R e s e a r c h   a r t i c l e

urn:lsid:zoobank.org:pub:BE6ED0BD-4A61-4F50-A8C2-BE84C6F00656

Living on the edge – first survey of loriciferans along the Atacama Trench

Martin V. SØRENSEN [1,*], Maria HERRANZ [2], Katarzyna GRZELAK [3],
Mauricio SHIMABUKURO [4], Reinhardt M. KRISTENSEN [5] & Daniela ZEPPILLI [6]

[1,2,5] Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen, Denmark.
[2] Department of Biology, University of Copenhagen, 2100 Copenhagen, Denmark.
[3] Marine Ecology Department, Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland.
[4,6] Univ. Brest, CNRS, Ifremer, UMR6197 Biologie et Écologie des Ecosystèmes marins profonds,
29280 Plouzané, France.
[4] Department of Biology, HADAL & Nordcee, University of Southern Denmark,
5230 Odense, Denmark.
[4] Institute of Oceanography, Federal University of Rio Grande, Rio Grande, RS 96203-900, Brazil.

[*] Corresponding author: mvsorensen@snm.ku.dk
[2] Email: maria.herranz@bio.ku.dk
[3] Email: kgrzelak@iopan.pl
[4] Email: shimabukuro@furg.br
[5] Email: rmkristensen@snm.ku.dk
[6] Email: Daniela.Zeppilli@ifremer.fr

[1] urn:lsid:zoobank.org:author:4143D650-12FC-4914-93F5-2C39339A7156
[2] urn:lsid:zoobank.org:author:6806936F-E381-4098-9D02-620D4847956E
[3] urn:lsid:zoobank.org:author:ABFE9734-0BD8-4ED9-A780-469D0058FCED
[4] urn:lsid:zoobank.org:author:EEE05E1C-C9F5-4FCC-A6C6-5A1D55FF5407
[5] urn:lsid:zoobank.org:author:4BA89040-D79E-41C1-A17C-539FBB9B6BA4
[6] urn:lsid:zoobank.org:author:6EDD442D-4DB9-46CA-A19D-29C67A055180

Abstract. The fauna of Loricifera along a north-south longitudinal transect following the Atacama Trench was explored. Whereas no loriciferans were collected from the actual trench, the continental slope and surrounding abyssal plains yielded two species of *Rugiloricus* and two of *Pliciloricus*. All four species are considered as new to science, but only one of them could be formally described. The new species, *Pliciloricus ukupachaensis* sp. nov., is closely related with the North Atlantic *Pliciloricus leocaudatus*, and the two species share different morphological traits, including an enlarged anal field with conspicuous pentagonal and hexagonal fields formed by strong, cuticular ridges. Among other peculiar traits, the new species is characterised by having strongly reduced trichoscalid plates and no double trichoscalids. Comparison with previously published, unidentified specimens suggests that the new species' distributional range might reach as far as Oregon off the US west coast.

Keywords. Deep-sea, HADES-ERC, Loricifera, meiofauna, *Pliciloricus ukupachaensis* sp. nov., *Rugiloricus*.

Introduction

Even 40 years after the discovery of Loricifera (Kristensen 1983), our knowledge about this animal phylum is still extremely limited, in terms of biodiversity as well as geographic distribution. For instance, the loriciferan fauna of the entire Southeast Pacific, from the Equator to Antarctica and between the East Pacific Rise and South America, is completely unexplored. Outside this enormous area, the nearest reports of loriciferans are from the Tropical Central and East Pacific (Kristensen *et al.* 2019; Fujimoto & Murakami 2020) and from Galapagos (Heiner & Neuhaus 2007; Neves & Kristensen 2016).

The present study reports the first occurrence of loriciferans from the Southeast Pacific, and is based on samples taken during the HADES-ERC Cruise SO261 – a study of the Atacama Trench and surrounding continental slope and abyssal plains. Meiofaunal observations from the Atacama Trench system confirmed elevated meiofaunal densities at the trench axis as compared to abyssal sites on oceanic plates (Shimabukuro *et al.* 2022). A recent study based on the same material addressed the potential sister group of loriciferans – the Kinorhyncha (Grzelak *et al.* 2021).

Loriciferans are known from all major oceans throughout the world, but still, their known bathymetric distribution is extremely patchy. Out of the fourteen described genera only three, *Australoricus* Heiner *et al.*, 2009, *Nanaloricus* Kristensen, 1983 and *Armorloricus* Kristensen & Gad, 2004, appear to be restricted to depths between a few to 200 m (e.g., Heiner 2004; Kristensen & Gad 2004; Heiner *et al.* 2009; Neves *et al.* 2021). Nearly all remaining genera accommodate species living below 1000 m (e.g., Kristensen & Shirayama 1988; Gad 2005, 2009; Neves *et al.* 2019; Sørensen *et al.* 2022), suggesting that loriciferans in general are well-adapted to the deep sea.

Whereas most genera of Loricifera are fairly small, from monotypic to accommodating up to five species, two of the commonly encountered deep-sea genera are slightly more diverse: *Pliciloricus* Higgins & Kristensen, 1986, with currently fourteen described species, is the most diverse loriciferan genus, followed by *Rugiloricus* Higgins & Kristensen, 1986 with eight species. Together, the two genera constitute most of the family Pliciloricidae Higgins & Kristensen, 1986, which (among several other characters) is characterised by an adult lorica composed of numerous folds – the so-called plicae (Higgins & Kristensen 1986). Oppositely, the lorica of the other major family, Nanaloricidae Kristensen, 1983, is made up by lorica plates (Kristensen 1983). Adults of *Rugiloricus* and *Pliciloricus* are most easily distinguished by the number of plicae in their lorica (ca 20 in *Pliciloricus*; >20 (typically 30–60) in *Rugiloricus*) and the morphology of the trichoscalids, i.e., the appendages on the neck (all trichoscalids are composed of a single appendage in *Rugiloricus*; half of the trichoscalids have an accessory appendage in *Pliciloricus*). Higgins larvae of the two genera can be distinguished in different ways, but the two most easily recognisable characters are the shape of the toes (short and thick in *Rugiloricus*; long and thin in *Pliciloricus*) and the absence (in *Rugiloricus*) or presence (in *Pliciloricus*) of terminal setae, i.e., a pair of relatively conspicuous setae between the bases of the toes (Neves *et al.* 2016; Fujimoto & Kristensen 2020).

Despite their 'high diversity' (in Loricifera terms), extremely few species of Pliciloricidae have been reported from the Pacific. In fact, only a single identified species has been reported from the East Pacific, i.e., *Rugiloricus californiensis* Neves *et al.*, 2019 from the US west coast. In the same study, Neves *et al.* (2019) reported the presence of additional Pliciloricidae spp., but all of them were in a condition that

did not allow identification or description. In addition, Heiner & Neuhaus (2007) studied the Loricifera fauna of Galapagos and reported the presence of unidentified *Pliciloricus* spp., *Rugiloricus* spp., and an undescribed pliciloricid genus that Fujimoto *et al.* (2020) subsequently suggested most likely was *Wataloricus*. Finally, Kristensen *et al.* (2019) reported the presence of two undescribed species, of *Rugiloricus* and *Pliciloricus* respectively, from manganese nodule fields of the tropical East Pacific Clarion-Clipperton Zone. All remaining reports of Pacific Pliciloricidae are from the West Pacific, near New Zealand (Heiner & Neuhaus 2010; Sørensen *et al.* 2022), Australia (Heiner *et al.* 2009) and Japan (Kristensen & Shirayama 1988; Fujimoto *et al.* 2020).

Thus, the present study is the first addressing the Southeast Pacific loriciferan fauna and, concordantly, the first to explore the loriciferans of the Atacama Trench system. While the samples did not yield any loriciferans from the actual trench, we describe a new species of *Pliciloricus* from the continental slope, and report three additional, putatively undescribed species, *Pliciloricus* sp. and *Rugiloricus* spp., from the slope and the abyssal plain that borders the trench.

Material and methods

Samples were collected by the German research vessel R/V *Sonne* (Cruise SO261) through March 2018 as part of the HADES European Research Council (HADES-ERC) framework. Sampling was done with a multicorer along a 450 km long north-south directed transect, covering the Atacama Trench and surrounding continental slope and abyssal plains. Loriciferans were recovered from three of the nine stations (Table 1; Fig. 1).

Samples were immediately fixed in 10% formalin and stored for further processing. At the IFREMER Labs, meiofauna was extracted from the samples by LUDOX centrifugation (Vincx 1996), and the specimens were sorted to main group. Unmounted specimens of Loricifera were shipped in vials to the Natural History Museum of Denmark (NHMD) for further examination. After tentative identification of unmounted specimens to genus and life stage, the specimens were split into a portion for light microscopy (LM) and one for scanning electron microscopy (SEM). Specimens for LM were dehydrated through a graded series of glycerine, mounted in Fluoromount-G between two cover slips, and attached to a plastic H-S slide. The specimens were examined with an Olympus BX51 light microscope with differential interference contrast, and photographed with an Olympus DP27 camera. After examination with conventional light microscopy, selected specimens were studied further with a Nikon Eclipse Ti2 confocal laser scanning microscope (CLSM). The autofluorescent signal from the specimens was detected with a laser excitation wavelength of 488 nm, and optical sections were obtained through a 40× oil objective. Specimens for SEM were dehydrated through a graded alcohol-acetone series, critical point dried, and mounted on aluminium stubs. The mounted specimens were sputter coated with a platinum/palladium mix and examined with a JEOL JSM-6335F Field Emission scanning electron microscope. Line art was based on information compiled from LM, CLSM and SEM imaging, and constructed in Adobe Illustrator CS6. The same software was used for all other figure plates. CLSM Z-projections were compiled in Fiji ImageJ software ver. 2.0.0. Three-dimensional reconstructions based on the acquired Z-stacks were made with Imaris ver. 9.5.1 software. All examined specimens are stored in the collection of NHMD.

For comparison with the new species, an unidentified specimen of *Pliciloricus* sp. (NHMD 225904) from the US West Coast, as well as unpublished SEM images (from co-author RMK) and selected types of *Pliciloricus leocaudatus* Heiner & Kristensen, 2005 (NHMD 100757, 100759 to 100762) were examined.
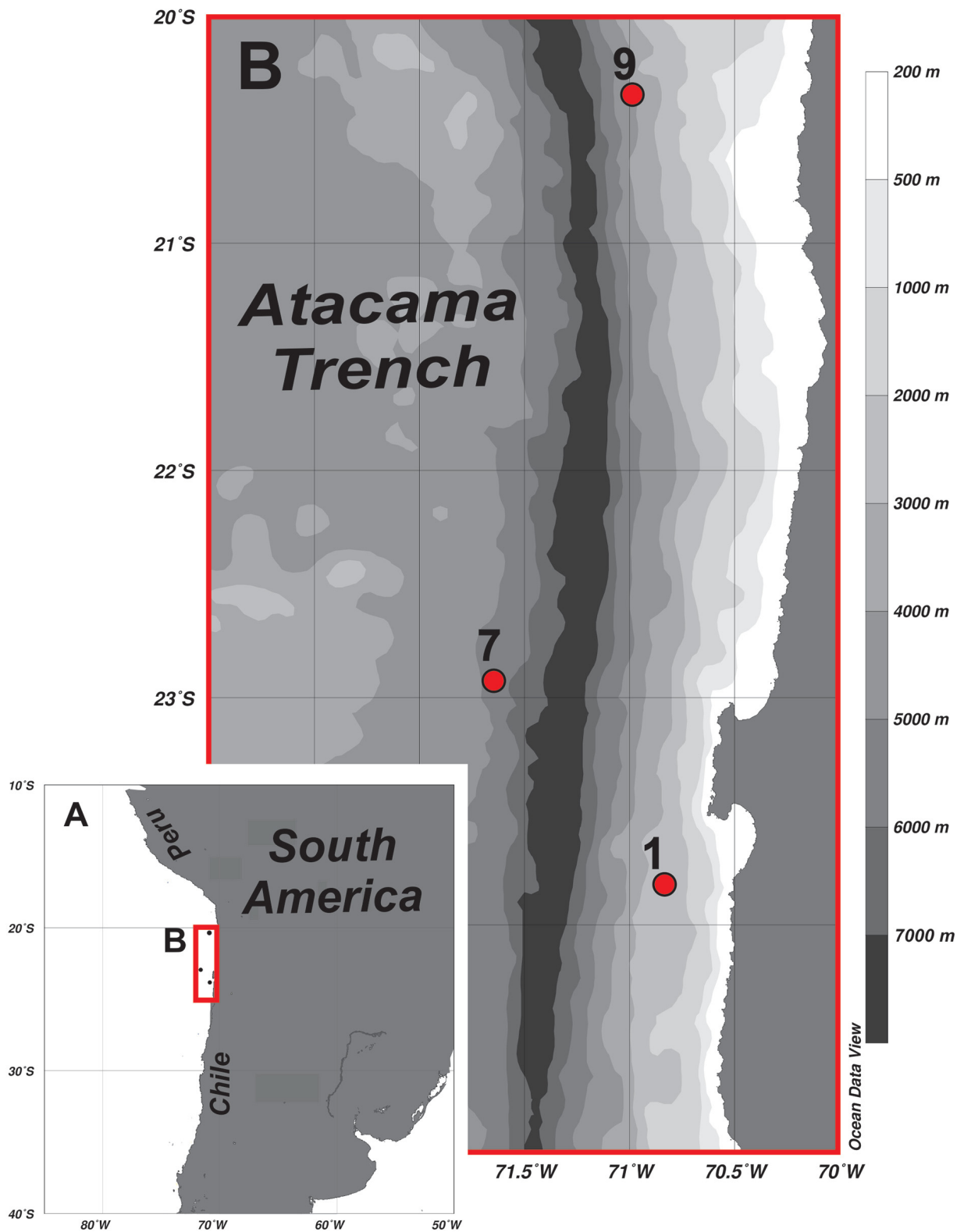
Fig. 1. Map showing the three stations near the Atacama Trench where loriciferans were collected. Station numbers refer to Grzelak *et al.* (2021).

