Article

Towards a better understanding of deep-sea tardigrade biogeography: numerous new records from the Southern Ocean

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Abstract

To date, only eight species of marine tardigrades have been recorded from the Southern Ocean. A total of 1210 tardigrade specimens were collected during various marine expeditions with R/V POLARSTERN: ANDEEP-1, ANDEEP-2, ANDEEP-3 and ANDEEP-SYSTCO. The sampled tardigrades belong to five families (Batillipedidae, Coronarctidae, Halechiniscidae, Styraconyxidae and Echiniscoididae), seven genera (*Batillipes*, *Coronarctus*, *Moebjergarctus*, *Angursa*, *Styraconyx*, *Tholoarctus*, *Isoechiniscoides*) and 15 species (*Batillipes wyedeleinorum*, *Coronarctus dissimilis*, *Coronarctus tenellus*, *Coronarctus* cf. *tenellus*, *Moebjergarctus clarionclippertonensis*, *Angursa* sp., *A. abyssalis*, *A. antarctica*, *A. capsula*, *A. lanceolata*, *A. lingua*, *Styraconyx qivitoq*, *S. takeshii*, *Tholoarctus oleseni*, *Isoechiniscoides* aff. *sifae* sp. can.). For the genera *Batillipes*, *Coronarctus*, *Moebjergarctus*, *Tholoarctus* and *Isoechiniscoides*, these new distribution data are the southernmost records and first reports from the Southern Ocean. Furthermore, the genera *Styraconyx*, *Batillipes* and *Isoechiniscoides* are reported from the abyssal zone for the first time. These new findings significantly expand our previous knowledge of both geographic and bathymetric distribution of marine Tardigrada.

Key words: Tardigrada, meiofauna, abyssal fauna, taxonomy

Introduction

Tardigrada is a phylum of microscopic invertebrates within Panarthropoda and is likely the sister group of Arthropoda (Schmidt-Rhaesa 2001; Dunn *et al.* 2014). Species of this phylum may live in almost every kind of habitats that contain at least a thin film of water and can occur even in deserts but also down to the abyssal plains (Artois *et al.* 2011). They are famous for their ability to survive in harsh environmental conditions, such as desiccation or freezing, but this applies mainly to limno-terrestrial species rather than to marine species (Nelson *et al.* 2015, Jørgensen & Møbjerg 2015). Limno-terrestrial tardigrades (class Eutardigrada) have a relatively uniform external morphology across the majority of species: a barrel-shaped body with four pairs of lobopodous legs terminated with claws. Marine tardigrades (class Heterotardigrada excluding most Echiniscoidea) are characterized by not only a greater variety of foot morphologies, as exemplified by the genus *Batillipes*, whose representatives have suction discs on their toes as an adaptation to rather turbulent habitats (Kristensen & Renaud-Mornant 1983), but also by various body shapes, enlarged sensory organs, and some further unique structures such as alae and caesti (procuticular processes, see, *e.g.* Fontoura *et al.* 2017). For example, in the genus *Florarctus*, alae are strongly developed as floating devices, while species of the genus *Tanarctus* possess long, hair-like, or branched sensory organs on the leg IV (Kristensen & Renaud-Mornant 1983, Fontoura *et al.* 2017).

Marine species are far less known than limno-terrestrial ones, especially from the deep sea and the polar regions. The main gaps concern species diversity, geographic and bathymetric distribution, ecology and organism biology such as ontogenesis or cryptobiosis (Kaczmarek *et al.* 2015, Nelson *et al.* 2015, Jørgensen & Møbjerg 2015). Given the incomplete knowledge of deep-sea tardigrades, particularly those of the genus *Angursa*, every new record is highly valuable. Even sporadic findings can gradually enhance our understanding of the species' distribution ranges and ecological requirements. Several species regarded hitherto as endemic or at least with restricted distribution, more likely have ocean-wide if not cosmopolitan distributions (Fujimoto & Hansen 2019, Trokhymchuk & Kieneke 2024).

There are different definitions of the boundaries (limits) of the Southern Ocean depending on the source to which one refers (*e.g.* IHO 1953, IHO 2000). Some of our research areas are rather located in the South Atlantic Ocean, but in the paper we will use "Southern Ocean" for a more simplified perception. Additionally, we will indicate more precise sea regions in the biogeographical sections (see Tables). It is well-known that the Southern Ocean has played a pivotal role in the evolution of various groups of deep-sea invertebrates such as Isopoda, Octopoda and Hirudinea (Brandt *et al.* 2007, Strugnell *et al.* 2008, Utevsky *et al.* 2023). Our current study aims to add some new data of a so-far only weakly investigated taxon in this region, namely the Tardigrada.

Only eight marine tardigrade species/subspecies have been reported from the Southern Ocean so far: *Angursa antarctica* Víllora-Moreno, 1998 from 352 and 416 m depth off Livingston Island, and 149 m depth from Lützow Holm Bay; *Bathyechiniscus tetronyx* Steiner, 1926 from 385 m depth of Gauss Station of East Antarctica; *Styraconyx takeshii* Fujimoto *et al.*, 2020 from 149 m depth of Lützow-Holm Bay; *Styraconyx* cf. *qivitoq* Kristensen & Higgins, 1984 from 149 m depth of Lützow-Holm Bay; and littoral species: *Neoechiniscoides horningi* Miller & Kristensen, 1999 from Aerial Cove, Macquarie Island; *Echiniscoides porphyrae* De Zio Grimaldi *et al.*, 2000 from Macaroni Bay, Prince Edwards Islands; *Echiniscoides verrucariae* De Zio Grimaldi *et al.*, 2000 from Macaroni Bay, Prince Edwards Islands and *Echiniscoides travei* Bellido & Bertrand, 1981 from Port Bizet, Île Longue, Kerguelen Islands (Steiner 1926, Bellido & Bertrand 1981, Sáiz-Salinas *et al.* 1997, Víllora-Moreno 1998, Miller & Kristensen 1999, De Zio Grimaldi *et al.* 2000, Fujimoto *et al.* 2020).

Our study aims to summarise the available and new data about the Southern Ocean marine tardigrades. With these combined data, we furthermore aim to provide answers to the following general research questions (RQs):

RQ 1. Do deep-sea tardigrade species show either endemic, or cosmopolitan patterns of distribution? Biogeographical studies of meiofauna such as nematodes show that only one-third of all families are cosmopolitan, while even more than 90% of genera are endemic in terms of habitat and depth (especially in the deep sea, see Danovaro & Gambi 2022). The initial assumption of the "Everything is everywhere but environment selects" hypothesis at least in limno-terrestrial tardigrades likely does not reflect an actual state for many species (Artois *et al.* 2011; Morek *et al.* 2021; Gąsiorek 2023), although cryptobiotic stages can be transported over long distances (*e.g.* by wind or birds). Traditional taxonomic studies (i.e., those not yet using DNA sequence data) have already demonstrated that so-called "cosmopolitan" species are often complexes of multiple species, each with more restricted distribution ranges (see Darling & Carlton 2018, Santos *et al.* 2019, Gąsiorek 2023 and references therein). A recent phylogeographic study furthermore demonstrated that many species of the limno-terrestrial taxon *Milnesium* are restricted to single zoogeographic realms, with instances of long-distance dispersal being very rare and ancient (Morek *et al.* 2021). Molecular studies of marine Tardigrada are sparse, focusing mostly on phylogeny and taxonomy (*e.g.* Jørgensen *et al.* 2010, Fujimoto *et al.* 2020).

RQ 2. Do marine tardigrade species have preferences in their bathymetric distribution? Marine tardigrades are known from all depths. Among many genera, such as *Angursa*, there are both shallow and deep-water species, and some representatives occur along the whole depths range (Fujimoto & Hansen 2019, Trokhymchuk & Kieneke 2024). However, other genera, such as *Moebjergarctus*, are currently known only from the abyssal zone (Bai *et al.* 2020, Saulenko *et al.* 2022, Wang *et al.* 2023).

RQ 3. Is there a change in Tardigrada density with depth, such as an increase or decline? For several meiofaunal taxa that occur in abyssal depths of the Southern Ocean, including Tardigrada, it was reported that there is a decrease of abundances with depth (Gutzmann *et al.* 2004). Here, we aim to test this pattern using our expanded dataset, which covers a much larger depth range than earlier studies.

Materials and methods

Samples were collected during ANDEEP-I (PS61/3), ANDEEP-II (PS61/4, ANDEEP-III (PS67) and ANDEEP-SYSTCO (PS71) expeditions of the R/V Polarstern. Samples were taken along a depth gradient reaching from 1,088 m to 5,194 m at various stations of the Atlantic sector of the Southern Ocean (Fig. 1; Table 1; Sup. Table 2.1, 2.2; see Poore 2002, Arenas & Fahrbach 2005, Bathmann 2010). Operations of the sampling devices, winches and all works related with samples processing on the vessel were carried out by responsible teams of crew members and expedition participants (scientists and technicians).
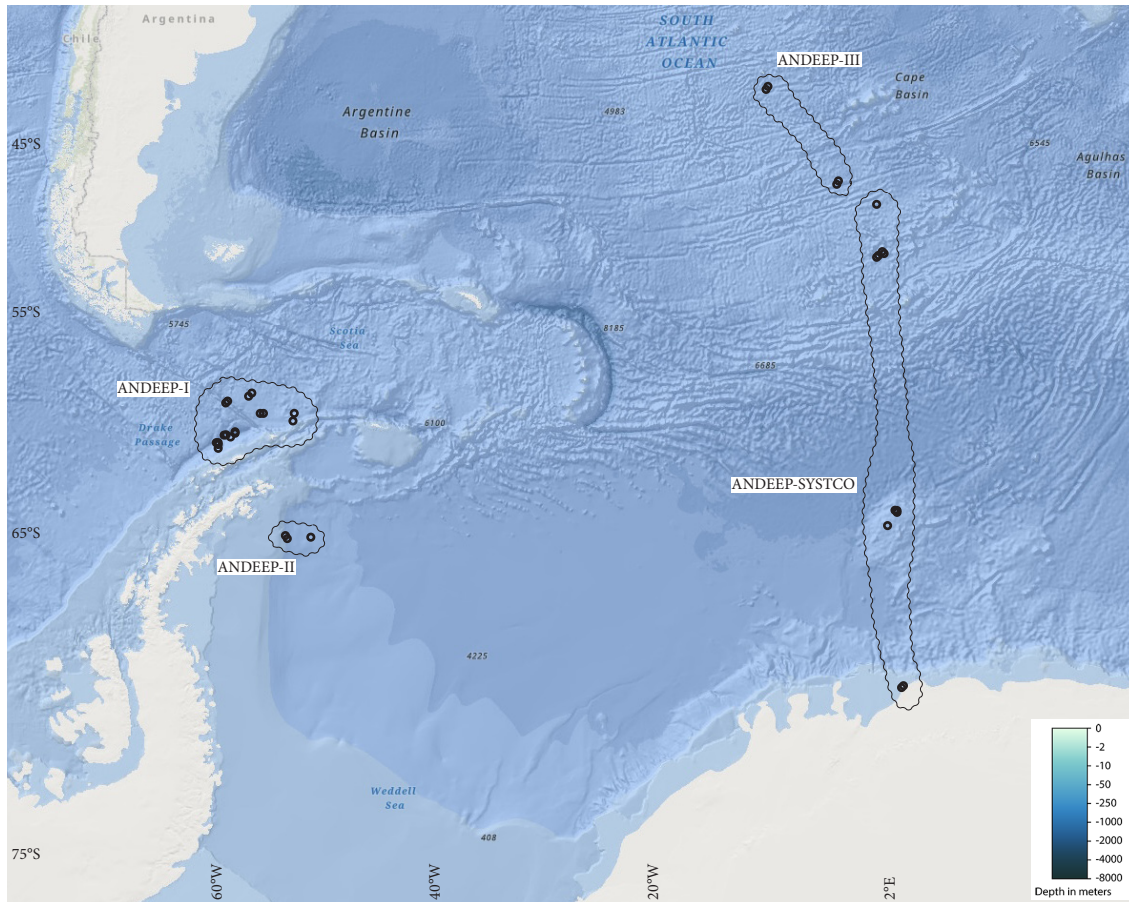
FIGURE 1. Atlantic sector of the Southern Ocean with all sampling stations (multiple corer or box corer) of expeditions ANDEEP-1 to 3 and ANDEEP-SYSTCO (encircled with black line) that yielded Tardigrada. Base map obtained from Bathymetric Data Viewer (www.ncei.noaa.gov/maps/bathymetry).

Samples were taken with a Barnett-Watson multiple corer (MUC) equipped with 12 core tubes of 57 mm internal diameter (25.5 cm² surface area, see Barnett *et al.* 1984) for ANDEEP-I and ANDEEP-II expeditions. In addition, the meiofauna was also analysed from two deployments of the box corer (0.5 × 0.5 m box; 2,500 cm² surface area). Sediment type for ANDEEP-I and ANDEEP-II was sand with silt (Poore 2002).

Samples were taken with a multiple corer (MUC) equipped with 10 core tubes of 95 mm internal diameter (70.85 cm² surface area) for the ANDEEP-III expedition. Sediment type for ANDEEP-III was sand (Arenas & Fahrbach 2005). For the ANDEEP-SYSTCO expedition samples were collected with a multiple corer (MUC) equipped with 12 plexiglass core tubes of 94 mm internal diameter (69.36 cm² surface area). In addition, the meiofauna was also analysed from one deployment of the box corer (0.5 × 0.5 m box; 2,500 cm² surface area). Sediment type for ANDEEP-SYSTCO was silt (Bathmann 2010). From every MUC deployment of each expedition, 1 to 3 sediment cores were sliced down to 20 cm (0–1 cm, 1–2 cm, 2–3 cm, 3–4 cm, 4–5 cm, 5–7 cm, 7–10 cm, 10–15 cm, 15–20 cm). However, tardigrades were only present in sediment layers not deeper than 5 cm. For the current study, we will not consider the small-scale distribution of Tardigrada inside the sediment.

TABLE 1. All corer deployments of expeditions ANDEEP 1, 2, 3 and ANDEEP-SYSTCO that contained Tardigrada. For two deployments at the Shona Ridge, no information about position and depth was available. GKG: boxcorer with 0.25 m² sampling area, MUC (A): multicorer with 0.25 m² sampling area, MUC (B): multicorer with 70.85 cm² sampling area per core tube, MUC (C): multicorer with 25.5 cm² sampling area per core tube, MUC (C): multicorer with 25.5 cm² sampling area per core tube

sea region	deployment	latitude	longitude	depth [m]	device	date	expedition	notes
N-W Cape Basin	PS67_016-6	41°7.61'S	9°56.05'W	4719	MUC (A)	25.01.2005	ANDEEP-III	
N-W Cape Basin	PS67_016-8	41°7.82'S	9°56.11'W	4726	MUC (A)	26.01.2005	ANDEEP-III	
S-W Cape Basin	PS67_021-4	47°40.00'S	4°15.13'W	4559	MUC (A)	29.01.2005	ANDEEP-III	
S-W Cape Basin	PS67_021-6	47°39.36'S	4°15.66'W	4564	MUC (A)	29.01.2005	ANDEEP-III	
S-W Cape Basin	PS71_90-2	49°0.95'S	0°0.03'E	n.a.	MUC (B)	29.01.2008	ANDEEP-SYSTCO	echosounder failure
Cape Basin Shona Ridge	PS71_013-12	52°2.22S	0°1.04'W	3000	MUC (B)	06.12.2007	ANDEEP-SYSTCO	
Cape Basin Shona Ridge	PS71_013-14	52°2.25S	0°1.11'W	2997	MUC (B)	06.12.2007	ANDEEP-SYSTCO	
Cape Basin Shona Ridge	PS71_85-5	52° 1.20' S	0° 0.20' E	2981	MUC (B)	26.01.2008	ANDEEP-SYSTCO	
Cape Basin Shona Ridge	PS71_85-7	52° 1.53' S	0° 0.16' E	2996	MUC (B)	27.01.2008	ANDEEP-SYSTCO	
Cape Basin Shona Ridge	PS71_019-12	n.a.	n.a.	n.a.	MUC (B)	n.a.	ANDEEP-SYSTCO	no info available
Cape Basin Shona Ridge	PS71_0187-12	n.a.	n.a.	n.a.	MUC (B)	n.a.	ANDEEP-SYSTCO	no info available
Lazarev Sea Maud Rise	PS71_39-10	64°28.83'S	2°52.48'E	2151	MUC (B)	03.01.2008	ANDEEP-SYSTCO	
Lazarev Sea Maud Rise	PS71_39-12	64°28.83'S	2°52.53'E	2151	MUC (B)	03.01.2008	ANDEEP-SYSTCO	
Lazarev Sea Maud Rise	PS71_39-14	64°28.84'S	2°52.49'E	2151	MUC (B)	03.01.2008	ANDEEP-SYSTCO	
Lazarev Sea Antarctic Shelf	PS71_017-12	70°4.86'S	3°22.59'W	1927	MUC (B)	22.12.2007	ANDEEP-SYSTCO	
Lazarev Sea Antarctic Shelf	PS71_017-13	70°4.97'S	3°21.54'W	1977	GKG	22.12.2007	ANDEEP-SYSTCO	
Lazarev Sea Antarctic Shelf	PS71_017-14	70°4.80'S	3°22.71'W	1960	MUC (B)	22.12.2007	ANDEEP-SYSTCO	

