on margin; outer ramus 1.4 times as long as inner ramus, acutely pointed, with many short robust setae on margin.

*Uropod 3* (Fig. 9C) 0.9 times as long as uropod 2; peduncle 0.4 times as long as inner ramus, increasing in width distally, with five short robust setae laterally; inner ramus broadest, moderately blunt apically, with sparse robust setae laterally; outer ramus as long as inner ramus, moderately blunt apically, with sparse robust setae laterally.

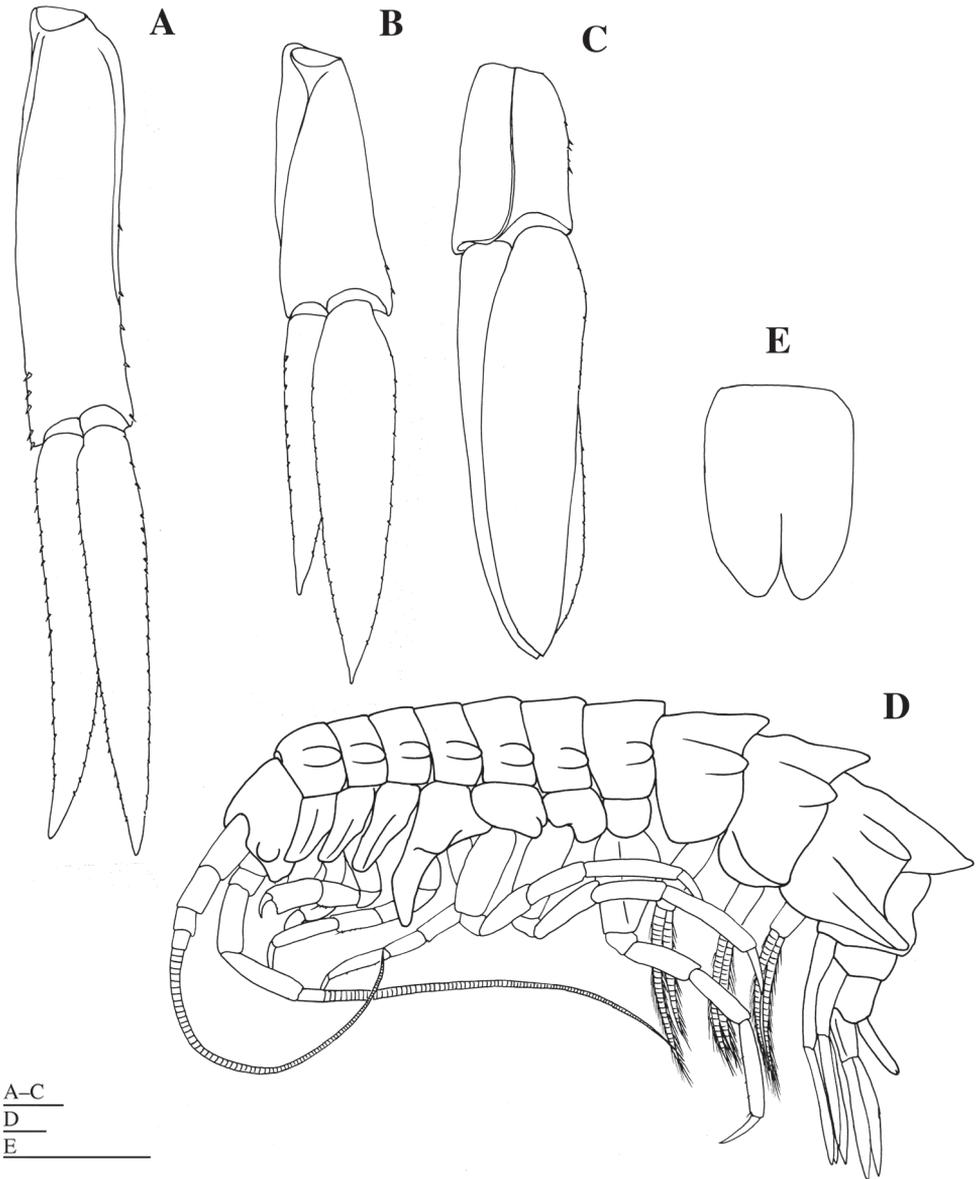
*Telson* (Fig. 1F) 1.5 times as long as wide, with deep and narrow Y-shaped excavation, without setae; distal cleft to 0.4 of total length of telson.

