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Two new *Hyalella* (Amphipoda: Hyalellidae) from the Puna and High Andean ecoregions of South America

Два новых вида *Hyalella* (Amphipoda: Hyalellidae) из экорегионов Пуна и Высокие Анды, Южная Америка

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KEY WORDS: taxonomy, Crustacea, *Hyalella oscari* sp.n.*,* *Hyalella inca* sp.n.*,* molecular analysis, Argentina, Peracarida.

КЛЮЧЕВЫЕ СЛОВА: таксономия, Crustacea, *Hyalella oscari* sp.n., *Hyalella inca* sp.n., молекулярный анализ, Аргентина, Peracarida.

ABSTRACT: This paper presents two species of *Hyalella*, *H. inca* sp.n. and *H. oscari* sp.n., discovered in the Puna and High Andes regions of Argentina, South America. From these findings, the total of *Hyalella* species in Argentina is now 16. The newly discovered species are comprehensively described, illustrated, sequenced, and compared to morphologically similar and phylogenetically related species. New cytochrome c oxidase I (COI) sequence data were obtained for both new species, revealing their phylogenetic relationships, particularly to species from Lake Titicaca. These findings offer new insights into the *Hyalella* lineages in the High Andes and Puna ecoregions of South America, emphasizing the need for a detailed molecular genetic study using various genetic markers to explore them more deeply.

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РЕЗЮМЕ: Дано сравнительное иллюстрированное описание *Hyalella inca* sp.n. и *H. oscari* sp.n. из регионов Пуна и Высокие Анды, Аргентина. С учетом новых находок, число видов рода *Hyalella* в Аргентине составляет 16. Данные по сиквенсам цитохром-с-оксидазы I (COI) новых видов показывают их филогенетическое сходство с видами *Hyalella* из озера Титикака. Для дальнейшего построения системы рода *Hyalella* необходимы дальнейшие молекулярно-генетические исследования с использованием разнообразных генетических маркеров.

Introduction

Peracarid Amphipoda comprise more than 170 families and approximately 10,160+ living species (although the actual number may be closer to 28,000–30,000 species) [Schram, Koenemann, 2021]. These organisms have colonized almost all aquatic ecosystems, and specially marine ones, as their greatest diversity and abundance are recorded in shallow-water marine benthic environments [Arfianti, Costello, 2020]. Additionally, members of the Talitridae Rafinesque, 1815 (superfamily Talitroidea) have successfully invaded terrestrial and semi-terrestrial habitats. Amphipoda is the most ubiquitous group of Peracarid crustaceans in freshwater ecosystems worldwide. This is particularly evident in ancient lakes such as the Titicaca, Baikal, and the Caspian Sea, where significant amphipod species radiations have been observed [Wellborn *et al*., 2015; Zapelloni *et al*., 2021].

The groups of freshwater amphipods are diverse, and each lineage has its own history of colonizing inland waters from marine ancestors. Currently, only two of the 10 known families of the superfamily Hyaloidea inhabit inland freshwater ecosystems, Hyalellidae Bulycheva, 1957 (one genus only, *Hyalella* Smith, 1874) and Chiltoniidae J.L. Barnard, 1972, with nine genera. Understanding the validity of taxa and relationships among Hyalellidae and Chiltoniidae have been the subject of numerous revisions and consequent changes of status. The morphological

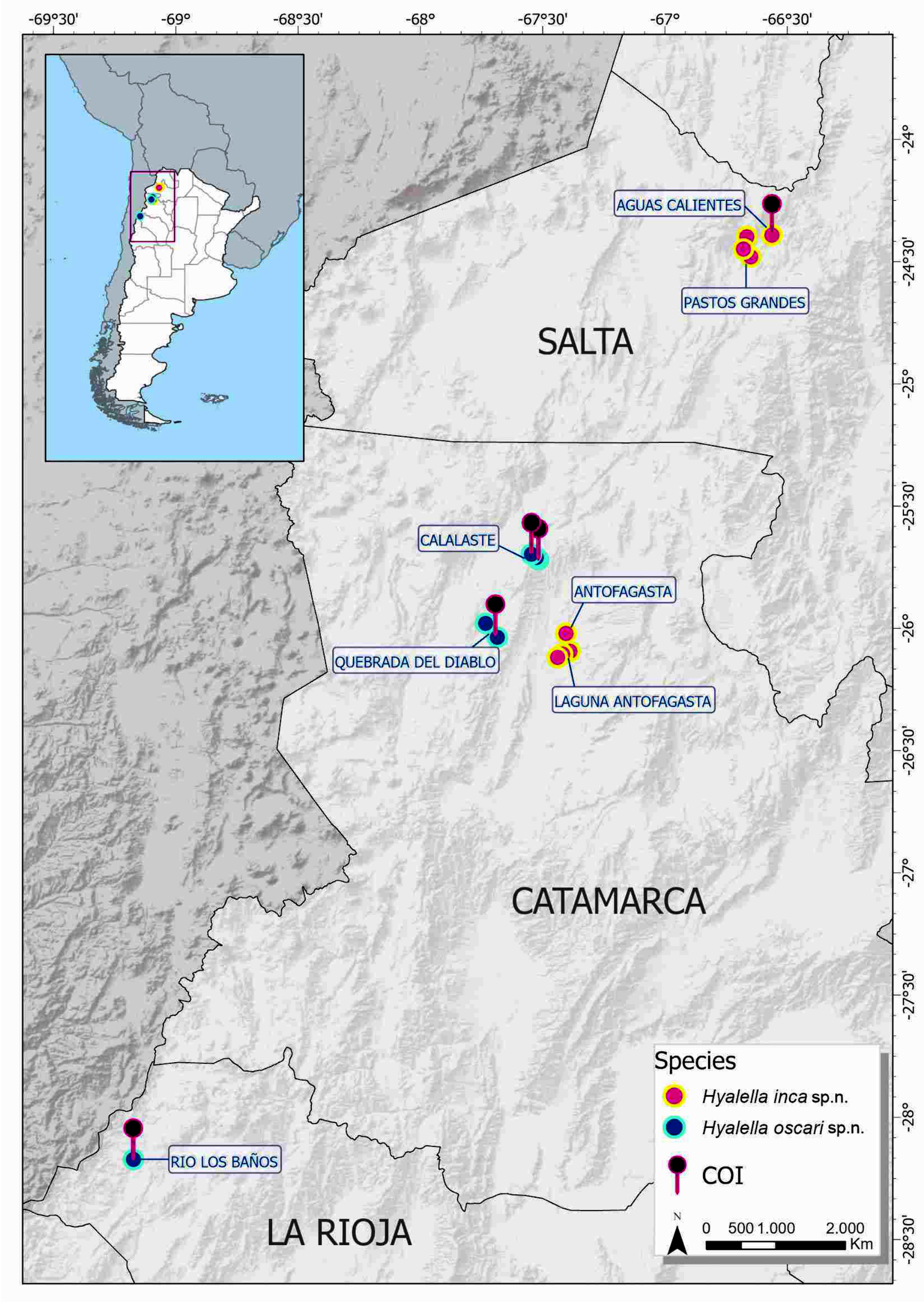

Fig. 1. Distribution map depicting each newly described species. The labeled points identified as COI indicate the localities subjected to molecular analysis.

Рис. 1. Карта распространения новых видов *Hyalella*. Выделены местонахождения, по материалам из которых был проведен молекулярный анализ.

similarity between taxa of both families is such that, in the past, some chiltoniids were originally attributed to the genus *Hyalella* or were grouped together with *Hyalella* in the family Hyalellidae. Thus, the type-species of *Chiltonia* (Chiltoniidae) is *Hyalella mihiwaka* Chilton 1898, original designation.

The knowledge of the diversity of freshwater amphipods is poor in the southern hemisphere, where Chiltoniidae and the great majority of Hyallellidae species are distributed. Chiltoniidae species are distributed in Australia, Tasmania, New Zealand, and South Africa, whereas *Hyalella* is endemic to America. A recent phylogenetic analysis based on data from two nuclear genes and one mitochondrial gene showed that Hyalellidae/Chiltoniidae conform a monophyletic group that could have possibly diverged from its marine ancestors during the Cretaceous

[Cannizzaro, Berg, 2022]. This early separation laid the foundation for the intricate evolutionary history of the genus *Hyalella*.

Hyalella is a complex genus with species-groups exhibiting minimal morphological differences and large hidden diversity. Numbering over 100 species [Mussini *et al.*, 2024], they are exclusively found in the Neotropical and Nearctic regions, inhabiting both epigean (rivers, streams, ponds, lakes and peatbog) and hypogean (caves, hyporheic, and hypotelminorheic habitats) freshwater systems [Grosso, Peralta, 1999]. In the South American High Andes, *Hyalella* amphipods play an essential role in aquatic macroinvertebrate communities. They frequently serve as parasite intermediate hosts, and play a critical role in aquatic food webs, acting as conduits of nutrients and energy to higher trophic levels [Väinölä *et al.*, 2008]. Particularly, in the Argentine Puna, a part of the Andean plateau, *Hyalella* is one of the most abundant groups of invertebrates [Rodrigues Capitulo *et al.*, 2014; Nieto *et al.*, 2017, 2018].

A recent molecular characterization of the *Hyalella* species found in Lake Titicaca has revealed at least five distinct evolutionary lineages [Adamowicz *et al.*, 2018]. Four *Hyalella* species have been identified in the Puna and High Andean ecoregions, along with 11 morphospecies [Hankel *et al.*, 2023]. These studies highlight the significant but underexplored diversity of *Hyalella* in mountain regions. Understanding this diversity is increasingly important in light of climate change [Tomikawa *et al.*, 2023; Oberdorff, 2022] and anthropogenic phenomena that result in a decline in water quality, such as *Hyalella* habitat fragmentation [Peralta, Isa-Miranda, 2023] and alterations in the structure of aquatic macroinvertebrate communities among other factors caused by human activities. Furthermore, the insights gained have practical applications, with *Hyalella* species serving as valuable indicators in monitoring programs [Graça *et al.*, 2002; Pineda-Alarcón *et al.*, 2023], a role that becomes increasingly critical in the face of the mounting threats to freshwater systems, particularly in the High Andean wetlands [Izquierdo *et al.*, 2018; Peralta, Isa-Miranda, 2023].

In this study, we describe two new *Hyalella* species from the Puna and High Andean regions, provide genetic data, and evaluate their phylogenetic relationships with congeners.

Materials and Methods

SAMPLING AND MORPHOLOGICAL EXAMINATION

The study area (Fig. 1), located in the Puna and High Andean ecoregions of NW Argentina, covers approximately 14,210,000 ha and includes parts of the Jujuy, Salta, Catamarca, La Rioja, and San Juan provinces. It encompasses elevations ranging from 3,200 to approximately 6,900 m above sea level (m a.s.l.), with peatlands covering an estimated 110,873 ha (0.78% of the total area) at elevations between 3,005 and 5,141 m a.s.l., with an average elevation of 4,056 m a.s.l. [Izquierdo *et al.*, 2015]. The climate is characterized by extreme aridity, with mean annual precipitation varying from less than 100 mm in the southwest to 400 mm in the northeast of the region. The average annual temperature ranges from 9°C to –4°C [Cabrera, 1976].

A geographic distribution map was digitally created using a hillshade model derived from the U.S. Geological Survey (USGS) elevation data [https://www.usgs.gov/]. Argentina and South America boundary shapefiles from the National Geographic Institute (IGN) [https://www.ign.gob.ar/] were integrated into the QGIS 3.34 Geographic Information System for its production.

The specimens of *Hyalella* were collected using a net (mesh of 300 μm) and immediately fixed in the field in 96% ethanol for molecular studies. Upon arrival at the laboratory, several specimens were transferred to 80% ethanol and dissected in Brunson solution (2 part distilled water, 1 part glycerina, and 1 part alcohol at 96%) under a stereomicroscope (Nikon 84978). The appendages were examined and illustrated using a Leitz Dialux camera lucida. The drawings were digitized with CorelDRAW® Graphics Suite 2020. Body measurements were performed from the tip of the head to the tip of the telson. Photographs of the habitus were taken using a stereomicroscope LEICA M165 C coupled with a LEICA DMC 2900 digital camera.

For scanning electron microscope (SEM) analyses of cuticular extensions, male specimens of *H. oscari* sp.n. FML-CRUST-01339 and *H. inca* sp.n. FML-CRUST-01340 were dehydrated in a graded ethanol series after ultrasonic cleaning for 30 s in a liquid medium. The samples were dried with carbon dioxide in a critical-point dryer, sputter-coated with gold, and examined using a Zeiss SUPRA 55-VP SEM.

The description of the new species was made based on previous taxonomic works on *Hyalella* species [Grosso, Peralta, 1999; González, Watling, 2001, 2003; Peralta, Isa-Miranda 2019; González *et al.*, 2020]. The terminology for setae and other cuticular structures follows Zimmer *et al.* [2009] and Isa-Miranda & Peralta [2023]. Specimens are deposited in the Crustaceans Collection of Fundación Miguel Lillo (FML) and Instituto de Biodiversidad Neotropical (IBN, CONICET-UNT), Tucumán, Argentina.

GENETIC DATA

We combined two distinct sources of data. We collected specimens of *Hyalella oscari* sp.n. and *Hyalella inca* sp.n. in peatlands, from Puna and High Andes ecoregions of Argentina. Additionally, we obtained COI sequences for species of Chiltoniidae, Dogielinotidae, Hyalellidae, Hyalidae, Najnidae, Talitridae, Pseudocrangonyctidae, and Brevitalitridae from the GenBank database.