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TABLE 1. (Continued)

sea region	deployment	latitude	longitude	depth [m]	device	date	expedition	notes
Weddell Sea	PS61/4_131-7	65°19.45'S	51°30.97'W	3057	MUC (C)	06.03.2002	ANDEEP-II	
Weddell Sea	PS61/4_133-6	65°20.18'S	54°14.36'W	1120	MUC (C)	07.03.2002	ANDEEP-II	
Weddell Sea	PS61/4_133-8	65°20.09'S	54°14.72'W	1088	MUC (C)	07.03.2002	ANDEEP-II	
Weddell Sea	PS61/4_133-10	65°20.30'S	54°14.67'W	1109	MUC (C)	07.03.2002	ANDEEP-II	
Ona Basin	PS61/3_42-5	59°40.39'S	57°35.74'W	3695	MUC (C)	28.01.2002	ANDEEP-I	
Ona Basin	PS61/3_42-7	59°39.49'S	57°34.51'W	3650	MUC (C)	28.01.2002	ANDEEP-I	
Ona Basin	PS61/3_43-4	60°27.05'S	56°04.77'W	3958	MUC (C)	03.02.2002	ANDEEP-I	
Ona Basin	PS61/3_43-6	60°27.00'S	56°04.24'W	3954	MUC (C)	03.02.2002	ANDEEP-I	
Ona Basin	PS61/3_46-4	60°38.12'S	53°57.67'W	2893	MUC (C)	30.01.2002	ANDEEP-I	
Ona Basin	PS61/3_46-6	60°38.64'S	53°57.27'W	2893	MUC (C)	30.10.2002	ANDEEP-I	
Shackleton Fracture Zone	PS61/3_129-5	59°52.39'S	59°57.78'W	3597	MUC (C)	23.02.2002	ANDEEP-I	
Shackleton Fracture Zone	PS61/3_129-7	59°52.30'S	59°57.63'W	3614	MUC (C)	23.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_99-5	61°07.09'S	59°16.50'W	5191	MUC (C)	12.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_99-7	61°07.06'S	59°15.53'W	5194	MUC (C)	12.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_105-2	61°24.14'S	58°51.15'W	2290	MUC (C)	14.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_105-4	61°23.81'S	58°50.24'W	2274	MUC (C)	14.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_105-6	61°23.73'S	58°50.26'W	2274	MUC (C)	14.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_114-5	61°43.52'S	60°44.13'W	2917	MUC (C)	18.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_114-6	61°43.57'S	60°43.97'W	2873	GKG	18.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_114-7	61°43.48'S	60°43.50'W	2900	MUC (C)	18.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_114-9	61°43.58'S	60°43.22'W	2875	MUC (C)	19.02.2002	ANDEEP-I	
South Shetland Trench	PS61/3_129-4	59°52.40'S	59°57.88'W	3598	GKG	23.02.2002	ANDEEP-I	

Processing of samples on board followed a standard procedure: the near bottom water inside the tube was poured over a 40 μm sieve and the filtrate was rinsed with filtered sea water into the sample bottle that already contained the sediment. Formaldehyde (37%, borax buffered) was added to the sample, and the bottle was then filled with filtered seawater to a final concentration of about 4% formaldehyde. Subsequently, meiofauna was separated from the sediment by density gradient centrifugation using silica colloid Levasil® and Kaolin® for stabilising the sediment during centrifugation (Higgins & Thiel 1988). The samples were centrifuged three times at 3,608 rpm, the supernatant was poured over sieves with a mesh size of 40 μm. For a better recognition of the meiofauna, Rose Bengal was added to the extracted samples in order to stain the specimens. Sorting was carried out in plankton counting chambers according to Bogorov (1927) and using dissecting microscopes with transmitted light illumination (*e.g.* Leica M80 or M125). Identification, counting and sorting of meiofauna higher level taxa was achieved by technicians of the German Centre of Marine Biodiversity Research (DZMB), Wilhelmshaven, Germany.

For the preparation of permanent microscopic slides, a single tardigrade specimen was placed by means of a thin wire loop into a small drop of glycerol on a glass slide that was surrounded by a thin ring of a mixture of beeswax and paraffin (ratio 1:2). The glycerol and the wax ring were then carefully covered with a cover slip and melted together on a heat plate at approximately 60 °C in a way that trapped air bubbles could emerge from the edge of the cover slip before the wax was solidifying again. The mentioned preparation of permanent microscope slides with tardigrades generally follows the procedure employed by Trokhymchuk & Kieneke (2024). All specimens were observed with an Olympus BX53 compound microscope equipped with differential interference contrast (DIC) and an adapted digital colour microscope camera euromex HD-Ultra VC.3036-HDS. Length and width measurements of certain morphological features were carried out with the software FiJi / ImageJ (Schindelin *et al.* 2012).

For the SEM preparation, after the light microscopic examination, the cover glasses were carefully removed from the permanent slides and the tardigrade specimens recovered with a thin metal needle. Next, they were transferred to 40% ethanol and then dehydrated with a graded series of ethanol (40-50-60-70-80-90-100%). In order not to lose the tiny specimens during the dehydration procedure, they were individually placed in minute metal cabinets sealed with an upper and a lower copper grid which are originally used as sample holders for ultrathin sections (Kieneke & Zekely 2008; Kieneke *et al.* 2015, Trokhymchuk & Kieneke 2024). After three exchanges of 100% ethanol, the specimen cabinets were transferred to the pressure chamber of a Leica CPD300 automatic critical point dryer. After complete discharge of CO_2 gas, each specimen was placed with an eyelash onto a round cover glass (diameter: 12 mm) that was coated with a very thin layer of Tempfix mounting resin (Plano GmbH, Wetzlar, Germany). After placement of every specimen, the cover glass may be warmed to 50 °C for 30 seconds in order to achieve a better adhesion of the specimens to the Tempfix. The cover glass was then glued on an aluminium stub and finally coated with gold-palladium using a Bal-Tec SCD 050 sputter-coater which operated 150 seconds at 40 mA current. SEM examination was carried out with a TESCAN VEGA3 using an acceleration tension of 10 kV and either the secondary (SE), or the backscattered electron (BSE) detector. Due to slight charging artefacts in some specimens, channel mixing of SE/BSE was also used.

Identification of genera was carried out with the aid of Fontoura *et al.* (2017) and Hansen & Kristensen (2020). Identification of species of Tardigrada was carried out using original species descriptions, taxonomic revisions and redescriptions if available. Results were cross-checked with all described species of the relevant genera according to the recent checklist of Tardigrada (Degma & Guidetti 2023) but also with recent papers *e.g.* Bartels *et al.* (2024). Drawings were made using the Procreate app.

We use the open nomenclature 'aff.' (Latin *affinis* = closely related, see, *e.g.* Bengtson 1988) in combination with 'sp. can.' (Latin *species candidatus* = candidate species) introduced by Dey *et al.* (2024) to denote that a presumptive new species belongs to a species complex. In the current study we therewith want to emphasize that the available characters allow us to assert a specimen represents a new species related to another and already described species. The 1210 microscopic slides and SEM stubs are deposited in the Tardigrada collection of the Senckenberg Natural History Museum, Frankfurt am Main, Germany, under the inventory numbers SMF 101 to SMF 1310 (accessible via https://search.senckenberg.de/aquila-public-search/search). All occurrence records of the 1210 determined specimens were furthermore submitted to the GBIF database (Senckenberg. Collection Tardigrada SMF. Occurrence dataset https://doi.org/10.15468/uvr84c accessed via GBIF.org on 2024-10-07).

Results

In total, 1,397 tardigrade specimens were extracted from the 130 sediment core samples of the four analysed deep sea expeditions ANDEEP 1, 2, 3, and ANDEEP-SYSTCO. Tardigrade densities were quite heterogeneous and ranged from 0.59 (N-W Cape Basin) to 9.01 individuals per 10 cm^2 deep sea bottom (Lazarev Sea closer to the Antarctic shelf). Apart from the latter sea area, also the Weddell Sea (2.12), the Ona Basin (3.71), and the South Shetland Trench (2.95) had rather high densities of Tardigrada (Table 2). However, the sample sizes varied significantly between sea regions, leading to relatively high standard deviations from the means (Table 2). A total of 1,210 tardigrade individuals could mostly be identified to species level, for 97 specimens only the genus could undoubtedly be identified; finally, 187 specimens were severely damaged and could only be identified as "Tardigrada". The identified specimens belong to five families, seven genera and 13 defined species that will be characterised in the following section. The abundances among the genera and species as well as between the sampled sea regions vary considerably (Tabs. 2, 3, 4). The genus *Angursa*, comprising five identified species, accounts for 96.9% of all identified tardigrades with 1,172 specimens. In contrast, the remaining six genera and eight species represent only 3.1% of the total (Table 3).

TABLE 2. Abundances and densities (individuals/10 cm^2) of Tardigrada in the different sea regions sampled during expeditions ANDEEP 1, 2, 3 and ANDEEP-SYSTCO. A total of 1,210 of the 1,397 individuals from a total of n=130 core samples were identified to genus and mostly to species level (see Tables 3–4).

	abundance (sum of cores)	abundance (mean)	SD	density (mean)	SD	n
N-W Cape Basin	21	4.20	2.04	0.59	0.29	5
S-W Cape Basin	43	7.17	5.34	1.01	0.75	6
Cape Basin Shona Ridge	79	6.08	4.80	0.88	0.69	13
Lazarev Sea Maud Rise	21	7.00	2.45	1.01	0.35	3
Lazarev Sea Antarctic Shelf	460	65.71	20.76	9.01	3.99	7
Weddell Sea	27	5.40	1.50	2.12	0.59	5
Ona Basin	322	9.47	6.88	3.71	2.70	34
Shackleton Fracture Zone	27	3.86	4.49	1.51	1.76	7
South Shetland Trench	397	7.94	6.61	2.95	2.55	50
total	1397					**130**

Within the genus *Angursa*, *A. capsula* and *A. abyssalis* are the two most abundant species, with 680 and 238 specimens, respectively (Table 4).

The raw summed abundance is generally dependent on the number of core samples analysed and the varying surface areas sampled by different devices. However, the comparably low number of core samples analysed from the Lazarev Sea close to the Antarctic Shelf nevertheless yielded a considerable number of 460 tardigrades, expressed as a likewise high density of 9.01 individuals per 10 cm^2 deep sea bottom (see Table 2).

The distribution of individual absolute abundances of each core sample across the sampled depth gradient shows an interesting pattern. Abundances of Tardigrada increase from the shallowest stations at about 1,100 m with less than 10 specimens per core to intermediate bathyal depths of about between 2,000 and 3,000 m with up to 25 specimens per core, but then decrease again from 3,500 to about 5,200 m (Fig. 2). There is a clear outlier from this trend: core samples from the Lazarev Sea closer to the Antarctic Shelf. Those samples yielded between 60 and more than 90 tardigrade individuals. The bathymetric trend in tardigrade occurrences described above remains evident when plotting the standardised densities of Tardigrada against depth. This plot again shows a peak around 2,000 meters, corresponding to samples from the Lazarev Sea near the Antarctic Shelf (Fig. 3). Linear regression indicates a slight overall decrease of tardigrade densities with depth, however, with a poor model fit (R^2 = 0.130).
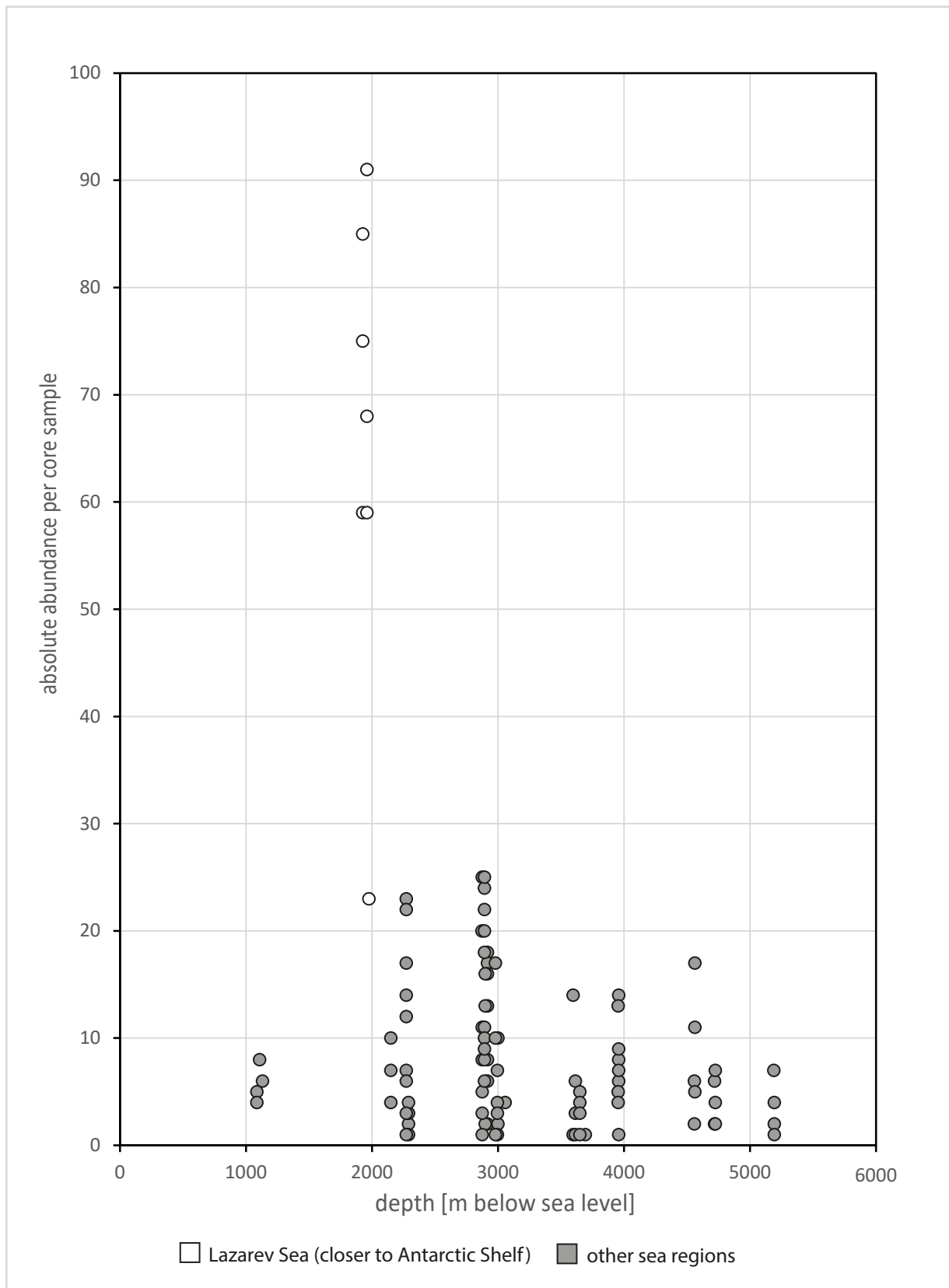
TABLE 3. Abundances of the identified genera of Tardigrada in the different sea regions sampled during expeditions ANDEEP 1, 2, 3 and ANDEEP-SYSTCO. In total, 1210 individuals were identified to genus (mostly to species) level, further 187 damaged specimens could only be recorded as Tardigrada (a total of 1,397 tardigrade records, see Table 2). Numbers in brackets refers to the number of samples (cores) that contained the respective taxon.

|	*Angursa*	*Batillipes*	*Coronarctus*	*Isoechiniscoides*	*Moebjergarctus*	*Styraconyx*	*Tholoarctus*	
N-W Cape Basin	20 (5)							
S-W Cape Basin	39 (5)		2 (1)					
Cape Basin Shona Ridge	59 (11)		8 (3)		1 (1)		1 (1)	
Lazarev Sea Maud Rise	20 (3)							
Lazarev Sea Antarctic Shelf	390 (7)					12 (4)	1 (1)	
Weddell Sea	17 (5)	1 (1)				1 (1)		
Ona Basin	297(33)	1 (1)		1 (1)	2 (2)		6 (4)	
Shackleton Fracture Zone	23 (6)				1 (1)			
South Shetland Trench	307 (49)							
total	**1172**(124)	**2** (2)	**10** (4)	**1** (1)	**4** (4)	**13** (5)	**8** (6)	1210

TABLE 4. Abundances and occurrences of the identified species of Tardigrada in the different sea regions sampled during expeditions ANDEEP 1, 2, 3 and ANDEEP-SYSTCO. In total, 1,210 individuals were identified to genus (mostly to species) level, further 187 damaged specimens could only be recorded as Tardigrada (a total of 1,397 tardigrade records, see Table 2).

