

# *Philibaetis* gen. nov., a new genus from the Philippines (Ephemeroptera, Baetidae)

Thomas Kaltenbach<sup>1,2</sup>, Jhoana M. Garces<sup>3</sup>, Jean-Luc Gattolliat<sup>1,2</sup>

<sup>1</sup> Museum of Zoology, Palais de Rumine, Place Riponne 6, CH-1005 Lausanne, Switzerland

<sup>2</sup> University of Lausanne (UNIL), Department of Ecology and Evolution, CH-1015 Lausanne, Switzerland

<sup>3</sup> Department of Biology, School of Science and Engineering, Ateneo de Manila University, Quezon City, 1108 Metro Manila, Philippines

<http://zoobank.org/458E5069-2CA2-436A-ABF5-BEFE6EBAC3F0>

Corresponding author: Thomas Kaltenbach (thomas.kaltenbach@bluewin.ch)

Academic editor: D. Zimmermann ♦ Received 8 October 2020 ♦ Accepted 4 November 2020 ♦ Published 5 January 2021

## Abstract

Investigations of type material and new material from the Philippines (Luzon) revealed that *Baetis luzonensis* Müller-Liebenau, 1982 and *B. realonae* Müller-Liebenau, 1982 do not belong to *Baetis* Leach, 1815. A new genus, *Philibaetis* gen. nov., is described to accommodate both species and both are re-described based on larvae. The new genus is characterised by having a rectangular labrum with a submarginal row of long, simple setae on the dorsal surface and ventrally on lateral margins long, simple, spine-like setae, on anterolateral margins long, feathered setae and medially long, bifid setae and a partial, submarginal row of lanceolate setae. Both mandibles have blade-like incisors and dorsally, a mediolateral patch of long, spine-like setae; additionally, the left mandible has a tuft of long, partly branched setae at the base of the subtriangular process. *Philibaetis* gen. nov. is further characterised by a hypopharynx with a medial tuft of stout setae and anterolaterally, two smaller tufts of stout setae, a galea-lacinia with the distal denti-seta tooth-like and directed against canines, a fore femur apically with stout setae, both on anterior and posterior side and without a femoral patch and a claw with one row of denticles and two or three subapical setae. The protogonostyli under the cuticle of male last instar larvae are folded in the *Labiobaetis* type, excluding their affiliation to the genus *Baetis*. COI sequences were obtained from both species. The genetic distance (Kimura 2-parameter) between them is 17.5% on average. Very limited genetic distances of 0% to 3% (0.75% on average) were found between specimens of *P. luzonensis* comb. nov.

## Key Words

COI, Labiobaetini, mayflies, morphology, subapical setae

## Introduction

The family Baetidae has the highest species diversity amongst mayflies, comprising ca. 1,100 species in 114 genera (Sartori and Brittain 2015, Jacobus et al. 2019, Cruz et al. 2020, Kluge 2020), which is close to one third of all mayfly species worldwide. They have a cosmopolitan distribution, except in Antarctica and New Zealand. Investigations of the molecular phylogeny of the order Ephemeroptera revealed the relatively-primitive status of the family (Ogden and Whiting 2005, Ogden et al. 2009, Ogden et al. 2019). The generic diversity of Baetidae is the highest in the Afrotropical realm (ca. 40 genera), followed by the

Neotropical (ca. 27 genera) and Oriental (ca. 28 genera) realms and finally the Nearctic (20 genera), Palaearctic (17 genera) and the Australasian (ca. 12 genera) realms (updated from Gattolliat and Nieto 2009). The number for the Oriental realm still seems to be rather low, taking into account that several regions with potentially high diversities (e.g. the Indian subcontinent, Indonesia incl. Borneo and the Philippines) belong to this realm. The last new genera of Baetidae from the Oriental region were described in 2020 from Indonesia and the Philippines (Kaltenbach et al. 2020a) and from Thailand (Suttinun et al. 2020).

The Philippines are a complex archipelago with more than 7500 islands, spanning the Asian-Australian faunal

zone interface directly at the Wallace Line. Its extraordinary biodiversity was presumably supported by the complex biogeographic history and isolation of the archipelago, including landmass movements, collisions between landmasses of different origin in Miocene and temporary Pleistocene land bridges which were possible colonisation pathways of species, but also by environmental gradients along steep volcanic slopes (Brown and Diesmos 2010, Freitag et al. 2016). Recent data suggest that even biogeographic regions, previously categorised as one single unit (e.g. Greater Luzon), are composed of distinct centres of endemism that correlate with tectonic features (Vallejo 2014), further explaining high endemism and niche specialisation of species found in the country.

Here we describe a new genus from the Philippines, based on the type material of *Baetis luzonensis* Müller-Liebenau, 1982 and *B. realonae* Müller-Liebenau, 1982, as well as larvae collected in 1997 and 2019 in four different locations in the Philippines (Luzon). Further collections of Ephemeroptera and especially of Baetidae in the Philippines and other parts of Southeast Asia will unveil more unknown genera and many more species in the future.

## Materials and methods

The new material was collected in 1997 and 2019 in four different locations in the Philippines (Luzon). Many more locations were sampled in this period without further findings of one of the two species (Kaltenbach et al. 2020b: figs 48, 49). The specimens were preserved in 70%–96% ethanol. The dissection of larvae was done in Cellosolve (2-ethoxyethanol) with subsequent mounting on slides with Euparal liquid, using an Olympus SZX7 stereomicroscope.

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

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

Drawings were made using an Olympus BX43 microscope. Photographs of larvae were taken using a Canon EOS 6D camera and the Visionary Digital Passport imaging system (<http://www.duninc.com>) and processed with Adobe Photoshop Lightroom (<http://www.adobe.com>) and Helicon Focus version 5.3 (<http://www.heliconsoft.com>). SEM pictures were taken using a FEI Quanta FEC

**Table 1.** Sequenced specimens.

Species	Locality	Specimens catalogue #	GenBank # (COI)	GenSeq Nomenclature
<i>P. luzonensis</i> comb. nov.	Philippines:	GBIFCH 00763644	MT873541	genseq-4
	Luzon	GBIFCH 00763652	MT873543	genseq-3
		GBIFCH 00763656	MT873545	genseq-3
		GBIFCH 00763653	MT873544	genseq-4
<i>P. realonae</i> comb. nov.	Philippines:	GBIFCH 00763650	MT873542	genseq-4
	Luzon			

250 electron microscope (Thermo Fisher). Photographs were subsequently enhanced with Adobe Photoshop Elements 13.

The distribution maps were generated with SimpleMappr (<https://simplemappr.net>, Shorthouse 2010), GEO-Locate (<http://www.museum.tulane.edu/geolocate/web/WebGeoref.aspx>) and Google Earth (<http://www.google.com/earth/download/ge/>) were used to attribute approximate GPS coordinates to sample locations of Müller-Liebenau (1982a).

The terminology follows Hubbard (1995) and Kluge (2004).

Abbreviations:

**AdMU** Ateneo de Manila University, Quezon City (Philippines)

**MZL** Museum of Zoology Lausanne (Switzerland)

**ZSM** Zoologische Staatssammlung München (Germany)

## Results

### *Philibaetis* Kaltenbach & Gattolliat, gen. nov.

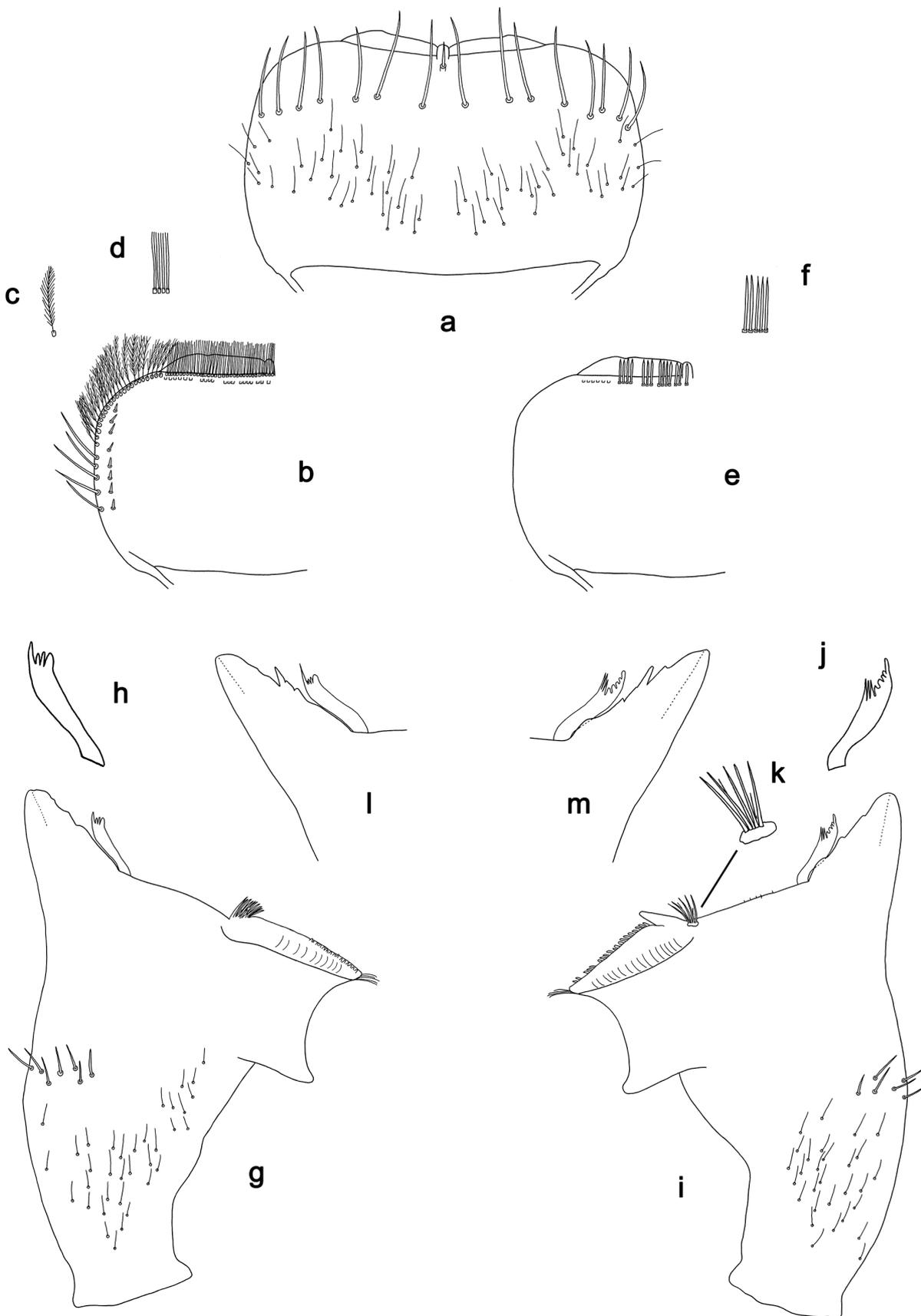
<http://zoobank.org/5C936E67-64CD-43BC-AC21-35709769C2ED>

