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Research Article

A new large predator (Amphipoda, Eusiridae) hidden at hadal depths of the Atacama Trench

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The deep ocean is a vast reservoir of new species to science, and each discovery improves our ecological understanding of these remote ecosystems. One island-like ecosystem is the Atacama Trench (Southeast Pacific Ocean), where the hadal depths (>6000 m) host a distinctive endemic community. Unlike the communities of other hadal subduction trenches, predatory (non-scavenging) amphipods have not been documented or collected from the Atacama Trench. In this study, we applied an integrative taxonomic approach to describe a new predatory amphipod in the Eusiridae Stebbing, 1888 family collected from 7902 m during the 2023 IDOOS Expedition and provide an updated global Eusiridae key with the 14th genus. Morphology and DNA barcoding robustly supported raising a new genus separate from the systematically similar genera *Dorotea. Dulcibella camanchaca* gen. nov. sp. nov. is a large amphipod (holotype: 38.9 mm length) with diagnostic features that include: a smooth dorsal body, 12 spines on the outer maxilla 1 plate, subsimilar and strongly subchelate gnathopods with broad carpus lobes, the pereopods 3 and 4 dactyli are 0.45× of the respective propodus and pereopods 5 to 7 dactyli are 0.6×, a distal spiniform process on the peduncle of uropod 1, and an elongated but weakly cleft telson. Together, *Dulcibella camanchaca* gen. nov. sp. nov. is a novel predator and reinforces the eco-evolutionary distinctiveness of the Atacama Trench.

http://zoobank.org/urn:lsid:zoobank.org:pub:95A6C497-AC8E-4C24-B451-C4B7F76CE687

Key Words: Deep ocean, DNA barcoding, Eusiridae key, Integrative taxonomy, Peru-Chile Trench

Introduction

The deep ocean is a vast reservoir of biodiversity that harbours unique species, communities, and ecosystems. Despite the significant expansion in biological sampling of the deep ocean over the past four decades, a substantial knowledge gap persists in the fundamental ecological unit of measure – the species (Rogers et al., 2023). However, each new species discovered and described serves as a crucial link to unravelling the ecology and the evolutionary history across the deep ocean (e.g., Chen et al., 2015; Linley et al., 2022; Rouse et al., 2016). Importantly, this knowledge is a powerful tool to counteract the biodiversity loss crisis resulting from increasing anthropogenic pressures and a changing climate (e.g., Glover et al., 2018; Paulus, 2021).

The hadal zone, or the deepest 45% of the ocean (6000–11,000 m), has high levels of undiscovered biodiversity. Most hadal features are trenches formed at the subduction zone between tectonic plates and shaped by a unique suite of extrinsic and intrinsic factors (Jamieson et al., 2010). The Atacama Trench, the southern sector of the Peru-Chile Trench, is one of the most geographically isolated hadal features and is situated below eutrophic surface waters and characterized by high sediment loads (Geersen, 2019; Stewart & Jamieson, 2018). The Atacama Trench is known to host a highly distinctive faunal community, driven by a combination of these isolating factors (Linley et al., 2022; Swan et al., 2021; Weston et al., 2021b, 2022). The hadal depths of the Atacama Trench

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were first measured during the expedition Downwind of 1957–1958 (Fisher & Raitt, 1962). Hadal fauna, including holothurians, bivalves, and foraminifera, were initially recovered by trawls and bottom grabs in 1962 and 1968 during R/V *Eltanin* and R/V *Akademik Kurchatov* expeditions (Belyaev, 1989). The benthic community was initially photographed down to 7196 m during the 1972 Southtow Expedition (Hessler et al., 1978). Using baited trap, amphipods were recovered from 7230 m during SIO BI72–20 (Ingram & Hessler, 1987) and subsequently on five expeditions between 1997 and 2022 (Atacama Trench International Expedition, Thurston et al., 2002; SO209, Fujii et al., 2013; SO261 and Atacamex Expedition, Weston et al., 2021a; ATACAMA HADAL, Gonzalez et al., in revision). From collected specimens, many species have been described as endemic to the Atacama Trench, including three amphipods (*Hirondellea sonne* Kilgallen, 2015, *Hirondellea thurstoni* Kilgallen, 2015, and *Eurythenes atacamensis* Weston & Espinosa-Leal, 2021), a snailfish (*Paraliparis selti* Linley, Gerringer & Canto-Hernández, 2022), a holothurian (*Elpidia atakama* Belyaev, 1971), two isopods (*Macrostylis dellacrocei* Aydogan, Wägele & Park, 2008 and *Munneurycope hadalis* Aydogan, Wägele & Park, 2008), and a mud dragon (*Echinoderes mamaqucha* Grzelak, Zeppilli, Shimabukuro & Sørensen, 2021). Due to the challenges of sample collection, more species remain uncollected and are likely novel species to science.

All known amphipods from the Atacama Trench hadal depths are bentho-pelagic scavengers. However, non-scavenging predatory species are present in other hadal features (Jamieson & Weston, 2023). One predatory family is the Eusiridae Stebbing, 1888, with at least eight species across the genera *Cleonardo* Stebbing, 1888, *Eusirella* Chevreux, 1908, *Eusirus* Krøyer, 1845, and *Rhachotropis* S.I. Smith, 1883, having been documented to occur at depths up to 9120 m in the Tonga Trench (Jamieson & Weston, 2023). These large predators have raptorial gnathopods and long, slender, and highly manoeuvrable bodies that make them effective at capturing, killing, and feasting on smaller benthic prey, such as lysianassoid amphipods (Bousfield & Hendrycks, 1995). However, predatory amphipods are rare in baited traps, the most common hadal collection method, leaving their diversity a gross underestimation (Jamieson et al., 2012; Jamieson & Weston, 2023; Lörz et al., 2012, 2018b).

In this study, we expanded the known diversity of the hadal Eusiridae by describing a new genus and species from 7902 m in the Atacama Trench recovered during the 2023 Integrated Deep-Ocean Observing System (IDOOS) Expedition. *Dulcibella camanchaca* gen. nov. sp. nov. is described by an integrative taxonomic approach, pairing morphology with DNA barcoding and systematics (Schlick-Steiner et al., 2010). We provide an updated key to the Eusiridae family with the raising of the 14th genus. Together, this species expands our understanding of the members of the hadal food web and provides further evidence that the island-like Atacama Trench is a hotspot for endemic diversity.

Material and methods

Sample collection and processing

Specimens were collected during the IDOOS Expedition to the Atacama Trench on the R/V *Abate Molina* on 1 October 2023, using a free-fall lander built by the Instituto Milenio de Oceanografia (IMO) and Centro de Instrumentación Oceanográfico (CIO). The lander was deployed at a single station at 7902 m (24°55′S, 71°27′W; Fig. 1). Three fish and invertebrate traps, baited with chicken, were mounted on the lander's moveable arm, which hinged to the seafloor once the lander landed. The lander was also equipped with an SBE 49 FastCAT CTD (Sea-Bird Scientific), an Optim SeaCam IP camera (DeepSea Power & Light), two SeaLite® LEDs (DeepSea Power & Light) set to 20%, and two 30-L Niskin bottles. However, the camera became non-functional during descent. The lander was recovered after 24 h on the seafloor using an acoustic release.

Following initial sorting on deck during the expedition, amphipods were preserved by flash-freezing in liquid nitrogen or RNA/DNA Shield (Zymo Research) and stored at −80 °C. For *Dulcibella camanchaca* gen. nov. sp. nov., one specimen was flash-frozen, and three were preserved in RNA/DNA Shield and not examined. The type material was selected post-expedition as the only specimen of the species not preserved in the RNA/DNA Shield and was transferred to 95% ethanol at room temperature.

Appendages of the holotype were dissected using a stereomicroscope (Leica EZ4W) and imaged with a Leica LAS EZ 3.4 DVD 272 camera with the Leica LAS EZ software. Appendages were also temporarily mounted with glycerol and examined on a Zeiss Axioskop 2 microscope. Following Horton and Thurston (2014), the length of appendage articles was measured from the proximal to the distal articular condyle (or closest estimated position) to control for the degree of limb flexing. Images were digitally inked using Inkscape v1.1.1, following a method adapted from Coleman (2003, 2009).

