

Two new species of the *Epimetopus mendeli* species group and notes on its adult and larval morphology (Coleoptera: Hydrophiloidea: Epimetopidae)

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Abstract. The *Epimetopus mendeli* species group is delineated based on characters of the head, elytra and male genitalia. Three species are included in the group: *E. mendeli* sp. nov. (Peru), *E. flavicaptus* sp. nov. (Ecuador) and *E. angulatus* Balfour-Browne, 1949 (Bolivia). The external morphology of *Epimetopus mendeli* sp. nov. is described and illustrated in detail, and the diagnostic characters for the other two species of the group are discussed and illustrated. Larval morphology, including the primary chaetotaxy of *E. mendeli* sp. nov., is described in detail based on first instar larvae from the egg case carried by an identified female. The larva is compared with the previously published description of larval *Epimetopus* Lacordaire, 1854 and the morphology of the abdominal apex is discussed, revealing only slight differences between various *Epimetopus* larvae. Larva of *E. mendeli* sp. nov. is also briefly compared with the larvae of remaining hydrophiloid families.

Key words. Epimetopidae, *Epimetopus*, new species, adult, larva, primary chaetotaxy, morphology, Neotropical Region, Bolivia, Ecuador, Peru

Introduction

The hydrophiloid family Epimetopidae includes 29 tropical species (HANSEN 1999, SHORT & FIKÁČEK 2011) characterized by the pronotum bearing several longitudinal ridges and largely covering the head, body surface covered by setiferous granules and elytra bearing high ridges or prominent tubercles. Little is known about the biology of the beetles: adults are usually collected at light, or at the edges of streams or standing water and appear to be

semiaquatic, larvae are predaceous and probably inhabit the same habitats as the adults (ARCHANGELSKY 1997).

Three genera are recognized: *Epimetopus* Lacordaire, 1854 from the Neotropical and southernmost Nearctic Regions, *Eumetopus* Balfour-Browne, 1949 from the Oriental Region, and *Eupotemus* Ji & Jäch, 1998 from the Afrotropical Region. While the taxonomy of the Oriental *Eumetopus* was recently revised (JI & JÄCH 1998, JÄCH 2002, SKALE & JÄCH 2003), the taxonomy of the remaining two genera remains largely unresolved. This is most critical in the Neotropical genus *Epimetopus*, which seems to contain by far the largest number of species. Several taxonomic notes about *Epimetopus* have been published over the last 60 years, describing a few new species from various parts of South America (BALFOUR-BROWNE 1949), or focusing on the fauna of Brazil (ROCHA 1969), Argentina (OLIVA 1986) and southern USA and Central America (PERKINS 1979). However, a large number of species appear to remain undescribed. A complete taxonomic revision is currently in progress by P. Perkins.

This contribution focuses on the species of *Epimetopus* of the herein defined *E. mendeli* species group from the higher altitudes of the Andean Mts. Two new species are described and compared with *E. angulatus* Balfour-Browne, 1949. As knowledge of the adult morphology of Epimetopidae is rather limited and recently published studies either lack illustrations of the morphological structures (HANSEN 1991) or illustrate only the Oriental genus *Eumetopus* (ARCHANGELSKY et al. 2005), we provide a detailed description and scanning electron micrographs of the external morphology of one of the newly described species. The presence of larvae in the egg case carried by one female paratype of *E. mendeli* sp. nov. allowed us also to describe the morphology and chaetotaxy of the first larval instar in detail and clarify at least partly the reasons which led to the incompatibility of the previously published larval descriptions (ROCHA 1967, 1969; COSTA et al. 1988, ARCHANGELSKY 1997).

Material and methods

The holotypes of all three species treated in this paper, as well as several paratypes of *Epimetopus mendeli* sp. nov., were dissected, and genitalia placed either on a transparent plastic strip below the specimen in water-soluble dimethyl hydantoin formaldehyde resin (DMHF) (the holotype of *E. angulatus*), or cleared in lactic acid and then transferred through 95% ethyl alcohol into a drop of Euparal resin on a small piece of glass attached below the specimen. One paratype of *E. mendeli* was cleared in 10% NaOH solution, disarticulated and mounted as a permanent microscopic slide using the Euparal resin (the slide is deposited in NMPC). Habitus photographs were taken using a Canon EOS 550D digital camera with an MP-E 65 mm macrolens. Drawings were traced from photographs taken with the same equipment (for lateral views of the head) or using Nikon TS100 light microscope (for male genitalia). Scanning electron micrographs of uncoated specimens were taken at the Department of Palaeontology, National Museum in Prague, using a Hitachi S-3700N scanning electron microscope.

Larvae were cleared in 10% NaOH solution for 1–2 hours at room temperature or at 40°C in order to macerate the musculature, and then examined as temporary glycerine slides allowing the examination in different views; the head of one specimen was dissected in order to examine in detail the morphology and chaetotaxy of the frontoclypeus and mouthparts. Drawings were prepared using a drawing tube attached to an Olympus BX41 compound microscope;

photographs of larvae were taken using a Nikon Coolpix P6000 equipped with an Ibendorf ocular adapter which allowed its direct attachment to the above microscope. After examination, specimens were transferred from the temporary slides through the 95% ethanol to the permanent microscopic slide using the Euparal resin (the slide is deposited in NMPC). Two larval specimens were examined using the scanning electron microscope after being transferred to the acetone through solutions with increasing acetone : ethanol ratio and subsequent critical point drying (CPD) to prevent the collapse of weakly sclerotized body parts. Gold-coated specimens were then observed using the JEOL 6380 LV scanning electron microscope at the Laboratory of Electron Microscopy of the Faculty of Science, Charles University in Prague. Due to the original preservation of the larvae in dry condition, the micrographs of larval body parts were not good enough for publication, but were used to check the details of some body parts and to prepare the drawings on Figs. 42–46.

Label data are cited verbatim for all specimens, using a slash (/) to divide separate rows and double-slash (//) to divide separate labels. GPS data cited are adapted from locality labels in all cases. Morphological terminology of the adults follows KOMAREK (2004) and LAWRENCE et al. (2010). Larval morphological terminology follows ARCHANGELSKY (1997) and MINOSHIMA & HAYASHI (2011), with partial reference to the outline of the general morphology of beetle larvae by LAWRENCE (1991); for primary chaetotaxy of the larval head we refer to FIKÁČEK et al. (2008) and BYTTEBIER & TORRES (2009). The nomenclature of leg sensilla introduced by TORRES et al. (2011) was not adopted here for two reasons: (i) the nomenclature was based on the highly derived swimming leg of *Tropisternus sahlbergi* (Sharp, 1883) (Hydrophilidae) with numerous additional setae, and (ii) pore-like sensilla were omitted by these authors. In the chaetotaxy descriptions, we use the term ‘pore’ for any kind of sensillum without any prominent portion.

In the description of the primary head chaetotaxy, we use the following abbreviations: AN – antenna; FR – frontale; gAN – group of apical antennal sensilla; gAPP – groups of sensilla of the inner appendage of the maxilla; gFR – group of sensilla on frontale; gLA – group of apical sensilla of labial palpus; gMX – group of apical sensilla of maxillary palpus; LA – labium; MN – mandible; MX – maxilla; PA – parietale; SE – antennal sensorium. Numbers of sensilla with uncertain homology are prefixed by a question mark (e.g., FR?12), groups of sensilla for which the homology cannot be reliably stated separately are marked by a range of respective sensilla numbers (e.g., PA23–24). The chaetotaxy of other body parts has not yet been homologized across hydrophiloid taxa and is therefore mentioned in a purely descriptive way.

Material examined is deposited in the following collections:

- BMNH Natural History Museum, London, UK (M. V. L. Barclay, C. Taylor);
- KSEM Natural History Museum, University of Kansas, Lawrence, USA (A. Short);
- NHMW Naturhistorisches Museum, Wien, Austria (M. Jäch, A. Komarek);
- NMPC National Museum, Prague, Czech Republic (M. Fikáček, J. Hájek);
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, USA (P. Perkins);
- MZUSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (C. Costa);
- QCAZ Pontificia Universidad Catolica del Ecuador, Quito, Ecuador [temporarily deposited in NMPC];
- UNMSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (L. Figueroa, M. Alvarado);
- USNM United States National Museum of Natural History, Washington D.C., USA (W. Steiner);
- YMC Yūsuke Minoshina collection, Sapporo, Japan.

Taxonomy

Epimetopus mendeli species group

All three members of this species group can be easily distinguished from all other described species of *Epimetopus* by the combination of the following characters:

1. eyes incompletely divided into dorsal and ventral portion: anterior ocular canthus present, posterior canthus absent [both anterior and posterior canthi are developed and meet each other in many other *Epimetopus* species, hence their eyes are completely divided into dorsal and ventral halves; both canthi are reduced in an unidentified species from KSEM examined during this study];
2. median lobe of the aedeagus complex, bearing lateral projections (Figs. 3–5, lap) in the basal portion, and two pairs on the apex – longer ventral ones (Figs. 26–29, vl) and shorter dorsal ones (Figs. 26–29, dl) [in contrast, the median lobe is simple in all other described *Epimetopus* species, lacking lateral projections at the base and not apically subdivided into two pairs of lobes];
3. elytra with alternating ridge-like and flat intervals, flat intervals without series of elongate tubercles [elytral intervals between elytral ridges bear serially arranged elongate tubercles in several other *Epimetopus* species];
4. body large, more than 2.2 mm long, and general body coloration dark brown [this distinguishes the species treated here from the species of the *E. costatus* group which also have eyes incompletely divided by a canthus, but are characterized by a small, rufescent body].

Based on the combination of these characters, it seems probable that the three species treated in this paper form a monophyletic group. Although this requires testing by a phylogenetic analysis in the future, we here formally define the group as the ‘*Epimetopus mendeli* species group’ in order to facilitate orientation within the genus prior to a complete taxonomic and phylogenetic revision.