Figures 1–11

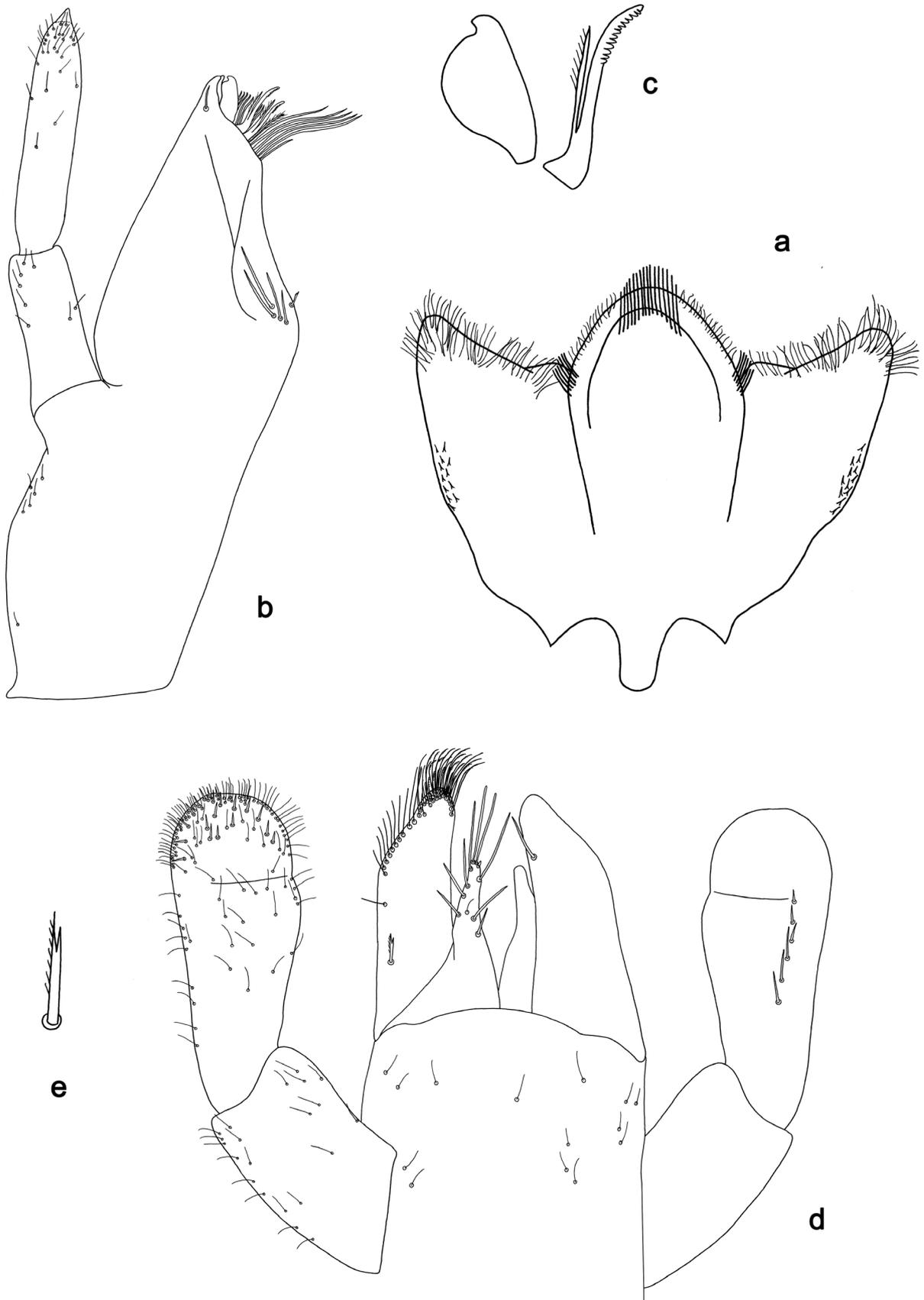
**Type species.** *Philibaetis luzonensis* (Müller-Liebenau, 1982) comb. nov., by present designation.

**Species included.** *Philibaetis realonae* (Müller-Liebenau, 1982) comb. nov.

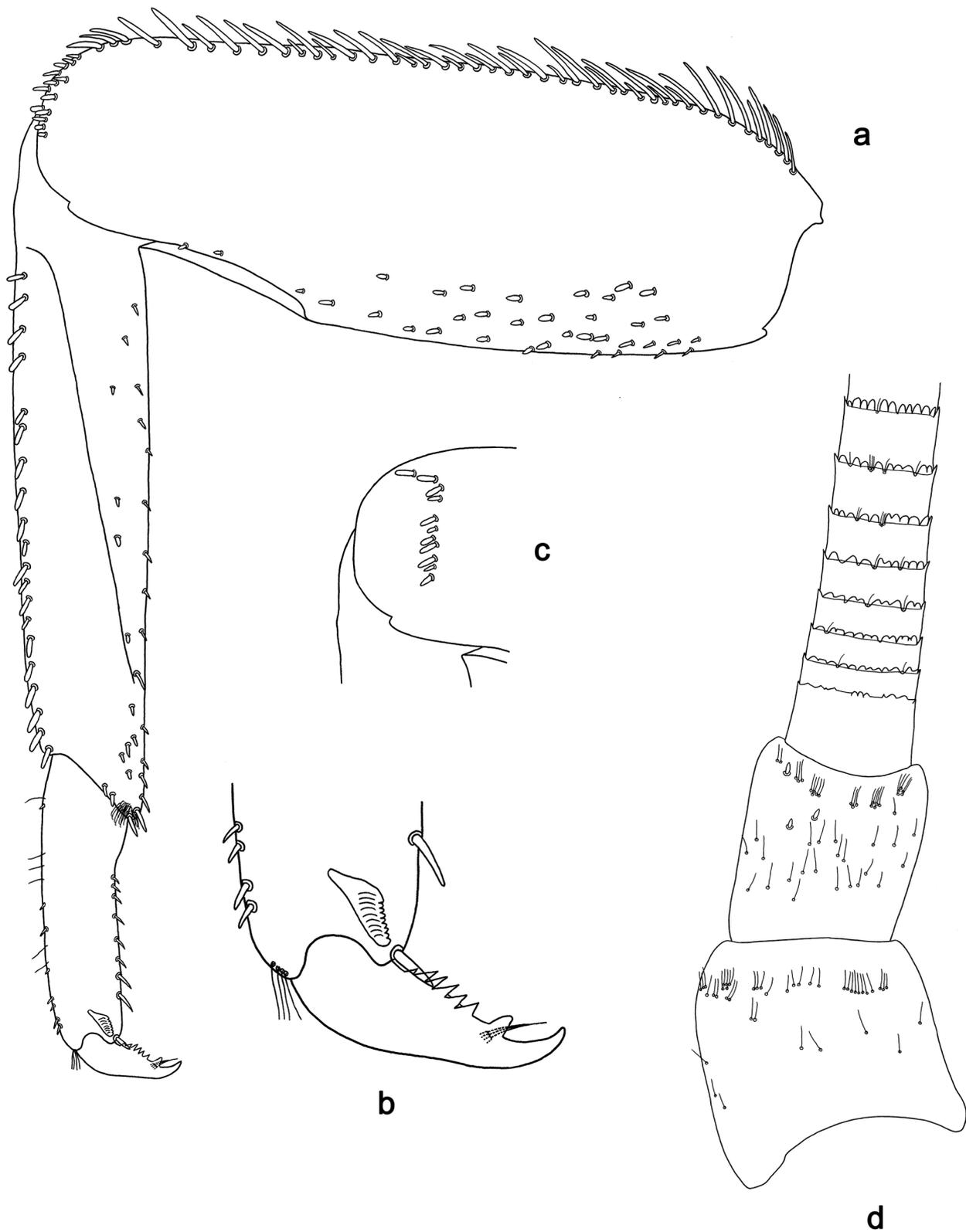
**Diagnosis. Larva.** This new genus is distinguished by a combination of the following characters: A) body elongate and slender, head clearly hypognathous (Fig. 5); B) bases of antennae not close to each other, without carina between them (Figs 5c, 8c); C) labrum rectangular, on dorsal surface with submarginal row of long, simple setae (Fig. 1a); ventrally on lateral margins long, simple, spine-like setae, on anterolateral margins long, feathered setae and medially long, bifid setae and a partial, submarginal row of lanceolate setae (Figs 1b–f, 6a, b); D) right mandible with blade-like incisor, stick-like, apically denticulate prosthema and dorsally mediolateral patch of long, spine-like setae (Fig. 1g, h, l); E) left mandible with blade-like incisor, slender prosthema apically denticulate and with comb-shaped structure; tuft of long, partly-branched setae at base of subtriangular process; dorsally mediolateral patch of long, spine-like setae



**Figure 1.** *Philibaetis luzonensis* comb. nov., larva morphology: **a.** Labrum, dorsal view; **b.** Labrum, ventral view; **c.** Seta on anterolateral margin; **d.** Medial setae; **e.** Labrum, ventral view, submarginal row of setae; **f.** Setae of submarginal row; **g.** Right mandible; **h.** Right prostheda; **i.** Left mandible; **j.** Left prostheda; **k.** Tuft of setae; **l.** Right incisor, kinetodontium and prostheda; **m.** Left incisor, kinetodontium and prostheda.



**Figure 2.** *Philibaetis luzonensis* comb. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Distal and middle denti-setae; **d.** Labium (left side: ventral view; right side: dorsal view); **e.** Posterolateral seta on ventral side of paraglossa.



**Figure 3.** *Philibaetis luzonensis* comb. nov., larva morphology: **a.** Foreleg; **b.** Claw; **c.** Apex of femur (posterior view); **d.** Basal part of antenna.

(Fig. 1i–k, m); F) hypopharynx with a medial tuft of stout setae and anterolaterally two smaller tufts of stout setae (Fig. 2a); G) galea-lacinia with three denti-setae, distal denti-seta tooth-like and directed against canines, middle and proximal denti-setae slender, bifid and pectinate; maxillary palp 2-segmented, apex of segment II constricted (Fig. 2b); H) glossae basally broad, narrowing towards apex, shorter than paraglossae, apically and on both margins with long, spine-like setae; paraglossae truncate in distal part, one stout, bifurcate seta in posterolateral area; labial palps segment II without protuberance (Fig. 2d, e); I) fore femur apically with stout setae both on anterior and posterior side, femoral patch absent; claw robust and pointed, with one row of denticles and 2–3 long subapical setae on posterior side and one short, fine, subapical seta on anterior side (Figs 3a–c, 11); J) paraproct with patch of notched scales (Fig. 4e, f); K) protogonostyli under larval cuticle folded in the *Labiobaetis* type (Fig. 10).

**Imagines.** Unknown.

**Etymology.** *Philibaetis* is an arbitrary combination of letters with allusion to the Philippines, where the genus occurs and to the genus *Baetis*. The latter is with reference to the superficial similarities between both genera and the fact that the species of *Philibaetis* gen. nov. were up to now assigned to *Baetis*. Gender is masculine.

**Description. Larva.** (Figs 1–11).

**Body.** Elongate and slender, head hypognathous (Fig. 5).

**Head.** *Antenna* (Figs 3d, 5c, 8c). More than 2× longer than head length, bases of antennae not close to each other, without carina between them (Figs 5c, 8c).

**Labrum** (Figs 1a–f, 6a, b). Rectangular, wider than long; on dorsal surface with submarginal row of long, simple setae; ventrally on lateral margin long, simple, spine-like setae, on anterolateral margin long, feathered setae and medially long, bifid setae and a partial, submarginal row of lanceolate setae.

**Right mandible** (Fig. 1g, h, l). Incisor and kinetodontium fused, incisor blade-like, kinetodontium with denticles; inner margin of innermost denticle of kinetodontium without row of thin setae; prosthema stick-like, apically denticulate; dorsally with mediolateral patch of long, spine-like setae.

**Left mandible** (Fig. 1i–k, m). Incisor and kinetodontium fused, incisor blade-like, kinetodontium with denticles; prosthema apically denticulate and with comb-shaped structure; with tuft of long, partly-branched setae at base of subtriangular process; dorsally with mediolateral patch of long, spine-like setae.

**Hypopharynx** (Fig. 2a). With medial tuft of stout setae and anterolaterally two smaller tufts of stout setae.

**Maxilla** (Fig. 2b, c). Apically with three stout canines and three denti-setae; distal denti-seta tooth-like, with opposite direction to canines, other denti-setae slender, bifid and pectinate; maxillary palp with two segments.

**Labium** (Fig. 2d, e). Glossae basally broad, narrowing towards apex, shorter than paraglossae; apically and on both margins with long, spine-like setae; paraglossae truncate in distal part, on apex with three rows of long,

robust, distally-pectinate setae and one stout, bifurcate seta in posterolateral area; labial palps segment II without protuberance, dorsally with row of spine-like setae near outer lateral margin.