	N-W Cape Basin	S-W Cape Basin	Cape Basin Shona Ridge	Lazarev Sea Maud Rise	Lazarev Sea Antarctic Shelf	Weddell Sea	Ona Basin	Shackleton Fracture Zone	South Shetland Trench	total
Angursa abyssalis	2	18	12	3	92	10	16	8	77	238
Angursa antarctica							62			62
Angursa capsula	14	12	37	12	251	2	130	8	214	680
Angursa lanceolata	2	3	2		3		22	1	3	36
Angursa lingua					4	2	56	3		65
Angursa sp.	2	6	8	5	40	3	11	3	13	91
Batillipes wyedeleinorum						1	1			2
Coronarctus dissimilis			1							1
Coronarctus sp.		2	4							6
Coronarctus tenellus			3							3
Isoechiniscoides aff. *sifae* sp. can.							1			1
Moebjergarctus clarionclippertonensis			1				2	1		4
Styraconyx qivitoq					12					12
Styraconyx takeshii						1				1
Tholoarctus oleseni			1		1		6			8
										1210

FIGURE 2. Absolute abundances of Tardigrada from all 130 analysed core samples of expeditions ANDEEP-1 to 3 and ANDEEP-SYSTCO to the Southern Ocean plotted against depth. Samples were taken at different working areas in the Cape Basin, in the Lazarev Sea, in the Weddell Sea, in the Ona Basin, and at different working stations in the Drake Passage.
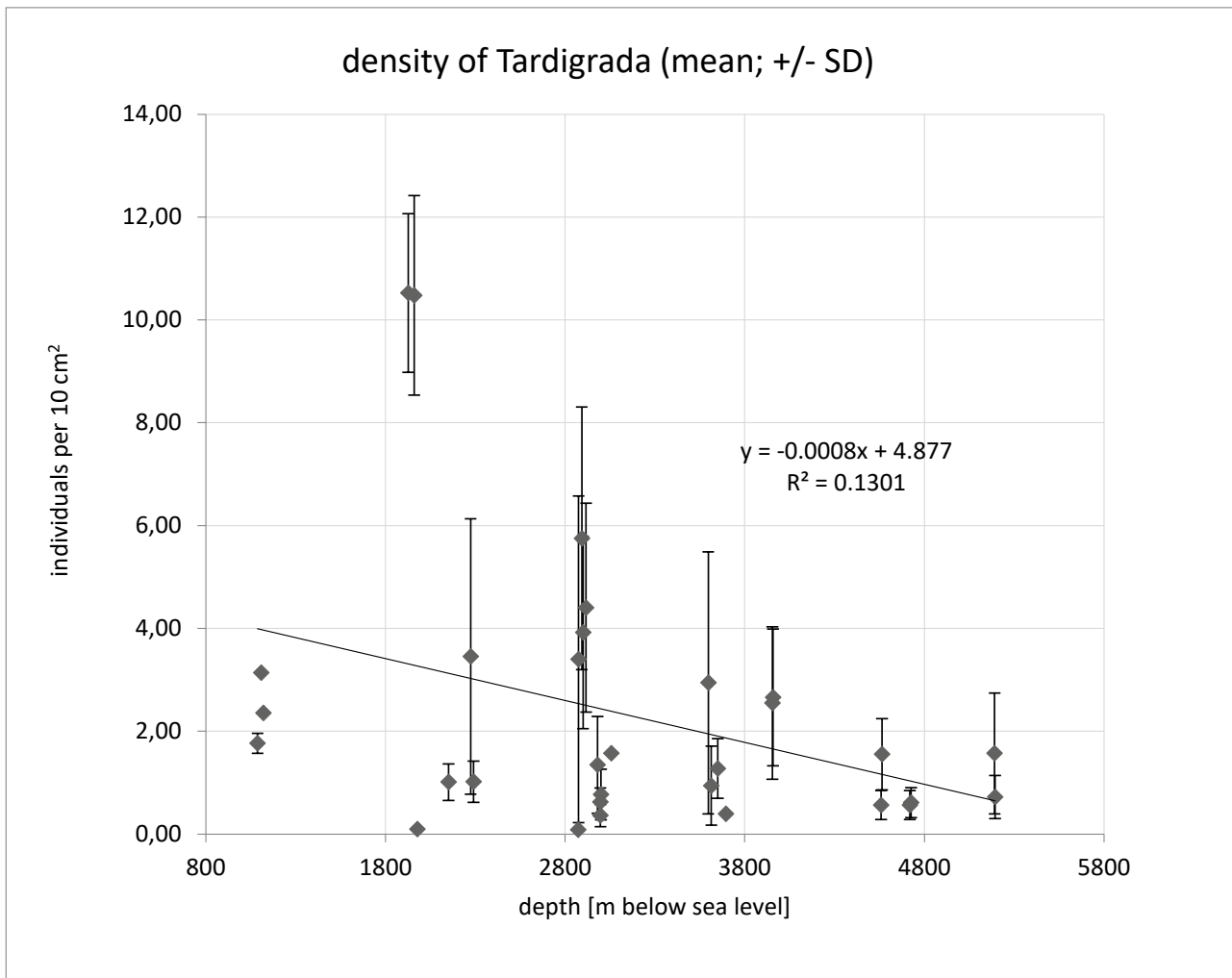
FIGURE 3. Means of Tardigrada densities (individuals per 10 cm^2) of all core samples per sampled depth plotted against depth. Linear regression indicates a slight decrease of tardigrade densities with depth but with a rather poor model fit (R^2=0.1301). Sediment core samples containing Tardigrada were obtained during expeditions ANDEEP-1 to 3 and ANDEEP-SYSTCO to the Southern Ocean.

Taxonomy

Phylum: Tardigrada Doyère, 1840

Class: Heterotardigrada Marcus, 1927

Family: Batillipedidae Ramazzotti, 1962

Genus: *Batillipes* Richters, 1909

***Batillipes wyedeleinorum* Bartels, Fontoura, Nelson & Kaczmarek, 2024**

N=2 specimens: 1 female, 1 juvenile
    occurrence: ANDEEP I; 60°38.12′S, 53°57.67′W; 2,893 m bsl (female); ANDEEP 2; 65°20.09′S, 54°14.72′W; 1,088 m bsl (juvenile).
    Both specimens are morphologically similar to the recently described species *Batillipes wyedeleinorum* Bartels *et al.*, 2024. However, we present our detailed description of an adult female since it adds important information to

the original description of *B. wyedeleinorum* regarding character variation and ecological preferences (*e.g.* deep sea occurrence).

Description of female
Figs 4–5, Supplementary Table 1.1

Body. Small *Batillipes* with total body length (from cephalic rim to the tip of caudal appendage) of 147 μm, and maximum body width of 46 μm between leg III and leg IV (Figs 4, 5A-C). Distinct trapezoid head, separated from the body by a distinct neck constriction and with conical lateral projections I of 7 μm length (Fig. 5C, G). Lateral projections between leg I and leg II (2.5 μm) are blunt. Lateral projections between leg II and III (3 μm) are conical. The lateral projections between leg III and leg IV (4 μm) are elongated (up to 20 μm) and rather blunt (Fig. 5C, G). Body cuticle punctuated with internal pillars (Fig. 5G–J).

Cephalic region. Cephalic cirri with cirrophores. Cephalic cirri tips have tufts with additional filaments (Fig. 5G, H). Cirri *A* are 24 μm in length. Unpaired median cirrus is 16 μm long. Internal cirri are 14 μm long and attached dorsally. External cirri are 11 μm long and situated close to the primary clavae. Primary clavae of 9.0 μm length are tube-shaped. (Fig. 5A). Primary clavae, cirrus *A* and external cirri all originate from a common lateral bulge of the head (Fig. 4). Secondary clavae are indistinct. Eyes not visible. Mouth cone is clearly visible (Fig. 5G, H). Ovoid pharyngeal bulb (15 × 10 μm) connected with the buccal tube with three placoids.

Legs. Sensory organs present on all telescopic legs (Fig. 5B). Sensory organs of legs I and II are about 7 μm long, of legs III to 10 μm. Sensory organs of legs IV with a cirrophore are 18 μm long and have frayed tips (Figs 5D, D2). Bases of legs I and legs II have a small (1.5–2.0 μm) dome-shaped projection. On legs I, digits 2 (4.0 μm) and 4 (5.5 μm) are the shortest (considering digit 1 the most cephalically), digits 3 (10.5 μm) and 5 (11.0 μm) are the longest and digits 1 (6.0 μm) and 6 (7.0 μm) are medium sized. The same pattern of digits on legs II and III (Fig. 5A). On legs IV, digits 3 (6.0 μm) and 4 (8.0 μm) are the shortest, and digits 1 (11.0 μm), 2 (14.5 μm), 5 (14.0 μm), 6 (11.0 μm) are the longest (Fig. 5D). Digits have disc-shaped suction discs (Figs 4, 5A, D, J). The specimen has some folded discs on legs II–IV (Fig. 4, 5I, J).

Caudal region. The caudal appendage is 8.5 μm long and looks like a single spine attached directly on the body. Rosette-shaped, six-lobed female gonopore and anus present (Fig. 5E, J). Putative smooth area between gonopore and anus is visible on light microscopy figures (Fig. 5E) but hidden by leg IV on SEM figures (Fig. 5J).

Remarks
There are only a few and slight morphological differences between *B. wyedeleinorum* and our specimen. We did not see the same medial groove in a smooth area between gonopore and anus. In addition, we were not able to observe the papillae on legs because of legs positioning after preparation for SEM (see *Additional remarks* in Bartels *et al.* 2024).

A possible ecological difference is evidenced by our new geographic and bathymetric record of this species.

Short description of juvenile
Fig. 5F; Supplementary Table 1.1

Four-toed juvenile 123.5 μm long with punctuated cuticle. Cephalic cirri with lance-shaped tips. Each leg with a sensory organ. Lateral projections on the neck region, between leg II and leg III are conical; projections between leg I and leg II, as well as between leg III and leg IV are blunt. On each leg digit 2 is shorter than the other. Short single conical caudal appendage presented.

Remarks
We identified this specimen as *Batillipes wyedeleinorum* because of overall morphological similarity. This individual has comparably shorter cirri *E*, a sensory organ on the leg IV and more elongated suction disks on digits. This kind of minor dissimilarities between mature and juvenile stages are known for other species of *Batillipes* (Kristensen & Mackness 2000). Furthermore, both specimens occur in a similar habitat, the Antarctic deep sea bottom, which is a rather unusual and unique habitat for species of the genus *Batillipes* (but see discussion).
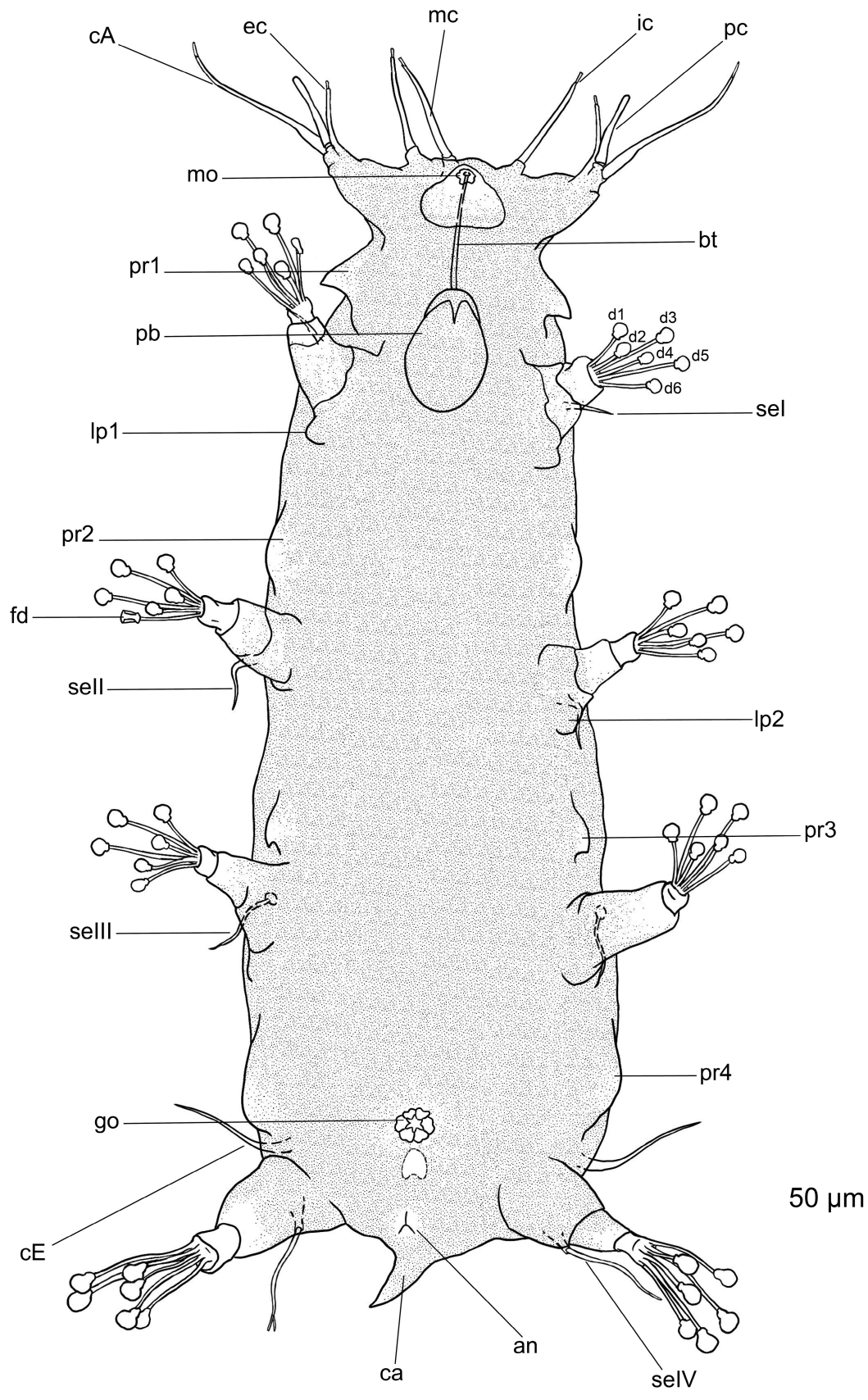
FIGURE 4. *Batillipes wyedeleinorum*, female, drawing (reconstruction) based on light microscopy (DIC) and SEM, ventral view. Abbreviations: an—anus, bt—buccal tube, cA—cirrus *A*, ca—caudal appendage, cE—cirrus *E*, d—digit, ec—external cirrus, fd—folded disc, go—gonopore, ic—internal cirrus, mc—median cirrus, mo—mouth opening, lp—leg projection, pb—pharyngeal bulb, pc—primary clava, pr—body projection, se—leg sensory organ.
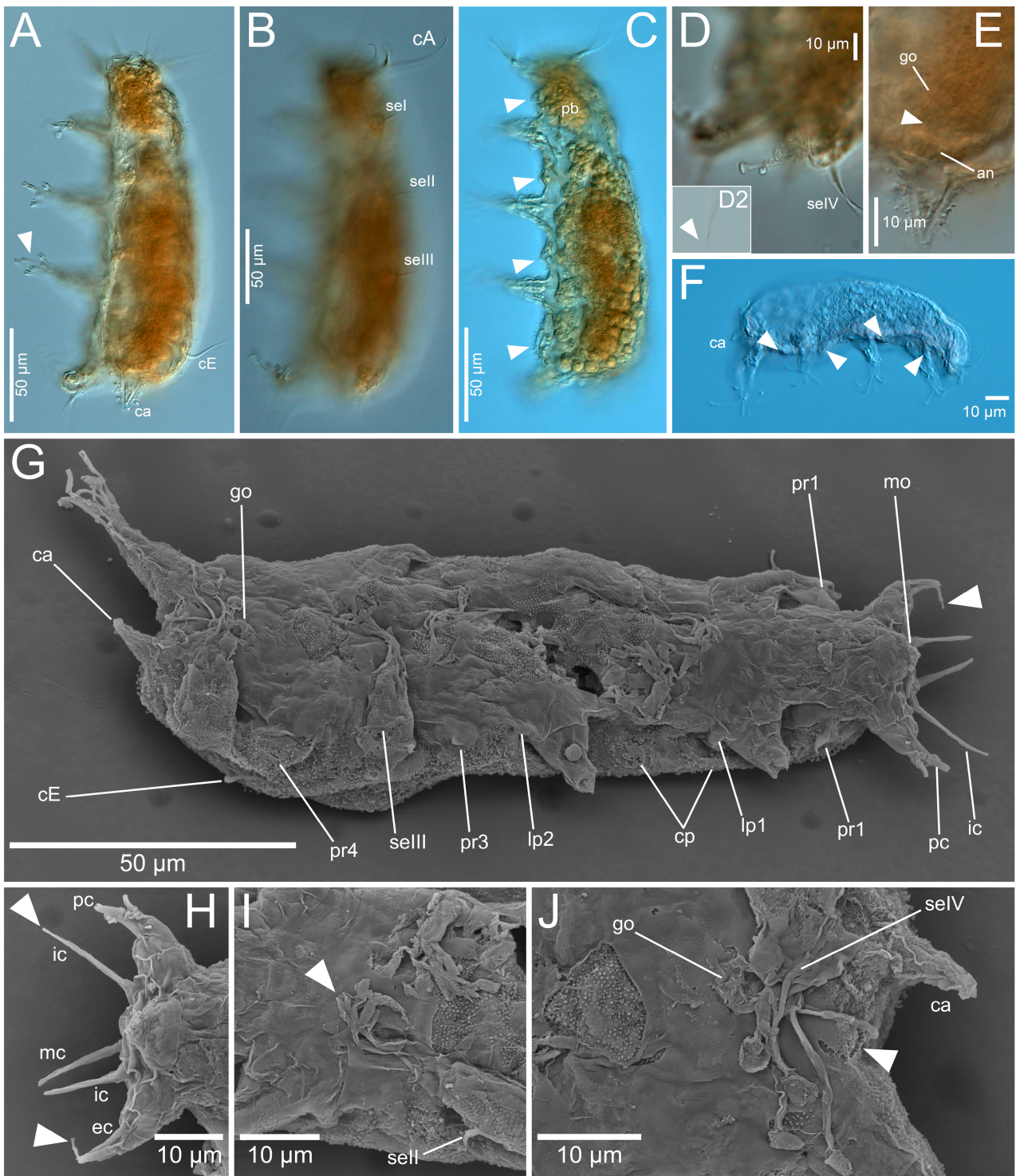
FIGURE 5. *Batillipes wyedeleinorum*. **A** female, light microscopy (DIC), ventro-sagittal view, note leg III digit arrangement (arrowhead). **B** female, light microscopy (DIC), ventro-sagittal view. **C** female, light microscopy (DIC), ventro-sagittal view, note body projections (arrowheads). **D** female, light microscopy (DIC), caudal region, note leg IV digits arrangement. **D2** female, light microscopy (DIC), leg IV sensory organ, note tuft of additional filaments (arrowhead). **E** female, light microscopy (DIC), caudal region, note smooth area (arrowhead). **F** *Batillipes wyedeleinorum*, juvenile, light microscopy (DIC), sagittal view, note body projections (arrowheads). **G** female, SEM, ventro-sagittal view, note cirrus *A* tip (arrowhead). **H** female, SEM, ventral view, cephalic region, note cephalic cirri tips (arrowheads). **I** female, SEM, ventral view, leg II region, note folded digits (arrowhead). **J** female, SEM, caudal region, ventral view, note cuticular pillars (arrowhead). Abbreviations: an—anus, ca—caudal appendage, cE—cirrus *E*, ec—external cirrus, go—gonopore, ic—internal cirrus, mo—mouth opening, lp—leg projection, pb—pharyngeal bulb, pc—primary clava, pr—body projection, se—leg sensory organ.

