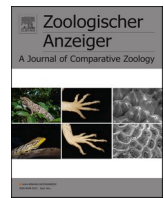




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Research paper

New genera of Neotropical Maindroniidae, with a redescription of *Maindronia neotropicalis* (Insecta, Zygentoma)[☆]

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ABSTRACT

Maindroniidae is a rarely-encountered monogeneric family of Zygentoma, of which only four species are described so far. Recent surveys in the Atacama Desert have revealed in the hyperarid core an astonishing molecular and morphological diversity of these insects. The present work aims to provide the basis for a systematic taxonomic analysis of this diversity. The former *Maindronia neotropicalis* from Chile is redescribed in a new genus as *Atacamus neotropicalis*, along with a second new genus and species, *Peruatacamus atunpacha* from Peru. Neotropical Maindroniidae are separated from Old World Maindroniidae and placed in the new subfamilies Atacaminae and Maindroniinae respectively.

1. Introduction

Maindroniidae is a monogeneric family of Zygentoma with a disjunct Palaearctic/Neotropical distribution, as recently summarized by Smith et al. (2020). Four species are known, but they are represented by only about 15 specimens mentioned in the literature over the last 125 years. Three of these species have been described from desert biomes in Sudan, the Arabian Peninsula and southern Iran, which points to an eastern Saharo-Sindic distribution. A single species, *Maindronia neotropicalis*, has been described from South America (Wygodzinsky, 1940), the type locality is a coastal habitat near Caleta Junin, a small coastal settlement in the Chilean Atacama Desert south of Pisagua, and this population is still the only one which has been morphologically analyzed (Wygodzinsky, 1940; Paclt, 1966).

Recent studies in the Chilean Atacama Desert revealed a surprising abundance and diversity in hyperarid environments with a number of genetically distinct lineages (Zúñiga-Reinoso and Predel, 2019). The present work aims to provide the basis for a systematic taxonomic analysis of these lineages, starting with a redescription of the former *M. neotropicalis* in a new genus, along with the description of a second new genus and species from Peru. For the first time in Zygentoma taxonomy, features of the proventriculus are used to complement the

detailed analysis of external morphology for species separation. A comparison of Neotropical with Old World material shows consistent morphological differences which, combined with the long separation implied by the disjunct distribution, merit distinction at subfamily level. Therefore, Neotropical Maindroniidae are separated from Old World Maindroniidae and placed in different subfamilies, respectively.

2. Material and methods

2.1. Sampling of specimens

Specimens from Chile were collected along the coast from Loa River mouth to Caleta Camarones in the Antofagasta and Tarapacá regions, including Caleta Junin, the type locality of *M. neotropicalis*. Specimens from Peru were collected 20 km southwest of Arequipa in Southern Peru (S16°30.55 W71°44.52, 1870 m a.s.l.; permit RD N° D000019-2022-MIDAGRI-SERFOR-DGGSPFFS-DGSPFS). Insects used for morphological analyses were immediately transferred into 70 % ethanol. Coloration was documented before on live specimens. Specimens from Caleta Junin were compared with the type material of *M. neotropicalis* (deposited in the Naturhistorisches Museum Basel) as well as specimens analyzed by Paclt (1966), deposited in the Museum der Natur

[☆] <http://zoobank.org/30332127-744E-4CDA-8C2F-89CE5CE7B89C>.

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Hamburg). Altogether, we analyzed material that originates from the collections listed below or that has been deposited there following this work:

AMNH: American Museum of Natural History, New York (USA)
 NMB: Naturhistorisches Museum Basel (Switzerland)
 MKB: Museum König Bonn (Germany)
 MNH: Museum der Natur Hamburg (Germany)
 MNHN: Museo Nacional de Historia Natural, Santiago (Chile)
 MZUC: Museo de Zoología de la Universidad de Concepción, Concepción (Chile)

2.2. Morphological analysis

Morphological features were first examined with a Zeiss Stemi 508 equipped with an AxioCam 105, a Zeiss Lumar.V12 stereomicroscope with objective NeoLumar S 1.5x, or an Axioskop 2 plus microscope equipped with a Zeiss AxioCam MRm camera (all Carl Zeiss GmbH, Göttingen, Germany). Subsequent micrographs were mostly generated on dried specimens using a Keyence VHX –2000 digital microscope (Keyence Deutschland GmbH, Neu-Isenburg, Germany). Proventriculi were dissected in 70 % ethanol with fine forceps and scissors, cleaned in 10 % KOH (2h, 60 °C), ultrasonicated, and documented first with the digital microscope. Subsequently, the sclerites were individually dissected, dried and mounted with superglue on stainless steel minute pins (0.15 mm), for SEM. If not otherwise stated, we followed the terminology used by [Smith et al. \(2020\)](#).

2.3. Scanning Electron Microscopy (SEM)

Previous to the SEM examination, insects stored in ethanol were dehydrated (2h absolute ethanol followed by 3 × 2h hexamethyldisilazane (HMDS), finally evaporation of HMDS at room temperature) or critical point dried using an Emitech K850 critical point dryer (Sample preparation division, Quorum Technologies Ltd., Ashford, England). Dried samples were either directly placed on carbon adhesive discs or Leit-C-Plast (both Plano, Wetzlar, Germany) on the specimen holder, or glued on the tip of minute pins; some of the latter samples (e.g. sclerites of proventriculus) were then mounted on a rotatable specimen holder ([Pohl, 2010](#)). SEM was either performed using a Phillips XL30 ESEM (Phillips, Amsterdam, Netherlands; [Figs. 6C/D, 12B/C, 13C-H, 18C, 19 B/C, 22 B/C, 25B, 26](#)) or a Zeiss Sigma 300–VP SEM (remaining figures); for the XL30 sputter coated with gold using the Emitech K 500, for the Sigma 300–VP using the Q150T ES (Quorum Technologies Ltd.).

2.4. Micro computed tomography (μCT), computer-based 3D reconstruction and 3D-models

The abdomen of one specimen from Peru containing the proventriculus was scanned in 100 % ethanol using the microtomography endstation of the imaging Beamline P05 ([Haibel et al., 2010](#); [Greving et al., 2014](#); [Wilde et al., 2016](#)) operated by the Helmholtz-Zentrum Geesthacht, Germany, using 20 KeV at the storage ring Petra III at Deutsches Elektronen-Synchrotron DESY, Hamburg, Germany. The projections have been recorded with a slight edge enhancement placing the detector at 10 cm distance to the sample using a custom developed 20 MP CMOS camera system with an effective pixel size of 643 nm in the projection images. For the tomographic scan, 4801 projections at equal intervals between 0 and π have been recorded. Tomographic reconstruction has been done using the filtered backprojection algorithm (FBP) implemented in a custom reconstruction pipeline ([Moosmann et al., 2014](#)) using matlab (Math-Works, Natick, MA, U.S.A.) and the Astra Toolbox. For processing the raw projections were binned two times resulting in an effective pixel size of the reconstructed volume of 1.29 μm .

Based on μCT -image stacks, the sclerites of the proventriculus were

segmented with Amira 5.6.0 (Thermo Fisher Scientific, Hillsboro, Oregon, U.S.A.).

The Amira macro ‘Multi Export’ ([Engelkes et al., 2018](#)) was used to create isosurfaces of the segmented material. After importing the material, we used Blender Ver. 3.3. (Amsterdam, Netherlands) to create the models and uploaded them to Sketchfab (New York, USA, Paris, France).

2.5. Sequencing of cytochrome oxidase subunit I

DNA extraction, amplification and sequencing of the cytochrome oxidase subunit I (COI) were performed as described in [Zúñiga-Reinoso and Predel \(2019\)](#).

3. Taxonomy

3.1. Family Maindroniidae ([Escherich, 1905](#)) sensu [Paclt, 1967](#)

3.1.1. Subfamily Maindroniinae stat. rev

Type genus: *Maindronia* [Bouvier, 1897](#).

Included species: *Maindronia mascatensis* [Bouvier, 1897](#), *Maindronia beieri* [Schremmer, 1964](#), *Maindronia bashagardensis* [Smith & Molero-Baltanás, 2020](#).

Distribution: Afghanistan, Iran, Oman, Sudan.

Diagnosis: Maindroniinae are characterised by the absence of distinct pronotal folds, well-developed tibial spurs with macrosetae, and 7 or 8 pairs of styli in adults. Tibiae ventrally with many bristle combs perpendicular to the lateral margins, the penultimate articles of labial palps are longer than wide.

Comments: [Bouvier \(1897\)](#) described the genus and species *M. mascatensis* as a ‘Thysanoure’ without referring it to a specific family. [Escherich \(1905\)](#) placed it in his newly created subfamily Maindroniinae under Lepismatidae. [Paclt \(1967\)](#) raised Maindroniidae to family level. We here re-introduce a subfamily Maindroniinae under Maindroniidae, now redefined to include only the Old World species of *Maindronia*, with all New World ‘*Maindronia*’ spp. being referred to different genera in another subfamily below. There is very little material of Maindroniinae available for examination, and available descriptions are often inadequate:

M. mascatensis is known only from the types, which were described as being in the Natural History Museum of Paris, France, but not found by [Smith et al. \(2020\)](#) and presumed lost. The original description is inadequate by modern standards and included no illustrations. One type specimen, also lost, was donated to [Escherich \(1905\)](#), who provided a partial redescription and some schematic illustrations, but many morphological details remained unknown.

M. beieri is known only from the types, purported to be in the Natural History Museum of Vienna, Austria, but could not be located there ([H. Bruckner, pers. comm. 2022](#)). The description and illustrations in [Schremmer \(1964\)](#) include adequate detail, but not all that is needed. The one male specimen that is described is obviously immature, judging by the small size, single pair of styli and unexpanded labial palp. On-line photographs from Sudan (<https://www.inaturalist.org/observations/9376998>) are presumably of this species but were of limited use due to low resolution; they were useful for confirming the lack of a colour pattern, but the specimen was not collected and no better resolution images are available ([A. Zboray, pers. comm. 2022](#)).

M. bashagardensis is known only from the holotype. The excellent description and illustrations ([Smith et al., 2020](#)) obviated any need to examine the type from the Australian Museum, Sydney. In addition, we have examined a specimen from Afghanistan that conforms to the description of *M. bashagardensis*. We believe this specimen to be the one published as *M. mascatensis* by [Wygodzinsky \(1962\)](#), because the sex and label data are identical. That specimen was published as being in the Biological Museum, Lund University, Sweden, but could not be located there ([E. Sandström, pers. comm. 2022](#)). Our specimen came from the AMNH, where it is incongruously labelled in Wygodzinsky’s own hand

as: '*M. neotropicalis*'. Material: AMNH_IZC 00395926: AFGHANISTAN, A. 480, Tour Kham, 20-I-1958, sous pierres, Lindberg. 1 male. The above information explains why our concept of *Maindronia* and Maindroniinae is based primarily on the description of *M. bashagardensis* and one examined specimen from Afghanistan, plus what little could be gleaned from the descriptions of the other two species.

M. bashagardensis has no distinct pronotal folds, and all three legs have prominent tibial spurs with several macrosetae. The holotype female had 7 pairs of styli, as had our male. The female was described and illustrated with grouped sensilla on the distal labial palp, but sensilla could not be clearly discerned on the male from Afghanistan; the penultimate article of the labial palp is longer than wide, and the tibiae show ventrally many bristlecombs perpendicular to the lateral margins.

Both *M. mascatensis* and *M. beieri* were illustrated without pronotal folds. The number of styli and shape of the penultimate article of labial palps are described and/or illustrated as expected for Maindroniinae. Labial palp sensilla were described only for juvenile males of *M. beieri* and they are grouped. Tibial setation is described/illustrated with bristlecombs perpendicular to lateral margins. The illustrated legs of neither species show tibial spurs, but we ascribe this to inaccurate illustration. Before the current era tibial spurs were routinely ignored in descriptions and simply omitted from illustrations, even though they occur in almost all Zygentoma (Irish, 1990). In the case of Escherich (1905) other species that are well known to have tibial spurs are illustrated on the same plate as *M. mascatensis* as lacking them.

Additional details in which *M. bashagardensis* differs from Neotropical Maindroniidae are listed in Table 1. Before one can confidently consider all to be subfamily level distinguishing characters some of these will need to be verified for the other two *Maindronia* spp. as well.

3.1.2. Subfamily Atacaminae Irish, Zúñiga-Reinoso & Predel, **subfam. nov**
<https://zoobank.org/A7904AFD-DC8D-4898-810F-0CDE4B29612E>.

Type genus: *Atacamus* Irish, Zúñiga-Reinoso & Predel, **gen. nov.**
Included species: *Atacamus neotropicalis* (Wygodzinsky, 1940) **comb. nov.**, *Peruatacamus atunpacha* Irish, Zúñiga-Reinoso & Predel, **gen. et sp. nov.**

Distribution: Chile, Peru.
Diagnosis: Atacaminae are characterised by the presence of distinct pronotal folds, tibial spurs without setae or completely reduced, and only 1 pair of styli in adults. Tibiae ventrally without bristlecombs perpendicular to the lateral margins, the penultimate article of the labial palp is as wide as long or wider. Other characters as in Table 1.

3.2. *Atacamus* Irish, Zúñiga-Reinoso & Predel, **gen. nov**

<https://zoobank.org/70F210CE-2FC3-461A-A94E-31DAE5C27DA1>.
Type species: *M. neotropicalis* Wygodzinsky, 1940.
Diagnosis: Genus characterized by strongly reduced to absent tibial

spurs, 3 + 3 macrosetae on pronotal collar, posterolateral macrosetae on thoracic nota, presence of macrosetae on posterior urotergites, 3 + 3 submedian bristlecombs on urosternites III – VII, 1 + 1 lateral discal macrosetae on urosternites III – VII, and epiprocts/paraprocts without distinct processes. Large species.
Etymology: Based on 'Atacama', the name for the Chilean desert in the indigenous Atacameña language (Vaisse et al., 1896), for which we specify the gender as masculine under ICZN article 30.2.2.

3.2.1. *Atacamus neotropicalis* (Wygodzinsky, 1940), **comb. nov**
M. neotropicalis Wygodzinsky, 1940: 25; Paclt, 1966: 158 (non Peña, 1985: 221).

There are two clear discrepancies between the description of *M. neotropicalis* and the holotype slides. Wygodzinsky (1940) described the species as having no dorsal setae on either the thoracic nota or on the urotergites, explicitly stating this as the primary character distinguishing his species from *M. mascatensis*. The holotype slides show that the urotergites are indeed setose. The thoracic nota could not be located on any of the type slides, not even on the one specifically labelled as including them, but in the examined material below they too are setose. Earlier, Paclt (1966) had already mentioned the presence of dorsal setation contrary to the description, after examining a non-type topotypical specimen of *M. neotropicalis*; we have re-examined Paclt's specimen and confirmed its identity. Furthermore, the holotype slides show the presence of 3–5 marginal setae on the posterolateral angles and 1 + 1 lateral discal bristlecombs on most urosternites in addition to the 3 + 3 posterior marginal combs described by Wygodzinsky (1940).

Description based on new material collected at the type locality at Caleta Junin (COI sequence see Supplementary Material 1A): Body length of adults 14–17 mm. Antennae and caudal filaments when intact longer than the length of the body. Ground colour of body white, visible through transparent integument. Dorsal body of males and females with a distinctive pattern formed by varying distribution and intensity of violaceous to brownish granular epidermal pigment (Fig. 1A and B). Dorsal pattern details vary individually but persistent elements include all or most of: a Rorschach pattern on the frons (Fig. 1B); a broad dark band along the lateral and posterior margins of the thoracic nota; unpigmented areas around the anterolateral pronotal folds (Fig. 1B), similarly unpigmented areas mediolaterally on the meso- and metanota; a broad dark band across the posterior half of each of urotergites I–IX, laterally these bands become narrower and encompass an unpigmented dot; a median longitudinal line from the pronotum to the metanotum, fairly wide with darker lateral edges on the pronotum, narrow on meso- and metanota; urotergite X mostly dark with 1 + 1 lighter discal comma-shaped spots. Dark pigmentation also on proximal half of clypeus, pedicellus, distal half of scapus, and around the bases of cerci and terminal filament, including paraprocts and epiproct. Lateral sides of mandibles and stipites, antennae and cerci uniformly lightly pigmented. Legs with a pigment spot on the apico-ventral femur and a pigmented line along the ventral face of the tibia. Ovipositor lightly pigmented, with transverse sutures and a weakly defined longitudinal line on each segment of gonapophyses unpigmented (Fig. 1A, inset). Otherwise the ventral body, including the labial palpi and styli, unpigmented.

All setae lacking barbs on shaft, larger macrosetae apically mostly bifid (unless specifically indicated differently, macrosetae mentioned in the text are bifid), sometimes (region-specific) only faintly bifid to truncated or apically roundish to acute. Body covered with scattered apically pointed and often curved setulae, but various forms exist and the term setulae is generally used here for very small setae (<50 µm).

Head wider than long, at most as wide as long, 1 + 1 trichobothria on disc of vertex directly posterior of postfrontal suture, halfway between origin of the coronal suture and the lateral margin (Supplementary Material 2A). Anteromedian part of the frons slightly concave, the adjoining proximal margin of clypeus distinctly bent upwards (frontal view). Periantennal frontal margins each with two combs, the anterior comb with 7–8 macrosetae extending from the anterolateral edge up to

Table 1
Morphological differences between the subfamilies of Maindroniidae. Character states for Maindroniinae based mainly on *Maindronia bashagardensis*, for Atacaminae on the taxa described here as well as all undescribed Neotropical Maindroniidae examined to date.

Character	Maindroniinae	Atacaminae
Distinct pronotal fold	absent	present
Tibial spurs	large, with setae	without setae or rudimentary
Number of styli in adults	7–8 pairs	1 pair on urosternite IX
Labial palp, penultimate article	much longer than wide	at least as wide as long
Frontal head setation	setal fields	setal rows
Supraocular seta	absent	present
Bristlecombs thoracic nota	present	absent
Bristlecombs on tibia	present	absent
Urotergite X	posteriorly concave	posteriorly convex or straight

the middle of the antennal socket, the posterior comb with 3–4 macrosetae (Fig. 2A). A single isolated macroseta posterior of the antennal socket (Fig. 2A). The bases of these macrosetae mostly along the unpigmented membranous suture descending from the dark pigmented margin of the frons (see Fig. 1B). Two isolated submarginal macrosetae at genal margin ventrad to posteroventrad of eye, a single supraocular macroseta (Fig. 2B). Clypeus laterally, at the distal margin of the pigmentation, with four setae of different size on each side, the larger ones as strong as the macrosetae at the frontal margin (Fig. 2A, inset). Labrum with prominent 1 + 1 transverse setal fields of about 14 macrosetae, arranged in somewhat indistinct double rows. Near the apical margin of labrum on both sides of the middle with 8–10 thin and acutely pointed setae of different length, some of them as long as the above-mentioned macrosetae of the labrum (Fig. 2C).

Mandibles typical of Maindroniidae, outer surface evenly rounded (Fig. 3A, inset) and with rosette-like structures (Fig. 3B), incisor region concealed by labrum (Fig. 2C); four-toothed, between the two dorsal teeth less incised (Fig. 3A, B, C) and the outer surface area of the two dorsal teeth unevenly striated longitudinally (Fig. 3B); base of mandibles evenly striated on inner side (Fig. 3C). The distinct bristlecomb along the dorsal inner edge of incisivi consist of 14–16 macrosetae gradually shortening distally, the distal 6–8 macrosetae very stout and arranged in a row, the proximal ones clustered and some of these proximal setae very long, thin and with extremely forked tips (Fig. 3C, inset). Outer exposed surface of mandible with 14–20 mostly isolated

macrosetae in the middle part and a single isolated macroseta posteriad (Fig. 3A and B).

Lacinia fairly robust, little curved, about the same length as galea (galea becomes shorter in dried specimens), with strongly sclerotized tip (Fig. 3A–D); inner side subapical with an almost vertical row of up to 4 closely fitting spines with strongly decreasing size ventrally (Fig. 3H). Galea concavely hollowed (Fig. 3D), slightly convex on the outer side (Fig. 3E), with 5–7 macrosetae at the base, a group of 3–5 macrosetae anterior of it, and apically of the latter group both on the outer and inner sides along the margins 8–10 small and mostly curved setae with acute tips, usually arranged in single rows; the outer row includes at least two transverse pairs of setae (Fig. 3E). Inner row distally bent dorsad, just behind the tip of the galea, forming a separate transverse row of 4–6 setae (Fig. 3E). Tip of galea rather soft and strongly shrinking in dried specimens (compare Fig. 3D and E), with a small glandular area (Fig. 3F and G). Cardo with 1–3 macrosetae, stipes apically with a group of 3–4 and proximally 1–2 isolated macrosetae.