**Thorax.** *Hind protoptera* (Fig. 4g). Absent.

**Foreleg** (Fig. 3a–c). **Femur** with dense row of curved, spine-like setae on dorsal margin, on apex short, stout setae on anterior and posterior side; femoral patch absent; **tibia** with patellotibial suture, dorsal margin with row of medium, clavate setae; **claw** robust and pointed, with one row of denticles, 2–3 long subapical setae on posterior side and one short, thin subapical seta on anterior side.

**Abdomen.** *Gills* (Figs 4a–d). Seven pairs of gills on segments I–VII, dorsally orientated. Margin with minute denticles intercalating fine, simple setae.

**Paraproct** (Figs 4e, f). Without prolongation at posterior margin, with stout, marginal spines; surface with patch of notched scales.

**Caudal filaments** (Fig. 5a, d). Inner margin of cerci with long, thin setae; paracercus bilaterally with long, thin setae.

**Imago.** Unknown.

**Distribution** (Fig. 12). Philippines: Luzon.

## Redescription

### *Philibaetis luzonensis* (Müller-Liebenau, 1982) comb. nov.

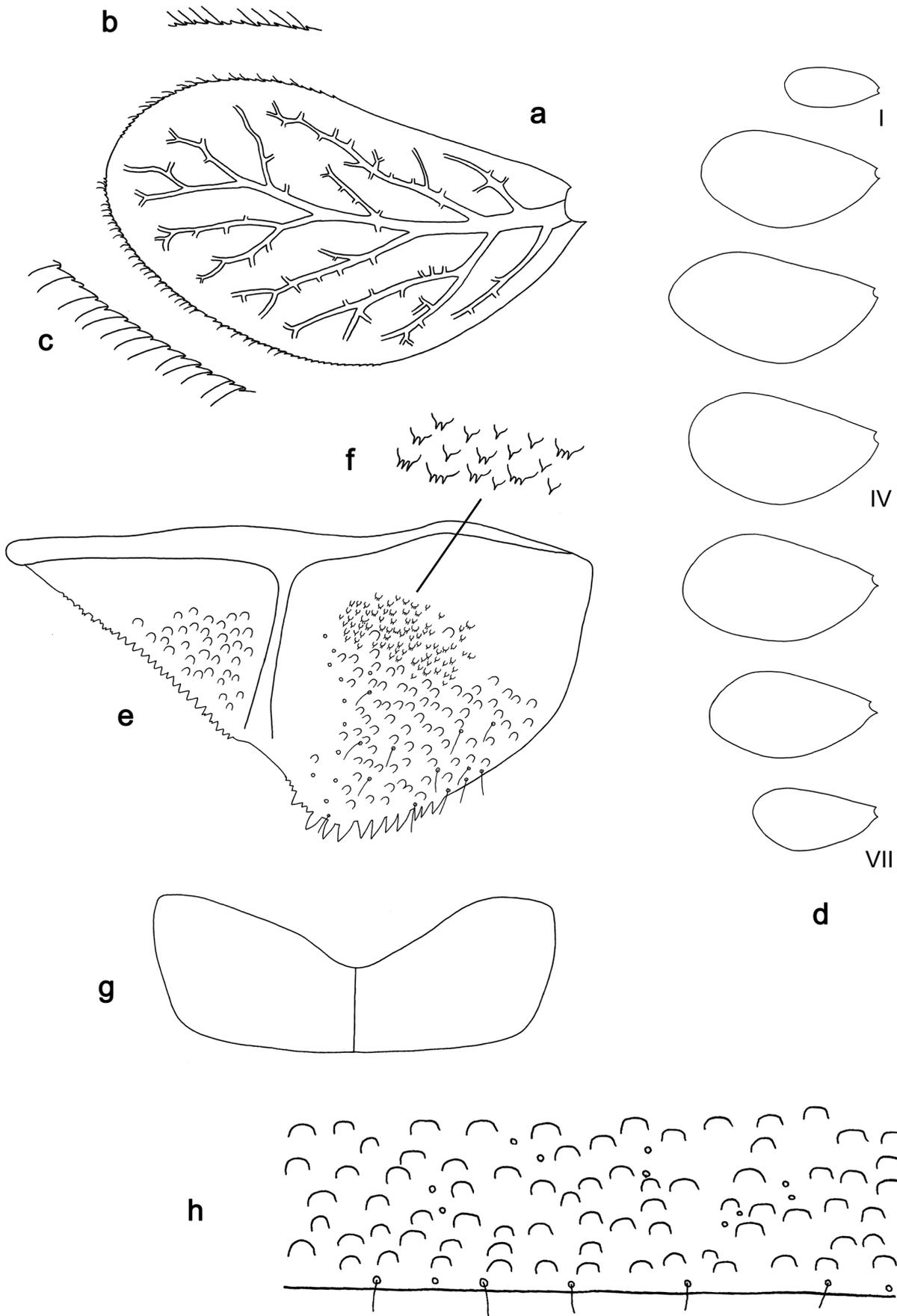
(Müller-Liebenau 1982a)

Figures 1–5, 10a, 11a–c, 12

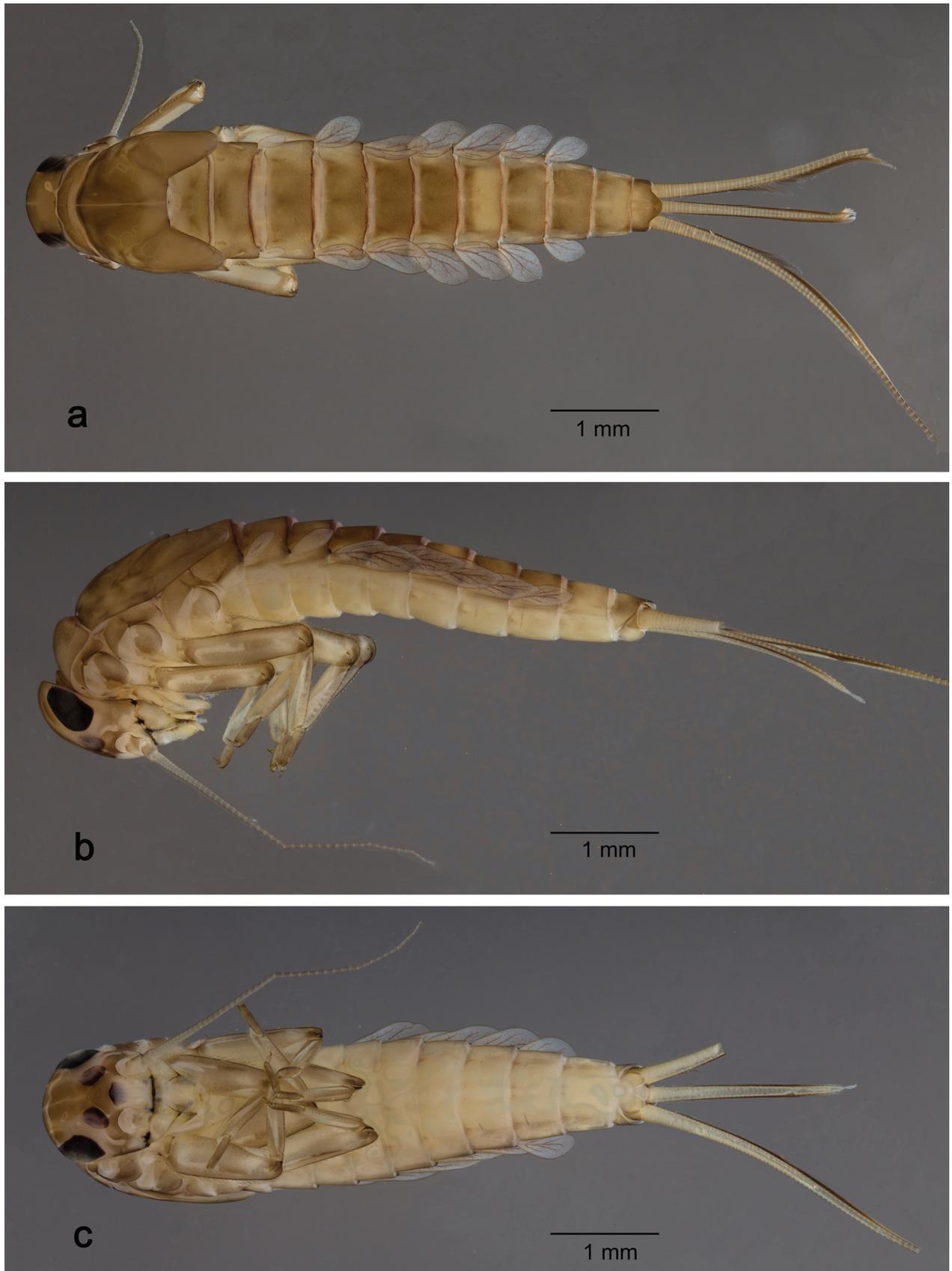
**Differential diagnosis. Larva.** The following characters distinguish *P. luzonensis* comb. nov. from *P. realonae* comb. nov.: A) abdominal tergite IV without spines at posterior margin; B) tarsus dorsal margin with row of short, stout setae and fine, simple setae; C) tarsus relatively broad and short, length 4× width in middle part and length ca. 0.4× length of tibia; D) claw with mostly three long subapical setae.

**Material examined. Holotype.** PHILIPPINES • larva; Luzon, Mountain Province, Banaue, Sumigar, Sumigar stream; 03.x.1967; leg. M.L. Pescador; on slide; ZSM.

**Other material.** PHILIPPINES • 80 larvae; Luzon, Ifugao, Banaue, Sumigar Bridge; 16°59'37"N, 121°02'51"E; 1700 m alt.; xi. 1997; leg. W. Mey; 3 on slides; GenBank MT873543; GBIFCH 00763652, 00592354, 00515336; MZL; 34 in alcohol; GBIFCH 00515509, 00515516, 00515507, 00515513; MZL; 1 on slide; GenBank MT873545; GBIFCH 00763656; AdMU; 42 in alcohol; GBIFCH 00515512, 00515511, 00515471, 00515508; AdMU • 27 larvae; Luzon, Mountain Province, Bauko, mineral rich mountain creek; 17°03'53"N, 120°05'10"E; 1820 m alt.; xi. 1997; leg. W. Mey; 1 on slide; GBIFCH 00592353; AdMU; 16 in alcohol; GBIFCH 00515517; AdMU; 2 on slides; GenBank MT873541; GBIFCH 00763644, 00592367; MZL; 8 in alcohol; GBIFCH 00515510, 00515470, 00515506;



**Figure 4.** *Philibaetis luzonensis* comb. nov., larva morphology: **a.** Gill IV; **b.** Inner margin of gill IV; **c.** Outer margin of gill IV; **d.** Gills I–VII; **e.** Paraproct; **f.** Patch of notched scales; **g.** Metanotum; **h.** Tergite IV.



**Figure 5.** *Philibaetis luzonensis* comb. nov., habitus, larva: **a.** Dorsal view; **b.** Lateral view; **c.** Ventral view.

MZL; • 12 larvae; Luzon, Ifugao, Tinoc; 16°40'58"N, 120°56'59"E; 1400 m alt.; xi. 1997; leg. W. Mey; 7 in alcohol; GBIFCH 00515514, 00515515; AdMU; 1 on slide; GenBank MT873544; GBIFCH 00763653; MZL; 4 in alcohol; GBIFCH 00515524; MZL.

**Description. Larva.** (Figs 1–5). *Body length* 5.6–9.0 mm (females), 5.6–7.5 mm (males). *Cerci* little longer than body length, *paracercus* ca. ½ of cerci length.

**Colouration** (Fig. 5a–c). Head, thorax and abdomen dorsally brown, abdominal segments VI and IX brighter, fore protoptera brown. Head, thorax and abdomen ventrally light brown. Legs with femur and tibia light brown, with darker pattern as in Fig. 5a–c, tarsus brown. Caudalii light brown.