Family: Coronarctidae Renaud-Mornant, 1974

Genus: *Coronarctus* Renaud-Mornant, 1974

***Coronarctus dissimilis* Gomes-Júnior, Santos, da Rocha, Santos & Fontoura, 2020**

N=1 specimen: female
     occurrence: ANDEEP-SYSTCO; 2,981 m bsl.
     Fig. 6; Supplementary Table 1.2

Short description
     Large female (273 μm, n=1) with claw heteromorphy (Fig. 6A). On the dorsal side a median cirrus is placed close between the posterior edges of the secondary clavae (Fig. 6B). Edges of secondary clavae are also clearly visible on the ventral side (Fig. 6C, C2). Both external and internal claws are with accessory spines on each leg (Fig. 6B, D). The presence of gonopore and seminal receptacles allows us to be secure with sex determination.

Remarks
     C. dissimilis is recognisable by the secondary clavae shape and median cirrus placed on the posterior end of secondary clavae. This representative exhibits claw heteromorphy and accessory spines as in the original description of Gomes-Júnior *et al.* (2020).

***Coronarctus tenellus* Renaud-Mornant, 1974**

N=3 specimens: 1 female, 1 male, 1 juvenile
     occurrence: ANDEEP-SYSTCO; 2,891 m bsl.
     Fig. 6; Supplementary Table 1.3

Short description
     Large tardigrades (205–294 μm, n=2) of elongated body, with coelomocytes and other spherical cells. Secondary clavae have clearly visible ventral side shape as in original description (Fig. 6G, G2). On the dorsal side the median cirrus is placed between the secondary clavae (Fig. 6F). Claws without heteromorphy. Accessory spines only on the internal claws of leg IV (Fig. 6H). Juvenile (205 μm) with internal claws and sometimes with external claws developing inside the femur (Fig. 6I). The female has a gonopore and seminal receptacles.

Remarks
     C. tenellus is recognisable by the secondary clavae shape and median cirrus position. All representatives have accessory spines on each leg IV internal claw (Renaud-Mornant, 1974).

Coronarctus* cf. *tenellus

N=7 specimens
     occurrence: ANDEEP-SYSTCO; 2,891 m bsl.

Remarks
     We are convinced that most of these seven specimens belong to the species *Coronarctus tenellus* Renaud-Mornant, 1974. However, since they are in a rather poor condition compared to the three specimens above, we decided to report them as *Coronarctus* cf. *tenellus*.

TROKHYMCHUK *ET AL.*
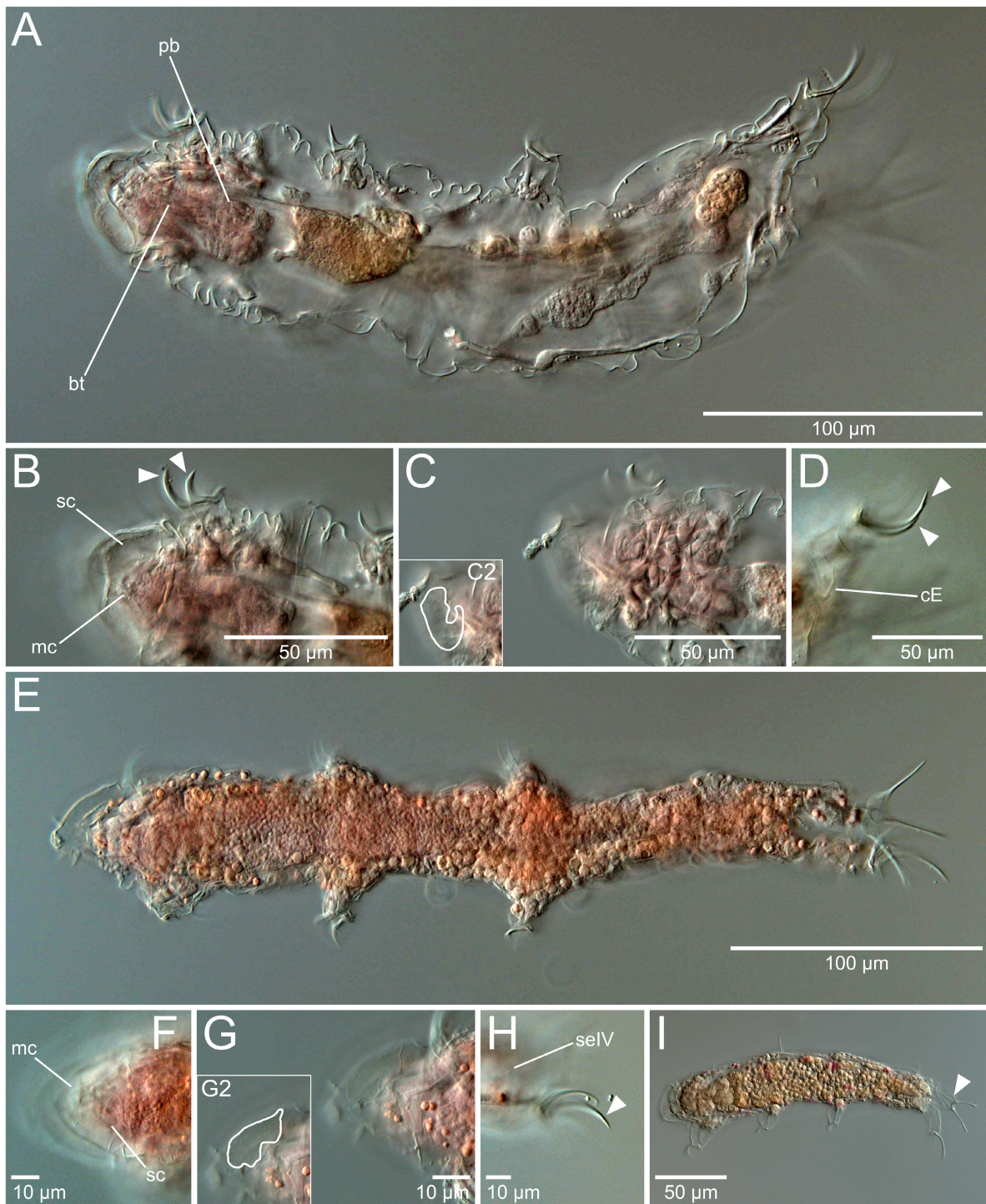
FIGURE 6. Genus *Coronarctus*. **A** *Coronarctus dissimilis*, female, light microscopy (DIC), ventro-sagittal view. **B** *Coronarctus dissimilis*, female, light microscopy (DIC), head, dorsal view, note leg I accessory spines on the external and internal claws (arrowheads). **C** *Coronarctus dissimilis*, female, light microscopy (DIC), head ventral view. **C2** *Coronarctus dissimilis*, female, light microscopy (DIC), head ventral view, secondary clava indicated. **D** *Coronarctus dissimilis*, female, light microscopy (DIC), leg IV, note leg IV accessory spines on the both external and internal claws (arrowheads). **E** *Coronarctus tenellus*, male, light microscopy (DIC), ventral position. **F** *Coronarctus tenellus*, male, light microscopy (DIC), head, dorsal view. **G** *Coronarctus tenellus*, male, light microscopy (DIC), head, ventral view. **G2** *Coronarctus tenellus*, male, light microscopy (DIC), head, ventral view, secondary clava indicated. **H** *Coronarctus tenellus*, light microscopy (DIC), leg IV, note leg IV accessory spines just on the both internal claw (arrowhead). **I** *Coronarctus tenellus*, juvenile, light microscopy (DIC), sagittal position, note leg IV with two internal claws and two growing external claws (arrowhead). Abbreviations: bt—buccal tube, cE—cirrus *E*, mc—median cirrus, pb—pharyngeal bulb, sc—secondary clava, se—leg sensory organ.
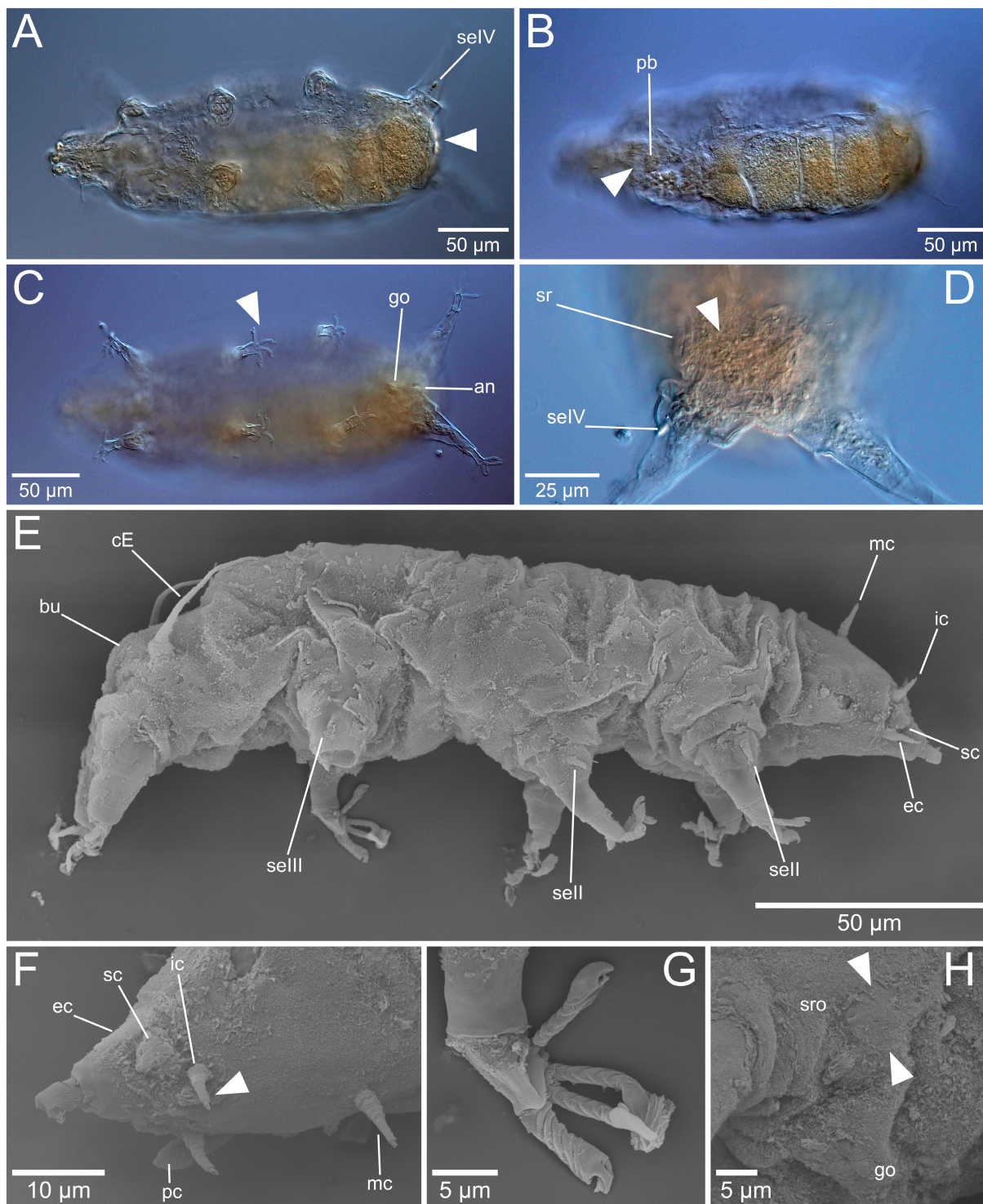
FIGURE 7. *Moebjergarctus clarionclippertonensis*. **A** *Moebjergarctus clarionclippertonensis*, female, light microscopy (DIC), dorsal view, note caudal bulge (arrowhead). **B** *Moebjergarctus clarionclippertonensis*, female, light microscopy (DIC), dorsal view, note buccal apparatus' stylet (arrowhead). **C** *Moebjergarctus clarionclippertonensis*, female, light microscopy (DIC), ventral view, note leg II digits (arrowhead). **D** *Moebjergarctus clarionclippertonensis*, female, light microscopy (DIC), caudal region, note patched seminal receptacle opening (arrowhead). **E** *Moebjergarctus clarionclippertonensis*, female, SEM, sagittal view. **F** *Moebjergarctus clarionclippertonensis*, female, SEM, head, dorsal view, note smooth portion of internal cirrus (arrowhead). **G** *Moebjergarctus clarionclippertonensis*, female, SEM, leg III digits. **H** *Moebjergarctus clarionclippertonensis*, female, SEM, posterior ventro-sagittal view, note seminal receptacle opening patch borders (arrowheads). Abbreviations: an—anus, bu—caudal bulge, cE—cirrus *E*, ec—external cirrus, go—gonopore, ic—internal cirrus, mc—median cirrus, pb—pharyngeal bulb, pc—primary clava, sc—secondary clava, se—leg sensory organ, sro—seminal receptacle opening.

Family: Halechiniscidae Thulin, 1928

Subfamily: Euclavarctinae Renaud-Mornant, 1983

Genus: *Moebjergarctus* Bussau, 1992

***Moebjergarctus clarionclippertonensis* Bai, Wang, Zhou, Lin, Meng & Fontoura, 2020**

N=4 specimens: 2 females, 2 with undetermined sex
 occurrence: ANDEEP 1, ANDEEP-SYSTCO; 3,551–3,650 m bsl.
 Fig. 7; Supplementary Table 1.4

Short description
 Large and robust tardigrade 148–283 µm long and 52.3–99.7 µm width (n=2). Buccal apparatus with stylets (Fig. 7B). Cephalic cirri with annulated base, smooth portion of the scapus and short flagellum (Fig. 7E, F). Each leg with a sensory organ (Fig. 7E). Internal and external digits are of the same size and wrinkled (Fig. 7C, G). Caudal region is covered with a thick cuticular layer shown as a bulge (Fig. 7A, E). All the females have a patched seminal receptacle opening (Fig. 7D, H).

Remarks
 The identification of this species is certain because of the morphology of cephalic cirri (annulated base, smooth scapus and short flagellum). The internal and external digits of all limbs are the same size that distinguishes this species from *M. okhotensis* (Bai *et al.* 2020, Saulenko *et al.* 2022). This species was previously reported from Pacific deep-sea plains with a high abundance of manganese or polymetallic nodules (Bai *et al.* 2020). At least the sampling stations of expedition ANDEEP 1 that contained *M. clarionclippertonensis* (Shackleton Fracture Zone, 59°52.30′S, 59°57.63′W) at the deep sea bottom of the Drake Passage are also close to areas with polymetallic sulfide deposits and hydrothermal vent activity (see discussion for details).

Family: Styraconyxidae Kristensen & Renaud-Mornant, 1983

Genus: *Angursa* Pollock, 1979

N=1,172 specimens

***Angursa abyssalis* Renaud-Mornant, 1981**

N=238 specimens
 occurrence: ANDEEP I, II, III, ANDEEP-SYSTCO; 1,088–5,213 m bsl.
 Fig. 8A–D; Supplementary Table 1.5

Short description
 Angursa with slender body (120–180 µm long, 20–35 µm width, n=5) and primary clavae longer than cirri *A*. Secondary and tertiary clavae are usually clearly visible (Fig. 8A, B, B2). Distance between both secondary clavae on the dorsal side of the head is 1.5–4.0 µm (Fig. 8B, B2). Cirrus *E* short (8.0–12.0 µm, n=5) (Fig. D). The hemispherical sensory organ with a small apical spine on leg IV is sometimes a bit elongated (as in *Angursa capsula*) (Fig. 8C).