The holotype material was deposited at the Museo Nacional de Historia Natural, Santiago, Chile (MNHNCL). GenSeq nomenclature follows Chakrabarty et al. (2013).

DNA barcoding and phylogenetics

Genomic DNA was extracted from pleopods 1 and 2 using the E.Z.N.A.® Mollusc & Insect DNA Kit (Omega

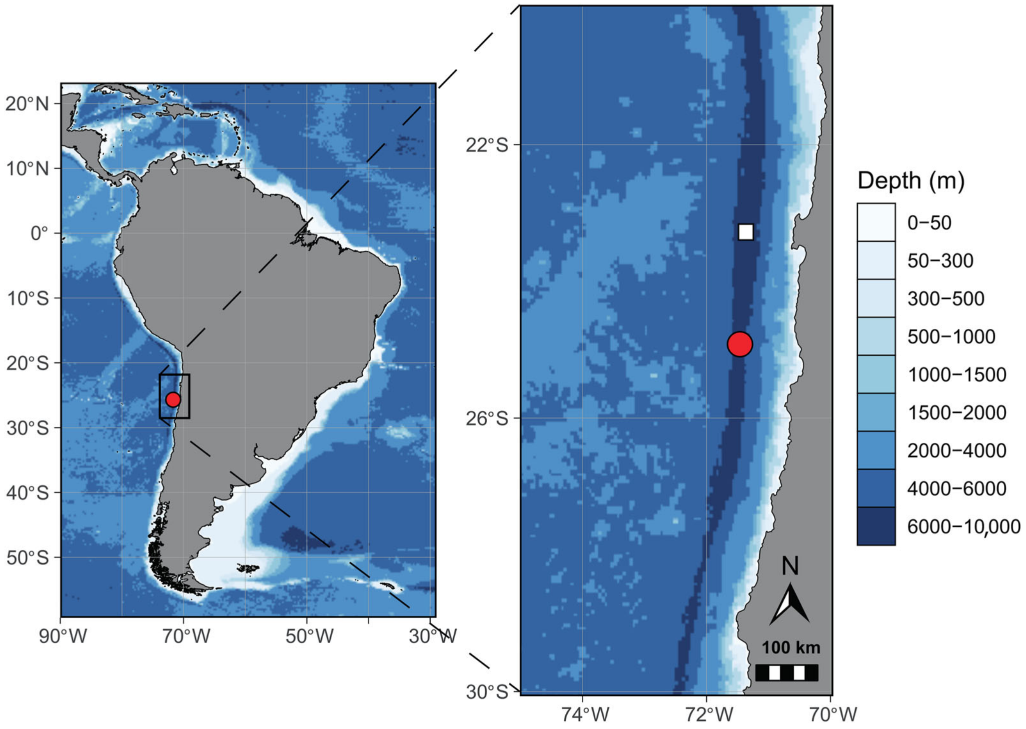

Fig. 1. Atacama Trench along the west coast of South America (left), where the black box indicates the sampling region (right). The red circle denotes the 2023 IDOOS Expedition lander station (7902 m) and type locality of *Dulcibella camanchaca* gen. nov. sp. nov. (7902 m, 23°55′S, 71°27′W). The white square denotes the deepest point of the Atacama Trench.

Bio-Tek). Samples were incubated with lysis buffer and proteinase K for 3 hours (González et al., 2020), with final elution in molecular-grade water. Concentration and quality were assessed using a Qubit 4 (Thermo-Fisher) with 1× dsDNA high-sensitivity reagents and a Nanodrop. Two mitochondrial barcoding regions, 16S rRNA (16S) and cytochrome oxidase I (COI), were amplified using published primer sets and AccuPower® Taq PCR PreMix (Bioneer). A target ∼440 bp region of 16S was amplified with 16SFt_amp (5′ GCRGTATI YTRACYGTGCTAAGG 3′) and 16SRt_amp2 (5′ CTGGCTTAAACCGRTYTGAACTC 3′) primers at an annealing temperature of 50 °C (Lörz et al., 2018b). A target ∼650 bp region of COI was amplified with LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAA AATCA-3′) primers at an annealing temperature of 45° C (Folmer et al., 1994).

PCR products were purified, and Sanger sequenced at both ends with an ABI 3730xl system by Macrogen Chile (Santiago, Chile) or Austral-Omic Sequencing Center (Santiago, Chile). Sequences were assembled, and primer sequences were removed in Geneious Prime 2024 (Kearse et al., 2012). Initial sequence identity and absence of contamination were verified using NCBI BLASTn and the Barcode of Life Data System (BOLD) v4 (Ratnasingham & Hebert, 2007). The nucleotide sequences of COI were translated into amino acid sequences to check for the presence of stop codons.

The phylogenetic relationship among the new species was assessed across the Eusiridae family and with the morphologically similar *Dorotea. Lanceola* sp. (Amphipoda) and *Pleuromamma abdominalis* (Lubbock, 1856) (Copepoda) were selected as outgroups in the COI alignment, as these Atacama Trench-dwelling species are in separate superfamilies and sufficiently divergent from the Eusiridae species (Ritchie et al., 2015). In the 16S dataset, only *Pleuromamma abdominalis* was used due to the low sequence length of *Lanceola* sp. The initial phylogenetic trees of all available representatives classified as Eusiridae revealed high levels of potential misidentification. Thus, the final alignments consisted of representatives with robust identifications, which were defined as (1) fully identified to the species level, indicating high confidence identifications, (2) identified to species with moderate confidence, as denoted by the presence of a cf., and (3) identified by one of the co-authors (i.e., *Cleonardo* sp. 1 JW-2019 (Weston et al., 2021b). Additionally, we limited the robust identification to three individuals per species. The final alignments for each gene fragment were performed using the MUSCLE (Edgar, 2004) plug-in in Geneious Prime 2024.07. The 16S and COI alignments comprised 12 individuals across

5 genera (328 bp) and 43 individuals across 7 genera, respectively (412 bp; Table 2).

Phylogenetic analysis of the 16S and COI alignments were conducted using maximum likelihood (ML) and Bayesian inference (BI) methods. For the ML approach, the analysis was fit in IQTREE v2.2 (Minh et al., 2020), where the ModelFinder (Kalyaanamoorthy et al., 2017) identified TIM+F + I + G4 as the best-fit model. Nodal support was assessed using 5000 ultrafast bootstrap replicates (Hoang et al., 2018). Bayesian analyses were conducted using BEAST v2.7 (Bouckaert et al., 2019). The evolutionary models were determined to be HKY+G for 16S and TIM3 + G for COI by the bModelTest (Bouckaert & Drummond, 2017) and run in BEAST, employing a strict clock under a Yule model, with 1×10^7 iterations. Four simultaneous runs were performed, sampling every 1000 generations. All estimated parameters had effective sample size values exceeding 200 in Tracer v1.4 (Rambaut & Drummond, 2007). The initial 25% of the trees were discarded as burn-in, and a consensus tree was generated using TreeAnnotator v1.8.4 (Drummond et al., 2012) with the maximum credibility clade criterion and median node weights.

The phylogenetic hypotheses were assessed using one tree-based and one distance-based species delimitation method to determine species boundaries. All analyses were performed without outgroups. The tree-based approach was a Bayesian implementation of the Poisson Tree Processes model (bPTP; Zhang et al., 2013) using the settings of 200,000 MCMC generations, thinning of 100, and a 0.25 burn-in. The distance-based method was Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021). The K80 substitution model was selected with a transition/transversion rate of 2.0. In addition, uncorrected p-distances pairwise distances with 1000 bootstrapping were calculated among the Eusiridae family using Mega X. The ASAP species delimitation results were used to define the species group in the p-distance analyses.