**Head. Antenna** (Figs 3d, 5b) with scape and pedicel subcylindrical, length ca. 3× head length.

**Labrum** (Fig. 1a–f). Rectangular, length 0.6× maximum width. Distal margin with shallow medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus 6–7 long, simple setae. Ventrally with marginal row of setae composed of lateral long, simple setae, anterolateral long, feathered setae and medial long, bifid setae; medially additional, partial, submarginal row of fine, lanceolate setae. Ventral surface with ca. eight short, spine-like setae near lateral margin.

**Right mandible** (Fig. 1g, h, l). Incisor blade-like; kinetodontium with three denticles, inner margin of innermost denticle without row of thin setae; prostheca stick-like, apically denticulate. Margin between prostheca and mola straight. Tuft of setae at apex of mola present.

**Left mandible** (Fig. 1i–k, m). Incisor blade-like; kinetodontium with three denticles. Prostheca apically denticulate and with comb-shaped structure. Margin between prostheca and mola straight, with few minute denticles. Subtriangular process long and slender, above level of area between prostheca and mola. Basally of subtriangular process with tuft of long, partly-branched setae. Tuft of setae at apex of mola present.

Both mandibles with lateral margins convex. Dorsally with fine, simple setae scattered over basal surface and mediolaterally with patch of long, spine-like, simple setae.

**Hypopharynx and superlinguae** (Fig. 2a). Lingua longer than superlinguae, longer than wide; with well-developed medial tuft of stout setae, anterolaterally with two smaller tufts of stout setae. Superlinguae distally almost straight, lateral margins slightly rounded; long, fine, simple setae along distal margin.

**Maxilla** (Fig. 2b). Galea-lacinia ventrally with one simple, apical seta under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like and directed against canines, other denti-setae slender, bifid and pectinate. Medially with one spine-like seta and four medium to long, simple setae. Maxillary palp ca. 1.2× as long as length of galea-lacinia; palp segment II 1.8× length of segment I; short, fine, simple setae scattered

over surface of segments I and II; apex of segment II distally constricted and pointed.

**Labium** (Fig. 2d, e). Glossa basally broad, narrowing towards apex, shorter than paraglossa; inner margin with three medium to long, spine-like, simple setae; outer margin with four long, spine-like, simple setae; apex with two long and one very short, spine-like setae; ventral surface with very few short, fine, simple setae. Paraglossa distally truncate, slightly curved inwards; ventrally with three rows of long, robust, distally-pectinate setae in apical area, row of long, simple setae on anterolateral margin, one short, simple seta in mediolateral area and one robust, bifurcate seta in posterolateral area; dorsally with one long, spine-like seta near inner margin. Labial palp with segment I 0.6× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II without protuberance; ventral surface with short, fine, simple setae; dorsally with row of ca. six spine-like setae near outer margin. Segment III almost semicircular; length 0.8× width; ventrally covered with short, spine-like setae and short to medium, fine, simple setae.

**Thorax. Hind protoptera** (Fig. 4g). Absent.

**Foreleg** (Figs 3a–c, 11a–c). Ratio of fore femur:tibia:tarsus:claw 1.2:1.0:0.4:0.2. **Femur**. Rather broad, length ca. 3× maximum width. Dorsal margin with row of ca. 40 long, curved, spine-like setae; length of setae mostly ca. 0.2× maximum width of femur. Apex rounded, with several curved, spine-like setae and many short, stout setae; on posterior side, arc of short, stout setae. Stout, lanceolate setae scattered along ventral margin; femoral patch absent. **Tibia**. Dorsal margin with row of medium, clavate setae. Ventral margin with row of short, spine-like setae, on apex some longer, spine-like setae and tuft of fine, simple setae. Anterior surface scattered with short, stout, lanceolate setae. Patellotibial suture present on basal ¾ area. **Tarsus**. Dorsal margin with row of short, stout and fine, simple setae. Ventral margin with row of short to medium, curved, spine-like setae. **Claw** robust and distally pointed, with one row of ca. seven denticles; generally three and sometimes two long, subapical setae.

**Abdomen. Tergites** (Fig. 4h). Surface with irregular rows of U-shaped scale bases, scattered micropores and fine, simple setae along posterior margin. Posterior margin of tergite IV without spines.

**Gills** (Fig. 4a–d). Seven pairs of gills on segments I–VII. Margin with minute denticles intercalating fine, simple setae. Tracheae extending from main trunk to inner and outer margins. Gill I as long as length of half segment II. Gill IV as long as length of segments V and half VI combined. Gill VII as long as length of segment VIII.

**Paraproct** (Fig. 4e, f). Without prolongation at posterior margin, with ca. 16 stout, marginal spines. Surface scattered with U-shaped scale bases and fine, simple setae; with a patch of notched scales. Cercotractor with small, marginal spines.

*Protogonostyli* (Fig. 10a) in male, last instar larvae ready to moult folded under larval cuticle in the *Labiobaetis* type.

**Distribution.** Philippines: Luzon (Fig. 12).

**Biological aspects.** The specimens were collected in mountain creeks at altitudes from 1400 m to 1820 m, mainly on bottom gravel or on rock surface in runs or riffles. They occurred together with *Labiobaetis sumigarensis* (Müller-Liebenau, 1982), *L. acei* Kaltenbach, Garces & Gattolliat, 2020 and *L. aldabae* Kaltenbach, Garces & Gattolliat, 2020 (see also Müller-Liebenau 1982a: 77).

## Re-description

### *Philibaetis realonae* (Müller-Liebenau, 1982) comb. nov.

(Müller-Liebenau 1982a)

Figures 6–9, 10b, 11d, e and 12

**Differential diagnosis. Larva.** The following characters distinguish *P. realonae* comb. nov. from *P. luzonensis* comb. nov.: A) abdominal tergite IV with triangular spines at posterior margin; B) tarsus dorsal margin with fine, simple setae; C) tarsus relatively slender and long, length 6.5× width in middle part and length ca. 0.5× length of tibia; D) claw with two long subapical setae.

**Material examined. Paratype.** PHILIPPINES • larva; Luzon, Laguna, College, rapids in Molawin Creek; 28.vii.1977; leg. C.R. Realon; on slide; ZSM.

**Other material.** PHILIPPINES • 10 larvae; Luzon, Ilocos Sur, Cervantes Municipality, Losong Bridge; 16°59'06"N, 120°46'11"E; 700 m alt.; 16. iv. 2019; leg. H. Freitag, J. Garces and C.V. Pangantihon; 3 in alcohol; GBIFCH 00515505; AdMU; 1 on slide; GenBank MT873542; GBIFCH 00763650; ZSM; 2 in alcohol; GBIFCH 00515472; ZSM; 1 on slide; GBIFCH 00592351; ZSM; 2 on slides; GBIFCH 00592349, 00592352; AdMU; 1 in alcohol; GBIFCH 00515337; AdMU.

**Description. Larva.** (Figs 1–5). *Body length* 4.7–4.9 mm (Müller-Liebenau 1982a: 4–5 mm). *Cerci* ca. as long as body length (Müller-Liebenau 1982a), *paracercus* less than half of cerci length.

*Colouration* (Fig. 9a–c). Head, thorax and abdomen dorsally brown, abdominal segments VI and IX brighter, fore protoptera brown. Head, thorax and abdomen ventrally light brown. Legs with femur and tibia light brown, with darker pattern as in Fig. 9a–c, tarsus brown. Caudalii light brown.

**Head. Antenna** (Fig. 7f) with scape and pedicel subcylindrical, length ca. 3× head length.

**Labrum** (Fig. 6a, b). Rectangular, length 0.6× maximum width. Distal margin with shallow medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus 6–7 long, simple setae. Ventrally with marginal row of setae composed of lateral long, simple setae, anterolateral long, feathered setae and medial long, bifid setae; medially an additional,

partial, submarginal row of fine, lanceolate setae. Ventral surface with ca. eleven short, spine-like setae near lateral margin.

**Right mandible** (Fig. 6c, d). Incisor blade-like; kinetodontium with three denticles, inner margin of innermost denticle without row of thin setae; prostheca stick-like, apically denticulate. Margin between prostheca and mola straight. Tuft of setae at apex of mola present.

**Left mandible** (Fig. 6e–g). Incisor blade-like; kinetodontium with three denticles. Prostheca apically denticulate and with comb-shaped structure. Margin between prostheca and mola straight. Subtriangular process long and slender, above level of area between prostheca and mola. Basally of subtriangular process with tuft of long, partly-branched setae. Tuft of setae at apex of mola present.

Both mandibles with lateral margins convex. Dorsally with fine, simple setae scattered over basal surface and mediolaterally with patch of long, spine-like, simple setae.

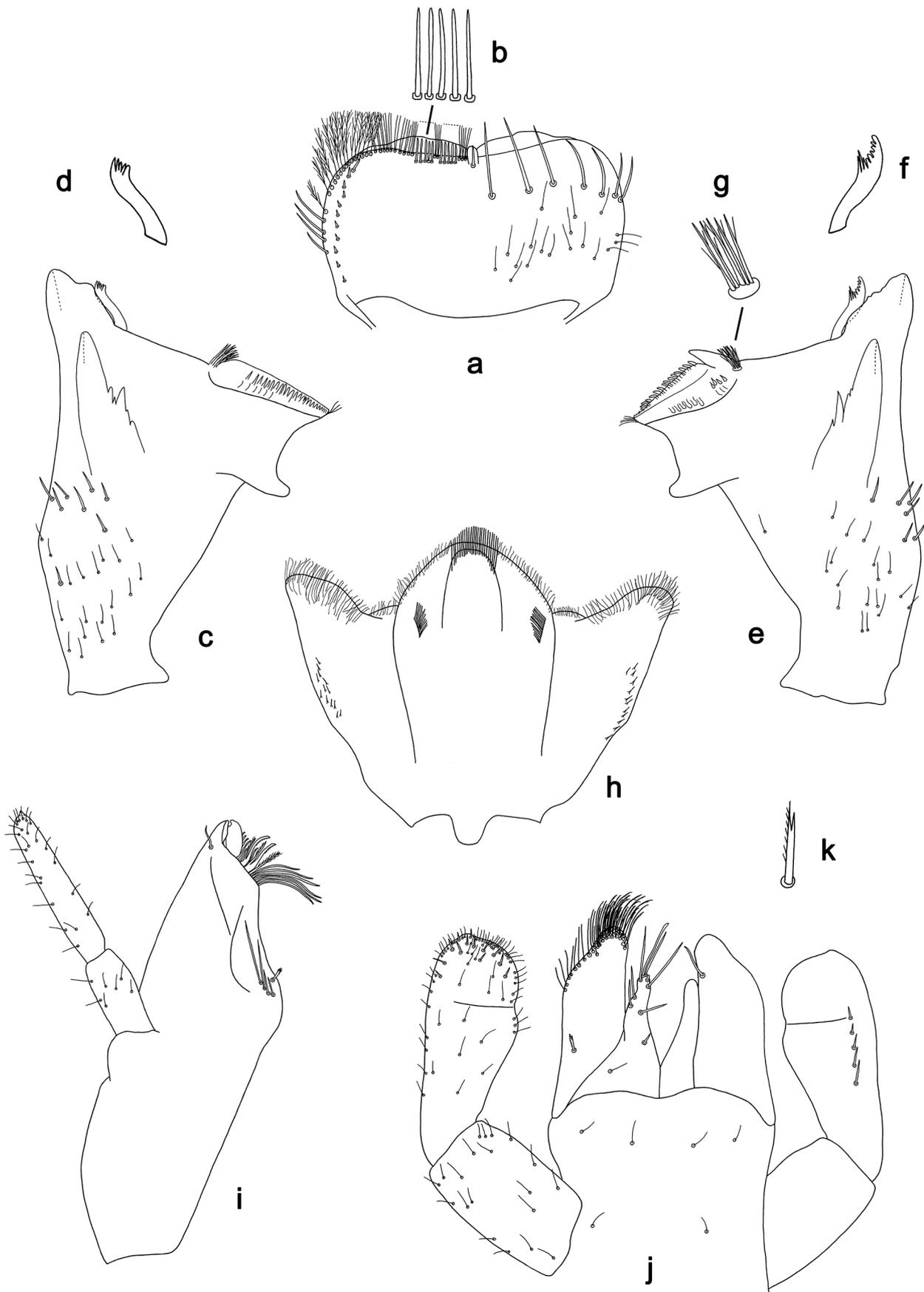
**Hypopharynx and superlinguae** (Fig. 6h). Lingua longer than superlinguae, longer than wide; with well-developed medial tuft of stout setae, anterolaterally with two smaller tufts of stout setae. Superlinguae distally almost straight, lateral margins almost straight; long, fine, simple setae along distal margin.