Maxillary palpi slender, ultimate article (article 5) about six times longer than wide, slightly curved inwards (Fig. 4A, inset). Setae of articles 3–5 apically pointed to barely visible bifid, slightly bent forwards, and on ultimate article denser along outer side. Article 2 with a mixture of apically pointed macrosetae and some bifid macrosetae, the short proximal article with 4–6 bifid macrosetae on ventral side. Tip of ultimate article of dried specimens often with concave indentation along the outer side, possibly due to weaker sclerotization. Near distal end of

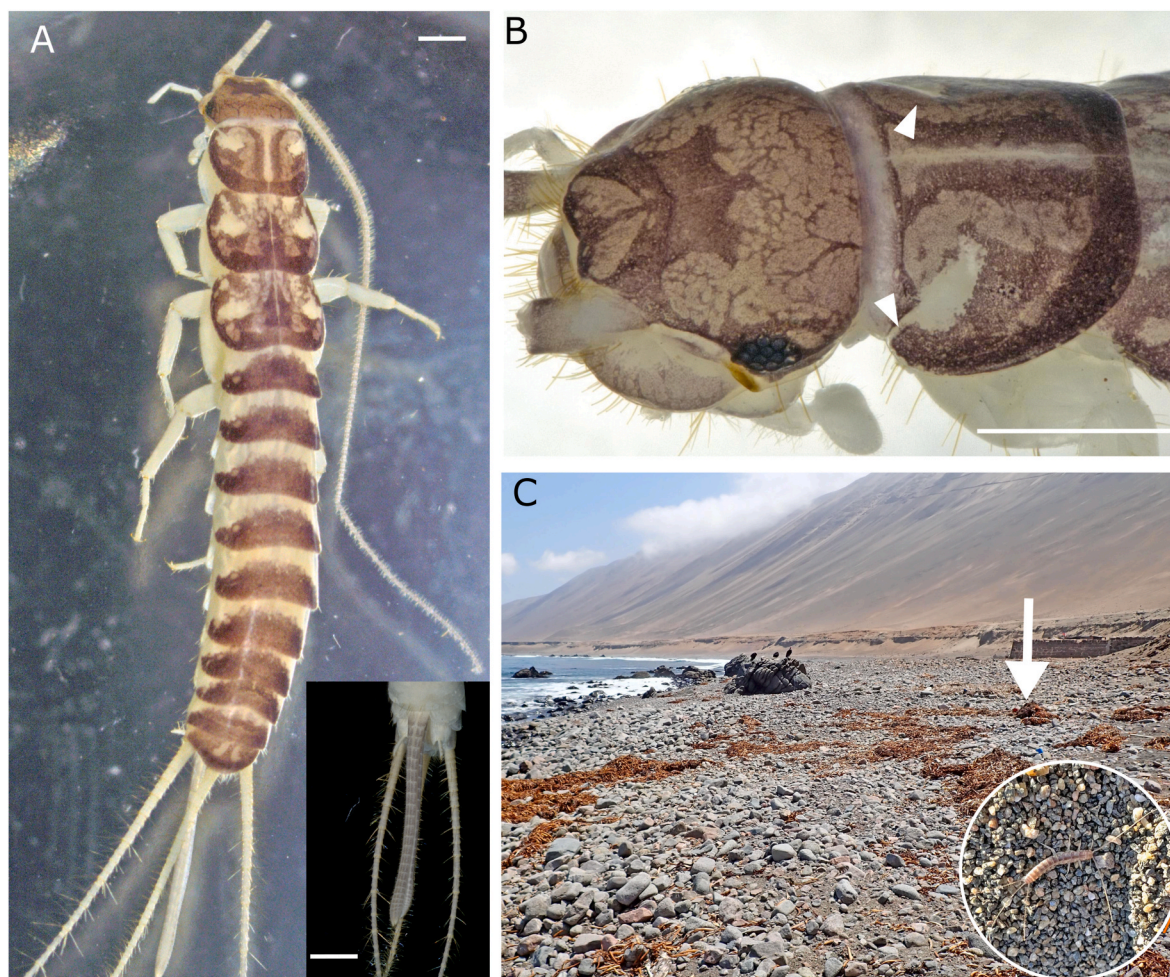


Fig. 1. *Atacamus neotropicalis*. **A)** Colour pattern of female specimen, stored in ethanol, from type locality at Caleta Junin (dorsal view); image slightly overexposed to recognize main patterns more easily (weak pigmentation not visible); inset: pigmentation of the ovipositor (ventral view). **B)** Dorsolateral view of head and pronotum. Anterolateral pronotal folds (arrowheads) associated with unpigmented areas. **C)** Collecting spot at type locality; inset shows a living specimen. Scale bars: 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

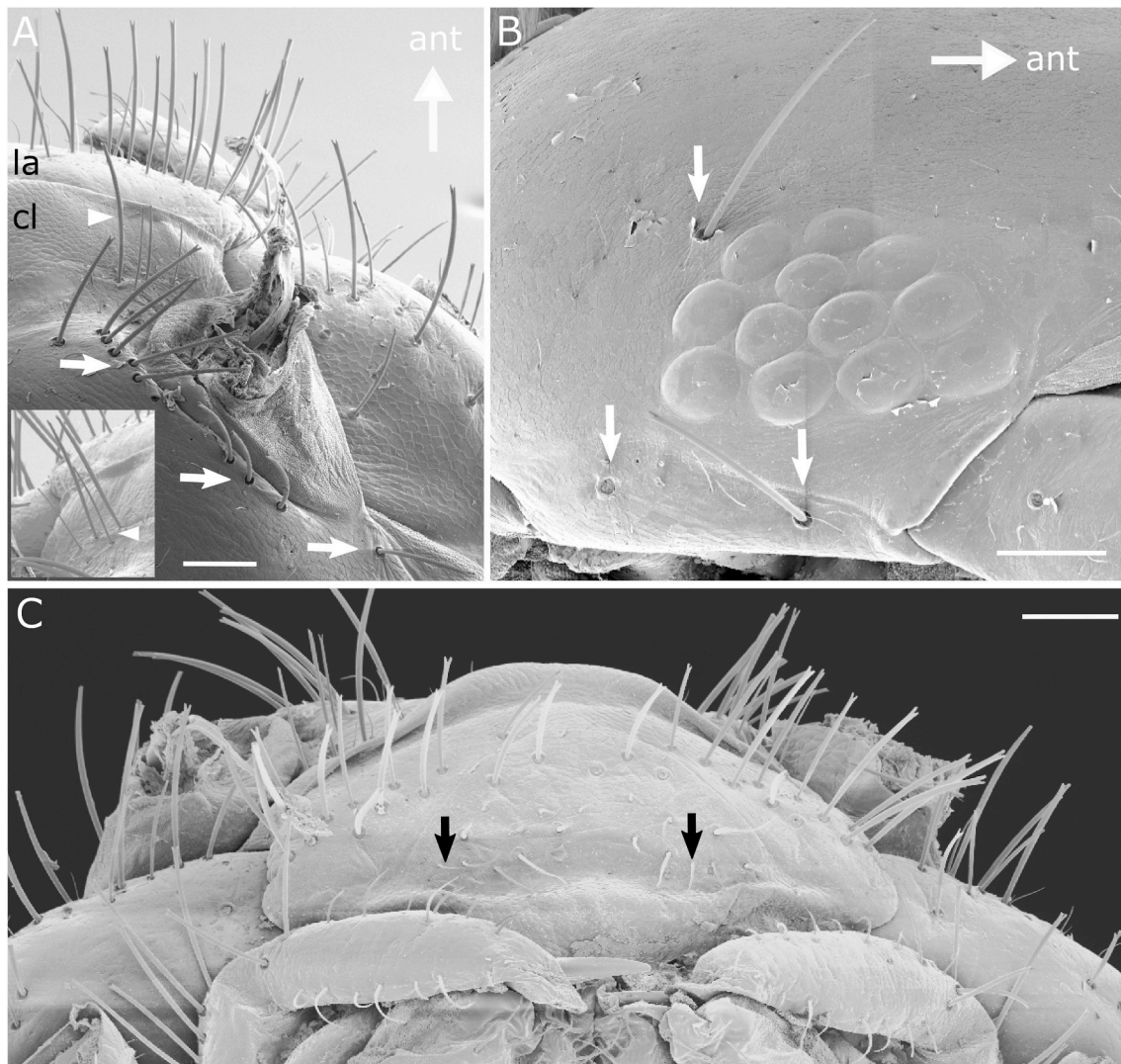


Fig. 2. *Atacamus neotropicalis*; setation head (SEM). **A**) Dorsal view with periantennal macrosetae (arrows), setation on clypeus (arrowheads; inset shows opposite side), and macrosetae of labrum; antenna removed. **B**) Lateral view with macrosetae of eye region (arrows). **C**) Frontoventral view on labrum, with proximal row of bifid macrosetae and distally with much thinner cilia/setae with acute tips (arrows). Scale bars: 100 μ m.

ultimate article four styloconic sensilla (pronged apical sensilla; see Molero-Baltanás et al., 2024) with 3–4 apical sensory cones that insert into a cylindrical base (style) (Fig. 4A). A single sensillum basiconicum type F (according to Adel, 1984; also resembles a somewhat raised poculiform sensillum; see Fig. 2F in Molero-Baltanás et al., 2024) located near the two distal styloconic sensilla (Fig. 4A and B). This sensillum accompanied by four fairly elongated sensilla basiconica type B, a fifth sensillum basiconicum type B is located more proximal (Fig. 4A). Scattered campaniform sensilla and rosette-like structures (see Matushkina, 2010) distributed over the ultimate article, the rosette-like structures mostly associated with wide-open cavities that resemble gland orifices (Fig. 4C).

Labium broader than long (Fig. 5A and B), postmentum with 1 + 1 anterolateral macrosetae and 1 + 1 much smaller anteromedian setae (Fig. 5A), the latter only slightly bifid. Prementum along the proximal margin with a row of 6–8 stout setae of different lengths, on disc with 14–18 similar but mostly larger macrosetae of different lengths; slightly anterior to the proximal margin a medial row of 3–4 thinner but still slightly bifid macrosetae on each side, the tips of the innermost of these cross each other medially in the premental cleft (Fig. 5C). Paraglossae with 5–7 stout macrosetae on outer disc, 1–2 similar macrosetae on the inner part; the inner part additionally with 8–12 less robust, inwardly

curved and mostly pointed setae with dome-shaped bases. About 6–8 setae of the latter type near the distal end of the glossae (Fig. 5C), the area covered by these setae with a larger number of campaniform sensilla. Sutures between prementum and paraglossae indistinct on outer half. Labial palps as in Fig. 5A and B, penultimate article about as wide as long; disc with evenly distributed macrosetae, along the inner margin some very long macrosetae. Ultimate article of the labial palps 2–2.5 times wider than long, the exact ratio varies due to different degrees of concavity. Papillae arranged in two bands not reaching the lateral margin of a brush-like sensilla field with tightly packed setae, the distal band longer than the proximal one (Fig. 5D). Bands mostly consist of 2–3 (proximal band) or 3–4 (distal band) rows of slender incisor-like ending and basally tapering sticks, that stand on similarly long, slightly inflated cylindrical bases (Fig. 5E). These sticks clearly separated from each other, no setae between bands. Sensilla field distal to the bands brush-like (distance between sockets less than their diameter) with short, mostly straight and apically rounded to acute sensilla, proximal to the bands with tightly packed short, apically needle-like setae bent towards the bands (Fig. 5E); the proximal sensilla field less extensive. Rest of article less densely covered with a mixture of acute to slightly bifid setae. A single basiconic sensillum type F and 2–3 basiconic sensilla type B, shape of both types of sensilla identical to those described above for

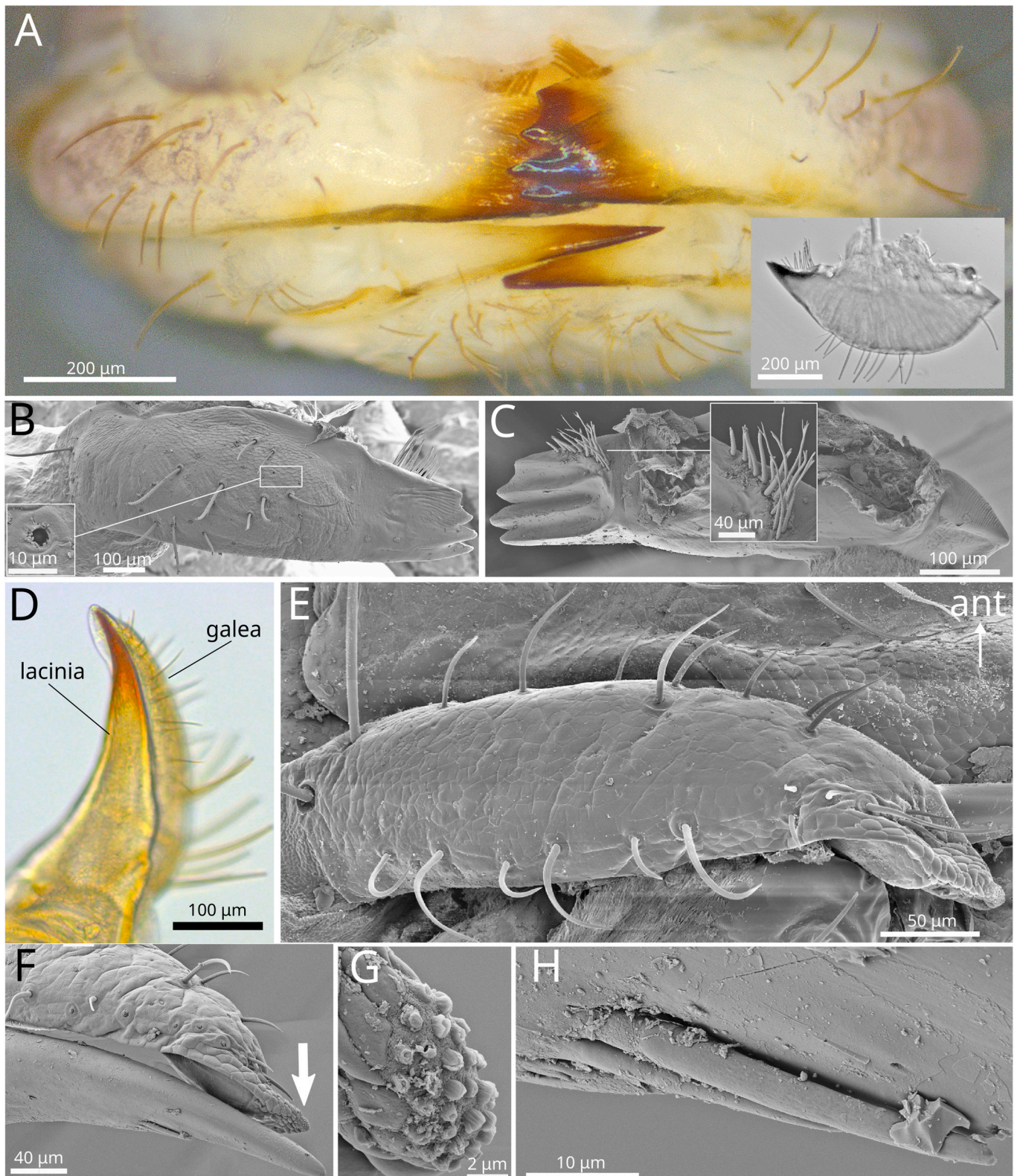


Fig. 3. *Atacamus neotropicalis*; mouth parts. **A)** Frontal view with mandibles and laciniae; labrum, galea, and antennae removed: inset with dissected mandible in lateral view. **B)** Outer side of mandible with rather isolated macrosetae, a triplet of rosette-like structures (see inset for single structure), and the group of macrosetae at the dorsal edge of incisivi. **C)** Inner side of opposite mandible from the same individual, the inset demonstrates the different forms of macrosetae at the tip. **D)** Inner side of isolated lacinia and galea, specimen not dried. The tip of galea covers the tip of lacinia. **E)** Outer side of dried galea with two rows of small, curved and apically acute setae, tip of galea clearly shrunk. **F)** Distal ends of lacinia and galea from inner side with a sensory/glandular field at the tip (arrow). **G)** Distalmost end of galea with condensed sensory/glandular field. **H)** Rudimentary bristle-like (?) structures near the inner apical tip of lacinia. A, D: micrograph; remaining figures: SEM.

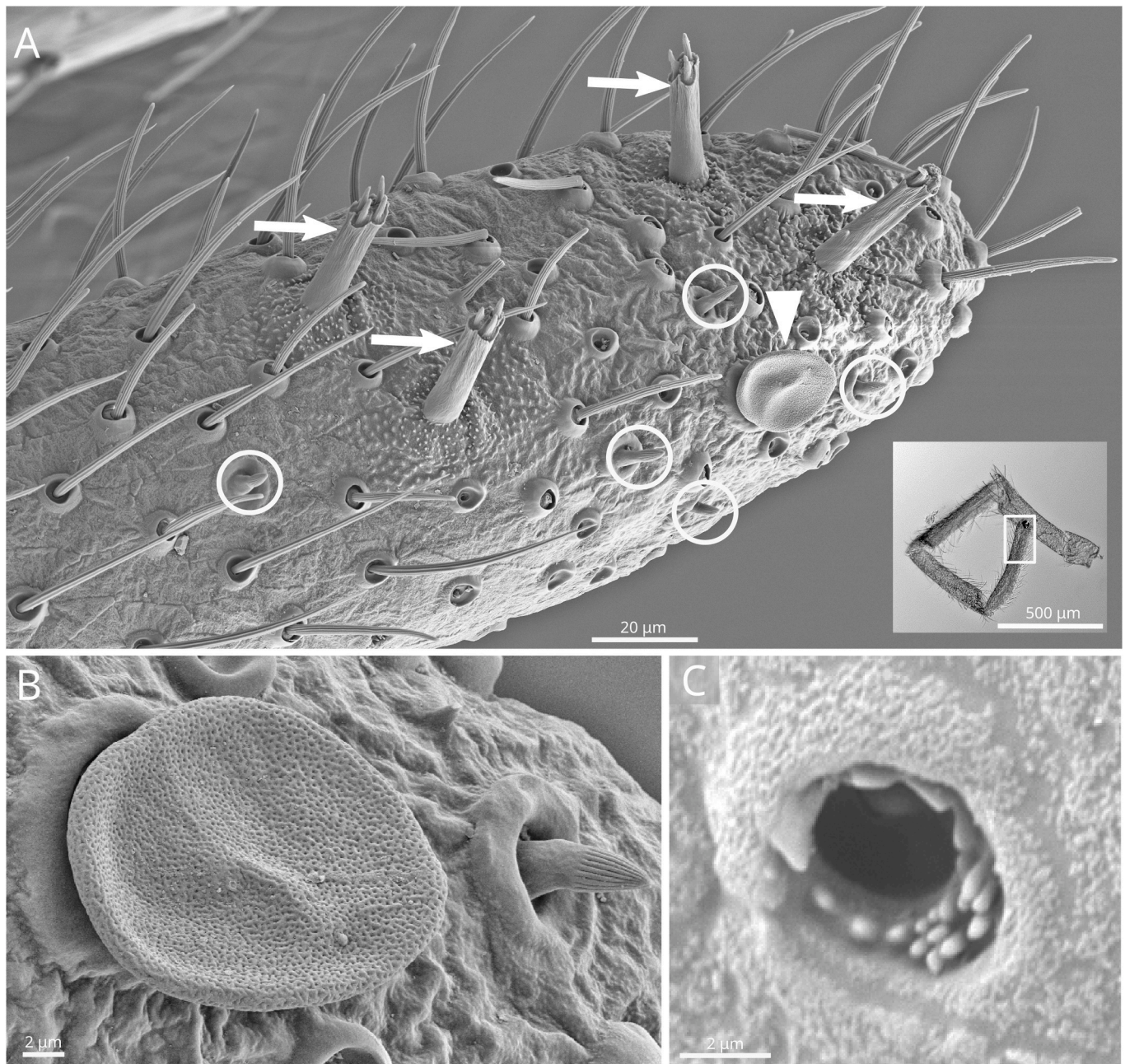


Fig. 4. *Atacampus neotropicalis*; ultimate segment of maxillary palp (SEM). **A)** Distal part with fairly fixed positions of sensilla on outer side; inset: complete maxillary palp (micrograph). Arrows, styloconic sensilla; arrowhead, basiconic sensillum type F; circles, basiconic sensilla type B. **B)** Details of basiconic sensillum type F and basiconic sensillum type B. **C)** Rosette-like structure with associated wide open cavity.

the maxillary palps, in the peripheral area (Fig. 5F). Rosette-like structures as in ultimate segment of maxillary palp, partially with wide open cavities (Fig. 5F), few campaniform sensilla medially. The side opposite the papilla-bearing one with few long and apically acute to slightly bifid macrosetae along lateral margins, the proximal margin only at the outer side with a row of 4–5 setae. This side on disc with 14–16 macrosetae, the inner side with only 4–5 isolated submarginal setae. Middle region without setae and cilia, no sensilla observed, few rosette-like structures.