Results

Taxonomic account

Order Amphipoda Latreille, 1816
Suborder Amphilochidea Boeck, 1871
Superfamily Eusiroidea Stebbing, 1888
Family Eusiridae Stebbing, 1888
Dulcibella gen. nov. *Weston & González*

Zoobank. https://zoobank.org/NomenclaturalActs/2795CA18-20DF-4B27-9C39-5A0A49CFF0FF

Type species. *Dulcibella camanchaca* sp. nov.

Etymology. The new genus is morphologically similar to *Cleonardo* Stebbing, 1888 and *Dorotea* Corbari, Frutos & Sorbe, 2019. Both genera's names were taken as characters from Cervantes's novel Don Quixote de la Mancha. This new genus, *Dulcibella*, extends this tradition with an homage to the character Dulcinea del Toboso. She is the imagined unrequited love of Don Quixote, and the source of all inspiration for love, bravery, and faith. However, the name *Dulcinea* is preoccupied by *Dulcinea* Péringuey, 1907 in the insect order Coleoptera. To adhere to Article 52 of the International Code of Zoological Nomenclature (ICZN, 1999), we are paying tribute to the tradition with the name "*Dulcibella*." Similarly, Dulcibella appears in medieval English poetry and literature as an archetypal name for a sweetheart or idealized woman. Derived from dulcis (sweet) and bella (beautiful), Dulcibella reinforces themes of sweetness and beauty.

Diagnosis. Body dorsally smooth. Pigmented eyes lacking. Antenna 1 longer than antenna 2, accessory flagellum 1-articulated, flagellum calceolate. Mandible incisor ends in a strong, blunt tooth; lacinia mobilis 5-dentate; setal row with 9 setae; molar trituration. Maxilla 1 inner plate with 3 subapical setae; outer plate with 12 apical spines. Maxilliped inner plate with 3 apical teeth; inner margin of palp article-4 denticulate. Coxa 1 not produced anteriorly and shorter than coxa 2. Coxae 5–6 bilobate. Gnathopods 1–2 subsimilar, strongly subchelate; carpal lobes broad; propodus large, palm oblique. Pereopods 3–4 merus longer than carpus, dactylus simple and elongate (0.45× of propodus). Pereopods 5–7 subequal in form and size; basis with small posterodistal lobe; dactylus simple and elongate (0.6× of propodus). Uropods 1–2 outer ramus shorter than inner ramus; distal spiniform process on uropods 1 peduncle. Uropod 3 rami subequal. Telson elongate, weakly cleft (<20%), with blunt apices.

Remarks. *Dulcibella* shares many morphological characteristics with *Dorotea* and *Cleonardo*, including a lack of dorsal teeth on the pleon and eyes, shallow coxa 1–4, and accessory flagellum 1-articulate. With *Dorotea*, *Dulcibella* specifically shares a weakly cleft telson (~20%) and a distal spiniform process on the peduncle of uropod 1. However, several features across multiple types of appendages are distinctively different (Table 1), including: (1) *Dulcibella* displays apparent gigantism (Timofeev, 2001) >3 cm and at least 2.5× larger than *Dorotea* and *Cleonardo*, (2) outer plate of maxilla 1 has 12 apical spines (10 in *Dorotea* and 11 in *Cleonado*), (3) the P3-7 dactyls are of medium length, ranging from

0.45–0.6× as long as the propodus (0.3× in *Dorotea* and 1× in *Cleonado*), (4) the rami of uropod 3 are subequal (inner ramus longer than outer in *Dorotea* and *Cleonardo*), and (5) the telson is distinctly bilobate and reduces to blunt apices (dehiscent lobes in *Dorotea*).

Identification key to Eusiridae genera. (Expanded from Bousfield and Hendrycks (1995) and Corbari et al. (2019)).

1– Gnathopods 1–2 of strong eusirid form (carpus slender, elongate, without or with narrow hind lobe, attached antero-distally to propodus)..............................2

– Gnathopods 1–2 not eusirid-like (carpus short and deep or, if elongate, hind lobe broad, attached proximally to propodus)..6

2– Gnathopods 1–2 carpus without hind lobe … … … *Triquetramana* Hendrycks & Conlan, 2003

– Gnathopods 1–2 carpus with narrow hind lobe.......3

3– Gnathopod 1 propodus distinctly larger than in gnathopod 2 … .*Eusirogenes* Stebbing, 1904

– Gnathopod 1 propodus smaller than in gnathopod 2 4

4– Coxae 1–4 deep. Accessory flagellum 1-articulated.......................................*Eusirus* Krøyer, 1845

– Coxae 1–4 shallow. Accessory flagellum scale-like or lacking 5

5– Pereopods 3–7 distally plumose-setose. Pleon dorsally smooth. Mandibular molar reduced ....*Eusiropsis* Stebbing, 1897

– Pereopods 3–7 normally dactylate and spinose distally. Pleon weakly toothed mid-dorsally. Mandibular molar normal, triturative surface large … … … .*Pareusirogenes* Birstein & Vinogradov, 1955

6– Pereopods 3–4 merus not longer (often distinctly shorter) than carpus. Coxa 1 produced anteriorly...........7

– Pereopods 3–4 merus longer than carpus. Coxa 1 little produced or rounded anteriorly. 8

Table 1. Morphological comparison among (a) *Cleonardo longipes*, the type species for the *Cleonardo* genus (Stebbing, 1888), (b–c) the two species in the *Dorotea* genus (Bellan-Santini & Ledoyer, 1987; Corbari et al., 2019), and (d) *Dulcibella camanchaca* (present study). The table is expanded from Corbari et al. (2019). Key morphological differences of *Dulcibella camanchaca* are in bold.

	Cleonardo longipes **Stebbing, 1888**	***Dorotea aberrantis*** **(Bellan-Santini & Ledoyer, 1987)**	***Dorotea papuana*** **Corbari, Frutos, & Sorbe, 2019**	***Dulcibella camanchaca*** **gen. nov. sp. nov.**
Distinctive characters				
Total length of holotype	Unclear	12 mm	14.8 mm	**38.9 mm**
Depth range and locality	3246 m, South-west of Juan Fernandez Islands, Chile	180 – 500 m, Marion and Prince Edward Islands, Sub-Antarctic	593 m, Papua New Guinea	**7902 m**, Atacama Trench
Setal row of mandible (left)	8 setae	7 setae	6 setae	9 setae
Inner plate of maxilla 1	2 subapical setae	1 subapical setae	3 subapical setae	3 subapical setae
Outer plate of maxilla 1	11 setae	10 setae	10 setae	**12 setae**
Maxilla 2	No mediofacial seta on inner or outer plates	1 mediofacial setae on inner plate, none on outer plate	No mediofacial seta on inner or outer plates	No mediofacial seta on inner plate, 1 setae on outer plate
Outer plate of maxilliped	No facial stout seta	No facial stout seta	4 facial stout setae	No facial stout seta
Dactylus of maxilliped	10 seta-like spines	No seta-like spines	4 seta-like spines	10 seta-like spines
Palmar margin of gnathopods 1–2				
Shape	Convex	Slightly convex	Straight	Slightly convex
Setae	7 setae	4 stout setae	6–7 stout setae	7 & 9 stout setae
Ratio of P3/P4 propodus to dactylus	1×	0.3×	0.3×	**0.45×**
Ratio of P5/P6/P7 propodus to dactylus	1×	0.3×	0.3×	**0.6×**
Uropod 3 rami length	Inner longer than outer	Inner longer than outer	Inner longer than outer	**Subequal**
Telson				
Length/max width ratio	2.31	1.96	1.76	1.77
Dorsal-lateral ornamentation	No seta	2 pairs of setae	No seta	No seta
Cleft	75%	19.2%	21%	17.8%

7– Lateral lobes of head strongly produced. Pleon 1–3 usually dorsally toothed, mucronate *Rhachotropis* S.I. Smith, 1883

Rostrum large. Pleon 1–3 smooth..... *Metarhachotropis* Ariyama & Kohtsuka, 2022

8– Gnathopods 1–2 propodus slender, carpus elongate. Maxilla 1 palp short, proximal article longer than distal one.................................. *Eusirella* Chevreux, 1908