Remarks
 The two species *A. abyssalis* and *A. capsula* are quite similar in the shape of the sensory organ of leg IV (Hansen and Fujimoto 2019). However, the main identifying trait for this species is the short (less than 4 µm) distance between the secondary clavae and the shorter cirri *E* (Fig. 8D).
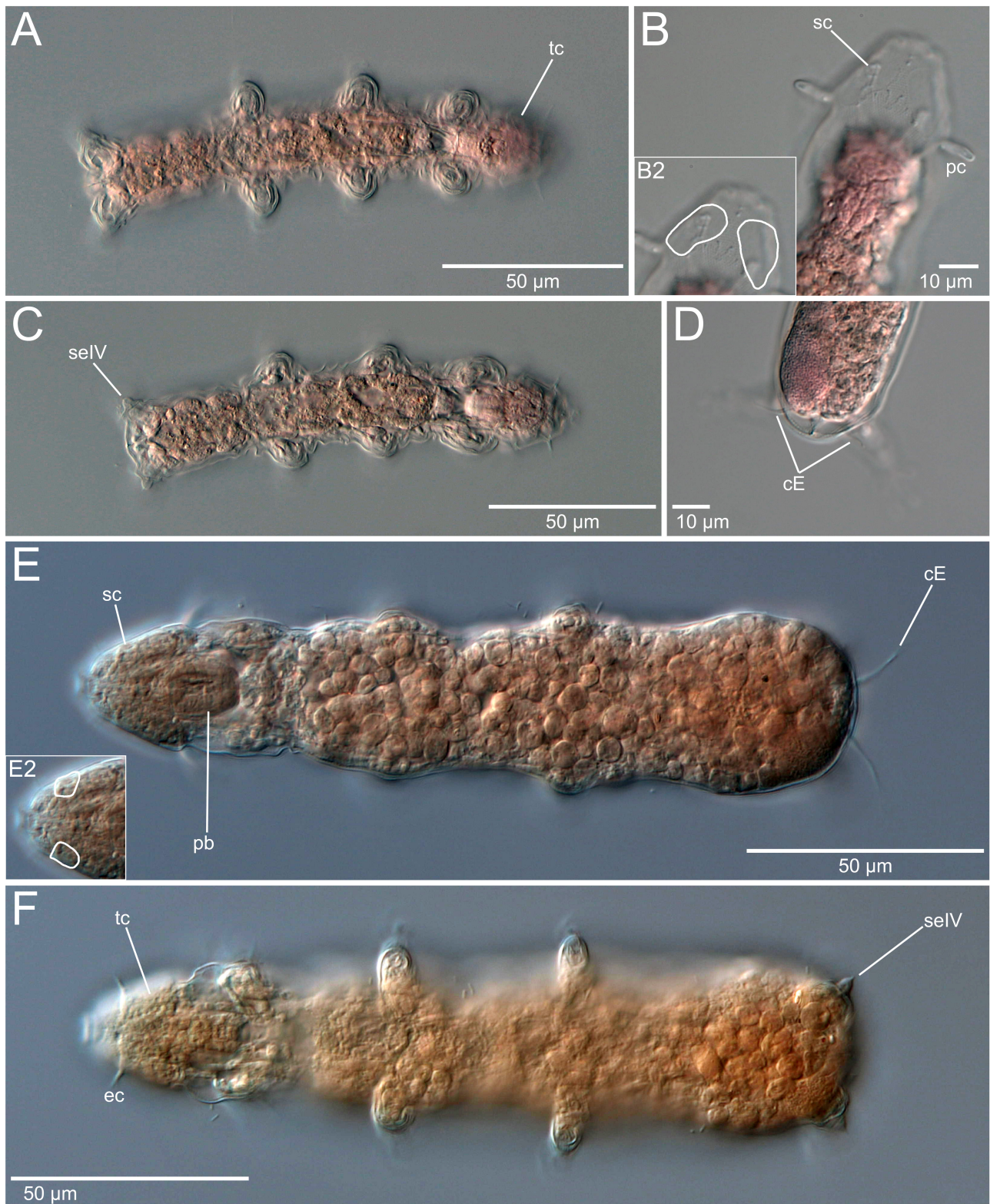
FIGURE 8. *Angursa bicuspis* group. **A** *Angursa abyssalis*, male, light microscopy (DIC), ventral view. **B** female, light microscopy (DIC), head, dorsal view. **B2** female, light microscopy (DIC), head, dorsal view, secondary clavae indicated. **C** male, light microscopy (DIC), dorsal view. **D** female, light microscopy (DIC), caudal region. **E** *Angursa capsula*, female, light microscopy (DIC), dorsal view. **E2** *Angursa capsula*, female, light microscopy (DIC), dorsal view, secondary clavae indicated. **F** *Angursa capsula*, female, light microscopy (DIC), ventral view. Abbreviations: cE—cirrus *E*, ec—external cirrus, pb—pharyngeal bulb, pc—primary clava, sc—secondary clava, se—leg sensory organ, tc—tertiary clava.

Angursa capsula Bussau, 1992

N=680 specimens
    occurrence: ANDEEP I, II, III, ANDEEP-SYSTCO; 1,088–5,213 m bsl.
    Fig. 8 E–F; Supplementary Table 1.6

Short description
    Angursa with a slender body (120–176 µm long, 20–30 µm width, n=5) and primary clavae longer than cirri *A*. Distance between both secondary clavae on the dorsal side of the head is 6.3–11.0 µm (Fig. 8E, E2). Capsules-like sensory organs on legs IV (Fig. 8F). Cirri *E* long (13.0–19.0 µm, n=5) (Fig. 8E).

Remarks
    One of the most difficult species to identify because of unclear borders of the secondary clavae. On the sagittal position of the specimen we mostly used the length of cirri *E* as a species-specific trait, which are longer than 11 µm (Hansen & Fujimoto 2019).

Angursa sp.

Remarks
    In total 91 individuals are damaged and do not show characters that allow their identification further than to the genus level. However, all of them belong to the *Angura bicuspis* complex with cirrus *A* shorter than primary clava (Fujimoto & Hansen 2019) and could either belong to *A. abyssalis* or *A. capsula*.

Angursa antarctica Víllora-Moreno, 1998

N=62 specimens
    occurrence: ANDEEP I; 2,893 m bsl.
    Fig. 9A–B; Supplementary Table 1.7

Short description
    Small *Angursa* with slender body (106–150 µm long, 19–22 µm width, n=5) and primary clavae shorter than cirri *A*. Individuals with long cephalic cirri and cirri *E*. Secondary clavae are present (Fig. 9A, A2). Short hemispherical sensory organs on legs IV present (Fig. 9A). Males have gonopore as in the original description (Fig. 9B).

Remarks
    A. antarctica belongs to the *A. lanceolata* group with primary clavae shorter than cirri *A* (Fujimoto & Hansen 2019). This species is recognisable by hemispherical leg IV sensory organs. Annulated scapi of cirri *E* sometimes not clearly visible (Víllora-Moreno, 1998).

Angursa lanceolata Renaud-Mornant, 1981

N=36 specimens
    occurrence: ANDEEP I, III, ANDEEP-SYSTCO; 1,927–5,213 m bsl.
    Fig. 9 C; Supplementary Table 1.8

Short description
    Angursa with slender body (101–150 µm long, 15.7–24.0 µm width, n=4) and primary clavae shorter than cirri *A*. Secondary and tertiary clavae present. Elongated leg IV sensory organs. Cirri *E* with lance-shaped ending.

Remarks
    A. lanceolata belongs to the *A. lanceolata* group with primary clavae shorter than cirri *A* (Fujimoto & Hansen 2019). Species with easily recognisable lance-shaped cirri *E* (Renaud-Mornant, 1981).
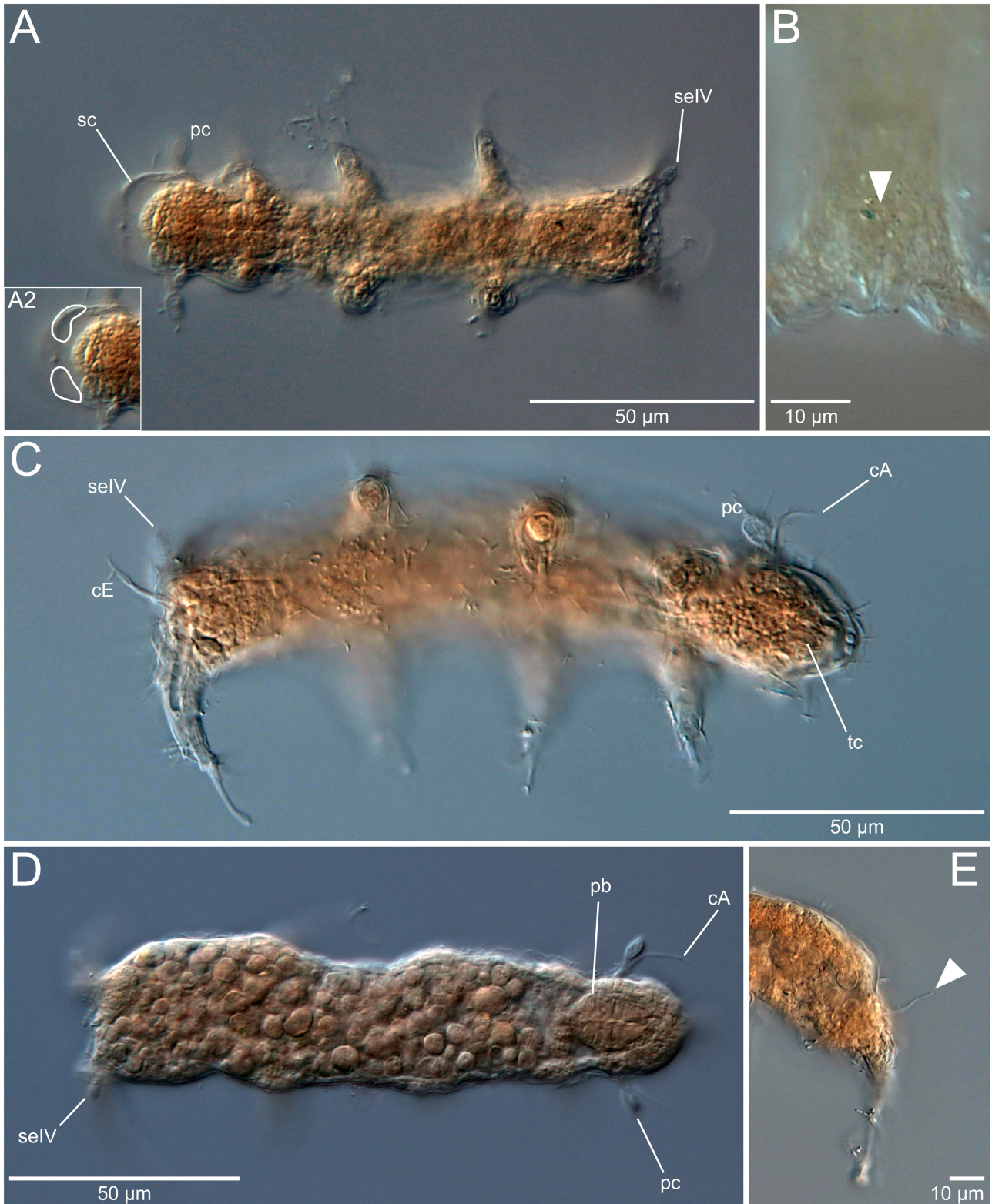
FIGURE 9. *Angursa lanceolata* group. **A** *Angursa antarctica*, male, light microscopy (DIC), dorsal view. **A2** *Angursa antarctica*, male, light microscopy (DIC), dorsal view, secondary clavae indicated. **B** *Angursa antarctica*, male, light microscopy (DIC), ventral view, note male gonopore (arrowhead). **C** *Angursa lanceolata*, female, light microscopy (DIC), ventral view. **D** *Angursa lingua*, female, light microscopy (DIC), dorsal view. **E** *Angursa lingua*, light microscopy (DIC), sagittal view, note cE (arrowhead). Abbreviations: cA—cirrus *A*, cE—cirrus *E*, pb—pharyngeal bulb, pc—primary clava, sc—secondary clava, se—leg sensory organ, tc—tertiary clava.

Angursa lingua Bussau, 1992

N=65 specimens
    occurrence: ANDEEP I, II, ANDEEP-SYSTCO; 1,088–3,555 m bsl.
    Figs 9D, E; Supplementary Table 1.9

Short description

Angursa with slender body (137–172 µm long, n=5) and primary clavae shorter than cirri *A* (Fig. 9D). Secondary and tertiary clavae present. Elongated leg IV sensory organs. Cirri *E* with tongue-shaped ending (Fig. 9E).

Remarks

A.lingua belongs to the *A. lanceolata* group with primary clavae shorter than cirri *A* (Fujimoto & Hansen 2019). Species with easily recognisable traits, such as tongue-shaped cirri *E* and elongated sensory organs on legs IV (Fig. 9E) (Bussau, 1992).

Genus: *Styraconyx* Thulin, 1942

Styraconyx qivitoq Kristensen & Higgins, 1984

N=13 specimens: 13 males
    occurrence: ANDEEP-SYSTCO; 1,927–1,960 m bsl.
    Figs 10A–E; Supplementary Table 1.10

Short description

We observed only dwarf males (72–108 µm long) unique for this species. Ovoid primary clavae and long cephalic cirri present (Fig. 10A). Secondary clavae are present (Fig. 10B). Neck region with folded cuticle (Fig. 10C). All digits are covered with a cuticular hood. Peduncles are large (Fig. 10D). Inconspicuous tubular-shape male gonopore is present (Fig. 10E).

Remarks

All the described characters are species-specific and correspond well to the original description (Kristensen & Higgins, 1984), so the identification is sound.

Styraconyx takeshii Fujimoto, Suzuki, Ito, Tamura & Tsujimoto, 2020

N=1 specimen: female
    occurrence: ANDEEP II; 1,109 m bsl.
    Figs 10F–I; Supplementary Table 1.11

Short description

Adult female (145 µm long, n=1) with the typical character combination of this species. Dorsal cuticle undulated (Fig. 10F). Primary clavae elongated (Fig. 10F). Large secondary clavae are present (Fig. 10G). Head cirri are divided into three regions (Fig. 10G). Thick seminal receptacle duct openings with no terminal swelling as lateral projections (Fig. 10H). Digits with proximal pads and small peduncles (Fig. 10I). Leg IV sensory organs as elongated papillae (Fig. 10H).

Remarks

Styraconyx takeshii is well recognisable by the shape of dorsal cuticle with transversal ridges, elongated form of primary clavae, small peduncles and robust seminal receptacle opening (Fujimoto *et al.* 2020).
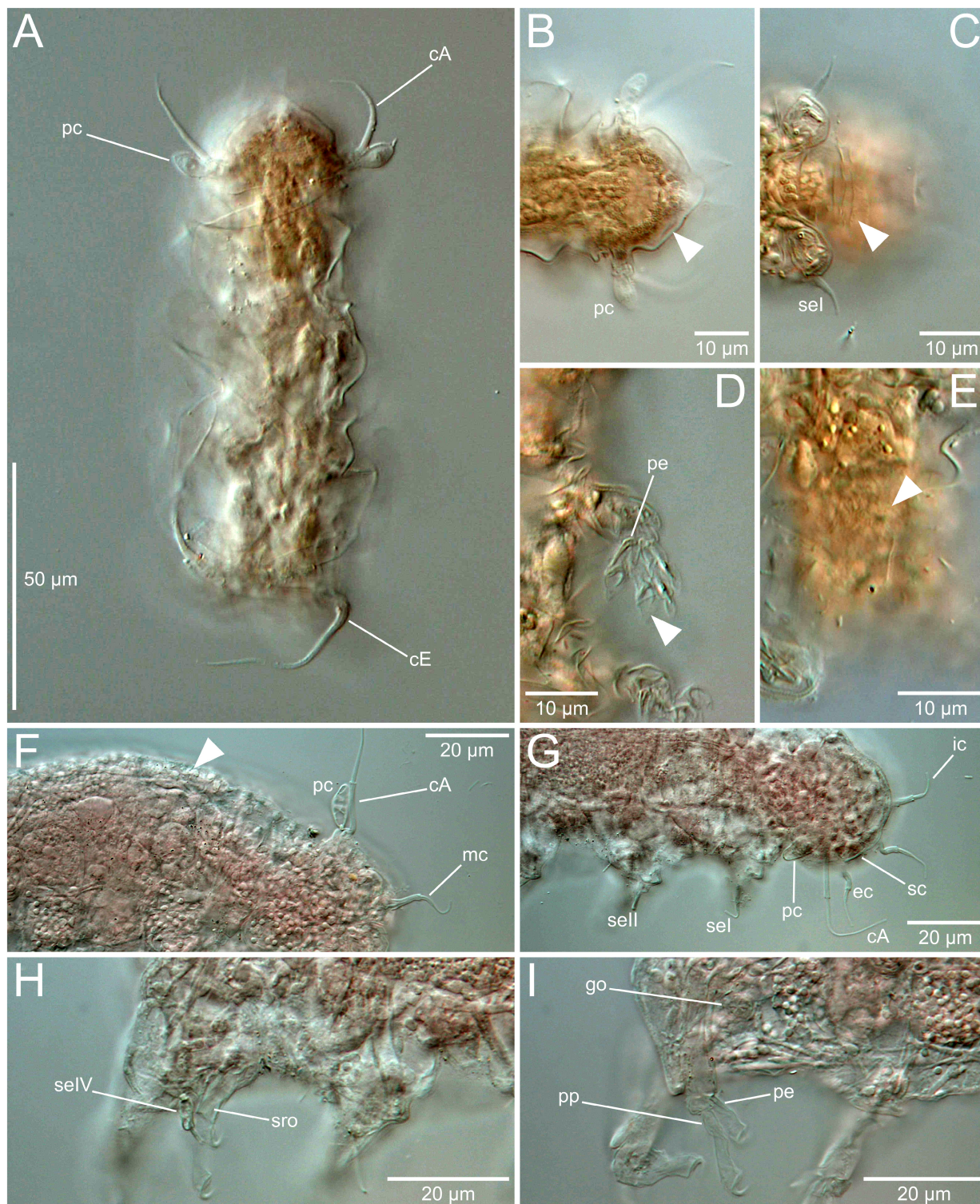
FIGURE 10. Genus *Styraconyx*. **A** *Styraconyx qivitoq*, male, light microscopy (DIC), dorsal view. **B** *Styraconyx qivitoq*, male, light microscopy (DIC), head, dorsal view, note secondary clava (arrowhead). **C** *Styraconyx qivitoq*, male, light microscopy (DIC), head, ventral view, note neck folds (arrowhead). **D** *Styraconyx qivitoq*, male, light microscopy (DIC), leg III, note digit covered with a cuticle hood (arrowhead). **E** *Styraconyx qivitoq*, male, light microscopy (DIC), caudal region, note male gonopore (arrowhead). **F** *Styraconyx takeshii*, female, light microscopy (DIC), sagittal view, note undulated dorsal cuticle (arrowhead). **G** *Styraconyx takeshii*, female, light microscopy (DIC), sagittal view. **H** *Styraconyx takeshii*, female, light microscopy (DIC), sagittal view. **I** *Styraconyx takeshii*, female, light microscopy (DIC), sagittal view. Abbreviations: cA—cirrus *A*, cE—cirrus *E*, ec—external cirrus, go—gonopore, ic—internal cirrus, mc—median cirrus, pc—primary clava, pe—peduncle, pp—proximal pad, se—leg sensory organ, sro—seminal receptacle opening.