Table 1. Summary of data on stations, species identities, and catalogue numbers (NHMD) for specimens stored in the Natural History Museum of Denmark.

Station	Location	Date	Latitude (S)	Longitude (W)	Depth (m)	Species	Specimens, types and catalogue nos
St. 1	continental slope	6 Mar. 2018	23°48.72′	70°50.04′	2560	*Pliciloricus ukupachaensis* sp. nov.	♀, holotype (NHMD 1177413); 1 ♀, paratype (NHMD 1177421); 1 Higgins larva, paratype (NHMD 1177414)
St. 7	abyssal plain	20 Mar. 2018	22°56.22′	71°37.08′	5500	*Pliciloricus* sp.	1 Higgins larva (NHMD 1177415)
						Rugiloricus sp. 1	1 Higgins larva (NHMD 1177416); 1 postlarva (NHMD 1177417)
St. 9	continental slope	28 Mar. 2018	20°19.97′	70°58.70′	4050	*Pliciloricus* sp.	2 Higgins larvae (MVS personal collection)
						Rugiloricus sp. 2	2 Higgins larvae (NHMD 1177418–1177419); 1 adult (uncertain sex) (NHMD 1177420)

Abbreviations

The following abbreviations are used on the figures:

af   = anal field
als   = anterolateral seta
an   = anus
avs   = anteroventral seta
cu_{ad} = cuticle adult
cu_{HI} = cuticle Higgins larva
cu_{pl} = cuticle postlarva
fl   = flosculus
ia   = internal armature
ir   = interplical radii
mc   = mouth cone
ms   = midventral mouth cone seta
mvp   = midventral plica
os   = oral stylet
ot   = oral tooth
pds   = posterodorsal seta
pl   = plica
pls   = posterolateral seta
sc_{ad} = scalids of adult
sc_{HI} = scalids of Higgins larva
$sc1_{cl}$ = clavoscalid of Row 1
$sc2_{do}$ = double organ of Row 2
$sc2_{ls}$ = leg-shaped scalid of Row 2
$sc2\text{–}8_{sp}$ = spinoscalids of Rows 2–8
$sc4_{cs}$ = claw-shaped scalid of Row 4
$sc9_{bs}$ = beak-shaped scalid of Row 9
to   = toe
tp2–3   = trichoscalid plates of Rows 2–3
tr   = trichoscalid
ts   = terminal setae

Results

Phylum Loricifera Kristensen, 1983
Family Pliciloricidae Higgins & Kristensen, 1986
Genus *Pliciloricus* Higgins & Kristensen, 1986

Pliciloricus ukupachaensis sp. nov.
urn:lsid:zoobank.org:act:AEF3321F-BCFB-4FF2-A8EC-81BF8E929462
Figs 2–8

Diagnosis

Adult *Pliciloricus* with a mouth cone with narrow basis, but getting conspicuously broader, before gradually narrowing again towards distal end. Introvert Row 1: females with eight regular, club-shaped clavoscalids with 23–25 annulated rings on distal ⅓; Introvert Row 2: three regular spinoscalids alternating with four leg-shaped scalids with three, articulating proximal units and long, spinous end-piece; double organ with fused bases, extending into long, tapering distal tips. Introvert Row 4: fifteen claw-like scalids with serrated shafts, articulating with thinner distal parts, with curved tips. Neck with fifteen single trichoscalids. Trichoscalid plates inconspicuous. Lorica with 22 plicae inclusive broader midventral plica. Anterior lorica margin smooth. Posterior part of lorica forming large anal field with distinct, asymmetrical ornamentation of pentagonal and hexagonal fields, formed by external cuticular ridges. Male morphology unknown.

Etymology

The species name, '*ukupachaensis*', is derived from 'Uku Pacha' – the underworld or 'inner world' according to Incan mythology. The name refers to the habitat of this species, in close proximity to the Atacama Trench that reaches into the underworld.

Material examined

Holotype

CHILE • ♀; continental slope off Antofagasta, and near the rim of the Atacama Trench; st. 1; 23°48.72′ S, 70°50.04′ W; depth 2560 m; 6 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for LM in Fluoromount G on HS slide; NHMD 1177413.

Paratypes

CHILE • 1 ♀; same collection data as for holotype; mounted for SEM; NHMD 1177421 • 1 Higgins larva containing a postlarva with an adult inside; same collection data as for holotype; mounted for LM in Fluoromount G on HS slide; see also Table 1 and Fig. 1; NHMD 1177414.

## Description

Adult female

Adult females consist of a head with mouth cone and introvert with nine rows of scalids, a neck region with one row of trichoscalids, a plicated lorica and an anal field with asymmetrically arranged fields (Figs 2A, C, 3–6, 7A). The female holotype measures 240 μm in total length and 100 μm in width at its widest point, i.e., near the anterior lorica margin. The mouth cone measures 68 μm in length, has a narrow basis, but broadens out to reach its maximum width of 25 μm about ⅕ from basis, before gradually tapering again towards the distal tip (Figs 2A, 4A–B, 6A). It is slightly retracted in both the holotype and adult paratype, which makes it appear broadest basally. The mouth cone is supported by oral ridges, and a narrow buccal tube is visible inside it. The pharynx does not have any distinct internal structures, and no placoids were observed.
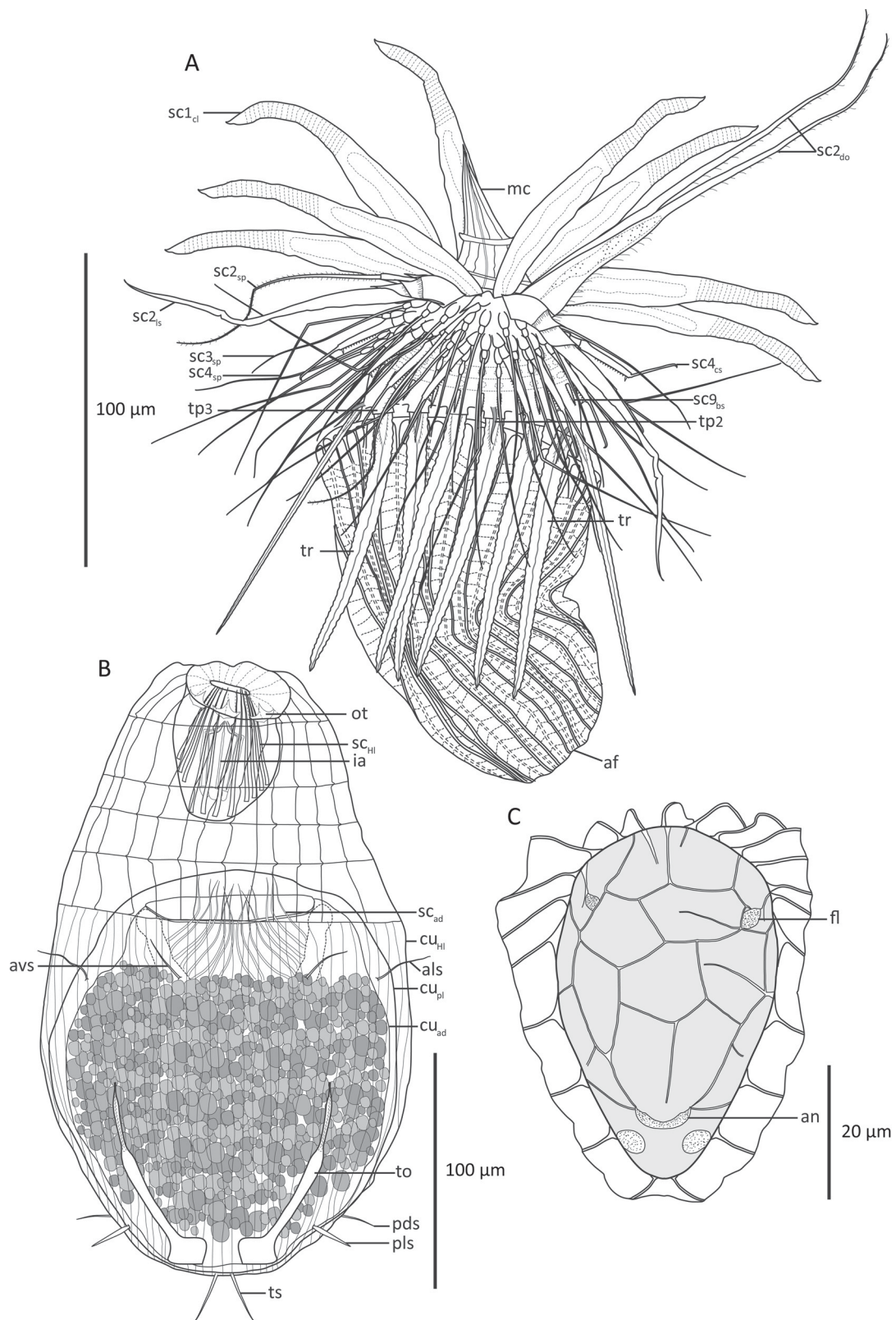
Fig. 2. Line art illustrations of *Pliciloricus ukupachaensis* sp. nov. **A**. Holotype, ♀ (NHMD 1177413), lateral view; for visibility, some Row 6 to 8 scalids have been omitted and their attachment sites are indicated by circles with dashed lines. **B**. Higgins larva containing a postlarva with an adult (NHMD 1177414), ventral view. **C**. Detail of anal field in adult (NHMD 1177421); dorsal side is up.

The introvert has nine rows of scalids (Fig. 3). The anteriormost Row 1 consists of eight club-shaped, 134 μm long clavoscalids. The clavoscalids are covered with extremely fine hairs and consist of a narrow base, a smooth, flattened part representing ⅔ of the total scalid length, and a distal end-piece with about 23–25 annulations; they terminate in small, anteriorly bent hooks (Figs 2A, 3, 4A–B, 5A–C, 6A–B, 7A).