– Gnathopods 1–2 propodus, and carpus stout. Maxilla 1 palp normal, proximal article shorter or subequal to distal one 9

9– Eyes lacking. Accessory flagellum 1-articulated . 10

– Eyes present. Accessory flagellum lacking............11

10– Telson tapering, ≥66% cleft, lobes not apically divergent. Peduncle of uropod 1 without distal spiniform process..................................... *Cleonardo* Stebbing, 1888

– Telson not tapering, ≤25% cleft, lobes apically divergent. Peduncle of uropod 1 with distal spiniform process...13

11– Coxae 1–4 small, shallow *Harcledo* Barnard J.L., 1964

– Coxae 1–4 deep 12

12– Pleonites 1–2 dorsally toothed...... *Sennaia* Bellan-Santini, 1997

– All pleonites dorsally smooth ... *Meteusiroides* Pirlot, 1934

13– Pereopod 5–7 dactylus to propodus ratio 0.3×. Uropod 3 outer ramus shorter than inner ramus. Telson lobes apically divergent with blunt apices .... *Dorotea* Corbari, Frutos, & Sorbe, 2019

– Pereopod 5–7 dactylus to propodus ratio 0.6×. Uropod 3 outer and inner rami subequal. Maxilla 1 outer plate with 12 apical stout setae........ *Dulcibella* **gen. nov.**

Dulcibella camanchaca sp. nov. *Weston & González* (Figs 2–5)

Zoobank. https://zoobank.org/NomenclaturalActs/4521ac42-dddd-4bfb-84c8-e30fa9d29f91

Type material. Holotype, mature female, total body length 38.9 mm, MNHNCL AMP-15974, genseq-1 16S (PP960594), genseq-1 COI (PP823946).

Type locality. Atacama Trench, eastern South Pacific Ocean (23°55′S, 71°27′W), IDOOS Expedition, R/V *Abate Molina*, station 1, depth 7902 m.

Etymology. Named for "camanchaca", a dense, low coastal fog that forms by the Atacama Desert and moves inland. "Camanchacas" was also the name given to some of the littoral inhabitants of this desertic region. Finally, "camanchaca" has also been attributed to mean "darkness" in the languages of the peoples from the Andes region and, in our case, signifies the deep, dark ocean from where this species predates.

Diagnosis. Same as for the new genus.

Description. BODY (Fig. 3): *Body* laterally compressed, dorsally smooth. *Colour* before preservation white to light tan. *Oostegites* on coxae 2–5; margins with long setae. *Gills* on pereopods 2–7, simple, oblong.

HEAD (Fig. 3): 0.68× smaller than pereonites 1 + 2. Rostrum short. Lateral cephalic lobe well-developed,

Fig. 2. Post-preservation photo of *Dulcibella camanchaca* gen. nov. sp. nov. Holotype female (MNHNCL AMP-15974).

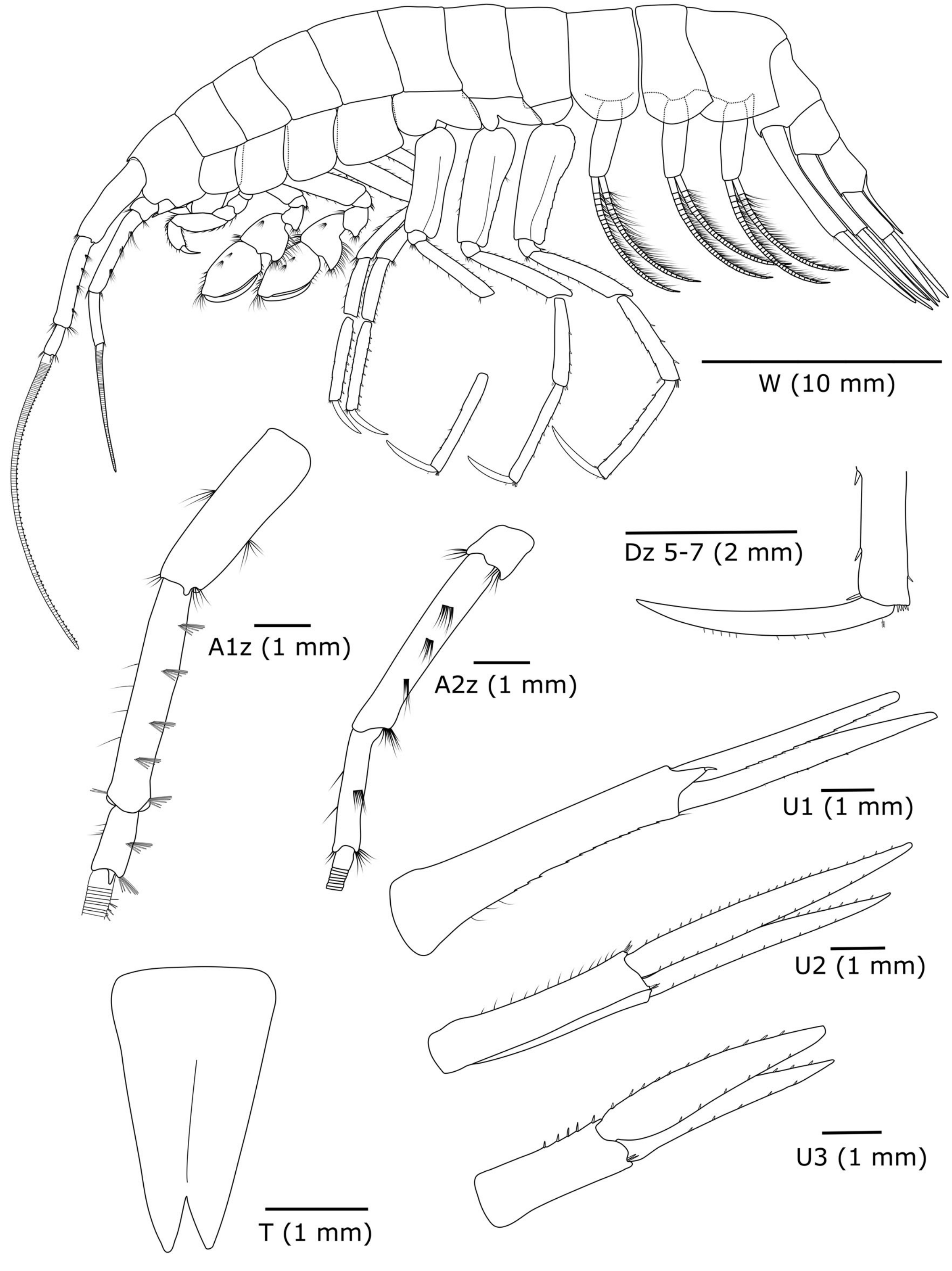

Fig. 3. *Dulcibella camanchaca* gen. nov. sp. nov. Holotype female (MNHNCL AMP-15974). W – whole, left side. A1 – left antenna 1 zoom. A2 – left antenna 2 zoom. D – left dactylus from pereopod 5–7 zoom. U1 – left uropod 1 ventral side. U2 – left uropod 2 dorsal side. U3 – left uropod 3 dorsal side. T – telson.