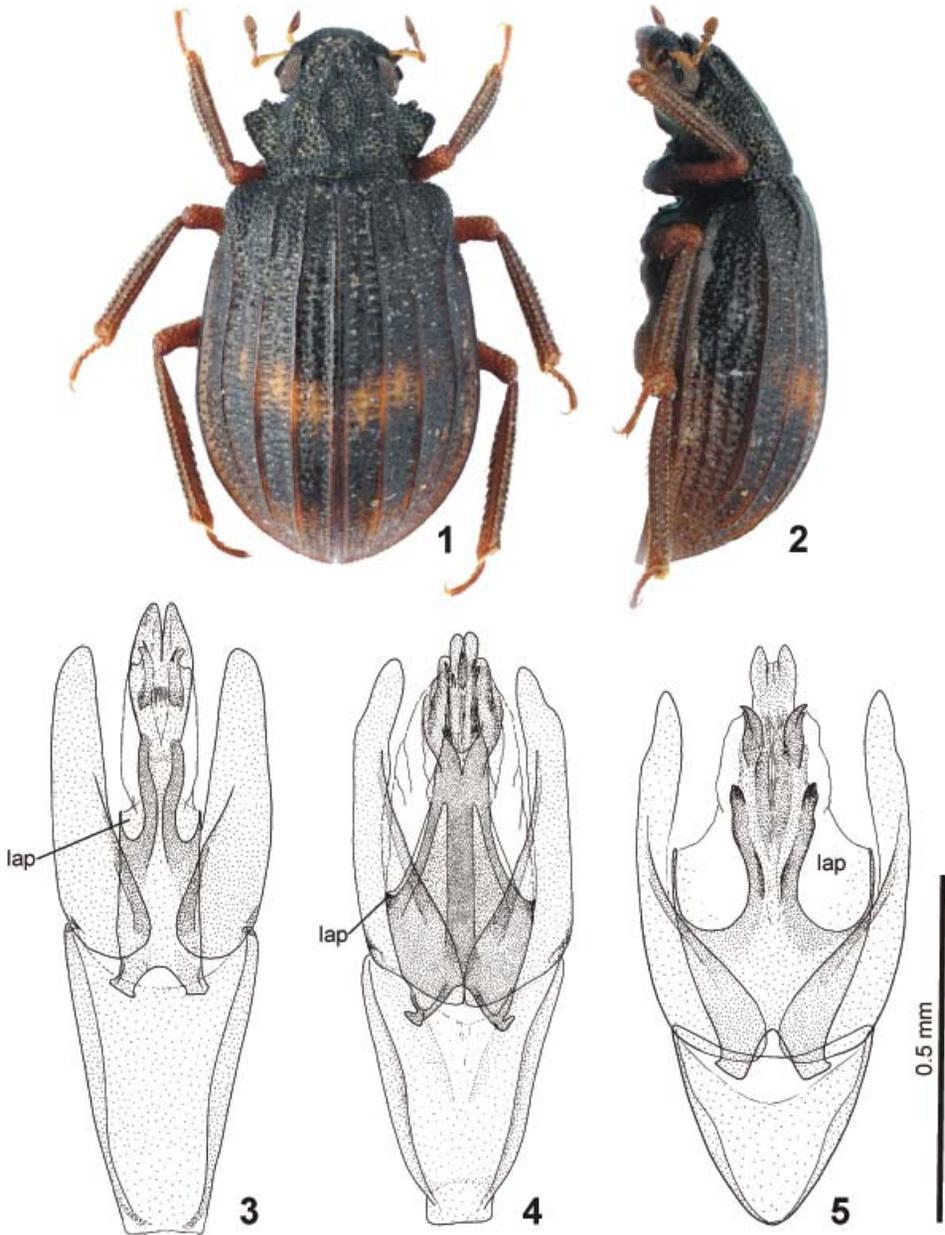
All three species included in the *E. mendeli* species group are very similar in external characters, and can only be reliably distinguished by the morphology of the aedeagus.

Epimetopus mendeli sp. nov.

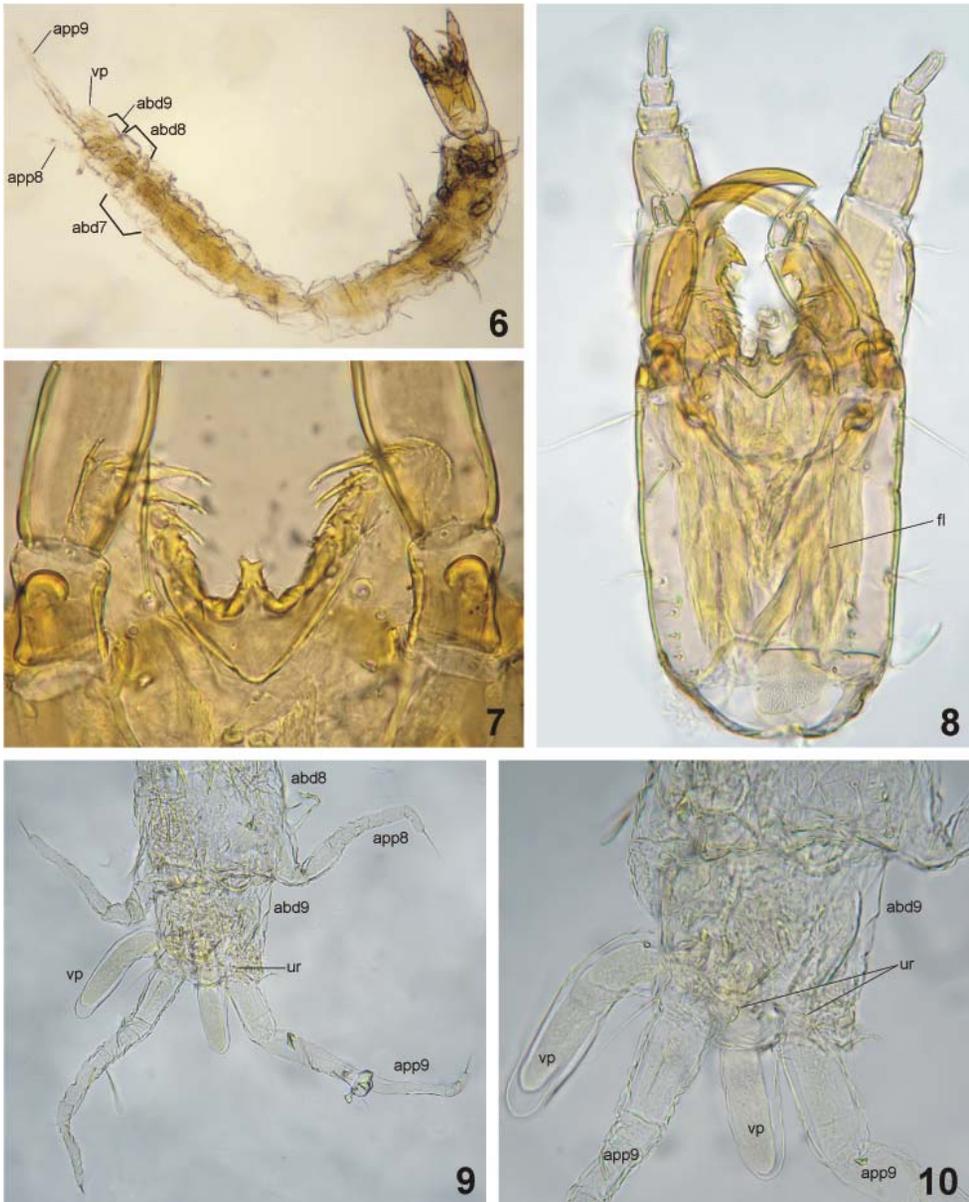
Type locality. Peru, Cuzco district, Kosñipata Valley, Cock of the Rock Lodge, 71°32'44.6"W 13°03'21.8"S, 1500 m a.s.l.

Type material. HOLOTYPE: ♂ (UNMSM): ‘Peru, Cuzco District / Kosñipata Valley / Cock of the Rock Lodge / W71°32'44.6"; S13°03'21.8" / 20.xi.–15.xii.2009, 1500m / Mendel, H. & Barclay, M.V.L. // BMNH{E} / 2009-126 / under stones/ by torrent’. PARATYPES: 18 spec. (BMNH, NMPC, KSEM, MCZ, NHMW, UNMSM): same label data as the holotype; 9 spec. (BMNH, NMPC, NHMW, UNMSM): ‘Peru, Cuzco District / Kosñipata Valley / Cock of the Rock Lodge / W71°32'44.6"; S13°03'21.8" / 20.xi.–15.xii.2009, 1500m / Mendel, H. & Barclay, M.V.L. // BMNH{E} / 2009-126 / light sheet’; 1 ♂ (KSEM): ‘PERU: Madre de Dios / Panliacolla Lodge [= Pantiacolla Lodge], Monk Saki Trail / Alto Madre de Dios River, 400m / 12°39'22"S, 71°13'55"W / 25 OCT 2000; R. Brooks / PERU1B00 098A ex: at black light’; 4 ♂♂ 3 ♀♀ (USNM): ‘PERU: Cuzco / Quince Mil / 28 Jan. 1979 / W. E. Steiner’; 1 ♀ (USNM): same label data plus ‘larvae from the egg case / carried by this specimen / used for description by / Fikáček et al. (2011)’.

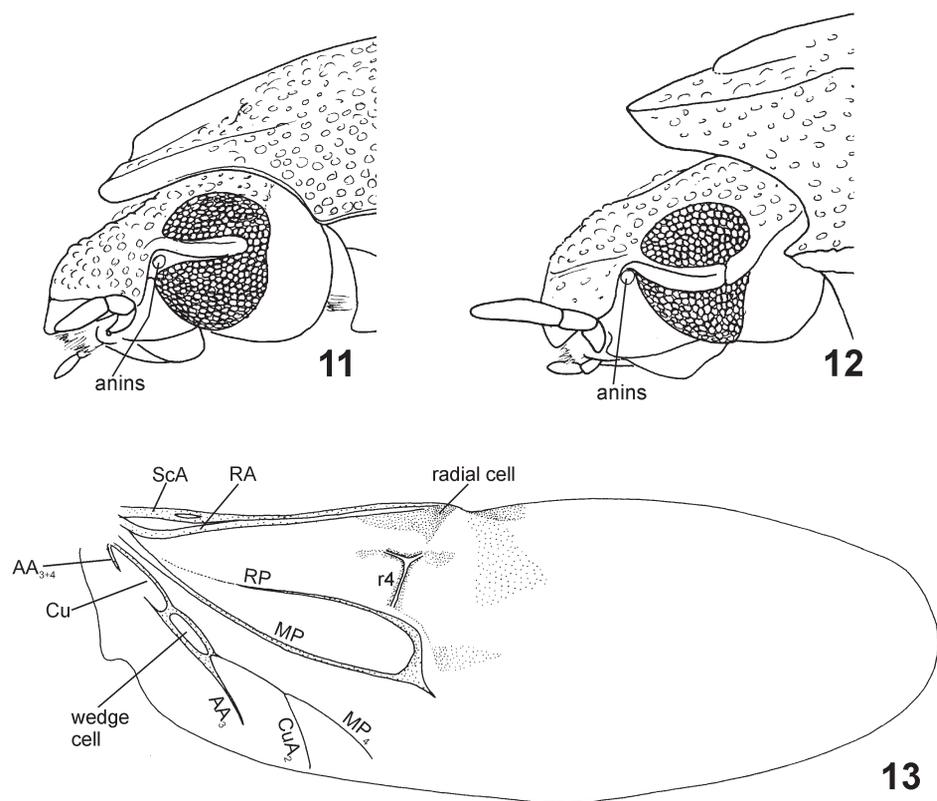
Additional adult material examined. 1 ♀ (USNM): ‘PERU: Cuzco / 25km SW Pilcopata / 16 Feb. 1979 / W. E. Steiner’.



Figs. 1–5. General habitus and aedeagi of *Epimetopus*. 1–2 – *E. mendeli* sp. nov., general habitus (body length 3.4 mm): 1 – dorsal view; 2 – lateral view. 3–5 – aedeagus of the holotype: 3 – *E. mendeli* sp. nov., 4 – *E. flavicaptus* sp. nov., 5 – *E. angulatus* Balfour-Browne, 1949. Abbreviations: *lap* – lateral process of median lobe.



Figs. 6–10. First instar larva of *Epimetopus mendeli* sp. nov. 6 – general habitus in ventrolateral view; 7 – detail of frontoclypeus; 8 – head capsule in dorsal view; 9 – abdominal apex in dorsolateral view; 10 – abdominal apex in dorsolateral view. Abbreviations: *abd7–9* – abdominal segments 7–9; *app8* – lateral projection of the abdominal segment 8; *app9* – lateral projection of the abdominal segment 9; *fl* – frontal line; *ur* – urogomphus; *vp* – ventral papillae.



Figs. 11–13. Morphological features of *Epimetopus*. 11–12 – head in lateral view: 11 – *E. mendeli* sp. nov.; 12 – *E. trogooides* (Sharp, 1875). 13 – hind wing of *E. mendeli* sp. nov. Abbreviations: AA – anterior branch of anal vein; *anins* – antennal insertion; *CuA* – anterior branch of cubital vein; *MP* – posterior branch of media; *r4* – transverse radial vein; *RA* – anterior branch of radius; *RP* – posterior branch of radius; *ScA* – anterior branch of subcosta.