Row 2 consists of four leg-shaped scalids, three regular spinoscalids, and two scalids fused into a ventral double organ. Each leg-shaped scalid (length: 125 μm) consists of a proximal part with three,
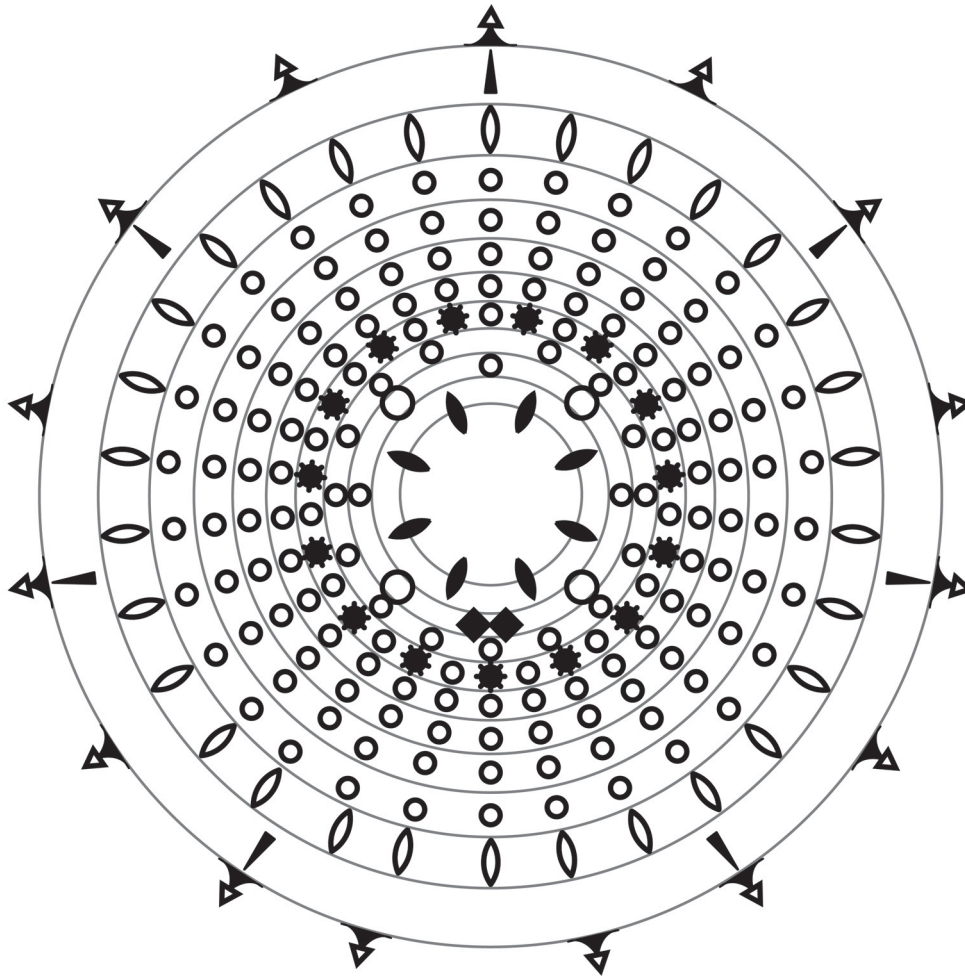

Introvert Rows	Scalids	Total	Neck Rows	
01 clavoscalids ●	8●	8	01 Trichoscalid plates	-
02 leg-shaped scalids ⃝ spinoscalids ○ and double organ ◆◆	4⃝+3○ +2◆	9	02 Trichoscalid plates	7
03 spinoscalids ○	15○	15	03 Trichoscalid plates + single trichoscalids	+15
04 spinoscalids ○ and claws ✸	15○+15✸	30		
05 spinoscalids ○	30○	30		
06 spinoscalids ○	30○	30		
07 spinoscalids ○	30○	30		
08 spinoscalids ○	30○	30		
09 beak-shaped scalids	30●	30		
Total scalids		212		

Fig. 3. Diagram of introvert in *Pliciloricus ukupachaensis* sp. nov., showing distribution of scalids and trichoscalid plates.

fringed, articulating units and a spinous end-piece with two partial constrictions about ⅓ from the distal, anteriorly curved tip. The three regular spinoscalids (length: 91 μm) alternate with the leg-shaped scalids and are located middorsally and midlaterally on the introvert. Each spinoscalid is composed of three units: a short, proximal basis with a distal spike, a short cylindrical mid-piece, and a long, acicular end-piece, covered with minute hairs; the end-piece represents more than ⅘ of the total scalid length, and has a distinct bend ⅓ from the distal bending tip. The double organ consists of two appendages (length: 134 μm) with swollen and fused bases, representing ⅓ of the total length; they narrow abruptly into considerably thinner, distally curved end-pieces; the bases have a line of hair along their inferior margins, whereas the end-pieces have hair along both the inferior and superior margins (Figs 2A, 3, 4A–B, 5A–C, 6B, D, 7A).
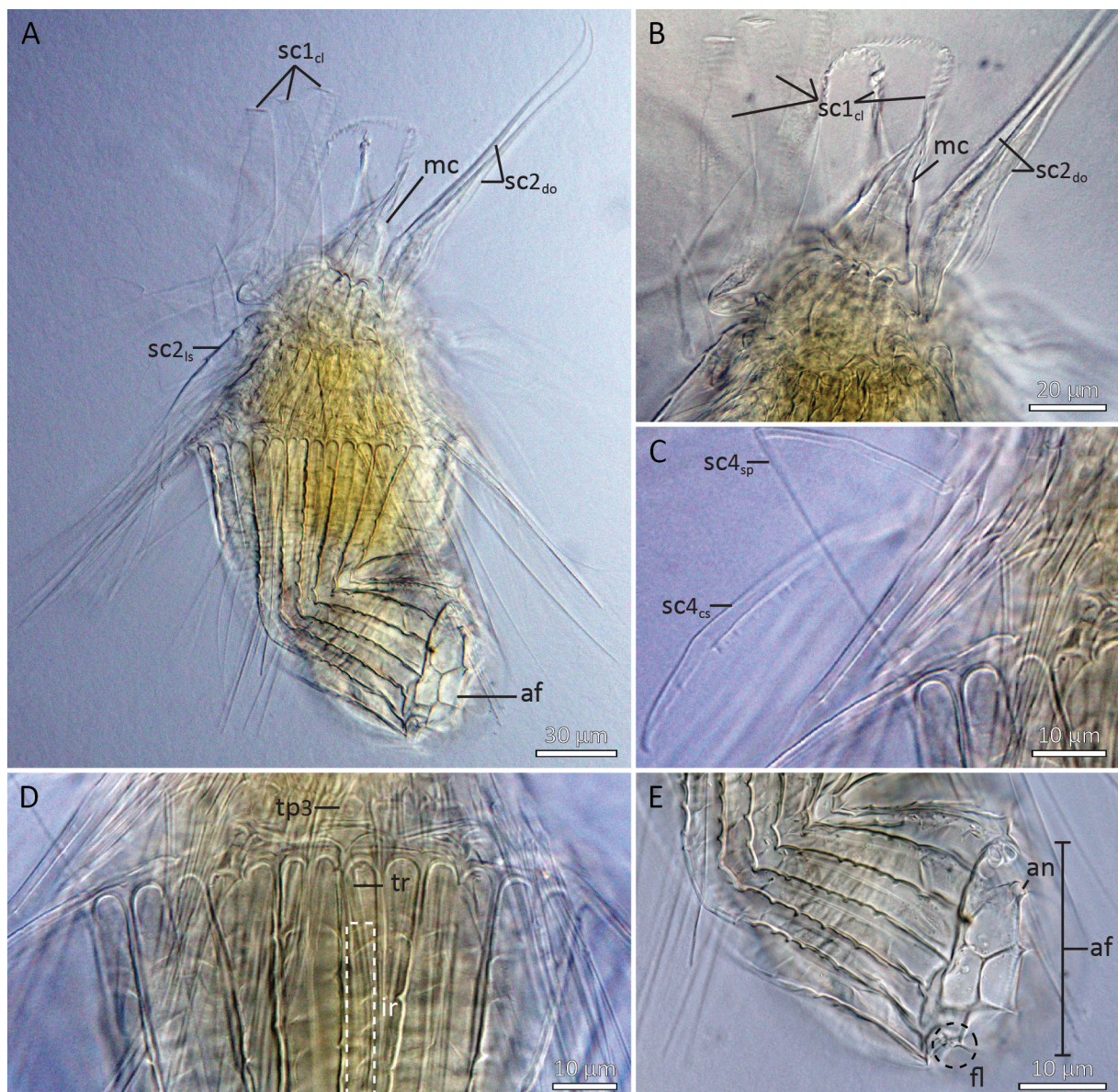
Fig. 4. Light micrographs showing overviews and details of holotype, adult ♀ of *Pliciloricus ukupachaensis* sp. nov. (NHMD 1177413). **A**. Lateral overview; dorsal is left and ventral is right. **B**. Detail of head showing mouth cone, clavoscalids and double organ. **C**. Detail of introvert showing scalids of Rows 4 to 8, inclusive claw-shaped scalids of Row 4. **D**. Detail of neck region and anterior part of lorica. **E**. Posterior part of lorica and lateral half of the anal field.

Row 3 consists of fifteen uniform spinoscalids (length: 58 µm), composed of two short, articulating, ovate bases and a long acicular end-piece, densely covered with minute hairs (Figs 2A, 3, 5A, 6D).

Row 4 consists of fifteen regular spinoscalids alternating with fifteen claw-like scalids. The spinoscalids (length: 98 µm) are composed of two short, articulating, ovate bases and a long acicular end-piece with a distinct bend ⅓ from its proximal end; end-pieces are covered with minute hairs. Each claw-like scalid (length: 44 µm) is composed of a short basis with hairy, distal margin, a shaft (½ of scalid length) with serration along its inferior margin, and a thinner distal part, with a curved tip; some claw-shaped scalids bend medially, suggesting an articulation between the shaft and the end-piece (Figs 2A, 3, 4C, 5A–B, 6C, 7A).

Rows 5 to 8 with spinoscalids that are very uniform. Each row has thirty spinoscalids (lengths: 68 to 73 µm), each consisting of a short basis composed of two ovate units and a long, smooth acicular end-piece with short hairs along their lateral margins (Figs 2A, 3, 6D).

Row 9 consists of thirty short, beak-shaped scalids (length: 10 µm) (Figs 2A–B, 3, 5B, 6D).

The neck has fifteen uniform, single trichoscalids (Figs 2A, 3, 4D, 5A–B, 6D). The trichoscalids are 79 µm in length, blade-shaped, with a median, longitudinal ridge, and a small, triangular plate covering the proximal attachment point.

Trichoscalid plates are extremely weakly defined. There might, however, be a very weak indication of a row with fifteen trichoscalid plates at the base of each trichoscalid. This indication can only be observed with LM though (Fig. 4D), and not with SEM, which suggests that the plates are mostly intracuticular thickenings, rather than external structures. Interestingly, however, minute (13 µm long) appendages are attached anterior to seven of the fifteen indistinct trichoscalid plates (Figs 2A, 3, 6D inset). These appendages are arranged with one in middorsal position anterior to the corresponding trichoscalid, and are otherwise present radially anterior to every second trichoscalid. This pattern corresponds to the arrangement of Row 2 trichoscalid plates in other species of *Pliciloricus* (see for instance the description of *P. apteryx* Sørensen *et al.*, 2022), and we therefore interpret these short appendages (Fig. 6D inset) as Row 2 trichoscalid plates. Accordingly, the weakly defined trichoscalid plates with attached trichoscalid represent Row 3, whereas there are no trichoscalid plates of Row 1 (Fig. 3).

No particular structures were noted in the thorax region. The lorica is composed of 22 plicae, including a broader midventral plica. Numerous, oblique structures, referred to as 'interplical radii', radiate from the primary double ridges of the plicae. The interplical radii are easily observed in LM as well as SEM (Figs 4D, 5D, 6C). The anterior lorica margin is straight, and there is no indication of marginal spikes (Figs 2A, 4D). In both adult specimens, the holotype and the paratype mounted for SEM, the lorica has a highly characteristic, nearly 90° bend on the ventral side (Figs 4A, 5, 7A).

Posteriorly, the lorica forms a large anal field (Figs 2A, C, 4A, E, 5A, D, 6E–F). The anal field is ovoid and limited by a strong ridge, which also marks the posterior limit of the lorical plicae. Numerous cuticular ridges present within the anal field form different pentagonal and hexagonal fields. Whereas the fields closest to the ventral side show a certain level of bilateral symmetry, the shape and arrangement of the remaining fields are more irregular, and overall the anal field ornamentation must be considered as asymmetrical. A single pair of P-flosculi are present in the dorsalmost portion of the anal field; a crescentic anal opening, flanked by a pair of oval thickenings, is present close to the ventral margin of the area.

Internal anatomy was difficult to observe, but two groups of circular muscles are present in the trunk, arranged as an anterior and a posterior group.