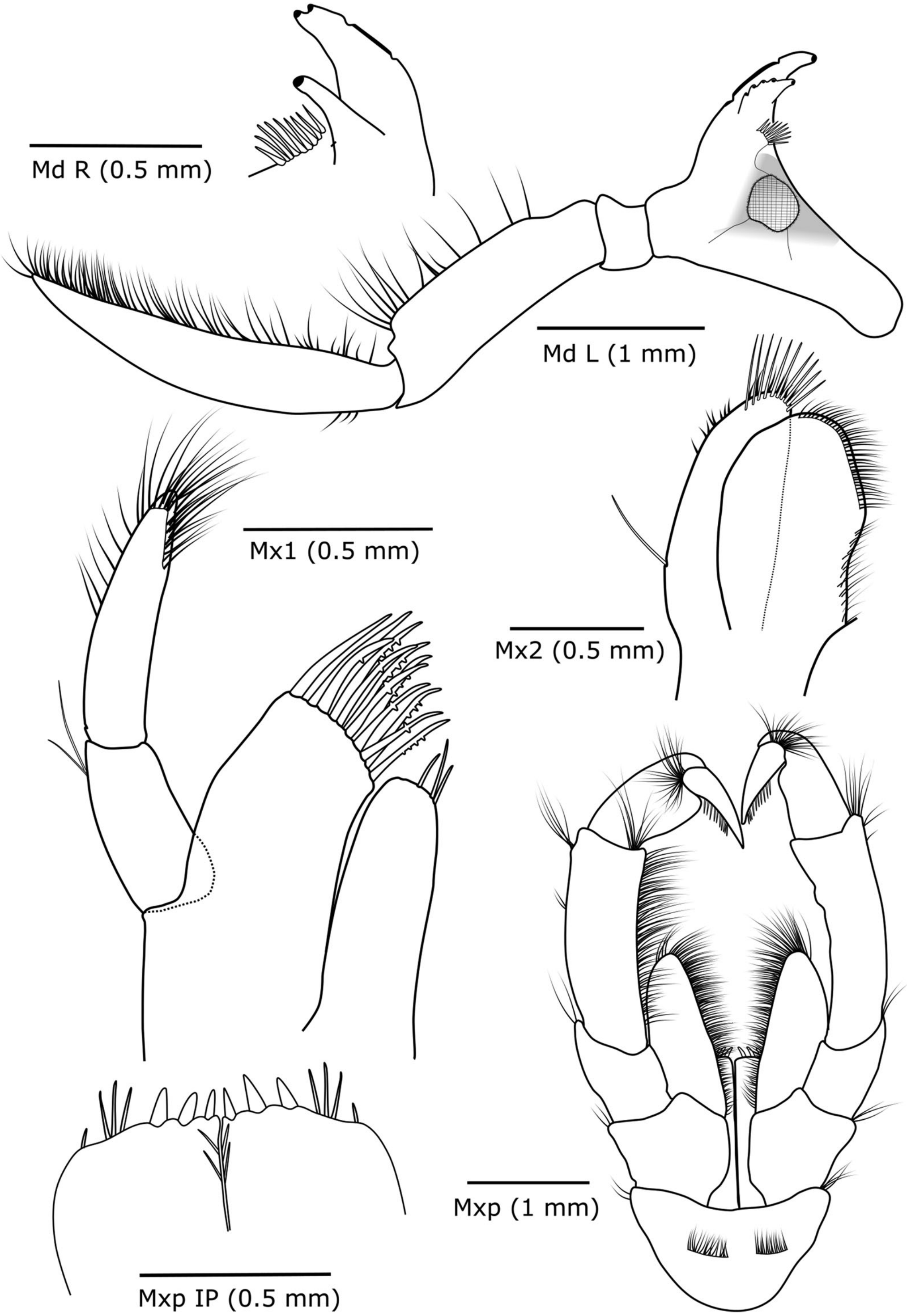

Fig. 4. *Dulcibella camanchaca* gen. nov. sp. nov. Holotype female (MNHNCL AMP-15974). Md R – right mandible zoom. Md L – left mandible. Mx1 – left maxilla 1. Mx2 – left maxilla 2. Mxp – maxilliped whole. Mxp IP – maxilliped inner plate zoom.

broadly rounded; antero-ventral corner subquadrate. Eyes absent prior to preservation. *Antenna 1* 2× longer than antenna 2 and 0.6× as long as body; peduncle 0.8× shorter than main flagellum; article 1 sub-equal to article 2, produced antero-distally hoodlike over base of article 2, 1 rounded antero-distal cusp; article 3 0.3× as

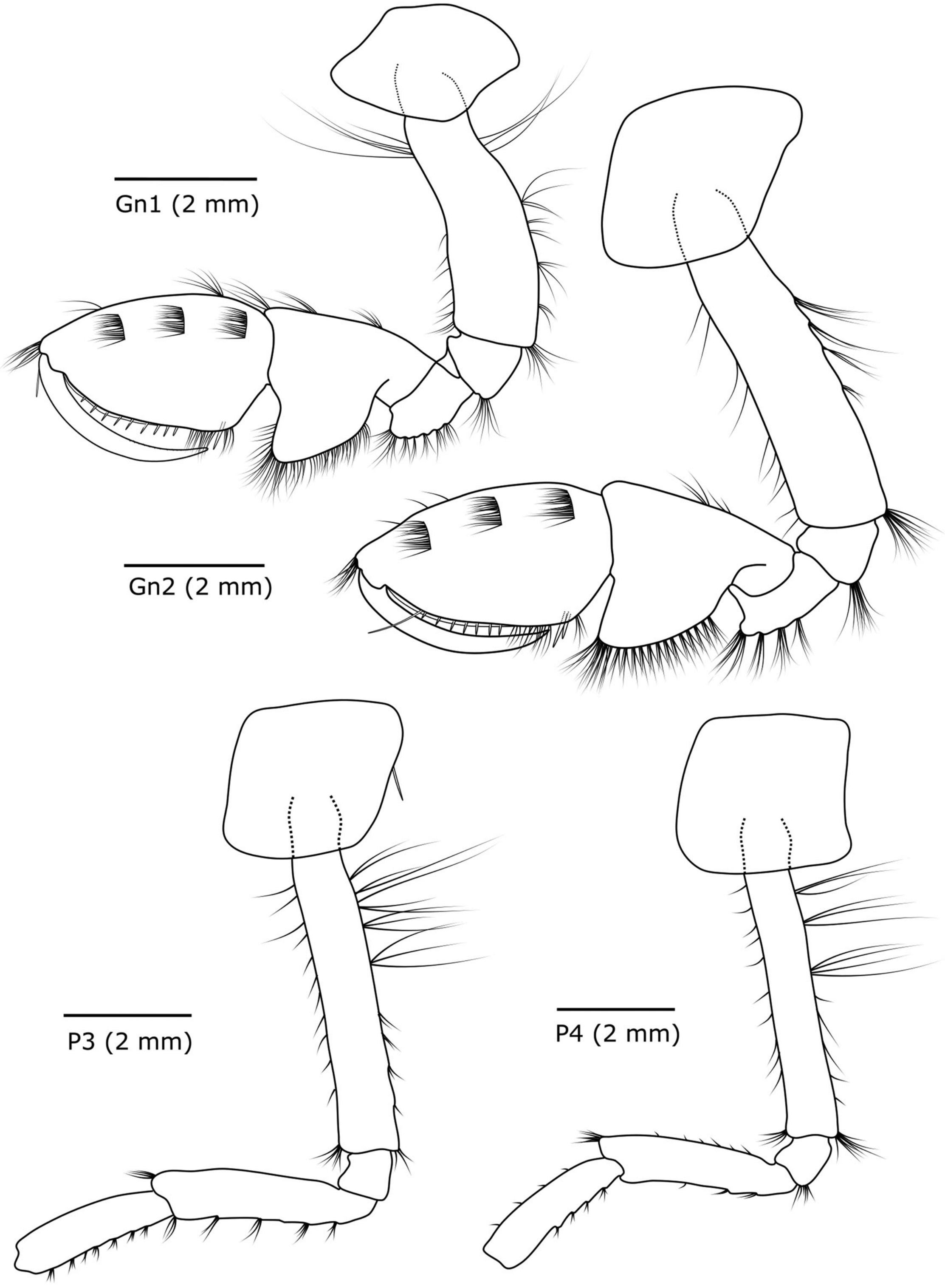

Fig. 5. *Dulcibella camanchaca* gen. nov. sp. nov. Holotype female (MNHNCL AMP-15974). Gn1 – left gnathopod 1. Gn2 – left gnathopod 2. P3 – left pereopod 3. P4 – left pereopod 4.

long as article 2. Flagellum with 152-articulate, calceoli of type 5 [see Lincoln, 1981] present on approximately every third article, proximal article elongate. Accessory flagellum 1-articulate. *Antenna 2* article 4 length 0.8× of article 5. Flagellum with no calceoli, first proximal article elongate, 54-articulate.