Description. Body widely elongate (Figs. 1–2), widest at posterior third of elytra, moderately convex in lateral view. Dorsal surface piceous brown, elytra with a pale reddish half-moon-shaped spot at ca. posterior 0.4 of intervals 1–5. Ventral surface piceous black, epipleura turning reddish brown posteriorly; antennae reddish with brown antennal club, maxillary palpi reddish with palpomere 4 brown; trochanters and bases of femora dark brown to brown, distal portions of femora and entire tibiae and tarsi reddish. Body length 2.3–3.5 mm (holotype 3.1 mm), body width 1.3–1.8 mm (holotype 1.5 mm).

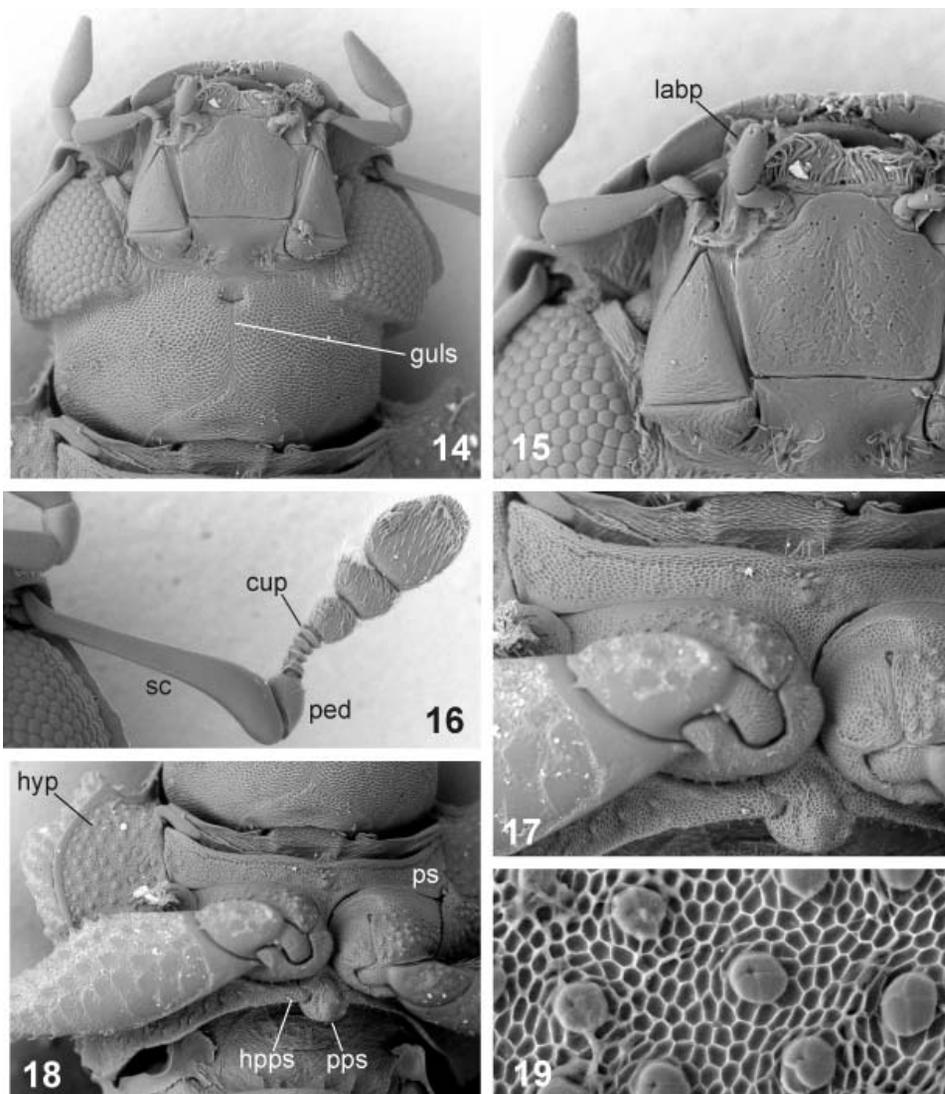
Head. Clypeus with uniform rather dense granulation, clypeus feebly concave, without marginal rim, lacking ‘systematic punctures’. Frons with granulation similar to that of clypeus, lacking ‘systematic punctures’ at inner margin of eyes. Eyes large, consisting of rather large ommatidia; elongate oval in dorsal view, incompletely divided into dorsal and ventral portion in anterior 0.7 by a wide canthus; ventral portion large, slightly larger than dorsal portion,

delimited posteriorly by short but distinct postocular bridge. Gular sutures widely joined in anterior 0.7, widely divergent in posterior 0.3. Labrum large, exposed, lacking granulation and 'systematic punctures'. Maxillary palpi moderately long, palpomeres 2 and 4 subequal in length, each ca. 2.5× as long as palpomere 3; palpomere 4 strongly asymmetrical, nearly straight on outer margin, widened in basal 0.4 on inner margin; cardo and stipes lacking 'systematic punctures'. Mentum ca. as long as wide, flat, bearing fine punctation; labial palpus short, basal palpomere the smallest, palpomere 2 ca. half as long as palpomere 3, palpomere 3 lacking spiniform sensillae, bearing only a few pore-like sensillae apically. Antenna with 9 antennomeres; scape slightly longer than antennomeres 2–9 combined, widest at distal margin; pedicel small, bulbous; antennomeres 3–6 very short, subequal in length, antennomere 6 (cupula) not differentiated from antennomeres 3–5 in size and shape; antennomeres 7–9 forming large pubescent club, first club antennomere the shortest and narrowest, 9th antennomere the longest and widest, ca. as long as antennomeres 7–8 combined.

Prothorax. Pronotum slightly wider than long; anterior lobe large, covering large basal portion of head up to anterior margin of eyes, bearing a deep distinct groove at anterior margin mesally; lateral lobes large, directed anterolaterad, nearly rectangular in shape. Pronotal sculpture consisting of four elevated ridges; two median ones close to each other, slightly sinuate in shape and joining each other anteriorly, high and distinct especially in their anterior third, defining a median groove; lateral ones weak and rather indistinct. Entire surface of pronotum except for medioanterior margin and anterior third of median ridges covered by moderately dense granulation similar to that of clypeus. Prosternum ca. as long as half of procoxal cavity, flat, bearing a reticulate microsculpture on the whole surface with a few isolated granules at midwidth; prosternal process strongly narrowing between procoxae, but widened again posteriorly, joining the hypomeral process posteriorly (hence, procoxal cavities closed posteriorly). Hypomeron divided by a ridge into the lateral narrow granulate portion and large mesal portion bearing the reticulate microsculpture and scattered granules.

Mesothorax. Scutellar shield slightly longer than wide, rounded posteriorly. Elytra narrowest subanteriorly, widest in posterior 0.3. Each elytron with 10 longitudinal punctuate striae, punctures large, close to each other, not connected by a longitudinal tubercles; scutellar stria absent. Each elytron elevated on sutural interval and bearing three additional high elevated ridges on intervals 3, 5 and 7; ridge on interval 5 interrupted in anterior 0.2, ridges on intervals 3 and 7 complete, ridge on interval 7 reaching large humeral bulge; all ridges reaching subapically. Remaining intervals (i.e. those not elevated to ridges) bearing irregular series of scattered granules; 'systematic punctures' absent from all elytral intervals. Elytral interval 11 with additional highly elevated ridge forming a false elytral margin in dorsal view. Epipleuron not divided into pubescent inner and bare outer portions, wide throughout, reaching elytral apex. Mesoventrite distinctly divided from mesanepisterna, bearing highly elevated transverse ridge on mesoventral process. Anapleural sutures nearly straight, joining anteriorly; mesanepisterna joining mesally. Anterior collar of mesothorax well defined, widest mesally. Mesepimeron large, subtriangular. Whole ventral surface of mesothorax except for anterior portion of mesoventrite and anterior collar bearing reticulate microsculpture, posterior portions of mesoventrite, mesanepisterna and whole mesepimera with scattered granules. Mesoventral process short, loosely contacting metaventral process.

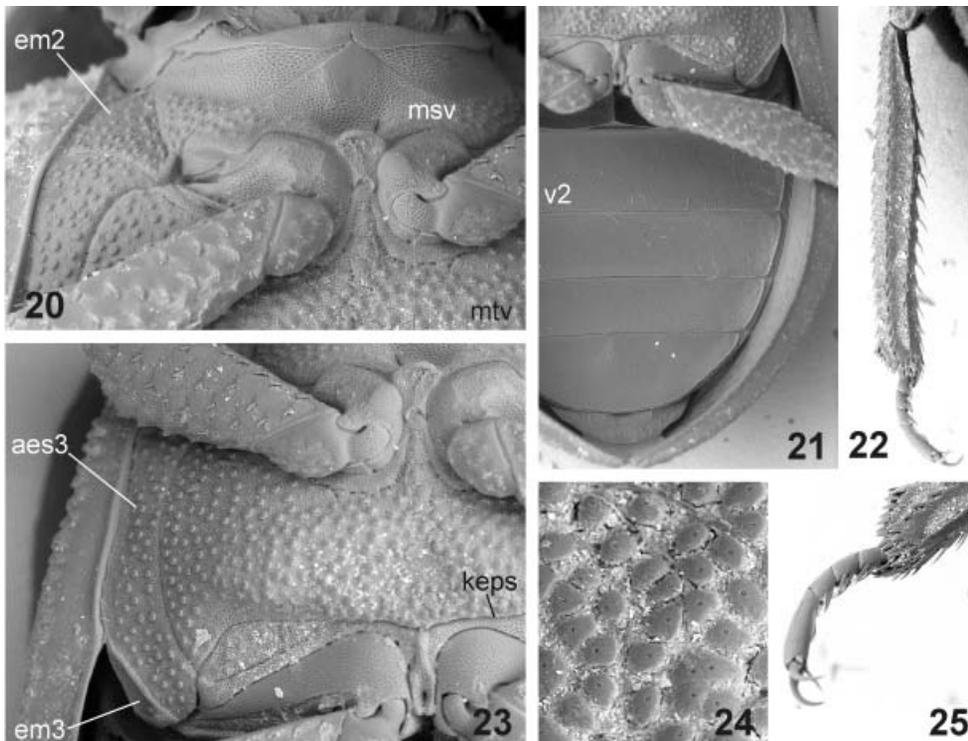
Metathorax. Ventral portion of metathorax slightly longer than mesoventrite, bearing reticulate sculpture and scattered granules over its entire surface. Metaventral process long and rather wide, projecting far between mesocoxae; anterolateral rim of metaventrite distinct, reaching submesally. Katepisternum very wide sublaterally, divided by very distinct



Figs. 14–19. External morphology of *Epimetopus mendeli* sp. nov. 14 – head, ventral view; 15 – detail of mouthparts; 16 – antenna; 17 – detail of prosternum; 18 – prothorax, ventral view; 19 – microsculpture of prothoracic hypomeron. Abbreviations: *cup* – cupula; *guls* – gular sutures; *hpps* – hypomeral process; *hyp* – hypomeron; *labp* – labial palpus; *ped* – pedicel; *pps* – prosternal process; *sc* – scapus.

katapisternal suture, bearing large deeply bifurcate metacoxal process. Metanepisternum ca. 7.5× as long as wide, lacking anterior transverse ridge strongly widened and projecting mesad anteriorly (nearly contacting mesocoxal cavity), bent mesad posteriorly and delimiting the outer wall of metacoxal cavity. Posteroventral portion of metepimeron widely exposed sublaterally. Metacoxal cavities not reaching lateral portion of metathorax. Hind wing well developed, with rather large distal area lacking any veins; RP preserved nearly from base, basal cell incompletely delimited due to interrupted AA_{3+4} ; wedge cell well developed, very small, AA_3 well developed, bifurcation of MP_4 and CuA_2 preserved as weak remnants only; jugal lobe preserved.