Last instar Higgins larva and postlarva

Last instar Higgins larva with head and trunk, the latter divided into a thorax region and a loricated abdomen (Figs 2B, 7B–E, 8). It measures 267 µm in length and 158 µm in width at its broadest point, medially on the abdomen.
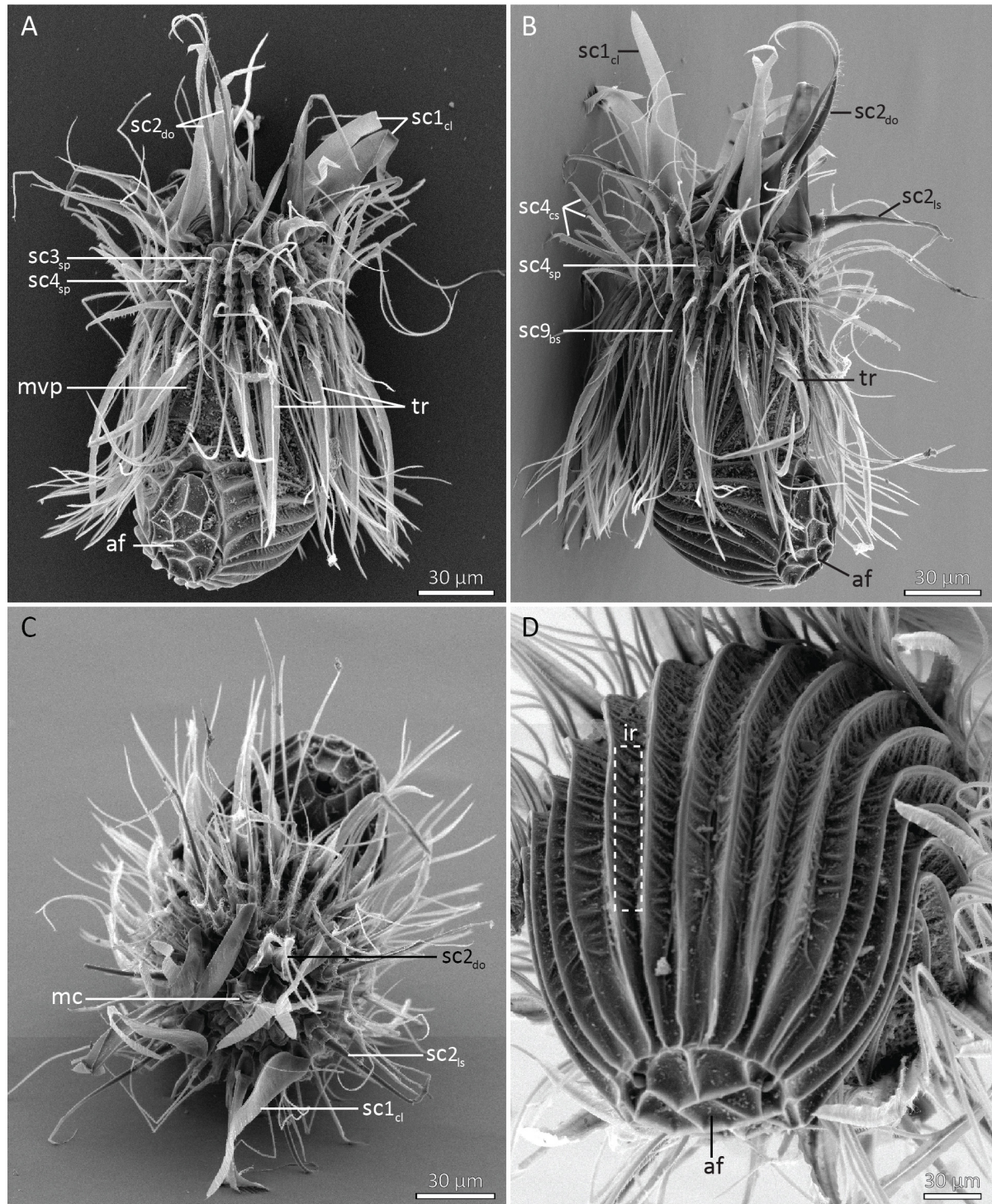
Fig. 5. Scanning electron micrographs showing overviews of adult paratypic ♀ of *Pliciloricus ukupachaensis* sp. nov. (NHMD 1177421). **A**. Ventral overview. **B**. Right side lateral overview. **C**. Frontal overview. **D**. Lorica, dorsocaudal view.
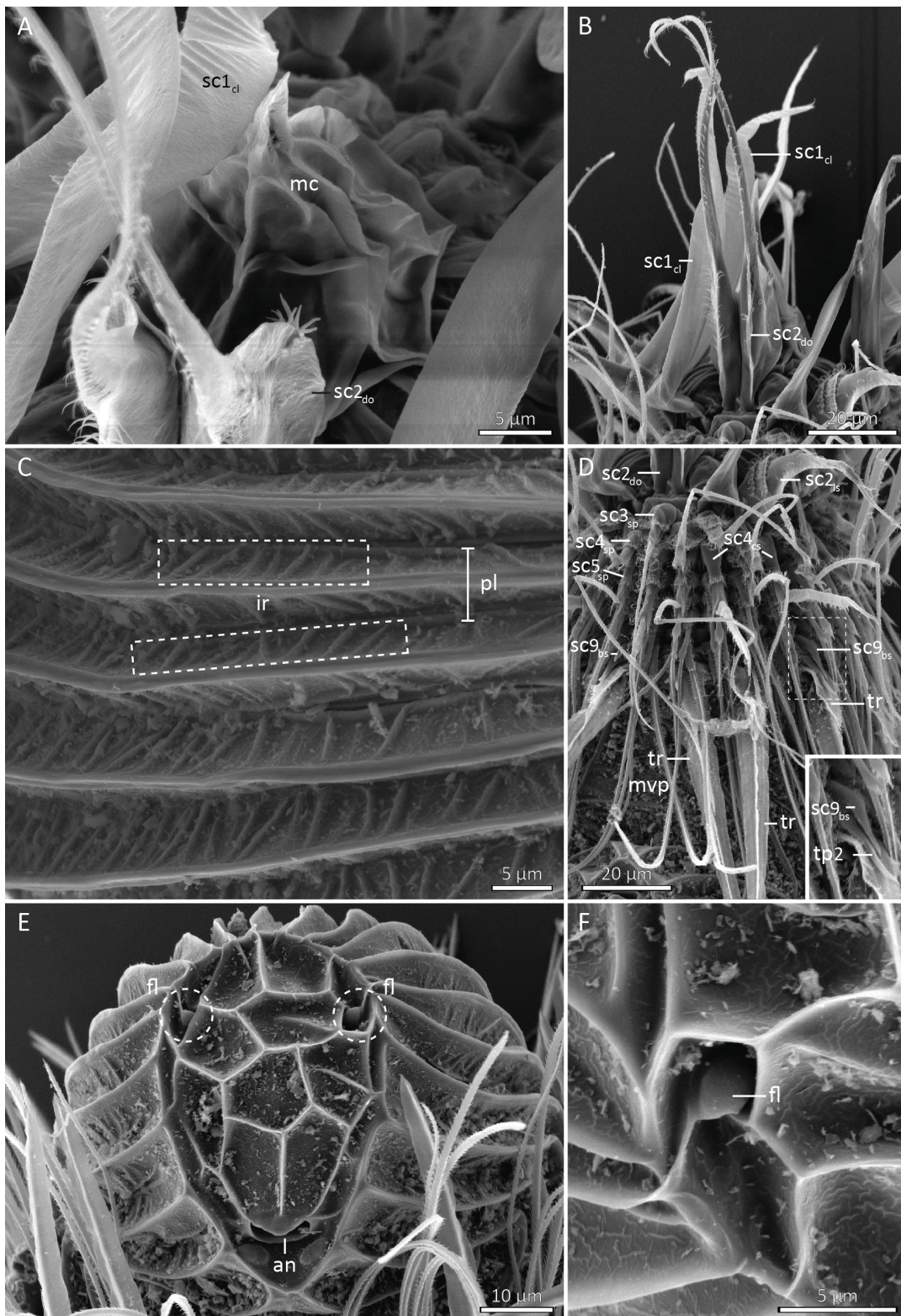
Fig. 6. Scanning electron micrographs showing details of adult paratypic ♀ of *Pliciloricus ukupachaensis* sp. nov. (NHMD 1177421). **A**. Mouth cone and basal parts of double organ. **B**. Double organ with clavoscalids in the background. **C**. Detail showing the interplical radii on the dorsal side of the lorica. **D**. Scalids and trichoscalids on the ventral side of the introvert and neck; inset shows close-up of area marked with dashed frame. **E**. Anal field; dorsal side is up. **F**. Detail showing flosculus on the anal field.

