ISSN 2075-5457 (print), ISSN 2220-9697 (online)

DOI: 10.26565/2075-5457-2024-43-6
UDC: 574.587:(595.188+595.412)

New records of deep-sea Gastrotricha and Tardigrada from Iberian and Canary Basins (Northeast Atlantic) with comments on abyssal meiofauna composition and the meiofauna paradox

R. Trokhymchuk, A. Kieneke

The "meiofauna paradox" refers to the amphi-oceanic or even cosmopolitan distribution of species of this ecological group, i.e. the marine meiofauna, as opposed to their weak dispersal potential. Dissolving this paradox includes on the one hand the discovery of complexes of genetically distinct but morphological cryptic species with much more limited distribution areas, but also involves the investigation of "stepping stone habitats" like the shelf area of oceanic islands and summits of seamounts. Such biotopes subdivide long distances, e.g. from one continent to the other, into shorter sections. However, what needs to be excluded is a possible distribution of "shallow water meiofauna" simply via population growth and range expansion at the abyssal plains of the world's oceans. In order to test if the abyssal plains may represent a barrier against dispersal of certain marine meiofauna taxa, we studied the composition of the meiofauna from six samples (stations) taken during the expedition IceDivA (SO280) of the R/V Sonne to the Iberian and Canary Basins from abyssal depths (4904-5485 m). The taxonomic focus was put on the Gastrotricha and Tardigrada. The dominant taxa in all samples were nematodes (13.0 - 97.7 ind./cm^2) and copepods (0.4 - 9.6 ind./cm^2), followed by annelids, kinorhynchs and ostracods. Three Gastrotricha species (*Desmodasys* sp. iberianA, *Desmodasys* sp. langsethA, *Musellifer* sp. iberianA (*Musellifer* aff. *tridentatus*)) and one tardigrade (*Coronarctus dissimilis*) were registered and examined using light microscopy (DIC and CLSM) and SEM. All gastrotrichs from the examined samples presumably represent new and still undescribed species. The range of geographic and bathymetric distribution of *Coronarctus dissimilis* increases to the Iberian Basin and to a depth of 4163 m. This finding further hints to a potential amphi-Atlantic distribution of this species. We compare our data with those from other studies on seamounts, oceanic islands and from the deep-sea and conclude that the abyssal plains represent a significant barrier against long distance dispersal for most genera (and species) of Gastrotricha and for a certain fraction of genera of Tardigrada, too.

Key words: Atlantic Ocean, biodiversity, biogeography, deep sea, *Desmodasys*, *Musellifer*, *Coronarctus*.

Cite this article: *Trokhymchuk R., Kieneke A. (2024). New records of deep-sea Gastrotricha and Tardigrada from Iberian and Canary Basins (Northeast Atlantic) with comments on abyssal meiofauna composition and the meiofauna paradox. The Journal of V. N. Karazin Kharkiv National University. Series Biology, 43, p. 66-84. https://doi.org/10.26565/2075-5457-2024-43-6*

About the authors:
Roman Trokhymchuk – V. N. Karazin Kharkiv National University, Svobody Maidan, 4, 61022, Kharkiv, Ukraine; German Centre for Marine Biodiversity Research (DZMB), Senckenberg am Meer, Suedstrand 44, 26382, Wilhelmshaven, Germany; rtrokhymchuk@gmail.com; https://orcid.org/0000-0001-9570-0226
Alexander Kieneke – German Centre for Marine Biodiversity Research (DZMB), Senckenberg am Meer, Suedstrand 44, 26382, Wilhelmshaven, Germany; alexander.kieneke@senckenberg.de; https://orcid.org/0000-0001-8180-2483

Received: 05.09.2024 / Revised: 16.10.2024 / Accepted: 18.10.2024

Introduction

Meiofauna (meiobenthos) is the community (ecological group) of aquatic, microscopic metazoans passing a sieve of 1 mm, but being retained on the sieve of 40 μm mesh size (Higgins & Thiel 1988). Although the definition of this fraction of the benthic fauna is defined just by this measure of mesh size, it represents an ecological guild of high biodiversity and complexity in trophic interactions within this community, but also with other trophic levels. Species of the meiofauna occupy all kinds of aquatic habitats of our planet ranging from the deep-sea floor (Shimabukuro et al., 2022), over intertidal sediments (Armonies & Reise, 2000, Martínez et al., 2020), running and stagnant inland water bodies to phytotelms (Kolicka 2016) and even moist terrestrial biotopes such as leaf litter or bryophytes (Higgins & Thiel, 1988, Kreuzinger-Janik et al., 2021, Minowa et al., in press). While taxa of the "limno-terrestrial" meiofauna may produce various dormant stages that are also highly suitable for long distance dispersal via anemochory or zoochory, e.g. the characteristic "barrel-shaped tuns" of Tardigrada (Nelson et al., 2015, Gąsiorek, 2023) or the resting eggs of Rotifera (Fontaneto & Plewka, 2021), marine meiofaunal organisms are supposedly much more limited in dispersion by the absence of such stages. However, frequently amphi-oceanic or even cosmopolitan distributions are observed in marine meiofaunal species. This phenomenon, i.e. the mismatch between wide distribution areas and the absence of life stages suitable for long distance dispersal is called the “meiofauna paradox” (Giere, 2009). However, during the past two decades several studies using DNA sequence data have revealed complexes of cryptic species with restricted distribution ranges within nominal species of various taxonomic groups that were before assumed as widespread or even cosmopolitan (e.g., Magpali et al., 2021, Jörger et al., 2012, Derycke et al., 2008, Cerca et al., 2020). The linked phenomena of stasis and recent speciation and further issues such as erroneous application of determination keys have let Cerca et al. (2018) conclude that the “meiofauna paradox” most likely does not exist. In addition, some real cases of widely distributed species might be potentially explained by natural dispersion e.g. via sea turtles (Ingels et al., 2020), as well as by anthropogenic distribution via marine traffic (e.g., in sediment of ballast water tanks; Radziejewska et al., 2006).

Different geomorphological features of the ocean floor may furthermore promote the spread of marine organisms – including the meiofauna – in different ways. In particular seamounts and likewise oceanic islands play an important role in the distribution of meiofauna. It has been suggested that seamounts can provide the function of “stepping stones” in the distribution of shallow-water meiofauna: exchange of individuals, and with this gene flow, is simply much more likely between adjacent seamounts and/or oceanic islands, than over long distances from the coast of one continent to the other (George, 2013 and references therein). At the same time, seamounts can also be “trapping stones” that stuck species there: arriving specimens can contribute to the formation of new populations and over time even new species may form through independent evolution and a strong restriction of gene flow (George, 2013, Cerca et al., 2018). Therefore, when exploring seamounts, one can in principle expect both, to observe shallow water (interstitial) meiofaunal species from adjacent areas or endemic species (George, 2013). In case of the concept of geographic rarity as an expanding issue for endemism, species restricted to such a limited distribution area like the summit plateau of a guyot seamount may appear to have a small population size, making them vulnerable to extinction (Fattorini, 2017).

If we want to learn about the function of seamounts and oceanic islands in conjunction with the biogeography of interstitial meiofauna, we need to study their inhabitants at species level. For the two systematic groups in focus of the current study, namely Tardigrada and Gastrotricha, there aren’t very many of such taxonomically detailed studies yet.