Abdomen with 5 visible ventrites. Ventrite 1 with large metacoxal grooves covering nearly its whole surface. Ventrites 2–5 flat, lacking pubescence; ventrites 2–3 and anterior portion of ventrite 4 with fine punctation (i.e. having shagreened appearance when examined under the binocular at 90× magnification), posterior portion of ventrite 4 and whole ventrite 5 shiny, without punctation; lateral margins of ventrites 2–4 and posterior margin of ventrite 5 with fine submarginal ridge. Posteromedian portion of ventrite 5 without emargination.



Figs. 20–25. External morphology of *Epimetopus mendeli* sp. nov. 20 – mesothorax, ventral view; 21 – abdomen; 22 – middle leg; 23 – metathorax, ventral view; 24 – detail of pronotal granulation; 25 – detail of middle tarsus. Abbreviations: *aes3* – metanepisternum; *em2* – mesepimeron; *em3* – metepimeron; *keps* – katapisternal suture; *msv* – mesoventrite; *mtv* – metaventrite; *v2* – second abdominal ventrite.

Legs. Profemora widest in basal third, covered with large tubercle-like projections on ventral face, bearing dense pubescence in basal third dorsally; mesofemora apparently widened at midlength, bearing stout decumbent sparsely arranged setae on ventral surface; metafemora long and slender, only indistinctly widened in distal third, ventral surface with same setation as mesofemora. All femora without tibial grooves. Pro- and mesotibiae distinctly longer than femora, metatibiae ca. as long as metafemora; all tibiae narrowest basally, slightly widened subbasally and then conical throughout in meso- and metatibiae, protibiae distinctly widened ca. at midlength; all tibiae bearing series of equidistant series of stout setae, those on inner face of metatibiae longer and thinner than remaining ones. Tibial spurs short, only slightly longer than other spines on tibial apices. Tarsi with five tarsomeres, tarsomere 1 shortest, rather indistinct in ventral view, tarsomeres 2–4 subequal in length, ca. as long as tarsomere 5 when combined; each tarsomere with few stout erect setae ventrally and few short decumbent setae on dorsal face. Claws moderately large, semicircular.

Male genitalia (Figs. 3, 26–27). Aedeagus 0.9 mm long. Phallobase symmetrical, widely rounded basally, slightly shorter than parameres. Paramere wide throughout, continuously arcuate on outer margin, apex widely rounded. Median lobe narrower than paramere; basal portion narrow, forming ca. 0.4 of length of median lobe, projecting into small lateral and large median projections ca. at midlength; apical portion bilobate, bearing two sets of spines subapically. Sternite 9 with semicircular median portion. Sternite 8 without median antieriad-directed projection.

Variation. The type material varies particularly in size, which seems to be connected to sex (all dissected male specimens are smaller and less robust than female specimens (recognized by the presence of an egg case and/or projecting cerci). The shape of the lateral margin of lateral lobes of the pronotum varies from straight to slightly concave or shallowly excised. The pale spot on the elytra is rather indistinct in several paratypes. All specimens examined are constant in the characters mentioned in the differential diagnosis, including those of male genitalia.

Etymology. The species is dedicated to one of its collectors, Howard Mendel, recently retired Head of Collections at the Natural History Museum, London. His persistence in climbing down the ravine to extend the type series of this new species mirrors his persistence in fighting for the best interests of the Entomology Collections throughout his successful career.

Biology. The holotype and 18 paratypes of this species were collected under loose rocks and rock litter lying on or partly buried in wet gravel substrate, close to the edge of a very fast flowing mountain stream. Males and females (generally with egg cases) were found in groups under stones. The stream flows through good quality cloud forest, but can be accessed by climbing down a ravine beneath a road bridge close to the entrance to ‘Cock of the Rock Lodge’. The habitat is not species-rich, although *Oxycheila pseudonigroaenea* (Horn, 1938) (Carabidae: Cicindelinae, det. By F. Cassola) and some smaller Carabidae were abundant, and the Torrent Duck *Merganetta armata* Gould, 1842 (Aves: Anatidae), a predator in fast flowing Andean streams, was present. An additional 9 paratypes of *E. mendeli* were collected at MV light within a few hundred meters of the stream.

Distribution. The species is known from three rather closely situated localities on the eastern slope of the Andes Mts. in the Cusco and Madre de Dios provinces, Peru.

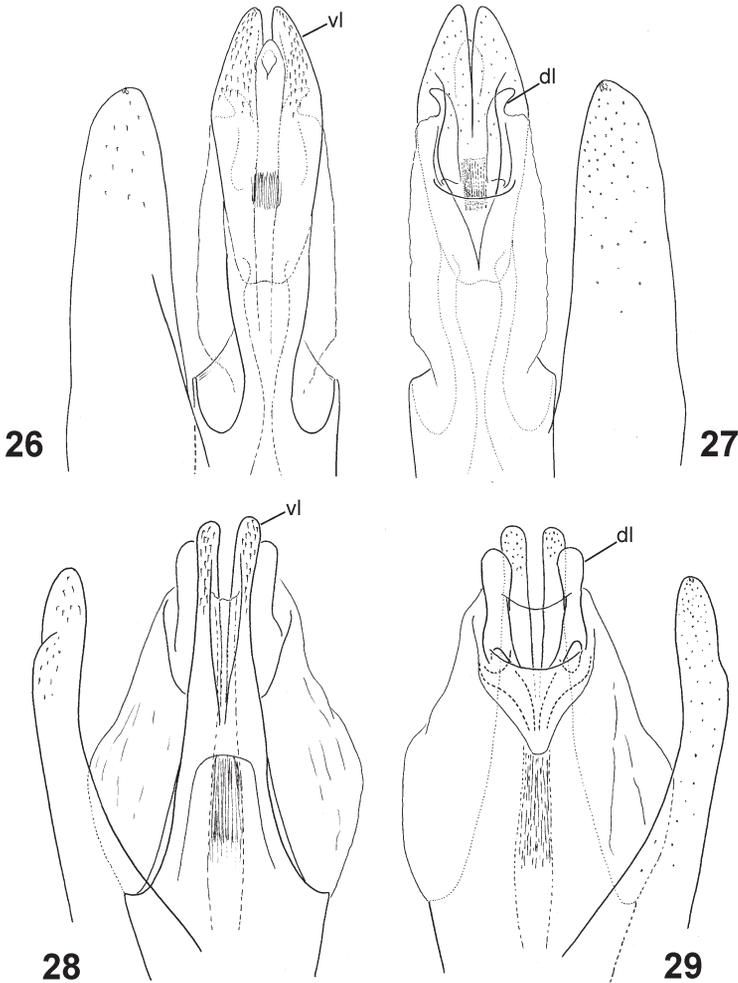
Epimetopus flavicaptus sp. nov.

Type locality. Ecuador, Napo Province, 4.4 km NNW of El Chaco, 00°18'48"S 77°50'21"W, 1680 m a.s.l.

Type material. HOLOTYPE (QCAZ): ♂, 'ECUADOR, prov. Napo / 4.4 km NNW of EL CHACO / S00°18'48" W77°50'21" / 28–30.xi.2006; 1680 m / M. Fikáček & J. Skuhrovec lgt. // YPT [= yellow pan trap]: on the gravel banks of a / stony stream in the primary / forest (very rainy weather)?

Additional material examined. 3 ♀♀ (USNM): 'ECUADOR: / Napo / Tena / 27 May 1977 / W. E. Steiner'

Differential diagnosis. Body length 2.7 mm, body width 1.5 mm. Corresponding with *E. mendeli* sp. nov. in all described external characters except the following: elytral pale half-



Figs. 26–29. Details of the aedeagal morphology. 26–27 – *Epimetopus mendeli* sp. nov., paratype from the type locality: 26 – ventral view; 27 – dorsal view. 28–29 – *E. flavicaptus* sp. nov., holotype: 28 – ventral view; 29 – dorsal view. Abbreviations: *dl* – dorsal lobe; *vl* – ventral lobe.

moon-shaped spot very indistinct; abdominal ventrites with slightly uneven surface, shiny and lacking shagreen on whole surface except for extreme base.

Male genitalia. Aedeagus (Figs. 4, 28–29) 0.8 mm long. Phallobase symmetrical, narrowing basad, rectangular basally, slightly shorter than parameres. Paramere rather narrow in apical half, outer margin with a low blunt tooth in apical fifth, slightly concave on outer margin subapically, apex narrowly rounded. Median lobe wider than paramere; basal portion moderately wide, projecting into small lateral projections at basal third and small submedian projection in apical third; apical portion quadrilobate, with two sets of small hooks subapically.

Etymology. The species name refers the fact that the type specimen was collected in a yellow pan trap (*flavus* = yellow, Lat.; *captus* = that which is taken, Lat.). Adjective.

Biology. The holotype was collected in a yellow pan trap installed on the stony bank of a mountain stream flowing from the primary cloud forest.

Distribution. Known from two localities ca. 80 km apart on the eastern slope of the Andes Mts. in the Napo Province, Ecuador. However, as reliable identification is only possible using characters of the male genitalia, the identification of the above females is tentative and needs to be confirmed by a male from the same area.

Epimetopus angulatus Balfour-Browne, 1949

Type locality. Bolivia, La Paz Department, Yungas valley.

Type material examined. HOLOTYPE: ♂ (BMNH): ‘Type // Yungas Valley / Bolivia. / 12–19.vi.1937 // H. E. Hinton / collector // Epimetopus / angulatus Type! / Balfour-Browne det. // Hinton Coll. / B.M.1939-583’. PARATYPES: 2 spec. (BMNH): same label data as the holotype, but with the first label ‘Para- / type’.

Differential diagnosis. Body length 2.8 mm, body width 1.6 mm. Corresponding with *E. mendeli* sp. nov. in all described external characters except for elytral pale half-moon-shaped spot absent. For detailed description see BALFOUR-BROWNE (1949).

Male genitalia (Fig. 5). Aedeagus 0.8 mm long. Phallobase symmetrical, strongly narrowing basad, subangulate basally, much shorter than parameres. Parameres very narrow in apical half, without a trace of a blunt tooth subapically, slightly concave on outer margin in apical fourth, subangulate at apex. Median lobe much wider than paramere, basal portion rather wide basally, strongly widened at midlength of median lobe projecting into large lateral and large submedian projections ca. at midlength of median lobe. Apical portion quadrilobate, with rather large sets of subapical hooks.

Biology. Unknown.

Distribution. Known from the type locality in Bolivia (BALFOUR-BROWNE 1949) and from the Tucumán Province in northern Argentina (OLIVA 1986).

Larval morphology

Epimetopus mendeli sp. nov.

Larval material examined. 12 first instar larvae found in the egg case carried by the female paratype with the following label data: ‘PERU: Cuzco / Quince Mil / 28 Jan. 1979 / W. E. Steiner // larvae from the egg case / carried by this specimen / used for description by / Fikáček et al. (2011)’ [one slide-mounted larva and two larvae in glycerine

deposited in NMPC, two larvae in glycerine in YMC, three larvae in glycerine in a microvial attached to the specimen and returned to USNM, one gold-coated larva mounted on the label returned to USNM].

General morphology. Body (Fig. 6) elongate, thorax and abdomen combined ca. $8\times$ longer than head, slender, almost parallel-sided. Body length ca. 1.6 mm (measured in partly distorted specimens).