General architecture and segmentation of antennae as described in detail for *M. bashagardensis* (Smith et al., 2020). Scapus longer than wide (~1.7–1.9; Fig. 6A and B) with a subapical ring reduced to 5–6 macrosetae on ventral/inner side (antennae facing forwards) and 6–8 macrosetae across the dorsal outer face; in addition, 6–8 discal macroseta proximal of the group of setae on inner/ventral side. Pedicellus shorter

than scapus, with a ring of subapical macrosetae, some of them very long; in addition, several shorter macrosetae on the inner and outer side proximal of the subapical ring. Scapus and pedicellus proximally each with 5 longitudinal rows of 4–6 very small and apically slightly double-lobed setae. Diverse types of setae along the flagellum. A typical mid-section of the flagellum, around annuli 80 to 100, is shown in Fig. 6. The T-annulus in this section shows an apical ring of forwards curved trichoid sensilla with ‘helmed’ sockets and acute tips (Fig. 6A, inset 1), interspersed several trichobothria with their characteristic half-serrated sockets (Fig. 6A, inset 2). Proximal ring of T-annuli with different types of chaetic setae, apically slightly bifid or acute and with different sockets. Segment proximal of T-annuli with ring of strongly bifid setae; slightly posterior of it six alternating setae with bent base (oval sockets; Fig. 6A, inset 3). Diverse sensilla with region-specific pattern,

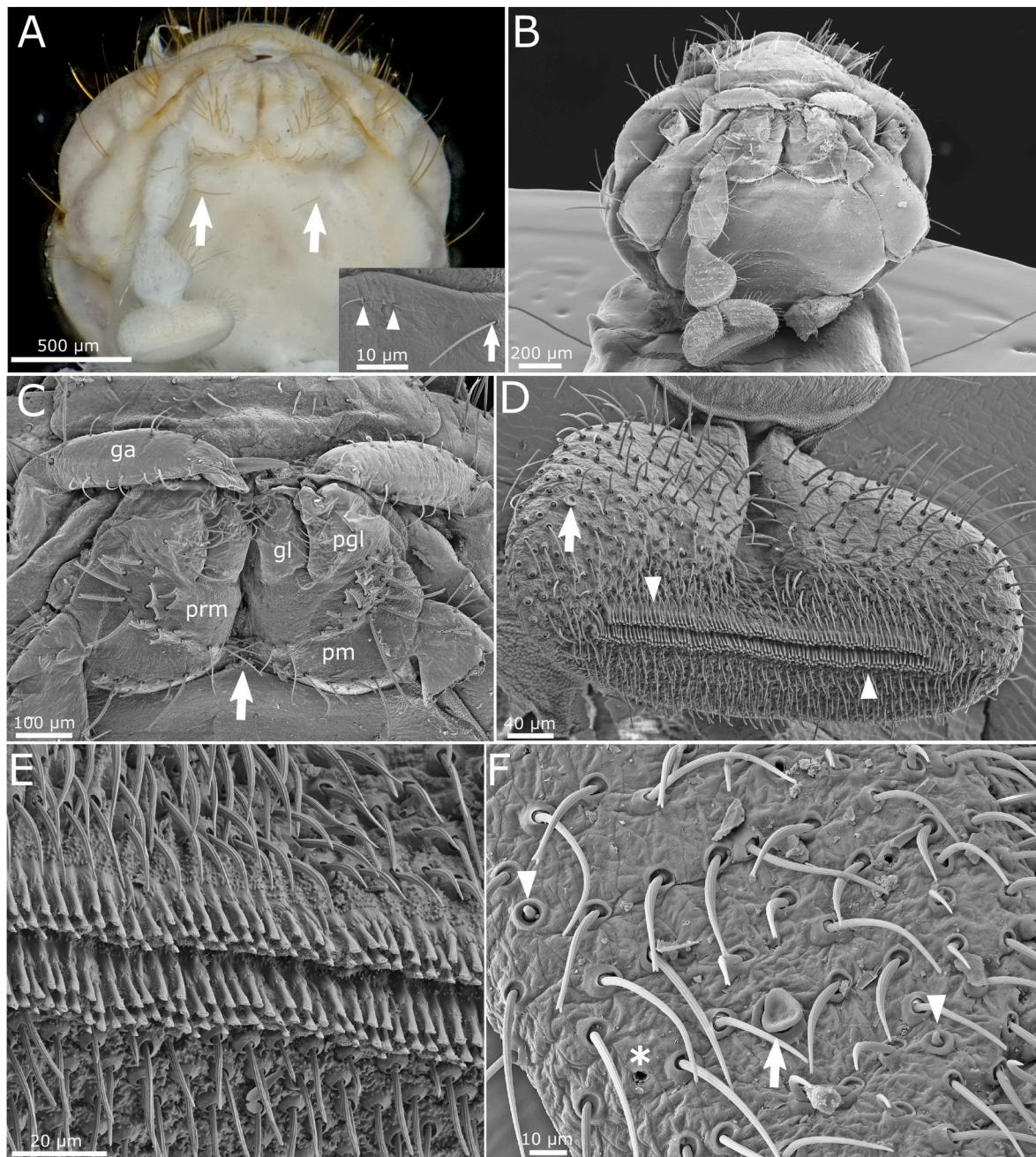


Fig. 5. *Atacamus neotropicalis*, labium. **A)** head ventral view. On the postmentum the anterolateral macrosetae are marked (arrows); the inset (SEM) also shows the much smaller anteromedian setae (arrowheads) and interspersed setulae. **B)** head ventral view, SEM. **C)** Overview of labium; macrosetae crossing the premental cleft marked by an arrow. ga, galea; gl, glossa; pgl, paraglossa; pm, postmentum; prm, prementum. **D)** Slightly eccentric ultimate article of labial palp with sensilla bands (arrow heads) and a single basiconic sensillum type C1 (arrow). **E)** Enlarged section with the two sensilla bands and adjacent setal/sensilla fields. **F)** Enlarged section with single basiconic sensillum type F (arrow), two basiconic sensilla type C2 (arrowheads), and a rosette-like structure with wide open cavity (asterisk). A: micrograph, remaining figures: SEM.

exemplarily shown in Fig. 6B for sensilla located opposite to the side shown in Fig. 6A.

Pronotum wider than long (~1.25–1.30), widest at around the middle, anterolateral edge not visible in dorsal view; with slightly indented posterior margin and shallow median depression. Pronotal collar flat and fairly wide (0.15 of total length pronotum), with 3 + 3 lateral macrosetae and an uniseriate fringe of about 20 mostly bent setulae along posterior margin (Fig. 7A and B). Pronotal folds fairly deep, slightly sigmoid from semilateral view, medially shallow and narrowed anterolaterally (Fig. 1B and 7A, B). Raised lateral margin as in all thoracic nota well-developed and roundish in cross section (Fig. 7A

and B), fading anteriorad and postero-mediad (posterior margins medially not raised at all). Anterolateral with 2 + 2 macrosetae anterior to the raised lateral margin, additionally 3–5 + 3–5 (rarely up to 7) macrosetae of different length on the raised lateral margin in the posterior half, and 1 + 1 submarginal posterolateral macrosetae (Fig. 7B). Two submarginal trichobothria posterior of the anterolateral macrosetae. Meso- and metanotum with similar patterns (Fig. 7C and D), but mostly with 3 + 3 anterolateral macrosetae, 4 + 7 macrosetae on the raised lateral margin in the posterior half, a further submarginal single macroseta (in addition to the submarginal posterolateral macroseta) behind the anterior group, and the two lateral submarginal trichobothria located in the middle

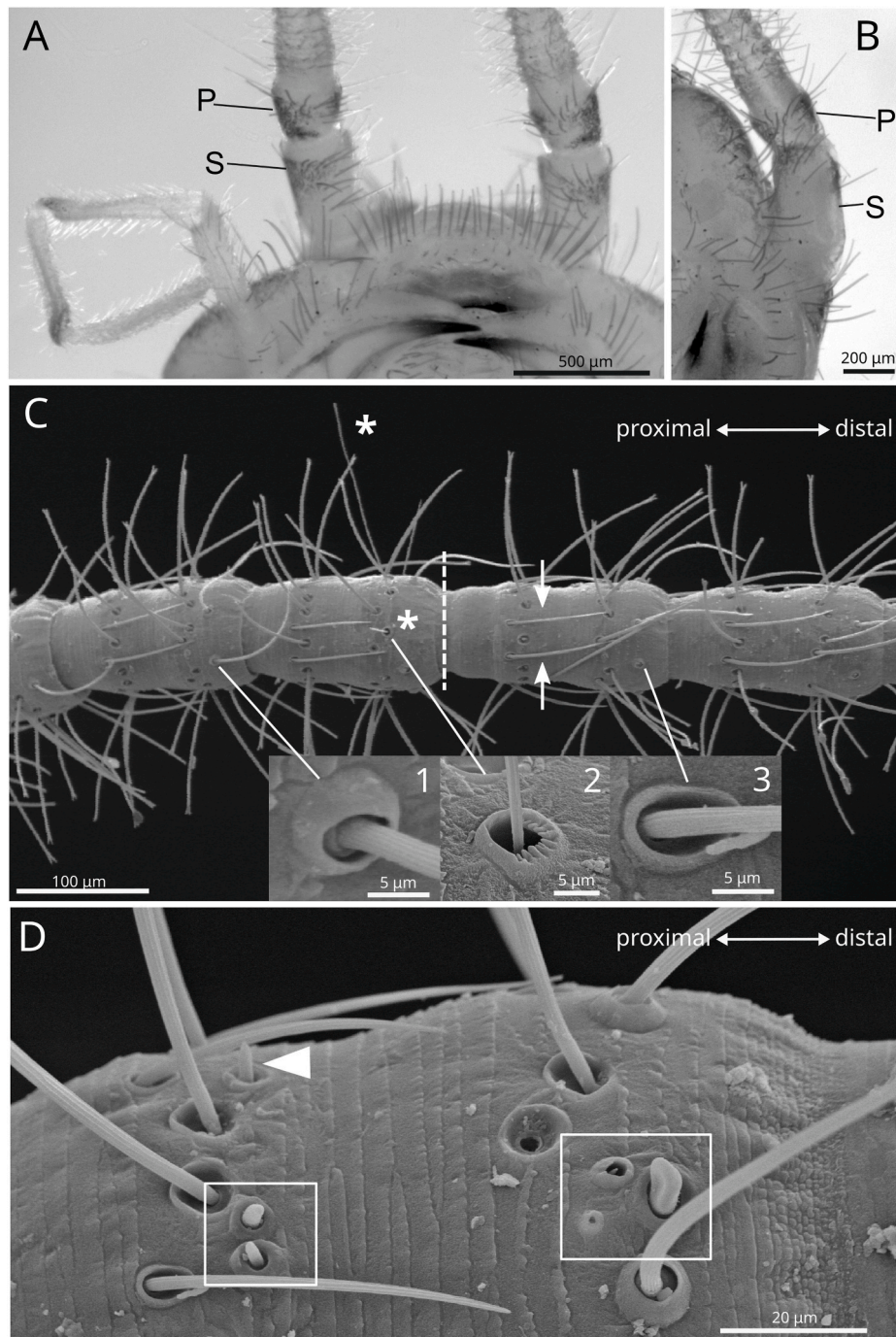


Fig. 6. *Atacamus neotropicalis*, antenna (SEM). A) and B) Anteroventral views with basal parts of antennae (different specimens); S: scapus, P: pedicellus. C) Overview of middle section of with diverse types of setae, the dashed line marks the boundary of an interval. Trichobothria of T-annulus with half-serrated sockets (asterisks; see inset 2), bent-based setae with pointed tips and oval sockets (arrows, see inset 3), trichoid sensillum of the apical ring (socket see inset 1). D) Examples of sensilla located opposite to the side shown in C). The more distal sensilla form a triad with basiconic sensillum F – basiconicum A – coeloconicum, the proximal sensilla consist of paired basiconic sensilla B (different subtypes) and a single basiconic sensillum C (arrowhead). A, B: micrograph; C, D: SEM.

(mesonotum) or in the posterior half (metanotum, posterior trichobothrium usually slightly behind the first macroseta of the raised posterolateral margin). Meso- and metanota slightly broader than pronotum, indentation on posterior margins more distinct, median furrow fine and narrow.

Basisterna of thorax large and flat, probasisternum tapering anteriorly and with 1 + 1 anterolateral bristlecombs perpendicular to the lateral margin and consisting of 2–4 bifid macrosetae each (Fig. 8A). Propres- ternum trapezoid, tapering posteriorly and protruding between large episternal (?) sclerites (Fig. 8A); when viewed from lateral running

anterodorsad and meeting the postmentum at an almost right angle. All spinasterna broadly transverse and with deep sutures to basisterna (Fig. 8A–C). Meso- and metapresterna are transverse sclerites separated by straight sutures from the respective basisterna and the spinasterna of the anterior segment. Meso- and metabasisterna anterior of the middle with 1 + 1 lateral bristlecombs perpendicular to the lateral margin and with 4–6 macrosetae each (Fig. 8A–C). Three mostly arch-like subcoxal sclerites, the one articulating on the coxa (trochantinus?) with a row of 5–6 (prosternum) or 2–3 (meso-, metasternum) macrosetae, the middle one with 2–4 macrosetae, and the most proximal of these sclerites

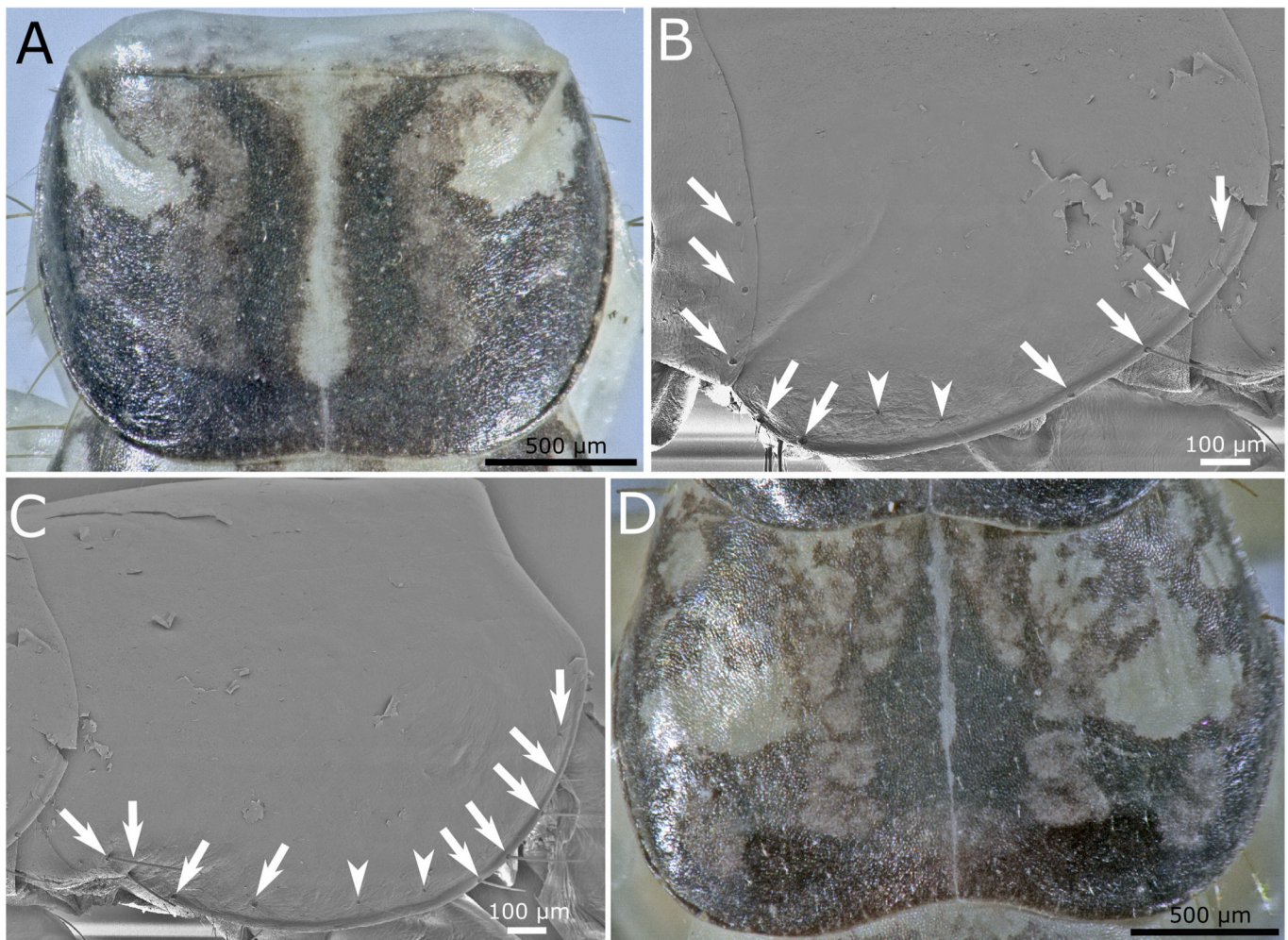


Fig. 7. *Atacampus neotropicalis*, thoracic nota. **A)** Pronotum, dorsal view. **B)** Pronotum with distinct fold, semi-lateral view (left side). Most macrosetae broken off, but bases (bold arrows) clearly visible. Trichobothria marked by arrowheads. **C)** Mesonotum, semilateral view (left side). **D)** Metanotum, dorsal view. A, D: micrograph; B, C: SEM.

without macrosetae (Fig. 8A and B).

Legs strongly lengthening posteriad (Fig. 9A), tibia III about 1.5 times length of tibia I and with L/W ratio of 4:1. Coxae ventrally perpendicular to the outer margin with 4–5 bristlecombs of 3–4 macrosetae each, on inner margin 2–3 bristlecombs of 2–4 macrosetae each, and 10–14 macrosetae along apical margin (among these 2–3 much longer macrosetae at apical inner edge facing the trochanter); occasionally single macrosetae between bristlecombs. In addition, two isolated marginal macrosetae on outer margin, one slightly proximal to the most proximal bristlecomb and the other (rarely two on procoxa) halfway between the proximal bristlecomb and the coxal insertion. Only on procoxa, a median submarginal macroseta (rarely 2) on proximal margin. Trochanters with 3–5 mostly marginal macrosetae and several smaller apically directed submarginal/discal setae, mainly on tibia-facing side. Femora with 3–4 straight spines on inner/posterior margin (the more distal on apical edge), intermingled with apically directed smaller setae that also cover the inner/posterior half of the ventral side (anterior area bare) and the anteroapical region. The anteroapical edge with a comb of three carrot-shaped macrosetae facing the tibia (their tips give the impression of being cut off, but appear with a slight notch at high magnification), few smaller setae posterior to this group, a single carrot-shaped submarginal macroseta with a more or less median position both on the ventral and dorsal side of the apical margin, and 3–5 stout (carrot-shaped) macrosetae along the outer/anterior margin (the distal one as large as the other carrot-shaped macrosetae of

femur, the other distinctly smaller). A single medioproximal macroseta on dorsal side of femora, particularly strong on profemur. Tibiae along both sides of posterior margin with 10–14 (protibia) or 6–10 (meso-, metatibia) long spines (Fig. 9B and C). The carrot-shaped macrosetae are arranged in a regular pattern over the ventral side, two each anteriorly, posteriorly and submarginal on the apical margin (Fig. 9B and C; [Supplementary Material 2C](#)), on the probiae often a third carrot-shaped macroseta proximally of the posterior couple. In addition, the ventral side densely covered ventrally with apically directed smaller setae (less dense on dorsal side), a seta-free band in front of the midline (Fig. 9B and C). Tibial spurs minute and variable between specimens, usually triangular (Fig. 9D), but occasionally undetectable even using a SEM; generally, hardly visible under the light microscope. Four-segmented tarsi densely covered with the fine apically directed setae and stronger macrosetae, the latter arranged in two sometimes indistinct ventrolateral rows on tarsal segments; 1–2 stout spines lateral on distal end of first tarsal segment. Pretarsal claws mildly curved apically, outer surface smooth, inner side at the base partly granulated, distal area slightly striated; empodium straight, about half of total length of claws, and with more or less developed microtrichia (Fig. 9E).

Urotergites I–IX each with a series of 4 + 4 (range 3–5) evenly spaced isolated marginal macrosetae on the posterolateral angles, 1 + 1 adjacent submarginal discal macrosetae on the posterolateral angles, and 1 + 1 mediolateral discal macrosetae (Fig. 10A and B). Especially on the posteriad urotergites, the mediolateral macrosetae are located on the

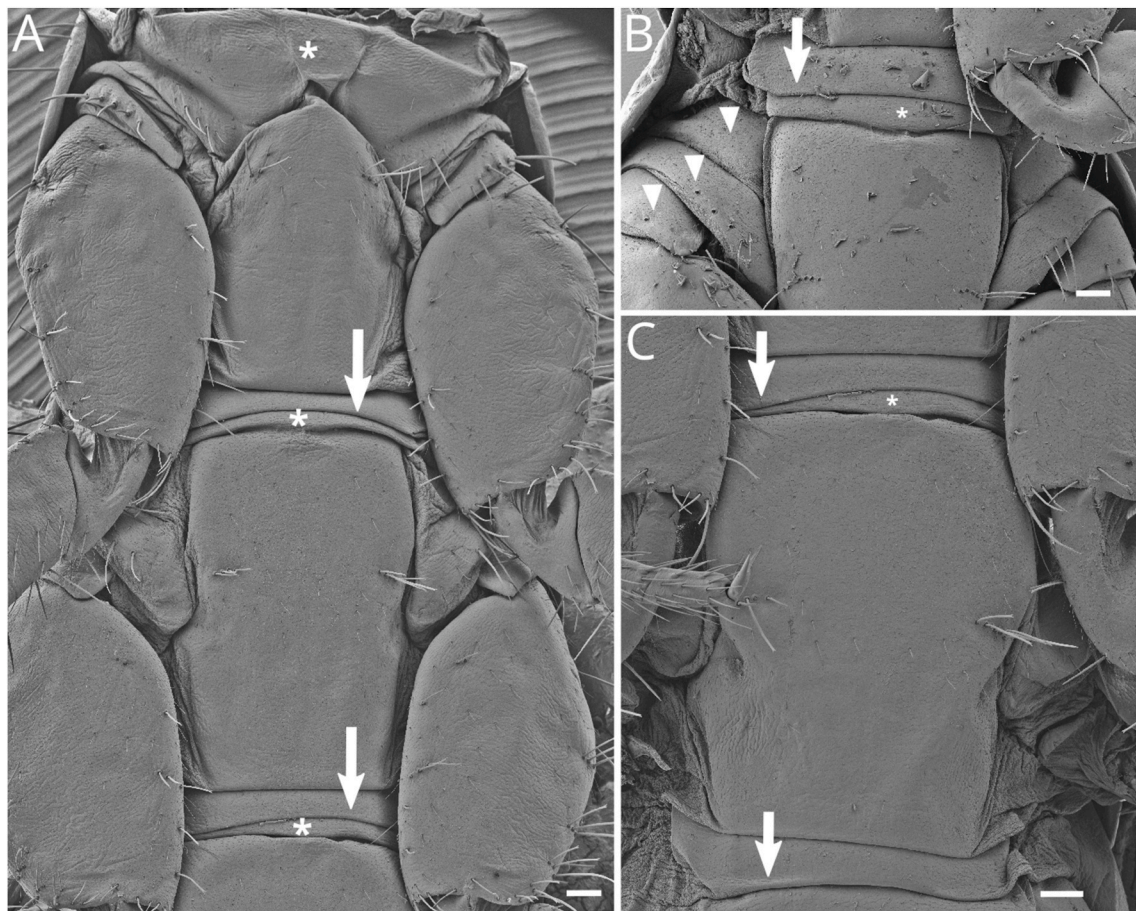


Fig. 8. *Atacamus neotropicalis*, thorax ventral (SEM); presternites marked by asterisks, spinasternites marked by arrows. **A)** Overview pro- and mesothorax (male). **B)** Mesothorax (female) with arch-like subcoxal sclerites (arrowheads). **C)** Overview metathorax (male). Scale bars: 100 μ m.

ventrally downfolded lateral parts and can only be seen in lateral aspect, these macrosetae missing on urotergite IX. Urotergite X along the convex part (middle part) of the hind margin with 6–10 + 6–10 evenly distributed and posteromedially directed straight macrosetae of different size; in addition, few much smaller posterolateral submarginal setae. Uniseriate rows of posteroventrad directed very small setae (setulae?) lateral/submarginal on inner sides of urotergites I–VII, less so on thoracic nota and urotergites VIII and IX. Disc of urotergites IX and X with abundant setulae in the posterior third, bare in front of it. Posterior margins of urotergites I–VIII weakly concave, that of urotergite IX more or less straight, urotergite X evenly rounded posteriorly (Fig. 10C).