Table 2. Species in the Eusiridae family, GenBank sequence accession numbers, and references for phylogenetic analysis of *Dulcibella camanchaca* gen. nov. sp. nov.

Species	16S	COI	Reference
Ingroup			
Cleonardo neuvillei	MZ197459	MZ197284	Kniesz et al., 2022
Cleonardo sp. JW-2019		MN262170	Weston et al., 2021b
Dulcibella camanchaca gen. nov. sp. nov.	PP960594	PP823946	This study
Dorotea papuana		MK260193	Corbari et al., 2015
Eusirus cf. *giganteus*	OK489458	OK489458	Salabao et al., 2022
Eusirus cf. *giganteus*	OK489459	OK489459	Salabao et al., 2022
Eusirus cuspidatus		DQ889150	Costa et al., 2007
Eusirus cuspidatus		FJ581636	Radulovici et al., 2009
Eusirus cuspidatus		FJ581637	Radulovici et al., 2009
Eurirus hirayamae	LC334112		Nakano & Tomikawa, 2018
Eusirus holmi		MG521152	Jażdżewska et al., 2018
Eusirus holmi		MG521143	Jażdżewska et al., 2018
Eusirus holmi		MG521124	Jażdżewska et al., 2018
Rhachotropis abyssalis	OQ622399	OQ622280	Lörz et al., 2023
Rhachotropis abyssalis	OQ622397	OQ622279	Lörz et al., 2023
Rhachotropis abyssalis	OQ622394	OQ622277	Lörz et al., 2023
Rhachotropis aculeata		LC671674	Kodama & Henmi, 2023
Rhachotropis aculeata		LC671675	Kodama & Henmi, 2023
Rhachotropis aculeata		LC671673	Kodama & Henmi, 2023
Rhachotropis chathamensis		GU804300	International Barcode of Life (iBOL)
Rhachotropis chathamensis		GU804298	International Barcode of Life (iBOL)
Rhachotropis chathamensis		GU804299	International Barcode of Life (iBOL)
Rhachotropis helleri		JQ412478	Lörz et al., 2012
Rhachotropis helleri		JQ412484	Lörz et al., 2012
Rhachotropis helleri		JQ412482	Lörz et al., 2012
Rhachotropis inflata		JQ412491	Lörz et al., 2012
Rhachotropis inflata		JQ412493	Lörz et al., 2012
Rhachotropis inflata		JQ412492	Lörz et al., 2012
Rhachotropis lomonosovi		MG521156	Jażdżewska et al., 2018
Rhachotropis macropus		MG521142	Jażdżewska et al., 2018
Rhachotropis macropus		MG521123	Jażdżewska et al., 2018
Rhachotropis macropus		MG521146	Jażdżewska et al., 2018
Rhachotropis marinae		MF409445	Lörz et al., 2018a
Rhachotropis marinae		MF409446	Lörz et al., 2018a
Rhachotropis marinae		MF409444	Lörz et al., 2018a
Rhachotropis rossi		JF498593	Steinke et al., unpublished
Rhachotropis saskia	MN228703	MH272122	Lörz et al., 2018b
Rhachotropis saskia	MH272097	MH272107	Lörz et al., 2018b
Rhachotropis saskia	MH272098	MH272111	Lörz et al., 2018b
Rhachotropis thordisae		MG521140	Jażdżewska et al., 2018
Rhachotropis thordisae		MG521150	Jażdżewska et al., 2018
Rhachotropis thordisae		MG521157	Jażdżewska et al., 2018
Outgroup			
Lanceola sp.		KP713953	Ritchie et al., 2015
Pleuromamma abdominalis	LC078972	LC492499	Hirai, 2020

MOUTHPART BUNDLE (Figs 3, 4): *Epistome* protruding, triangular. *Mandible* left incisor 2-dentate separated by incurved cutting edge, ending in a strong blunt tooth; right incisor 3-dentate with concave cutting edge, ending in bifurcated strong teeth; left lacinia mobilis 5-toothed, ending in a strong tooth, the others much smaller; right lacinia mobilis single-toothed. Molars medium, triturative, grinding surface ringed by short blades, higher than wide. Setal rows with 9 setae. Palp 3-articulate, elongate; article 3 1.5× longer than article 2, slightly sickle-shaped, tapering distally; article 2 1.4× wider than article 3. *Maxilla 1* inner plate with 3 subapical setae; outer plate with 12 apical stout setae (11 cuspidate and 1 simple); palp 2-articulate, article 1 with 2 simple setae on outer margin, article 2 1.6× the length of article 1 with 2 rows of simple setae on distal half inner margin and 6 simple setae on distal half outer margin. *Maxilla 2* inner plate 1.4× broader

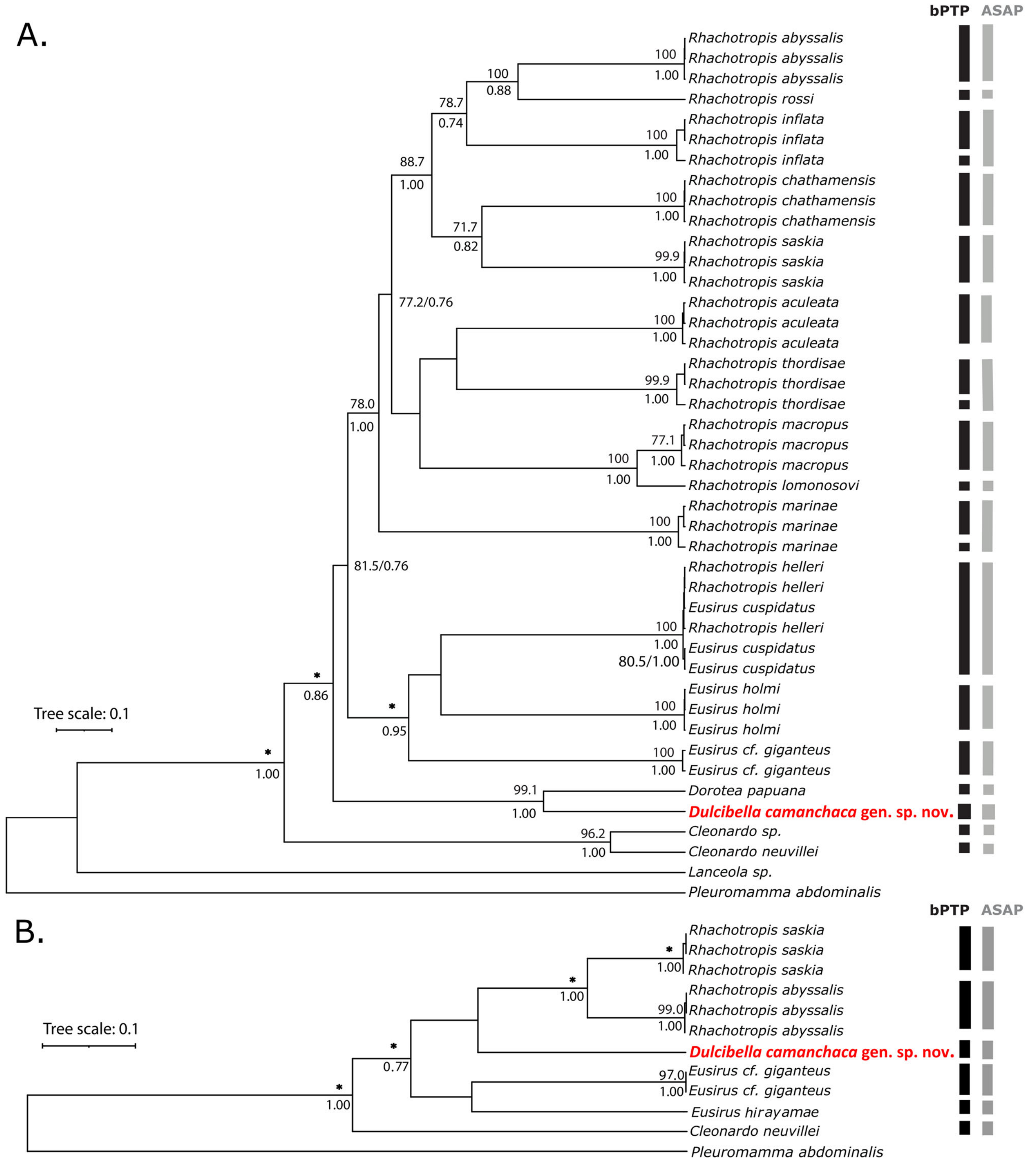

Fig. 6. Bayesian phylogeny showing the inferred relationship of *Dulcibella camanchaca* gen. nov. sp. nov. (red bold) within the Eusiridae family based on (A.) COI (413 bp) and (B.) 16S (328 bp). References for comparative sequences are in Table 1. Branch nodes have maximum likelihood bootstrap support values (top) and Bayesian posterior probabilities (below). Values less than 70 or 0.7 are not stated or depicted by an asterisk. Species delimitation inferences by the bPTP and ASAP analyses are presented on the right side of the phylogeny.