Head (Figs. 8, 30–31) subquadrate in shape, elongate, ca. $1.5\times$ longer than wide, hyperprognathous, with occipital foramen shifted dorsally. Head width 0.15–0.17 mm ($n = 4$). Frontal lines U-shaped, arising on outer margin of antennal socket and reaching posterior margin of head capsule, slightly bent mesad at midlength; coronal line indistinct. Antennal sockets situated on the laterodorsal portion of head. Frontoclypeus (Fig. 32) symmetrical; nasale small, in shape of slightly asymmetrical quadrate projections. Epistomal lobes large, symmetrical, largely overlapping nasale, well-sclerotized mesally with few teeth on inner margin between epistomal (gFR2) setae, largely membranous laterally, lateral margin with fine membranous finger-like projections. Dorsal mandibular articulation covered laterally by a projection of parietale (Fig. 35). Stemmata indistinct in examined larvae. Gular suture absent, posterior tentorial pits distinct, situated anteromesally. Cervical sclerites indistinct (probably absent) in examined larvae.

Antenna (Fig. 36) 3-segmented, short and rather stout. Scape ca. half as long as pedicel, flagellum ca. as long as scape. Pedicel with only one sensorium (SE1), sensorium as long as flagellum.

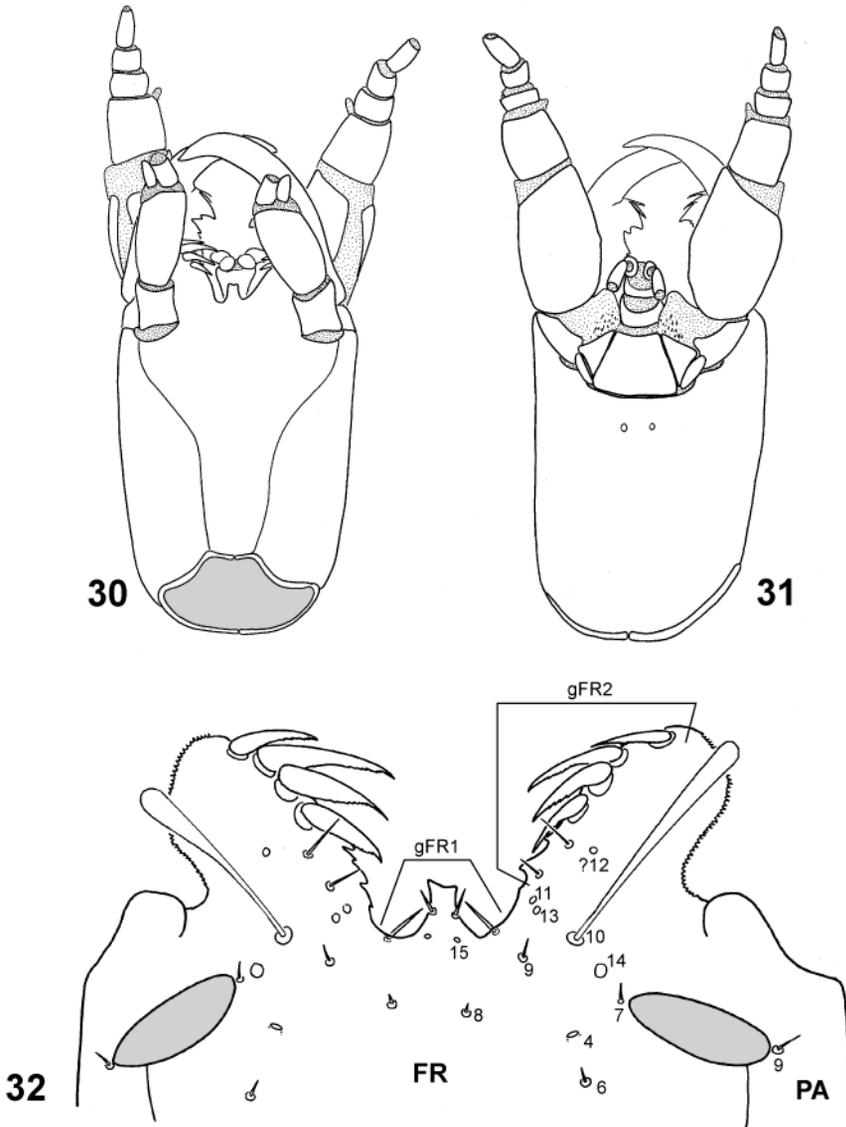
Mandibles (Fig. 39) symmetrical, with falcate apical portion. Retinaculum with two teeth; distal tooth small, bearing a spine-like cuticular projection apically; basal tooth large, anvil-shaped, partly underlying the basal portion of distal tooth, bearing a set of spiny semimembranous projections apically as well as basally (Fig. 42). Basal inner face with several small teeth bearing spines at apices, and with a basal field of fine spine-like cuticular projections.

Maxilla (Figs. 37–38) 6-segmented (including cardo), massive, ca. twice as long as antenna. Cardo large, situated laterally, and associated with two additional sclerites lying between cardo and labium. Stipes the longest and widest, cylindrical, largely sclerotized ventrally, but only partially sclerotized dorsally; sclerotized dorsal portions with fine series of spicules. Maxillary palpus with 4 segments, palpomere 1 ca. half as long as stipes, completely sclerotized; palpomeres 2–3 short, palpomere 4 thin and elongate; inner appendage small, largely membranous. Maxillary articulating area in shape of a membranous lobe bearing fine spines mesally.

Labium (Figs. 40–41) freely articulated with parietale at straight submental line (ventral anterior margin of parietale straight, not excised); submentum large, trapezoidal, rather tightly associated with laterally lying triangular sclerite of maxillary articulating area. Mentum and prementum short, transverse. Labial palpus 2-segmented, with basal palpomere ca. $3\times$ shorter than distal palpomere; ligula absent. Labium largely covered by frontoclypeus in dorsal view.

Thorax. Prothorax wider than head capsule. Proscutum (Fig. 47) formed by a large plate subdivided mesally by a sagittal line. Ventral portion of prothorax (Fig. 48) with a pair of triangular presternal sclerites articulating posterolaterally with a precoxal sclerite connecting the presternum with coxal articulation; remaining parts largely membranous except for very weakly sclerotized laterotergites. Mesonotum with a pair of large subtriangular sclerites

meeting mesally in anterior half of mesothorax, posterior portion membranous without clear sclerites. Metathorax membranous, without distinct sclerotized areas. Legs moderately long, clearly visible in dorsal view, all pairs similar in shape; prothoracic legs slightly shorter than meso- and metathoracic ones. Leg 5-segmented (Figs. 49–50); procoxae nearly contiguous



Figs. 30–32. Head capsule of the first larva of *Epimetopus mendeli* sp. nov. 30–31 – general view of the head capsule: 30 – dorsal view; 31 – ventral view. 32 – detail of frontoclypeus.

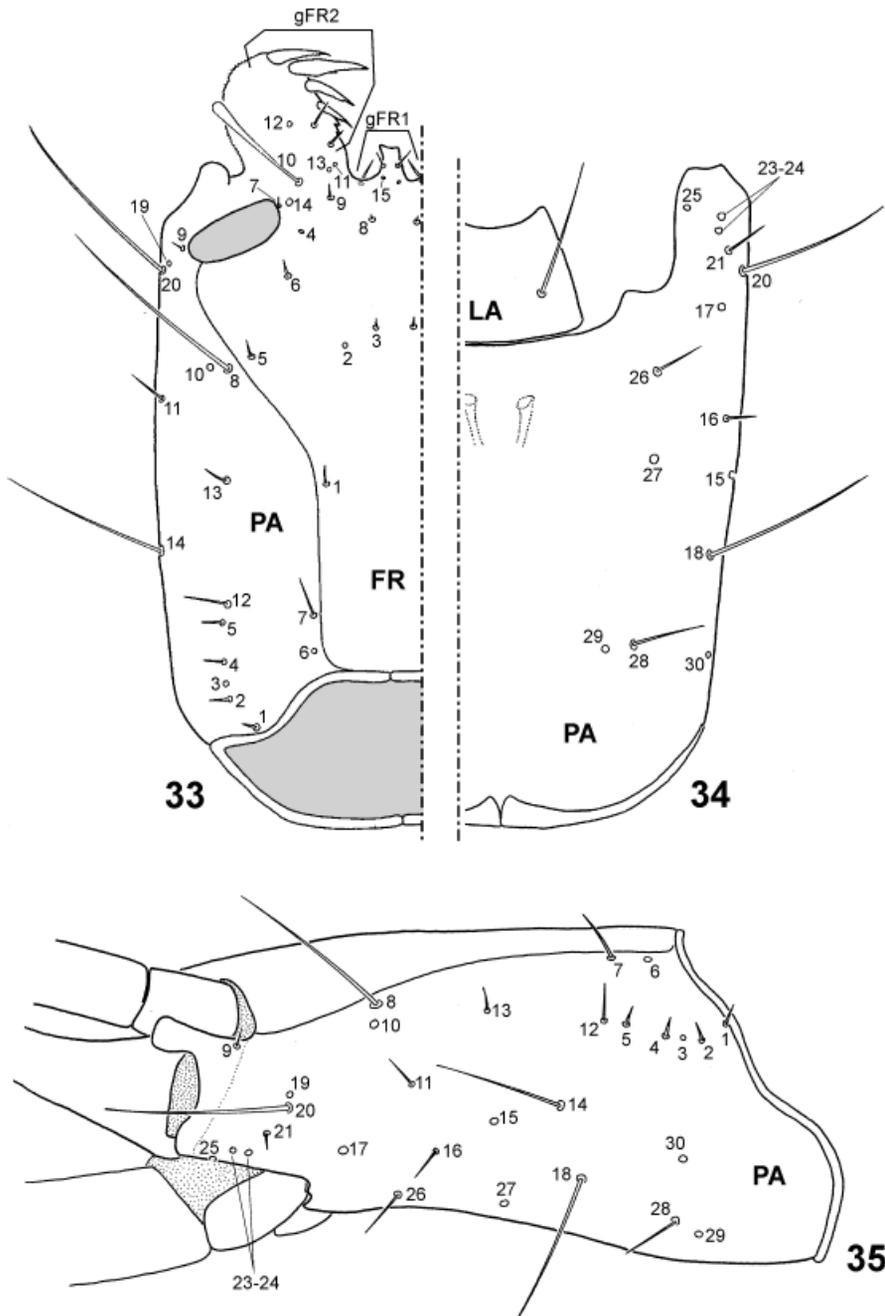
mesally, meso- and metacoxae well separated from each other; trochanter ca. as long as femur, rather firmly joined to each other; tibiotarsus slender, slightly shorter than trochanter and femur combined. Claw slightly shorter than tibiotarsus, apically slightly bent ventrad.

Abdomen with 9 well developed membranous segments. Segments 2–8 each subdivided into shorter anterior fold and longer posterior fold (Figs. 51–52; af, pf). Segment 1 bare ventrally, ventral portions of segments 2–7 each with a transverse mound bearing several transverse rows of fine cuticular spines on anterior part of the posterior fold (Fig. 52), the spines larger laterally, reduced to nearly indistinct mesally. A pair of spiracles situated dorsolaterally on larger fold of each segment, spiracles biforous, but largely reduced in size (Figs. 51–52, sp7). Posterior part of segment 8 (Figs. 9, 53–54, abd8) with a low spiracular tubercle dorsolaterally and a long unsegmented finger-like projection laterally on each side. Segment 9 (Figs. 9–10, 53–54; abd9) with a pair of long membranous projections laterally and a pair of tiny urogomphi dorsally (Figs. 9–10, 53; ur); ventral portion with a pair of large membranous finger-like projections ('ventral papillae', Figs. 9–10, 53–54; vp). Spiracular atrium not developed.