Urosternite I with 1 + 1 submarginal submedian bristlecombs on posterior margin with 2–3 macrosetae each and 2–4 tiny widely spaced marginal setae on the posterolateral angles, urosternites II–VII (II–VIII in males) with 3 + 3 submedian bristlecombs of 3–6 macrosetae each, slightly distant from the posterior margin and with the outermost macroseta of the outer submedian bristlecomb noticeably more robust than the rest; 3–5 mostly small and widely spaced, posteriad directed marginal setae on the posterolateral angles; 1 + 1 posterolateral bristlecombs of 1–4 (mostly 1–2) macrosetae, and 1 + 1 lateral discal bristlecombs of 2–4 macrosetae each (Fig. 11A), the latter missing on urosternite II and male urosternite VIII. Posterior margins of urosternites I–VI (females) and I–VIII (males) with weak concave indentation, urosternite VII of females straight to evenly rounded posteriorly (Fig. 11B). Coxites VIII in females with the outer submedian bristlecomb described above for urosternites anterior thereof as well as the posteriorly directed marginal setae on the posterolateral margin and a single large posterolateral submarginal macroseta; the posteromedian (inner) margin of these coxites with a row of 8–12 setae (Fig. 11B). The stylus-

bearing coxites IX of females each with a densely packed field of >30 macrosetae of different lengths along the inner margin of the inner process, these setae partially intermingling with the numerous long and acute setae originating from the paraproct (Fig. 11B, inset). Inner and outer process of coxite IX with 1–2 isolated apical discal macrosetae each (Figs. 11B) and 3–4 posteriorly directed macrosetae on the posterior margin of the outer process (Fig. 11B, inset). Inner process apically pointed-triangular extended, same length or slightly longer than the posteriorly broadly rounded outer process. Both sexes with one pair of rather slender styli with 8–9 stout spines (acute or truncated) running in a line along the slightly convex ventral side, then around the tip and ending with at least two spines on the dorsal side. This series of stout macrosetae joined on the both sides by 8–12 smaller macrosetae. Inner process of coxite IX of male same length as outer process, both processes rounded triangular, each with 2–3 macrosetae on disc (Fig. 11C), the outer process also with the marginal macrosetae on posterior margin. Unlike in females, the macrosetae along the inner edge of the inner process extend far onto the disc (Fig. 11C).

Male parameres medium-sized, shorter than inner process of coxites IX, pseudoarticulated (Fig. 11C, inset), densely covered with long pointed macrosetae, otherwise without special features (Fig. 11C). Penis short, reaching to the base of the parameres, the wide opening with a ring of short pin-shaped styles on inner margin. Epiproct and paraprocts without processes; paraprocts with a dense tuft of long pointed macrosetae on disc, anteriad with two much stronger bifid macrosetae (Fig. 11C).

Ovipositor of primary type and moderately long, slightly inflated in front of tip, with 22–26 divisions (Figs. 12A), 0.28–0.32 x body length; tip of gonapophyses 9 with a distinct hiatus (Fig. 12B). Each division

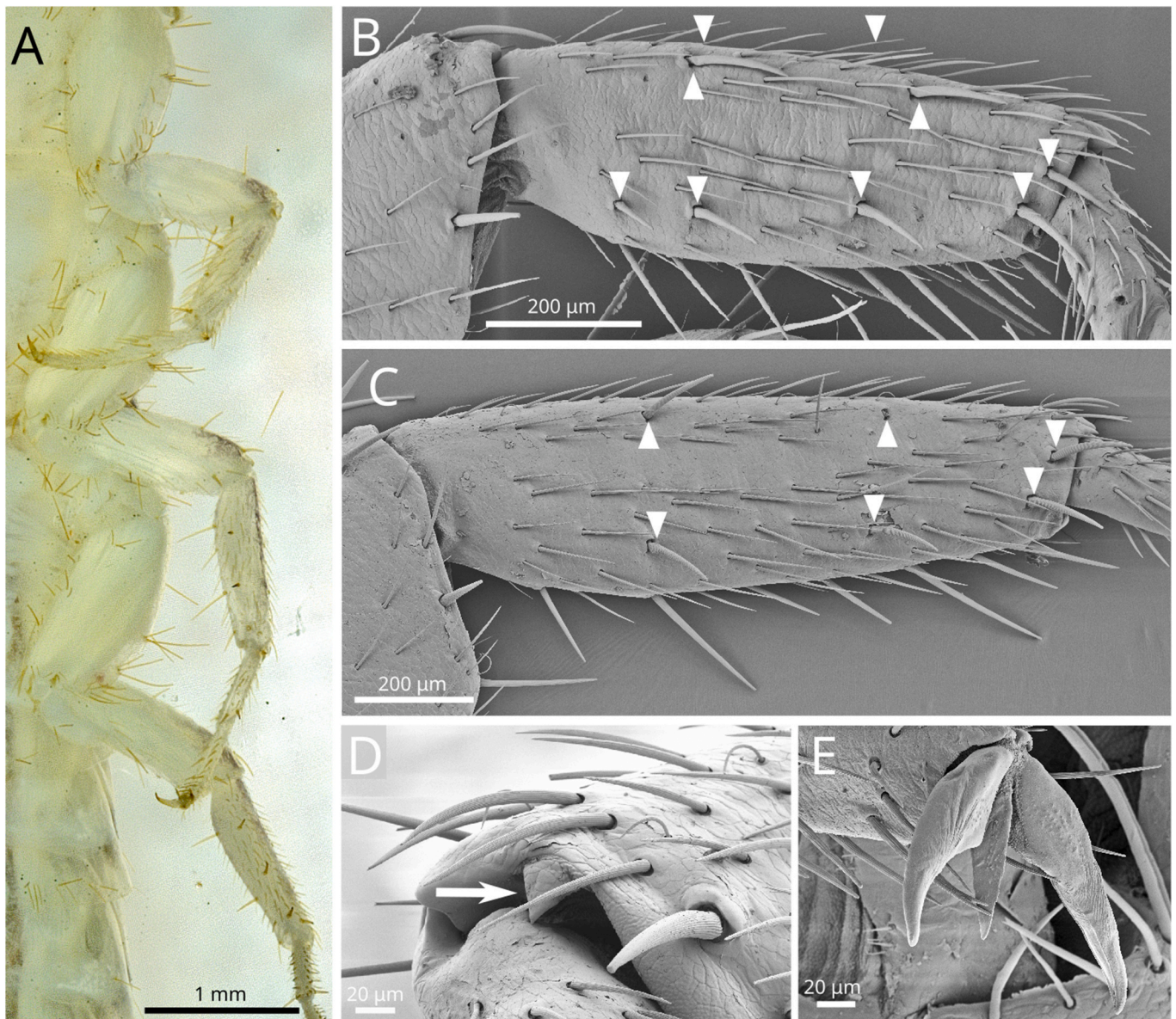


Fig. 9. *Atacamus neotropicalis*, legs ventral view. **A)** overview. **B)** Protibia with many smaller apically-directed setae, carrot-shaped spines (arrowheads), and a dense row of longer spines along both sides of the posterior margin. **C)** Mesotibia with similar pattern of spines and setae as in protibia, but less spines along the posterior margin. **D)** Apical tip of mesotibia with reduced tibial spur (arrow). **E)** Pretarsal claw and empodium of mesotarsus. A: micrograph; remaining figures: SEM.

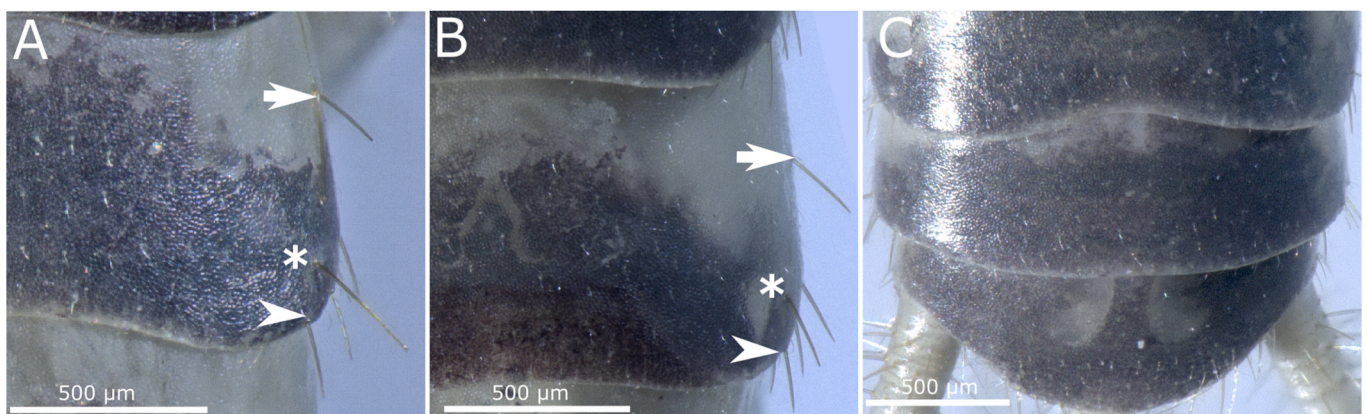


Fig. 10. *Atacamus neotropicalis*; urotergites (micrographs). **A)** Urotergite I with posterolateral marginal (arrowheads), posterolateral submarginal (asterisk) and mediolateral (arrow) macrosetae. **B)** Urotergite IV. **C)** Urotergites VIII–X.

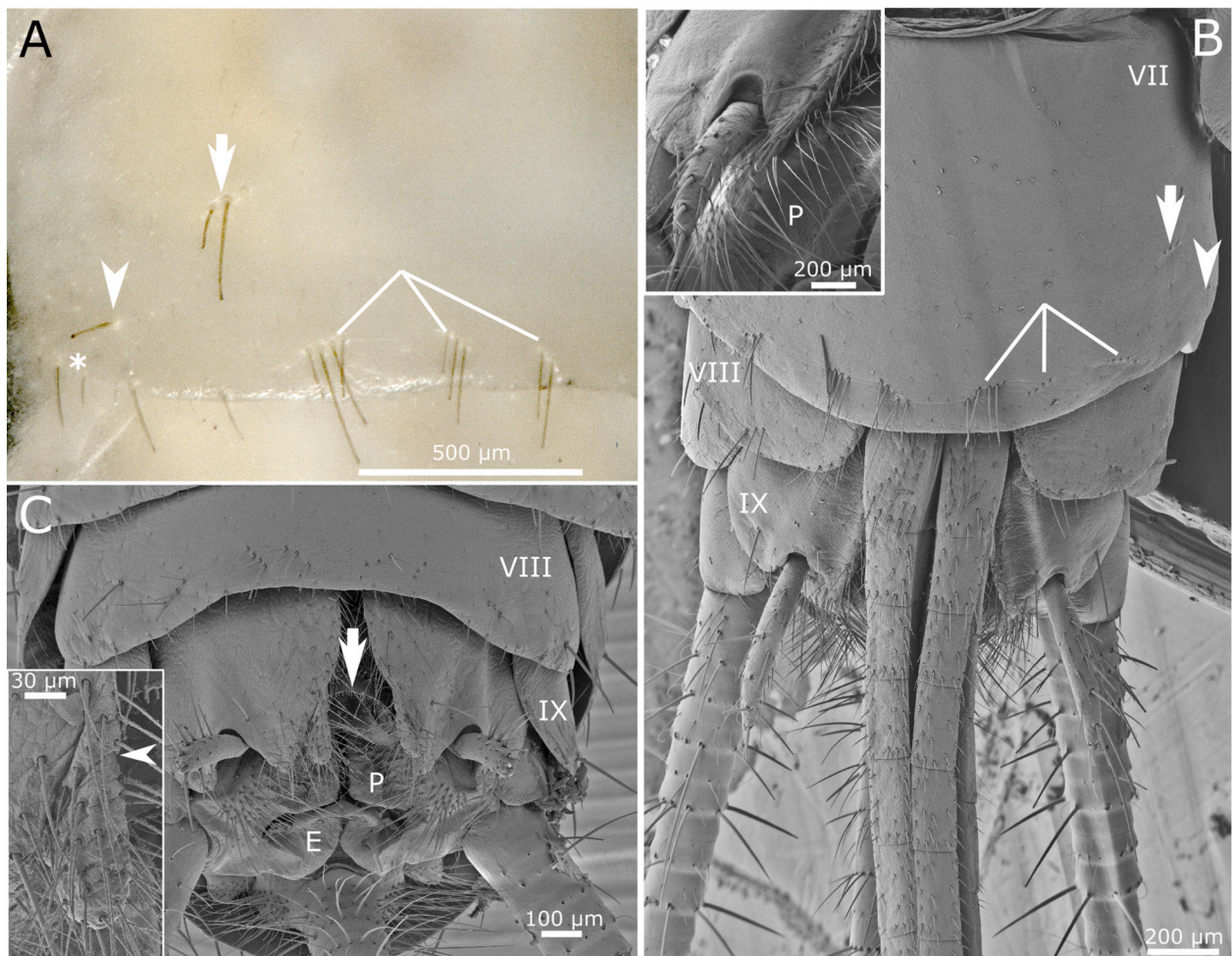


Fig. 11. *Atacamus neotropicalis*, abdomen ventral. **A)** Setation of urosternite VI (left side) with submedian bristlecombs (with lines), posterolateral marginal setae (asterisks), posterolateral submarginal macrosetae (arrowhead), and lateral discal bristlecombs (arrows, light microscopic image). **B)** Posterior sternites female (markings as in A), inset shows coxite IX and setation of paraproct (P); ovipositor removed. **C)** Posterior sternites male with parameres, penis (arrow), paraprocts (P) and epiproct (E); inset shows pseudoarticulated paramere (arrowhead). A: micrograph; B, C: SEM.

with moderately long and acutely pointed setae, those of gonapophysis 9 with setation restricted to a lateral band. Setae shorter, slightly conical to bulbous and with curved needle-shaped tips at apical divisions (Fig. 12C). Distalmost tip of ovipositor with more densely grouped setae (socket diameter wider than distance between them), the ultimate division proximal of the tip with a number of basiconic sensilla type C2 (Fig. 12C).

Proventriculus with six large sclerites, tentatively labelled as ventral sclerite (V_{prov}), paired lateroventral sclerites (LV_{prov}), paired laterodorsal sclerites (LD_{prov}), and dorsal sclerite (D_{prov}) (Fig. 13A and B). Sclerite V_{prov} obovate; middle area concave and without bristles; bristle-free area ovate, tapering towards the tip and the base (Fig. 13C). Sclerite D_{prov} with longitudinal ridge facing the lumen, anteriad evenly broadened; the posterior $\frac{3}{4}$ of ridge with bristles that cover the entire width; the bristle-free anterior area spatula-like and slightly concave to plane (Fig. 13D); ridge weakly curved from lateral view; sickle-shaped frontal edge (Fig. 13E). Sclerite LV_{prov} with distinct anteriorly-directed protrusion (Fig. 13F and G); distal end of protrusion rather plane and with 4 rounded terminal lobes; socket with distinctly raised lateral crests, the area in between depressed (Fig. 13G); the crest facing V_{prov} slopes at about 45° , middle part of it with scattered bristles and moderate convexity (Fig. 13F); sclerite LD_{prov} with asymmetrical anteriorly-directed slightly bilobed protrusion arising from a longitudinal dorsal indentation, posteriorly within the depression densely covered by strong bristles; the margin facing D_{prov} slightly roundish raised in lateral view,

sloping anteriorly at a very obtuse angle to the protrusion (Fig. 13H).

Material examined: Holotype, male, NMB. Dissected with different parts mounted on each of five microscope slides. Each slide with three handwritten labels, respectively to the left (a), right (b) and bottom right (c) of the central cover slip. Mounting medium strongly blackened in some cases, but contents remain visible with bright backlighting.

- Slide 1, labelled: a) *M. neotropicalis* Wygod. Junin/Chile, IX-1909; b) Kopf mit kopfhänge, L2026. TYPUS [later printed label]; c) Naturh. Museum Basel, Insecta I.C.20. Pr.I/94. Coll. Wygodzinsky. Almost completely black, contains: head capsule, fragments of antennae, 2 mandibles, 2 maxillae with palps, no labium.
- Slide 2, labelled: a) *M. neotropicalis* Wygod. Junin/Chile, IX-1909. b) Urosternite 1–9. L2027. c) Naturh. Museum Basel, Insecta I.C.20. Pr. I/95. Coll. Wygodzinsky. Brownish, contains: most urotergites and urosternites.
- Slide 3, labelled: a) *M. neotropicalis* Wygod. Junin/Chile, IX-1909. b) Beinpaare 1, 2, 3. Terga 1, 2, 3. L 2029. c) Naturh. Museum Basel, Insecta I.C.20. Pr.I/97. Coll. Wygodzinsky. Brown to black, contains: three thoracic sterna plus attached legs (three legs consist of coxae only, one leg free-floating), no thoracic terga.
- Slide 4, labelled: a) *Maindronia neotropicalis* Wygod. Junin/Chile, Coll. Masarey. b) Cercus L 2008. c) Naturh. Museum Basel, *Maindronia neotropicalis* Wyg., Junin/Chile. Insecta I.C.20. Pr.I/92. Coll. Wygodzinsky. Clear slide, contains: almost complete right cercus.

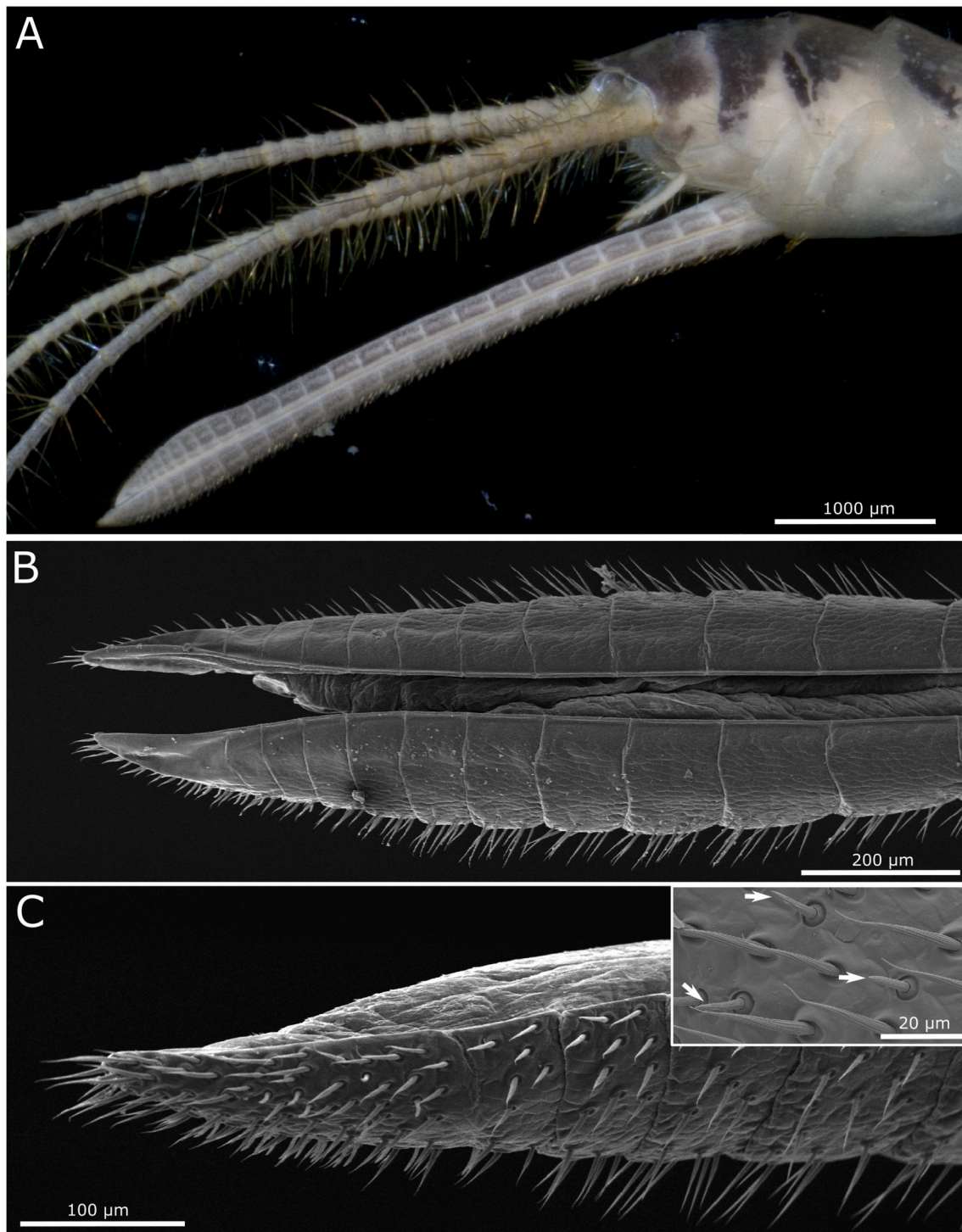


Fig. 12. *Atacamus neotropialis*, ovipositor. **A)** Overview from lateral. **B)** Dorsal view of gonapophysis 9; setation restricted to a lateral band, tip with hiatus-like cleft. **C)** Tip of gonapophysis 8 (lateral view) showing dense and slightly conical to bulbous setae with needle-shaped tips, curved at apical divisions. Sensilla basiconica C (inset, see arrows) between setae. A: micrograph; B, C: SEM.