Table 3. Pairwise p-distances (minimum–maximum) within and among available genera in the Eusiridae family based on COI alignment (413 bp).

Genus	*Cleonardo*	*Dorotea*	*Dulcibella*	*Eusirus*	*Rhachotropis*
Cleonardo	0.1131				
Dorotea	0.2720–0.2755				
Dulcibella	0.2508–0. 2653	0.1733			
Eusirus	0.1860–0.2653	0.1759–0.2317	0.1808–0.2325	0.1773–0.2295	
Rhachotropis	0.2118–0.2809	0.2290–0.2618	0.2016–0.2539	0.1442–0.2618	0.0955–0.2623

and 0.9× shorter than outer plate, submarginal row of simple setae on distal half inner margin, medial setae proximal inner margin; outer plate with apical simple setae, 1 long simple setae proximal outer margin. *Maxilliped* ordinary, heavily setose; inner plate with 3 stout apical spines, 4 setae on apical margin; outer plate large reaching 0.4× length of palp article 2; palp, 4-articulate, ordinary, inner margin of article 4 with 10 robust setae.

PEREON (Figs 3, 5): *Coxae* 1–4 medium, about as deep as broad, subquadrate, ventral margin rounded. Coxa 1 0.7× shorter than coxae 2–4, not produced distally. Coxa 3 bearing one long stout seta on posterior margin. Coxa 4 weakly excavate posteriorly. Coxae 5–6 posterolobate. Coxa 7 smallest, unilobate. *Gnathopods 1–2* similar, subequal, strongly subchelate. Merus strongly spinose, strongly produced and rounded ventral margin; carpal lobes broadly pronounced and rounded; propodus ovate; palm strongly oblique, 2× length of carpus attachment margin, with 9 (G1) and 7 (G2) stout setae, proximally limited by 1 (G1) or 2 (G2) stout setae for dactylus insertion, one long sub-proximal setae on palm of G2; dactylus curved, one long sub-proximal setae on anterior margin of G1, posterior margin sparsely setulated. *Pereopods 3–4* ordinary; merus 1.2× longer than carpus; dactylus 0.45× of propodus length, simple, weakly styliform and slightly curved. *Pereopods 5–7* homopodous, elongate, simple; basis with small rounded posterodistal lobe, posterior margin of P6–7 basis slightly denticulate; dactylus simple, weakly styliform and slightly curved, 0.6× of propodus length.

PLEON (Fig. 3): *Epimeron 1* posterodistal corner rounded. *Epimeron 2* posterodistal corner subquadrate with a tiny cusp. *Epimeron 3* posterodistal corner quadrate. No setae on distal margins.

UROSOME (Fig. 3): *Uropod 1* peduncle 1.1× longer than rami, with a row of short stout setae on outer margin, blunt distoventral process bearing a distal stout seta; inner ramus 1.2× longer than outer, stout setae on outer margins. *Uropod 2* peduncle 0.8× length of rami, stout setae on inner margin; inner ramus 1.2× longer than outer; inner and outer margin of both rami with stout setae. *Uropod 3* peduncle 0.7× length of rami, stout setae on inner margin; inner ramus subequal outer one; inner and outer margins of both rami with stout setae, except at apex. *Telson* elongated, 1.8× as long as broad, cleft 17.8%, lobes apically divergent with blunt apices, without distal armament.

Habitat and ecology. *Dulcibella camanchaca* gen. nov. sp. nov. is known only from the type locality at the Atacama Trench. Further sampling may reveal this species' wider vertical range and distribution across the trench. As an eurisid with a long, slender body and robust gnathopods, this amphipod is considered to have a predatory lifestyle. This predator was collected in the trap with two scavenging amphipods, *Eurythenes atacamensis* and Stegocephalidae gen. sp., where *Eurythenes atacamensis* were highly dominating in abundance.

Molecular identification and phylogenetics. The holotype of *Dulcibella camanchaca* gen. nov. sp. nov. was sequenced, annotated, and deposited to GenBank for the partial mitochondrial barcoding regions 16S (439 bp; PP960594) and COI (642 bp; PP823946).

Dulcibella camanchaca gen. nov. sp. nov. was supported as a distinct genus within the Eusiridae family based on the DNA barcoding data (Fig. 6). *Dulcibella camanchaca* gen. nov. sp. nov. was phylogenetically placed as sister to *Dorotea papuana* Corbari, Frutos, & Sorbe, 2019, with high support values (BI = 1.00, ML = 99.1), based on the COI phylogeny (Fig. 6A). The species delimitation analyses concurrently delineated *Dulcibella camanchaca* gen. nov. sp. nov. as distinct from *Dorotea* with a p-distance difference of 17.3% (SI Table 1; Table 3). *Dulcibella camanchaca* gen. nov. sp. nov. averaged 22.9% pairwise p-distance among the family, with a maximum difference of 26.5% with *Cleonardo* sp. JW-2019.

Across the family, the two methods delineated different numbers of species within the COI phylogeny, with 20 species per bPTP and 17 species per ASAP (Fig. 6A). Specifically, this delineation discordance was present within individuals identified as *Rhachotropis inflata* (G.O. Sars, 1883), *Rhachotropis thordisae* Thurston, 1980, and *Rhachotropis marinae* Lörz, Jażdżewska & Brandt, 2018. Additionally, specimens with *Rhachotropis helleri* (Boeck, 1871) and *Eusirus cuspidatus* Krøyer, 1845 identifications were delineated as the same species by both methods. The p-distance differences averaged 23.2% among the genera, and the within-genera averaged 11.3% for *Cleonardo*, 20.4% for *Eusirus*, and 21.4% for *Rhachotropis* (Table 3).

Discussion

The Atacama Trench hosts a distinctive faunal community, and *Dulcibella camanchaca* gen. nov. sp. nov. adds to the high degree of endemism found at hadal depths. Most notably, *Dulcibella camanchaca* gen. nov. sp. nov. contrasts with the other known hadal-dwelling amphipods of the Atacama Trench by having a predatory rather than a scavenging lifestyle. This predatory lifestyle is evidenced by their raptorial gnathopods, slender and agile body morphology, and mouthparts primed for shredding.

Morphologically *Dulcibella camanchaca* gen. nov. sp. nov. strongly fits in the Eusiridae family, particularly the powerful subchelate gnathopods and accessory flagellum of antenna 1 being 1-articulated (Figs 3, 4). At the first examination, *Dulcibella camanchaca* gen. nov. sp. nov. is most closely aligned with *Dorotea*, particularly with the spiniform process on uropod 1 and an elongate but weakly cleft telson (Fig. 3). These two distinctive characters are only seen in *Dorotea* and *Dulcibella*, although their function remains unknown. The cleft state follows the findings of Verhey et al. (2016), who found the cleft to be highly homoplasious and challenged using cleftness to characterize taxonomic groups. However, the combination *Dulcibella camanchaca* gen. nov. sp. nov. possesses a unique combination of novel characteristics. The most unique one within the family is the outer plate of the maxilla 1, having 12 apical spines; across the family, the number of spines is either 10 or 11 (Bousfield & Hendrycks, 1995). This additional spine's function is unclear, possibly a response to food preference (Fig. 4; Watling, 1993). Another distinguishing feature is the relative length of the pereopod dactyli, which is longer than that of *Dorotea* but shorter in *Cleonardo* (Fig. 3; Table 1). The length and slenderness of the dactylate pereopods appear to be an important functional trait for Eusiridae, representing an indicator of the habitat substrate type in which they await their prey (Bousfield & Hendrycks, 1995). Corbari et al. (2019) suggested that *Dorotea*'s short dactyli indicated a hard substrate preference, as opposed to long-dactyli for soft bottom sediment. *Dulcibella camanchaca* gen. nov. sp. nov. have medium-length dactyli, suggesting that a combination of soft and hard sediment types may be available to them, thus increasing the chances of predatory success in the food-limited environment.