Marine gastrotrich communities have been studied from the Faroe Bank in the Northeast Atlantic (Clausen, 2004), from the islands of Lanzarote, Canary Islands (Riera & Todaro, 2012, Todaro et al., 2019, Martínez et al., 2019), and from São Miguel, Azores (Araújo & Hochberg, 2021). From the 20 species of Gastrotricha that were identified on the Faroe Bank,10 species also occur at several other east Atlantic sites and four were even known from the Atlantic coast of North America. These widespread North Atlantic distributions of marine gastrotrichs, with intermediate occurrences on the Faroe Bank, were interpreted as a possible indication of the so-called “Thule land bridge” in the Tertiary as a potential gateway for shallow water meiofauna distribution (Clausen, 2004). The impressive number of 61 species of marine Gastrotricha reported from Lanzarote (Canary Islands) yielded a high number of putative new species, but also 32 known species with a wider distribution in the Atlantic Ocean, or even from further Ocean basins (Todaro et al., 2019). Species such as *Dactylopodola typhle* (Remane, 1927) or *Acanthodasys aculeatus* Remane, 1927, with a reported trans-Atlantic distribution, can already be regarded as an indication of a stepping stone function of Lanzarote island. Furthermore, eight species that were already known from the Mediterranean Sea, but not from northern European sites, were discussed in the conjunction of the re-invasion of the Mediterranean after the Messinian crisis (Todaro et al., 2019). With a focus on endemism, Martínez et al. (2019) also studied the soft-bodied meiofauna of Lanzarote, including the Gastrotricha. Their analysis also yielded evidence for the “trapping stone” function of oceanic islands and seamounts as a number of at least 10 Canarian endemic gastrotrich species were identified (Martínez et al., 2019).

Analyses of tardigrade communities with a high taxonomic resolution have been carried out from the Faroe Bank (Hansen et al., 2001, Jørgensen & Kristensen, 2001, Hansen et al., 2003, Hansen et al., 2012, Hansen & Kristensen, 2021), from the Condor Seamount, Azores (Kristensen & Renaud-Mornant, 1983, Kristensen et al., 2015) and from the Great Meteor Seamount Plateau (Tchesunov, 2018). Reported from the Faroe Bank, 19 determined species of tardigrades were registered. The composition of genera is similar to that of shallow sublittoral sediments of the Mediterranean Sea and Florida, USA, but differs by the presence of the “deep-sea genus” *Coronarctus* (Hansen et al., 2001). *Tholoarctus natans* Kristensen & Renaud-Mornant, 1983 reported from the Faroe Bank and the Azores is also known from all other Oceans

(Kaczmarek et al., 2015). Such a cosmopolitan distribution in this species is possibly enabled by its ability to buoyancy with the bell-shaped cuticle (Kristensen & Renaud-Mornant, 1983). The marine tardigrade fauna of the Azores currently consists of two determined species and further undetermined representatives of genera *Chrysoarctus, Coronarctus* and *Tanarctus* (Kristensen & Renaud-Mornant ,1983, Kristensen et al., 2015). With only one reported endemic species, the Great Meteor Seamount Plateau is the exception rather than the rule (Tchesunov, 2018).

So far, we have only regarded the communities of putative “stepping stone” and/or “trapping stone” biotopes. However, it is furthermore of high relevance to regard the vast deep sea plains surrounding those isolated “underwater island biotopes” as well (see also “concluding remark 2” of George, 2013), if we try to understand their role in biogeography and dispersal of meiofauna. Are the abyssal plains a barrier against distribution of these microscopic organisms at all, or are they simply inhabited by species that also occur on seamount summits or island shelfs? Gastrotricha and Tardigrada are frequently reported from deep sea sediments, however, their occurrence is patchy and the densities are mostly very low compared to most other meiobenthic higher level taxa (see, e.g., Vincx et al., 1994 and references therein, Gutzmann et al., 2004). Furthermore, most studies only report the occurrence of both phyla without any further taxonomic resolution. The only deep sea records of Gastrotricha on species level are so far those of *Desmodasys abyssalis* Kieneke & Zekely, 2008 from a Pacific hydrothermal vent site and of *Thaumastoderma antarctica* Kieneke, 2010 from the South Atlantic Drake Passage (Kieneke & Zekely, 2008, Kieneke, 2010). Deep-sea tardigrades, unlike gastrotrichs, are better studied, but rather mosaically (Kaczmarek et al. 2015). However, some genera such as *Coronarctus* and *Mjobergarctus* can be distinguished as explicit deep-sea taxa (Kaczmarek et al., 2015, Trokhymchuk & Kieneke, 2024, Trokhymchuk et al., 2024). Meanwhile, as shown by extensive studies of the deep sea tardigrade fauna (more than 1000 individuals from the Southern Ocean), some “shallow-water genera” may also have deep-water species, but with relatively low densities compared to the dominant species. This applies especially to the genus *Isoechiniscoides*, a putative new species of which is reported for the first time from the abyssal zone – the same situation as with the gastrotrich species *Thaumastoderma antarctica* (Kieneke, 2010, Trokhymchuk et al., 2024).

The current study shall help to understand if the sedimentary abyssal plains, one of the largest ecosystems on earth (Ramirez-Llodra et al., 2010), represent a barrier against long distance dispersal of certain meiobenthic and interstitial taxa like the Gastrotricha and Tardigrada. Such a knowledge will further sharpen our understanding about the role of isolated oceanic islands, archipelagos and seamounts for the dispersal and biogeography of marine meiobenthic organisms. We have studied the composition of meiobenthic higher level taxa of a selected subset of deep sea sediment samples from the northeast Atlantic (Iberian Basin and Canary Basin) taken with a multiple corer during expedition SO280 of the R/V Sonne. The recovered specimens of Gastrotricha and Tardigrada have been determined to species level and compared with data from relevant literature.

Materials and methods

Core samples with deep sea sediment were collected in the Northwest Atlantic (Fig. 1, Tab. 1) during the IceDivA1/SO280 expedition of the German R/V SONNE (Kieneke & Brix 2021, Brix et al. 2024). A multiple corer (MUC) with 12 independently closing acrylic glass tubes (Octopus GmbH, Hohenweststedt, Germany) was used as sampling gear for the deep-sea meiofauna. The inner radius of the core tubes is 4.75 cm, the sampled bottom area per core tube thereby covered 70.85 cm^2. After dismounting a core tube from the support frame of the MUC, the near bottom water was immediately poured over a 40 µm sieve. Subsequently, the filtrate containing the epibenthic fauna and a sediment slice of 5 cm height (sediment volume of ca. 354.25 cm^3) was rinsed into a Kautex® wide neck container (1000 ml) with a roughly isosmotic aqueous solution of 7% $MgCl_2$ (w/v) using a spray bottle. The samples were left in the wet laboratory of the research vessel for about 10 minutes until fixation. The use of isosmotic magnesium chloride solution prior to fixation was to anesthetize soft-bodied meiofauna organisms in order to avoid body contractions through muscle spasms (Todaro & Hummon, 2008). For the fixation, a 37% and borax-buffered formaldehyde solution was added to the sample and the Kautex® wide neck container was filled up with filtered seawater to a final concentration of about 4% formaldehyde.