**Maxilla** (Fig. 6i). Galea-lacinia ventrally with one simple, apical seta under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like and directed against canines, other denti-setae slender, bifid and pectinate. Medially with one spine-like seta and four medium to long, simple setae. Maxillary palp ca. 1.1× as long as length of galea-lacinia; 2-segmented; palp segment II 1.9× length of segment I; short, fine, simple setae scattered over surface of segments I and II; apex of segment II distally constricted and pointed.

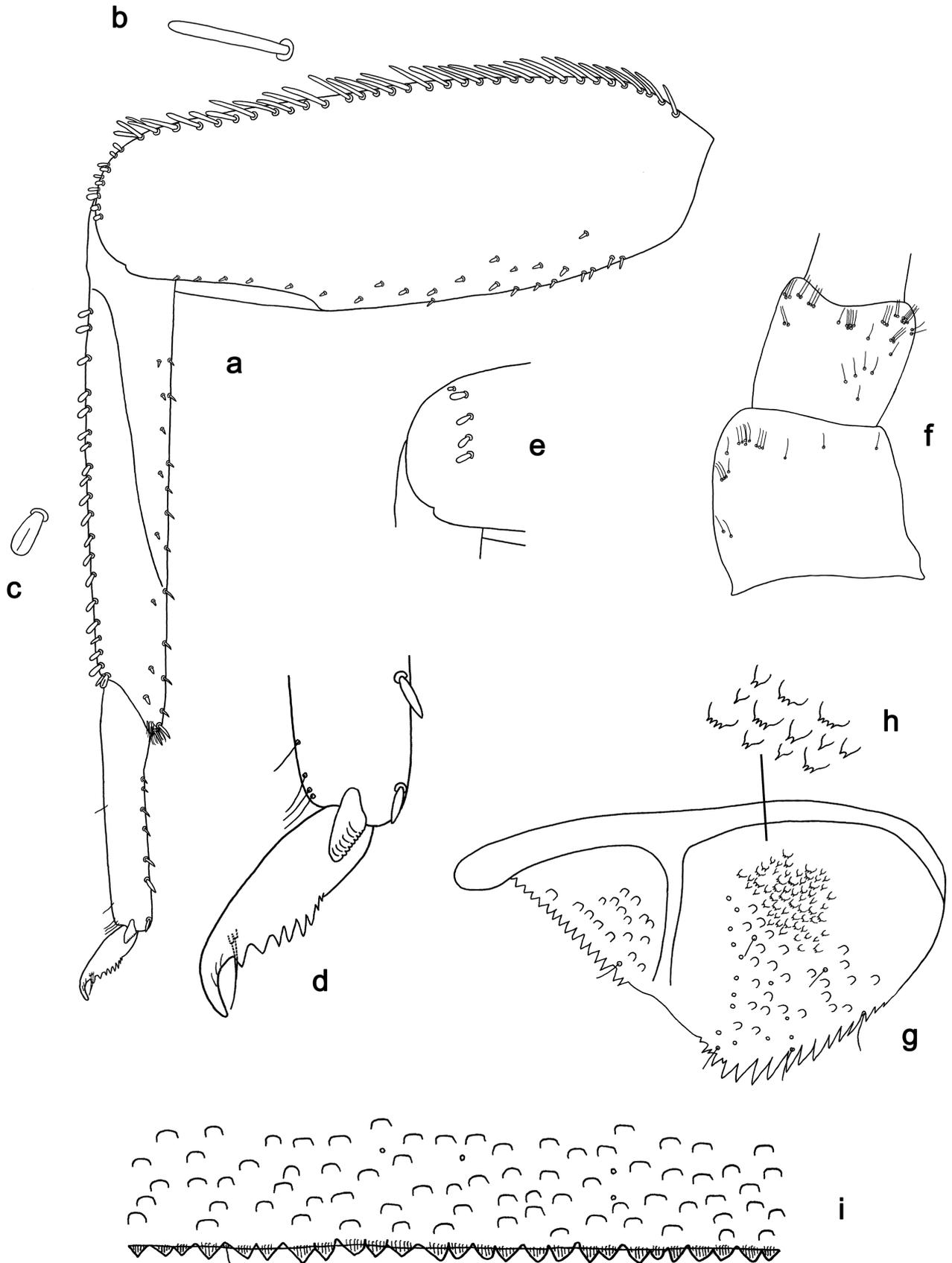
**Labium** (Fig. 6j, k). Glossa basally broad, narrowing towards apex, shorter than paraglossa; inner margin with three short to long, spine-like, simple setae; outer margin with three long, spine-like, simple setae; apex with two long and one very short, spine-like setae; ventral surface with very few short, fine, simple setae. Paraglossa distally truncate, slightly curved inwards; ventrally with three rows of long, robust, distally pectinate setae in apical area, row of long, simple setae on anterolateral margin, one short and one robust, bifurcate seta in posterolateral area; dorsally with one long, spine-like seta near inner margin. Labial palp with segment I 0.7× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II without protuberance; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III almost semicircular, apically slightly pointed; length 0.8× width; ventrally covered with short, spine-like setae and short to medium, fine, simple setae.

**Thorax. Hind protoptera.** Absent.

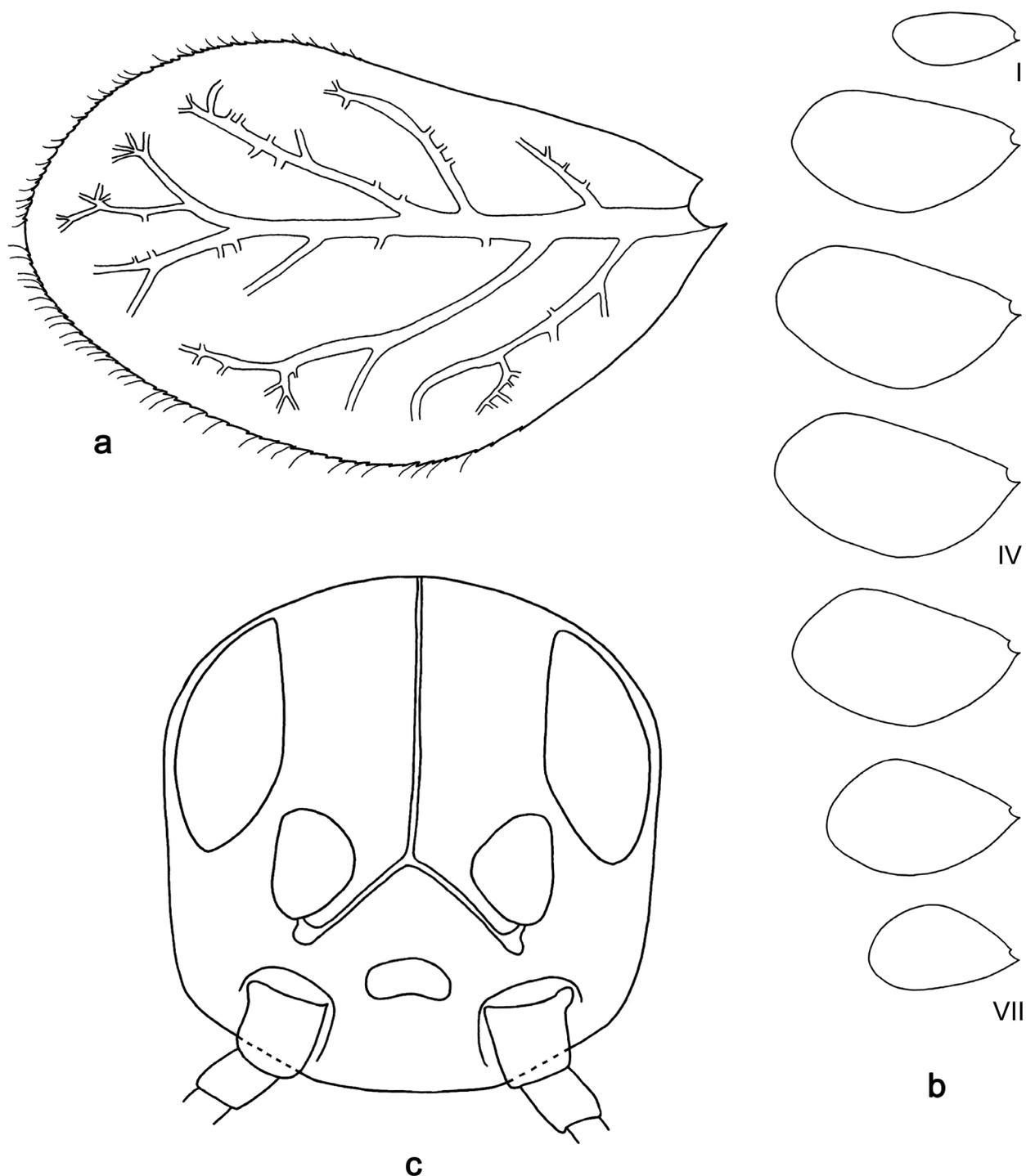
**Foreleg** (Figs 7a–e, 11d, e). Ratio of fore femur:tibia:tarsus:claw 1.2:1.0:0.5:0.2. **Femur.** Rather broad, length ca. 3× maximum width. Dorsal margin with row of ca. 31



**Figure 6.** *Philibaetis realonae* comb. nov., larva morphology: **a.** Labrum; **b.** Setae of submarginal row (ventral view); **c.** Right mandible; **d.** Right prostheca; **e.** Left mandible; **f.** Left prostheca; **g.** Tuft of setae; **h.** Hypopharynx and superlinguae; **i.** Maxilla; **j.** Labium (left side: ventral view; right side: dorsal view); **k.** Posterolateral seta on ventral side of paraglossa.



**Figure 7.** *Philibaetis realonae* comb. nov., larva morphology: **a.** Foreleg; **b.** Seta on dorsal margin of femur; **c.** Seta on dorsal margin of tibia; **d.** Claw; **e.** Apex of femur (posterior view); **f.** Base of antenna; **g.** Paraproct; **h.** Patch of notched scales; **i.** Tergite IV.