Total genomic DNA was extracted from ethanol-preserved specimens and purified using the salting-out protocol. In this protocol 300 uL TNES lysis buffer (50 mM Tris, 400 mM NaCl, 20 mM EDTA, 0.5% SDS) and 16 uL proteinase K (20 mg/mL final concentration) were added to each sample. Samples were vortexed for 30 s, and the tube spun down for 5 min at 14000 rpm. Tubes were incubated at 51 °C overnight. Thereafter, 300 uL NaCl (5 M) was added to each sample. The supernatant was transferred to fresh tubes. An equal volume of 99% ethanol was added to each sample, mixed well, and incubated at –4 °C for 1 h. Samples were then centrifuged for 5 min at 14000 rpm. The pellet was washed with 70% ethanol, dried, and finally resuspended in 20–50 uL sterile dH2O.

The mitochondrial Cytochrome *c* Oxidase subunit (COI) DNA was amplified by the polymerase chain reaction (PCR) method using the primer sets LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 ((5'-TAAACTTCAGGGTGACCAAAAAATCA-3') [Folmer *et al.*, 1994]. Amplifications were carried out in 25 μL reactions: 14.8 μL ddH2O, 5 μL 10X Taq PCR buffer (containing 20 mM MgCl2), 1.25 μL of each 10 μM primer, 0.5 μL 10 μM dNTPs, 0.2 μL Taq DNA polymerase (Promega), and 2 μL genomic DNA template.

Fig. 2. Habitus of *Hyalella oscari* sp.n. from the type locality: *a* — male holotype, FML-CRUST 01337; *b* — preserved male and female in copulation, FML-CRUST 01338.

Рис. 2. Внешний вид *Hyalella oscari* sp.n. из типового местонахождения: *a* — голотип самец, FML-CRUST 01337; *b* — копулирующие самец и самка, FML-CRUST 01338.

Amplification cycles were performed on a Biometra Tadvance (Analytik Jena) as follows: 4 °C for 3 min; 30 amplification cycles of 94 °C for 45 s, 45 °C for 45 s, 72 °C for 1 min; and a final step for 5 min at 72 °C. Amplification products were visualized on 1% agarose electrophoresis. All sequencing reactions were performed by Macrogen South Korea Inc (https://dna.macrogen.com/).

Chromatograms were edited and visualized using SeqTracer [Stucky, 2012]. For subsequent analysis the COI sequences were aligned using the MUSCLE algorithm (Multiple Sequence Comparison by Log-Expectation, Edgar 2004).

PHYLOGENETIC ANALYSIS

The phylogenetic analyses were conducted based on sequences of mithochondrial COI. *Pseudocrangonyx yezonis* [Akatsuka, Komai, 1922] was selected as the outgroup of the analyses. SeqTrace software [Stucky, 2012] was employed for data analysis, encompassing the alignment and quality check of both forward and reverse sequences. Furthermore, manual inspection of chromatograms was carried out to address any ambiguities in base pairs. Additionally, AliView [Larsson, 2014] was utilized for the alignment and refinement of the COI genes. Phylogenetic relationships were constructed by Bayesian Inference (BI) and Maximum Likelihood (ML), partitioned by the 1st, 2nd and 3rd codon positions for COI. The evolutionary model was selected based on Tomikawa *et al.* [2023]. For COI 1st codon HKY+F+G4; for COI 2nd codon, TNe+I+G4; for COI 3rd codon, TVM+F+I+G4. ML phylogenies were conducted using IQ-TREE software [Nguyen *et al.*, 2015] with 1000 ultrafast bootstrap replicates [Hoang *et al.*, 2018]. BI tree and

Bayesian posterior probabilities were estimated using MrBayes [version 3.2.7, Ronquist *et al.*, 2012], with Markov chains of 10 million generations.

Results

SYSTEMATICS

Order AMPHIPODA Latreille, 1816
Suborder SENTICAUDATA Lowry et Myers, 2013
Superfamily HYALOIDEA Bulycheva, 1957
Family HYALELLIDAE Bulycheva, 1957
Genus *Hyalella* S.I. Smith, 1874

***Hyalella oscari* sp.n.**

Figs 2–7.

Hyalella sp. 6 — Hankel *et al.,* 2023

MATERIAL EXAMINED. **Holotype**. **Argentina**: 1 ♂, Catamarca Province, Calalaste, –25.70791° S –67.52827° W, alt. 4429 m a.s.l, 16.X.2020, J. Rodriguez leg., (FML-CRUST 01337), 9.6 mm. **Paratypes**: 1 ♀ measuring 6.18 mm, and 2 ♂♂ and 1 ♀ (FML-CRUST 01338), 2 ♂♂ and 2 ♀♀ (IBN-EcoPP-25D), same data as holotype. Additional material: **Argentina**: 5 ♂♂ and 4 ♀♀, La Rioja Province, Río Los Baños, –28.1725° S –69.17408° W, 3915 m a.s.l., 24.II.2016, 3 ♂♂ and 2 ♀♀, Catamarca Province, Quebrada del Diablo, –26.02902778° S –67.69330556° W, 3955 m a.s.l, 15.V.2017, 3 ♂♂, Calalaste, –25.7135° S –67.52336° W, 4392 m a.s.l, 15.XII.2015, J. Rodriguez leg.

DIAGNOSIS. Body smooth. Antenna II slightly longer than head and longer than Antenna I. Maxilla I palp with a medial constriction and with two plumose setae on tip. Gnathopod I propodus with sinuous palm margin exhibiting slight medial concavity; palm angle with four cuspidate setae. Two short setae placed subdistally on outer surface of basis of pereiopod 7. Sternal gills present on pereonites 3 to 7. Epimeral plate 1 rounded, plates 2 and 3 slightly acuminate. Uropod 1 not sexually-dimorphic.

TYPE LOCALITY AND REFERENCE SEQUENCES. Calalaste peatbog, –25.70791° S –67.52827° W, 4429 m a.s.l, Catamarca Province, Argentina. GenBank accession numbers: *COI*: OR726343, OR726347, OR726345, OR726346 (Fig. 1).

ETYMOLOGY. The species was named in honour of the first author's grandfather.

DESCRIPTION OF MALE

Body: Stout and smooth. Maximum length observed 9.78 mm. *Head*: Eye ellipsoid, pigmented.

Antenna I: shorter than antenna II but slightly longer than its peduncle. Peduncular segments 1-3 with few simple setae and numerous plumose setae C2, alongside microsetae (Ib type). The flagellum consists of nine articles with groups of simple setae A1, additionally featuring distally positioned aesthetascs, occurring between articles 5–7 (Fig. 3*a*, *b*).

Antenna II: longer than Antenna I, with its peduncle approximately equal to the length of the head. Peduncular segment 4 much shorter than 5. Peduncular segment 3 with a plumose thin seta; segments 3–5 with distal and medial simple A1 or plumose setae C2. Flagellum comprises 11 articles, each bearing groups of simple setae (Fig. 3*c*, *d*).

Upper lip: ordinary, with minute setae on the distal part (Fig. 4*a*).

Mandible: Right mandible incisor 6-denticulate, lacinia mobilis complex bifurcate, setal row with 4 pappose setae (Fig. 4*b*). Left mandible incisor 5-denticulate, lacinia mobilis 4-denticulate, setal row with six pappose setae (Fig. 4*c*). Both mandibles with well-developed triturative molars.

Lower lip: ordinary, outer lobes covered with minute setae (Fig. 4*d*).

Maxilla I (Fig. 4*e*): palp unsegmented, long and narrow, with a medial constriction, reaching more than half the length of the distance between the base of the palp and the apex of the outer plate, with two plumose distal setae on tip. Outer plate with nine serrate setae type F4, some of them larger and spatulate, as can be observed in detail in the SEM image (Fig. 4*e*). Inner plate shorter than outer one, with two apical papposerrate setae, and several marginal setules.

Maxilla II (Fig. 4*f*): Inner plate subequal in length to the outer with 1 strong pappose seta on inner margin; outer and inner plates with few hair-like setae.

Maxilliped (Fig. 4*g*): Inner plate longer than wide, with three stout robust cuspidate B1 setae, accompanied by additional pappose setae and setules on both apex and margins. Outer plate with simple setae on inner and distal margins. Palp 4-segmented, second one as long as wide; segment 4 short and unguifom; segments 1–3 with simple setae at outer distal end; segment 3 distally ornamented with denticles of type t5, featuring setae of both simple type A1 and serrated type F3.

Gnathopod I (Fig. 5*a*): subchelate. Coxal plate longer than wide, with microtrichs (type Ia) along margin. Basis with four simple setae on posterior margin. Propodus (Fig. 5*b*) hatchet-shaped, longer than its maximum width, with group of slender simple setae at anterodistal corner; inner face with oblique row of seven serrate setae (F3) arranged in two groups; palmar margin sinuous; palm angle equipped with four cuspidate setae and comb/setose-scales. Dactylus claw-like, with denticles on the inner margin. Additionally, microtrichs of type Ib are observed on the dactylus and surface of the propodus. Palmar Index (sensu Ruffo [1973]) = 0.49.

Gnathopod II (Fig. 5*c*): subchelate. Basis approximately three times longer than its maximum width, bearing four groups of setae at posterior margin. Basis, ischium and merus each with group of setae on postero-distal angle. Posterior lobe of carpus with pectinate border lined with row of serrate setae. Propodus ovate; palm margin oblique, slightly longer than posterior margin; palm margin with several strong, short to medium-length setae; palm angle with two cuspidate setae B5 with accessory seta and comb/setose scales. Dactylus claw-like, congruent with palm, carrying single thin plumose seta dorsally. Palmar Index (sensu Ruffo [1973]) = 0.34.

Pereiopods 3 and 4 (Fig. 6*a*, *b*): similar in size and shape. Coxal plates: pereiopod 3 longer than wide; pereiopod 4 excavated posteriorly, longer than wide; both coxal plates with margins lined with thin simple setae (type Ia); posterior margin of basis, merus, carpus and propodus with simple or cuspidate setae; dactylus short, less than half length of propodus.

Pereiopods 5–7 (Fig. 6*c*–*e*): pereiopod 5 notably shorter than pereiopods 6 and 7, which are subequal in length. Coxal plates: pereiopod 5: wider than long, posterior lobe deeper than anterior; pereiopod 6: as long as wide with a significantly reduced anterior lobe; pereiopod 7: wider than long; all coxal plates with thin, simple setae along their margins (type Ia). Basis: posterior margin expanded, notably more in pereiopod 7 than in pereiopods 5 and 6, finely serrated; additionally, the seventh pereiopod has two reduced setae subdistally on outer surface; anterior margin of basis of pereiopod 5 bearing group of four plumose setae. Anterior and posterior margins of ischium, merus, carpus, and propodus with simple or cuspidate setae. Dactylus short, like pereiopods 3 and 4.

Coxal gills: sacciform, present on gnathopod II to pereiopod 6 (Fig. 6*a*–*d*). Sternal gills tubular (Fig. 6*d*), present on pereonites 3 to 7.

Pleopods: Biramous, similar; peduncle shorter than rami, with retinacula; rami multi-annulated and bearing long plumose setae.