**Description of the paratype female (KMNH IvR 500907).** Similar to holotype in morphology of all appendages (Figs 9D, E, 10A–C). Pleonites 1–3 (Fig. 9D) with dorsal carinae and posterolateral processes; dorsal carinae of pleonites 1 and 2 reaching apex of posterolateral processes. Epimeral plate 3 (Fig. 9D) with pointed posteroventral angle, reaching apex of dorsal carina of pleonite 3.

*Telson* (Fig. 9E) 1.4 times as long as wide, with deep and narrow Y-shaped excavation, without setae.



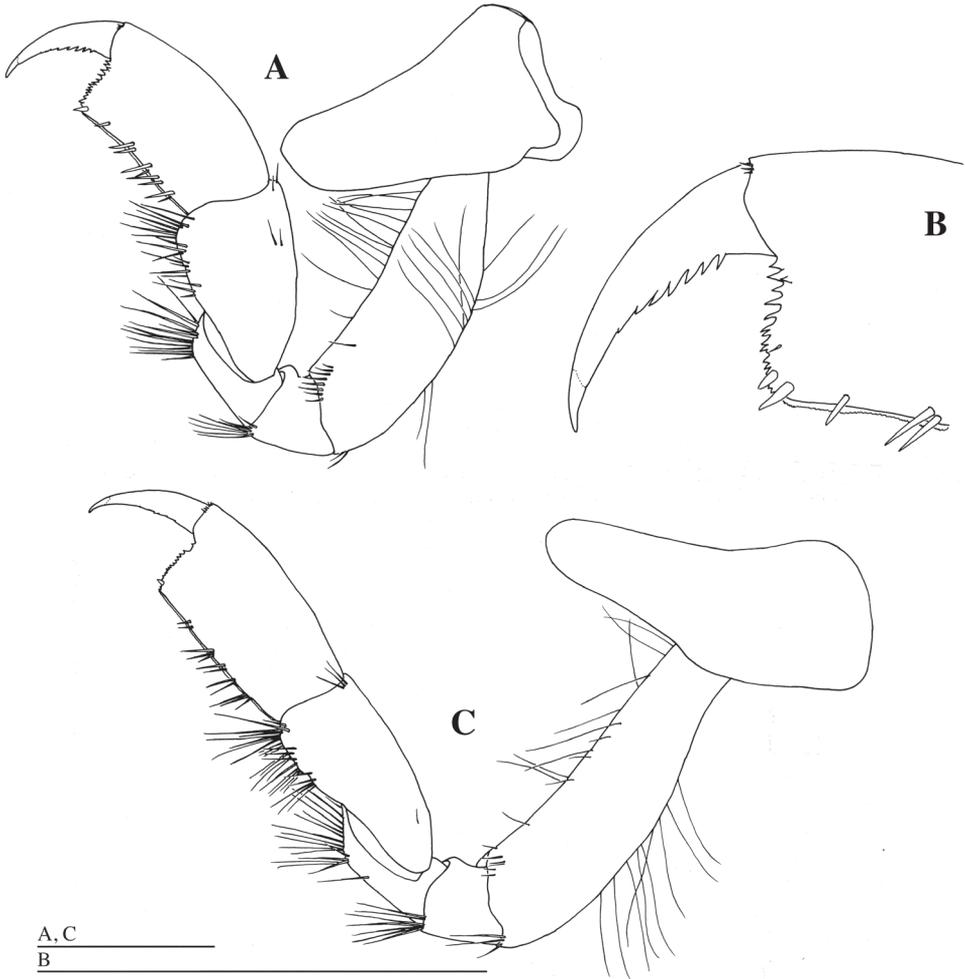
**Figure 8.** *Epimeria abyssalis* sp. n., holotype female: **A** left pereopod 7, lateral **B** distal part of propodus of left pereopod 7, lateral **C** left pleopod 1, dorsal **D** coupling hooks on peduncle of left pleopod 1, dorsal **E** seta on peduncle of left pleopod 1, dorsal **F** seta on outer ramus of left pleopod 1, dorsal. Scale bars: 1 mm.