Genus: *Tholoarctus* Kristensen & Renaud-Mornant, 1983

***Tholoarctus oleseni* Jørgensen, Boesgaard, Møbjerg, & Kristensen, 2014**

N=8 specimens: 1 female, 4 males, 3 with undetermined sex
occurrence: ANDEEP I, ANDEEP-SYSTCO; 1,927–2,997 m bsl.
Fig. 11; Supplementary Table 1.12

Short description

Tardigrades with slender body and bell-shaped outer epicuticle (Fig. 11A, C). Short primary clavae and large secondary clavae present (Fig. 11A). Sexual dimorphism concerning body size (female is 336 µm long and 79 µm wide, n=1; males are 165–173 µm long and 40 µm wide, n=3) (Fig. 11A compared with Fig. 11C). Sensory organs on each leg present (Fig. 11B, D).

Remarks

Tardigrades with clear sexual dimorphism in size (mature females are twice as big as males). Short spine-like sensory organ present also on the legs II and III. Outer epicuticle with various levels of inflation so we measured length and width by inner cuticle borders, which corresponded to the original description by Jørgensen *et al.* (2014).

Order: Echiniscoidea Richters, 1926

Family: Echiniscoididae Kristensen & Hallas, 1980

Genus: *Isoechiniscoides* Møbjerg, Kristensen, & Jørgensen, 2016

***Isoechiniscoides* aff. *sifae* sp. can.**

N=1 specimen: female
occurrence: ANDEEP I; 60°27.05′S, 56°04.77′W; 3,958 m bsl.
Figs 12–14; Supplementary Table 1.13

Description

Body. Small *Isoechiniscoides* of 113 µm body length and 46 µm width. Dorsal cuticle has warts arranged in transverse rows. They are penetrated by epicuticular pillars (Fig. 14F). A pair of mid-dorsal, kidney-shaped cuticular sculptures of 5 × 3 µm and without warts is present on the posterior region (Fig. 14I).

Cephalic region. Two mouth plates form the mouth opening region (Figs 12B, 13D, E). Pharyngeal bulb inconspicuous and pharyngeal apparatus not visible. Eyes are absent. Primary clavae ovoid (3.5 µm long) with a small pore on the anterior end. The base of the primary clava has an elongated plate (4.5 µm) that lacks warts and pillars (Fig. 13B, C, 14E, F); the elongated plate of the right primary clava is either hidden on the SEM images due to a backward folding of cirrus *A*, or it could be completely blown-up due to a preparation artefact (Fig. 14G). However, its contours are visible on the light microscope image (Fig. 13B, C). Secondary clavae (7.5 × 8 µm) dome-shaped (Figs 13D, E, E2, 14G). External (2.5 µm) and internal cirri (3.5 µm) have a small ring-shaped base (Fig. 13D, 14G). Cirri *A* are 10.5 µm long and have a thicker and folded cirrophore (Fig. 14F, G).

Legs. Leg I sensory organ is an elongated papilla (2.5 µm) with short spiny tip (Fig. 14A). Leg II sensory organ is a 3.3 µm long spine (Fig. 14B). Leg III sensory organ is a spine (5.5 µm) with annulated base (Fig. 14C). Leg IV sensory organ is a spherical papilla (4.0 µm) with a short spiny tip (Fig. 14I). Each leg has six sickle-shaped claws with cuticular folds (Fig. 14H).

Caudal region. Cirri *E* are 14.5 µm long and have a thicker annulated cirrophore (Fig. 14E, I). Rosette-shaped, six-lobed female gonopore is present on the ventral side between legs III and IV (Figs 13F, 14D). The anus is located in the terminal body end and present as an inconspicuous three-lobed unit (Figs 12B, 13F).
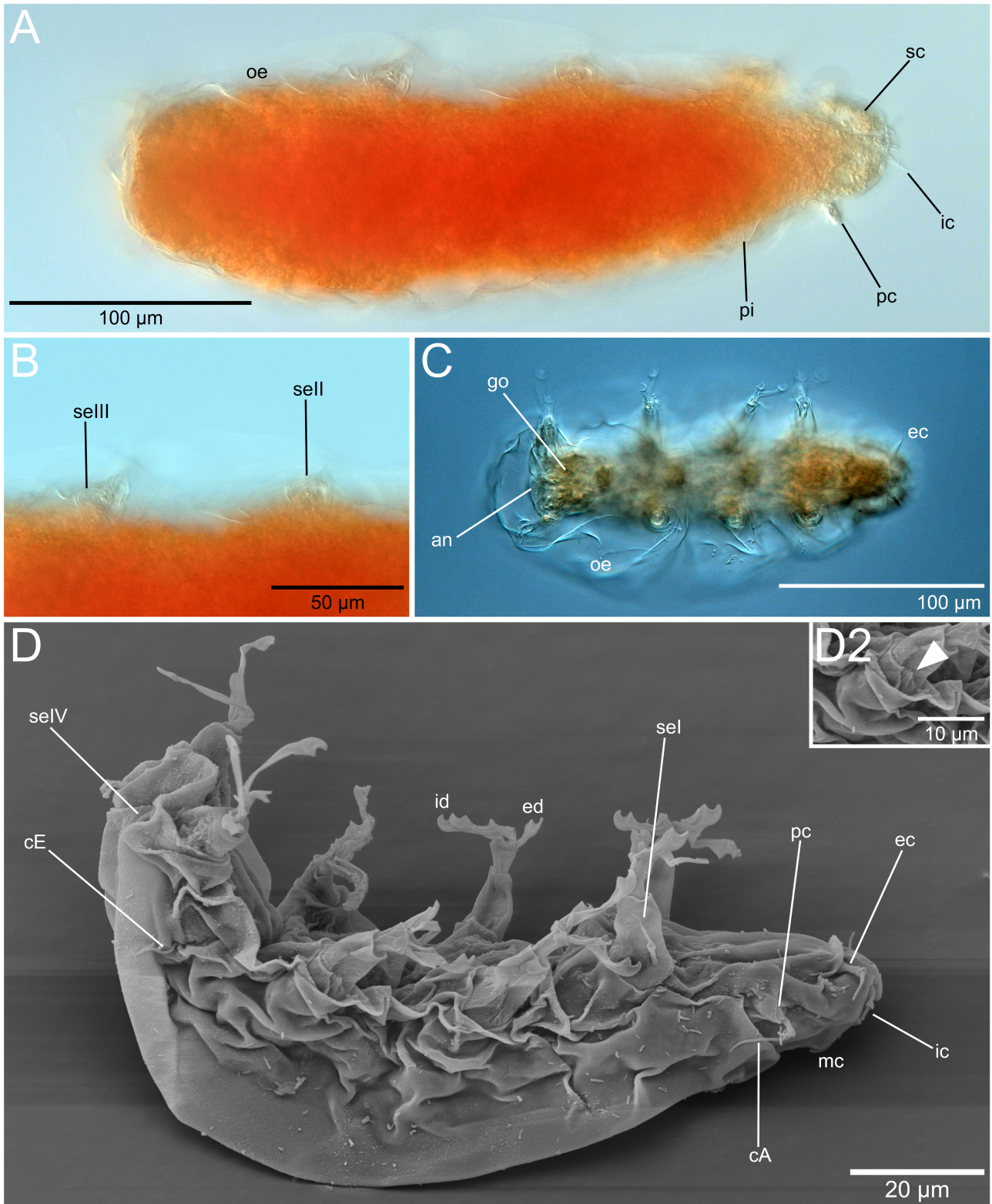
FIGURE 11. *Tholoarctus oleseni*. **A** *Tholoarctus oleseni*, female, light microscopy (DIC), dorsal view. **B** *Tholoarctus oleseni*, female, light microscopy (DIC), leg II (right) and leg III (left) region, dorsal view. **C** *Tholoarctus oleseni*, male, light microscopy (DIC), ventral view. **D** *Tholoarctus oleseni*, male, SEM, ventro-sagittal view. **D2** *Tholoarctus oleseni*, male, SEM, leg III, note sensory organ (arrowhead). Abbreviations: an—anus, cA—cirrus *A*, cE—cirrus *E*, ec—external cirrus, ed—external digit, go—gonopore, ic—internal cirrus, id—internal digit, mc—median cirrus, oe—outer epicuticle, pc—primary clava, pi—cuticular pilars, sc—secondary clava, se—leg sensory organ.
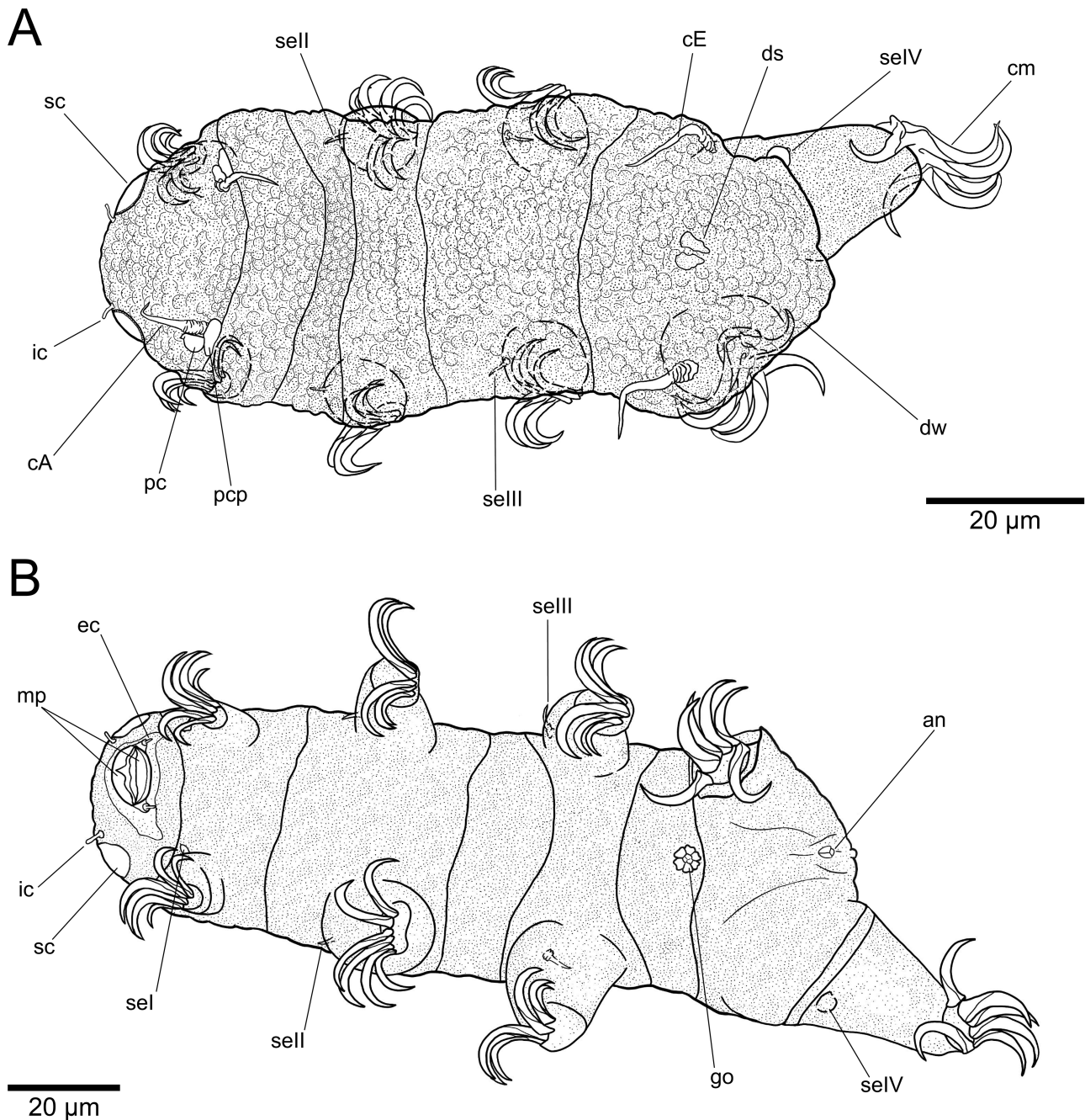
FIGURE 12. *Isoechiniscoides* aff. *sifae* sp. can., female, drawing (reconstruction) based on light microscopy (DIC) and SEM. **A** *Isoechiniscoides* aff. *sifae* sp. can. female, dorsal view. B female, ventral view. Abbreviations: an—anus, cA—cirrus *A*, cE—cirrus *E*, cm—claw membrane, ds—dorsal sculpture of the caudal segment, dw—dorsal wart with pillars, ec—external cirrus, go—gonopore, ic—internal cirrus, mp—mouth plates, pc—primary clava, pcp—primary clava plate, sc—secondary clava, se—leg sensory organ.

Differential diagnosis

With its body length of 113 μm, *Isoechiniscoides* aff. *sifae* sp. can. is a rather tiny deep-sea representative compared to the already described *I. higginsi* and *I. sifae*, which measure up to 329 and 188 μm, respectively (Hallas & Kristensen 1982, Møbjerg *et al.* 2016). In order to exclude the possibility of a shrinkage that might have occurred during desiccation by CPD, we have also measured the specimen when still mounted on a glycerol-mounted slide and there was no shrinkage observable. Therefore, this species can be well separated from *I. higginsi* by the smaller size, but additionally by the length of the sensory organs of leg I, II, III and IV (4.0, 12.0, 14.0 and 6.5 μm in *I.*

higginsi holotype female to 2.5, 3.3, 5.5 and 4.0 µm in *I.* aff. *sifae* sp. can. female), mid-dorsal plates without warts and the unique elongate primary clavae plate. Morphologically, *Isoechiniscoides* aff. *sifae* sp. can. is very similar to *I. sifae*, however, the body size, length of leg sensory organs (3.5, 8.0, 11.6 and 4.9 µm in *I. sifae* holotype female to 2.5, 3.3, 5.5 and 4.0 µm in *I.* aff. *sifae* sp. can. female) and the presence of primary clavae plates are significant differences between both species, which could represent a pair of sister species.

We refrain from erecting the new species of *Isoechiniscoides* due to the rather poor condition of the specimen and the lack of supporting molecular data.
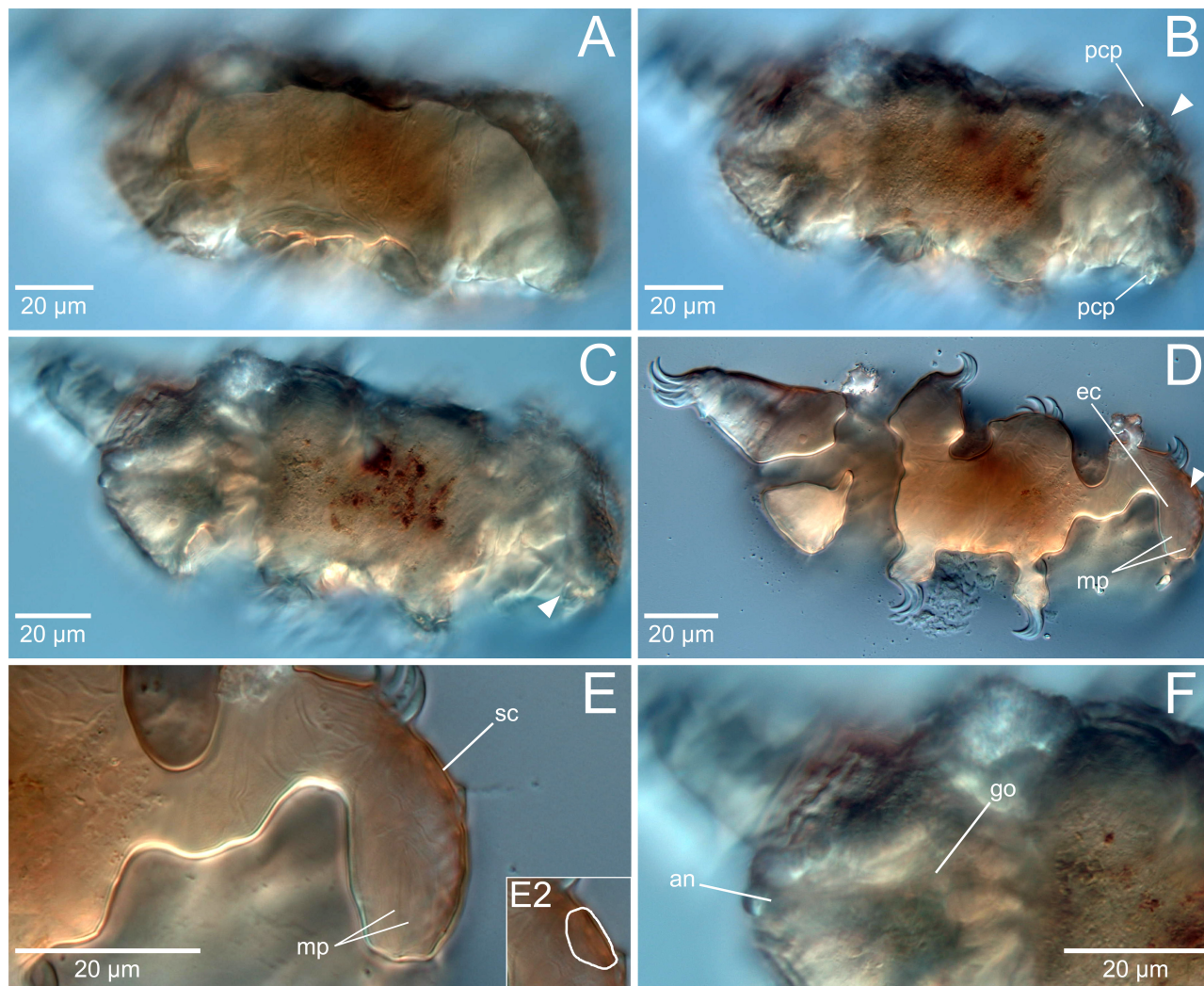
FIGURE 13. *Isoechiniscoides* aff. *sifae* sp. can., female, light microscopy (DIC). **A** dorsal view. **B** dorsal view, note primary clava (arrowhead). **C** dorsal view, note primary clava (arrowhead). **D** ventral view, note secondary clava (arrowhead). **E** ventral view. **E2** ventral view, secondary clava indicated. **F** ventral view, caudal region. Abbreviations: an—anus, ec—external cirrus, go—gonopore, mp—mouth plates, pcp—primary clava plate, sc—secondary clava.