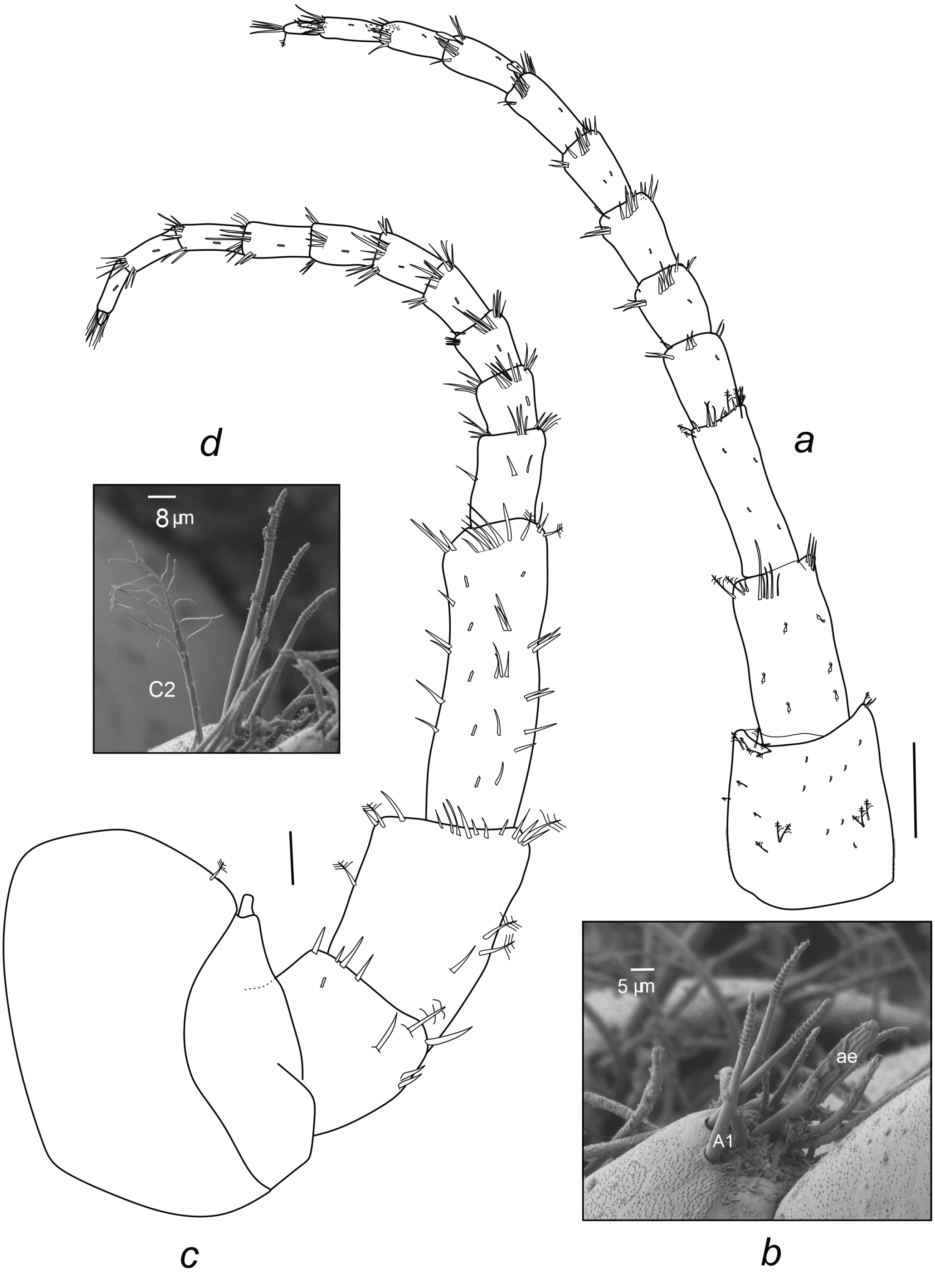

Fig. 3. *Hyalella oscari* sp.n., male holotype, FML-CRUST 01337: *a* — antenna I; *b* — SEM picture showing an article of the flagellum of antenna I featuring a1-type setae and 1 aesthetasc; *c* — antenna II; *d* — SEM picture showing the setae of a segment of the peduncle of antenna II. Scale bars: 0.1 mm.

Рис. 3. *Hyalella oscari* sp.n., голотип самец, FML-CRUST 01337: *a* — антенна I; *b* — членик флагеллума антенны I с щетинками типа a1 и 1 эстетаском, СЭМ; *c* — антенна II; *d* — щетинки сегмента стебелька антенны II, СЭМ. Масштаб: 0,1 мм.

Uropod 1 (Fig. 7*a*): Peduncle longer than rami, with four proximal cuspidate setae on dorsal surface and two other distal cuspidate setae all aligned in a longitudinal row; rami subequal in length; outer ramus with three dorsal and four distal cuspidate setae; inner ramus with two dorsal and five distal cuspidate setae, without modified curved seta on inner side. Microtrichs of type Ib on both peduncle and rami.

Uropod 2 (Fig. 7*b*): shorter than uropod 1. Peduncle longer than rami, with three dorsal cuspidate setae aligned in a longitudinal row and other cuspidate setae on dorsolateral and dorsomedial distal margin; inner ramus with two dorsal and six distal cuspidate setae, one of them longer than rest; outer ramus with one dorsal and three distal cuspidate setae, one of them longer than rest. Microtrichs of type Ib on peduncle and rami.

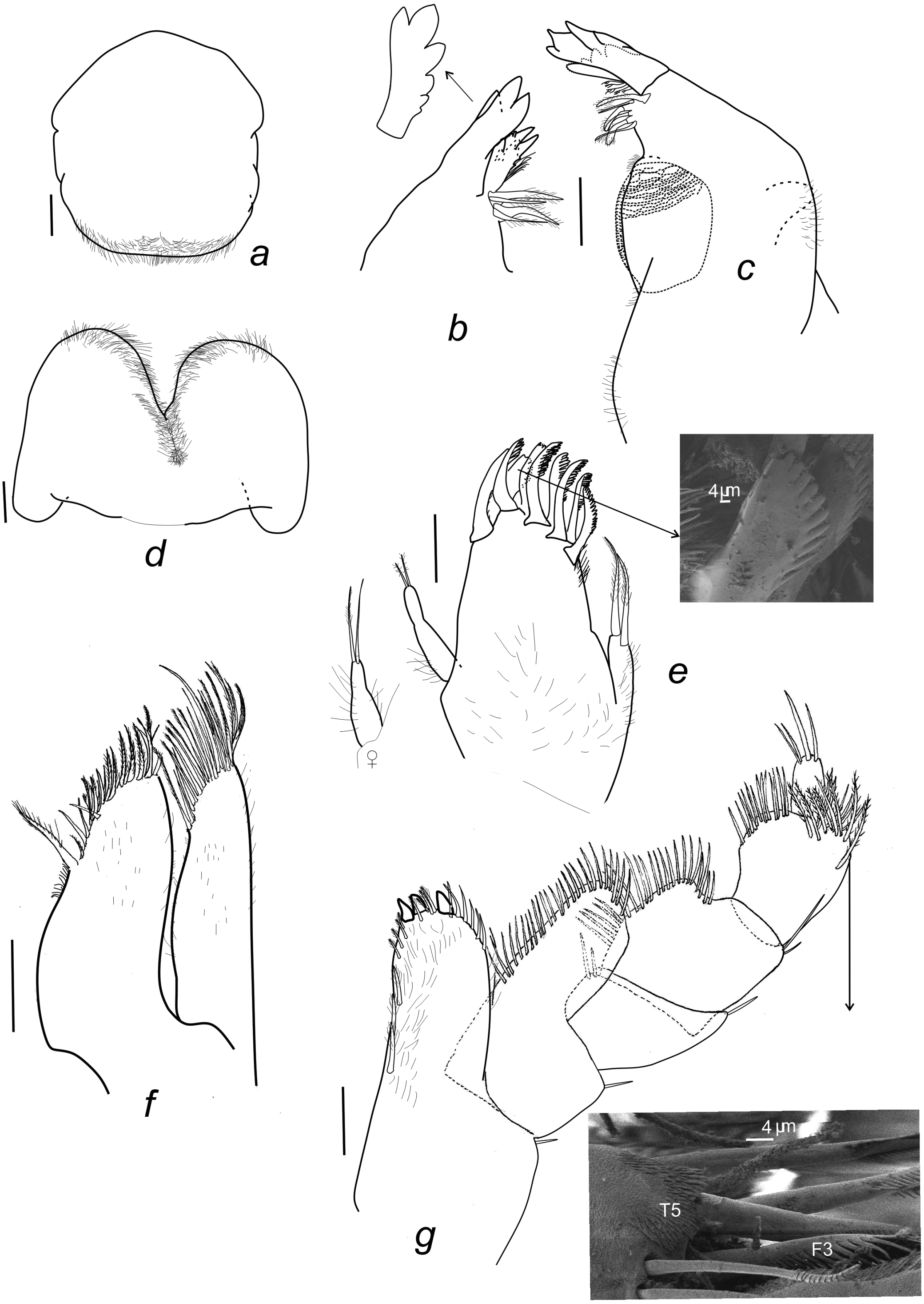

Fig. 4. *Hyalella oscari* sp.n., male holotype, FML-CRUST 01337: *a* — upper lip; *b* — right mandible, with detail of incisor; *c* — incisor and lacinia mobilis of left mandible; *d* — lower lip; *e* — maxilla I, with detailed view of the large spatulated seta; to the left: detail of the palp of maxilla I in the female paratype; *f* — maxilla II; *g* — maxilliped, SEM image showing details of article 3 of the palp. Scale bars: 0.1 mm.

Рис. 4. *Hyalella oscari* sp.n., голотип самец, FML-CRUST 01337: *a* — верхняя губа; *b* — правая мандибула, отдельно показана деталь строения резца; *c* — резец и подвижный зубец левой мандибулы; *d* — нижняя губа; *e* — максилла I, по стрелке показаны детали строения большой лопатчатой щетинки, слева — щупик максиллы I паратипа самки; *f* — максилла II; *g* — максиллипед, отдельно показана вершина членика 3 щупика, СЭМ. Масштаб 0,1 мм.

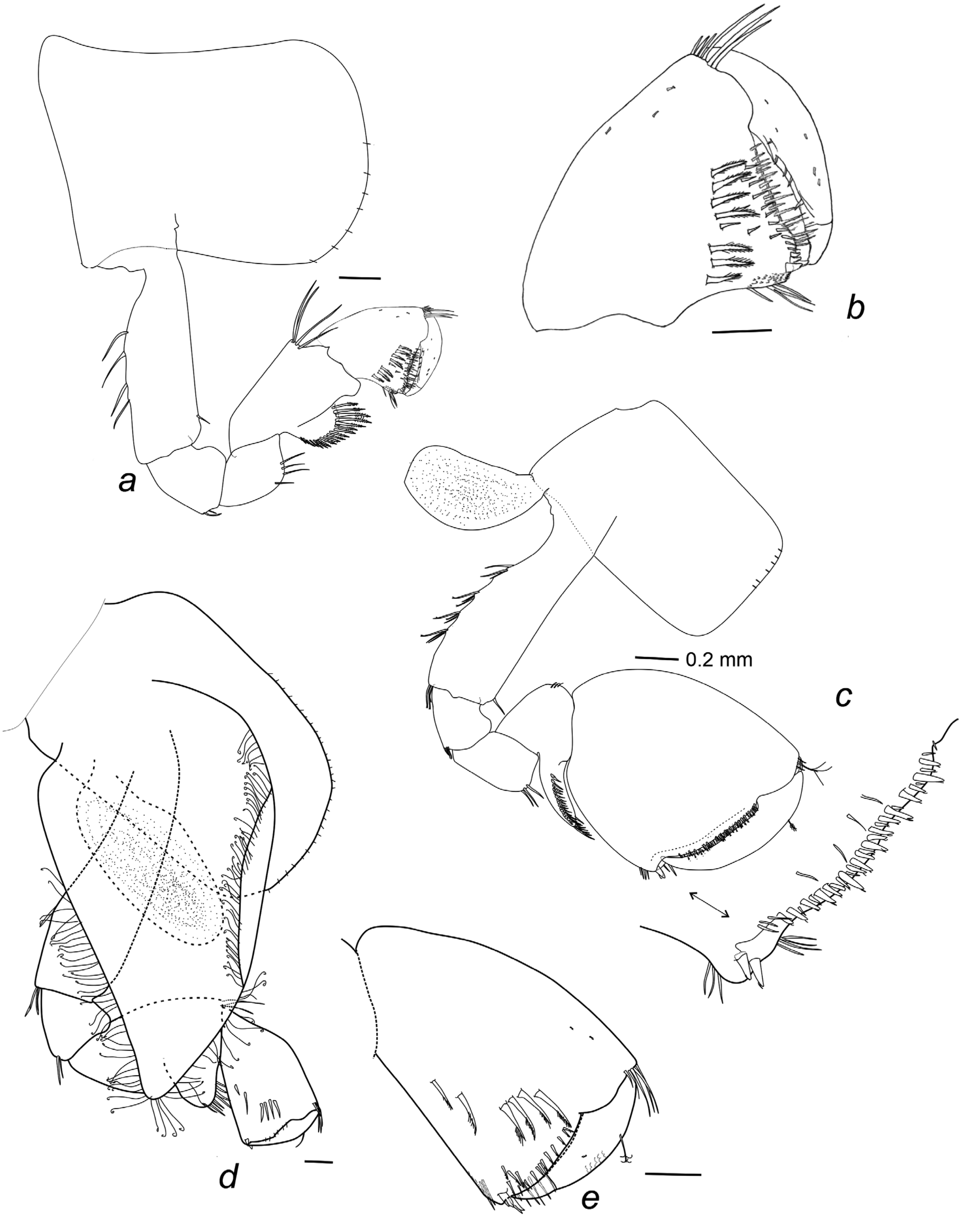

Fig. 5. *Hyalella oscari* sp.n., male holotype, FML-CRUST 01337 (*a–c*) and female paratype FML-CRUST 01338 (*d–e*): *a* — gnathopod I; *b* — propodus of gnathopod I; *c* — gnathopod II, with inset of palm margin; *d* — gnathopod II; *e* — propodus of gnathopod II. Scale bars: 0.1 mm.

Рис. 5. *Hyalella oscari* sp.n., голотип самец, FML-CRUST 01337 (*a–c*) и паратип самка FML-CRUST 01338 (*d–e*): *a* — гнатопод I; *b* — проподит гнатопода I; *c* — гнатопод II, отдельно показано вооружение края лопасти; *d* — гнатопод II; *e* — проподит гнатопода II. Масштаб 0,1 мм.

Uropod 3 (Fig. 7*c*): shorter than peduncle of uropod 2. Peduncle much wider than ramus, as long as wide, with five strong cuspidate distal setae and other six thin simple setae on ventral face; ramus stout, shorter than peduncle, apex with one simple seta and five strong cuspidate setae.

Telson (Fig. 7*e*): wider than long, entire, with many thin simple setae on distal margin and microtrichs type Ib; dorsal surface with a scale pattern. The telson of a male paratype features only two simple setae at each side (Fig. 7*d*).