The head of the single, paratypic larva was retracted and detailed information on the introvert morphology could not be obtained. Pharyngeal armature consists of oral teeth with tripartite anterior tips and inner armature (Figs 2B, 7D, 8A, C–D). The thorax has four transverse folds and numerous (>22) longitudinal
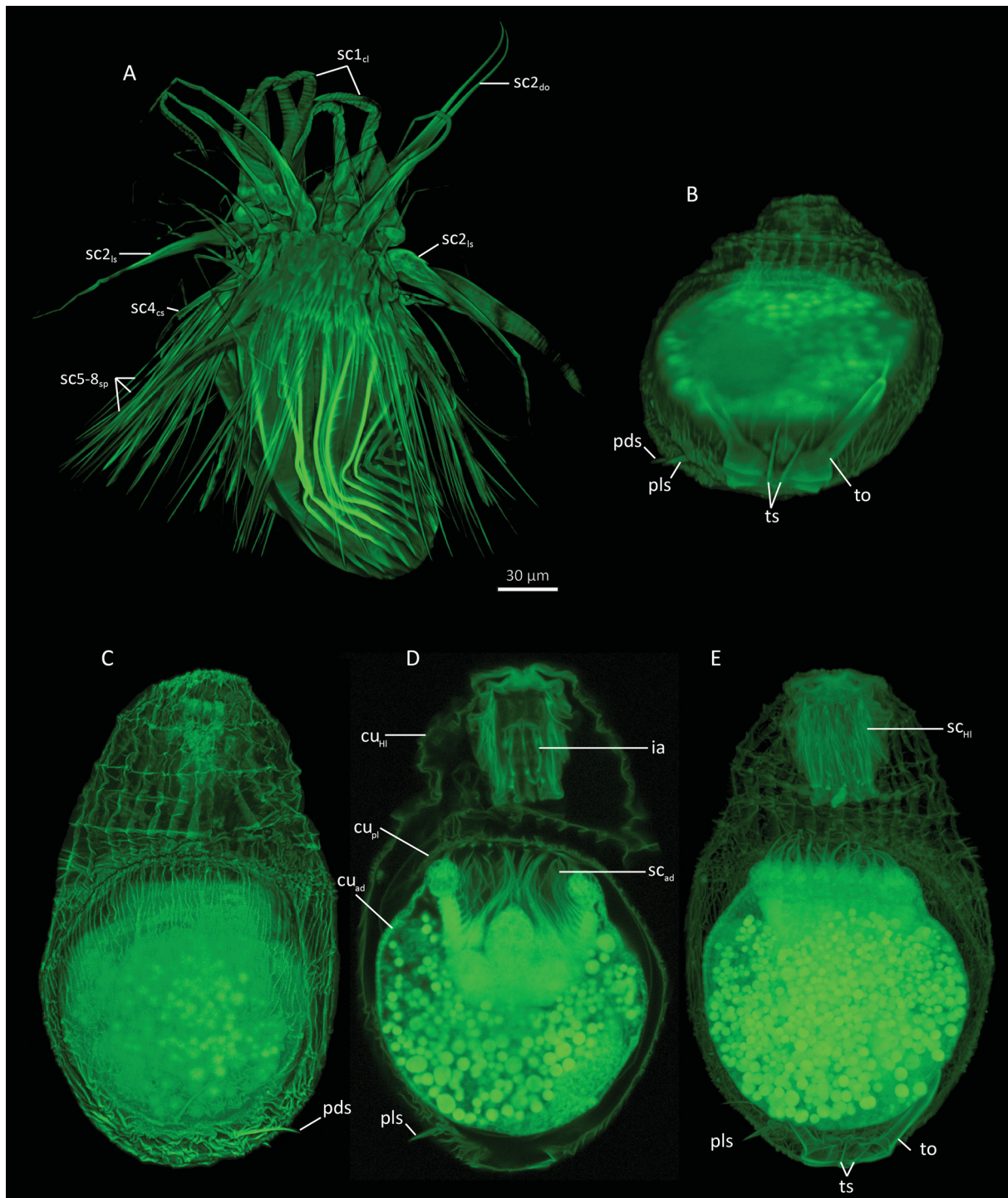
Fig. 7. Confocal laser scanning micrographs of *Pliciloricus ukupachaensis* sp. nov. showing 3D reconstruction of (A) adult ♀ holotype (NHMD 1177413) and Z-stack projections (B–E) of paratypic Higgins larva containing a postlarva with an adult (NHMD 1177414). **A**. Lateral overview; dorsal is left and ventral is right. **B**. Caudal view; ventral side is up. **C**. Dorsal overview. **D**. Overview focused medially in specimen. **E**. Ventral overview.
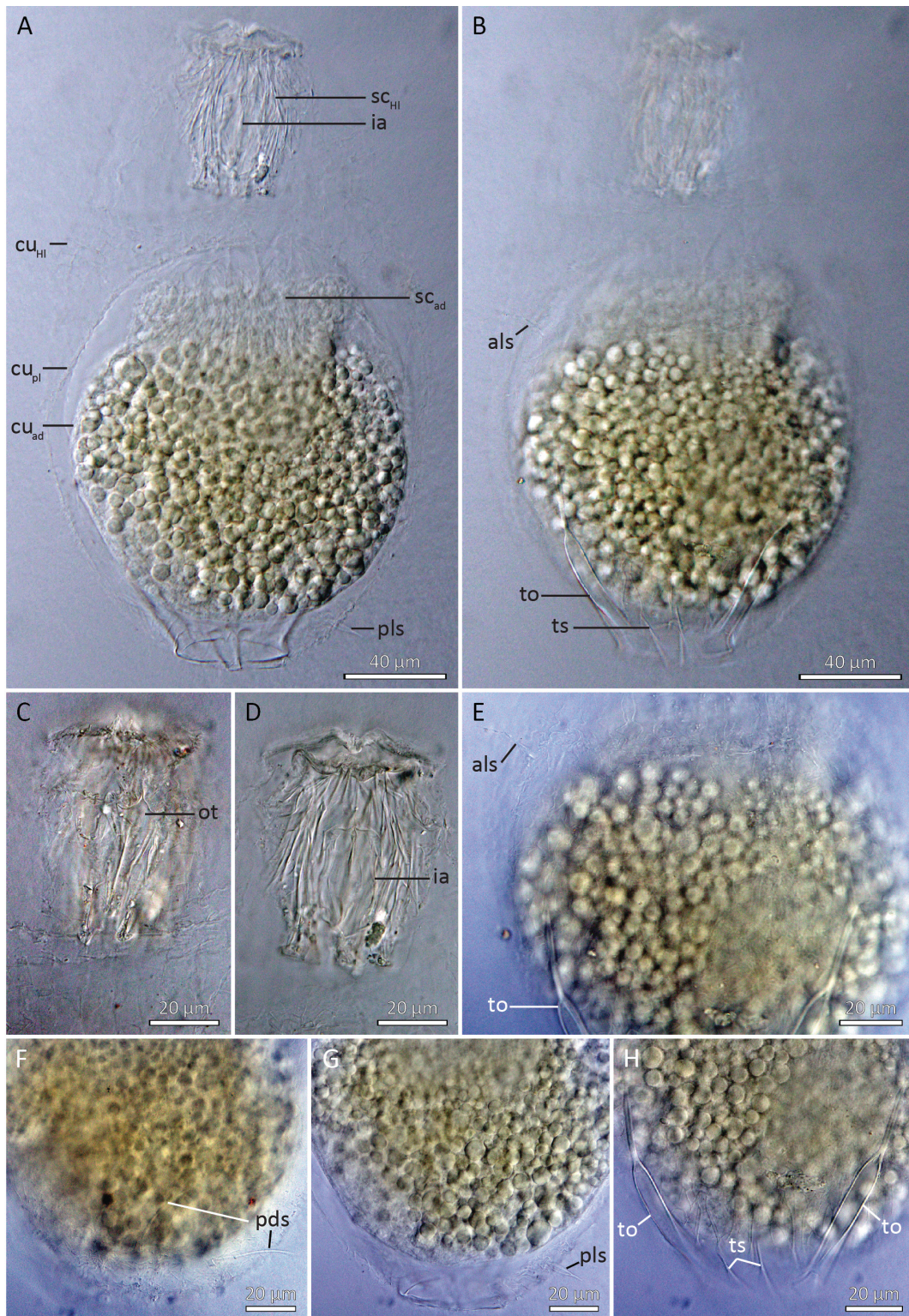
Fig. 8. Light micrographs showing overviews and details of paratypic Higgins larva of *Pliciloricus ukupachaensis* sp. nov., containing a postlarva with an adult (NHMD 1177414). **A**. Overview, focused medially in specimen. **B**. Ventral overview. **C**. Prepharyngeal armature, focused on oral teeth. **D**. Prepharyngeal armature, focused on internal armature. **E**. Anterior part of lorica, ventral view. **F**. Posterior part of lorica, dorsal view. **G**. Posterior part of lorica, focused medially in specimen. **H**. Posterior part of lorica, ventral view.

folds. The abdomen has numerous (>90) indistinct longitudinal lines, which are so weakly developed that they can hardly be referred to as plicae. Two pairs of anterior, simple, unbranched setae are located on the abdomen about ¼ from its anterior margin: anterolateral setae measure 25 μm in length, whereas anteroventral setae are slightly shorter, measuring 22 μm in length. Posterior setae include thin and simple posterodorsal setae (length: 36 μm), swollen and stiff posterolateral setae (length: 18 μm), and the acicular and rigid terminal setae (length: 25 μm) attaching between the toes (Figs 2B, 7B–E, 8A–B, E–H).

The toes are long and slender (total toe length: 91 μm) and divided into three portions: relatively broad bases (62 μm), slender mid-pieces each with a central, internal canal (length: 24 μm), and short, abruptly narrowing tips (length: 5 μm) (Figs 2B, 7B, E, 8B, E, H).

The Higgins larva contains a postlarva, which is nothing but a cuticle without any further, observable structures. The postlarva is nearly globular and about 152–155 μm in diameter. A developing adult stage of unknown sex is present inside the postlarva, filled with refringent vesicles. The adult scalids of the introvert appear to be well-developed, but internal organs are still not developed, and the lorica is so thin that it appears undifferentiated (Figs 2B, 7B–E, 8A–B).
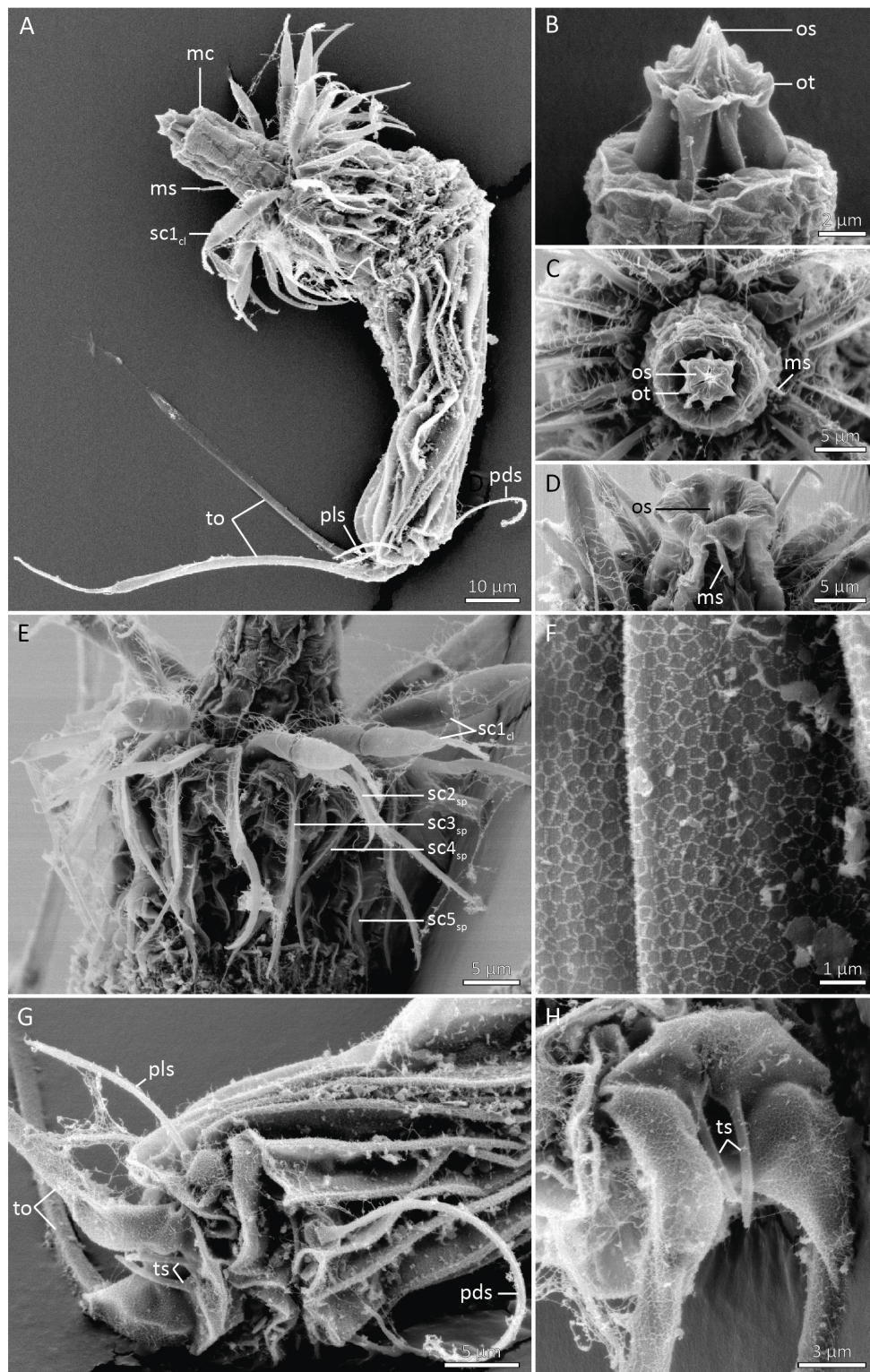
Pliciloricus sp.
Figs 9, 10A

Material examined

CHILE • 1 Higgins larva; abyssal plain, on the west side of the Atacama Trench; st. 7; 22°56.22′ S, 71°37.08′ W; depth 5500 m; 20 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for LM in Fluoromount G on HS slide; NHMD 1177415 • 2 Higgins larvae; continental slope off Iquique, and near the Atacama Trench; st. 9; 20°19.97′ S, 70°58.70′ W; depth 4050 m; 28 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for SEM; see also Table 1 and Fig. 1; personal reference collection of MVS.

Short description of Higgins larvae

The single larva mounted for LM has its head retracted and contains another stage that appears to be a postlarva (Fig. 10A). The contracted trunk length is 224 μm and maximum width is 160 μm, measured on the anterior part of the abdomen. The thorax region has six transverse folds, and the abdomen has eleven longitudinal folds on each side, suggesting the presence of 22 plicae. Anterior setae are thin, simple and unbranched (anterolateral seta length=30 μm; anteroventral seta length=45 μm). Posterodorsal (length =47 μm) and posterolateral (length=38 μm) setae have the same simple appearance as the anterior ones, whereas the terminal setae (length=34 μm) are slightly thicker and appear more rigid. Toes are slender and long (length=118 μm), and divided into a thicker proximal part (length=83 μm) that narrows abruptly into a thinner, distal end-piece (length=35 μm).

Specimens mounted for SEM of what is assumed to be the same species have protruded mouth cones and introverts (Fig. 9A). The mouth cone has six oral styles surrounded by six oral teeth (Fig. 9B–C). A short seta is present in midventral position on the mouth cone (Fig. 9C–D). The introvert has five rows of scalids, with eight clavoscalids in the first row. Each clavoscalid is composed of a short basis, two broad and flattened mid-pieces, and a short, thin tip (Fig. 9A, E). Row 2 has 10 scalids, composed of a laterally flattened proximal part and a sickle-shaped end-piece. The exact number of scalids in Rows 3 and 4 could not be determined, but in both rows the scalids are composed of two, relatively uniform units. Scalids of Row 5 are shorter, and consist of a proximal plate with a short, flexible distal appendage (Fig. 9E). All scalids carry long, but extremely thin, undulating hairs.