Discussion

Diversity and dominance

During ANDEEP-1, ANDEEP-2, ANDEEP-3 and ANDEEP-SYSTCO expeditions, 1,397 individuals of marine tardigrades were recorded, 1,210 were identified to genus and mostly also to species level. With 1,172 of these 1,210 individuals, the collected tardigrades are strongly dominated by the genus *Angursa*. Within this genus, *Angursa capsula* is the dominant species with 58.02% of all specimens, and *Angursa abyssalis* is the subdominant one with 20.31%. There is a species diversity of 13 taxa in total, but with much lower abundance among the tardigrades other than the two species of *Angursa* mentioned above (see Table 4).
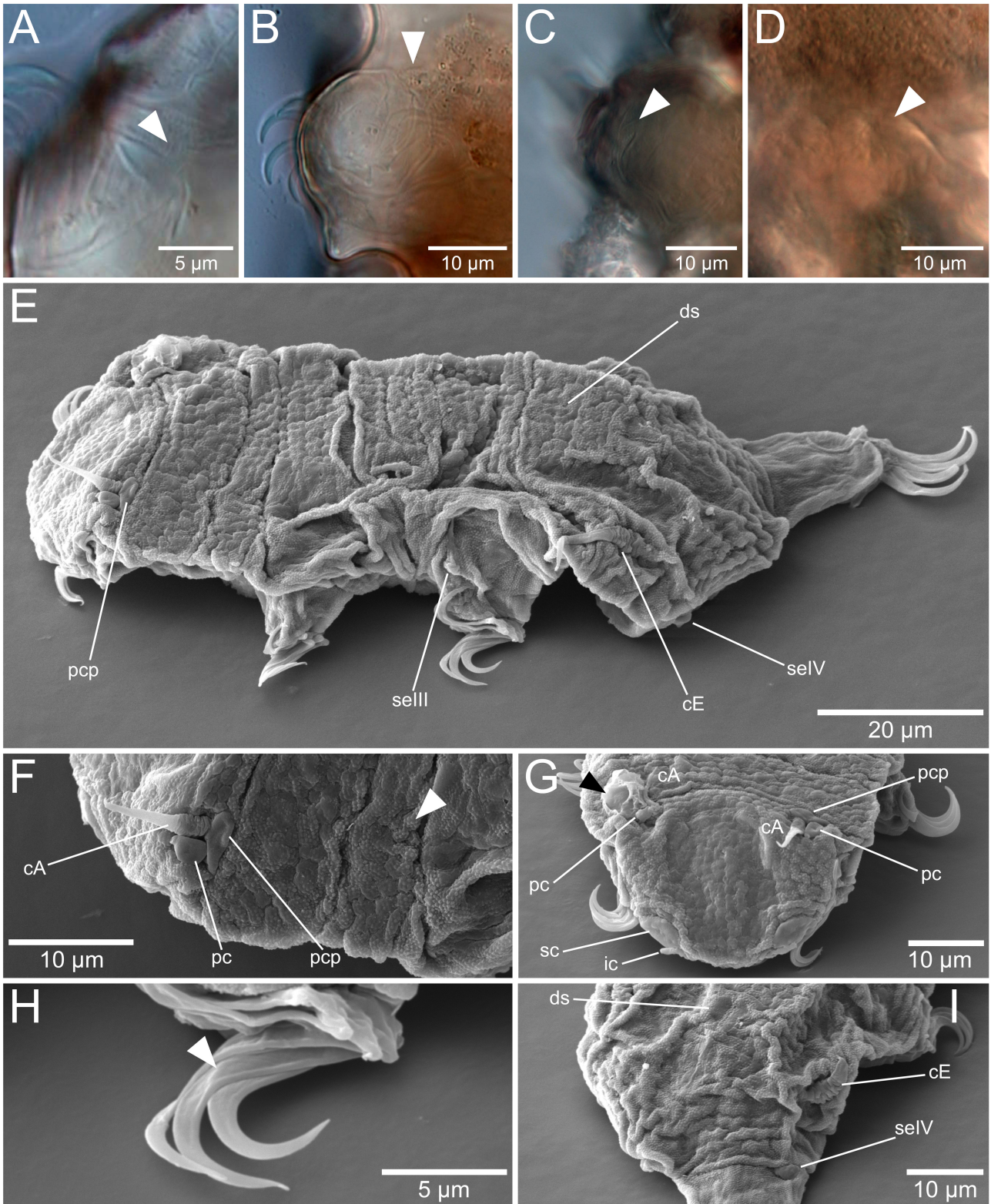
FIGURE 14. *Isoechiniscoides* aff. *sifae* sp. can., female, light microscopy (DIC) from A to D, SEM from E to I. **A** leg I, note sensory organ (arrowhead). **B** leg II, note sensory organ (arrowhead). **C** leg III, note sensory organ (arrowhead). **D** caudal region, note female gonopore (arrowhead). **E** dorso-sagittal view. **F** head, dorsal view, note dorsal wart with pillars. **G** head, frontal view, note damaged primary clava plate (arrowhead). **H** leg III claws, note claw membrane (arrowhead). **I** caudal region, dorsal posterior view. Abbreviations: cA—cirrus *A*, cE—cirrus *E*, ds—dorsal sculpture of the caudal segment, ic—internal cirrus, pc—primary clava, pcp—primary clava plate, sc—secondary clava, se—leg sensory organ.

Biogeography

The knowledge about the biogeography of Tardigrada is quite heterogeneous. Especially among the limno-terrestrial Eutardigrada, quite a lot of supposedly cosmopolitan species have been reported, such as *Milnesium tardigradum* (Doyère, 1840) (Morek *et al.* 2021). However, despite their extraordinary abilities to form desiccation stages that should have a high capacity for long distance-dispersal with wind or biological vectors (Nelson *et al.* 2015, Jørgensen & Møbjerg 2015, Morek *et al.* 2021), studies of 18S rRNA, 28S rRNA, ITS-2, COI and transcriptome sequencing have revealed that species which were formerly regarded as having a widespread or even cosmopolitan distribution, are in fact complexes of cryptic species, like in the case of genus *Richtersius* (Stec *et al.* 2020). Such studies gradually improved our understanding of the biogeography of limno-terrestrial Tardigrada in a way that we can today conclude that a universal, ubiquitous "everything is everywhere" pattern is questionable. Instead, the understanding of their biogeography needs to be replaced by a "regional structuring" approach (Gąsiorek 2023). According to a thorough analysis of numerous studies of the past decades, a pattern becomes evident that limno-terrestrial tardigrade communities are assembled mostly by species with more restricted distributional ranges (*e.g.* endemic to a certain zoogeographic region) and a lower number of more widespread to even true cosmopolitan species (Gąsiorek 2023 and references therein). Concerning the marine realm, which is mostly populated by species of the Heterotardigrada, our knowledge about the distribution of species and biogeographic patterns is even much more fragmentary compared to the Eutardigrada. There are also reports of widespread species such as *Styraconyx qivitoq* that occurs in Greenland (Kristensen & Higgins 1984), the Faroe Islands (Hansen *et al.* 2001), the Mediterranean Sea (D'Addabbo Gallo *et al.* 2001, Grimaldi de Zio & D'Addabbo Gallo 2001, Grimaldi *et al.* 2003, D'Addabbo *et al.* 2007, Accogli *et al.* 2011), the Black Sea (Kharkevych 2012), the Indian Ocean (Gallo *et al.* 2007) and the Lutzow-Holm Bay (reported as *Styraconyx* cf. *qivitoq*) in East Antarctica (Fujimoto *et al.* 2020), but the larger part of marine tardigrade species, however, is only reported from a rather restricted area possibly indicating endemism. *Angursa antarctica* for instance, is only known from the South Shetland Islands and the Lutzow-Holm Bay (Víllora-Moreno 1998; Fujimoto *et al.* 2020). We need to keep in mind that such limited or even singular finds may often be biased by a quite scattered sampling and research activity (Bartels *et al.* 2015; Kaczmarek *et al.* 2015). Genetic data is difficult to achieve for marine tardigrades from remote habitats like the deep sea, but also occurrence records based on a morphological identification can already provide some new indications of distributional patterns: a recent analysis of just a small subset of deep-sea samples from the Northwest Atlantic, for instance, already enhanced our understanding of the distribution of some species of the genus *Angursa* (Trokhymchuk & Kieneke 2024). In the following, we compare our new records from the Southern Ocean deep sea with the already known distribution of the respective species. There is always a possibility of observing a complex of species with highly similar morphology rather than a truly widespread species like in the case of *Batillipes pennaki*, which could be revealed as consisting of at least three different lineages delimitable by quantitative morphological traits (Santos *et al.* 2019). Taking into account the above-mentioned sampling difficulties, the results of the current study are regarded as first steps in understanding the biogeography of the deep-sea tardigrades. In accordance with Gąsiorek (2023), we are aware that any meaningful analysis of tardigrade biogeography needs to be carried out with the corroboration of genetic data. Only with such it is possible to detect a possible hidden diversity within morphologically defined species, as for example in the intertidal and barnacle-associated tardigrades of the genus *Echiniscoides* (Faurby & Barber 2015).

The genus *Batillipes* is one of the most frequently occurring marine tardigrade genera (Kaczmarek *et al.* 2015). However, this genus was hitherto unknown from the polar regions. The most southern reported species are *Batillipes amblypyge* Menechella *et al.*, 2017, *Batillipes lingularum* Menechella *et al.*, 2017 and *Batillipes acuticauda* Menechella *et al.*, 2015 from the Argentina coast (Menechella *et al.* 2015, 2017) and *Batillipes lesteri* Kristensen & Mackness, 2000 from the Southern Australia coast (Kristensen & Mackness 2000). Our record is the first from the Southern Ocean (Ona Basin and the Weddell Sea) and the most southern *Batillipes* record so far. *Batilipes wyedeleinorum* has been recorded from the Bahamas (Bartels *et al.* 2018) and the Great Camanoe Island (Bartels *et al.* 2024). Our new records provide evidence for a possible South-Atlantic distribution of *Batilipes wyedeleinorum*.

Coronarctus dissimilis was previously registered near Brazil (Gomes-Júnior *et al.* 2020) and from the Newfoundland basin (Trokhymchuk & Kieneke 2024). We report this species for the first time from the Southern Ocean (Cape Basin Shona Ridge). This new record provides further evidence for a possible amphi-Atlantic distribution of *C. dissimilis*, as already suggested by Trokhymchuk & Kieneke (2024). The known distribution of the species *Coronarctus tenellus* was restricted to the deep sea off the eastern coast of Africa near Somalia (Indian

Ocean, Somali Basin) and off the western coast of Africa near Namibia (Atlantic Ocean, Angola Basin; Renaud-Mornant 1974). We registered this species from the Southern Ocean for the first time. The new record (present study) somehow "lines up" with the previous ones of Renaud-Mornant (1974) and enlarges the known distribution range of *C. tenellus* further southwards from the Angola Basin to the Cape Basin. Together with the record from the Indian Ocean, this could point to a circum-global distribution in the southern hemisphere which needs, however, support from further records of this species from the Pacific sector of the Southern Ocean and definitely supporting DNA sequence data in order to validate such species records.

The genus *Moebjergarctus* has so far been exclusively reported from specific abyssal seafloor regions containing manganese or polymetallic nodules, such as the Pacific Clarion-Clipperton Zone (type locality of *M. clarionclippertonensis*, Bai *et al.* 2020) and the deep South China Sea (Wang *et al.* 2023). In this study, we registered *Moebjergarctus clarionclippertonensis* from the deep sea bottom of the Ona Basin, Shackleton Fracture Zone and Shona Ridge. These regions are also known for numerous polymetallic sulfide deposits and hydrothermal vent sites such as black smokers (Miller *et al.* 2018) and therefore correspond well to the other records of this genus. Our record is the first for the genus and species from the Southern Ocean at the transition zone from the Atlantic Ocean to the Pacific Ocean basin, *i.e.* the Drake Passage.

Recently, Fujimoto & Hansen (2019) reviewed the taxonomy and distribution records of the genus *Angursa*. Amongst others, they concluded that several previous records of especially *A. abyssalis* need to be regarded as records of *Angursa* sp. instead, due to non-reliable identification (see discussion of Trokhymchuk & Kieneke 2024). Reliable records of *Angursa abyssalis* stem from off the Angola coast, the Northeast Atlantic, the Kuril Basin and the Newfoundland basin (Renaud-Mornant 1981, Fujimoto & Hansen 2019, Saulenko *et al.* 2022, Trokhymchuk & Kieneke 2024). We here report this species for the first time from the Atlantic sector of the Southern Ocean from all expeditions and almost every sampling station at the Drake Passage/Scotia Sea, Weddell Sea, Lazarev Sea, and the Cape Basin. These numerous southern data points provide strong support for an at least Atlantic-wide deep-sea distribution of this species. The records from the northwest Pacific (Saulenko *et al.* 2022) even suggest a cosmopolitan abyssal distribution of *A. abyssalis*.

Angursa antarctica was previously reported from the South Shetland Islands and the Lutzow-Holm Bay (Víllora-Moreno 1998; Fujimoto *et al.* 2020). We report *Angursa antarctica* from a rather close location in the deep sea of the Drake Passage northwest of the South Shetland Islands. These new records match with the hypothesised endemicity of this species. *Angursa capsula* was previously reported from only two and quite far apart locations, the Peru basin in the eastern Pacific and the Newfoundland basin in the northwestern Atlantic (Bussau 1992, Trokhymchuk & Kieneke 2024). Trokhymchuk & Kieneke (2024) pointed out that this could indicate a worldwide distribution of *A. capsula*. The numerous novel records of this species from the Southern Ocean (Drake Passage/Scotia Sea, Weddell Sea, Lazarev Sea, Cape Basin) provide further support for a putative cosmopolitan (deep-sea) distribution and nicely "link" the former records geographically. *Angursa lanceolata* is currently known from deep sea sites off the Angola coast and the Newfoundland basin abyssal plain (Renaud-Mornant 1981, Trokhymchuk & Kieneke 2024). We report this species for the first time from several stations of the Atlantic sector of the Southern Ocean (Drake Passage, Lazarev Sea and Cape Basin). These new records provide further evidence for a possible amphi-Atlantic distribution of *A. lanceolata*. The hitherto known distribution of *Angursa lingua* could so far only be deduced from two records. One is from the Peru basin (Bussau 1992) and the second from off the Coast of Brazil (da Rocha *et al.* 2013). We report this species for the first time from the Atlantic sector of the Southern Ocean (Drake Passage, Weddell Sea and Lazarev Sea), a region intermediate between both previous records. This can be regarded as further evidence for a putative cosmopolitan (deep-sea) distribution as in the case of *A. abyssalis* and *A. capsula*, or at least a circum-global distribution in the southern hemisphere as hypothesised for *Coronarctus tenellus* (see above).

Styraconyx qivitoq is a bryozoan parasite reported from Greenland (Kristensen & Higgins 1984), the Faroe Islands (Hansen *et al.* 2001), the Mediterranean Sea (D'Addabbo Gallo *et al.* 2001, Grimaldi de Zio & D'Addabbo Gallo 2001, Grimaldi *et al.* 2003, D'Addabbo *et al.* 2007, Accogli *et al.* 2011), the Black Sea (Kharkevych 2012), the Indian Ocean (Gallo *et al.* 2007) and the Lutzow-Holm Bay (reported as *Styraconyx* cf. *qivitoq*) in East Antarctica (Fujimoto *et al.* 2020). The current findings of *S. quivitoq* from Lazarev Sea provide further southern records of this species. It may have a potentially bipolar origin with further dispersal to the (sub-) tropics, like some bryozoans have (Kuklinski & Barnes 2010), their potential hosts. This could therefore represent an interesting example of coevolution of distribution ranges between host and parasite and definitely needs further future attention. *Styraconyx takeshii* has been only reported from its type locality in the Lutzow-Holm Bay of East Antarctica so far (Fujimoto
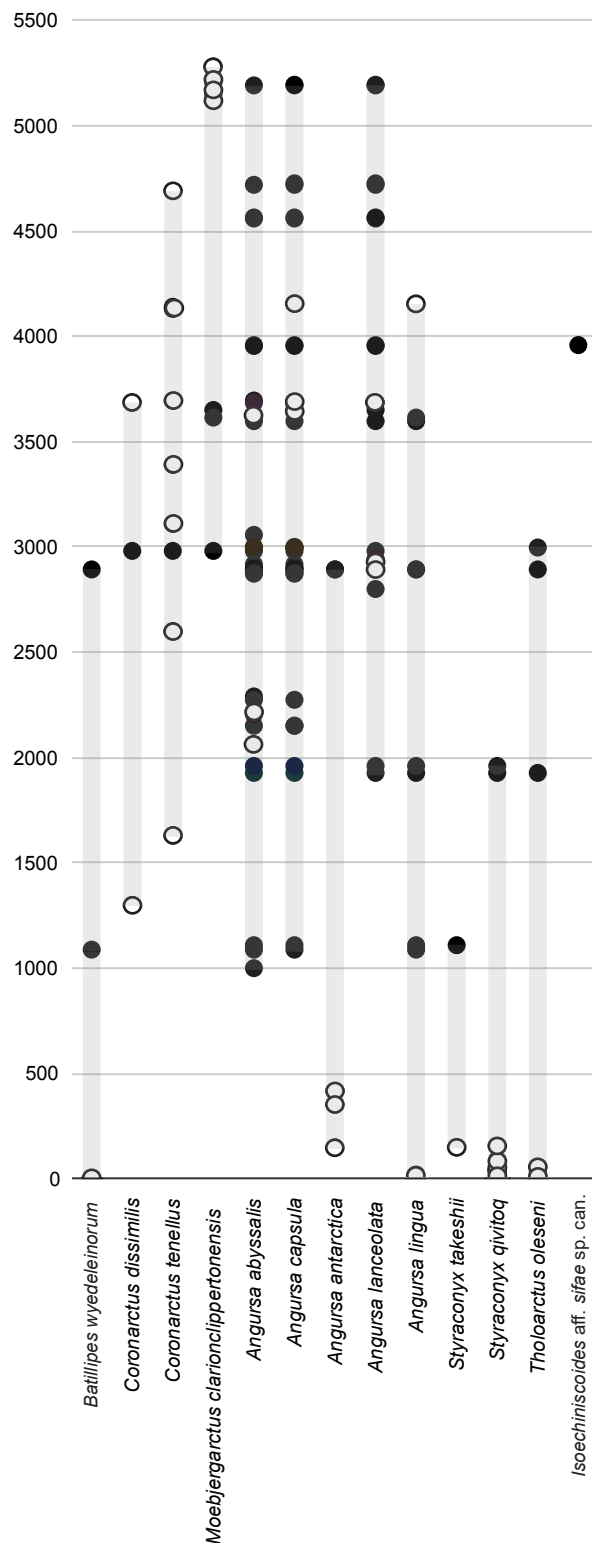
FIGURE 15. Bathymetric distribution of the thirteen species of Tardigrada sampled during expeditions ANDEEP-1 to 3 and ANDEEP-SYSTCO. Black circles indicate depth records obtained by the current study, empty circles indicate previously published depth records, grey bars indicate potential bathymetric distribution ranges of each species. Depth in m below sea level.