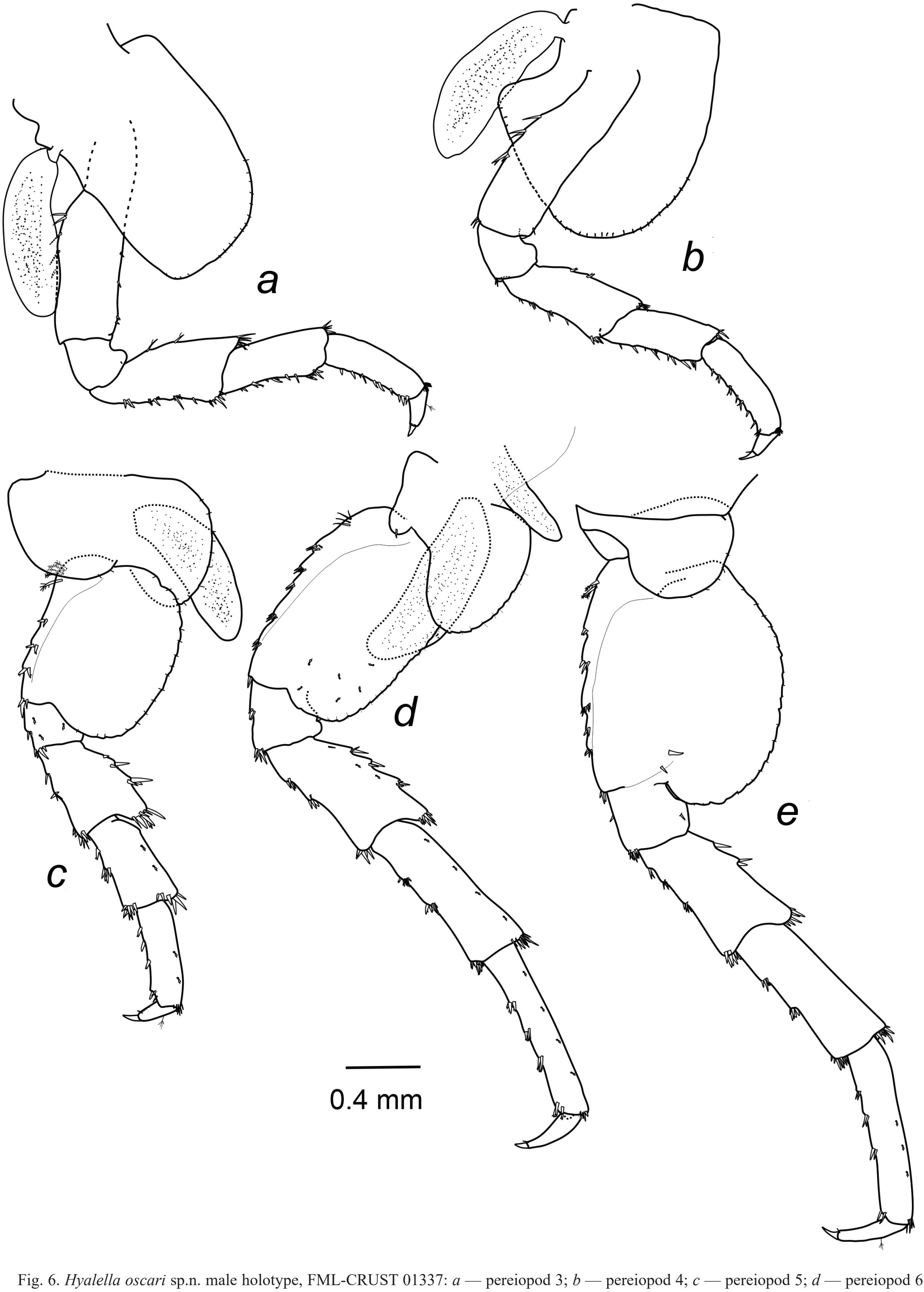

Fig. 6. *Hyalella oscari* sp.n. male holotype, FML-CRUST 01337: *a* — pereiopod 3; *b* — pereiopod 4; *c* — pereiopod 5; *d* — pereiopod 6; *e* — pereiopod 7.

Рис. 6. *Hyalella oscari* sp.n., голотип самец, FML-CRUST 01337: *a* — переопод 3; *b* — переопод 4; *c* — переопод 5; *d* — переопод 6; *e* — переопод 7.

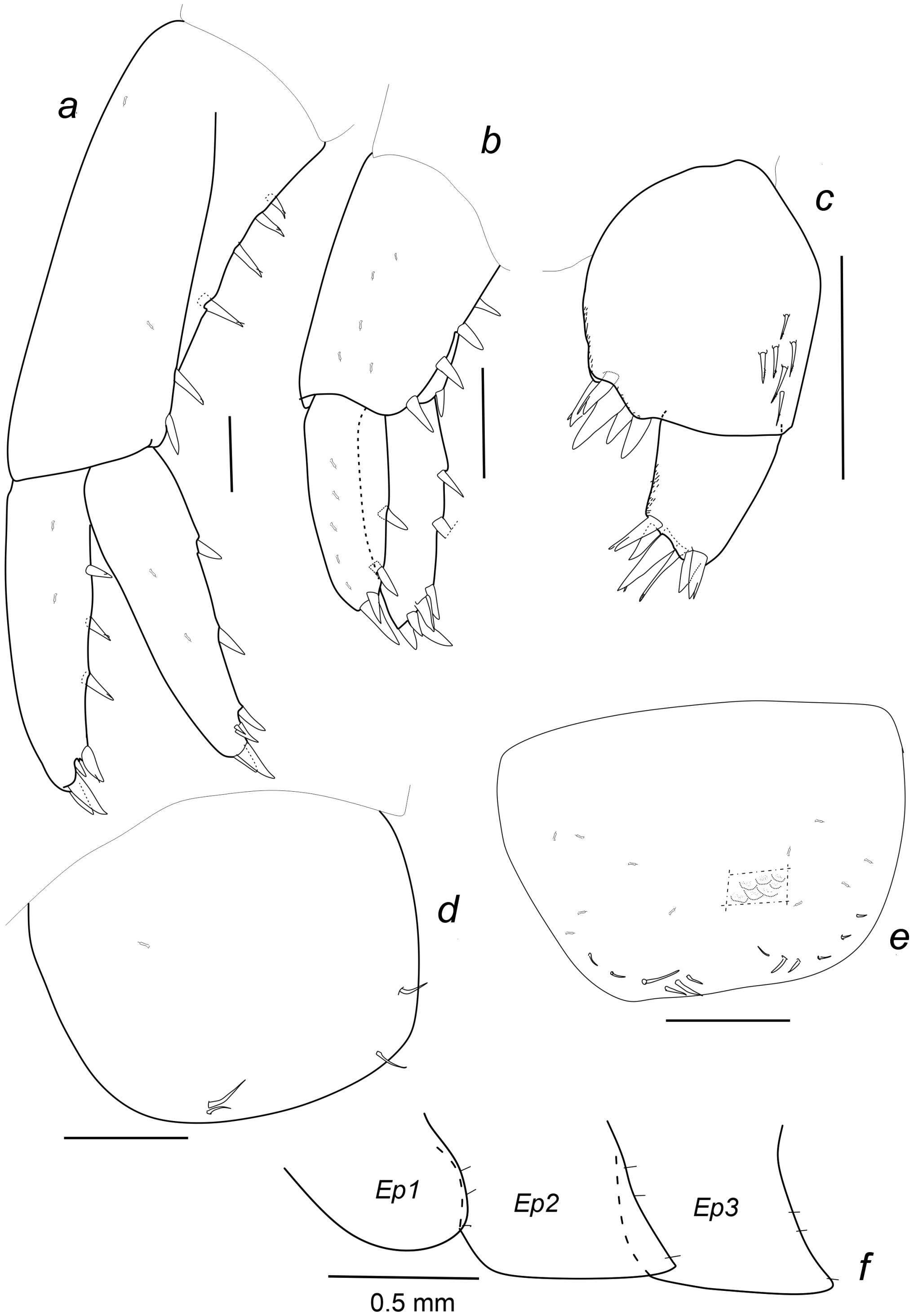

Fig. 7. *Hyalella oscari* sp.n., male holotype, FML-CRUST 01337: *a* — uropod 1; *b* — uropod 2; *c* — uropod 3; *d* — telson of male paratype; *e* — telson; *f* — epimeral plates. Scale bars: 0.1 mm.

Рис. 7. *Hyalella oscari* sp.n., голотип самец, FML-CRUST 01337: *a* — уропод 1; *b* — уропод 2; *c* — уропод 3; *d* — тельсон паратипа самца; *e* — тельсон; *f* — пластинки эпимер. Масштаб 0,1 мм.

Epimeral plates (Fig. 7*f*)*:* Plate 1 is rounded posterodistally, while Plates 2 and 3 are slightly acuminate; all posterior margins bear a few setules.

Intraspecific Variability in males: some males (IBN-EcoPP-23C) exhibit six setae on the inner face of gnathopod I propodus, while others display nine, in contrast to the seven displayed by the holotype. Variability was observed also in the setae count at telson and uropod 2 apices; in one of the male paratypes (FML-CRUST 01338), the telson exhibited only two simple setae on each side (Figs. 7*d*, *e*), while the inner ramus of uropod 2 apex carries seven setae.

Fig. 8. *Hyalella inca* sp.n., male holotype, FML-CRUST 01335. Habitus, lateral view.
Рис. 8. *Hyalella inca* sp.n., голотип самец, FML-CRUST 01335. Внешний вид, латератльно.

FEMALE (PARATYPES). Maximum body length observed 7.76 mm. Habitus similar to male except for the following characters: palp of maxilla I shorter, with two significantly longer setae at apex compared to male (Fig. 4*e*). Gnathopods I and II closely resemble each other in size and shape, inner face of gnathopod I displaying seven serrate setae, while gnathopod II features six. Gnathopod II differs from its male counterpart in both shape and the relatively smaller size of its propodus (Fig. 5*d*, *e*). Oostegites broad and subtriangular, with larger curled setae on the margins (Fig. 5*d*).

Hyalella inca sp.n.
Figs 8–13.

Hyalella aff. puna — Hankel *et al.*, 2023

MATERIAL EXAMINED. **Holotype. Argentina**: ♂, Catamarca Province, Laguna Antofagasta, –26.1058° S –67.42058° W, alt. 3338 m a.s.l, 13.XII.2015, J. Rodríguez leg., (FML-CRUST 01335), 9.8 mm. **Paratypes**: 1 ♀ measuring 7.35 mm, 2 ♂♂ and 1 ♀ (FML-CRUST 01336); 4 ♂♂and 2 ♀♀ (IBN-EcoPP-23C); same data as holotype. Additional material: **Argentina**: 5 ♂♂ and 1 ♀, Salta Province, Aguas Calientes, –24.39164° S –66.56256° W, 3795 m a.s.l., 3.II.2014, 3 ♂♂ and 2 ♀♀, Pastos Grandes, –24.42852° S –66.67161° W, 4048 m a.s.l, 3.II.2014, 4 ♂ ♂and 2 ♀♀, Catamarca Province, Laguna Antofagasta, –26.10413889° S –67.4185° W, 3331 m a.s.l, 14.XII.2015. J. Rodríguez leg.

DIAGNOSIS. Body smooth. Palp of maxilla I asymmetrical, with right branch bearing two setae on tip vs. only one on left branch. Sternal gills present on pereonites 2 to 7. Epimeral plate 1 rounded; plates 2 and 3 acuminate. Uropod 3 elongated, peduncle longer than ramus; ramus thin, approximately twice as long as wide. Uropod 1 sexually-dimorphic, with male inner ramus displaying a distinct modified seta (‘copulatory spine’ of Bousfield, 1996).

TYPE LOCALITY AND REFERENCE SEQUENCES. Laguna Antofagasta, –26.1058° S –67.42058° W, 3338 m a.s.l, Catamarca Province, Argentina. GenBank accession numbers: *COI*: OR726344 (Fig. 1).

ETYMOLOGY. The term “Inca” in the specific epithet should be interpreted as a noun in conjunction with the generic name, in reference to the Inca Empire, which historically occupied vast areas of South America, including the highland and Puna regions.

DESCRIPTION OF MALE

Body: smooth. Maximum length observed 9.87 mm. *Head*: Eye ellipsoid, pigmented.