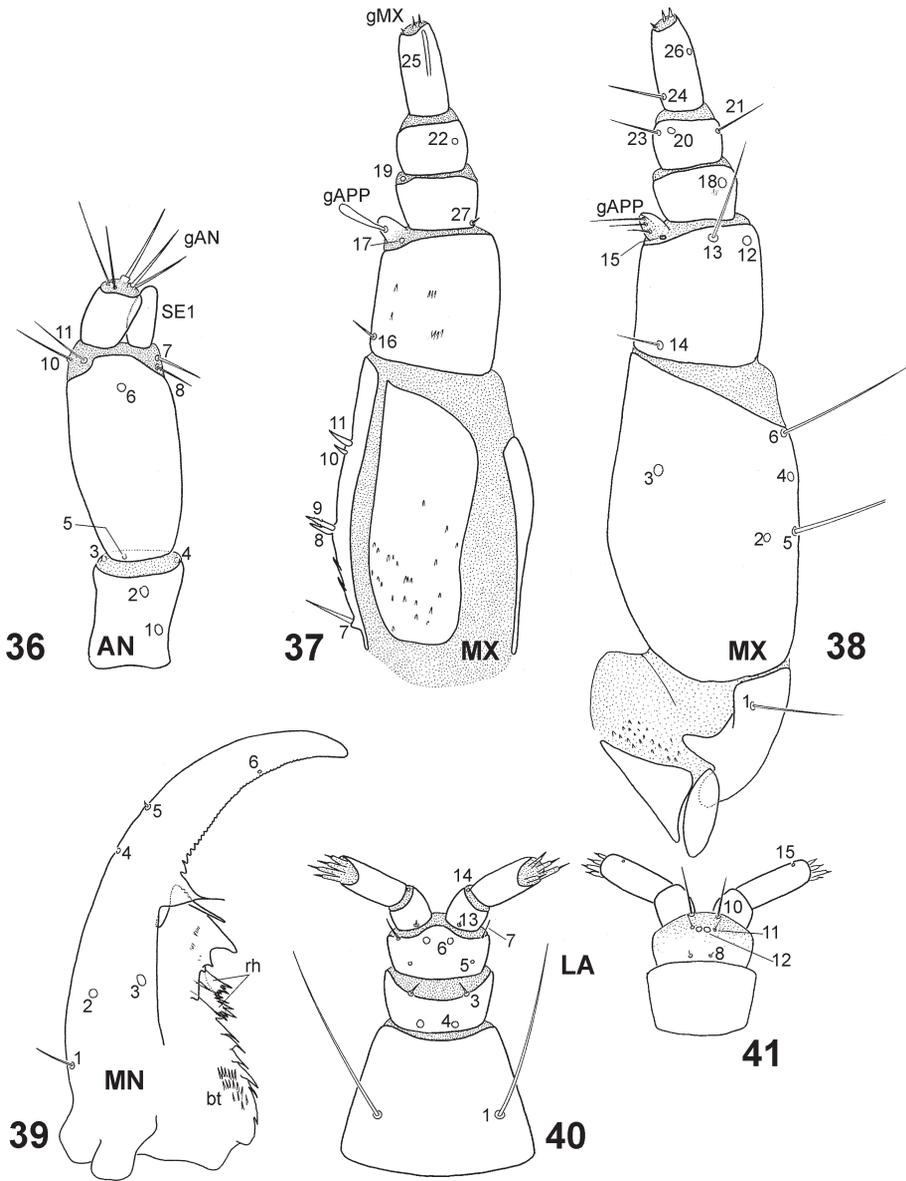
Primary chaetotaxy. Head. Frontale with 46 sensilla (Figs. 32–33). Central part with three pairs of sensilla diverging posteriad, small seta FR1 situated at frontal line, pore FR2 and small seta FR3 close to each other more mesally. Lateral portions posterior to antennal socket each with two small setae and one pore: seta FR5 situated at frontal line, seta FR6 anteromesally of it, and pore FR4 even more anteromesally. Inner part of antennal socket with a small seta FR7, central portion of frontale between antennae with two pairs of small setae (FR8–9) diverging anteriad. Nasale with a group of four moderately long trichoid setae (gFR1) and with a basal pair of pores (FR15). Each epistomal lobe with a group of six setae (gFR2) situated on inner margin, two mesal short and trichoid, four lateral large, flat and with lobate margins (Fig. 43); a long scale-like seta FR10 situated anteromesally of antennal socket, a pore FR14 between the seta and antennal socket; two closely situated pores (FR11 and FR13) situated mesally at base of epistomal lobe, a pore FR12 in central portion of the lobe.

Parietale with 29 sensilla each (Figs. 33–35). Posterior portion with a row of five short setae (PA1–2, PA4–5 and PA12) and one pore (PA3) at midwidth of dorsal parietale portion, and with a pore (PA6) and a short seta (PA7) at frontal line. Anterior portion at frontal line with a pore (PA10) and a long trichoid seta (PA9). Lateral portion with a pore (PA30) posteriorly, two long setae (PA14 and PA18) situated more anteriorly, two short setae (PA11 and PA16) situated even more anteriorly, and pores PA15 and PA17 situated anteriorly of PA14 and PA16, respectively; anterior part with a long seta PA20, a pore (PA19) situated dorsally of it and a short seta (PA21) situated more ventrally; sensilla PA22 absent. Ventral portion at the mandibular articulation with three closely standing pores (PA23–25) and a longitudinal row of four sensilla: seta PA26 situated anteriorly, pore PA27 in anterior third, and seta PA28 and pore PA29 in posterior third.

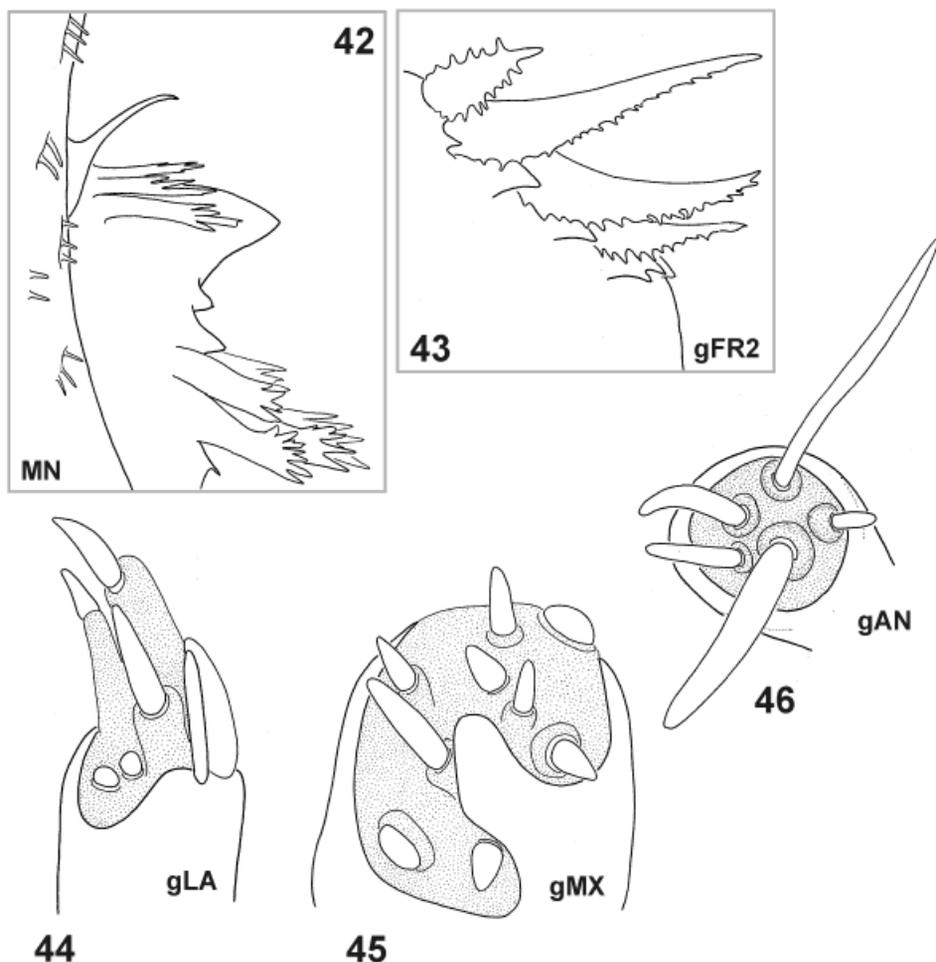
Antennae each with 14 sensilla (Fig. 36). Scape with two pores (AN1–2) situated dorsally and three pores (AN3–5) situated in intersegmental membrane, pedicel with one pore (AN6) dorsally in sclerotized area, two moderately long setae (AN10–11) situated mesally and two moderately long setae (AN7–8) situated laterally below antennal sensorium. Sclerotized portion of flagellum lacking sensilla, apical group of sensilla (gAN) bearing two long and three short setae (Fig. 46).



Figs. 33–35. Primary chaetotaxy of the head capsule of the first instar larva of *Epimetopus mendeli* sp. nov. 33 – dorsal view; 34 – ventral view; 35 – lateral view.



Figs. 36–41. Antenna and mouthparts of the first instar larva of *Epimetopus mendeli* sp. nov. 36 – antenna, dorsal view; 37 – maxilla, dorsal view; 38 – maxilla, ventral view; 39 – mandible, dorsal view; 40 – labium, ventral view; 41 – labium, dorsal view.

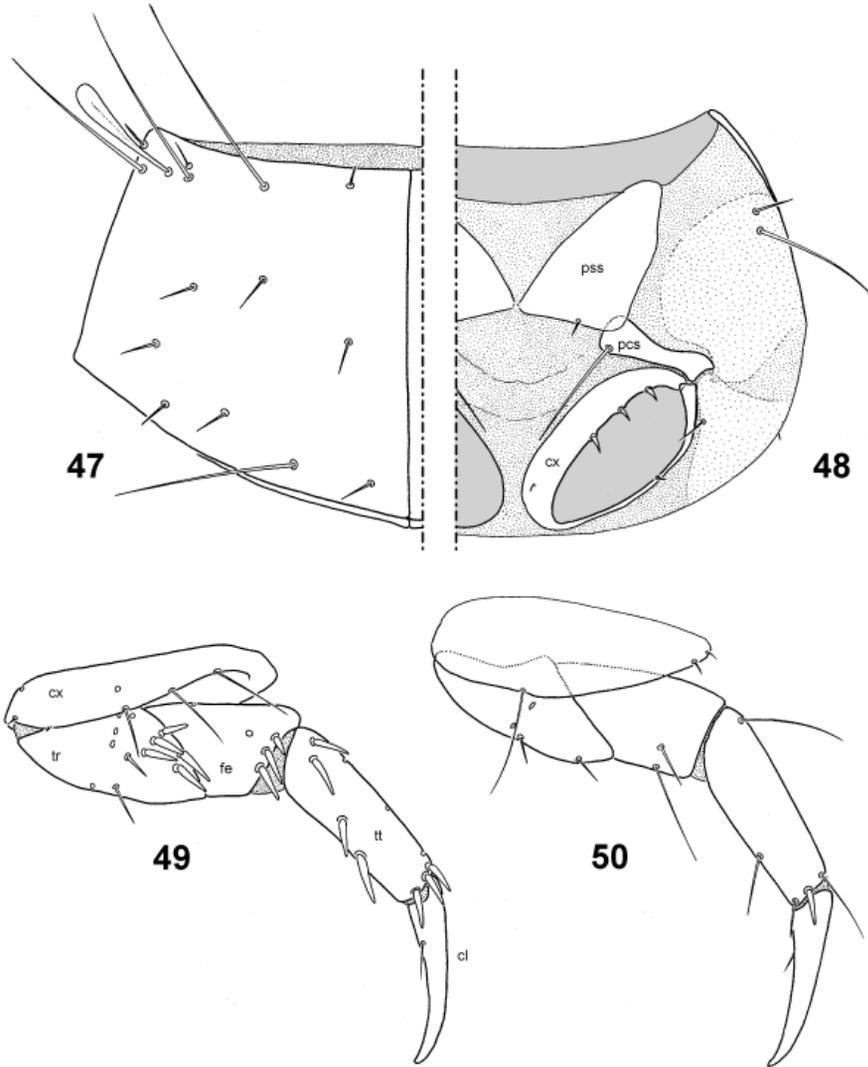


Figs. 42–46. Details of the head morphology of the first instar larva of *Epimetopus mendeli* sp. nov. (redrawn from SEM micrographs). 42 – retinaculum of the mandible, dorsal view; 43 – frontoclypeal setae gFR2, dorsal view; 44 – apical field of labial palpus, lateral view; 45 – apical field of maxillary palpus, apical view; 46 – apical field of antennal flagellum, apical view.