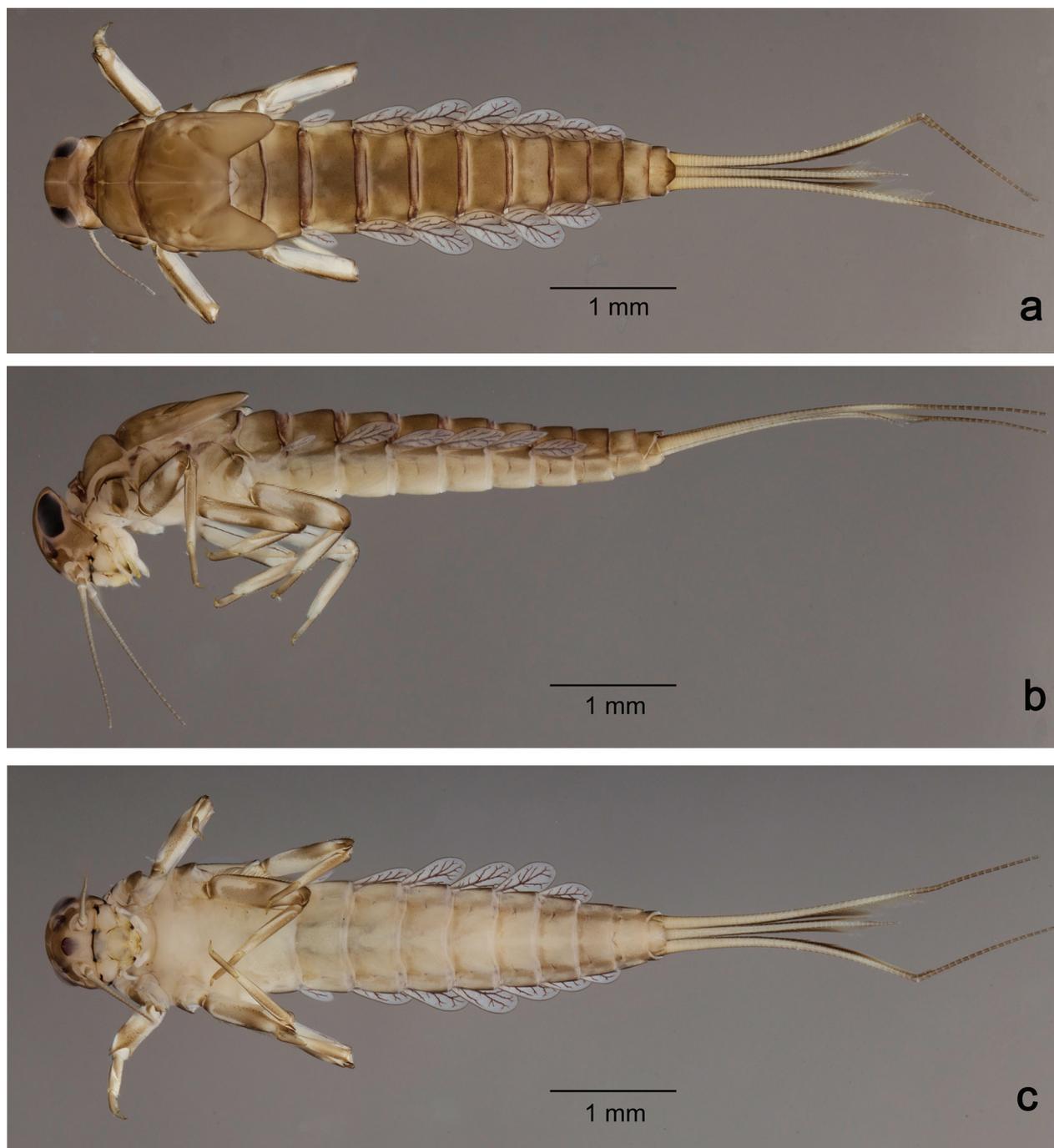


**Figure 8.** *Philibaetis realonae* comb. nov., larva morphology: **a.** Gill IV; **b.** Gills I–VII; **c.** Head.

long, curved, spine-like setae; length of setae mostly ca.  $0.2\times$  maximum width of femur. Apex rounded, with two pairs of curved, spine-like setae and many short, stout setae; on posterior side, arc of short, stout setae. Stout, lanceolate setae scattered along ventral margin; femoral patch absent. *Tibia.* Dorsal margin with row of medium, clavate setae. Ventral margin with row of short, spine-like setae, on apex, some longer, spine-like setae and tuft of fine, simple setae. Anterior surface scattered with short, stout, lanceolate se-

tae. Patellotibial suture present on basal  $\frac{3}{4}$  area. *Tarsus.* Dorsal margin with some fine, simple setae. Ventral margin with row of short to medium, curved, spine-like setae. *Claw* robust and distally pointed, with one row of eight or nine denticles; with ca. three stripes; two long, subapical setae.

**Abdomen.** *Tergites* (Fig 7i). Surface with irregular rows of U-shaped scale bases and scattered micropores. Posterior margin of tergite IV with triangular spines, wider than long.



**Figure 9.** *Philibaetis realonae* comb. nov., habitus, larva: **a.** Dorsal view; **b.** Lateral view; **c.** Ventral view.

**Gills** (Fig. 8a, b). Seven pairs of gills on segments I–VII. Margin with minute denticles intercalating fine, simple setae. Tracheae extending from main trunk to inner and outer margins. Gill I as long as length of  $\frac{2}{3}$  segment II. Gill IV as long as length of segments V and half VI combined. Gill VII little longer than length of segment VIII.

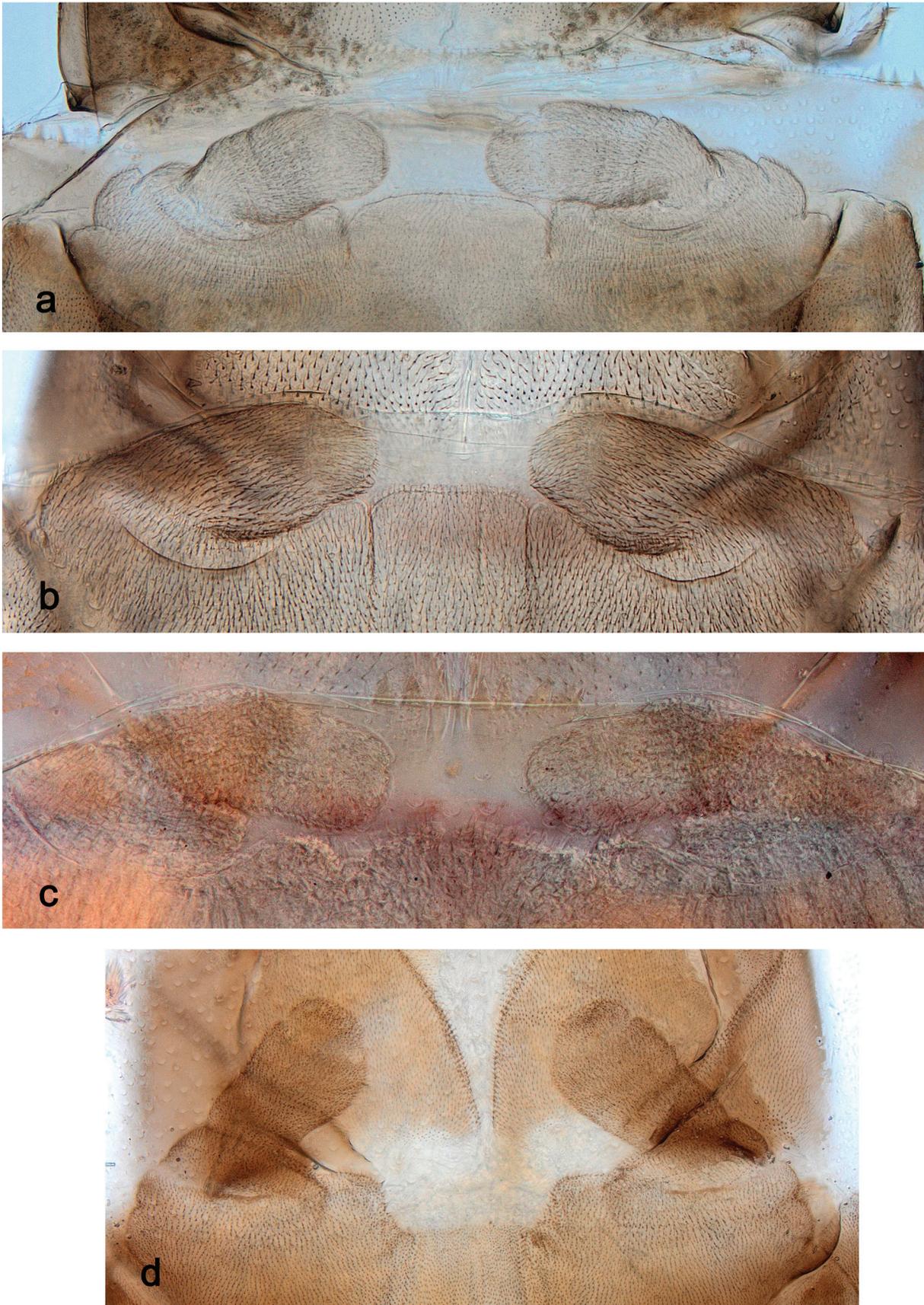
**Paraproct** (Fig. 7g, h). Without prolongation at posterior margin, with ca. 18 stout, marginal spines. Surface scattered with U-shaped scale bases, fine, simple setae

and micropores; with patch of notched scales. Cercotractor with small, marginal spines.

**Protogonostyli** (Fig. 10b) in male, last instar larvae ready to moult folded under larval cuticle in the *Labiobaetis* type.

**Distribution.** Philippines: Luzon (Fig. 12).

**Biological aspects.** The specimens were collected at altitudes of 30 m and 700 m, partly together with *Labiobaetis molawinensis* (Müller-Liebenau, 1982) (see also Müller-Liebenau 1982a: 80).



**Figure 10.** Protogonostyli developing under cuticle of male last instar larvae: **a.** *Philibaetis luzonensis* comb. nov.; **b.** *Philibaetis realonae* comb. nov.; **c.** *Labiobaetis* type of folding, *Labiobaetis pelingeni* Kaltenbach, Garces & Gattolliat, 2020; **d.** *Baetis* type of folding, *Baetis rhodani* (Pictet, 1843).

## Discussion

### Assignment, morphological differences and similarities

*Philibaetis* gen. nov. obviously belongs to the family Baetidae, based on the developing turbinate eyes of late instar male larvae, the long, slender body shape, the larval Y-shaped frontal suture reaching ventrally to lateral ocelli (Fig. 8c), the labrum with distinctly-expressed median incision, the shape of left and right prostheca, the kinetodontium fused with mandible and with incisor, the shape of glossae (basally widened, most part narrow) and the anterior outer projection of femur apex, which is directed towards inner side of femur (Figs 3a, 7a) (Wang and McCafferty 1996, Kluge 2004, Kluge and Novikova 2011). It further belongs to the subfamily Baetinae sensu Kazlauskas (1972) and the Anteropatellata, because of the presence of the patellotibial suture on the forelegs of the larvae (Kluge and Novikova 2011). It can be assigned to the non-*Baetis* complex of Baetinae (Waltz et al. 1994, Waltz and McCafferty 1997), also referred to as Baetungulata-non-Baetofemorata (Kluge and Novikova 2011), because of the claw with one row of denticles on inner-anterior side and the lack of a femoral patch. The folding of the protogonostyli developing under the cuticle of last instar male larvae is of the *Labiobaetis* type (Fig. 10; Kluge 2004: fig. 29E–J). Therefore, *Philibaetis* gen. nov. is preliminarily placed within the tribe Labiobaetini Kluge and Novikova (2016) since the final placement can be only definitely done once the male imago is described as well.