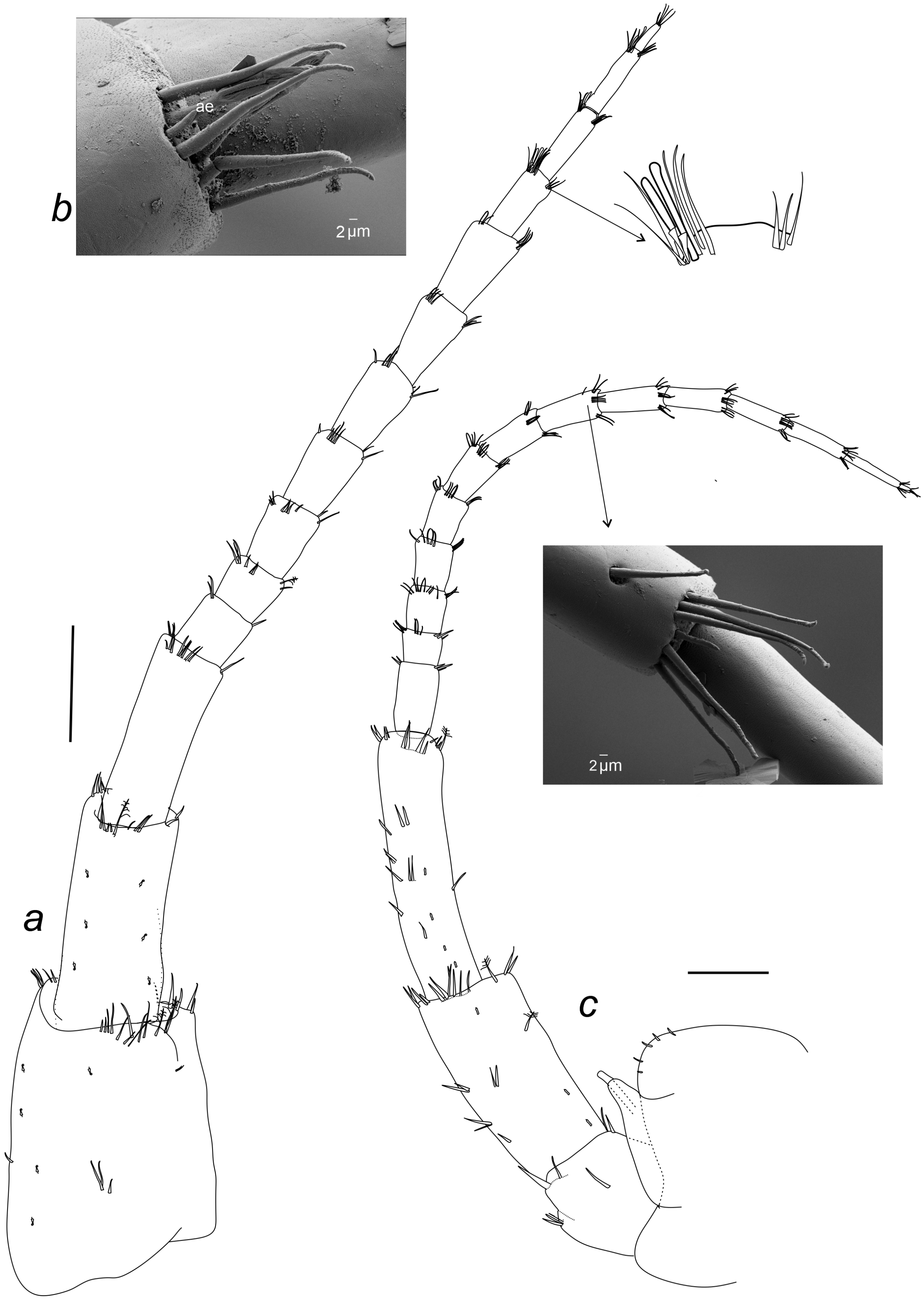

Fig. 9. *Hyalella inca* sp.n., male holotype, FML-CRUST 01335: *a* — antenna I, with details of its distal part; *b* — SEM picture showing an article of the flagellum of antenna I featuring a1-type setae and two aesthetascs; *c* — antenna II, SEM photo detailing its setae.

Рис. 9. *Hyalella inca* sp.n., голотип самец, FML-CRUST 01335: *a* — антенна I, отдельно показаны детали строения одного из дистальных члеников; *b* — членик флагеллума антенны I с щетинками типа a1 и 2 эстетасками, СЭМ; *c* — антенна II, отдельно показаны щетинки одного из члеников, СЭМ.

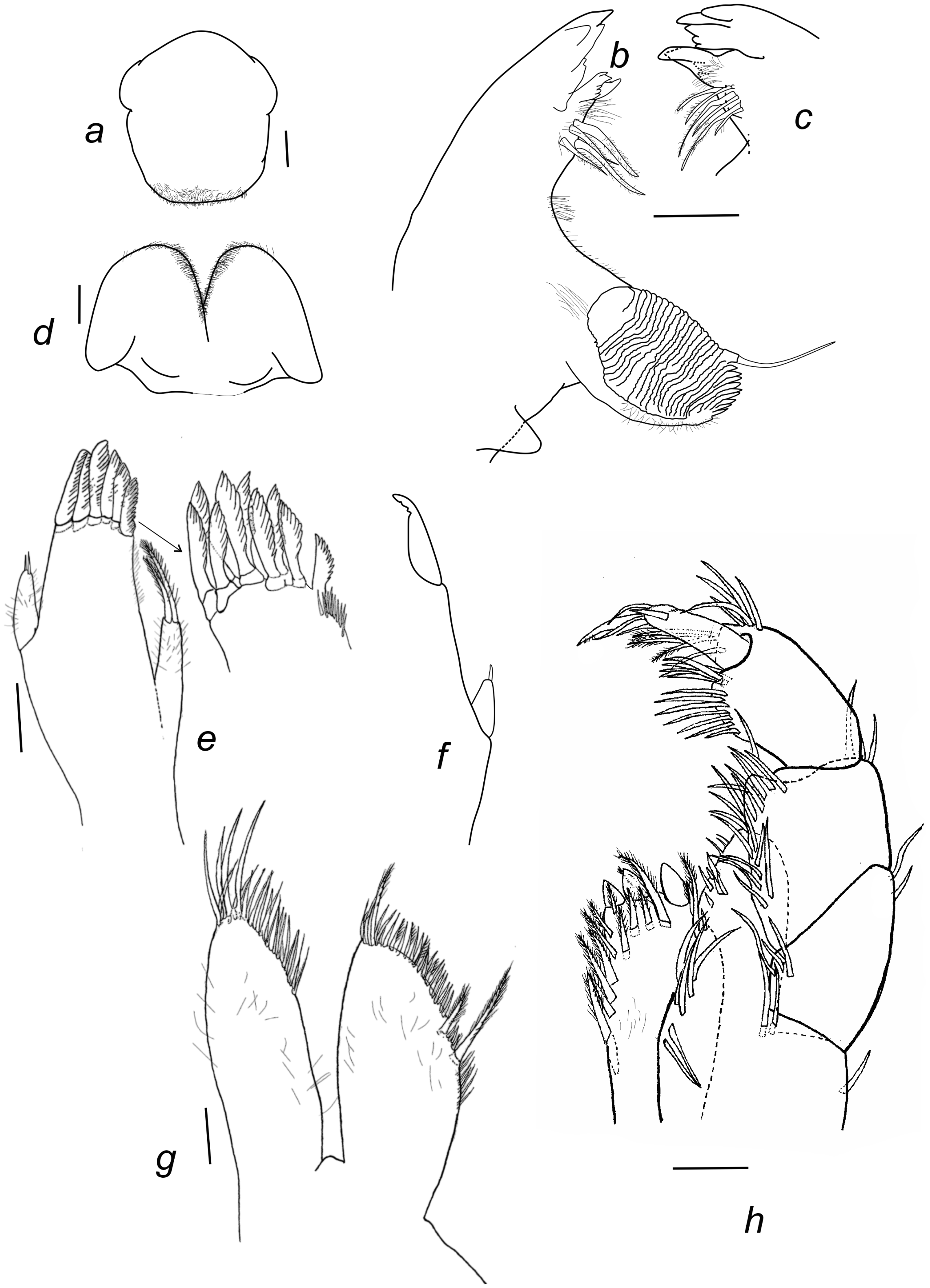

Fig. 10. *Hyalella inca* sp.n., male holotype, FML-CRUST 01335: *a* — upper lip; *b* — right mandible; *c* — incisor and lacinia mobilis of left mandible; *d* — lower lip; *e* — maxilla I, with details of the setae on the outer plate; *f* — left maxilla I, palp and a portion of the outer plate; *g* — maxilla II; *h* — maxilliped. Scale bars: 0.1 mm.

Рис. 10. *Hyalella inca* sp.n., голотип самец, FML-CRUST 01335: *a* — верхняя губа; *b* — правая мандибула; *c* — резец и подвижный зубец левой мандибулы; *d* — нижняя губа; *e* — максилла I, отдельно показаны щетинки наружной пластинки; *f* — левая максилла I, щупик и часть наружной пластинки; *g* — максилла II; *h* — максиллипед. Масштаб 0,1 мм.

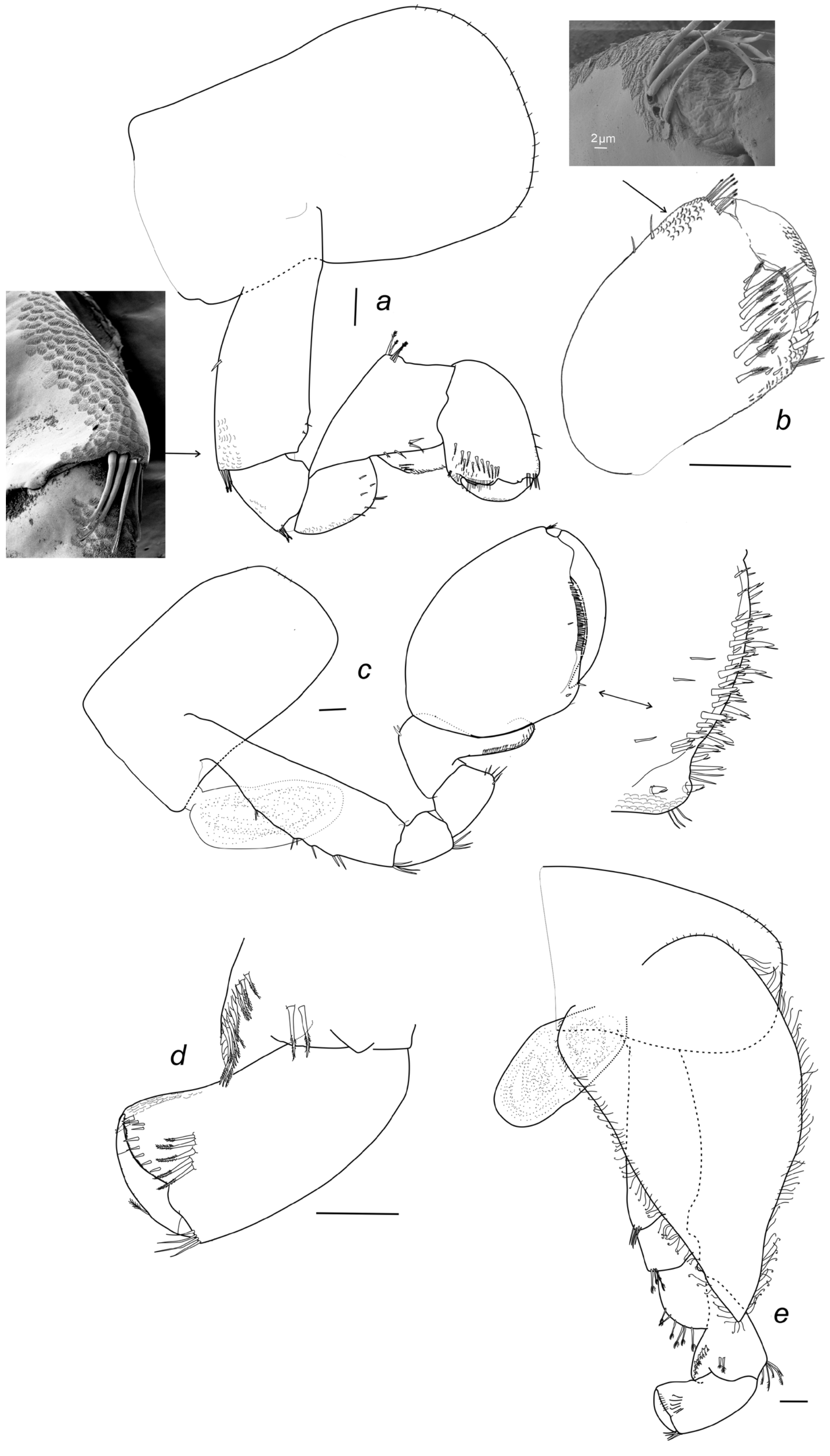

Fig. 11. *Hyalella inca* sp.n., male holotype, FML-CRUST 01335 (*a*–*c*) and female paratype FML-CRUST 01336 (*d*–*e*): *a* — gnathopod I, with detail of the denticles on the basis; *b* — propodus of gnathopod I, SEM image displaying the denticles; *c* — gnathopod II, with inset of palm margin; *d* — propodus of gnathopod II; *e* — gnathopod II. Scale bars: 0.1 mm.

Рис. 11. *Hyalella inca* sp.n., голотип самец, FML-CRUST 01335 (*a*–*c*) и паратип самка, FML-CRUST 01336 (*d*–*e*): *a* — гнатопод I, отдельно показаны зубчики основного членика; *b* — проподит гнатопода I, отдельно показано размещение зубчиков, СЭМ; *c* — гнатопод II, отдельно показано вооружение края лопасти; *d* — проподит гнатопода II; *e* — гнатопод II. Масштаб 0,1 мм.