Mandible each with 6 sensilla (Fig. 39). A moderately long seta (MN1) situated basally on outer face, two pores (MN2–3) on dorsal surface in basal third, a pore (MN4) and a short seta (MN5) on outer face in distal third and a small pore (MN6) subapically on inner face.

Maxillae (Figs. 37–38) each with one long seta (MX1) situated ventrally on cardo. Stipes with five spine-like setae on inner surface: MX7 situated at very base, MX8–9 in basal third, one ventrally of the other, MX10–11 in distal third. Ventral surface with one pore (MX3), lateral surface with two pores (MX2 and MX4) and two long setae (MX5–6). Palpomere 1

with two moderately long setae situated basally on lateral surface, MX14 ventrally of MX16; distal margin ventrally with a seta (MX13) and a pore (MX12). Base of inner appendage with one pore ventrally (MX15) and one dorsally (MX17). Inner appendage (gAPP) with two moderately long seta and a long scale-like seta. Palpomere 2 with one tiny seta (MX27) basally and one pore (MX18) distally. Palpomere 3 with a series of sensilla at distal margin,



Figs. 47–50. Thorax of the first instar larva of *Epimetopus mendeli* sp. nov. 47 – proscutum; 48 – ventral portion of prothorax; 49 – metathoracic leg, anterior view; 50 – metathoracic leg, posterior view. Abbreviations: *cl* – claw; *cx* – coxa; *fe* – femur; *pcs* – precoxal sclerite; *pss* – presternal sclerite; *tr* – trochanter; *tt* – tibiotarsus.

setae MX21 and MX23 laterally, pores MX20 and MX22 dorsally or ventrally, respectively. Palpomere 4 with a long basal seta (MX24) and a pore MX26 and a digitiform sensilla situated subapically. Apical membranous area with 9 short to very short sensilla (gMX, Fig. 45).

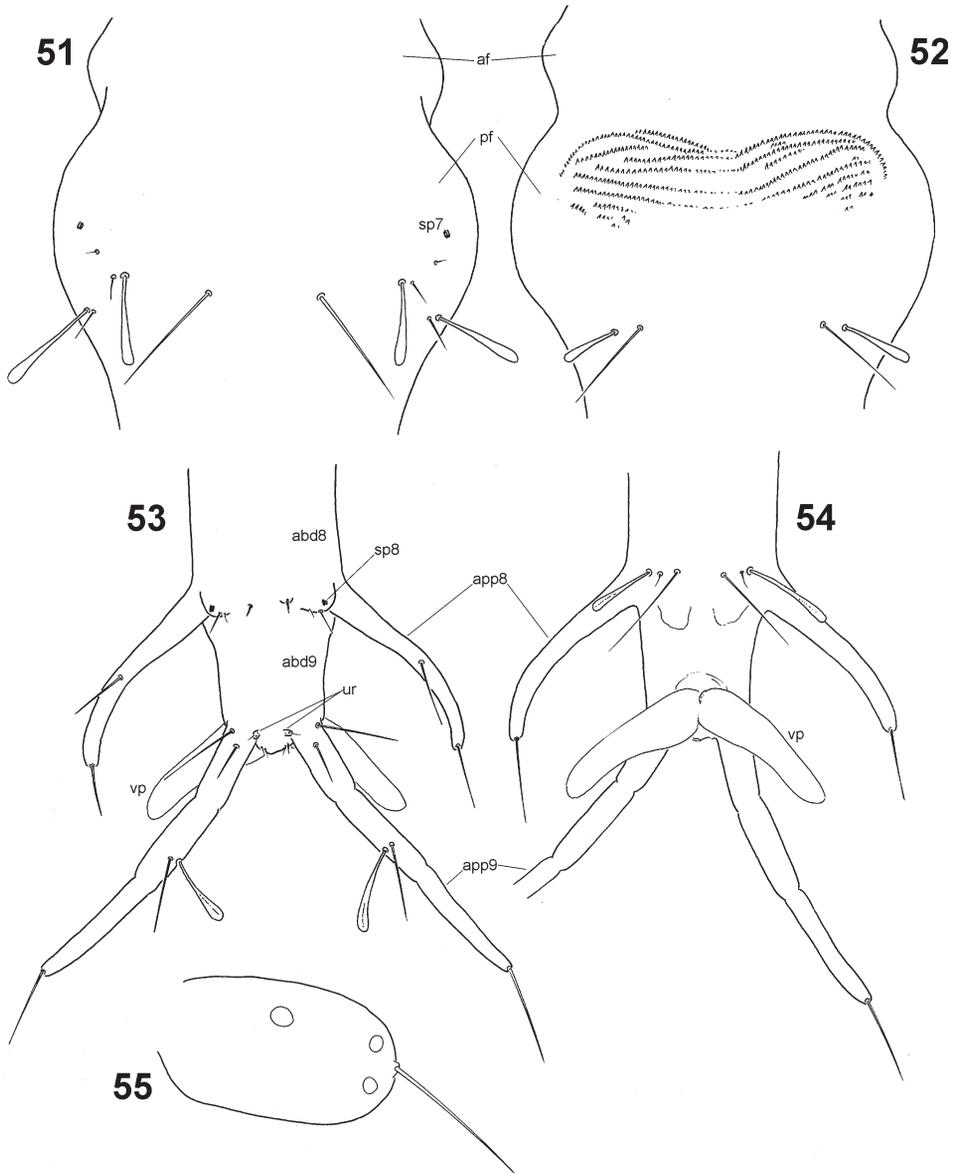
Labium (Figs. 34, 40–41). Submentum with one pair of long setae (LA1), LA2 absent. Mentum with basal pair of pores (LA4) and distal pair of short setae on ventral surface. Prementum with two pairs of pores (LA5–6) ventrally, one short seta (LA7) laterally on each side, one pair of basal tiny setae (LA8) dorsally and a group of two setae pairs (LA10–11) and a pair of pores (LA12) between palpal bases. Palpomere 1 with one tiny seta (LA13) basally and one pore (LA14) on intersegmental membrane, palpomere 2 with a subapical pore (LA15). Apical membranous field with two peg-like sensilla laterally, three short setae on long membranous extensions, and two tiny cap-like sensilla (gLA, Fig. 44).

Thorax. Proscutum with 15 setae on each half situated in three transverse rows; anterior row with three short trichoid, three long trichoid and one long scale-like setae; irregular series at midlength with four short trichoid setae, posterior row with three short and one long trichoid setae. Ventral portion with one short seta on posterior margin of each presternal sclerite and one long trichoid seta on anteromesal margin of precoxal sclerite. Lateral portion with a pair of trichoid setae (one long, one short) below proscutal margin, and one short seta dorsally of coxal articulation. Meso- and metanotum with a chaetotaxy similar to that of dorsal portion of abdominal segments.

Metathoracic leg. Coxa with three long and one short setae on a ridge anteriorly above trochanter articulation, and with two pores; posterior portion with two tiny setae proximally and one long seta below trochanter articulation. Trochanter with a group of five stout setae and one trichoid seta on anterodistal surface, ventral face with three moderately long setae and one pore; a series of elongate pore-like sensilla on both anterior and posterior surfaces situated across midlength of trochanter. Femur with three stout setae along anterodistal margin and with two long trichoid setae situated posterodistally, anterior surface with one pore. Tibiotarsus with an oblique row of four stout setae on anterior face, dorsal face with one long seta basally, ventral face with one seta distally, distal portion with four stout and two trichoid setae around claw articulation. Claw unisetose.

Abdomen (Figs. 51–55). Each abdominal segment with a transverse row of setae posteriorly, consisting on each side of one long trichoid, two long scale-like and two short trichoid setae dorsally and one long trichoid and one long scale-like setae lateroventrally. One tiny seta situated between the transverse row and the spiracle. Chaetotaxy of segments 8 modified, consisting on each side of one short seta situated mesally and two short setae situated on spiracular tubercle, ventrally with three closely standing setae including one long scale-like seta; lateral projection with one long seta in apical third and one long seta apically. Segment 9 lacking sensilla except for two pairs of tiny setae on its posterior margin; lateral projections each with a pair of basal setae, one long trichoid and one long scale-like setae at midlength and one trichoid seta apically; urogomphus with one seta and two pores apically, and one pore at midlength (Fig. 55). Ventral papillae lacking sensilla.

Comparative notes. The larva of *E. mendeli* sp. nov. seems to correspond with the Brazilian larvae of '*Epimetopus* sp. 2' (see below) in the morphology of the head, head appendages, thorax and abdomen (including the presence of two pairs of long projections at the end of the



Figs. 51–55. Abdominal morphology of the first instar larva of *Epimetopus mendeli* sp. nov. 51–52 – abdominal segment 7 (51 – dorsal view; 52 – ventral view); 53–54 – abdominal apex (53 – dorsal view; 54 – ventral view); 55 – detail of urogomphus. Abbreviations: *abd8–9* – abdominal segments 8–9; *af* – anterior fold of abdominal segment; *app8–9* – lateral projection of abdominal segments 8–9; *pf* – posterior fold of abdominal segment; *sp7–8* – spiracles on the abdominal segment 7–8; *ur* – urogomphus; *vp* – ventral papila.

abdomen, but it lacks ventral papillae) as well as in the general pattern on the head chaetotaxy including the presence of the scale-like setae (however, the Brazilian larvae were examined only on temporary slides without any previous treatment). Stemmata are clearly seen on the Brazilian larvae.

Epimetopus sp. 1

Larval material examined. 5 first instar larvae (MZUSP): **BRAZIL:** SÃO PAULO: Campos do Jordão (Bosque da Galharada), 5.x.1993, lgt. expedition MZUSP, rearing number 9 (9A and 9B respectively).

Adult material examined. 3 ♀♀ (MZUSP): same label data as the larvae (the larvae were reared from the egg cases carried by these specimens).

Comparative notes. The larvae of this species correspond with those of *E. mendeli* sp. nov. in the morphology of the head, head appendages, thorax and abdomen (including the presence of two pairs of long projections at the end of the abdomen) as well as in the general pattern on the head chaetotaxy including the presence of scale-like setae (however, the larvae were examined only on temporary slides without any previous treatment). Stemmata are clearly seen on these specimens: they are aggregated in two groups, anterior and posterior one, divided from each other by a space; the anterior group is larger than the posterior, but each seem to be composed of three original stemmata. Ventral papillae of the abdominal segment 10 are absent.

Identification. The adult specimens from whose egg cases the larvae were reared fit the diagnosis of the *E. mendeli* species group by the characters (1), (2) and (4) mentioned above. Male genitalia were not examined as all available specimens are females. The larvae examined by us are the same as those upon which ARCHANGELSKY (1997) based his description of *E. trogoidea* (Sharp, 1875) [even though the rearing number is not mentioned by ARCHANGELSKY (1997), we suppose that the description cannot concern the syntopically occurring *Epimetopus* sp. 2 (see below) as only one larva in poor condition is available for that species]. Hence, even though the precise identification of the larva described by ARCHANGELSKY (1997) and reexamined by us remains unspecified (pending the examination of males), the identification of the larva as *E. trogoidea* by ARCHANGELSKY (1997) must be considered incorrect – the larva probably belongs to the *E. mendeli* group.