In order to separate the fixed meiofauna from the clayish sediment, the density gradient centrifugation was applied (Higgins & Thiel, 1988). For preparing a suspension with higher density than the organisms, we used the silica colloid Levasil®. An addition of Kaolin® should stabilize the sediment

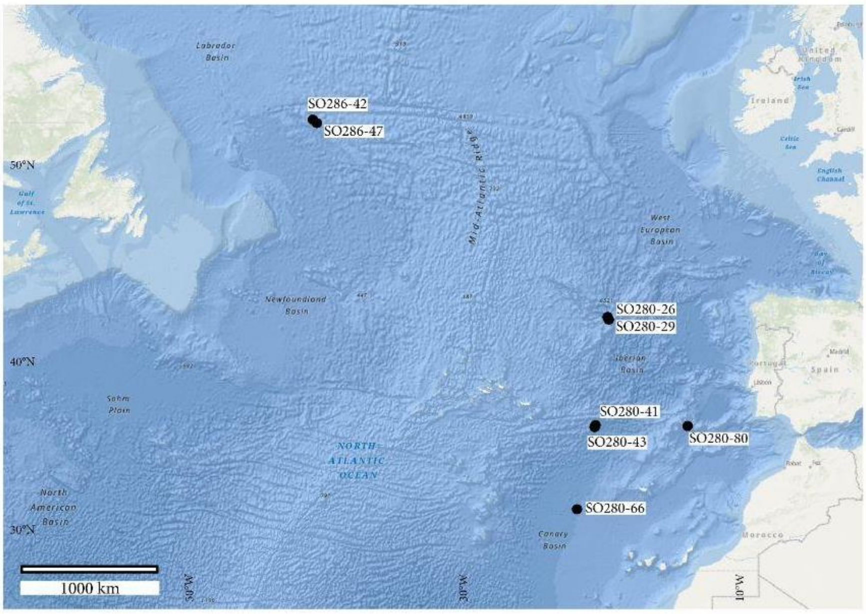

Figure 1. IceDivA/SO280 and IceDivA2/SO286 (see Trokhymchuk & Kieneke, 2024) expedition deployments (stations) we investigated. Map source: https://www.ncei.noaa.gov/maps/bathymetry/

Table 1. Selected deep-sea core samples (MUC) of expedition SO280 of which the meiofauna community was studied. Superscript letter G: core contained gastrotrichs, T: core contained tardigrades

station	latitude	longitude	depth	sea region
SO280-26, MUC 8^{G}	41° 57.540' N	018° 58.787' W	4904 m	Iberian Basin abyssal plain
SO280-29, MUC 6	41° 57.570' N	018° 58.823' W	4906 m	Iberian Basin abyssal plain
SO280-41, MUC 1^{G}	36° 02.059' N	019° 00.799' W	5485 m	Iberian Basin abyssal plain
SO280-43, MUC 9	36° 02.057' N	019° 00.832' W	5485 m	Iberian Basin abyssal plain
SO280-66, MUC 4^{G}	32° 01.989' N	022° 00.711' W	5121 m	Canary Basin; Madeira Abyssal Plain
SO280-80 MUC 2^{T}	36° 26.006' N	014° 00.025' W	4163 m	Iberian Basin; SE of Josephine Bank seamount

during the centrifugation, which was carried out three times at 3608 rpm. For sieving the supernatant containing the meiofauna organisms a mesh size of 40 μm was chosen. We added the dye Rose Bengal for a better recognition of the meiofauna organisms during sorting, which was carried out in Bogorov chambers (Bogorov, 1927) under dissecting microscopes with transmitted light illumination (Leica M80 or M125 stereo microscopes). We have investigated six MUC samples so far (Tab. 1), one from each of the six major working areas of expedition SO280 with bottom sampling (Kieneke & Brix 2021, Brix et al. 2024).

The single tardigrade specimen was stained with Acid Fuchsin and Congo Red 1:1 overnight for the further confocal laser scanning microscope (CLSM) examination with Leica TCS SP5 CLSM (DM5000B base). For this purpose, the specimen was mounted in pure glycerol on a temporary slide. We operated with the argon laser (488 nm) and the DPSS laser (561 nm). After CLSM investigation, the specimen was transferred to a glycerol drop on a slide surrounded with beeswax and paraffin mixture 1:2; covered with coverslip and heated until the wax melted (Trokhymchuk & Kieneke, 2024).

After careful investigation, photographing and filming with an Olympus BX53 light microscope equipped with DIC optics and an attached euromex HD Ultra digital camera, we carried out a well-established preparation method in order to prepare three gastrotrichs for the scanning electron microscope

(SEM) examination (see, e.g., Kieneke & Zekely, 2008, Kieneke et al., 2015, Trokhymchuk & Kieneke, 2024). The coverslip was carefully removed from the temporary slide and the specimen was transferred with an eyelash to a special cage, (invented by Dr. Wilko Ahlrichs) immersed in 40% ethanol (as in Trokhymchuk & Kieneke, 2024). Dehydration was carried out in steps of 10% to 100%, and finally dried in a Leica CPD300 critical point dryer. After removal from the cabinet, the specimen was placed on a round coverslip covered with a mounting resin (Tempfix, Plano GmbH, Wetzlar, Germany) and heated to about 50°C for 30 seconds to adhere the sample to the surface. The coverslip with the specimen glued to it was mounted on an aluminum stub. Gold-palladium coating was performed on the Bal-Tec SCD 050 sputter-coater operated within 150 seconds at 40 mA. SEM examination was conducted using a TESCAN VEGA3 SEM with an acceleration tension of 10 and 30 kV and both, the secondary and the backscattered electron detectors. Three specimens of gastrotrichs, each on individual SEM-stubs (specimens SO280-26-8_1v1, SO280-41-1_1v1, SO280-66-4_1v1 on stubs SN-240911-1, SN-240911-3 and SN-240911-2, respectively) are kept in the private collection of A. Kieneke, Senkenberg am Meer, Wilhelmshaven, Germany. The permanent slide with the tardigrade (SO280-80-2 1v1) is deposited in the Tardigrada collection of the Senckenberg Natural History Museum, Frankfurt am Main, Germany with the same permanent slide number but also with the SMF number 1311 (accessible via https://search.senckenberg.de/aquila-public-search/search). The occurrence record of the tardigrade was submitted to the GBIF database. For comparison with one of our gastrotrichs, a specimen of *Desmodasys* sp. langsethA collected from the central Arctic Langseth Ridge during the expedition PS101 with the research icebreaker "Polarstern" (Boetius & Purser, 2017) was likewise investigated with SEM (specimen PS101-194-3_7v98 on SEM-stub SN-200227-3).

Genus-level identification of the Gastrotricha was carried out with the aid of Kieneke et al. (2020). Tardigrada genus determination dealt with Fontoura et al. (2017). Species identification was made with taxonomic papers containing original species descriptions and redescriptions (see taxonomic part for references). For individuals that are not identified to any known species, we used a combination of the locality of first occurrence and a capital letter plus the prefix "sp." as a "working species name", e.g., "*Desmodasys* sp. iberianA" (unknown species reported from the Iberian Basin), instead of a usual naming of working species like simply "*Desmodasys* sp.1". This shall enable a clear and explicit reference of such working species in future comparative taxonomic studies (as already used in Hummon 2001-2010).

The figure plates were made in Adobe InDesign CS5.5 with single microscopic images, or using stacked images made with Picolay (www.picolay.de). The measurements were made according to the methodology of the original genus/species descriptions (see taxonomic part for references), using the light microscopic images and the image-processing software FIJI/ImageJ (Schindelin et al., 2012).

Abbreviations used in the text below:

BL – body length, ec – external cirrus length, fu – furca length, hw – head width, ic – internal cirrus length, mc – median cirrus length, pc – primary clava length, TbA – anterior adhesive tubes, TbP – posterior adhesive tubes, tw – total (trunk) width, seIV – leg IV sensory organ length, spIV – leg IV coxal process length.

Results

Meiofauna communities

The meiofauna communities of the analysed samples consisted of Nematoda, Copepoda, Annelida (Polychaeta), Kinorhyncha and Ostracoda, with Nematoda and Copepoda as the first and second most abundant taxa (Tab. 2). Nauplii (potentially copepod larvae) were also more abundant than major taxa, while Gastrotricha, Tardigrada and Mollusca only occurred in few or single core samples and always with very low densities (Tab. 2).

Table 2. Densities (individuals per surface area of 10 cm²; one core per station) of meiofauna, Northeast Atlantic Ocean, expedition IceDivA/SO280.