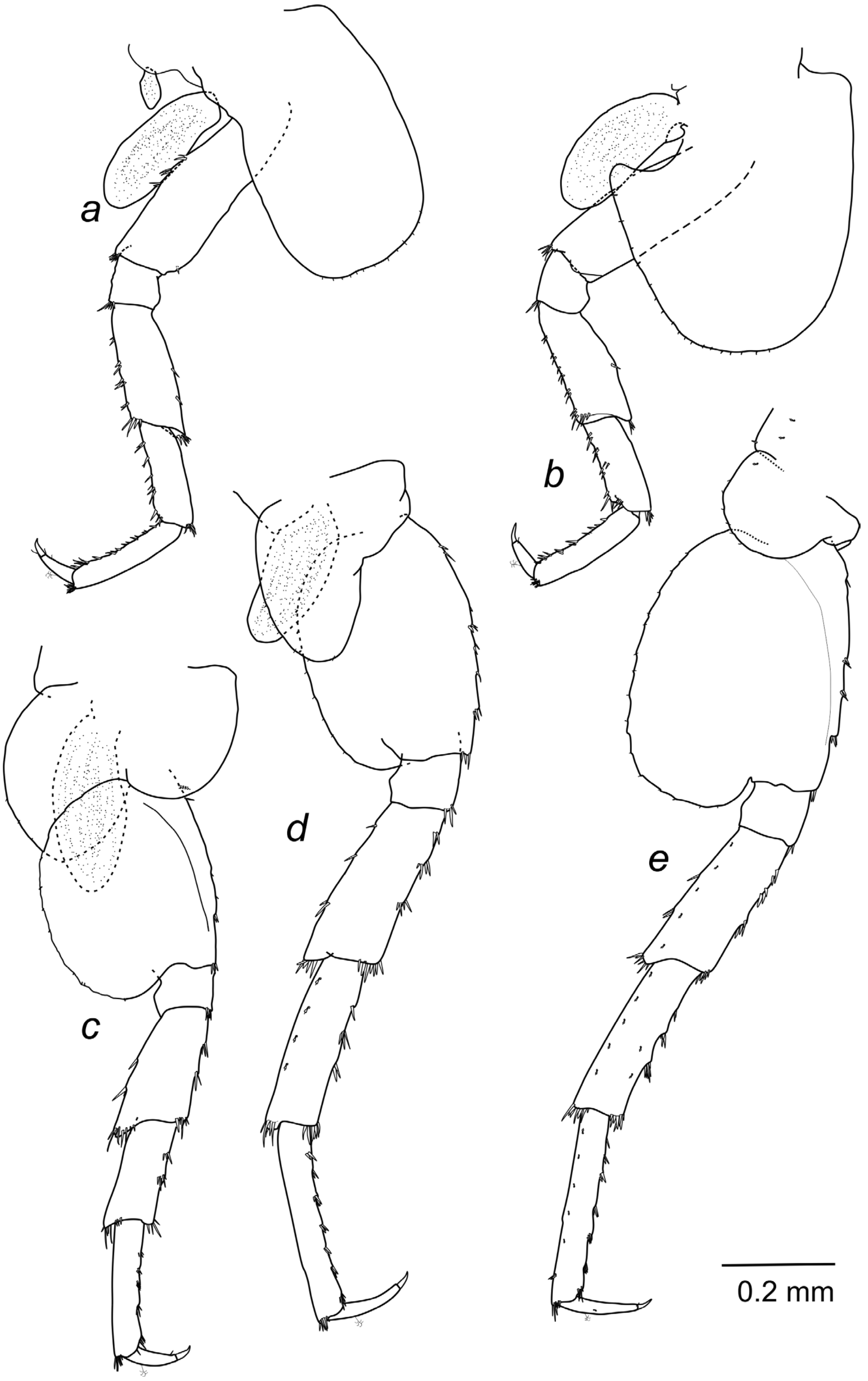

Fig. 12. *Hyalella inca* sp.n., male holotype, FML-CRUST 01335: *a* — pereiopod 3; *b* — pereiopod 4; *c* — pereiopod 5; *d* — pereiopod 6; *e* — pereiopod 7.

Рис. 12. *Hyalella inca* sp.n., голотип самец, FML-CRUST 01335: *a* — переопод 3; *b* — переопод 4; *c* — переопод 5; *d* — переопод 6; *e* — переопод 7.

Antenna I (Fig. 9*a*, *b*): shorter than antenna II but longer than its peduncle. Peduncular segments 1–3 progressively shorter, all segments with many simple and plumose setae, along with microtrichs Ib. Flagellum with eleven articles, with groups of simple setae (type A1) and some isolated plumose setae; aesthetascs ordinary occurring distally between articles 8–10.

Antenna II (Fig. 9*c*): less than half body length. Peduncular segments 3–5 bearing groups of simple and plumose setae. Flagellum comprising 14 articles each bearing distal and subdistal simple setae of type A1.

Upper lip: Ordinary, with minute setae on the distal part (Fig. 10*a*).

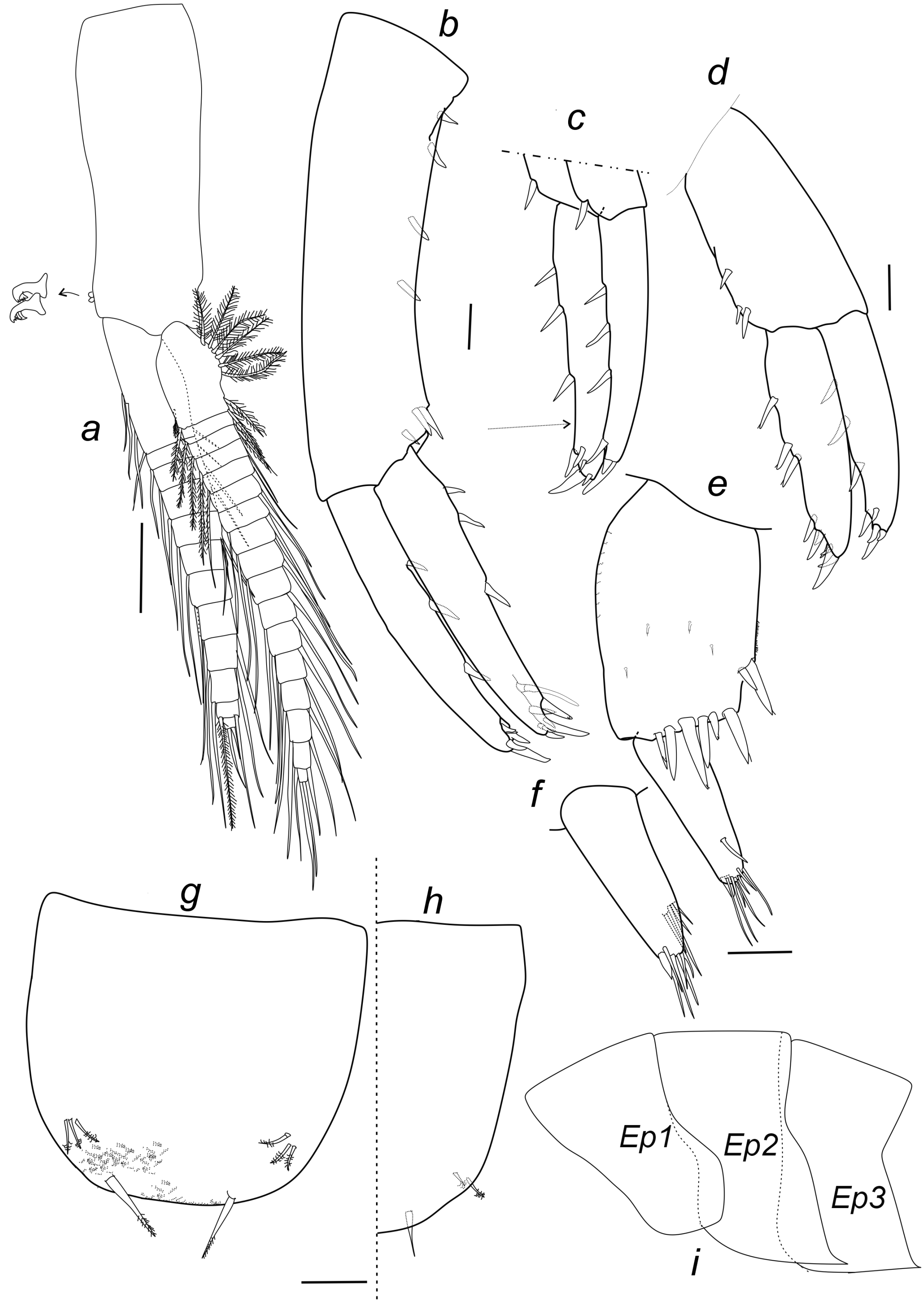

Fig. 13. *Hyalella inca* sp.n., male holotype, FML-CRUST 01335 (*a–b*, *d–i*) and female (FML-CRUST 01336) (*c*): *a* — pleopod 1; *b* — uropod 1; *c* — uropod 1 rami and a portion of the apical part of the peduncle; the absence of the curved seta is shown; *d* — uropod 2; *e* — right uropod 3; *f* — left ramus of uropod 3; *g* — telson of male paratype; *h* — portion of the telson; *i* — epimeral plates. Scale bars: 0.2 mm.

Рис. 13. *Hyalella inca* sp.n., голотип самец, FML-CRUST 01335 (*a–b*, *d–i*) и самка (FML-CRUST 01336) (*c*): *a* — плеопод 1; *b* — уропод 1; *c* — ветви уропода 1 и фрагмент апикальной части стебелька; показано отсутствие изогнутых щетинок; *d* — уропод 2; *e* — правый уропод 3; *f* — левая ветвь уропода 3; *g* — тельсон паратипа самца; *h* — часть тельсона; *i* — пластинки эпимеры. Масштаб 0,2 мм.

Mandible: Right mandible (Fig. 10*b*) incisor 5-denticulate (three long, two short); lacinia mobilis complex with many denticles; setal row with 4 pappose setae; molar triturative, well developed. Left mandible (Fig. 10*c*) incisor broadened, 5-denticulate; lacinia mobilis 4-denticulate (two long, two short); setal row with six pappose setae.

Lower lip: Ordinary, outer lobes covered with minute setae (Fig. 10*d*).

Maxilla I: Asymmetrical. Outer plate with nine robust serrate setae F4 and setules on the inner surface. Inner plate shorter than outer one, with two apical papposerrate setae, and several marginal setules. Palp of right Maxilla I longer than wide, reaching more than half the length of the distance between the base of the palp and the apex of the outer plate, bearing two simple apical setae (Fig. 10*e*). Palp of left maxilla shorter than right counterpart, with only one simple distal seta (Fig. 10*f*).

Maxilla II (Fig. 10*g*): Inner plate slightly shorter than outer plate, with 2 unequal strong pappose setae on inner margin; outer and inner plates with simple and plumose setae distally and few setules on the surface.

Maxilliped (Fig. 10*h*): Inner plate with three apical robust cuspidate setae; distal and medial margins with plumose setae. Outer plate ovate, longer than first segment of palp; distal and medial margins with simple setae. Palp longer than plates, 4-segmented; segment 3 slender, longer than wide; segments 1–3 bearing both simple and serrated setae on medial margin and lateral margins; segment 4 unguiform, shorter than segment 3, with simple setae shorter than nail placed distally.

Gnathopod I (Fig. 11*a*): Subchelate, coxal plate longer than wide, margin with small simple setae (type Ia). Basis hind margin with a single simple seta; basis, ischium and merus with denticles type T1 on margins. Posterior margin of basis and ischium with groups of 5 serrated setae. Carpus longer than wide, posterior pectinate lobe bordered with serrate setae. Propodus (Fig. 11*b*) longer than broad, hammer-shaped, anterodistal margin with A1-type simple setae, inner face with 10–11 serrate setae type F3 arranged obliquely; palm margin bearing a subrectangular hump near the dactylus, lined with A1-type setae; palm angle with T1-type denticles, and two cuspidate setae with accessory seta. Dactylus with T1-type denticles. Palmar Index (sensu Ruffo [1973]) = 0.37.

Gnathopod II (Fig. 11*c*): Subchelate. Coxal plate longer than wide. Basis, ischium and merus with groups of simple setae on posterior margin. Carpus subtriangular, notably shorter than propodus. Propodus ovate, with oblique palm; palm margin bordered with several rows of simple setae; palm angle with two cuspidate setae and T1-type denticles. Dactylus claw-like, congruent with the palm. Palmar Index (sensu Ruffo [1973]) = 0.43.

Pereiopods 3 and 4 (Fig. 12*a*, *b*): Similar in size. Coxal plates: pereiopod 3 subrectangular, longer than wide; pereiopod 4 broad, excavated posteriorly, 1.2x as long as wide; both coxal plates with margins lined with thin simple setae type Ia; posterior margin of basis, ischium, merus, carpus and propodus with simple or cuspidate setae; dactylus elongated, approximately ½ length of propodus.

Pereiopods 5–7 (Fig. 12*c*–*e*): Pereiopod 5 shorter than pereiopods 6 and 7, with the last two being equal in length. Coxal plate of pereiopod 5 bilobated, wider than long, with posterior lobe deeper than anterior lobe; coxa of pereiopod 6 as long as wide, with significantly reduced anterior lobe; coxa of pereiopod 7 wider than long; all coxal plates with thin simple setae along their margins (type Ia). Basis of pereiopods 5–7 expanded and finely serrated, anterior and posterior margin of ischium, merus, carpus and propodus with simple or cuspidate setae and few microtrichs type Ib. Dactylus of all limbs elongated, similar to pereiopods 3–4.

Coxal gills: Sacciform, present on gnathopod II to pereiopod 6 (Fig. 12*a*–*d*). Sternal gills also sacciform but shorter, present on pereonites 2 to 7 (Fig. 12*a*).