Epimetopus sp. 2

Larval material examined. 1 first instar larva (MZUSP): **BRAZIL:** SÃO PAULO: Campos do Jordão (Bosque da Galharada), 5.x.1993, lgt. expedition MZUSP, rearing number 10.

Adult material examined. 2 ♀♀ (MZUSP): same label data as the larva (the larva was reared from the egg cases carried by these specimens).

Comparative notes. The larva agrees with those of *E. mendeli* sp. nov. in the general morphology of the head and thorax, the abdomen is not preserved. Head capsule is of the same proportions as in *E. mendeli* (i.e., longer than wide) and the general pattern of the chaetotaxy of the head capsule seems to be identical to *E. mendeli* (the larva was studied only in tem-

porary slide without any previous treatment). The presence or absence of the scale-like setae on the head and thorax cannot be confirmed or excluded, as the respective setae are broken. Abdomen is missing in the larva and was not examined.

Identification. The females from which the larva was reared are relatively large and have completely divided eyes, according to which they may be assigned to *E. trogoidea* species group.

Discussion

The knowledge of larval morphology of the family Epimetopidae is rather limited so far – only the larvae of the genus *Epimetopus* are known, whereas the immature stages of the remaining two genera, *Eupotemus* and *Eumetopus*, remain unknown. Larvae of two species of the genus *Epimetopus* have been described on the basis of the first instar larvae found in the egg case carried by females: larvae of *E. trogoidea* (Sharp, 1875) by ROCHA (1967), COSTA et al. (1988, partly based on the same material) and ARCHANGELSKY (1997), and the larva of *E. thermarum* Schwarz & Barber, 1918 by ROCHA (1969). The descriptions of larval *E. trogoidea*, moreover, show two different morphological types of larvae. Those described by ROCHA (1967) and COSTA et al. (1988) have a short head capsule and bear on abdominal apex one pair of long projections, whereas the description by ARCHANGELSKY (1997) shows the larva with an elongate head capsule and with two pairs of projections on the abdomen. The reasons for this incompatibility remained largely unclear until now (FIKÁČEK 2007; M. Archangelsky, pers. comm. 2006, 2011).

The reexamination of the specimens on which ARCHANGELSKY (1997) based his description of larvae of *E. trogoidea* revealed that the associated adults were misidentified and may actually belong to *E. mendeli* species group (see *Epimetopus* sp. 1 in Larval morphology section for details). This seems, at least in part, to explain the discordance between the published descriptions of *E. trogoidea*. Unlike *Epimetopus mendeli*, *E. trogoidea* (as well as *E. thermarum*, larva of which was described by ROCHA (1969)) is a representative of the large-sized species with completely divided eyes (Fig. 12) referred to herein as *E. trogoidea* species group. Observed differences in the head and abdomen morphology between the ‘long-headed’ and ‘short-headed’ larvae may in fact represent the differences between the larvae of the *E. trogoidea* and *E. mendeli* species groups. However, the single poorly preserved larva of *Epimetopus* sp. 2 examined for this study seems to belong to *E. trogoidea* group based on the morphology of the adult females from which egg case it was reared, and still it bears the elongate head and differs therefore clearly from the larvae of *E. trogoidea* and *E. thermarum* described by ROCHA (1967, 1969) and COSTA et al. (1988). The incorrect association with adults could be a possible explanation, as both *Epimetopus* sp. 1 (possibly belonging to *E. mendeli* group) and *Epimetopus* sp. 2 (belonging to *E. trogoidea* group) used for the rearings were collected syntopically and on the same day, but other possibilities cannot be excluded either (e.g. that both short-headed and long-headed larvae are found in different species of *E. trogoidea* group). Still more larval material as well as a detailed taxonomic revision of the adults are needed to properly understand the larval morphology of *Epimetopus*.

FIKÁČEK et al. (2008) considered the primary chaetotaxy of the larval head of the Hydrophiloidea rather stable in presence/absence, size and shape of the sensilla. This was documented in

detail for several groups of the Hydrophilidae (BYTTEBIER & TORRES 2009, TORRES et al. 2011, MINOSHIMA & HAYASHI 2011) and briefly summarized for the Helophoridae, Spercheidae and Hydrochidae by FIKÁČEK et al. (2008). Based on our study, we may confirm the same is the case for *Epimetopus* as well – the head capsule bears all sensilla found in *Hydrobius fuscipes* (Linnaeus, 1758) except setae PA22 (which is however missing even in *Helophorus* Fabricius, 1775), the mouthparts seem to differ from *Hydrobius* Leach, 1815 only in the absence of the submental seta LA2 (which is, however, absent also from other basal hydrophiloid families examined). On the other hand, *Epimetopus* largely differs from *Hydrobius* as well as *Helophorus* especially in the position of the sensilla on the parietale and on the maxillary segments (stipes and palpomere 1). Interesting is the presence of the scale-like setae on the head (frontale and inner appendage of the maxilla) as well as on thorax and abdomen – this type of setae was recently documented for the hydrophilid genera *Helochaeres* Mulsant, 1844 and *Agraphydrus* Regimbart, 1903 (MINOSHIMA & HAYASHI 2011) and is here documented for the first time outside of the Hydrophilidae.

In general, the larval morphology of *Epimetopus* seems to be a mix of characters shared with *Helophorus* and/or *Georissus* Latreille, 1809, and characters resembling some hydrophilid taxa. Characters shared by *Epimetopus*, *Helophorus* and *Georissus* are as follows: (i) frontoclypeus with single median projection of the nasale and large epistomal lobes projecting further than nasale, (ii) the presence of retinacular spines on the mandible, (iii) relatively long maxillary palpomere 1, (iv) sensilla PA6–7 situated close to each other, (v) sensilla PA22 absent, (vi) stipital setae MX5–6 distant from each other, (vii) abdomen without spiracular atrium, and (viii) the ventral portion of prothorax with presternal and precoxal sclerites [shared also with *Spercheus* Kugelann, 1798 and *Hydrochus* Leach, 1817, whereas one plate is developed in most Hydrophilidae). A few further characters are shared only with *Georissus*, but not with *Helophorus*: (i) setae of gFR2 large and with lobate margins, (ii) lateral margins of epistomal lobes membranous and bearing finger-like projections, (iii) submentum freely articulated with parietale at straight submental line (ventral anterior margin of head capsule straight, not excised). Characters resembling the hydrophilid taxa include (i) antenna with one sensorium [shared with all Hydrophilidae, Spercheidae and Hydrochidae]; (ii) mandibular retinaculum complex with numerous spiny projections [resembling *Laccobius* Erichson, 1837 and *Berosus* Leach, 1817]; (iii) closely aggregated stemmata [resembling *Chaetarthria* Stephens, 1835 and Megasternini; but the group is not subdivided into anterior and posterior ones in these taxa], (iv) labium rather small, not overlapping nasale [resembling *Laccobius* and *Berosus*]. Those characters shared with *Laccobius* and Megasternini seem to represent convergences as these hydrophilid taxa are deep inner groups of the Hydrophilidae based on published phylogenetic studies (HANSEN 1991, ARCHANGELSKY 2004). The relevance of the characters shared with *Berosus* (which seems to stand basal in the Hydrophilidae; BERNHARD et al. 2009), *Chaetarthria* (which is often considered as sister-group to Berosini; HANSEN 1991, ARCHANGELSKY 2004), Spercheidae and Hydrochidae should be tested in a phylogenetic analysis as they may be informative for higher phylogeny of the Hydrophiloidea.

Abdominal morphology differs markedly between the two types of *Epimetopus* larvae based on our study and published descriptions. The ‘short-headed’ larval type bears one pair of long projections on abdominal segment 9, which were interpreted as three-segmented urogomphi by ROCHA (1967, 1969) and COSTA et al. (1988) as well as by some subsequent

authors (HANSEN 1991). In contrast, ARCHANGELSKY (1997) and our results show that the 'long-headed' larval type bears two pairs of long unsegmented abdominal projections, one pair on segment 8 and one pair on segment 9. ARCHANGELSKY (1997) considered the projections on segment 9 of the 'long-headed' larval type as non-homologous with urogomphi and mentioned that urogomphi are short and one-segmented in his specimen. This was later adopted e.g. by BEUTEL & LESCHEN (2005) and is confirmed also by our study of the larva of *E. mendeli* in this paper. In agreement with ARCHANGELSKY (1997), we consider a dorsal pair of tiny projections on the abdominal segment 9 (Figs. 9–10, 53; ur) to represent highly reduced urogomphi. The homology of these projections with urogomphi is supported (i) by their position (reduced urogomphi are situated dorsally on abdominal segment 9 in the Hydrophilidae and Georissidae; BØVING & HENRIKSEN 1939, ARCHANGELSKY 1997, MINOSHIMA & HAYASHI 2011); (ii) their chaetotaxy (other projections on the abdominal apex of *Epimetopus* except for lateral projections lack sensilla; the three-segmented urogomphus of first instar *Helophorus* bears six sensilla); (iii) the reasons denying the homology of lateral projections of abdominal segment 9 (see the next paragraph).

In spite of the different interpretation of their segmentation (unsegmented according to ARCHANGELSKY (1997) and this study; three-segmented according to ROCHA (1967, 1969) and COSTA et al. (1988)), the lateral projections of abdominal segment 9 are clearly homologous between 'long-headed' and 'short-headed' larvae. This is supported not only by their position, but also by their chaetotaxy, which is completely identical between the larva of *E. trogoidea* drawn by ROCHA (1967) and the larva of *E. mendeli*. The similarities in position, morphology and chaetotaxy of both pairs of long abdominal projections of *E. mendeli* indicate, moreover, that both pairs may be serially homologous, which would exclude the homology of posterior pair with segmented urogomphi. The projections of *E. mendeli* are completely membranous, but sometimes also show slight constrictions along their length which may evoke the segmentation. Both SEM observations of larvae of *E. mendeli* and examination of the well-preserved larvae of *Epimetopus* sp. 1 showed no trace of segmentation, indicating that the infrequently observed constrictions are just artifacts. If the serial homology of the projections is adopted, a pair of short lateral setiferous projections of abdominal segment 8 illustrated by ROCHA (1967, 1969) and COSTA et al. (1988) for 'short-headed' larvae may in fact be homologous with the long lateral projections of *E. mendeli*. Hence, the 'short-headed' and 'long-headed' *Epimetopus* larvae seem to differ only in the length of the projections on abdominal segment 8 and their abdominal morphology is otherwise very similar.

The third pair of projections present in the larvae of *E. mendeli* (called temporarily 'ventral papillae' here) was not mentioned in the previous descriptions and it is absent from the larva of *Epimetopus* sp. 1 examined for this study. The projections are totally membranous and lack any chaetotaxy, for which reasons they cannot be considered to represent urogomphi. Instead, the ventral position of these projections may indicate that they are actually derived from a reduced pygopodium (the remnant of abdominal segment 10) and may be therefore analogous (but surely not homologous) to the prostyli of the larvae of the Hydrophilidae: Hydrophilini (BØVING & HENRIKSEN 1939, MINOSHIMA & HAYASHI 2011). Ventral spinose lobes of abdominal segments 2–7 seems, by their position, to correspond to the spinose areas on these segments in larval *Helophorus* (in which the spines are, however, irregularly arranged and not lying on

a mound). In contrast, the larvae of *Georissus* lack similar cuticular spines on the abdominal segments. Spiracles of *Epimetopus* are considered as functional by ARCHANGELSKY (1997) even though they are rather small in size at least compared to the larvae of *Helophorus*. However, they correspond well to the size of the abdominal spiracles in *Georissus*.

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