**Figure 9.** *Epimeria abyssalis* sp. n., **A–C** holotype female, **D, E** paratype female (KMNH IvR 500907): **A** left uropod 1, dorsal **B** left uropod 2, dorsal **C** left uropod 3, dorsal **D** habitus, lateral **E** telson, dorsal. Scale bars: 1 mm.

**Coloration.** Body (Fig. 11) and appendages excluding maxilliped cream-colored; distal part of maxilliped brownish red.

**Remarks.** *Epimeria abyssalis* sp. n. can be identified and separated from other species of the genus by the following combination of characters: rostrum short, 0.2 times



**Figure 10.** *Epimeria abyssalis* sp. n., paratype female (KMNH IvR 500907): **A** left pereopod 1, lateral **B** distal part of propodus and dactylus of left pereopod 1, lateral **C** left pereopod 2, lateral. Scale bars: 1 mm.

as long as head; eyes absent; pereonites 1–7 without dorsal carinae; palmar margins of propodi of gnathopods 1–2 transverse, strongly serrate; coxae 1–3 each with blunt apex; coxa 4 produced into posterodistal cusp directed posterodistally, laterally projected at mid part; anterior margin of coxa 4 slightly concave; coxa 5 as wide as coxa 4, subrectangular, without anterodistal and posterodistal projections; anterior margin of coxa 5 broadly rounded; basis of pereopod 7 broadest, as long as basis of pereopod 6, 1.6 times as wide as basis of pereopod 6; and telson 1.5 times as long as wide, with deep and narrow Y-shaped excavation, without setae.

*Epimeria abyssalis* sp. n. is close to *E. pelagica* and *E. yaquinae*, with which it shares a short rostrum, pereon without dorsal carinae, and coxa 5 lacking posterodistal projection



**Figure 11.** *Epimeria abyssalis* sp. n., paratype female (KMNH IvR 500906) photographed on board shortly after sampling. Scale bar: 10 mm.

are shared by *E. pelagica* and *E. yaquinae*. *Epimeria abyssalis* is distinguished from *E. pelagica* by the following features (those of *E. pelagica* in parentheses): eyes absent (present); article 1 of antenna 1 twice as long as wide (as long as wide); posterodistal angle of propodi of gnathopods 1 and 2 nearly right angle squared, (obtuse angle); coxa 3 blunt distally (pointed distally); coxa 4 moderately broad at basal part (narrow); propodi of pereopods 5 and 6 moderately short, 1.4 times as long as carpi (long, 1.7–1.9 times as long as carpi); basis of pereopod 7 broad, posterior margin convex (narrow, posterior margin slightly concave); inner ramus of uropod 1 broad, as long as outer ramus (narrow, shorter than outer ramus); and telson with deep and narrow Y-shaped excavation, without setae (deep and broad V-shaped excavation, with two pairs of setae distally). *Epimeria abyssalis* differs from *E. yaquinae* in the following features (those of *E. yaquinae* in parentheses): palmar margins of propodi of gnathopods 1 and 2 without projections (with pointed projections); labrum with shallow notch distally (without notch); uropod 3 slightly shorter than uropod 2 (longer than uropod 2); rami of uropod 2 broad (narrow); and telson with deep and narrow Y-shaped excavation (deep and broad V-shaped excavation).