Pleopods: Biramous. Peduncle with pair of retinacula. Rami multiarticulate, provided with long plumose setae (Fig. 13*a*).

Uropod 1 (Fig. 13*b*): Peduncle longer than rami, with four dorsal cuspidate setae aligned in a longitudinal row and other three cuspidate setae on dorsolateral and dosomedial distal margin. Rami subequal in length with three dorsal cuspidate setae; inner ramus with seven distal setae, one of which notably elongated, slender and slightly curved, surpassing tip of ramus (‘copulatory spine’ sensu Bousfield [1996]); outer ramus with five distal setae, one of them larger than rest.

Uropod 2 (Fig. 13*d*): slightly shorter than peduncle of uropod 1. Peduncle slightly longer than rami. Peduncle and both rami each with three dorsal cuspidate setae. Outer ramus with seven distal cuspidate setae, one notably longer and more robust than rest; inner ramus bearing five distal cuspidate setae, one of which longer and stronger than rest.

Uropod 3 (Fig. 13*e*): subequal in length to peduncle of uropod 2; peduncle rectangular, wider and longer than ramus, with six robust distal setae and two additional marginal setae, all cuspidate. Outer ramus basal width nearly 2.5 times width at tip of ramus, with six to seven simple setae and one shorter cuspidate seta distally; another group of subdistal setae placed close to apex consisting of row of four long, thin simple setae (left uropod 3; Fig. 13*f*) or only one seta (right uropod 3) (Fig. 13*e*).

Telson: subrectangular, with two widely spaced, long simple setae on distal margin (setae serrate in one of male paratypes); additionally, other two short plumose setae placed subdistally on each side (three setae in one of male paratypes) on dorsal surface of telson (Fig. 13*g*, *h*).

Epimeral plates (Fig. 13*i*): Plate 1 is rounded posterodistally; Plates 2 and 3 are acuminate posterodistally with angle strongly produced.

Intraspecific variability in males: Variations were observed, including differences in the setation of ramus of uropod 3, as outlined in the main description. Additionally, in one male an apparent notch was observed on coxa 5, and two setae were absent on the anterodistal part of the gnathopod I propodus. Some individuals exhibited 13 articles in antenna II flagellum (14 in holotype). Further variations were noted in the number and type of setae on the telson, as described in the main text.

FEMALE (PARATYPES). Maximum body length observed 7.32 mm. Female gnathopod II propodus (Fig. 11*d*) smaller and slenderer than in male, with five serrate setae on the inner face. Oostegites subtriangular, featuring curled setae along margin (Fig. 11*e*). Female Uropod 1 without modified seta (‘copulatory spine’) on inner ramus (Fig. 13*c*).

TAXONOMICAL REMARKS

Hyalella oscari sp.n. was discovered in the Puna and High Andes ecoregions, specifically in Catamarca and La Rioja provinces to the east of the Andes, Argentina, at elevations ranging from approximately 3900 to 4400 m a.s.l. This species bears a close resemblance to *Hyalella fatimae* Isa-Miranda et Peralta, 2022, yet it can be primarily distinguished by distinct morphological features. Notably, *H. oscari* sp.n. is characterized by the morphology and chaetotaxy of maxilla I palp, particularly the presence of two plumose setae vs. only one seta present in *H. fatimae*, the former being a feature unique within the genus *Hyalella*. Additionally, in *H. fatimae*, the antenna II extends notably longer than the head, about 25% of the body length, whereas in *H. oscari* sp.n., it is only slightly longer. The propod of male gnathopod I of *H. oscari* sp.n. has a slightly concave palm margin gradually increasing in height towards the palmar angle (vs. it is regularly convex in *H. fatimae*). The excavation of

Table 1. Morphological differences among male *Hyalella* species distributed in the Puna and High Andes.
Таблица 1. Морфологические различия между самцами видов *Hyalella*, распространенных в Пуне и Высоких Андах.

Character	***H. kochi* González et Watling, 2001**	***H. puna* Peralta et Isa-Miranda, 2019**	***H. fatimae* Isa-Miranda et Peralta, 2022**	***H. fossamancinii* Cavalieri, 1959**	***H. oscari* sp.n.**	***H. inca* sp.n.**
Antenna 1: articles of flagellum	9	9–10	8	9–10	9	11
Antenna 2: articles of flagellum	11	10–14	10	11–14	11	14
Maxilla 1, palp length	Minute, short	Reaching almost half of the distance between base of palp and base of setae on outer plate	Reaching more than half of the distance between base of palp and base of setae on outer plate	Reaching more than half of the distance between base of palp and base of setae on outer plate	Long, with a medial constriction, reaching more than half the length of the distance between the base of the palp and the apex of the outer plate	Reaching more than half the length of the distance between the base of the palp and the apex of the outer plate
Gnathopod 1 propodus shape and number of setae on distal anterior margin	Hammer-shaped, with one seta	Hammer-shaped, without setae	Hatched-shaped, without setae	Hatched-shaped, without setae	Hatched-shaped, without setae	Hammer-shaped, with two setae
Gnathopod 1 propodus: number of setae on inner face	7	7	7–9	More than 10	7–8	10–11
Pereiopod 7 basis, presence/absence of two setae placed subdistally on outer surface	Absent	Absent	Absent	Absent	Present	Absent
Uropod 1 with modified setae on inner ramus	Present	Absent	Absent	Absent	Absent	Present
Ramus of uropod 3: slender or robust	Slender	Slender	Robust	Robust	Robust	Slender
Ramus of uropod 3 length: subequal or shorter than peduncle	Subequal than peduncle	Shorter than peduncle	Shorter than peduncle	Shorter than peduncle	Shorter than peduncle	Shorter than peduncle
Sternal gills on pereionites	3 to 7	2 to 7	2 to 7	2 to 7	3 to 7	2 to 7
Telson: number of simple apical setae	4–6	2–4	2	8–12	4–6	2

coxa 4 in *H. oscari* sp.n. is more pronounced than in *H. fatimae*, and the former exhibits four cuspidate setae on the palm angle (vs. three in *H. fatimae*).

Hyalella oscari sp.n. also shows resemblances to *H. fossamancinii* Cavalieri, 1959, also reported in the Puna and High Andean region. However, notable differences exist, particularly in maxilla I: in *H. fossamancinii* the palp is straight and bears only one simple distal seta, whereas *H. oscari* sp.n. features a slightly arched palp with a constriction and two plumose setae on tip. Additionally, regarding the setation on the peduncle of uropod 3, *H. oscari* sp.n. bears numerous fine marginal setae, which are absent in *H. fossamancinii*. The shape of gnathopod I propodus male differs between the species, with *H. fossamancinii* having a straight palm margin while *H. oscari* sp.n. exhibits a sinuous one.

Hyalella oscari sp.n. is further distinguished from both *H. fatimae* and *H. fossamancinii* by the presence of two short external setae on the basis of pereopod 7, a feature not observed in the other species. The only species exhibiting this trait is *Hyalella gonzalezi* Jaume, 2021, endemic to Lake Titicaca, yet it differs primarily due to differences in uropod 3 setation, the distinctive maxilla I palp of *H. oscari* sp.n., and the longer and sharper coxa 4 in *H. gonzalezi* compared to *H. oscari* sp.n. Additionally, the body of *H. gonzalezi* presents a faint but distinct transverse hump along the posterodorsal margin of pereionites and pleonites, a feature not observed in *H. oscari* sp.n.

In molecular phylogenetic analyses, *H. oscari* sp.n. is genetically closely affiliated with *H. armata*, *H. krolli*, and *H. franciscae*. It is worth mentioning that *H. oscari* sp.n. displays a ‘smooth’ body whereas *H. armata* (endemic to Lake Titicaca) exhibits extremely elongated, laterally directed spines on each of the pereiopodal coxal plates I–IV. In comparison to *H. franciscae* (found in Patagonia, Chile, and southern South America), similarities were noted in the length of palp of maxilla I and setae on peduncle of uropod 3. However, distinctions arise in the length of uropod 3 ramus, a more 'triangular' male propod of male gnathopod II, and presence of 16 setae on the inner face of propodus of gnathopod I. In contrast to *H. krolli* (from Lake Titicaca), similarities were observed in the length of palp of maxilla I, but differences were evident, as *H. krolli* has a compact body, shorter antennae I and II, and notably elongated and narrow coxal plates.

Hyalella inca sp.n. was found in the Puna and High Andes ecoregions, precisely within the Salta and Catamarca provinces, situated to the east of the Andes, at elevations ranging from approximately 3300 to 4000 m a.s.l. This species exhibits several similarities to *H. puna* Peralta et Isa-Miranda 2019, which initially led to its designation as "*Hyalella aff. puna*" in the study conducted by Hankel *et al.* [2023]. However, there are several diagnostic traits enabling the differentiation of both species. Notably, some individuals of *H. puna* exhibit postero-dorsal flanges on pleonites I–III, while other individuals of the same species have a smooth body. In contrast, *H. inca* sp.n. possesses a consistently smooth body (therefore, this feature cannot be used to distinguish these two species). Furthermore, in *H. inca* sp.n., the right maxilla I palp is longer than in *H. puna*, and it features two simple setae at the apex, as opposed to *H. puna*, which has only one. These two setae were also observed in *Hyalella echinus* (Faxon, 1876) from Lake Titicaca, although with significant differences, primarily associated with body structure, as *H. echinus* has spines on each body somite. The left and right maxilla I are similar in *H. puna*, while in *H. inca* sp.n., they are asymmetrical. Concerning the setation of male gnathopod I propodus, *H. inca* sp.n. features two reduced setae on dorsal margin, in contrast to *H. puna*, which shows an unarmed margin.

Additionally, *H. inca* sp.n. has a notably larger uropod 3 ramus, with a basal width exceeding twice the height of the ramus, whereas *H. puna* maintains a 1.7 ratio of base width to ramus height. Another distinguishing trait is the presence of a row of setae on the ramus of uropod 3 in *H. inca* sp.n., which is absent in *H. puna*. *H. inca* sp.n. possesses also a modified seta on the inner ramus of uropod 1, not found in *H. puna*. In molecular phylogenetic trees, *H. inca* sp.n. is closely related to *H. kochi*, *H. montforti*, and *H. simplex.* They share the modified seta on the inner ramus of the male uropod 1. This curved seta is a diagnostic morphological character of the "curvispina species complex" used by Bousfield [1996] to propose the subgenus *Hyalella* (*Mesohyalella*). The new species shares similarities with *H. montforti* (Lake Titicaca) in the overall morphology of the male gnathopod II and male gnathopod I propodus. They differ primarily in the distinctive the dorso-posterior flanges on peraeon segments 7, pleonites 1, 2, and 3 of *H. montforti* (compared to the smooth body of *H. inca* sp.n.), and the size and shape of the peduncle and ramus of uropod 3, which in *H. montforti* is much smaller and stouter than in *H. inca* sp.n. Compared to *H. simplex* (Southern Chile), there are similarities in the morphology and setation of the telson, as well as in the long palp of maxilla I. However, distinctions arise in the morphology and setation of uropod 3, and it is noteworthy that *H. simplex* exhibits sternal gills on somites 3 to 7. Similarities with *H. kochi* and the new species extend to the morphology of the propodus of male gnathopod I. However, notable differences are primarily observed in the reduced length of palp of maxilla I, the equal length of ramus and peduncle of uropod 3, and the presence of sternal gills on somites 3 to 7 in *H. kochi*.

Table 1 presents a comparison of the main morphological characters of the species recorded from the Puna and High Andes of Argentina, including the two new species.

PHYLOGENETIC ANALYSES

Our phylogenetic analyses include a total of 36 species of both Hyaloidea (with 4 families represented) and Talitroidea (with 2 families represented) (Table 2).

When considering South American species of *Hyalella*, there have been identified four clades (we maintained the same terminology for these clades as proposed previously by Adamowicz *et al.* [2018]). Clade A, housing *H. kochi* González et Watling, 2001, *H. nefrens* González et Watling, 2003, *H. longipalma* (Faxon, 1876), *H. cuprea* (Faxon, 1876), and *H. hirsuta* Jaume, 2021, was strongly supported only by Bayesian inference (BI: 100) and weakly supported by maximum likelihood (ML: 79). Clade C (BI: 100, ML: 97) including *H. franciscae* González et Watling, 2003, *H. gonzalezi* Jaume, 2021 in Jaume *et al.* [2021], *K. krolli* Jaume, 2021 in Jaume *et al.* [2021], *H. armata* (Faxon, 1876) plus the new species *H. oscari*. Clade D (BI: 100, ML: 95) comprised species exclusively confined to the altiplano (Titicaca), namely *H. tiwanaku* González et Watling 2003, *H. longipes* (Faxon 1876), and *H. neveulemairei* Chevreux 1904. Clade E (BI: 100, ML: 98) including *H. montforti* Chevreux 1907, *H. simplex* Schellenberg 1943, *H. kochi* González et Watling 2001, and the new species *H. inca*. All analyses agreed on locating the two new species within the clades C and E respectively (Fig. 14*a*, *b*).