Station	core	Nematoda	Copepoda	Nauplii	Annelida	Kinorhyncha	Ostracoda	Gastrotricha	Tardigrada	Mollusca
SO280-26	8	70.0	9.6	1.7	0.3	0.3	0.1	0.1	0.0	0.0
SO280-29	6	86.8	7.3	7.9	1.3	0.0	0.3	0.0	0.0	0.0
SO280-41	1	97.7	4.8	5.9	1.4	0.6	0.4	0.1	0.0	0.1
SO280-43	9	74.2	4.1	3.5	0.8	0.3	0.1	0.0	0.0	0.0
SO280-66	4	13.0	0.4	1.7	0.0	0.0	0.0	0.1	0.0	0.0
SO280-80	2	26.7	2.8	2.1	0.8	0.1	0.1	0.0	0.1	0.0

Gastrotricha
Phylum Gastrotricha Metschnikoff, 1865
Order Macrodasyida Remane, 1925 [Rao and Clausen, 1970]
Family Turbanellidae Remane, 1926
Genus *Desmodasys* Clausen, 1965
***Desmodasys* sp. iberianA**
Fig. 2 A – F, 3 A – D
1 adult (hermaphrodite)
Sample: SO280-26, 4904 m depth
Measurements: BL 310 µm; hw 46 µm; tw 60 µm

Description: This *Desmodasys* has a roughly spindle-shaped, elongate body with an anterior end gradually narrowing towards the mouth opening (Figs. 2A-B, 3A-B). Posterior body end is drawn-out into a pair of lobes in a fin-like, acute-triangular shape of about 20 µm length (Fig. 3A, C-D). However, only the right lobe was observable under the SEM, the left one seems to be broken off (Fig. 3A). As characteristic for the genus *Desmodasys*, adhesive tubes are only present in an anterior (TbA) and in a posterior group (TbP), but there are no further tubes along the body. There are about 22 TbA per body side arranged in a quite peculiar way: on each body side the TbA are grouped as a transverse row with a ventrolateral to ventral position. On the ventral side, there is only a narrow gap of about 15 µm between both groups of TbA (Figs. 2C, 3A-B). At the external (lateral) end of each group, there are two elongated and thicker TbA of 25 µm length, while all other TbA measure about 10 µm (Figs. 2A, 3A-B). However, also at the inner (median) end of each group a few TbA seem to be slightly longer and thicker than the others (Fig. 3A-B). On the posterior lobes, there is a number of 14 TbP that measure up to 12.5 µm in length (Fig. 3C-D). The specimen has a massive and about 120 µm long myoepithelial pharynx that gradually increases in width from anterior to posterior (ca. 30 µm diameter at the anterior part and 45 µm in the posterior part, anterior to the pharyngeal bulbs). Close to the posterior end of the pharynx, there is a pair of pharyngeal bulbs leading to the pharyngeal pores. Due to the positioning of the specimen, the exact shape of the mouth opening was not determinable with certainty, but it leads to a spacious, cylindrical buccal cavity of about 12 x 15 µm. The pharynx leads to the intestine that is more than 50 µm wide and spacious in the middle third of the trunk and its epithelium contains a rather high abundance of refractive vesicles. Epidermal gland openings could be observed only under the SEM and only in the anterior end of the animal (Fig. 3A, B). This specimen of *Desmodasys* was an adult hermaphrodite with a mature and yolk-containing egg in a dorsal position of the posterior third of the trunk and paired testes in the middle third of the trunk. We were neither able to observe the pattern of ventral cilia under the light microscope, nor under the SEM. Cilia were obviously already lost during the centrifugation of the sample.

Remarks: So far, there are three described species in the genus *Desmodasys: D. phocoides* Clausen, 1965, *D. borealis* Clausen 2000, and *D. abyssalis* Kieneke & Zekely, 2008 (Clausen, 1965, 2000, Kieneke & Zekely, 2008). All these species have a quite similar appearance concerning their habitus, however, the two “shallow water species” *D. phocoides* and *D. borealis* are significantly larger than the deep-sea species *D. abyssalis* (see Kieneke & Zekely, 2008). A comparable body length, the absence of numerous and large epidermal glands along the entire body, and the shared occurrence in abyssal depth make the investigated specimen from expedition SO280 most similar to *D. abyssalis*. However, the number of anterior adhesive tubes in each tuft is much higher in the investigated specimen (22) than the number of TbA in the three known species (up to ten in *D. abyssalis*; 12-14 in *D. phocoides*; up to 16 in *D. borealis*). Furthermore, the pattern of two strongly elongated and thickened lateral-most TbA and the very narrow gap between both groups/rows of TbA distinguishes the specimen from SO280 from all known species of *Desmodasys* and especially from the most similar *D. abyssalis*. Since these character differences are significant, we cannot consider this individual to be a representative of any known species and regard it as a member of a new species of *Desmodasys*. Although species descriptions of Gastrotricha based on single specimens are frequently being carried out (e.g., Kieneke, 2010, Kieneke & Todaro, 2021), we refrain from doing so in this case because of the poor condition of the specimen and because there are further core samples available from the SO280 expedition that most likely contain further specimens.

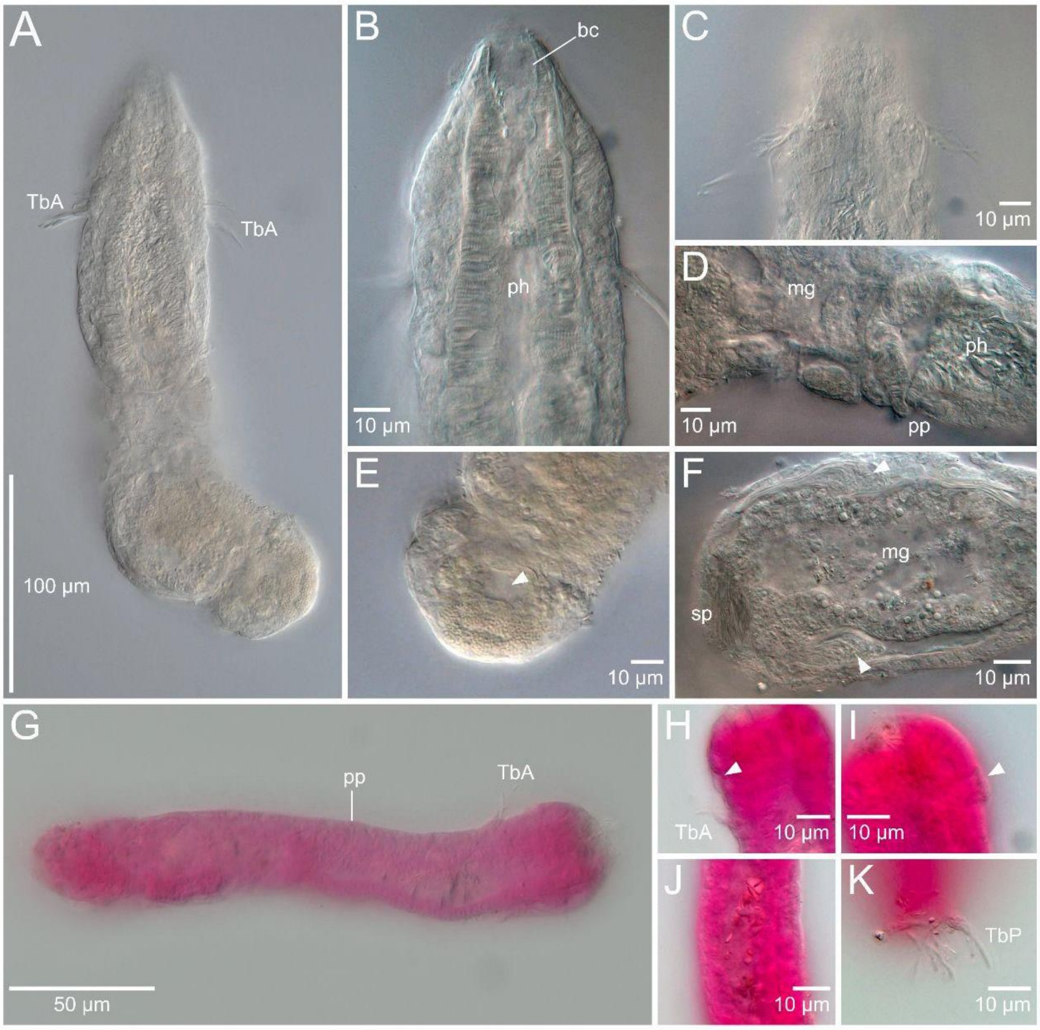

Figure 2. *Desmodasys* sp. iberianA, adult (A – F) and *Desmodasys* sp. langsethA, juvenile (G – K). **A** habitus; **B** anterior end; **C** anterior adhesive tubes; **D** pharynx region; **E** oocyte, note the nucleus (arrowhead); **F** midgut region, note testis (arrowheads); **G** juvenile, habitus; **H** anterior end, note sensory device (arrowhead); **I** anterior end, note sensory device (arrowhead); **J** debris in midgut; **K** posterior adhesive tubes. A – K light microscopy (DIC). Abbreviations: bc – buccal cavity; mg – midgut; ph – pharynx; pp – pharyngeal pore; sp – spermatozoa; TbA – anterior adhesive tubes; TbP – posterior adhesive tubes.