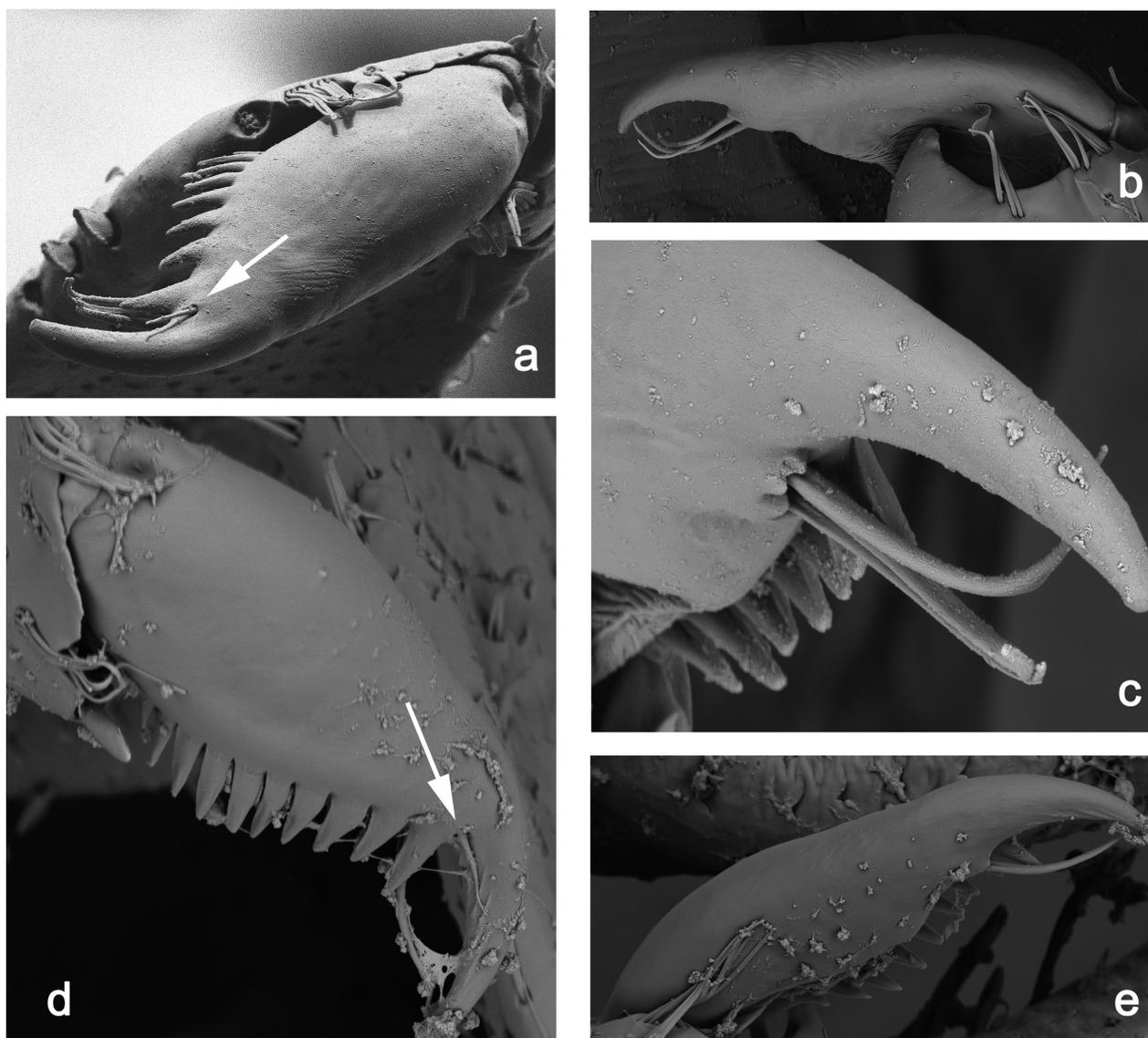
Apart from the unique combination of characters as described in the diagnosis, the following characters differentiate *Philibaetis* gen. nov. from all other genera of Baetinae: labrum ventrally on lateral margin with long, simple, spine-like setae, on anterolateral margin with long, feathered setae and medially with long, bifid setae and a partial submarginal row of lanceolate setae (Figs 1b–f, 6a, b); both mandibles with blade-like incisor and dorsally, a mediolateral patch of long, spine-like setae, left mandible additionally with a tuft of long, partly-branched setae at base of subtriangular process (Figs 1g–m, 6c–g); galea-lacinia with distal denti-seta tooth-like and directed against canines (Figs 2b, c, 6i); claws with one row of denticles and 2 or 3 long, subapical setae on posterior side and one reduced subapical seta on anterior side (Figs 3b, 7d, 11a–e).

Most of the characters are not unique autapomorphies of *Philibaetis* gen. nov. as they can be found in other related or not related genera as well. However, none of these genera is sharing several of the characters and they always present other important differences, for example, *Asiobaetodes* Gattolliat, 2012, has a similar labrum, but not the additional submarginal row of setae on ventral side (Gattolliat 2012: fig. 1); blade-like incisors of the mandibles are also described in some *Labiobaetis* Novikova & Kluge, 1987 (Kaltenbach and Gattolliat 2018: figs 16a, b, 17b, d, 19b, d), in *Baetis* Leach, 1815

(Müller-Liebenau 1981: fig. 1e, Müller-Liebenau 1984: fig. 1e, Müller-Liebenau and Hubbard 1985: fig. 4e) and in *Liebebiella* Waltz & McCafferty, 1987 (Müller-Liebenau 1982b: fig. 1E); the distal denti-seta directed against the canines is also present in *Bungona* Harker, 1957 (Marle et al. 2016: figs 6a, 24), as well as in several genera of Protopatellata; the labial palp segments II are comparable with species of *Baetis*, *Bungona* (Shi and Tong 2019: figs 39, 61) and *Tenuibaetis* Kang & Yang, 1994 (Kaltenbach and Gattolliat 2019b: fig. 2h); the comb-like structure on the left mandible of *Cheleocloeon* Wuillot & Gillies, 1993 (Gattolliat and Sartori 2008: fig. 15) and *Bungona* (Marle et al. 2016: fig. 5) is at a different place basally from the subtriangular process and of different shape than the tuft of long setae of *Philibaetis* gen. nov.; both structures, are therefore, not comparable.

### Subapical setae of claws

Müller-Liebenau described both species of *Philibaetis* gen. nov. (but previously assigned to *Baetis*) with one subapical seta only (Müller-Liebenau 1982a: figs 2H, 3H). This can be explained by the fact that the subapical setae of this genus often appear as one single seta in slide preparations or under a binocular. However, our slides, as well as SEM pictures, revealed the number and complex structure of these subapical setae. *P. luzonensis* comb. nov. generally has three long subapical setae on the claws of all legs (posterior side) and *P. realonae* comb. nov. always two; additionally, there is always one reduced subapical seta on the anterior side in both species (Figs 3b, 7d, 11a–e). All subapical setae on the posterior side of the same claw have separate insertions, standing very close together. They seem to have different lengths and partly different shapes, which could facilitate the arrangement to one single, broader seta under natural conditions. The separation of these combined setae seems to happen under unnatural conditions by the influence of chemicals like alcohol and Cellosolve (2-ethoxyethanol) during slide preparation; or by dehydration during preparation for SEM pictures, but not always. Several long, subapical setae on the same side of a claw are very rare in Baetidae. Other exceptions, besides *Philibaetis* gen. nov., are *Lugoiops* McCafferty & Baumgartner, 2003, with five subapical setae (McCafferty and Baumgartner 2003: fig. 10) and *Moribaetis* Waltz & McCafferty, 1985, with two (Lugo-Ortiz and McCafferty 1996: fig. 9). One single, long subapical seta is widespread in Baetidae (e.g. *Baetis*, *Baetodes* Needham & Murphy, 1924, *Gratia* Thomas, 1992, *Indobaetis* Müller-Liebenau & Morihara, 1982) and one on each side was described from, for example, the different genera of the *Centroptiloides* complex, *Madaechinopus* Gattolliat & Jacobus, 2010, *Offadens* Lugo-Ortiz & McCafferty, 1998, *Liebebiella* Waltz & McCafferty, 1987, *Monocentroptilum* Kluge, 2018 as well as a few species of *Baetis* (Müller-Liebenau and Morihara 1982, Müller-Liebenau 1982b, Müller-Liebenau 1984, Thomas 1992, Lugo-Ortiz and McCafferty 1998, 1999,



**Figure 11.** Claws and subapical setae, SEM photos: **a–c.** *Philibaetis luzonensis* comb. nov., **a.** Fore claw, anterior view; **b.** Middle claw, posterior view; **c.** Hind claw, posterior view; **d, e.** *Philibaetis realonae* comb. nov., **d.** Fore claw, anterior view; **e.** Middle claw, posterior view.

Gattolliat 2002, Dominguez et al. 2006, Kluge 2018, Yanai et al. 2018). However, the subapical setae have variable positions on the claw between some of the genera.

## Genetics

The interspecific genetic distance between the two species of *Philibaetis* gen. nov. is 17%–18% (K2P; Table 2). This is in line with interspecific distances reported from *Labiobaetis* in Indonesia (11%–24%), Borneo (19%–25%) and the Philippines (15%–27%) (Kaltenbach and Gattolliat 2019a, 2020, Kaltenbach et al. 2020b). Ball et al. (2005) reported a mean interspecific, congeneric distance of 18% for mayflies from the United States and Canada. The intraspecific distances for *P. luzonensis* comb. nov. are very low as expected, ranging from 0% to 3% (average 0.75%; K2P; Table 2).

**Table 2.** Intraspecific and interspecific genetic distances between sequences of the mitochondrial COI gene in the genus *Philibaetis* gen. nov. (Kimura 2-parameter; %).

	Species	Specimens catalogue #	1	2	3	4
1	<i>P. luzonensis</i> comb. nov.	GBIFCH 00763644				
2		GBIFCH 00763652	3			
3		GBIFCH 00763653	3	0		
4		GBIFCH 00763656	3	0	0	
5	<i>P. realonae</i> comb. nov.	GBIFCH 00763650	17	18	17	18

## Distribution

So far, both *P. luzonensis* comb. nov. and *P. realonae* comb. nov. were found on Luzon only, but at very different altitudes (Table 3, Fig. 12). This could be an indication that the two species were differentiating along elevational and environmental gradients, as discussed for some species of *Labiobaetis* on the same island (Kaltenbach et al. 2020b and citations therein).



Figure 12. *Philibaetis* gen. nov., distribution, Philippines.

**Table 3.** GPS coordinates and altitudes of locations of examined specimens.

Species	Locality	Altitude	GPS coordinates
<i>P. luzonensis</i> comb. nov.	Philippines: Luzon	1820 m	17°03'53"N, 121°05'10"E
		1700 m	16°59'37"N, 121°02'51"E
		1400 m	16°40'58"N, 120°56'59"E
<i>P. realonae</i> comb. nov.	Philippines: Luzon	700 m	16°59'06"N, 120°46'11"E
		30 m	14°09'53"N, 121°14'48"E

The number of sampled localities and different habitats is still limited in the Philippines and there are large regions without any collection activities so far. Therefore, we may assume that the number of taxa will continue to increase with further collections in the future.

## Acknowledgements

We sincerely thank Lars Hendrich (Zoologische Staatssammlung München, ZSM) for the loan of precious type material and Wolfram Mey (Museum für Naturkunde, Humboldt Universität, Berlin, Germany), as well as Hendrik Freitag and his team (Biodiversity Laboratory, Ateneo de Manila University, Quezon City, Philippines) for the collection of new material. Collection in the Philippines was made possible with the Gratuitous Permit (GP 0133-17 and renewals) for the collection of aquatic wildlife as kindly issued by the Bureau of Fisheries and Aquatic Resources (BFAR), Quezon City. We are also grateful to Michel Sartori (MZL) for his constant interest and support for our project, to Maud Liégeois (University of Lausanne, UNIL) for her support with lab work and preparation of the COI barcodes, to Geneviève L'Eplattenier for her support in the preparation for the SEM pictures and to Antonio Mucciolo (University of Lausanne, UNIL), who took the SEM pictures. Lastly, we are thankful to Cassandra Caedo (USA) for corrections and improvements of the English language and to the reviewers of our manuscript, Ernst Bauernfeind, Luke Jacobus and Michel Sartori, for their valuable comments.

## References

Ball SL, Hebert PDN, Burian SK, Webb JM (2005) Biological identifications of mayflies (Ephemeroptera) using DNA barcodes. *Journal of the North American Benthological Society* 24: 508–524. <https://doi.org/10.1899/04-142.1>

Brown RM, Diesmos AC (2010) Philippines, Biology. In: Gillespie RG, Clague DA (Eds) *Encyclopedia of Islands*. University of California Press, Berkeley, Los Angeles, London, 723–732.