- Slide 5, labelled: a) *Maindronia massareyi neotropicalis* Junin/Chile, 1909, Coll. Masarey. b) Cercus & filum terminale, L 2009. c) Naturh. Museum Basel, *Maindronia neotropicalis* Wyg., Junin/Chile. Insecta I.C.20. Pr.I/93. Coll. Wygodzinsky. Clear slide, contains: urotergite X plus almost complete left cercus and part of filum terminale.

Material of [Paclt \(1966\)](#): 1 ♀ (in ethanol), labelled: Junin, R. Paessler, leg. 3.VIII.1911, lect. 11.X.1911; *M. neotropicalis* (det. J. Paclt) dazu 2 Präparate (MNH). (The microscope slides, that according to the

publication include one leg and some fragments of terminal filaments, were not seen.)

New material:

AMNH_IZC 00395921 (in ethanol): CHILE, Tarapacá, Pisagua, 28.9.57, Kuschel leg., 3♀♀, 5♂♂.

AMNH_IZC 00395923 (in ethanol): Iquique, en la playa, 8.9.57, L.E. Peña, Kuschel, 3♀♀, 1♂, 1 subadult.

AMNH_IZC 00395924 (in ethanol): Iquique, en La playa, 5.10.57, L. E. Peña, Kuschel, 6♀♀, 5♂♂.

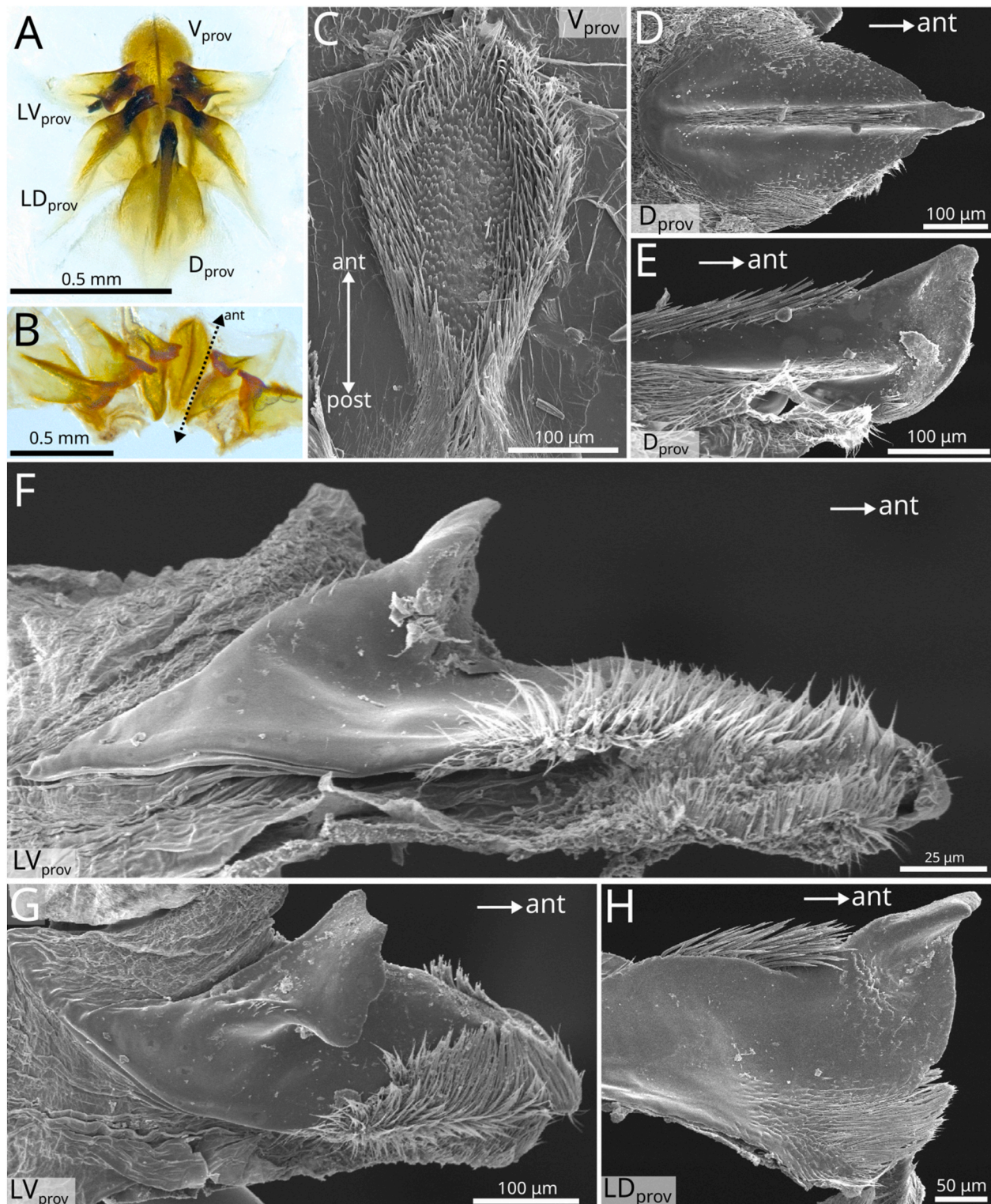


Fig. 13. *Atacamus neotropicalis*, sclerites of proventriculus. **A)** Overview of sclerites in natural position, frontal view; **B)** Proventriculus opened for dissection of the individual sclerites; **C)** Sclerite V_{prov} ; **D)** Sclerite D_{prov} , lumen-oriented; **E)** Sclerite D_{prov} , lateral view; **F)** Sclerite LV_{prov} , lateral view; **G)** Sclerite LV_{prov} , lumen-oriented; **H)** Sclerite LD_{prov} , lateral view. A, B: micrograph; C–H: SEM.

CHILE, Caleta Camarones (voucher code: B33, in ethanol), S19°11.64 W70°15.80', 30 m a.s.l., under stones. 16.3.2022, leg. R. Predel. 2♀♀, 1♂: 1♀ (MZUC), 1♀, 1♂ (MNH).

CHILE, Caleta los Verdes (voucher code: B38, in ethanol), S20°26.05 W70°09.65, 5 m a.s.l., under stones. 10.10.2017, leg. A. Zúñiga-Reinoso, A. Jara. 1♂ (MZUC).

CHILE, Caleta Junin (voucher code: F02, in ethanol), S19°39.51 W70°10.13, 5 m a.s.l., under dry kelp. 18.3.2022, leg. A. Zúñiga-Reinoso, R. Predel, A. Jara. 11 specimens: 2♂♂, 2♀♀ (MNH), 2♂♂, 2♀♀ (MNH), 2♂♂, 1♀ (MZUC). Same place and habitat as above, 17.03.2025, leg. R. Predel. 3 specimens: 2♂♂, 1♀ (MKB).

CHILE, 12 km S of Rio Loa mouth (voucher code: F15, in ethanol),

S21°32.35 W70°04.52, 2 m a.s.l., under dry kelp. 20.3.2022, leg. A. Zúñiga-Reinoso, R. Predel, A. Jara; 3♀♀, 1♂ (MZUC), 1♀ (MNHN), 1♀ (MKB).

Distribution: Collected along the coast from Quebrada Camarones in the north to 12 km S of Rio Loa mouth in Chile.

Habitat of type locality: Different stages of *A. neotropicalis* were collected by hand a few meters above the sea level along a rather narrow zone on the beach at Caleta Junin; mainly under dry or almost dry kelp, but occasionally also under stones (Fig. 1C). The beach borders on the steeply rising Coastal Cordillera, the transition from beach to Coastal Cordillera is abruptly hyperarid and without vegetation. Similar habitats are also typical for the other populations collected.

Remarks: The COI sequence of at least a single specimen of each newly collected population was analyzed, these specimens showed sequence identities to specimens from the type locality of 96.4 % or higher (616 bp). All described characters visible by light microscopy were confirmed to be identical for the specimens of these populations.

3.3. *Peruatacamus* Irish, Zúñiga-Reinoso & Predel, **gen. nov**

<https://zoobank.org/12D6D886-72F6-4D97-9063-7980ABAD6B93>.

Type species: *P. atunpacha* Irish, Zúñiga-Reinoso & Predel, **sp. nov.**

Diagnosis: Genus characterized by well-developed tibial spurs without setae, absence of macrosetae on pronotal collar, absence of posterolateral macrosetae on thoracic nota, absence of macrosetae on posterior urotergites, 2 + 2 submedian bristlecombs on urosternites III – VII, absence of lateral discal macrosetae on urosternites III – VII, and epiprocts/paraprocts with distinct processes. Large species.

Etymology: A combination of ‘Peru’, the country where the species was discovered, and *Atacamus*, the new genus name for the first species of Maindroniidae described from South America; we specify the gender as masculine under ICZN article 30.2.2.

3.3.1. *Peruatacamus atunpacha* Irish, Zúñiga-Reinoso & Predel, **sp. nov**

<https://zoobank.org/74633F3F-8136-4F27-8A0F-BD4C042BC757>.

Description based on material collected at the type locality within a distance of about 50 m (COI sequence see [Supplementary Material 1B](#)):

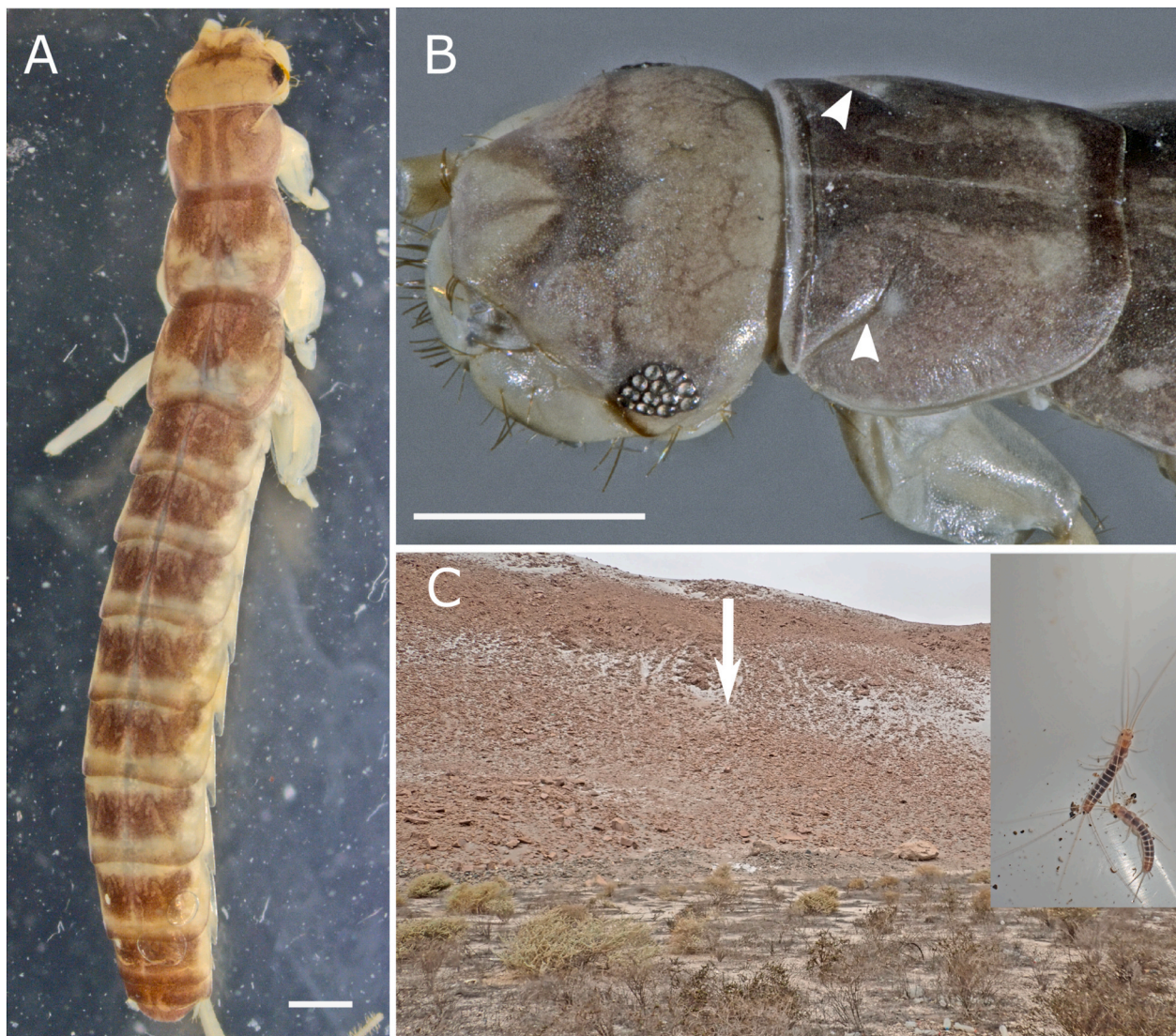


Fig. 14. *Peruatacamus atunpacha*. **A)** Colour pattern of female specimen (paratype used for SEM), stored in ethanol, from type locality near Arequipa (dorsal view); image slightly overexposed to recognize main patterns more easily. **B)** Dorsolateral view of head and pronotum. Anterolateral pronotal folds marked by arrowheads. **C)** Collecting spot at type locality (arrow); *Peruatacamus* (or Maindroniidae) have not been found in the area with shrubs in the foreground. Inset: Living specimens, probably males, after collecting in the field. The blackish colour results from the filled foregut, which extends far into the abdomen. Scale bars: 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Body length of adults 14–20 mm (largest specimen measured alive 19.4 mm), of holotype: 16.1 mm. Antennae and caudal filaments when intact at least twice as long as the body; longest intact cercus three times longer than body.

Ground colour of body white, dorsal body with a distinctive pattern formed by varying distribution and intensity of brownish to blackish granular epidermal pigment (Fig. 14A and B). Dorsal pattern details vary individually but persistent elements include all or most of: a dark Rorschach pattern on the frons (Fig. 14B); dark edges to the lateral and posterior margins of the thoracic nota and urotergites (narrow on urotergites), with a lighter submarginal band and a darker basal disc; narrow unpigmented light lines at the pronotal folds, shorter unpigmented areas mediolaterally at a similar position on the meso- and metanota; a median longitudinal line, with darker lateral edges on the pronotum, from the pronotum to urotergite X (part of which may be the dorsal

haemolymph vessel visible through the transparent integument); urotergite X mostly dark with 1 + 1 lighter discal comma-shaped spots. Entire ventral body, including maxillary/labial palpi and styli, unpigmented. Legs, antennae, clypeus, caudal filaments and ovipositor usually unpigmented, at most lightly pigmented; tibia on ventral and dorsal side with more regular weak pigmentation. In living animals, brownish pigmentation on most urotergites and posterior nota often unrecognizable due to dark foregut content visible through the body (Fig. 14C, inset). In these cases, only the white submarginal posterior band and white lateral side well visible. Types of setae as in *A. neotropica*.

Head wider than long, 1 + 1 trichobothria on disc of vertex directly posterior of postfrontal suture, halfway between origin of the coronal suture and the lateral margin (Supplementary Material 2B). Anterior margin of frons nearly straight (Fig. 14B), the adjoining proximal margin of clypeus slightly bent upwards (frontal view). Periantennal

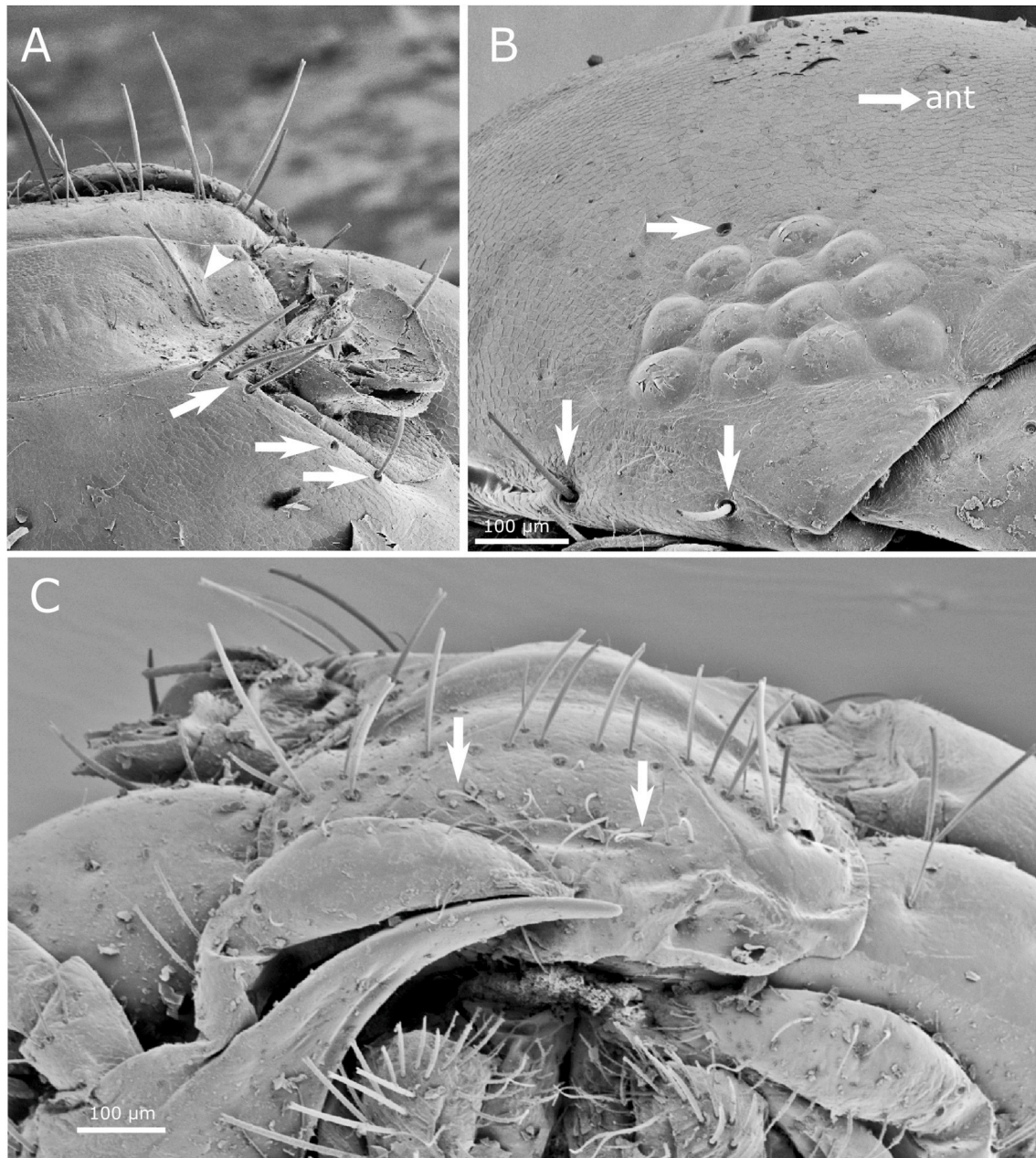


Fig. 15. *Peruatacamus atunpacha*; setation head (SEM). A) Dorsal view with periantennal macrosetae (arrows), single macroseta on clypeus (arrowhead), and macrosetae of labrum; antenna removed. B) Lateral view with macrosetae of eye region (arrows). C) Frontal view on labrum, with proximal row of bifid macrosetae and distally with much thinner cilia/setae with acute tips (arrows). Scale bars: 100 µm.

frontal margins each with two combs, the anterolateral comb with 4–5 macrosetae and the posterior comb with only 2 macrosetae (Fig. 15A). A single isolated macroseta posterior of the antennal socket (Fig. 15A). The bases of these macrosetae mostly along the unpigmented membranous suture descending from the dark pigmented margin of the frons. Two isolated submarginal macrosetae at genal margin ventrad to posteroventrad of eye, a single supraocular macroseta (Fig. 15B). Clypeus laterally each with a single strong macroseta (Fig. 15A). Labrum with prominent 1 + 1 transverse setal fields of 12–18 macrosetae, arranged in somewhat indistinct double rows. Near the apical margin of labrum on

both sides of the middle with 8–10 thin and acutely pointed setae of different length, of which at least two are longer than the above-mentioned macrosetae of the labrum (Fig. 15C).