Tholoarctus oleseni was reported from the Tasman Sea Fish Rock Cave (Jørgensen *et al.* 2014). We report this species from the Atlantic sector (Ona Basin and Cape Basin) of the Southern Ocean. This could be a first indication of a putative circum-global distribution of *T. oleseni* in the southern hemisphere.

The family Echiniscoididae is present in the Southern hemisphere by just shallow water species (Kaczmarek *et al.* 2015). Closest to the Southern Ocean are species reported from the Prince Edward Islands—*Echiniscoides porphyrae* and *Echiniscoides verrucariae* (Grimaldi de Zio *et al.* 2000); the Kerguelen Islands—*Echiniscoides travei* (Bellido & Bertrand 1981); the Macquerie Islands—*Neoechiniscoides horningi* (Miller & Kristensen 1999). We report for the first time a representative of the family Echiniscoididae from the deep Southern Ocean. The genus *Isoechiniscoides* so far includes two littoral species, *I. higginsi* and *I. sifae*, from the USA east coast (Hallas & Kristensen 1982, Faurby *et al.* 2012) and the French Atlantic coast, accordingly (Møbjerg *et al.* 2016). We report a species of *Isoechiniscoides*, *I.* aff. *sifae* sp. can., from the Southern Ocean, the first record of the genus from high southern latitudes. This new record provides further evidence for a possible amphi-Atlantic distribution of the genus *Isoechiniscoides*. If this species is endemic to that area can only be clarified with new sample material from different circum-Antarctic stations.

Coming back to our first general research question (**RQ 1**), we cannot provide a simple "yes or no" answer, depending on the species we regard to. We were able to demonstrate that marine deep-sea tardigrades much likely show different distribution patterns ranging from amphi-oceanic distributions (e. g. *Coronarctus dissimilis*), occurrences in two oceans indicating putative cosmopolitan distributions (e. g. *Angursa capsula*), southern hemisphere circum-global distributions (*e.g. Coronarctus tenellus*), but also patterns of possible endemicity (e. g. *Angursa antarctica*). It has to be stressed, though, that species such as *Angursa lanceolata* were for a long time only known from their type locality and therefore considered endemic. However, recent research has revealed a wider area of distribution for this species (Trokhymchuk & Kieneke 2024, this study). The challenge in identifying endemism in marine meiofaunal animals is the generally fragmentary sampling in such a vast ecosystem as the deep-sea plains. There is currently no way to demonstrate the absence of species in a series of local samples as a true absence of those species in the studied area, because of the patchy distribution coupled with very low abundances of many meiofaunal taxa (Giere 2009). If the grid of sampling stations would be dense enough, maybe rare species that were thought to be endemic would be re-discovered also in other regions. This imbalance of sampling and research effort also causes a bias if areas of endemism shall be identified using a community-based approach (*e.g.* Garraffoni & Balsamo 2017).

Bathymetric distribution

Compared to the inadequate knowledge of the biogeography of marine Tardigrada and in particular of deep-sea tardigrades, we also only have a weak idea of the true bathymetric distribution (occurrence) and, linked to this, the ecological demands of the different species. The majority of heterotardigrades has been reported so far only from eulittoral or shallow sublittoral sandy sediments and less frequently from other substrata such as macroalgae, barnacles or stones (Kaczmarek *et al.* 2015). Some species or even few genera, however, are reported as 'typical deep-sea taxa' as for example *Moebjergarctus*, *Proclavarctus* and the genus *Coronarctus* (Renaud-Mornant 1974, 1983, Kaczmarek *et al.* 2015, Bai *et al.* 2020, Gomes-Júnior *et al.* 2020, Wang *et al.* 2023). Somehow intermediate between these two extremes, few species that are frequently observed from shallow water were also recorded from deeper sites of the shelf or from seamount summits like *Tanarctus ramazzottii* Renaud-Mornant, 1975 (Renaud-Mornant 1975, Grimaldi de Zio & D'Addabbo Gallo 2001, Grimaldi de Zio *et al.* 2003). An obstacle against the understanding of true bathymetric distributions of marine tardigrades is much likely the sampling effort again, which is either dedicated to the deep sea, or to shallow waters, with a huge gap in between. And, analogously to the biogeography, also the study of distribution patterns along depth gradients, or elevational gradients in limno-terrestrial Tardigrada, are in need of validation through genetic data (Gąsiorek 2023). Despite their limitations, in the following comparison of our data with those of the literature, we will figure out what can be learned from the new 1210 records that already span a considerable depth range of 1,088 to 5,194 m.

The deepest until recently known *Batillipes* record was the species *Batillipes similis* reported from the Faroe Bank, Atlantic Ocean, at 104-260 m depth (Hansen *et al.* 2001). There are further sublittoral records for unknown species of *Batillipes* from the Faroe Bank (Hansen *et al.* 2001; Hansen 2005), however, all remaining species of the genus are exclusively known from shallow water bottoms (see Kaczmarek e al. 2015). A recent record of a non-determined *Batillipes* sp. from the South China Sea at 1,517 m depth was the first one of this genus from a

deep-sea habitat (Wang *et al.* 2023). In the samples from the ANDEEP-1 expedition, we found a single *Batillipes wyedeleinorum* four-toed juvenile at 1,088 m depth and a single female specimen of *Batillipes wyedeleinorum* at 2,893.2 m depth (Drake Passage). These three records are the deepest of the genus *Batillipes* (and also Batillipedidae) so far and significantly increase our knowledge of the bathymetric distribution of this taxon. Furthermore, our new records of the recently described *Batillipes wyedeleinorum* considerably increases the known depth range of this species. So far, *B. wyedeleinorum* has been recorded from the Bahamas from 3 m depth (Bartels *et al.* 2018) and from the Great Camanoe Island from intertidal samples (Bartels *et al.* 2024). Therefore, the ecological demands of this species seem to differ considerably from its congeners that mostly live in the euphotic zone.

As already mentioned above, representatives of the genus *Coronarctus* are considered "typical" deep-sea tardigrades (Kaczmarek *et al.* 2015). *Coronarctus tenellus* has been recorded from the Namibian Coast at 3,694 m; the Somalian coast at range from 1,630 to 4,690 m depth (Renaud-Mornant 1974); *Coronarctus dissimilis* is known from the Campos Basin at 1,300 m, the Newfoundland Basin at 3,685 m depth (Trokhymchuk & Kieneke 2024). Our findings of these two species at a depth of 2,981 m completely support the idea of *Coronarctus* as an exclusively abyssal taxon.

Moebjergarctus is another exclusively deep-sea genus, usually recorded from polymetallic nodules (Bussau 1992, Bai *et al.* 2020, Saulenko *et al.* 2022, Wang *et al.* 2023). *Moebjergarctus clarionclippertonensis* was described from the Clarion-Clipperton Fracture Zone in the east Pacific with records from depths between 5,135–5,281 m (Bai *et al.* 2020). In this study, we record *Moebjergarctus clarionclippertonensis* from depths between 3,551 to 3,650 m in the Drake Passage which supports the abyssal distribution of this species, but also enlarges the known depth range of this species.

The genus *Angursa* primarily comprises deep-sea species (Kaczmarek *et al.* 2015; Fujimoto & Hansen 2019), with a few exceptions such as coastal records of *Angursa clavifera* Noda 1985 from the coast of Honshu (Noda 1985) or *Angursa* sp. in the Adriatic Sea according to D'Addabbo Gallo *et al.* 2001.

Angursa antarctica was described from the ocean bottom of the Scotia Sea at depths between 352 and 416 m (Fujimoto *et al.* 2020, Víllora-Moreno 1998). We found this species in samples from the geographically rather close Drake Passage (Ona Basin), but at 2,893 m depth. The known bathymetric distribution of this species therefore increases considerably to abyssal depths and now spans more than 2,500 m. The reliable records of *Angursa abyssalis* (see above) stem from a depths range of 2,063 to 3,685 m bsl (Fujimoto & Hansen 2019, Renaud-Mornant 1981, Saulenko *et al.* 2022, Trokhymchuk & Kieneke 2024). Our samples come from depths of 1,088 to 5,213 m of the Drake Passage and the Weddell Sea and therefore increase the known range of bathymetric distribution of this species considerably. *Angursa capsula* was described from the Peru Basin at depths of 4,140–4,170 m (Bussau 1992) and from the Newfoundland Basin at depths of 3,675 to 3,685 m (Trokhymchuk & Kieneke 2024). We record this species from 1,088 to 5,213 m depths in the whole Atlantic sector of the Southern Ocean and therewith also increase the known bathymetric distribution of this species. Both most abundant deep-sea tardigrade species of the Southern Ocean, *Angursa abyssalis* and *A. capsula* obviously share similar ecological demands, at least regarding the depth and linked physicochemical parameters (pressure, temperature, salinity etc.). *Angursa lanceolata* has previously been recorded from a depth range of 2,944 to 3,685 m (Renaud-Mornant 1981, Trokhymchuk & Kieneke 2024). In this study, we record this species from 1,927 m (Atlantic-Indian Basin) to 5,213 m (Drake Passage) depth. The species therefore has a much wider bathymetric distribution than previously known. *Angursa lingua* was described from the Peru Basin at 4,140–4,170 m depth (Bussau 1992). We record *Angursa lingua* from 1,088 m (Weddell Sea) to 3,555 m depth (Drake Passage) and therefore expanded the known bathymetric distribution of this species to much shallower bathyal depths.

The genus *Styraconyx* typically comprises shallow-water tardigrade species (e. g. Grimaldi de Zio *et al.* 2003); however, four species have been reported from the deeper sublittoral zone. *Styraconyx qivitoq*, for instance, has been reported from the Faroe Bank at 104–260 m depth (Hansen *et al.* 2001). In the course of this study, we record the same species *Styraconyx qivitoq* from 1,927 m to 1,960 m depth from the Lazarev Sea and now has a known bathymetric distribution from the shelf to bathyal depths. *Styraconyx takeshii* has so far only been reported from its type locality, the Lützow-Holm Bay, Antarctica, at 149 m depth (Fujimoto *et al.* 2020). We record *Styraconyx takeshii* from 1,109 m depths from the Weddell Sea and now this species has, as its congener, a known bathymetric distribution from the shelf to bathyal depths. These are by far the deepest records of the genus *Styraconyx* known so far.

The genus *Tholoarctus* consists of both shallow-water and deep-sea tardigrades (Kristensen & Renaud-Mornant 1983, Jørgensen *et al.* 2014). *Tholoarctus oleseni* was hitherto only known from a marine cave at the Tasman Sea at just 34 m depth where it occurs in coarse coralligenous and detritus-rich sand (Jørgensen *et al.* 2014). We recorded *Tholoarctus oleseni* from a depth range between 1,927 to 2,997 m in the Southern Ocean which is considerably deeper. The known bathymetric distribution of this species therefore increases to bathyal and abyssal depths. Furthermore, the range of inhabited sediment types is obviously much wider from silty or fine-sandy to coarse sandy.

The family Echiniscoididae so far exclusively comprised shallow water species (Gąsiorek & Kristensen 2022). For example, *Echiniscoides bruni* was recorded from various shallow water locations around Italy: Sardinia, Nuoro Province and the bottom of the Orosei Gulf at depths between 30 and 40 m and is the deepest occurring *Echiniscoides* species known so far (D'Addabbo Gallo *et al.* 1992; Kaczmarek *et al.* 2015). The genus *Isoechiniscoides* also consists of littoral species. Both *I. higginsi* and *I. sifae* have been recorded from the tidal zone (Hallas & Kristensen 1982, Faurby *et al.* 2012, Møbjerg *et al.* 2016). We record a single female specimen *Isoechiniscoides* aff. *sifae* sp. can. from 3,958 m. This is the first abyssal report of this genus and of the whole Echiniscoididae.

As demonstrated before, also our bathymetric records provide novel knowledge for many species and the known depth ranges have been greatly enlarged in parts (Fig. 15). Concerning our main research question **RQ 2**, there are obviously marine tardigrade species that do not prefer a narrow depth layer for their distribution such as *Angursa antarctica*, *Tholoarctus oleseni*, *Styraconyx qivitoq* and *S. takeshii* which may occur from shallow sublittoral or from the shelf down to bathyal or even abyssal depths. On the other hand, our new data also supported a narrow deep-sea (abyssal) occurrence of species such as *Coronarctus tenellus* and *C. dissimilis*. And in further species, *e.g. Angursa abyssalis*, *A. capsula* and *Moebjergarctus clarionclippertonensis*, we were able to confirm the abyssal occurrence, but were likewise also able to demonstrate a much larger bathymetric distribution that may also reach bathyal depths.

Bathymetric patterns of tardigrade densities

It is known that deep-sea tardigrades are less abundant compared to shallow water tardigrades (Nelson *et al.* 2018). In order to learn about general trends in the bathymetric distribution of marine Tardigrada, we compared the patterns of specimen abundances and densities of all tardigrade species combined. The observed trend of decrease of abundances with depth in many meiofaunal taxa inhabiting abyssal sediments of the Drake Passage was only reversed in the Gastrotricha and the Tantulocarida, that showed a slight increase of abundances with depth (Gutzmann *et al.* 2004). The mentioned study already covered Tardigrada counts of the expedition ANDEEP-1 (see Gutzmann *et al.* 2004), which are again included in our expanded dataset. However, the covered depth range was approximately from 2,300 to 5,200 m, but our data cover depths from 1,088 to 5,200 m. Especially the inclusion of "shallower" samples changed the currently known pattern. Although the trend of a general decrease of densities with depth was supported, we were also able to differentiate this overall pattern: there is a considerable increase of tardigrade abundances and densities from about 1,000 to 3,000 m and abundances and densities decrease again in samples deeper than 3,000 m (Figs 2, 3). It is possible that there are favourable conditions for marine tardigrades at depths between 2,000 and 3,000 m. This assumption fits the results of Saeedi *et al.* (2020) who identified maximum abundances of macro- and meiofauna between 500 and 5,000 m depth. Furthermore, we were able to observe a considerable 'peak' of abundance/density at depths of about 2,000 m (Figs 2, 3). All these samples originate from the Lazarev Sea closer to the Antarctic Shelf which has a well-known high secondary productivity due to accumulation and transfer of organic matter from the sympagic biota (under ice community) to the benthic habitat (Liu *et al.* 2010, Veit-Köhler *et al.* 2013, Flores *et al.* 2011). With the observed patterns, we can give a definite answer to our main research question **RQ 3**: based on our current comprehensive dataset from the Southern Ocean, it seems that tardigrade densities increase to bathyal depths and then decrease again within the abyssal zone. Hence, there is a clear change of densities with depth. However, if this represents a general pattern of marine tardigrade bathymetric distributions needs to be tested with further data and at best also from different geographic regions. Furthermore, highly productive regions of the world oceans such as upwelling zones may alter this general trend.

Conclusion

Although the deep-sea tardigrade fauna remains poorly understood and the biogeographic and evolutionary relationships of Sub-Antarctic and Antarctic tardigrades remain to be fully elucidated, we have obtained considerable new data on the diversity, biogeography and bathymetric distribution of tardigrades in the Southern Ocean. We registered 13 tardigrade species, 10 of these 13 species are new records for the Southern Ocean. Six species: *Angursa antarctica, Styraconyx qivitoq, S. takeshii, Tholoarctus oleseni, Batillipes wyedeleinorum* and *Isoechiniscoides* aff. *sifae* sp. can., are new records of deep-sea Tardigrada. Concerning our three main research questions, we have been able to find some answers: Our comprehensive dataset supports both potential endemic species and species with amphi-oceanic or even global distribution as well. Of course, these biogeographic results need validation by DNA sequence data in future studies. Furthermore, we could enlarge the known bathymetric distributions of some taxa and extend some of them even from the shallow sublittoral to the deep-sea (*e.g.* for Echiniscoididae). Finally, we observed a pattern of tardigrade density increasing to bathyal depths and decreasing again to abyssal depths. If the discovered patterns follow general rules, however, can best be tested if in future research further regions will be investigated like the Arctic region or the temperate and (sub-) tropical Atlantic Ocean.

Data availability

The datasets generated during and/or analyzed during the current study are available in the GBIF repository "https://doi.org/10.15468/uvr84c"

Conflicts of Interests

The authors declare no conflict of interests.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

SM.01 Raw morphometric measurements for species reported in the present study [XLSX file].

SM.02 Tardigrade species occurrence in ANDEEP-1, ANDEEP-2, ANDEEP-3 and ANDEEP-SYSTCO expeditions [XLSX file].