The DNA barcoding supported the phylogenetic distinctness of *Dulcibella camanchaca* gen. nov. sp. nov., providing a secondary line of robust evidence for raising a new genus (Fig. 6). *Dulcibella* was 17.3% different in p-distance from *Dorotea papuana*, falling beyond the benchmark of genus differentiation at >15% (Costa et al., 2007; Jażdżewska & Mamos, 2019). Their monophyletic placement on the COI tree reflects the morphological similarities shared among *Dorotea* and *Dulcibella*, particularly the weakly cleft telson and a distal spiniform process on the peduncle of uropod 1 (Fig. 6). However, contrary to the shared morphological features and name legacy, *Cleonardo* was placed basal to all other Eusirid genera. Noteworthily, the COI phylogeny only captures some of the described Eusirid diversity, with the nine genera missing baseline representation and most species missing from the represented genera. Of the presented Eusiridae diversity, the p-distances for within-genera *Eusirus* and *Rhachotropis* were elevated, suggesting higher and cryptic genera diversity (e.g., Mohrbeck et al., 2021). The Eusiridae family has been systematically dynamic, with the temporary inclusion of three other families in Eusiridae and the moving of Eusiridae from the suborder Senticaudata Lowry & Myers, 2013 into the suborder Amphilochidea Boeck, 1871 (Barnard & Karaman, 1991; Lowry & Myers, 2013, 2017). Future efforts should focus on phylogenetic systematics across the Eusiridae family and superfamily, which may lead to the discovery of cryptic diversity and systematic reorganization.

The presence of predators in the traps was unexpected. Compared with other hadal ecosystems, the Atacama Trench could be considered well-sampled for amphipods, which are the best-sampled hadal taxa (Jamieson & Weston, 2023), with six expeditions deploying at least 13 baited traps to depths >6000 m in the regional proximity of Richard's Deep (Ingram & Hessler, 1987; Thurston et al., 2002; Fujii et al., 2013; Weston et al., 2021a; Gonzalez et al., unpublished). However, a non-scavenging species had not been collected or noted in the video by any of those sampling events (Fujii et al., 2013; Linley et al., 2022; Swan et al., 2021; Thurston et al., 2002; Weston et al., 2021a). Additionally, two specimens of Stegocephalidae gen. sp. were recovered in the traps and will be described in a subsequent effort. The reason for their collection in the 2023 IDOOS traps is unknown. One speculative possibility is using chicken for bait instead of fish, such as mackerel, which may produce a differential odour plume (Sainte-Marie, 1992). Another possibility is that this station's seafloor habitat varied enough from other sampled depths, possibly supporting a slightly different community composition (Stewart & Jamieson, 2018). Unfortunately, the camera was non-functional on the seafloor. Regardless of the driving reason, the presence of *Dulcibella camanchaca* gen. nov. sp. nov. highlights that a higher sampling intensity is required to reach the asymptote on a species-accumulation curve, thus fully characterizing the diversity on the benthos (Ugland et al., 2003). Achieving this for amphipods and other fauna groups will require wider geographic and bathymetric sampling and a broader combination of sampling tools (Weston & Jamieson, 2022).

Dulcibella camanchaca gen. nov. sp. nov. is only known from the type locality of 7902 m, and future efforts will be important to expand the understanding of its full bathymetric range and role in the food web. The Atacama Trench hadal community is interesting because megafaunal predators, snailfishes such as *Paraliparis selti*, and decapods apparently do not extend deeper than ~7200 m, which is shallower than their physiological limit (Jamieson et al., 2021; Linley et al., 2022; Swan et al., 2021). Weston et al. (2021a) suggested that the bathymetric limit of snailfishes may influence the ontogenetic distribution of the predominant amphipod species, *Eurythenes atacamensis*, whereby large juveniles and females dominate below these depths, and small juveniles are at shallower depths with low hydrostatic pressure. It may be possible that *Dulcibella camanchaca* gen. nov. sp. nov. in part fills this predatorial niche at depths >7200 m. Eusiridae are known to predate lysianassoid amphipods. Even though *Dulcibella camanchaca* gen. nov. sp. nov. is large, displaying the pattern of deep-ocean gigantism (McClain et al., 2006; Timofeev, 2001), it is still smaller than the robust ~70 mm *Eurythenes atacamensis*, which likely puts it out of predatorial reach. More plausibly, *Dulcibella camanchaca* gen. nov. sp. nov. may predate on the smaller (~10 mm) *Hirondellea* spp. (Kilgallen, 2015), which were not collected during the IDOOS expedition owing to the trap hole size. Future work with higher available specimen numbers should perform gut content and stable isotope analyses to identify its food source and trophic placement more definitely and to understand the hadal food web in the eutrophic Atacama Trench.

Broadly, predatory Eusirid species are a present member of the hadal community, albeit in small numbers. Jamieson and Weston (2023) summarized that there are at least four genera with eight species across nine features. Of these hadal species, the most distinctive of the Eusiridae is *Rhachotropis*, with large species such as *Rhachotropis saski* Lörz & Jażdżewska, 2018 having a 3280 m bathymetric distribution in the Kuril-Kamchatka Trench (Lörz et al., 2018b). *Dulcibella camanchaca* gen. nov. sp. nov. expands these records by one more, representing the first record in the eastern South Pacific Ocean. Additionally, more species of *Dulcibella* may be present in the Pacific Ocean, with a non-public genetic record on BOLD from the Clarion-Clipperton Zone being ~90% similar to *Dulcibella camanchaca* gen. nov. sp. nov. While recognizing low data resolution, hints of a generalized biogeographic pattern of genera distribution may be present, with *Cleonardo* in the Indian Ocean, *Eusirella* and *Eusirus* in the Atlantic and western South Pacific, *Rhachotropis* in the North Pacific, and *Dulcibella* in the eastern South Pacific. Weston et al. (2022) showed clear regional clades of the scavenger *Bathycallisoma schellenbergi* (Birstein & Vinogradov, 1958) globally. A combination of hadal-feature intrinsic factors, such as temperature and dissolved oxygen, and the degree of geographic isolation drove the partitioning of distinct populations (Jamieson et al., 2010; Glud et al., 2021; Linley et al., 2022; Weston et al., 2022). For Eusiridae, if a biogeographic pattern is supported, this may provide insights towards understanding the drivers and timing of colonization and diversification across the hadal zone.

In summary, the ultra-deep ocean is ripe for discovering new species. Through an integrative approach, *Dulcibella camanchaca* gen. nov. sp. nov. represents another endemic species and predator in the Atacama Trench and may be one of the few megafaunal predators at depths >7200 m.

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Author contributions

JNJW: Conceptualization, Investigation (equal), Visualization, Writing (equal). CEG: Conceptualization, Specimen Collection, Data Curation, Methodology, Resources, Investigation (equal), Visualization, Writing.

RE: Funding Acquisition, Project Administration, Resources, Supervision, Writing – Review & Editing. OU: Funding Acquisition, Project Administration, Resources, Supervision, Writing – Review & Editing.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Supplemental material

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Data availability statement

All genetic sequences have been deposited into NCBI GenBank under accession numbers PP960594 and PP823946. The holotype is deposited at the Museo Nacional de Historia Natural, Santiago, Chile under number AMP-15974

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