*Epimeria abyssalis* is the deepest recorded *Epimeria* species. *Epimeria* was previously known down to 3710 m (*Epimeria glaucosa* J.L. Barnard, 1961).

**Etymology.** Species name was derived from *abyssus* (L.) referring to its deep-water habitat.

### Key to the north Pacific species of *Epimeria*

- 1        Rostrum short, not reaching half the length of article 1 of antenna 1; coxa 5 lacking posterodistal projection.....2
- Rostrum long, reaching half the length of article 1 of antenna 1; coxa 5 with posterodistal projection.....4

2	Telson with deep and broad V-shaped excavation.....	3
–	Telson with deep and narrow Y-shaped excavation.....	<i>E. abyssalis</i> sp. n.
3	Eyes absent; palmar margins of gnathopods 1 and 2 with posterior projection; coxa 4 rounded distally.....	<i>E. yaquinae</i>
–	Eyes present; palmar margins of gnathopods 1 and 2 without posterior projections; coxa 4 pointed distally.....	<i>E. pelagica</i>
4	Eyes present.....	5
–	Eyes absent.....	<i>E. subcarinata</i>
5	Coxa 5 projection nearly reaching epimeral plate 1.....	6
–	Coxa 5 projection not reaching epimeral plate 1.....	<i>E. cora</i>
6	Head ventral lobe not produced,.....	7
–	Head ventral lobe produced.....	<i>E. pacifica</i>
7	Telson 1.2 times as long as wide; uropodal peduncle longer than rami.....	<i>E. morronei</i>
–	Telson as long as wide; uropodal peduncle shorter than rami.....	<i>E. ortizi</i>

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We are grateful to Prof. Emeritus S. Ohta (University of Tokyo, Tokyo), director of the cruise and who facilitated the collection of the amphipod specimens. We would like to thank to the crew of the R/V “Hakuho-Maru” of the Ocean Research Institute, University of Tokyo, for their cooperation at sea. Also, many thanks are given to Dr. C. O. Coleman (Museum für Naturkunde), Dr. C. d’Udekem d’Acoz (Royal Belgian Institute of Natural Sciences), and an anonymous reviewer, for their valuable comments and suggestions on the manuscript. This research was supported in part by KAKENHI.

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# Corrigenda: Two new species of *Brachytrycherus* Arrow, 1920 from China (Coleoptera, Endomychidae). ZooKeys 595: 137–146. doi: 10.3897/zookeys.595.7569

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When describing the new species *Brachytrycherus conaensis* sp. n., the information of two female paratypes is incorrect and should be deleted. When describing another the new species, *Brachytrycherus curviantennae* sp. n., the information of one female paratype is incomplete and should be added “1700 m” altitude; the information of another female paratype should be reduced to “ditto except (CBWX)”, and in all the information of paratype, the word “Medgo” is a spelling error, and the correct spelling is “Medog”.

The correct information *Brachytrycherus conaensis* sp. n. and in *Brachytrycherus curviantennae* sp. n. should be as follows:

Paratypes, 1 female, same data as holotype. 3 males, 7 females, Xizang, Cuona, Lexiang, 2500 m, 6.VIII.2010, Wen-Xuan Bi leg. (CBWX); 5 males, 6 females, ditto except 15.VII.2011 (CBWX); 26 males, 11 females, ditto except 29–30.VI.2013 (CBWX); 1 male, 1 female, ditto except (MZPW); 18 males, 1 female, ditto except 2500–2600 m, 20–30.VI.2013 (CBWX); 1 female, ditto except 2700 m, 18.VI.2013 (CBWX).

Paratypes, 1 female, Xizang, Medog, Beibeng, Gelincun, 1700 m, 3.VIII.2014, Wen-Xuan Bi leg. (MHBU); 1 female, ditto except (CBWX).