Discussion

BIOGEOGRAPHY AND PHYLOGENETIC RELATIONSHIPS OF *HYALELLA* SPECIES

The present study explores some aspects of freshwater amphipod biodiversity in southern South America, focusing on the genus *Hyalella*, which stands out for its high diversity. In the Argentine Puna, Hankel *et al.* [2023] reported their occurrence of 11 morphospecies distinct from the *Hyalella* species already described. On the basis of that study, we present here the results of a molecular and morphological screening of two of those morphospecies, finally confirming their status as new species. This expands the list of species recognized within the Puna and High Andes regions of Argentina to include *Hyalella kochi*, *H. fatimae*, *H. fossamancinii*, *H. puna*, along with the recently designated *H. inca* sp.n. and *H. oscari* sp.n. The total number of *Hyalella* species for Argentina has increases to 16.

The initial molecular studies of *Hyalella* began in North America [Witt, Hebert, 2000; Witt *et al.*, 2006], and suggested the potential existence of many new, yet undescribed species. Advancing from this baseline, other researchers have recently added phylogenetic reconstructions from molecular data of *Hyalella* species from South America, particularly examining the cox1 gene [Adamowicz *et al.*, 2018; Jurado Rivera *et al.*, 2020]. These studies hinted at the presence of five main and distinct monophyletic clades (A, B, C, D and E) in localities comprising Lake Titicaca and other water bodies of the northern Altiplano.

Delving into the phylogenetic assignment of the newly identified species, *H. inca* sp.n. nests within clade

Table 2. DNA sequences used in this study. The data marked with an asterisk (*) are sequences obtained for the first time in this study.

Таблица 2. Сиквенсы ДНК, использованные в данном исследовании. Звездочкой (*) помечены сиквенсы, полученные впервые.

Family / Superfamily	Species	Locality	NCBI GenBank accession numbers
Chiltoniidae/ Hyaloidea	*Arabunnachiltonia murphyi* King, 2009	Strangways Springs, Australia	JX900303
Chiltoniidae / Hyaloidea	*Austrochiltonia clydensis* King et Leys, 2011	Tasmania, Australia	JN009888
Chiltoniidae/ Hyaloidea	*Austrochiltonia dalhousiensis* Zeidler, 1997	ND	KJ661046
Chiltoniidae/ Hyaloidea	*Austrochiltonia subtenuis* (Sayce, 1902)	VIC, Australia	JN009878
Chiltoniidae/ Hyaloidea	*Kartachiltonia moodyi* King et Leys, 2014	Kangaroo Island, Australia	KJ661125
Chiltoniidae/ Hyaloidea	*Stygochiltonia bradfordae* King, 2012	Yilgarn, Australia	KT958077
Chiltoniidae/ Hyaloidea	*Wangiannachiltonia guzikae* King, 2009	Great Artesian Basin, Australia	KT958093
Dogielinotidae/ Hyaloidea	*Haustorioides japonicus* Kamihira, 1977	Chirihama Beach, Hakui, Ishikawa, Japan	LC735834
Hyalellidae/ Hyaloidea	*Hyalella armata* (Faxon, 1876)	Lake Titicaca, Peru	OM513779
Hyalellidae/ Hyaloidea	*Hyalella azteca* (Saussure, 1858)	Lost Creek, USA	DQ464726
Hyalellidae/ Hyaloidea	*Hyalella cajasi* Alonso et Jaume, 2017	Ecuador	OM513890
Hyalellidae/ Hyaloidea	*Hyalella cuprea* (Faxon, 1876)	Perú	OM513846
Hyalellidae/ Hyaloidea	*Hyalella curvispina* Shoemaker, 1942	Uruguay	MZ754520
Hyalellidae/ Hyaloidea	*Hyalella franciscae* González et Watling, 2003	Chile	OM513892
Hyalellidae/ Hyaloidea	*Hyalella gonzalezi* Jaume, 2021	Perú	OM513801
Hyalellidae/ Hyaloidea	*Hyalella hirsuta* Jaume, 2021	Lake Titicaca, Perú	OM513782
Hyalellidae/ Hyaloidea	*Hyalella inca* sp.n.	Aguas Calientes, Salta, Argentina	OR726344*
Hyalellidae/ Hyaloidea	*Hyalella kochi* González et Watling, 2001	Perú	OM513871/ OM513725/ OM513827
Hyalellidae/Hyaloidea	*Hyalella krolli* Jaume, 2021	Bolivia	OM513807/ OM513808
Hyalellidae/ Hyaloidea	*Hyalella longipalma* (Faxon, 1876)	Perú	OM513815
Hyalellidae/ Hyaloidea	*Hyalella longipes* (Faxon, 1876)	Perú	OM513858
Hyalellidae/ Hyaloidea	*Hyalella montezuma* Cole et Watkins, 1977	USA	AY152807
Hyalellidae/ Hyaloidea	*Hyalella montforti* Chevreux, 1907	Perú	OM513888
Hyalellidae/ Hyaloidea	*Hyalella muerta* Baldinger, Shepard et Threloff, 2000	Texas Springs, USA	DQ464602
Hyalellidae/ Hyaloidea	*Hyalella nefrens* González et Watling, 2003	Perú	OM513809
Hyalellidae/ Hyaloidea	*Hyalella neveulemairei* Chevreux, 1904	Perú	OM513771
Hyalellidae/ Hyaloidea	*Hyalella oscari* sp.n.	Rio Los Baños, La Rioja, Argentina	OR726343*
		Quebrada del Diablo, Catamarca, Argentina	OR726347*
		Calalaste, Catamarca, Argentina	OR726345*
		Calalaste, Catamarca, Argentina	OR726346*
Hyalellidae/ Hyaloidea	*Hyalella sandra* Baldinger, Shepard et Threloff, 2000	Travertine Springs, USA	DQ464682

Table 2 (continued).
Таблица 2 (продолжение).

Family / Superfamily	Species	Locality	NCBI GenBank accession numbers
Hyalellidae/ Hyaloidea	*Hyalella simplex* Schellenberg, 1943	Chile	AF520434
Hyalellidae/ Hyaloidea	*Hyalella spinicauda* Soucek et Lazo-Wasem, 2015	USA	OQ918612
Hyalellidae/ Hyaloidea	*Hyalella texana* Stevenson et Peden, 1973	Clear Creek Springs, USA	MF990281
Hyalellidae/ Hyaloidea	*Hyalella tiwanaku* González et Watling, 2003	Perú	OM513865
Hyalellidae/ Hyaloidea	*Hyalella wellborni* Soucek et Lazo-Wasem, 2015	Three Pond Barrens Trail, St. Johns, Newfoundland, Canada	OQ985175
Hyalidae/ Hyaloidea	*Apohyale punctata* (Hiwatari et Kajihara, 1981)	Shari, Hokkaido, Japan	LC735835
Hyalidae/ Hyaloidea	*Protohyale triangulata* (Hiwatari, 2003)	Etajima, Hiroshima, Japan	LC735836
Najnidae/ Hyaloidea	*Najna consiliorum* Derzhavin, 1937	Lake Akkeshi, Hokkaido, Japan	LC735837
Brevitalitridae/Talitroidea	*Bousfieldia phoenixae* Chou et Lee, 1996	Pingtung, Chunri, Taiwan	LC566384
Talitridae/Talitroidea	*Mizuhorchestia urospina* Morino, 2014	Yamaguchi, Japan	LC566328
Talitridae/Talitroidea	*Morinoia japonica* (Tattersall, 1922)	Lake Biwa, Japan	LC566324
Talitridae/Talitroidea	*Yamatorchestia nudiramus* (Morino et Miyamoto, 2015)	Mie, Japan	LC566448
Talitridae/Talitroidea	*Platorchestia pacifica* Miyamoto et Morino, 2004	ND	OQ512290
Outgroup			
Pseudocrangonyctidae/ Crangonyctoidea	*Pseudocrangonyx yezonis* Akatsuka et Komai, 1922	Akita, Japan	LC171519

E, whereas *H. oscari* sp.n. finds its place within clade C. Robust support for these classifications stems from both molecular and morphological data. Clade-specific morphological traits play a crucial role in delineating these groups. Thus, specific characteristics such as the setation of gnathopod I propodus and its hammer-shaped form and the presence of modified curved setae in the inner ramus of male uropod 1 distinguish clade E species; however, this last feature is not exclusive to that clade because these setae are also developed in some species of clade A, as well as in two other species that could not be recovered within any clade: *H. curvispina* and *H. cajasi*; according to González [2003], the occurrence of curved setae on the inner ramus of male uropod 1 is a shared characteristic in various species exhibiting diverse general morphologies and sternal gill arrangements. The Clade C is characterized by elongated palp maxilla 1, stoutness of uropod 3 ramus, and hatched shape of gnathopod I propodus. Distinct species within clades A, C, D, and E shared traits involving the development of dorsal and lateral spines and flanges on the body, exemplified by species such as *Hyalella montforti*, *H. neveulemairei*, *H. nefrens*, and *H. armata*. Thus, the armoured spiny morphologies of some species suggest the independent evolution of this morphological traits across different lineages, a pattern congruent with Zapelloni *et al.* [2021] report of phenotypic plasticity and morphological convergence within *Hyalella*.

Further research, including molecular and morphological phylogenetic analyses, is expected to increase the number of valid *Hyalella* species and allow for a comprehensive analysis of the origin of North and South American Hyalellidae species.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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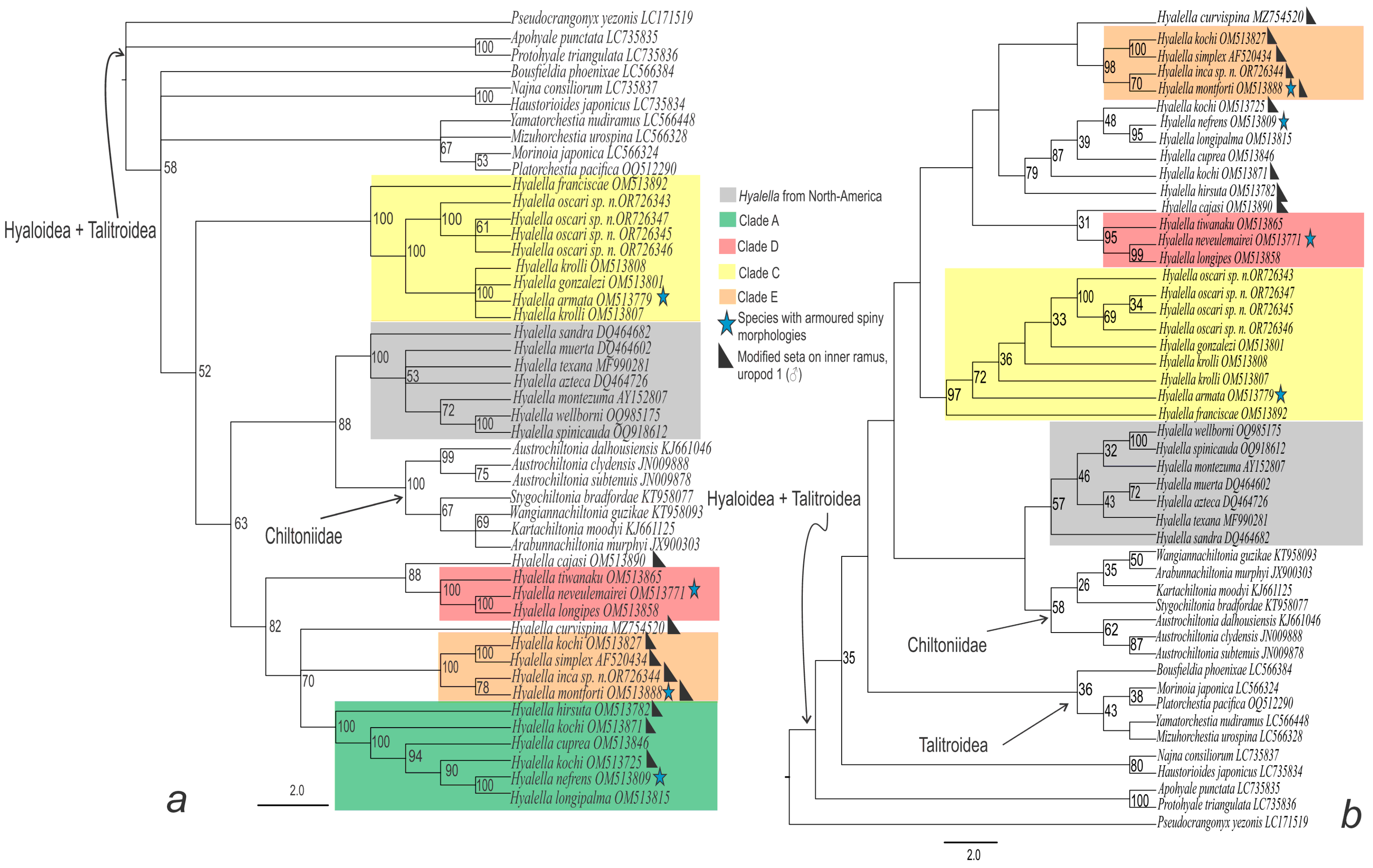

Fig. 14. Phylogenetic trees based on COI data set: *a* — Bayesian analysis with numbers at nodes indicating Bayesian posterior probabilities; *b* — maximum likelihood analysis with numbers at nodes indicating ultrafast bootstrap values. Unnumbered nodes have less than 25 support.

Рис. 14. Филогенетические взаимоотношения (деревья), основанные на наборе данных COI: а — Байесовский анализ с числами в узлах, указывающими байесовские постериорные вероятности; б — анализ методом максимального правдоподобия с числами в узлах, указывающими сверхбыстрые значения поддержки. Ненумерованные узлы с поддержкой менее 25.

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