***Desmodasys* sp. langsethA**

Fig. 2 G – K, 3 E – H
1 juvenile
Sample: SO280-66, 5121 m depth
Measurements: BL 192 µm; hw 35 µm; tw 28 µm

Description: This *Desmodasys* has a cylindrical, elongate body. The shape of the anterior end cannot be described with certainty, because the buccal cavity seems to be contracted and therefore it appears truncated (Figs. 2G, 3E-F). Posterior body end is drawn-out into a pair of lobes in a fin-like, acute-triangular shape of about 10 µm length (Fig. 3E, G). In this case, only the left lobe was observable under the SEM, the right lobe was folded down (Fig. 3G). As characteristic for the genus *Desmodasys*, adhesive tubes are only present in an anterior (TbA) and in a posterior group (TbP), but there are no further tubes along the body. There are only 5 TbA per body side and again both most external (lateral) tubes are strongly elongated and thicker and of 10 and 15 µm length, while the three internal (median) TbA measure only up

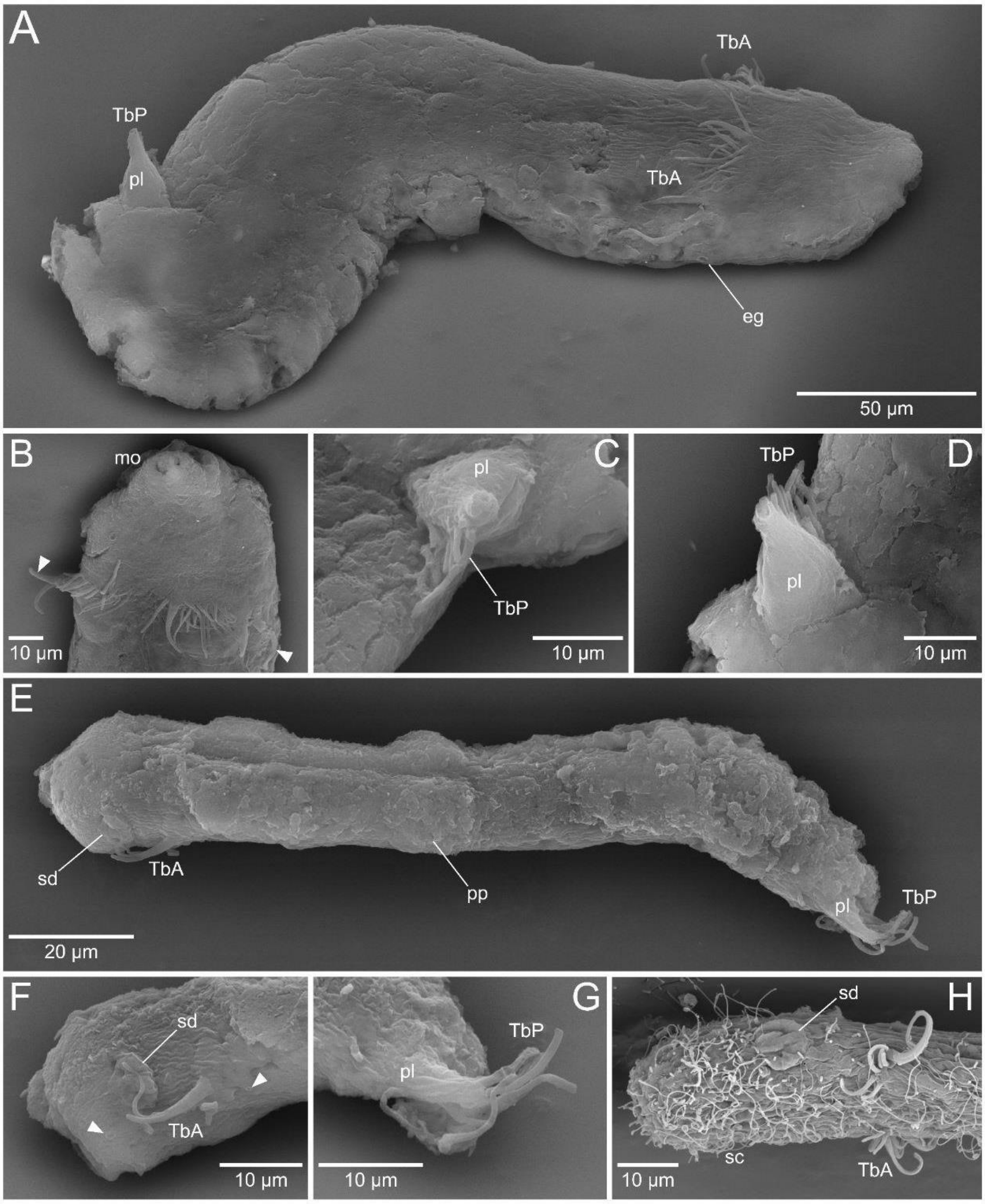

Figure 3. *Desmodasys* sp. iberianA, adult (A – D) and *Desmodasys* sp. langsethA, juvenile (E – G), *Desmodasys* sp. langsethA SN-200227-3**, adult (H). A** habitus; **B** anterior end, note bigger adhesive tubes (arrowheads); **C** posterior adhesive tubes; **D** posterior adhesive tubes; **E** juvenile, habitus; **F** anterior end, lateral view, note epidermal glands (arrowheads); **G** posterior adhesive tubes; **H** *Desmodasys* sp. langsethA from “type locality” (A. Kieneke private unpublished data). A – H scanning electron microscopy (SEM). Abbreviations: eg – epidermal gland; mo – mouth opening; pl – posterior lobe; pp – pharyngeal pore; sc – sensory cilia; sd – sensory device; TbA – anterior adhesive tubes; TbP – posterior adhesive tubes.

to 5 µm (Figs. 2G-H, 3E-F). There are a number of 6 TbP that measure up to 14 µm in length and are arranged on the inner margins of the posterior lobes (Figs. 2K, 3E, G). It was almost impossible to study internal organs of this specimen of *Desmodasys*, however, there were definitely no gonads indicating a juvenile or subadult specimen. Deduced from the position of the pharyngeal pores (Fig. 3E), the pharynx occupies the complete anterior half of the animal (Fig. 3E), another indication of the adolescence of this specimen. Although no proper information on the gut system can be made, we were able to document a peculiarity related to it: in a mid trunk position, there was an accumulation of cristaline splinters that are most likely debris from food items (Fig. 2J). Epidermal gland openings were detected under the SEM and again in the anterior part of the animal (Fig. 3F). As in the other specimen, we were neither able to observe the pattern of ventral cilia under the light microscope, nor under the SEM. Cilia were obviously already lost during the centrifugation of the sample. The most peculiar structure of this second specimen of *Desmodasys* is a protrusion on both sides of the anterior body end, anterior to the TbA and in a slightly more dorsal position (Figs. 2H-I, 3F). This structure consists of a curved bulge in a dorso-ventral alignment and one shorter bulge branching from the center of the curved bulge and projecting towards anterior. On the left body side, it has therefore the shape of a rounded and mirrored capital "Є" (Ukrainian letter [je]) (Fig. 3F). This presumably chemosensory organ has a size of about 5 x 10 µm.