Outer surface of mandibles with 10–14 mostly isolated macrosetae in the middle part and 1–2 isolated macrosetae posteriad (Fig. 16A); tip of incisor region four-toothed, between the two dorsal teeth less incised (Fig. 16A and B); proximal of the two dorsal teeth unevenly striated longitudinally (Fig. 16B); base of mandibles evenly striated on inner side (Fig. 16B). The distinct bristlecomb along the dorsal inner edge of incisivi consist of 14–16 macrosetae gradually shortening distally, the

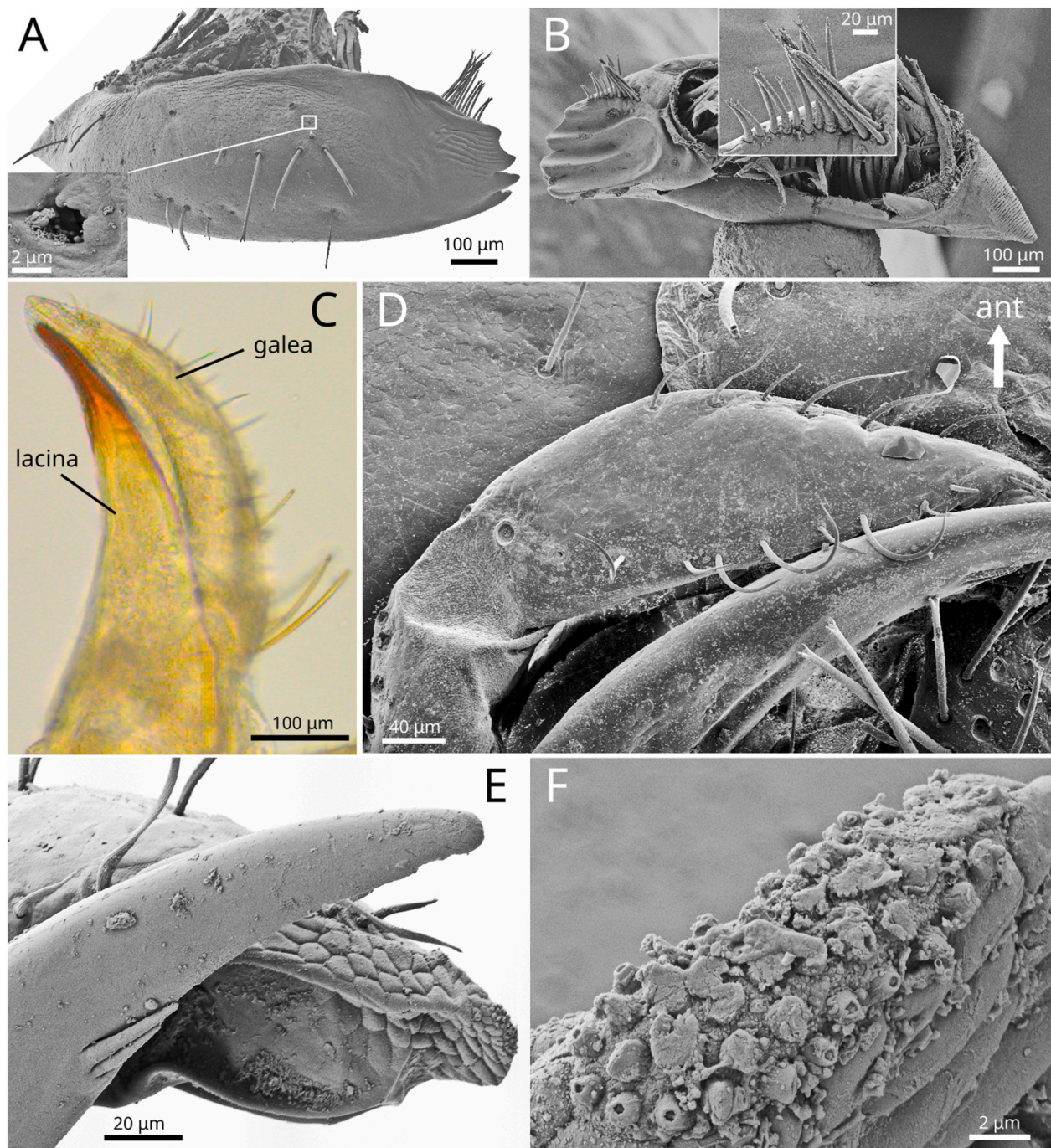


Fig. 16. *Peruatacamus atunpacha*, mouth parts. **A)** Outer side of mandible with rather isolated macrosetae, rosette-like structures (see inset for single structure), and the group of macrosetae at the dorsal edge of incisivi. **B)** Inner side of same mandible, the inset demonstrates the different forms of the tips of the macrosetae. **C)** Inner side of isolated lacinia and galea, specimen not dried. The tip of galea covers the tip of lacinia. **D)** Outer side of dried galea with two rows of small, curved and apically acute setae, tip of galea shrunk. **E)** Distal ends of lacinia and galea from inner side. **F)** Distalmost end of galea with condensed glandular field. **C:** micrograph; remaining figures: SEM.

distal 6–8 macrosetae very stout and arranged in a row, the proximal ones clustered and longer, with moderately forked tips (Fig. 16B, inset).

Lacinia fairly robust, little curved, about the same length as galea, with strongly sclerotized tip (Fig. 16C), inner side subapical with at least 2 closely fitting spines (the ventral spine smaller; Fig. 16E). Galea concavely hollowed, clearly convex on the side facing antieriad (Fig. 16C), with 4–6 macrosetae at the base, another group of 3–4 macrosetae anterior of it, and apically of the latter group on the dorsal and ventral sides along the outer margins with rows of 6–8 small and mostly curved setae with acute tips (Fig. 16D); the dorsal row includes at least one transverse pair of setae. Ventral row distally bent dorsad, just behind the tip of the galea, forming a separate transverse row of 3–5 setae. Tip of galea rather soft and shrinking in dried specimens, with a small glandular area (Fig. 16E and F). Cardo with 1–3 macrosetae, stipes apically with a group of 3–4 and proximally 1–2 isolated macrosetae.

Maxillary palpi slender, ultimate article about six times longer than wide, slightly curved inwards (Fig. 17A, inset). Setae of articles 3–5 apically pointed to slightly bifid, bent forwards, and on ultimate article denser along outer side. Article 2 with a mixture of apically acute macrosetae and bifid macrosetae, the short proximal article with 4–6 bifid macrosetae on ventral side. Tip of ultimate article of dried specimens often with concave indentation along the outer side. Near distal end of ultimate article three cylindrical styloconic sensilla, a fourth styloconic sensillum close to the middle, all with 3–4 cones (Fig. 17A and B). A single basiconic sensillum type F proximal to the three distal styloconic sensilla (Fig. 17A). Five short conical basiconic sensilla type B

form a more or less diagonal line which extends over almost the entire outer area (Fig. 17B). Slightly sunken rosette-like structures distributed over the ultimate article, usually not associated with widely open cavities.

Labium broader than long (Fig. 18A), postmentum with 1 + 1 anterolateral macrosetae and 1 + 1 slightly smaller anteromedian setae (Fig. 18B). Prementum along the proximal margin with a row of 4–5 stout setae of different lengths, on disc with 14–18 similar but mostly larger macrosetae of different lengths; slightly anterior to the proximal margin a medial row of 4–5 thinner and more pointed but still bifid macrosetae on each side, the tips of the innermost of these cross each other medially in the premental cleft (Fig. 18B). Paraglossae with 5–7 stout macrosetae on outer disc, the inner part additionally with 12–14 less robust, inwardly curved and mostly acute setae with dome-shaped bases. About 6–8 setae of the latter type near the distal end of the glossae, the area covered by these setae with a larger number of campaniform sensilla. Sutures between prementum and paraglossae indistinct on outer half. Penultimate article of labial palps slightly wider than long, disc with evenly distributed macrosetae and along the inner margin some very longer macrosetae (Fig. 18A, inset). Ultimate article of the labial palps 2.4–2.8 times wider than long, the distal sensilla band about the same length or slightly shorter than the proximal band, both extending to the lateral margins of a brush-like sensilla field that is more extensive proximal to the bands (Fig. 18C). Bands mostly consist of 3–4 (proximal band) or 4–5 (distal band) rows of robust incisor-like ending and basally only slightly tapering sticks, that stand on non-inflated

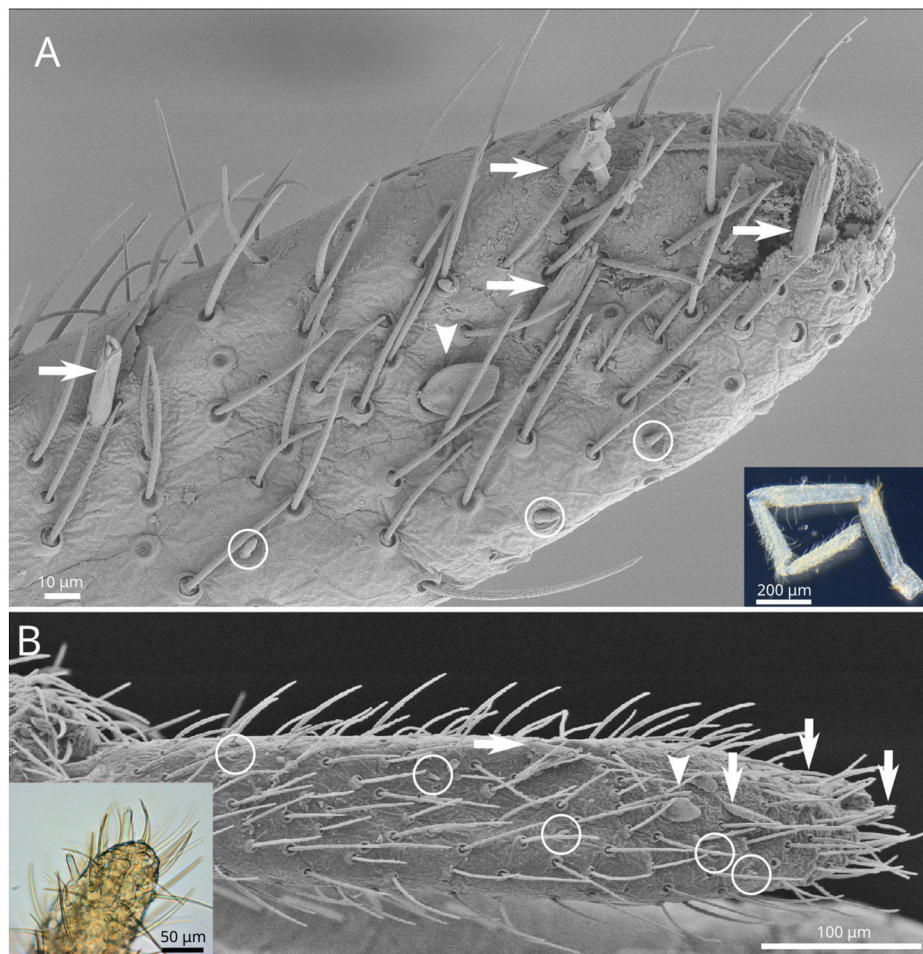


Fig. 17. *Peruatacamus atunpacha*; ultimate segment of maxillary palp (SEM). **A)** Distal part with fairly fixed positions of sensilla on outer side. Inset: complete maxillary palp (micrograph). Arrows, styloconic sensilla; arrowhead, basiconic sensillum type F; circles, basiconic sensilla type B. **B)** Complete segment from the other side of same specimen showing the proximal location of the fourth basiconic sensillum type F. Inset: micrograph of distal part with prominent styloconic sensilla.

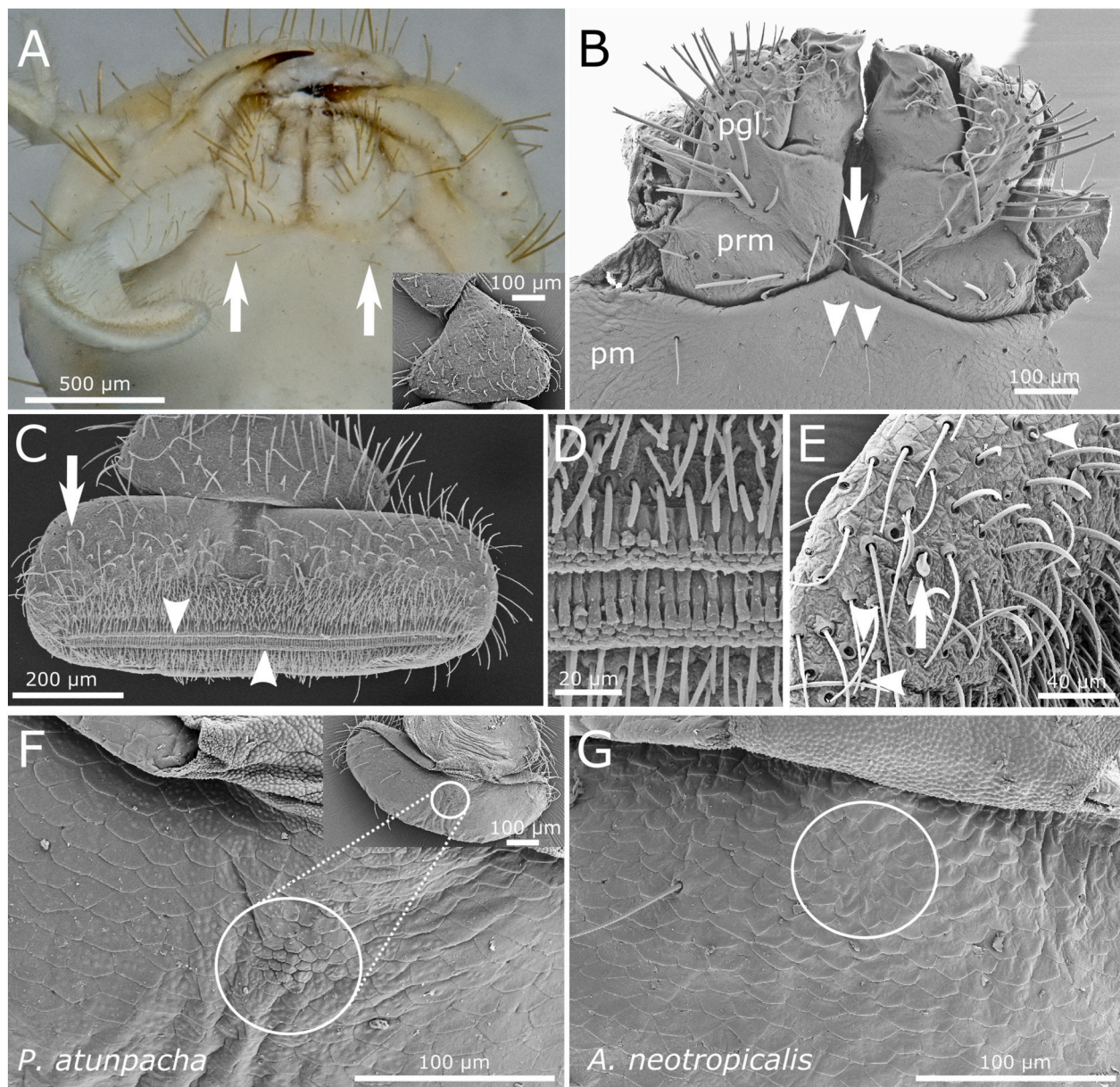


Fig. 18. *Peruatacamus atunpacha*, labium. **A)** head ventral view, the anterolateral macrosetae of postmentum marked by arrows. Inset: penultimate article of labial palp. **B)** dissected labium and anterior postmentum. Macrosetae crossing the premental cleft marked by an arrow; the two anteromedian setae (arrowheads) thinner, but nearly as long as anterolateral setae. Gl, glossa; pgl, paraglossa; pm, postmentum; prm, prementum. **C)** Slightly eccentric ultimate article of labial palp with sensilla bands (arrow heads) and a single basiconic sensillum type C1 (arrow). **D)** Enlarged section with the two sensilla bands and adjacent setae. **E)** Enlarged section with the single basiconic sensillum type F (arrow) and three basiconic sensilla type B (arrowheads). **F)** Opposite side of ultimate article with well-defined area of very small scale-like structures. **G)** Same area as in (F) shown for *N. neotropicalis*. A: micrograph, remaining figures: SEM.

cylindrical bases (Fig. 18D). Sticks tightly packed, no setae between bands. A single row of rod-like structures (see *M. bashagardensis*; Smith et al., 2020) immediately proximal to the inner band (Fig. 18C and D), barely delimited from the more proximal setae, with compact and very slightly inflated setae ending in incised tips. Brush-like sensilla field distal to the bands with densely packed and mostly straight setae with apically rounded to truncate sensilla, proximal to the bands with similar but more unevenly shaped setae, intermingled with compact setae resembling those of the rod-like structures described above. Rest of article less densely covered with slightly bifid setae. A single basiconic sensillum type F and 2–3 basiconic sensilla type B, shape of both types of sensilla identical to those described above for the maxillary palps, in the peripheral area (Fig. 18E). Rosette-like structures as described above for the maxillary palps. The side opposite the papilla-bearing one with few

long and apically slightly bifid macrosetae along lateral margins, the proximal margin only at the outer side with a row of 4–5 setae. This side on disc with 10–14 macrosetae, the inner side with 4–5 isolated setae of different size. A group of small scale-like structures in the middle (not so in *A. neotropicalis*, Fig. 18G); this region without sensilla, few rosette-like structures.

Antennae with types of setae as described above for *A. neotropicalis* (Fig. 19). Scapus only slightly longer than wide (~1.05–1.2) with sub-apical ring reduced to 4–6 macrosetae of different size around the middle of the inner/ventral side (antennae facing forwards) and 5–7 macrosetae across the dorsal outer face; in addition, an isolated discal macroseta proximal to each of these groups (Fig. 19A and B). Pedicellus shorter than scapus, with an almost complete ring of subapical macrosetae (Fig. 19A and B), some of them very long. Scapus and pedicellus

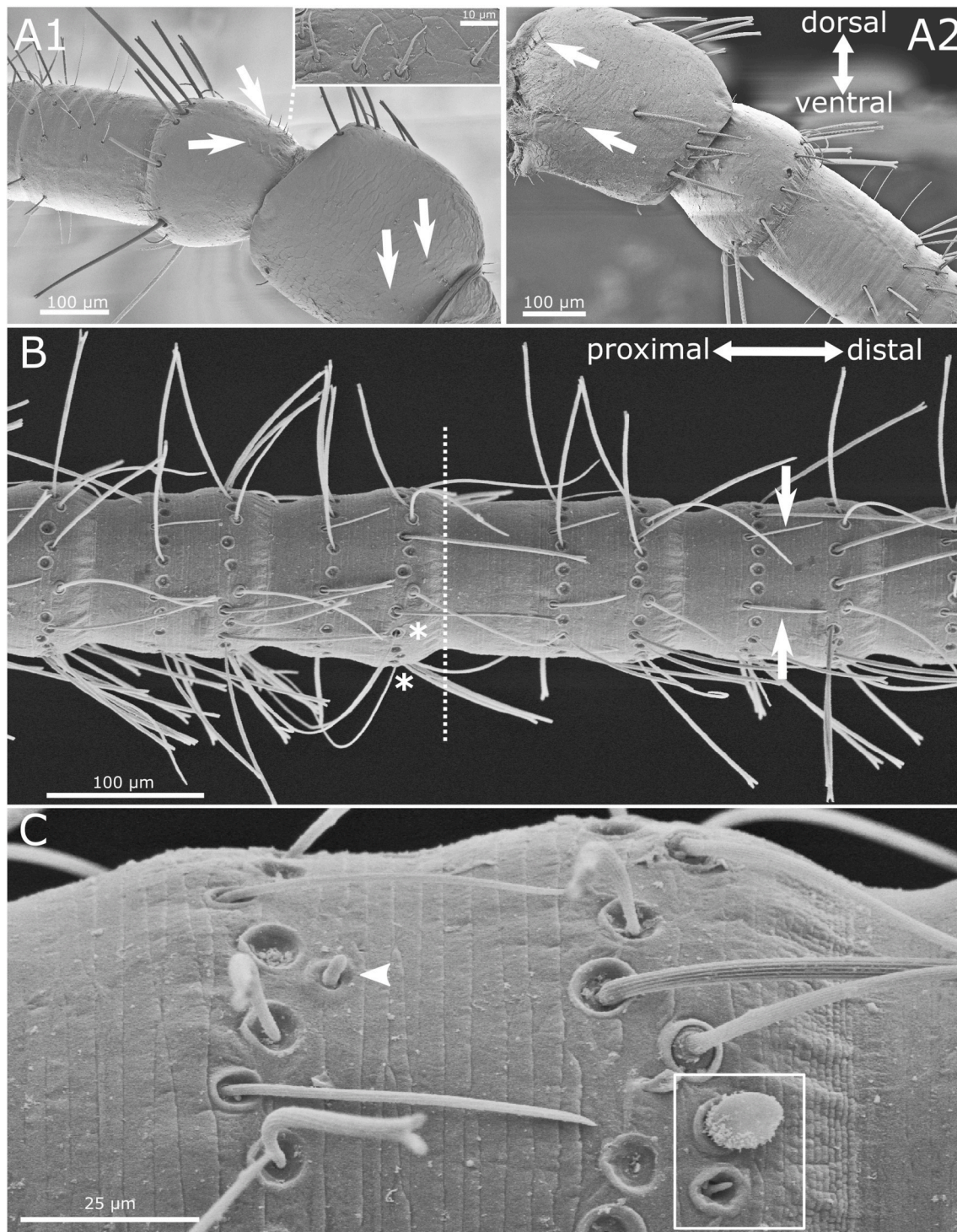


Fig. 19. *Peruatacamus atunpacha*, antenna (SEM). **A)** Basal section with scapus and pedicellus (A1: inner side, A2 outer side) with macrosetae and proximal rows of very small setae (arrows; see also inset). **B)** Overview of middle section of flagellum with diverse types of setae, the dashed line marks the boundary of an interval. **C)** Examples of sensilla located opposite to the side shown in B). The more distal sensilla form a pair with basiconic sensillum F – basiconicum A, the proximal sensilla is a single basiconic sensillum C (arrowhead).

proximally each with 5–6 longitudinal rows of 4–6 very small and apically slightly double-lobed setae (Fig. 19A, inset). Diverse types of setae along the flagellum. A typical mid-section of the flagellum is shown in Fig. 19B). Features of region-specific formation of sensilla along flagellum (Fig. 19C) slightly different from that of *A. neotropicalis*, but not studied in detail.