Fig. 9. Scanning electron micrographs showing overviews and details of Higgins larvae of unidentified *Pliciloricus* sp. from st. 9 (personal reference collection of MVS). **A**. Lateral overview. **B–C**. Distal tip of mouth cone with protruded oral styles and teeth; dorsal view (B) and frontal view (C). **D**. Distal tip of mouth cone with retracted oral styles and teeth, ventral view. **E**. Introvert, dorsal view. **F**. Detail showing irregular honeycomb ornamentation on lorica. **G**. Posterior end of lorica, dorsocaudal view. **H**. Detail showing toe bases and terminal setae.

The thorax region is partly contracted and difficult to examine, but it appears to have four or five transverse folds. Likewise, it was not possible to establish the exact number of plicae in the slender abdomen, but there seems to be around 20–22. The abdominal cuticle, as well as the cuticle of the toes, has a fine honeycomb ornamentation on their surface (Fig. 9F). Anterior setae were difficult to observe, but three pairs of posterior setae with similar morphology as those in the LM specimen are present (Fig. 9G–H).
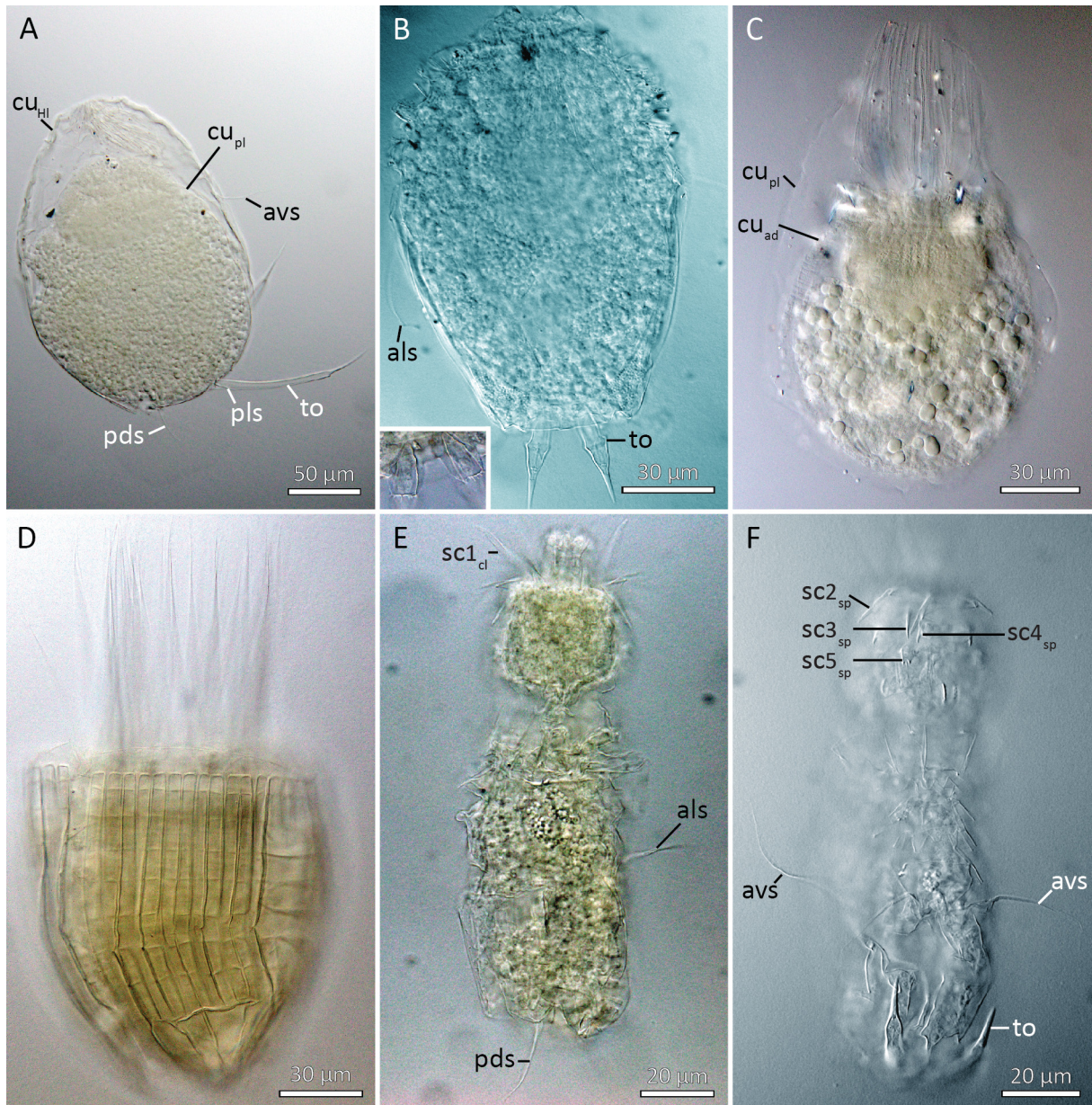
Fig. 10. Light micrographs showing overviews of unidentified specimens. **A**. *Pliciloricus* sp. Higgins larva from st. 7, lateral view (NHMD 1177415). **B**. *Rugiloricus* sp. 1 Higgins larva, ventral view (NHMD 1177416); inset shows close-up of plate-like toe bases with serrated margins. **C**. *Rugiloricus* sp. 1 postlarva with developing adult inside, focused medially in specimen (NHMD 1177417). **D**. *Rugiloricus* sp. 2 adult, lateral view with dorsal left and ventral right (NHMD 1177420). **E**. *Rugiloricus* sp. 2 Higgins larva, dorsal view (NHMD 1177418). **F**. Same, ventral view.

Genus *Rugiloricus* Higgins & Kristensen, 1986

Rugiloricus sp. 1
Fig. 10B–C

Material examined

CHILE • 1 Higgins larva; abyssal plain, on the west side of the Atacama Trench; st. 7; 22°56.22′ S, 71°37.08′ W; depth 5500 m; 20 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for LM in Fluoromount G on HS slide; NHMD 1177416 • 1 postlarva containing a developing adult; abyssal plain, on the west side of the Atacama Trench; st. 7; 22°56.22′ S, 71°37.08′ W; depth 5500 m; 20 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for LM in Fluoromount G on HS slide; see also Table 1 and Fig. 1; NHMD 1177417.

Short description of Higgins larva and postlarva

The Higgins larva (Fig. 10B) is strongly contracted (length = 136 μm and width = 97 μm). The lorica has longitudinal folds, but the exact number of folds could not be determined. Anterolateral setae are thin and unbranched (length = 56 μm); anteroventral setae were not observed. Posterior setae are also thin, flexible and unbranched, with long posterodorsal setae (length = 34 μm) and much shorter posterolateral ones (length = 12 μm). Terminal setae are not present. The toes are the most remarkable trait in the larva. Each toe consists of a cylindrical proximal part (length = 14 μm) and a gradually tapering distal part (length = 21 μm). The toes reach their maximum width in the transition point from cylindrical to tapering, and these medial thickenings give the toes their peculiar appearance (Fig. 10B). The entire cylindrical proximal part and half of the tapering part are hollow, and likely to contain some glandular tissue; the distal tips are compact. Ventrally, the toe bases are supported by plate-like extensions with serrated posterior margins (Fig. 10B inset).

The postlarva (Fig. 10C) is made up by a simple cuticle without any visible structures or ornamentation (length = 188 μm and width = 118 μm). It contains an adult at a very early developmental stage. The adult trunk is nearly globular (diameter = 100 μm) and contains mostly undifferentiated cells. The scalids of the introvert appear more developed and extend into the anterior part of the postlarval cuticle. They are long and slender, with the typical appearance of adult scalids, stressing that the specimen in the postlarval cuticle is not another larval stage.

Rugiloricus sp. 2
Fig. 10D–F

Material examined

CHILE • 2 Higgins larvae; continental slope off Iquique, and near the Atacama Trench; st. 9; 20°19.97′ S, 70°58.70′ W; depth 4050 m; 28 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for LM in Fluoromount G on HS slide; NHMD 1177418 to 1177419 • 1 adult of uncertain sex; continental slope off Iquique, and near the Atacama Trench; st. 9; 20°19.97′ S, 70°58.70′ W; depth 4050 m; 28 Mar. 2018; R/V Sonne SO261; deep-sea mud; mounted for LM in Fluoromount G on HS slide; see also Table 1 and Fig. 1; NHMD 1177420.

Short description of Higgins larvae and adult

One Higgins larva (NHMD 1177419) was so strongly contracted that it did not offer any significant information. The shape of the toes suggested though, that it is conspecific with the other, stretched and more well-preserved Higgins larva (NHMD 1177418). This larva has a fully protruded head and thin lorica with irregular, longitudinal folds (Fig. 10E–F). Body length (exclusive toes) is 140 μm, and

maximum width in the anterior part of the trunk is 48 µm. The introvert has five rows of scalids, with clavoscalids in the anterior row and scalids composed of two elongate, articulating units in Rows 2 to 4. Row 5 has short scalids formed by a proximal plate, with a short, flexible distal appendage. A short, hook-shaped scalid is present middorsally, posterior to Row 5. All setae on the lorica are thin, flexible and unbranched. Anterior setae are long (anterolateral seta length = 38 µm; anteroventral seta length = 40 µm), whereas the two posterior pairs are considerably shorter (posterodorsal seta length = 25 µm; posterolateral seta length = 12 µm). Terminal setae are absent. Each toe is 27 µm long and consists of an only slightly tapering proximal part, with a hollow cavity, and a compact distal part that tapers towards its terminal tip.

The adult specimen (Fig. 10D) is strongly contracted, which prevents any examination of the head structures. The lorica is 133 µm long and has a maximum width of 114 µm. The lateral and dorsal sides have about 32 plicae, whereas the ventral side has a larger, midventral field with five transverse folds, formed by the fusion of six to eight plicae. Plicae are also fused in the posterior part of the lorica, which seems to have about 12 triangular fields, which all point towards the terminal tip of the lorica.
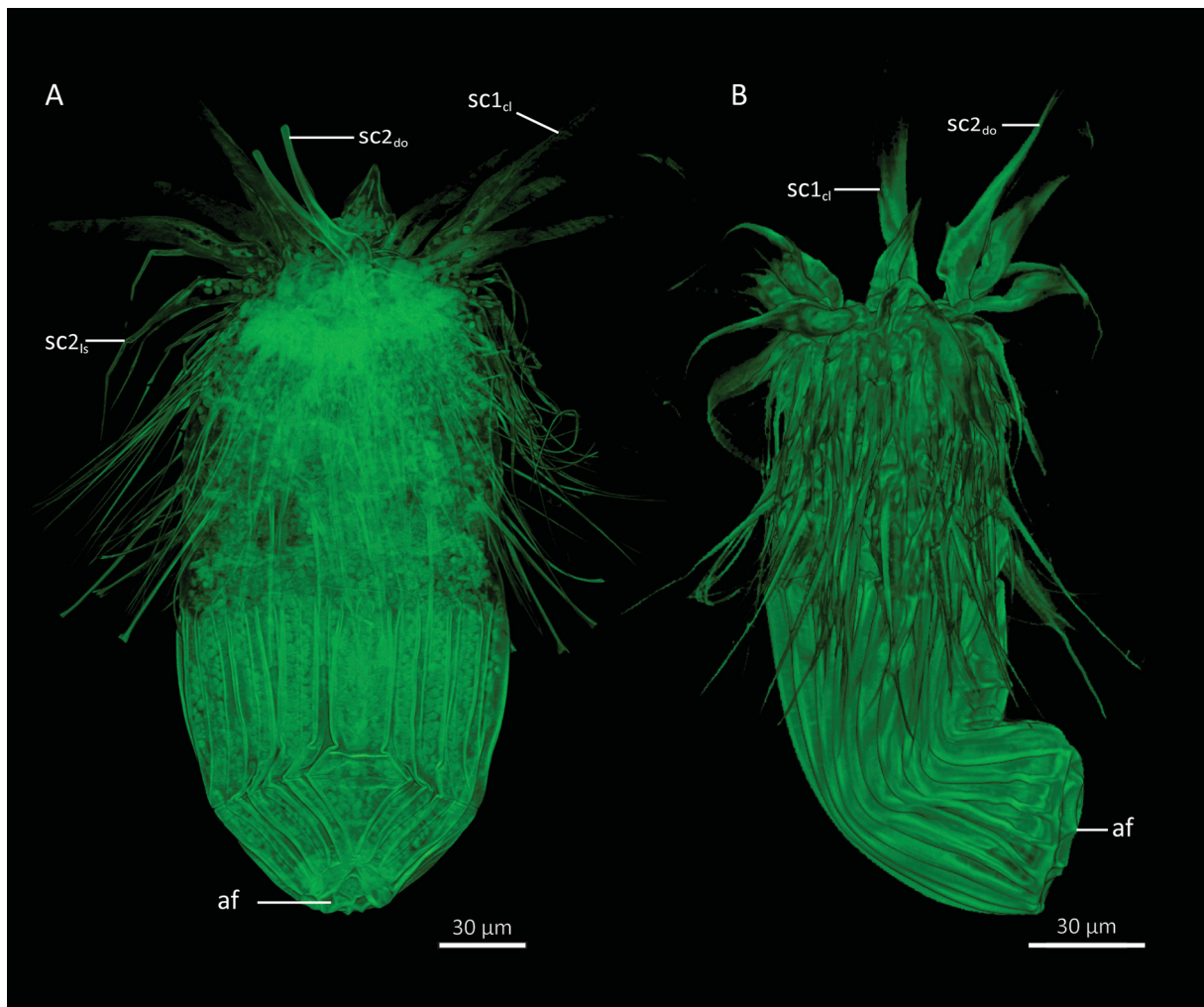
Fig. 11. Confocal laser scanning 3D reconstructions. **A**. *Pliciloricus leocaudatus*, ventral view, paratype (NHMD 100760). **B**. *Pliciloricus* aff. *ukupachaensis* collected off Oregon, US west coast, lateral view (NHMD 225904).