Remarks: As already mentioned above, due to the much smaller body size and the absence of large epidermal glands along the whole body, also the second specimen of *Desmodasys* definitely does not belong to the two "shallow water species" *D. phocoides* and *D. borealis*. Concerning the number of TbA and TbP, this second specimen possesses the least number of adhesive tubes compared to all three described species of *Desmodasys* and to the other specimen of expedition SO280 (see above). We need to keep in mind, though, that we here deal with a subadult specimen and measurements and numbers of adhesive tubes most likely differ in adult specimens. With the first specimen it shares the two elongated external TbA, however, this second specimen is unique in the possession of the peculiar Є-shaped structure on the sides of the anterior body end, presumably chemosensory organs. We need to emphasize that sample material from expedition PS101 of the German research icebreaker "Polarstern" to the Arctic Langseth Ridge (Boetius & Purser 2017) contained numerous specimens of *Desmodasys* with a similar putative sensory structure. A SEM image of one of those specimens is shown in Fig. 3H for comparison (private collection of A. Kieneke, unpublished data). Due to the striking similarity, we suggest this individual also belongs to the yet undescribed species "*Desmodasys* sp. langsethA" from the Central Arctic Basin. We refrain again from making a formal taxonomic species description, because of the poor condition of the specimen and because there are many more specimens from this undescribed species in a much better condition and preservation from the sample material of expedition PS101.

The midgut content is most likely non-organic debris of either calcareous or siliceous matter and could be foraminifera shell parts (see Traunspurger & Majdi 2017).

Order Chaetonotida Remane, 1925 [Rao and Clausen, 1970]
Family Muselliferidae Leasi & Todaro, 2008
Genus *Musellifer* Hummon, 1969
***Musellifer* sp. iberianA**
Musellifer aff. *tridentatus* Kånneby, Atherton & Hochberg, 2014
Fig. 4, 5
1 juvenile/subadult
Sample: SO280-41, 5485 m depth
Measurements: BL 96 µm; fu 64 µm; hw 33 µm; tw 33 µm

Description: The single specimen found so far in one core sample of expedition SO280 has the typical habitus of a member of the genus *Musellifer*, with an anteriorly tapering head region, a slightly broader and spindle-shaped trunk region, both regions separated by a distinct constriction, and a posterior furca with two elongate branches/TbP (Figs. 4A, 5A). The total body length is about 96 µm, however, due to a strong contraction and bending of the animal this measurement is biased. Since we could not trace any patterns of eggs or sperm, this is most likely a juvenile specimen. The conical anterior end ("head") is densely covered with cilia, the typical "muzzle" of species of the genus *Musellifer* (Fig. 4A-B, D). These cilia of the anterior body end were mostly lost during the preparation for SEM (Fig. 5A-B). Inside the head region there is the muscular pharynx with a triradiate lumen (Fig. 4E), a distinct constriction at the level of the junction between pharynx and midgut demarcates the border between "head" and trunk (Figs. 4A-E, 5A, D). The body surface of this specimen of *Musellifer* is covered by very thin and tight-fitting simple spined scales that continue on the furcal branches including the whole TbP (Figs. 4C, 5A, C-F). Each scale of the trunk section has a convex anterior edge that is only observable under the light microscope due to the broad overlap of each scale by its preceding scale (e.g. Fig 4D). The free posterior edge of the trunk scales describes a rather rhombic shape, but with a concave central indentation. The edges of this indentation are drawn-out into short pinnacles and in the center of the indentation arises a short and flexible appearing spine (Fig. 5A, C-D). This basic “stingray-shape” of the trunk scales also applies to the scales of the furcal base and those of the actual TbP, however, these scales are gradually decreasing in width (3 to 3.5 μm in the trunk scales, 2.5 to 3 μm in the furcal scales, 0.5 to 1.5 μm in the scales covering each TbP; Fig. 5E-F). On the trunk section, there are about 10 longitudinal columns of scales with 25 scales in each column on the ventral side. Such counts of the dorsal side are not possible due to the position of the specimen on the SEM-stub, however, we expect similar numbers of columns and scales. The peculiarity of this specimen of *Musellifer* is a “collar” of strong and curved spines on the head section. Here, about 12 μm from the anterior end of the animal, a sharp line demarcates the “muzzle” from this collar of spines (Figs. 4C, 5A-B). The collar is about 8 to 10 μm wide (anterior-posterior direction) and surrounds the whole body like a belt. The shape of the basal scales is difficult to determine even with the high resolution of the SEM. This is due to a strong overlap of single scales and much likely also because of the contraction of the specimen. However, the shape seems to be crest-shaped as in several species of the gastrotrich genus *Chaetonotus* (Fig. 5B). The strongly curved and claw-like spines are about 2 μm long. There are about 18 longitudinal columns of spines/scales with 10 scales in each column on the ventral side.

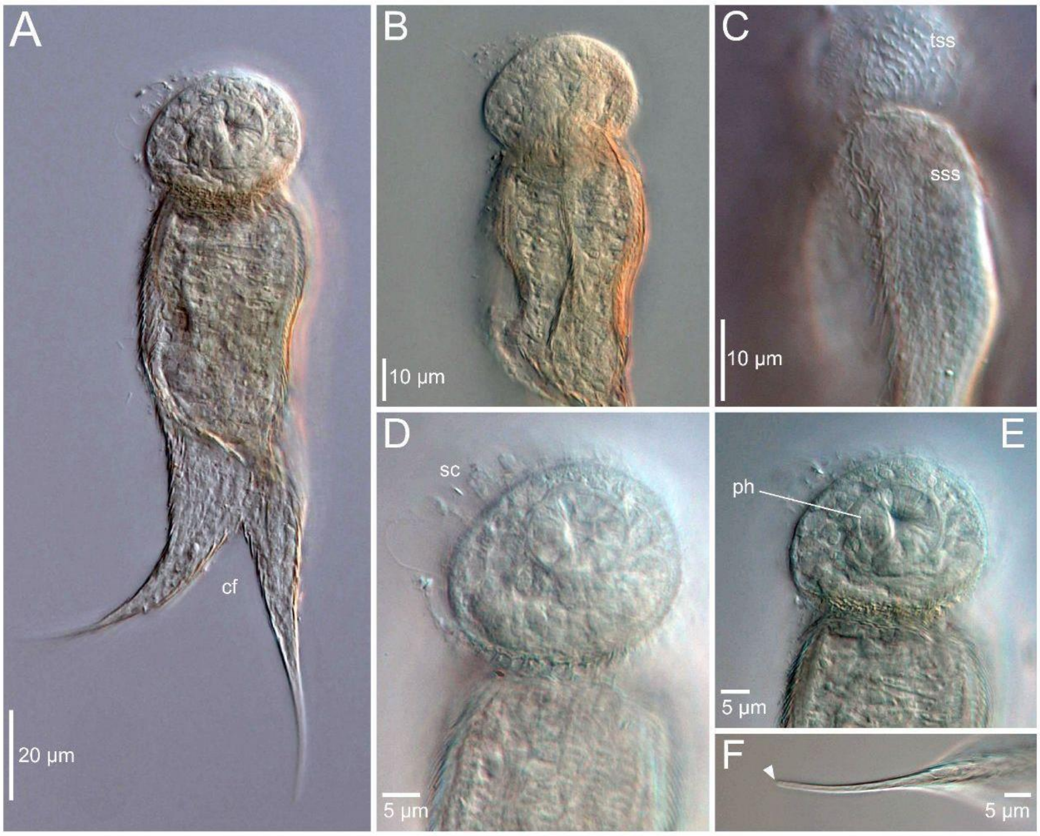

Figure 4. *Musellifer* sp. iberianA (*Musellifer* aff. *tridentatus*), juvenile. A habitus; **B** note two ventral locomotory cilia bands; **C** body scales; **D** anterior end; **E** anterior end; **F** tube of caudal furca, note scale simple spine (arrowhead). A – F light microscopy (DIC). Abbreviations: cf – caudal furca; ph – pharynx; sc – sensory cilia; sss – simple spined scales; tss – trident-shaped scales.