Pronotum wider than long (~1.20–1.25), widest towards the end of

the first third, with slightly indented posterior margin and shallow median depression (Fig. 20A). Pronotal collar narrow (~0.075 of total length pronotum), without macrosetae, 1 + 1 trichobothria near the midline, and a scattered row of about 10 mostly bent setulae along posterior margin. Pronotal folds deep and particularly narrow at the anterolateral corner, slightly sigmoid from semilateral view (Fig. 20B). Raised lateral margin as in all thoracic nota somewhat sharp-edged due

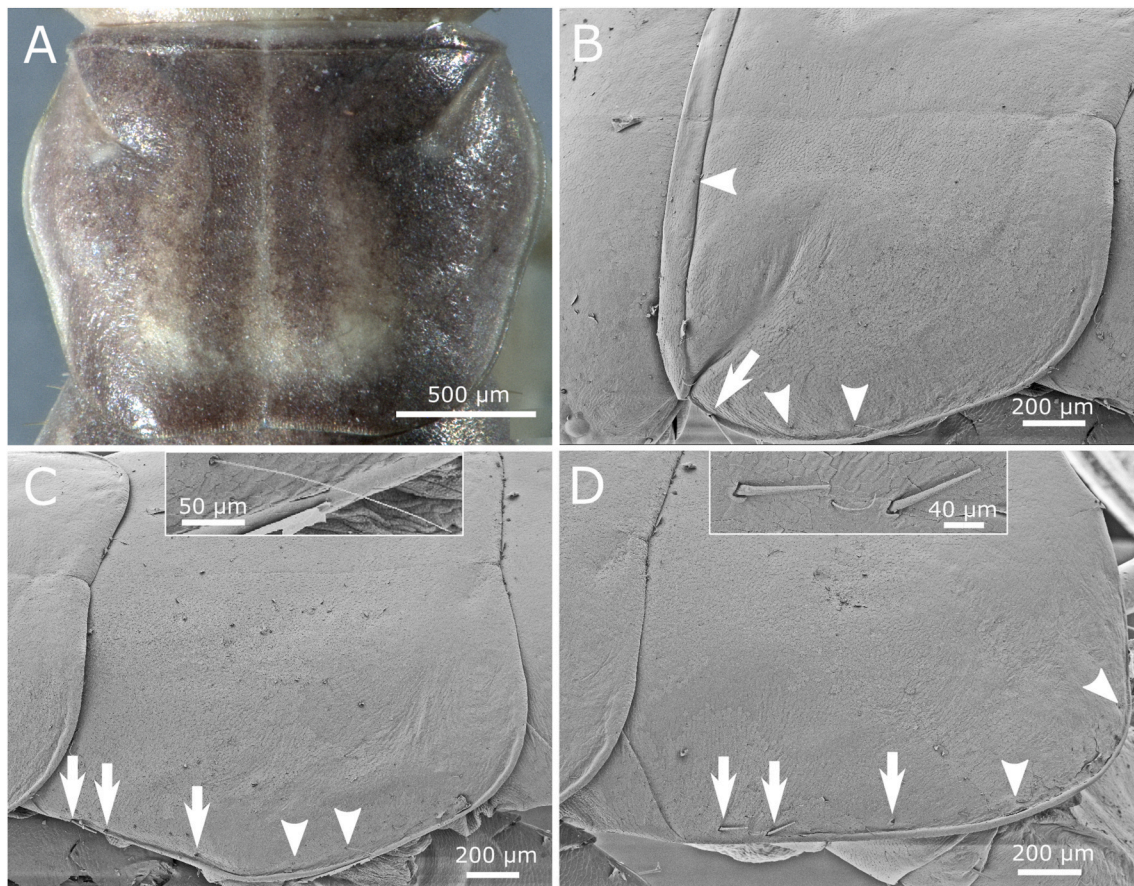


Fig. 20. *Peruatacamus atunpacha*, thoracic nota. **A)** Pronotum, dorsal view. **B)** Pronotum with deep anterolateral fold, semi-lateral view (left side). Single marginal macroseta accompanied by two submarginal trichobothria and a single trichobothrium on pronotal collar. **C)** Mesonotum, semilateral view (left side); inset: trichobothrium. **D)** Metanotum, semilateral view (left side); inset: anterolateral macrosetae. Bold arrows, macrosetae; thin arrows, trichobothria. A: micrograph; B–D: SEM.

to a distinct indentation on inner side (Fig. 20A–D), fading anterior and postero-medial (posterior margins medially not raised at all). Anterolateral with 1 + 1 marginal macrosetae and two submarginal trichobothria posterior of the anterolateral macroseta. Meso- and metanotum with 2 + 2 short anterolateral marginal setae, 1 + 1 submarginal macrosetae before (mesonotum) or in the middle (metanotum), and the two submarginal trichobothria more posteriorly (mesonotum: just behind the middle, metanotum: around the posterolateral corner). Meso- and metanota slightly broader than pronotum, indentation on posterior margins more distinct, median furrow fine and narrow.

Basisterna of thorax large and flat. Probasisternum tapering anterior and with 1 + 1 anterolateral bristlecombs perpendicular to the lateral margin and consisting of 3–5 macrosetae each (Fig. 21A). Propressternum trapezoid, tapering posterior and protruding between large episternal (?) sclerites (Fig. 21A). All spinasterna broadly transverse and with deep sutures to basisterna (Fig. 21A–C). Meso- and metapresterna are transverse sclerites separated by straight sutures from the respective basisterna and the spinasterna of the anterior segment. Meso- and metabasisterna anterior of the middle with 1 + 1 lateral bristlecombs of 3–6 macrosetae each, perpendicular to the lateral margin (Fig. 21B and C). Three mostly arch-like subcoxal sclerites, the one articulating on the coxa with a row of 5–6 (prosternum) or 2–3 (meso-, metasternum) macrosetae, the middle one with 2–3 macrosetae, and the most proximal of these sclerites without macrosetae.

Legs strongly lengthening posterior (Fig. 22A), tibia III about 1.8 times the length of tibia I and with L/W ratio of 5.5:1 (Fig. 22C); setation sparse and feeble. Procoxa ventrally perpendicular to the outer margin with 4 bristlecombs of 3–4 macrosetae each, on inner margin 2–3

bristlecombs of 2–3 macrosetae each, and 6–10 macrosetae along apical margin (among these 2–3 much longer macrosetae at apical inner edge facing the trochanter); occasionally single macrosetae between bristlecombs. On meso- and metacoxae bristlecombs often reduced and/or represented by single macrosetae only. In addition, two isolated marginal macrosetae on outer margin of coxae, one slightly proximal to the most proximal bristlecomb and the other halfway between the proximal bristlecomb and the coxal insertion. Only on procoxa, 1–2 median submarginal macrosetae on proximal margin. Trochanters with 3–4 mostly marginal macrosetae. Femora with three straight spines on inner/posterior margin (the more distal on apical edge). The anteroapical edge with a comb of three carrot-shaped macrosetae facing the tibia, 1–2 setae posterior to this group, a single carrot-shaped submarginal macroseta with a more or less median position both on the ventral and dorsal side of the apical margin, and 4–6 stout (carrot-shaped) macrosetae along the outer/anterior margin (the distal one larger than the other ones). A single medioproximal macroseta on dorsal side of femora, particularly strong on profemur. Tibiae along the posterior margin with 3–6 long spines (Fig. 22B and C). The fairly slender carrot-shaped macrosetae are arranged in a regular pattern over the ventral side, two anteriorly, usually three posteriorly and two submarginal on the apical margin (Fig. 22B and C; [Supplementary Material 2D](#)), rarely additional setae of that type present. On apical margin several submarginal macrosetae in addition to the two carrot-shaped setae; few smaller apically directed setae in line with the posterior carrot shaped macrosetae. Tibial spurs distinct but relatively small, with inflated base and claw-shaped tip, no setae (Fig. 22C, inset). Four-segmented tarsi with apically directed stout tarsal spines arranged in two distinct

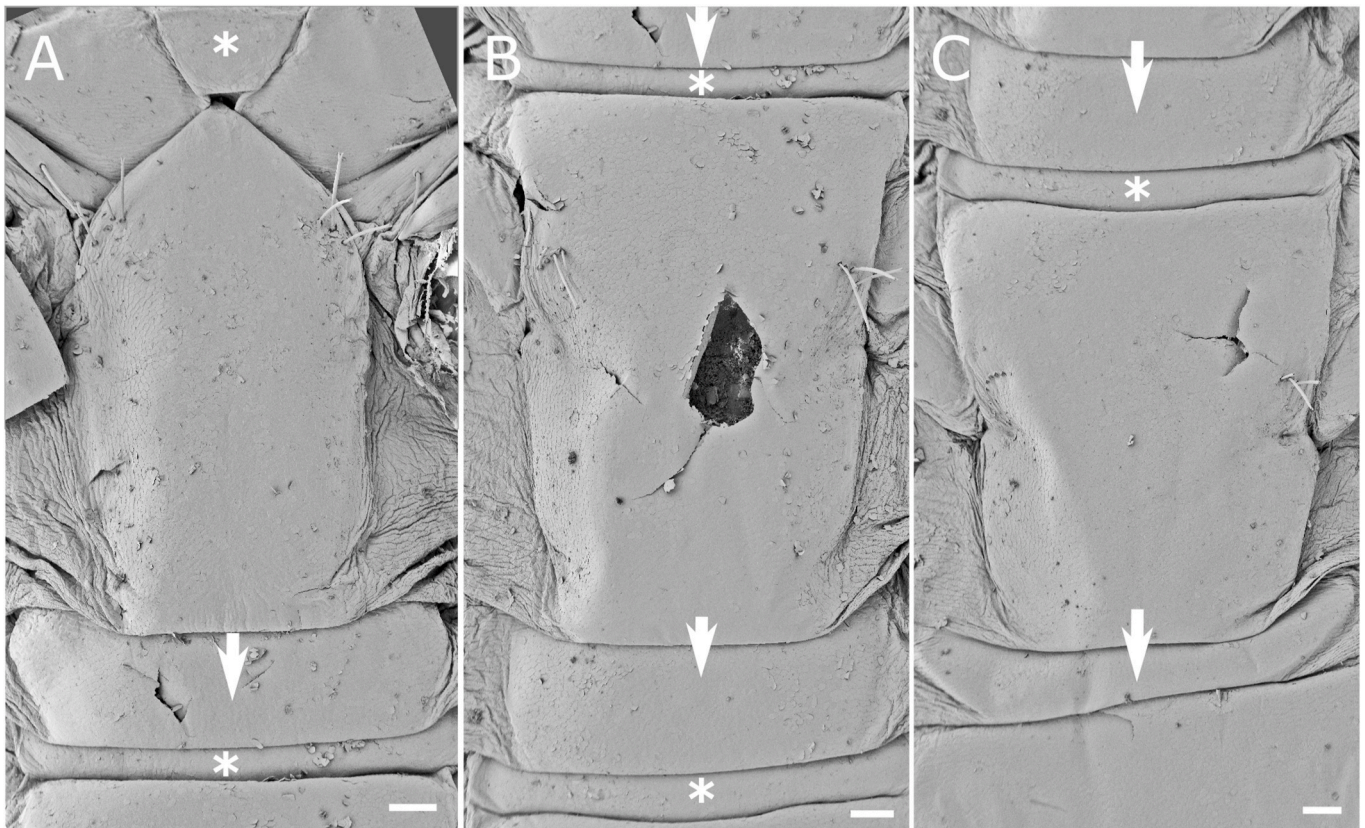


Fig. 21. *Peruatacamus atunpacha*, thorax ventral (SEM); presternites marked by asterisks, spinasternites marked by arrows. A) Prothorax, B) Mesothorax, C) Metathorax. Scale bars: 100 μ m.

ventrolateral rows, otherwise only very few apically directed smaller setae, and two spines lateral on distal ends of first three tarsal segments (Fig. 22D); the apex of the fourth tarsal segment with a setal fringe. Tarsal claws mildly curved apically, outer surface smooth, empodium straight and about half length of claws (Fig. 22D).

Urotergites I–IV (sometimes I–V) with 1 + 1 small posterolateral submarginal setae, the remaining urotergites bare, except for scattered setulae (Fig. 23). Posterior margins of the more anterior urotergites weakly concave, that of the posterior ones (sometimes only urotergite IX) more or less straight, urotergite X evenly rounded posteriorly (Fig. 23C).

Urosternite I with 1 + 1 submarginal submedian macrosetae, urosternite II with 2 + 2 submedian bristlecombs, urosternites III–VII (II–VIII in males) with 2 + 2 submedian bristlecombs and 1 + 1 posterolateral submarginal macrosetae (Fig. 24). The inner of the submedian bristlecombs with 2–3 macrosetae (on urosternite VII/VIII of females/males the outermost macroseta sometimes well separated from the other setae), the outer with 1 or 1–2 macrosetae (posterior urosternites). Posterior margins of urosternites I–VI in females and I–VII in males with concave indentation, those of urosternite VII in females/urosternite VIII in males slightly concave to straight. Coxites VIII in females with three isolated discal macrosetae, presumably homologous to the submedian/posterolateral macrosetae of the urosternites anterior to it (Fig. 24B); the posteromedian (inner) margin of these coxites with a row of 3–5 macrosetae (Fig. 24B). The stylus-bearing coxites IX of females each with 6–10 marginal macrosetae along the inner and posterior margin of the inner process (Fig. 24B). Inner and outer process of coxite IX each with 1–2 isolated macrosetae (Fig. 24B). Inner process rounded apically, somewhat thinner and slightly shorter than the outer, posteriorly broadly rounded process. Both sexes with one pair of robust styli which are slightly bent dorsad, the convex ventral side with a line of 6–8 antiad-directed stout spines (acute to truncated), the two apical spines

running around the tip (Fig. 24B and C); additionally, 3–4 smaller setae adjacent to the above row of stout spines. Inner process of coxite IX of male same length as outer process, both processes rounded triangular; the inner process with 2–3 macrosetae on disc and, unlike in females, the macrosetae along the inner/posterior margin extend onto the disc (Fig. 24C). Outer process with 1–2 macrosetae on disc and a single submarginal macroseta on the inner-apical tip.

Male parameres medium-sized and apically tapering, shorter than inner process of coxites IX, densely covered with medium-sized pointed macrosetae, otherwise without special features (Fig. 24C). Penis short, reaching to the base of the parameres, the wide opening with a ring of styles on inner margin. Epiproct anterolaterally with triangular processes, which face a similarly shaped posterolateral process of the paraprocts; the latter with a discal protrusion showing a dense tuft of long pointed macrosetae, two much stronger bifid macrosetae in the middle, and several smaller setae lateral of it (Fig. 24C).

Ovipositor of primary type and moderately long, slightly dilated in front of tip, with 18–20 divisions (Fig. 25); 0.17–0.2 x body length. Each division with a few short and stiff setae, those at distalmost tip of gonapophyses slightly shorter and denser (distance between the sockets greater than the socket diameter), not bulbous or with curved needle-like tips. A larger number of basiconic sensilla type C2 on apical divisions of gonapophyses (Fig. 25C); setation of gonapophysis 9 restricted to a lateral band.

General features of the proventriculus as described for *A. neotropialis*, a 3D reconstruction based on μ CT analysis is deposited under <https://skfb.ly/pu8vx>. Sclerite D_{prov} with longitudinal robust ridge facing the lumen, broadening antiad, but with distinct constriction posteriorly at about 2/3; the posterior 1/4 of the ridge with bristles that cover the dorsal midline (adjacent dorsal area bare; Fig. 26A); the bristle-free anterior area longitudinally indented (Fig. 26B) and weakly trapezoid from dorsal view (Fig. 26A); ridge

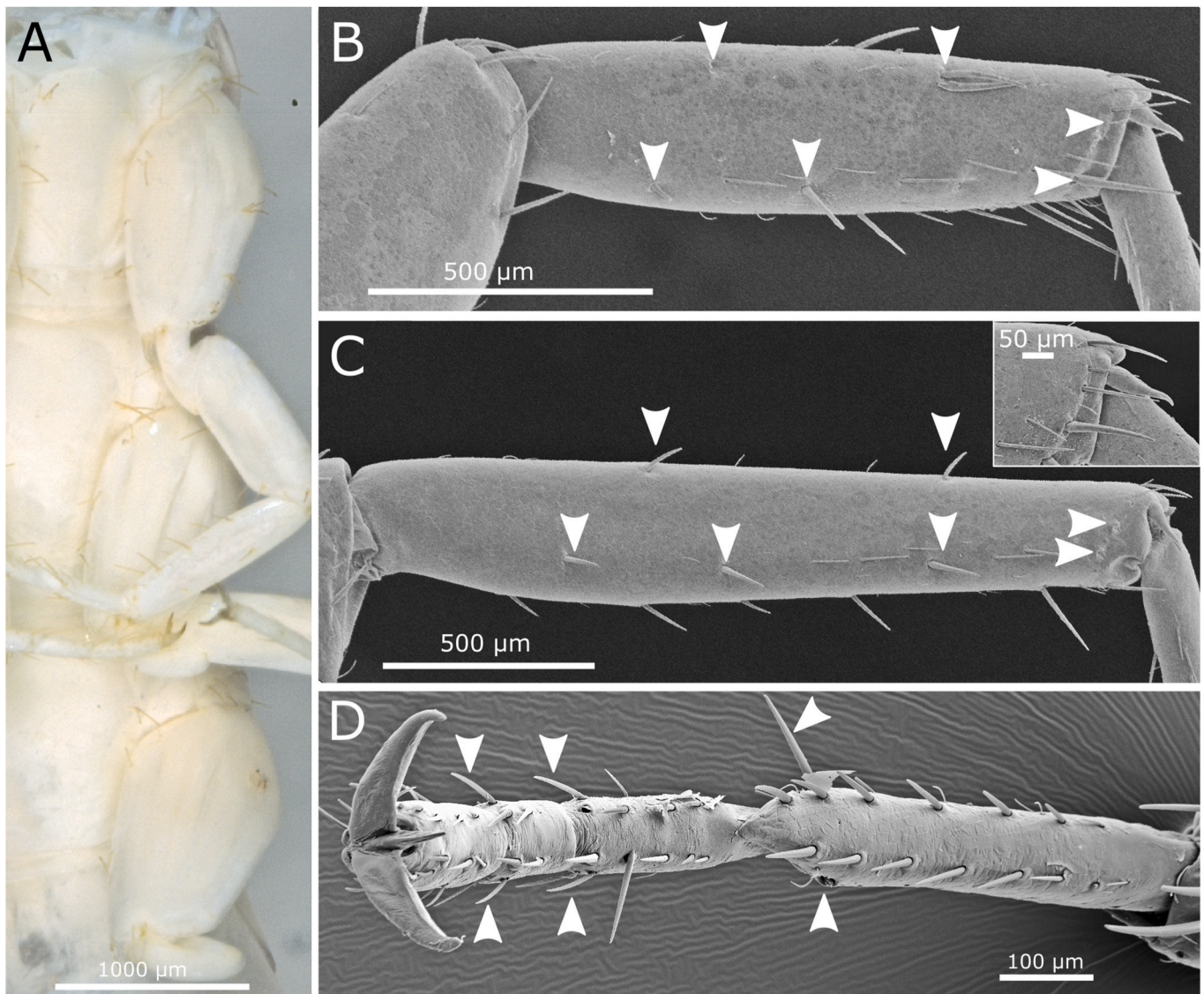


Fig. 22. *Peruatacamus atunpacha*, legs ventral view. **A)** overview. **B)** Protibia with few smaller apically-directed setae, conical spines (carrot-shaped) with fixed positions (arrowheads), several spines along both sides of the posterior margin, and a well-developed tibial spur. **C)** Metatibia with similar pattern of spines and setae as in protibia, the inset shows the tibial spur of the mesotibia. **D)** Ventral view on tarsus of midleg with distinct rows of anteriorly-directed stout spines and isolated lateral spines near the tip of segments (arrowheads). **A:** micrograph; remaining figures: SEM.

curved from lateral view, sickle-shaped frontal edge (Fig. 26B). Sclerite V_{prov} obovate to rhomboid, middle area concave and without bristles, the bristle-free area extends anteriorly as a narrow strip almost to the tip and widens shortly behind the midline before ending quite abruptly posteriorly (Fig. 26C). Sclerite LV_{prov} with anteriorly-directed protrusion (Fig. 26D and E); distal end of protrusion convex and with 4 somewhat pointed terminal lobes. The socket of the protrusion with a distinctly raised lateral crest facing V_{prov} , otherwise convex (Fig. 26E); the crest first runs from the protrusion in a straight line posteriorly and then slopes down at an almost right angle. This rectangular edge has a pronounced, dense bristle cover (Fig. 26D). Sclerite LD_{prov} with asymmetrical anteriorly-directed slightly bilobed protrusion arising from a weak depression that is densely covered by bristles; ridge facing D_{prov} strongly curved in lateral view, sloping anteriorly nearly (rounded) rectangular to the protrusion (Fig. 26F).

Material examined: Holotype (in ethanol), Peru, Arequipa (voucher code: PT32B), S16°30.55' W71°44.52', under stones/garbage on sandy hill. 25.5.2022, leg. A. Zúñiga-Reinoso, R. Predel, ♀, body length 16.1 mm (MNH).

Paratypes: same data as holotype, 2♀♀ (1 specimen in ethanol, 1 specimen prepared for SEM), 2♂♂ (1 specimen in ethanol, 1 specimen prepared for SEM) (MNH).

Diagnosis: Genus/species distinguished from Maindroniinae by the characters listed in Table 1 and from *A. neotropialis* by the characters listed in Table 2.

Distribution: Currently known only from the type locality near Arequipa in southern Peru.

Habitat: The animals were collected by hand mainly under wind-blown rubbish (cardboard, textiles) on a steep sand hill with scattered rocks and large stones, but no vegetation (Fig. 14C). Under a thin reddish layer, probably caused by abrasion of the rocks, very fine grained, whitish sand. This habitat is bordering a shallow, dry riverbed; the latter with an accumulation of larger shrubs where the runoff is blocked by a road (Fig. 14C). Not a single *P. atunpacha* could be collected in the latter habitat, although pitfall traps were set up for several weeks.

Etymology: From 'atunpacha', meaning 'giant' in the Quechua language of Peru (Rimaypi, 2018), treated as a noun in apposition, and referring to the large size.