Discussion

Identity of examined specimens

Common challenges in taxonomic studies of loriciferans are the shortage of specimens, their stage of preservation, which is often far from ideal, and difficulties in matching different developmental stages. In the present study, we were faced with all three challenges, but concluded after a close comparison of all specimens that the examined material included four species: two *Pliciloricus* and two *Rugiloricus*.

The two species of *Pliciloricus* are represented by two adults and one last instar Higgins larva containing a postlarva, all originating from st. 1 and identified as *P. ukupachaensis* sp. nov., and by three, putatively conspecific but unidentified Higgins larvae from stations 7 and 9. The three latter Higgins larvae are distinguished from *P. ukupachaensis* by differences in the shape of their posterolateral setae and toes. The unidentified Higgins larvae have thin and flexible posterolateral setae (Figs 9A, G, 10A), unlike the swollen and rigid setae of the new species (Figs 2B, 7D–E, 8G). Furthermore, their toes are considerably longer (118 µm versus 91 µm in the new species), and without the off-set tips (Fig. 9A, 10A) that characterise the toes of *P. ukupachaensis* (Figs 2B, 8H).

The three Higgins larvae do not show any clear similarity to any described species. Their exceptionally long and slender toes without offset tip show greatest similarity with the toes of *Pliciloricus hadalis* Kristensen & Shirayama, 1988, but the proportional lengths of the thicker proximal parts versus the thinner distal parts differ. In *P. hadalis* the thinner distal parts are longest (Kristensen & Shirayama 1988), whereas the thicker proximal parts represent more than ⅔ of the total toe length in the Atacaman specimens. The Higgins larvae of *P. hadalis* furthermore differ by having bifurcated anterior setae on the larval lorica.

The two species of *Rugiloricus* are represented by a Higgins larva and a postlarva containing a developing adult, both from st. 7, and two Higgins larvae and a strongly contracted adult from st. 9. Again, we use differences in the larval toe morphology to suggest that the populations at the two stations represent two different species. The toes of the larvae of *Rugiloricus* sp. 2 (Fig. 10F) from st. 9 look like common *Rugiloricus* toes, i.e., relatively short and stout toes that taper more or less gradually towards the tips (see, e.g., *R. carolinensis* Higgins & Kristensen, 1986, *R. manuelae* Pardos & Kristensen, 2013, and *R. polaris* Gad & Martínez Arbizu, 2005). The toes of the Higgins larva of *Rugiloricus* sp. 1 from st. 7 differ considerably from this common shape, by having an outline of each toe that resembles the nib of an old fashioned ink pen (Fig. 10B). Unlike the toes of other *Rugiloricus*, which are broadest at their bases, the toes of this larva from st. 7 are broadest medially, by the end of the cylindrical proximal part. The serrated plates supporting the bases of the toes are furthermore unusual (Fig. 10B inset) and have, to our knowledge, not been reported previously. This highly conspicuous toe morphology suggests that *Rugiloricus* sp. 1 from st. 7 represents an undescribed species of the genus. Unfortunately, there is not much additional information to add about the species' morphology, which prevents us from providing a formal description.

The specimens from st. 9, *Rugiloricus* sp. 2, are unfortunately preserved in a condition that does not allow complete identification or description. This single adult is so strongly contracted that only the lorical morphology can be examined (Fig. 10D). The lorica immediately draws attention to its caudal part, where the plicae merge into large, triangular fields. This lorical modification is uncommon within the genus and separates it from most of the known species, which either lack such fields or have fields that are much narrower, i.e., typically of the same width as the plicae. This differentiation of the lorica suggests that *Rugiloricus* sp. 2 is an undescribed species as well. Unfortunately, the Higgins larvae do not offer any particular evidence to support this assumption. Out of the eight described species of *Rugiloricus*, Higgins larvae are only known from three species (mentioned in the previous paragraph),

181

and the two available larvae from the present study do not show any traits that differ conspicuously from those of the described larvae.

Notes on *Pliciloricus ukupachaensis* sp. nov.

Differential characters

Adult specimens of *Pliciloricus* are characterised by the presence of a lorica with 22 plicae, midventral scalids of Row 2 modified into a double organ with fused bases, and a neck with alternating single- and double trichoscalids (Higgins & Kristensen 1986; Neves *et al.* 2016; Fujimoto & Kristensen 2020). The morphology of *P. ukupachaensis* sp. nov. generally follows this diagnosis (however, see discussion in the following section), which assigns the new species to *Pliciloricus*.

Pliciloricus currently accommodates fourteen described species, and the new species can easily be distinguished from most of them by its enlarged and conspicuously ornamented anal field (Figs 2C, 4E, 6E). The only other species with a similar anal field is *P. leocaudatus* (Fig. 11A), described from Faroe Bank in the North Atlantic (Heiner & Kristensen 2005). Most species of *Pliciloricus* display some kind of differentiated anal field, sometimes referred to as an 'anal cone' or 'anal field', but the anal fields of *P. leocaudatus* and *P. ukupachaensis* sp. nov. are larger than in other species and have a conspicuous pattern of pentagonal and hexagonal fields. The close similarity between the two species not only confirms the generic affinity of *P. ukupachaensis*, but it also strongly supports a close relationship between *P. leocaudatus* and *P. ukupachaensis*.

Thus, *P. ukupachaensis* sp. nov. can be distinguished from most congeners, except from *P. leocaudatus*, by its anal field with pentagonal and hexagonal fields. The characters that most easily differentiate the new species from *P. leocaudatus* include the exact arrangement of fields in the anal field, the position of the flosculi, and the morphology of the clavoscalids, double organ and trichoscalids. When comparing the ornamentation of the anal field in the two species, it is striking how the fields in *P. leocaudatus* follow a relatively strict bilateral symmetrical pattern (see Heiner & Kristensen 2005: figs 3, 5b), whereas the fields in *P. ukupachaensis* are distributed much more asymmetrically. *Pliciloricus leocaudatus* furthermore has three pairs of flosculi – two pairs in the caudal end of its ventrolateral plicae and one pair within the anal field. Only the latter pair, the one inside the anal field, is present in *P. ukupachaensis*. Also, the clavoscalids and double organs differ quite a bit between the two species. *Pliciloricus leocaudatus* has clavoscalids with 7–11 distal annulations, and the clavoscalids are longer than the short, none-tapered double organ scalids. In *P. ukupachaensis* the clavoscalids have more than twice as many annulations, and the scalids of the double organ gradually taper into long, thin distal tips which make them as long as the clavoscalids. Finally, the trichoscalids are conspicuously different. *Pliciloricus leocaudatus* has eight single and seven double trichoscalids, which follows the general and diagnostic pattern for species of *Pliciloricus*. In contrast, *P. ukupachaensis* sp. nov. has fifteen single trichoscalids – a configuration that otherwise only occurs outside the genus. This absence of the otherwise genus diagnostic double trichoscalids is addressed further in the following section.

Besides the new species reported in the present contribution, and *P. leocaudatus* from the Faroe Bank, we have a third example of a specimen with a large anal field. In their study of deep-sea Loricifera from the US west coast, Neves *et al.* (2019) described two new species, but they also reported the presence of various adult and larval specimens of Pliciloricidae that could be not identified or described. One of these was an adult specimen of *Pliciloricus* (Fig. 11B), collected at 3200 m depth near the margin of the Blanco Trench, off Oregon (see Neves *et al.* 2019: table 1). The authors did not provide any detailed notes on the specimen, but it was deposited in NHMD (catalogue number NHMD 225904), and the specimen was re-examined for the present study. Interestingly, it shows a great resemblance to *P. ukupachaensis* sp. nov. Its double organ in introvert Row 2 consists of scalids with long, gradually tapering tips that curve in a dorsal direction, which is exactly as described for *P. ukupachaensis*. The

general shape and dimensions of its lorica are also very similar to those of *P. ukupachaensis*. The lorica furthermore has a large anal field, and even though it cannot be examined in detail because of the specimen's orientation, it is clear that the area is large, and has strong ridges forming well-defined fields, as observed in *P. ukupachaensis* and *P. leocaudatus*. In addition, the lorica has a distinct ventral bend (Fig. 11B) – which is identical to the bend observed in *P. ukupachaensis* (Figs 4A, 5B, 7A). Also this bend is discussed further in the following.

We would hesitate to conclude that the *Pliciloricus* sp. reported by Neves *et al.* (2019) from the US west coast is identical to *P. ukupachaensis* sp. nov., but the similarity is so close that we would not reject the possibility either. The great distance between Chile and Oregon could perhaps suggest that conspecifity between the populations is unlikely, but in this context it is worth noticing that Grzelak *et al.* (2021) examined kinorhynchs from the same area, in and along the Atacama Trench, and recorded *Echinoderes juliae* Sørensen *et al.*, 2018 – a species described from the same abyssal plains off Oregon.

Notes on morphological traits

Pliciloricus ukupachaensis sp. nov. displays different unusual morphological traits that attract special attention. Most, if not all, loriciferan species have rows of cuticular thickenings in the neck region known as "basal plates" or "trichoscalid plates" (Kristensen 1983; Neves *et al.* 2016). They are usually easily visualised with both LM and SEM, but in *P. ukupachaensis* they were extremely difficult to identify. After very careful examination we identified with LM some vague lines that could indicate the presence of at least one row of trichoscalid plates (Fig. 4D). Since the trichoscalids seemed to attach on or very close to these indistinct trichoscalid plates, we interpreted them as belonging to Row 3 – the posteriormost trichoscalid plate row in the neck. The weak outline of these trichoscalid plates could be observed with LM, whereas neither SEM (e.g., Fig. 6D) nor CLSM imaging showed any indication of the plates. To test whether the lack of distinct trichoscalid plates in *P. ukupachaensis* was a primary condition or due to secondary reduction, we compared with the putatively closely related species *P. leocaudatus*. In this species, however, trichoscalid plates are well developed, which is documented in the description and confirmed by inspection of additional unpublished SEM imaging. Thus, it seems most likely that the trichoscalid plates of Row 3 in *P. ukupachaensis* sp. nov. are reduced.

Neck Row 2 in *P. leocaudatus* has only seven trichoscalid plates, and they are all longitudinally aligned with the species' double trichoscalids. Thus, the presence of a Row 2 trichoscalid plate is tightly linked with the presence of a double trichoscalid. Besides this relation, its Row 2 trichoscalid plates differ from those of other rows by extending into a long, pointed projection (see, e.g., Heiner & Kristensen 2005: fig. 5d). As described above, *P. ukupachaensis* sp. nov. breaks the frame of its genus diagnosis by not having double trichoscalids, but, interestingly, it has a row with seven pointed projections (Fig. 6D). These seven projections are arranged as one in middorsal position, anterior to the middorsal trichoscalid, and from this point, with a projection anterior to every second trichoscalid (Fig. 3). In other words, the projections attach exactly in positions where they would be aligned with double trichoscalids in other species of *Pliciloricus*. We therefore interpret these projections as rudiments of the otherwise reduced trichoscalid plates of Row 2. In conclusion, it appears that the trichoscalid plates in *P. ukupachaensis* have been through a transformation, where Row 1 plates have been lost completely, Row 2 plates have been so strongly reduced that only the external projection is left, and Row 3 plates are left as indistinct outlines.