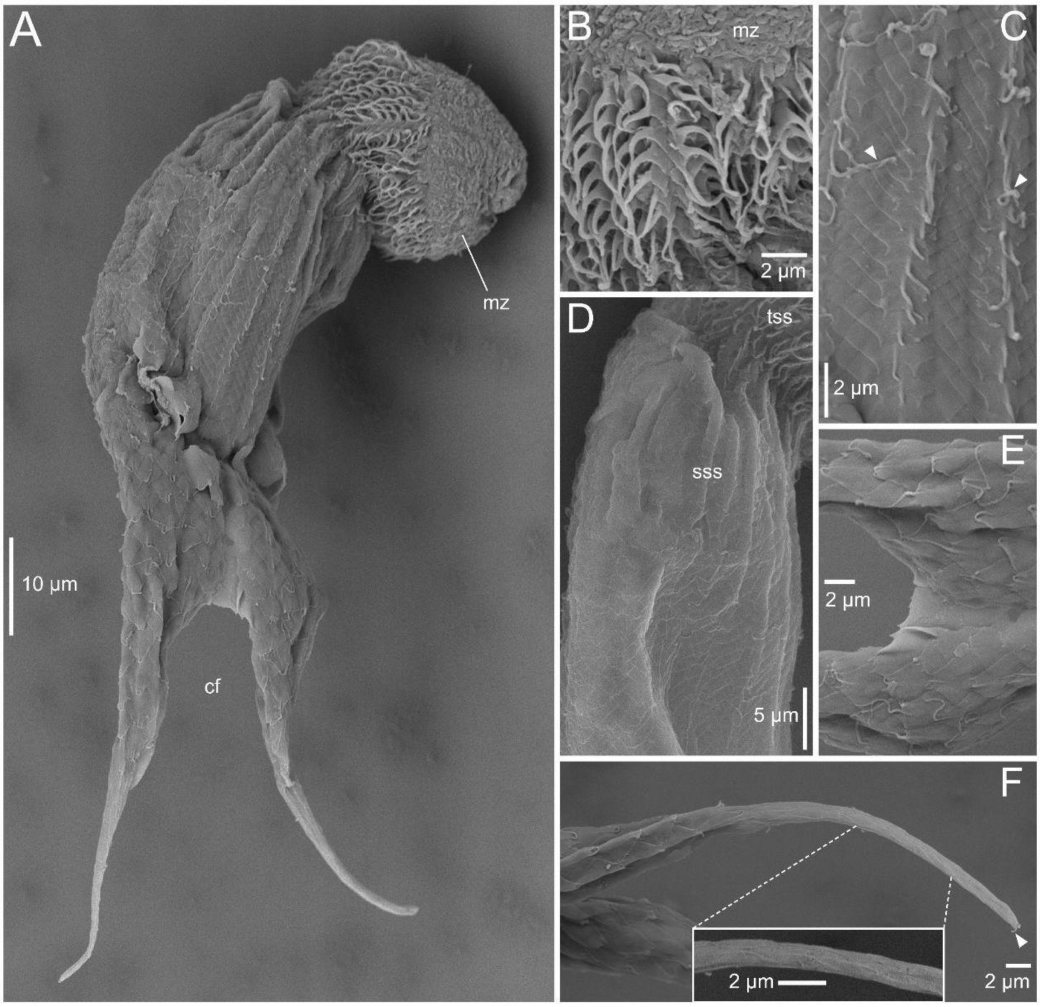

Figure 5. *Musellifer* sp. iberianA (*Musellifer* aff. *tridentatus*), juvenile. A habitus; **B** neck region spined scales; **C** ventral body scales, note locomotory cilia (arrowheads); **D** lateral side, neck-body region; **E** caudal furca scales; **F** tube of caudal furca, note scale simple spine (arrowhead), closeup area marked with dashed lines. A – F scanning electron microscopy (SEM). Abbreviations: cf – caudal furca; mz – muzzle; sss – simple spined scales; tss – trident-shaped scales.

Remarks: So far, five described species of the genus *Musellifer* are known. Four of these species, namely *Musellifer delamarei* (Renaud-Mornant, 1968), *Musellifer sublitoralis* Hummon, 1969, *Musellifer reichhardti* Kånneby, Atherton & Hochberg, 2014 and *Musellifer tridentatus* Kånneby, Atherton & Hochberg, 2014 occur in shallow sublittoral sandy sediments, while *Musellifer profundus* Vivier, 1974 is described and reported from deeper offshore sediments (e.g. Vivier, 1974, Sergeeva et al., 2019), but also from shallower bottoms (e.g., Leasi & Todaro, 2010). However, most of the species of *Musellifer*, including *M. profundus*, are characterized by a quite homogeneous cuticular armature, meaning there is only one type of scales on the whole body surface, only differing in size depending on the body region (head versus neck versus trunk etc.). It is only *M. tridentatus* that has an area of so-called trident-shaped scales on the anterior-most part of its head (Kånneby et al. 2014). In this regard, the specimen found in a core sample of expedition SO280 is most similar to *M. tridentatus*. However, there are three significant differences between both morphotypes: 1) The area with the different scale type of the specimen of the Iberian Basin forms a “collar” around the posterior part of the head section, while in *M. tridentatus* this area is in the anterior-most part of the head, at a comparable position where species of the freshwater-dwelling taxon Chaetonotidae possess the unpaired cephalion and paired pleurae. 2) The shape of these scales differs considerably, with the strong and curved spines in the deep-sea specimen and smaller scales with three keels in *M. tridentatus*.

3) *M. tridentatus* has a pair of peculiar elongated lateral spines about 20 µm anterior to the furca; such elongated spines are not present in the *Musellifer* found during expedition SO280. We again refrain from making a formal taxonomic species description, as in the other two cases, because of the poor condition of the specimen, which is strongly contracted and distorted. Furthermore, it is a juvenile specimen lacking taxonomically important reproductive traits (see discussion of Leasi & Todaro, 2010). In addition, there are further core samples available from the SO280 expedition that most likely contain further specimens of this undescribed *Musellifer*.