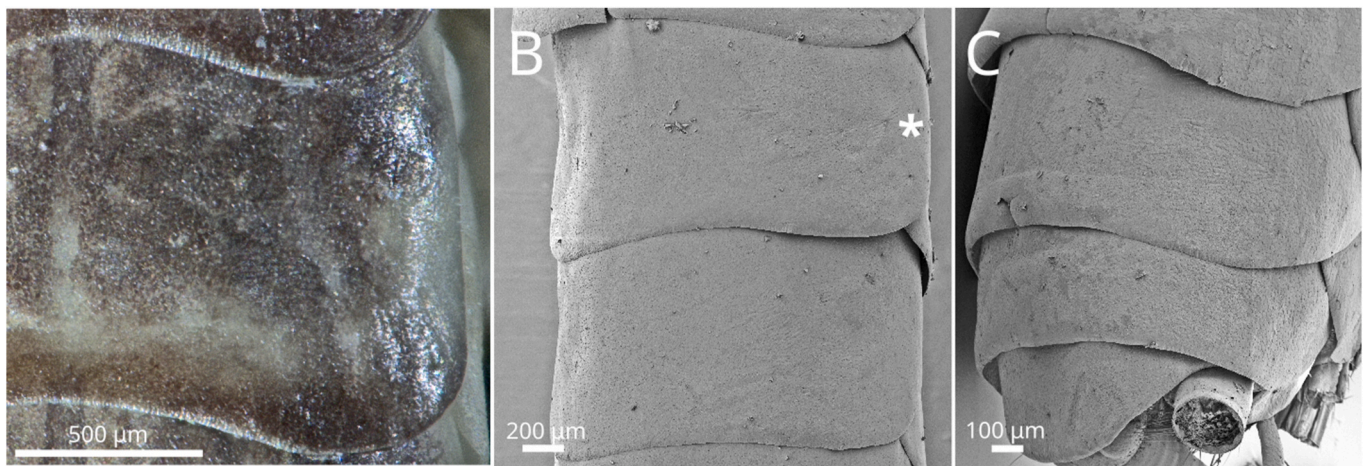


Fig. 23. *Peruatacamus atunpacha*; urotergites. **A)** Urotergite I, the asterisk indicates a single posterolateral submarginal seta (socket). **B)** Urotergite IV + V, only tergite IV with posterolateral seta (socket; arrowhead). **C)** Urotergites VIII–X without setae (seta visible at posterior tip of urotergite X belongs to a ventral sclerite). A: micrograph; B, C: SEM.

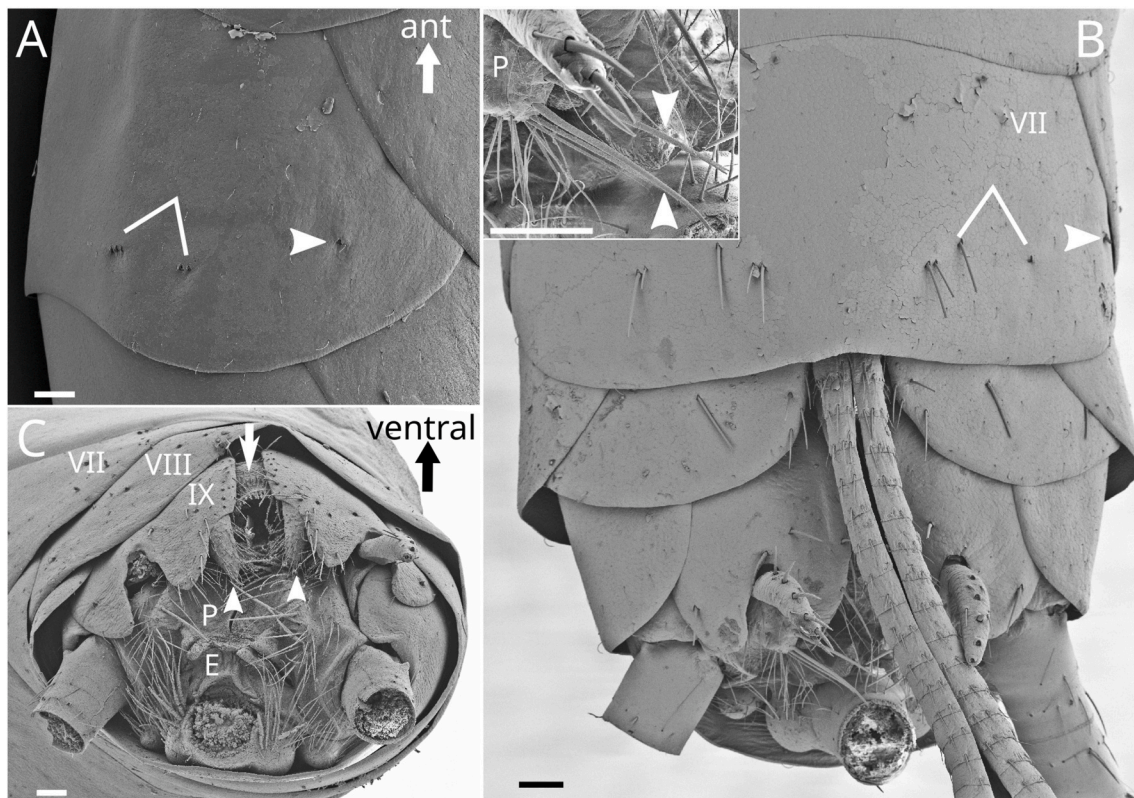


Fig. 24. *Peruatacamus atunpacha*, abdomen ventral (SEM). **A)** Urostermite V in ventrolateral view with sockets of two submedian bristlecombs (marked with lines) and a single posterolateral macroseta (arrowhead). **B)** Posterior sternites female (markings as in A), the inset shows setation of the lateral protrusion of the left paraproct (P) with two strong bifid macrosetae (arrowheads), remaining setae apically mostly acute. **C)** Posterior sternites of male with parameres (arrowheads), penis (arrow), paraprocts (P) and epiproct (E). Scale bars: 100 µm.

4. Discussion

The motivation to describe new taxa of Maindroniidae is the striking contrast between the very rare sightings of these insects in the past and their recently discovered abundance and molecular diversity in the hyperarid core of the Atacama Desert; an area that was considered poor or free of insects due to its Mars-like landscape (Zúñiga-Reinoso and Predel, 2019). Only a single species was known from South America (Wygodzinsky, 1940), which is placed here in the new genus *Atacamus*.

Our present study allows for a first assessment of the morphological differentiation within the South American Maindroniidae, which appears to be very pronounced. Both the genetic differentiation and the morphological differences between the two species examined here made it necessary to establish new genera; this also leads to the restriction of the genus *Maindronia* to the Old World species.

As a starting point, a detailed re-description of *A. neotropicalis* is provided, which belongs to clade B in Zúñiga-Reinoso and Predel, 2019. Although Paclt (1966) had already corrected some statements made in

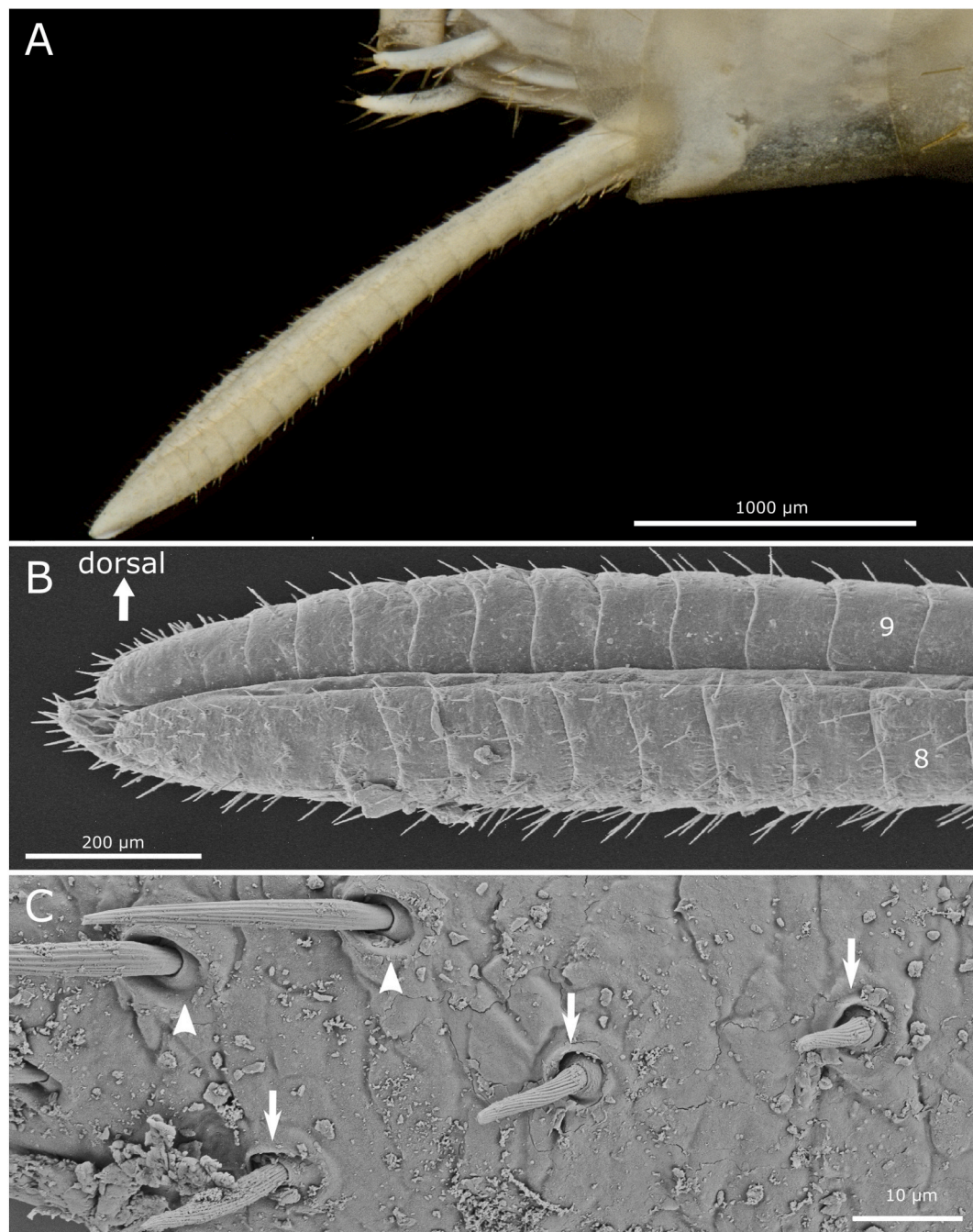


Fig. 25. *Peruatacamus atunpacha*, ovipositor. **A)** Overview from lateral. **B)** Lateral view with gonapophysis 8 and 9; setation of gonapophysis 8 restricted to a dorsolateral band. **C)** Detail from tip of gonapophysis 8 showing slightly conical setae with truncated/bifid tips (arrowhead) and (assumed) basiconic sensilla C (arrows). A: micrograph; B, C: SEM.

the original description by Wygodzinsky (1940), e.g. regarding dorsal setation, many characters of this species had been described quite generally or remained unknown. This lack of information is addressed in our study. In this context, we benefited from the extensive use of SEM to describe as many details as possible. Therefore, the description appears somewhat lengthy in parts, but this at least allows a selection of those features that appear relevant for future taxonomic studies on the Maindroniidae. The taxon we then selected for the description of a second South American species, *P. atunpacha*, is the largest species we collected so far; it does not belong to the genetically already analyzed populations described in Zúñiga-Reinoso and Predel (2019), but appears in preliminary analyses as sister group of a clade which comprises the smallest species of Atacaminae (yet undescribed); the latter distributed

in the southern Atacama Desert, but also entering the Altiplano (clade D in Zúñiga-Reinoso and Predel, 2019).

When evaluating the morphology of the two species/genera described here, it became apparent that, in addition to a number of features that differ only slightly between the species, there is a substantial number of features that diverge morphologically to such an extent that a taxonomic assignment is very easy. Among the characters that are quite similar in the two species studied, and presumably in other South American taxa, are most of the setation of the head (including mouth parts), thoracic sternites and coxae, but also the general morphology of the body, mouth parts (including sensilla), and antennae. In addition, the types of macrosetae and setulae appear to be very similar between species, including those described for *M. bashagardensis*

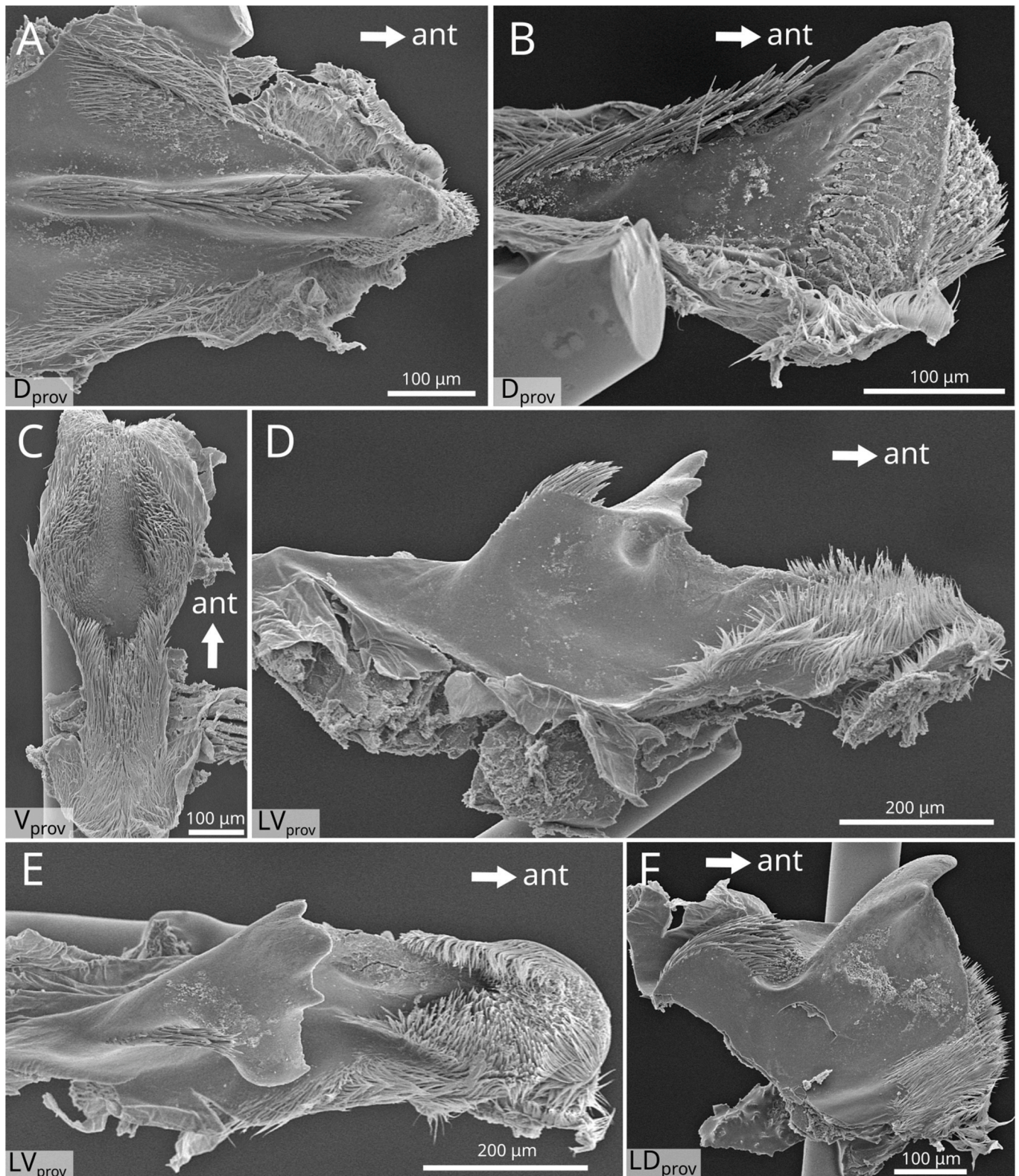


Fig. 26. *Peruatacamus atunpacha*, sclerites of proventriculus (SEM). **A)** Sclerite D_{prov} , lumen-oriented; **B)** Sclerite D_{prov} , lateral view; **C)** Sclerite V_{prov} ; **D)** Sclerite LV_{prov} , lateral view; **E)** Sclerite LV_{prov} , lumen-oriented; **F)** Sclerite LD_{prov} , lateral view.

in [Smith et al. \(2020\)](#).

Important (i.e., clearly different) and easily recognizable taxonomic characters that can be used for species identification are summarized in [Table 2](#). These include characters that are well established for species differentiation (see [Molero-Baltanás et al., 2024](#)), such as setation of

pronotal collar, thoracic nota, urotergites, urosternites, and legs. The color pattern is also clearly different. Other easily identifiable features that differ between species are the setation of the clypeus, the shape of pronotal folds + paraprocts/epiproct, and the size/development of tibial spurs. When using high resolution SEM, other important diagnostic

Table 2
Diagnostic differences in morphology between *Peruatacamus atunpacha* and *Atacamus neotropicalis*.

Character	<i>A. neotropicalis</i>	<i>P. atunpacha</i>
Pigmentation on urotergites I–VIII	central area without lateral margin	posterior half with lateral margin
Clypeus	4 + 4 lateral setae of different size	1 + 1 lateral macrosetae
Papilla bands labial palp	terminating distinctly before lateral margin, proximal band shorter	terminating close to lateral margin, proximal band longer
Setal field around papilla bands	proximal less extensive than distal, with pointed sensilla	proximal more extensive than distal, with rounded to slightly bifid sensilla
Pronotal fold	rather shallow, associated unpigmented area expands medially	deep and narrowed anterolaterally, associated unpigmented area narrow
Pronotal collar	wide, 3 + 3 macrosetae present	narrow, 1 + 1 trichobothria absent
Posterolateral setae thoracic nota		
apically directed fine setae on femur, tibia, tarsus	dense cover	few isolated setae
Tibial spur	minute	well developed
Macrosetae on lateral angles of urotergites VI–IX	present	absent
Urosternites III–VII	3 submedian bristlecombs, lateral discal macroseta present	2 submedian bristlecombs, lateral discal macroseta absent
Epiproct/paraprocts	without processes	with triangular processes
Setae of apical divisions ovipositor	needle-shaped tips	truncated to slightly bifid tips
Sclerite D proventriculus	ridge slender, no emargination	ridge massive, with emargination
Sclerite LV proventriculus: lateral crest socket protrusion	sloping slightly convex, with isolated bristles	sloping at an almost right angle, with dense bristle field at rectangular edge

features become visible, including in particular differences in the sensilla fields of labial palps, in the sensilla of the distal segments of the ovipositor, and the proventricular sclerites. The use of proventricular structures for taxonomic purposes suggested itself when one of us (JI) noticed proventricular diversity while dissecting Lepismatidae for description in the 1990's and was also proposed in a recent review (Molero-Baltanás et al., 2024), but never realized before the present study. As shown here, the proventriculus provides a wealth of taxonomic information. However, the complicated three-dimensional structure makes a correct interpretation of what is seen a tedious task; also because 'textbook knowledge' and terminology are still missing. For that reason, we have focused on few viewing angles which make a comparison rather easy. Most of the features described here using SEM images are also visible with light microscopy. Basically, the proventriculus of Zygentoma has six larger sclerites, among them two bilateral pairs. The latter are asymmetrical, meaning that the left/right views are different. This offers plenty of opportunities, both for identifying important diagnostic characters and for confusion. Nevertheless, we would like to encourage the inclusion of the proventriculus in the morphological description of hitherto little-studied Zygentoma groups, such as the Maindroniidae, whenever possible. In this context, it should be kept in mind that the shape of the proventriculus may have evolved differently in relation to specific food resources in the extreme environments they live.

The detailed morphological analysis of two South American species of Maindroniidae and our growing knowledge about the genetic differentiation of a number of already collected lineages, which might include several species each (solely the *Peruatacamus* lineage is known from a single location only), made it reasonable to introduce new genera. Among other reasons, this was done to avoid frequent changes to the generic names of Maindroniidae in view of the expected new

descriptions. This makes *Maindronia* a genus now restricted to the Old World. As a further change, we have introduced different subfamilies for the Old World and New World species, respectively. The morphological features used to separate these subfamilies are listed in Table 1 and include information we have already collected from the various lineages of Atacaminae. Whether this subfamily concept will hold in future analyses therefore depends mainly on more information about Old World taxa. Currently, the only species that was described in sufficient detail is *M. bashagardensis* (Smith et al., 2020), which is apparently closely related to the first described species of the Maindroniidae, *M. mascatensis* (Bouvier, 1897). A characteristic feature of the Atacaminae is the arrangement of papillae on the ultimate article of labial palps in form of bands. The single components of these papillae, which were occasionally found with paste-like excretions, are probably homologous to those seen in other Zygentoma (see e.g., Blanke et al., 2014; Tricholepidion). Whether the papillae bands are only typical of Atacaminae or represent a synapomorphy of Maindroniidae needs to be clarified in future analyses. Available information from the descriptions of Maindroniinae is somewhat vague; an illustration of a labial palp of *M. mascatensis* in Escherich (1905) indicates a single band (?), in the description of *M. beieri* the females are illustrated with a similar single band (in both cases it is presumably a papilla band; these structures are not mentioned in the texts), but a small subadult male is described with '5 Gruppen von palisadenartig dicht gepackt stehender kurzer Stäbchen', which is supplemented with comments about a possible glandular function of these sticks (Schremmer, 1964). Finally, Smith et al. (2020) favor a 3 + 2 or 3 + 2+1 arrangement of the papillae in *M. bashagardensis* (3 + 2 arrangements are found in many Lepismatidae), but these groups of papillae are very elongated, and the separate units could also have resulted from artificial deformation on the slides (Smith, pers. information 2024). In any case, other features of the ultimate article of labial palps also seem to be taxonomically very informative, but usually require SEM analysis. As was shown here, a previously described unique character of the Maindroniidae, the smooth inner part of lacinia (Escherich, 1905), appears somewhat different on SEM images, at least for the Atacaminae.

CRedit authorship contribution statement

John Irish: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Álvaro Zúñiga-Reinoso:** Writing – review & editing, Visualization, Investigation, Data curation, Conceptualization. **Hanna Cieszyński:** Writing – review & editing, Methodology, Investigation, Data curation. **Hans Pohl:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Reinhard Predel:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Reinhard Predel reports financial support was provided by German Research Foundation (Projektnummer 268236062 – SFB 1211). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jcz.2025.10.010>.

Data availability

Data will be made available on request.

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