The second, even more significant difference from the common morphological pattern also relates to a potential trichoscalid modification through reduction. One of the key diagnostic characters for species of *Pliciloricus* is the alternating occurrence of single and double trichoscalids (Higgins & Kristensen 1986; Neves *et al.* 2016; Fujimoto & Kristensen 2020). All species of *Pliciloricus* described so far have seven double trichoscalids, composed of a main scalid, resembling the single trichoscalids, and

an accessory appendage attached basally on the surface of the main scalid. This accessory appendage usually resembles the main scalid, but is slightly thinner and more flexible. However, in *P. ukupachaensis* sp. nov. none of the trichoscalids have this accessory appendage. All fifteen trichoscalids have the same uniform appearance, and they must all be considered as single trichoscalids. Since the presence of double trichoscalids so far has been considered as synapomorphic for species of *Pliciloricus*, the lack of such structures in *P. ukupachaensis* could potentially be considered a plesiomorphic condition, suggesting that the species represents the earliest branch within the genus. However, as discussed above, we find morphological evidence supporting a close relationship between *P. ukupachaensis* and *P. leocaudatus*, and since the latter has well-developed double trichoscalids, it seems more likely that the lack of accessory trichoscalid appendages in *P. ukupachaensis* is a secondary loss. This hypothesis also gets some support from the arrangement of Row 2 trichoscalid plates in this species, which are arranged as if double trichoscalids actually were present.

The lack of double trichoscalids in *P. ukupachaensis* sp. nov. obviously compromises the genus diagnosis for *Pliciloricus*. However, since the modified trichoscalids in the new species appear to be a secondary loss, the new findings do not have any phylogenetic implications, such as indicating potential paraphyly or polyphyly of the genus. But it does have some practical implications for generic identification. The dichotomous part of the identification key of Neves *et al.* (2016) lists the presence of seven double trichoscalids as one of three key characters to identify adult *Pliciloricus*, whereas it is the single character pointing to the genus in the key of Fujimoto & Kristensen (2020). Both keys are still valid, and extremely helpful tools in taxonomic work with loriciferans, but the neck morphology of *P. ukupachaensis* makes genus recognition more ambiguous and stresses the need to consult other characters.

A third morphological trait we would like to highlight is of a slightly more obscure kind. When examining the holotype of *P. ukupachaensis* sp. nov. we noticed that the lorica has a characteristic bend on its ventral side (Figs 4A, 7A) – something that seemingly could be a fixation artefact. We noted, however, that the paratype mounted for SEM has exactly the same bend (Fig. 5A–B); thus, this potential 'artefact' was consistently expressed in both available adult specimens. As mentioned above, the unidentified *Pliciloricus* sp. reported by Neves *et al.* (2019) might be conspecific or very close to *P. ukupachaensis*, and, interestingly, this specimen also has this ventral bend (Fig. 11B). Even if this is a fixation artefact, it cannot appear consistently in three specimens without in some way being related to their anatomy. Interestingly, both *P. ukupachaensis* and *Pliciloricus* sp. from Oregon have their circular trunk muscles arranged in two groups – anteriorly and posteriorly in the trunk – and the bend appears right at the space between the two muscle groups. If the ventral longitudinal muscles in this species contract, without a simultaneous contraction of the dorsal longitudinal muscles, the lorica would necessarily bend, and this bend would appear exactly where we observe it – in between the circular muscle groups. Thus, even though we cannot rule out that this is nothing but an artefact, the bend of the lorica is clearly connected with the species' muscular anatomy, which could suggest that live animals in fact are able to make this characteristic bend. In any case, it is noteworthy that this bend does not appear in other species (not even *P. leocaudatus*), but seems to be specific for *P. ukupachaensis* and *Pliciloricus* sp. from Oregon.

Conclusions

The continental slopes and abyssal plains along the Atacama Trench host at least four species of Loricifera. We were able to provide a description of *Pliciloricus ukupachaensis* sp. nov, whereas two species of *Rugiloricus* and one species of *Pliciloricus* could not be described based on the limited material. This is the first loriciferan described from the Southeast Pacific. It was only recorded from a single station near the Atacama Trench, but a highly similar specimen that previously was collected off the US west coast might indicate that the new species has a much wider distribution. If the North American specimen turns out to be identical with *P. ukupachaensis*, this would be the widest distributional range ever reported for a loriciferan species.

The new species is closely related to the North Atlantic *P. leocaudatus*, and they are characterised by a large anal field with distinct pentagonal and hexagonal fields. Other unusual characters in the new species include reduced trichoscalid plates, the presence of only single trichoscalids, and a peculiar ventral bend of the lorica, which was observed in both adults from the type locality and the potentially conspecific specimen from Oregon.

Acknowledgements

References

Fujimoto S. & Kristensen R.M. 2020. Loricifera. *In*: Schmidt-Rhaesa A. (ed.) *Guide to the Identification of Marine Meiofauna*: 415–427. Verlag Dr Friedrich Pfeil, Munich.

Fujimoto S. & Murakami C. 2020. A new genus and species of Nanaloricidae (Loricifera: Nanaloricida) from the Clarion-Clipperton Fracture Zone. *Zoologischer Anzeiger* 289: 177–188. https://doi.org/10.1016/j.jcz.2020.10.009

Fujimoto S., Yamasaki H., Kimura T., Ohtsuka S. & Kristensen R.M. 2020. A new genus and species of Loricifera (Nanaloricida: Pliciloricidae) from the deep waters of Japan. *Marine Biodiversity* 50: e103. https://doi.org/10.1007/s12526-020-01130-3

Gad G. 2005. Giant Higgins-larvae with paedogenetic reproduction from the deep sea of the Angola Basin – evidence for a new life cycle and for abyssal gigantism in Loricifera? *Organisms Diversity and Evolution* 5: 59–75. https://doi.org/10.1016/j.ode.2004.10.005

Gad G. 2009. *Culexiregiloricus*, a new genus of Nanaloricidae (Loricifera) from the deep sea of the Guinea Basin (Southeast Atlantic). *Zootaxa* 2096 (1): 33–49. https://doi.org/10.11646/zootaxa.2096.1.5

Gad G. & Martínez Arbizu P. 2005. First report of Arctic Loricifera – a new *Rugiloricus*-species from the Laptev Sea. *Marine Biology Research* 1: 313–325. https://doi.org/10.1080/17451000500327455

Grzelak K., Zeppilli D., Shimabukuro M. & Sørensen M.V. 2021. Hadal mud dragons: first insight into the diversity of Kinorhyncha from the Atacama Trench. *Frontiers in Marine Science* 8: e670735. https://doi.org/10.3389/fmars.2021.670735

Heiner I. 2004. *Armorloricus kristenseni* (Nanaloricidae, Loricifera), a new species from the Faroe Bank (North Atlantic). *Helgoland Marine Research* 58: 192–205. https://doi.org/10.1007/s10152-004-0185-3

Heiner I. & Kristensen R.M. 2005. Two new species of the genus *Pliciloricus* (Loricifera, Nanaloricida, Pliciloricidae) from the Faroe Bank, North Atlantic. *Zoologischer Anzeiger* 243 (3): 121–138. https://doi.org/10.1016/j.jcz.2004.05.002

Heiner I. & Neuhaus B. 2007. Loricifera from the deep sea at the Galápagos Spreading Center, with a description of *Spinoloricus turbatio* gen. et sp. nov. (Nanaloricidae). *Helgoland Marine Research* 61: 167–182. https://doi.org/10.1007/s10152-007-0064-9

Heiner I. & Neuhaus B. 2010. Phylum Loricifera: corset worms. *In*: Gordon D.P. (ed.) *New Zealand Inventory of Biodiversity, Volume 2: Kingdom Animalia: Chaetognatha, Ecdysozoa, Ichnofossils*: 472–475. Canterbury University Press, Christchurch, New Zealand.

Heiner I., Boesgaard T.M. & Kristensen R.M. 2009. First time discovery of Loricifera from Australian waters and marine caves. *Marine Biology Research* 5: 529–546. https://doi.org/10.1080/17451000902933009

Higgins R.P. & Kristensen R.M. 1986. New Loricifera from Southeastern United States coastal waters. *Smithsonian Contributions to Zoology* 438: 1–70. https://doi.org/10.5479/si.00810282.438

Kristensen R.M. 1983. Loricifera, a new phylum with Aschelminthes characters from the meiobenthos. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 21: 163–180. https://doi.org/10.1111/j.1439-0469.1983.tb00285.x

Kristensen R.M. & Gad G. 2004. *Armorloricus*, a new genus of Loricifera (Nanaloricidae) from Trezen ar Skoden (Roscoff, France). *Cahiers de Biologie marine* 45: 121–156. https://doi.org/10.21411/CBM.A.421701B2

Kristensen R.M. & Shirayama Y. 1988. *Pliciloricus hadalis* (Pliciloricidae) a new loriciferan species collected from the Izu-Ogasawara Trench, Western Pacific. *Zoological Science* 5: 875–881.

Kristensen R.M., Gooday A.J. & Goineau A. 2019. Loricifera inhabiting spherical agglutinated structures in the abyssal eastern equatorial Pacific nodule fields. *Marine Biodiversity* 49: 2455–2466. https://doi.org/10.1007/s12526-019-00962-y

Neves R.C. & Kristensen R.M. 2016. *Spinoloricus neuhausi* (Loricifera, Nanaloricidae), a new deep sea species from Galápagos Spreading Center. *Zoologischer Anzeiger* 265: 171–177. https://doi.org/10.1016/j.jcz.2016.01.001

Neves R.C., Reichert H., Sørensen M.V. & Kristensen R.M. 2016. Systematics of Phylum Loricifera: identification keys of families, genera and species. *Zoologischer Anzeiger* 265: 141–170. https://doi.org/10.1016/j.jcz.2016.06.002

Neves R.C., Kristensen R.M., Rohal M., Thistle D. & Sørensen M.V. 2019. First report of Loricifera from the North East Pacific Region, with the description of two new species. *Marine Biodiversity* 49: 1151–1168. https://doi.org/10.1007/s12526-018-0898-1

Neves R.C., Kristensen R.M. & Møbjerg N. 2021. New records on the rich loriciferan fauna of Trezen ar Skoden (Roscoff, France): description of two new species of *Nanaloricus* and the new genus *Scutiloricus*. *PLoS ONE* 16: e0250403. https://doi.org/10.1371/journal.pone.0250403

Pardos F. & Kristensen R.M. 2013. First record of Loricifera from the Iberian Peninsula, with the description of *Rugiloricus manuelae* sp. nov. (Loricifera, Pliciloricidae). *Helgoland Marine Research* 67: 623–638. https://doi.org/10.1007/s10152-013-0349-0

Shimabukuro M., Zeppilli D., Leduc D., Wenzhöfer F., Berg P., Rowden A.A. & Glud R.N. 2022. Intra- and inter-spatial variability of meiofauna in hadal trenches is linked to microbial activity and food availability. *Scientific Reports* 12: e4338. https://doi.org/10.1038/s41598-022-08088-1

Sørensen M.V., Rohal M. & Thistle D. 2018. Deep-sea Echinoderidae (Kinorhyncha: Cyclorhagida) from the Northwest Pacific. *European Journal of Taxonomy* 456: 1–75. https://doi.org/10.5852/ejt.2018.456

Sørensen M.V., Grzelak K., Kristensen R.M. & Herranz M. 2022. First account on Loricifera from New Zealand: a new species of *Pliciloricus*, and a Shira larva with postlarva representing the new genus and species *Patuloricus tangaroa* gen. et sp. nov. *Zoologischer Anzeiger* 299: 207–220. https://doi.org/10.1016/j.jcz.2022.06.004

Vincx M. 1996. Meiofauna in marine and fresh water sediments. *In*: Hall G.S. (ed.) *Methods for the Examination of Organismal Diversity in Soils and Sediments*: 214–248. CABI University Press, Cambridge, MA.