Chakrabarty P, Warren M, Page LM, Baldwin CC (2013) GenSeq: An updated nomenclature and ranking for genetic sequences from type and non-type sources. *ZooKeys* 346: 29–41. <https://doi.org/10.3897/zookeys.346.5753>

Cruz PV, Nieto C, Gattolliat J-L, Salles FF, Hamada N (2020) A cladistic insight into higher level classification of Baetidae (Insecta: Ephemeroptera). *Systematic Entomology* 2020: 1–12. <https://doi.org/10.1111/syen.12446>

Dominguez E, Molineri C, Pescador ML, Hubbard MD, Nieto C (2006) Ephemeroptera of South America. In: Adis J, Arias JR, Rueda-Delgado G, Wantzen KM (Eds) *Aquatic Biodiversity in Latin America*, Vol. 2. Pensoft Publishers, Sofia-Moscow, 646 pp.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299. [http://www.mbari.org/staff/vrijen/PDFS/Folmer\\_94MMBB.pdf](http://www.mbari.org/staff/vrijen/PDFS/Folmer_94MMBB.pdf)

Freitag H, Jäch MA, Wewalka G (2016) Diversity of aquatic and riparian Coleoptera of the Philippines: checklist, state of knowledge, priorities for future research and conservation. *Aquatic Insects* 37: 177–213. <https://doi.org/10.1080/01650424.2016.1210814>

Gattolliat J-L (2002) Two new genera of Baetidae (Ephemeroptera; Insecta) from Madagascar. *Aquatic Insects* 24: 143–159. <https://doi.org/10.1076/aqin.24.2.143.4903>

Gattolliat J-L (2012) Two new genera of Baetidae (Ephemeroptera) from Borneo (East Kalimantan, Indonesia). *Annales de Limnologie – International Journal of Limnology* 48: 187–199. <https://doi.org/10.1051/limn/2012012>

Gattolliat J-L, Nieto C (2009) The family Baetidae (Insecta: Ephemeroptera): synthesis and future challenges. *Aquatic Insects* 31: 41–62. <https://doi.org/10.1080/01650420902812214>

Gattolliat J-L, Sartori M (2008) Order Ephemeroptera. *Arthropod Fauna of the UAE* 1: 47–83.

Hubbard MD (1995) Towards a standard methodology for the description of mayflies (Ephemeroptera). In: Corkum LD, Ciborowski JJH (Eds) *Current directions in research on Ephemeroptera*. Canadian Scholar's Press, Toronto, 361–369.

Jacobus LM, Macadam CR, Sartori M (2019) Mayflies (Ephemeroptera) and their contributions to ecosystem services. *Insects* 10: 1–26. <https://doi.org/10.3390/insects10060170>

Kaltenbach T, Garces JM, Gattolliat J-L (2020a) A new genus of Baetidae (Insecta, Ephemeroptera) from Southeast Asia. *European Journal of Taxonomy* 612: 1–32. <https://doi.org/10.5852/ejt.2020.612>

Kaltenbach T, Garces JM, Gattolliat J-L (2020b) The success story of *Labiobaetis* Novikova & Kluge in the Philippines (Ephemeroptera, Baetidae), with description of 18 new species. *ZooKeys*, in press.

Kaltenbach T, Gattolliat J-L (2018) The incredible diversity of *Labiobaetis* Novikova & Kluge in New Guinea revealed by integrative taxonomy (Ephemeroptera, Baetidae). *ZooKeys* 804: 1–136. <https://doi.org/10.3897/zookeys.804.28988>

Kaltenbach T, Gattolliat J-L (2019a) The tremendous diversity of *Labiobaetis* Novikova & Kluge in Indonesia (Ephemeroptera, Baetidae). *ZooKeys* 895: 1–117. <https://doi.org/10.3897/zookeys.895.38576>

Kaltenbach T, Gattolliat J-L (2019b) A new species of *Tenuibaetis* Kang & Yang, 1994 from Indonesia (Ephemeroptera, Baetidae). *ZooKeys* 820: 13–23. <https://doi.org/10.3897/zookeys.820.31487>

Kaltenbach T, Gattolliat J-L (2020) *Labiobaetis* Novikova & Kluge in Borneo (Ephemeroptera, Baetidae). *ZooKeys* 914: 43–79. <https://doi.org/10.3897/zookeys.914.47067>

Kazlauskas RS (1972) Neues über das System der Eintagsfliegen der Familie Baetidae (Ephemeroptera). *Proceedings of the XIII International Congress of Entomology in Moscow*, 2–9 August 1968, Vol. 3, 337–338.

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120. <https://doi.org/10.1007/BF01731581>

- Kluge NJ (2004) The Phylogenetic System of Ephemeroptera. Kluwer Academic Publishers, Dordrecht, 442 pp. <https://doi.org/10.1007/978-94-007-0872-3>
- Kluge NJ (2018) A new Afrotropical genus *Monocentropilum* gen. nov. (Ephemeroptera: Baetidae: Protopatellata). *Zootaxa* 4486: 115–128. <https://doi.org/10.11646/zootaxa.4486.2.2>
- Kluge NJ (2020) Ephemeroptera of the world. <http://www.insecta.bio.spbu.ru> [retrieved 10.09.2020]
- Kluge NJ, Novikova EA (2011) Systematics of the mayfly taxon *Acentrella* (Ephemeroptera, Baetidae), with description of new Asian and African species. *Russian Entomological Journal* 20: 1–56. <https://doi.org/10.15298/rusentj.20.1.01>
- Kluge NJ, Novikova EA (2016) New tribe Labiobaetini tribus n., redefinition of *Pseudopannota* Waltz & McCafferty 1987 and descriptions of new and little known species from Zambia and Uganda. *Zootaxa* 4169: 1–43. <https://doi.org/10.11646/zootaxa.4169.1.1>
- Kumar S, Stecher G, Tamura K (2016) MEGA 7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lugo-Ortiz CR, McCafferty WP (1996) Phylogeny and classification of the *Baetodes* complex (Ephemeroptera: Baetidae), with description of a new genus. *Journal of the National American Benthological Society* 15: 367–380. <https://doi.org/10.2307/1467283>
- Lugo-Ortiz CR, McCafferty WP (1998) The *Centroptiloides* Complex of Afrotropical small minnow mayflies (Ephemeroptera: Baetidae). *Annals of the Entomological Society of America* 91: 1–26. <https://doi.org/10.1093/aesa/91.1.1>
- Lugo-Ortiz CR, McCafferty WP (1999) *Edmundsiops instigatus*: a new genus and species of small minnow mayflies (Ephemeroptera: Baetidae) from Australia. *Entomological News* 110: 65–69.
- Marle P, Salles FF, Gattolliat J-L (2016) Two new species of *Bungona* Harker, 1957 (Ephemeroptera: Baetidae) from Borneo, Indonesia. *Zootaxa* 4088: 221–235. <https://doi.org/10.11646/zootaxa.4088.2.4>
- McCafferty WP, Baumgartner DE (2003) *Lugoiops maya*, a new genus and species of Ephemeroptera (Baetidae) from Central America. *Proceedings of the Entomological Society of Washington* 105: 397–406.
- Müller-Liebenau I (1981) Review of the original material of the baetid genera *Baetis* and *Pseudocloeon* from the Sunda Islands and the Philippines described by G. Ulmer, with some general remarks (Insecta: Ephemeroptera). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 78: 197–208.
- Müller-Liebenau I (1982a) New species of the family Baetidae from the Philippines (Insecta, Ephemeroptera). *Archiv für Hydrobiologie* 94: 70–82.
- Müller-Liebenau I (1982b) Five new species of *Pseudocloeon* Klapálek, 1905, (Fam. Baetidae) from the Oriental Region (Insecta, Ephemeroptera) with some general remarks on *Pseudocloeon*. *Archiv für Hydrobiologie* 95: 283–295.
- Müller-Liebenau I (1984) New genera and species of the family Baetidae from West-Malaysia (River Gombak) (Insecta: Ephemeroptera). *Spixiana* 7: 253–284.
- Müller-Liebenau I, Hubbard MD (1985) Baetidae from Sri Lanka with some general remarks on the Baetidae of the Oriental Region (Insecta: Ephemeroptera). *Florida Entomologist* 68: 537–561. <https://doi.org/10.2307/3494855>
- Müller-Liebenau I, Morihara (1982) *Indobaetis*: a new genus of Baetidae from Sri Lanka (Insecta: Ephemeroptera) with two new species. *Gewässer und Abwässer* 68/69: 26–34.
- Ogden TH, Whiting MF (2005) Phylogeny of Ephemeroptera (mayflies) based on molecular evidence. *Molecular Phylogenetics and Evolution* 37: 625–643. <https://doi.org/10.1016/j.ympev.2005.08.008>
- Ogden TH, Breinholt JW, Bybee SM, Miller DB, Sartori M, Shiozawa D, Whiting MF (2019) Mayfly phylogenomics: initial evaluation of anchored hybrid enrichment data for the order Ephemeroptera. *Zoosymposia* 16: 167–181.
- Ogden TH, Gattolliat J-L, Sartori M, Staniczek AH, Soldan T, Whiting MF (2009) Towards a new paradigm in mayfly phylogeny (Ephemeroptera): combined analysis of morphological and molecular data. *Systematic Entomology* 34: 616–634. <https://doi.org/10.1111/j.1365-3113.2009.00488.x>
- Sanger F, Nicklen S, Coulson AR (1977) DNA sequencing with chain-terminating inhibitors. *Proceedings of the National Academy of Sciences USA* 74: 5463–5467. <https://doi.org/10.1073/pnas.74.12.5463>
- Sartori M, Brittain JE (2015) Order Ephemeroptera. In: Thorp J, Rogers DC (Eds) *Ecology and general biology: Thorp and Covich's Freshwater Invertebrates*. Academic Press, 873–891. <https://doi.org/10.1016/B978-0-12-385026-3.00034-6>
- Shi W, Tong X (2019) Genus *Bungona* Harker, 1957 (Ephemeroptera: Baetidae) from China, with description of three new species and a key to Oriental species. *Zootaxa* 4586: 571–585. <https://doi.org/10.11646/zootaxa.4586.3.12>
- Shorthouse DP (2010) SimpleMapp, an online tool to produce publication-quality point maps. [Retrieved from] <https://www.simplemapp.net> [Accessed August 03, 2020].
- Suttinun C, Gattolliat J-L, Boonsong B (2020) *Cymbalocleon* gen. nov., an incredible new mayfly genus (Ephemeroptera: Baetidae) from Thailand. *PLoS ONE* 15(10): 1–17. <https://doi.org/10.1371/journal.pone.0240635>
- Thomas A (1992) *Gratia sororculaenadinae* n. gen., n. sp., Ephémérop-tère nouveau de Thaïlande (Ephemeroptera, Baetidae). *Bulletin de la Société d'Histoire Naturelle de Toulouse* 128: 47–51.
- Vallejo BJ (2014) Biogeography of Luzon Island, Philippines. In: Telnov D (Ed) *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea*. The Entomological Society of Latvia, Riga, 47–59.
- Vuataz L, Sartori M, Wagner A, Monaghan MT (2011) Toward a DNA taxonomy of Alpine *Rhithrogena* (Ephemeroptera: Heptagenidae) using a mixed Yule-Coalescent Analysis of mitochondrial and nuclear DNA. *PLoS ONE* 6: 1–11. <https://doi.org/10.1371/journal.pone.0019728>
- Waltz RD, McCafferty WP (1997) New generic synonymies in Baetidae (Ephemeroptera). *Entomological News* 108: 134–140.
- Waltz RD, McCafferty WP, Thomas A (1994) Systematics of *Alainites* n. gen., *Dipheter*, *Indobaetis*, *Nigrobaetis* n. stat., and *Takobia* n. stst. (Ephemeroptera, Baetidae). *Bulletin de la Société d'Histoire Naturelle de Toulouse* 130: 33–36.
- Wang T-Q, McCafferty WP (1996) New diagnostic characters for the mayfly family Baetidae (Ephemeroptera). *Entomological News* 107: 207–212.
- Yanai Z, Gattolliat J-L, Dorchin N (2018) Taxonomy of *Baetis* Leach in Israel (Ephemeroptera, Baetidae). *ZooKeys* 794: 45–84. <https://doi.org/10.3897/zookeys.794.28214>