Tardigrada
Phylum Tardigrada Doyère, 1840
Class Heterotardigrada Marcus, 1927
Family Coronarctidae Renaud-Mornant, 1974
Genus *Coronarctus* Renaud-Mornant, 1974
Coronarctus dissimilis Gomes-Júnior, Santos, da Rocha, Santos & Fontoura, 2020
Fig. 6

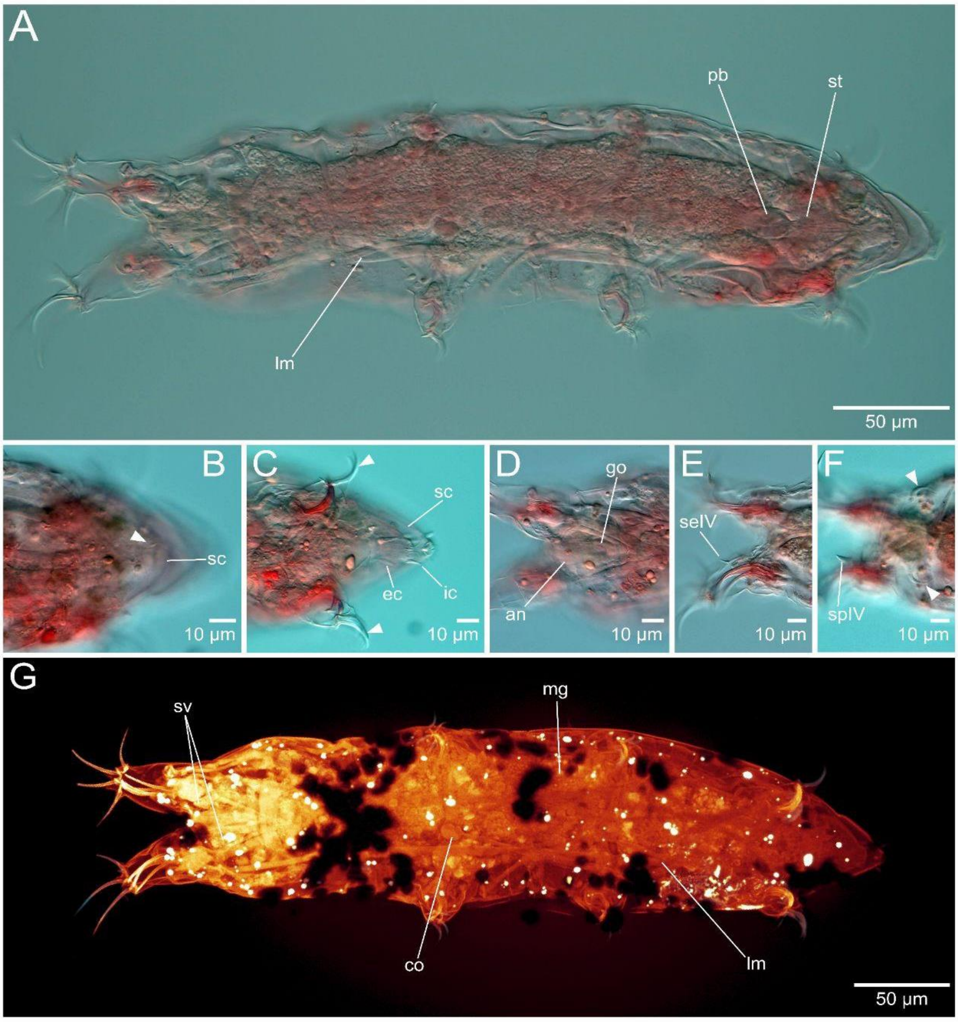

Figure 6. *Coronarctus dissimilis*, male. A habitus; **B** head, dorsal view, note median cirrus (arrowhead); **C** head, ventral view, note bigger internal claws on the leg I (arrowheads); **D** posterior body end, ventral view; **E** legs IV; **F** legs IV, note cirri E (arrowheads); **G** internal anatomy. A – F light microscopy (DIC), G – confocal microscopy (CLSM). Abbreviations: an – anus; co – coelomocyte; ec – external cirrus; go – gonopore; ic – internal cirrus; lm – longitudinal muscles; mg – midgut; pb – pharyngeal bulb; sc – secondary clava; seIV – leg IV sensory organ; spIV – leg IV coxal process; st – stylet, sv – seminal vesicle.

1 male

Sample: SO280-80, 4163 m depth

Measurements: BL 346 μm; tw 89 μm; pc 4.5 μm; ec 6.5 μm; ic 6 μm; mc 3 μm; spIV 9 μm; seIV 5 μm.

Description: Adult *Coronarctus* male with robust cylindrical, elongated body with smooth cuticle. Large longitudinal muscles are visible (Fig. 6A, G). Pharyngeal bulb 19 x 12 μm and stylets present (Fig. 6A). Primary clavae are oval and short. Secondary clavae lobated: they dorsally diverge before median cirrus insertion (Fig. 6B); ventral part of the secondary clava surrounds the external cirrus (Fig. 6C) and has a second lobe. Leg I claws show heteromorphy with internal claws bigger than external (Fig. 6C). Spine-like sensory organs IV (Fig. 6E) and leg IV coxal processes (Fig. 6F) are present. Accessory spines on the claws of each leg. Male has a well-observable anus and gonopore (Fig. 6D). Two lateral seminal vesicles around gonopore present (Fig. 6G).

Remarks: This individual belongs to the *Coronarctus tenellus* group (Gomes-Júnior et al. 2020) due to the short cephalic cirri (less than 10 μm) and claws on leg IV much longer than claws on legs I-III. The morphological data corresponded to the original description by Gomes-Júnior et al. 2020. Species specific traits include the insertion of median cirrus between diverged posterior part of secondary clavae; shape of secondary clavae from the ventral view; claws heteromorphy and presence of apical accessory spine on each claw.

Discussion

Meiofauna densities

Meiofauna communities of the northeast Atlantic deep-sea (Iberian and Canary Basins) showed a rather low density value for nematodes (max. of 97.7 ind./cm²) and copepods (max. of 9.6 ind./cm²), compared to shallower Atlantic sites such as the Condor seamount at 1900 m depth. At sampling site 8, for instance, nematode densities reached 152.6 ind./cm² and copepod densities 10.78 ind./cm² (Zeppilli et al., 2013). However, the general trend of nematode and copepod density decreasing with depth is already known, e.g., from the Bay of Biscay where nematode density at 4415 m depth (station 09-5) was 152 ind./cm² and copepod density was 15 ind./cm²; but at 4460 m depth (station 69-5) it was only 5 ind./cm² and 1 ind./cm², accordingly (Dinet & Vivier, 1977). The density values of “minor” meiofauna taxa in our samples is highly similar to those of other deep sea studies in the closest regions (Vincx et al., 1994).

Biogeographic considerations

The major aim of the current study was a further step towards clarifying the role of the abyssal plains as possible barriers against long-distance dispersal of certain meiofauna taxa, i.e. the Gastrotricha and Tardigrada. If the deep-sea bottom would not be a barrier, long-distance dispersal could purely happen by population growth and therewith through range expansion of species. But if these biggest ecosystems of our planet indeed function as barriers against dispersal, this would in turn underline the outstanding role of seamounts and oceanic islands promoting long-distance dispersal of (shallow water) meiofauna as “stepping stones” or “staging posts” (George, 2013).

As already mentioned in the introduction, studies of gastrotrich and tardigrade communities from seamount and island shelf biotopes on genus or even species level are still rare. However, this limited number of studies already yielded a genus-level diversity of 28 genera of Gastrotricha from the Faroe Bank, São Miguel and Lanzarote, with 19 genera of Macrodasyida, 8 genera of Paucitubulatina and the genus *Neodasys* (Araujo & Hochberg, 2021, Clausen, 2004, Martínez et al., 2019, Todaro et al., 2019; see Tab. 3). In contrast to this, we so far only know two macrodasyidan genera, i.e. *Desmodasys* and *Thaumastoderma*, and a single paucitubulatinan genus, *Musellifer*, from deeper offshore sediments to bathyal and abyssal depths (Vivier, 1974, Kieneke & Zekely, 2008, Kieneke, 2010, Sergeeva et al., 2019, current study). Apart from *Desmodasys*, the two other genera were also recorded from the Faroe Bank, São Miguel and Lanzarote (*Thaumastoderma*, see Tab. 3), or at least from Lanzarote (*Musellifer*, see Tab. 3), but *Desmodasys* is known from coastal shallow sublittoral sediments of Norway (Clausen, 1965, 2000). However, if we have a look on the species level, there is no overlap between deep-sea versus seamount, island, and continental-coastal biotopes: known deep-sea species of *Musellifer* are so far *M. profundus* and *M.* sp. iberianA (Vivier, 1974, Sergeeva et al., 2019, current study), but on Lanzarote *M. delamarei* was recorded (Martínez et al., 2019, Todaro et al., 2019); known deep-sea species of *Desmodasys* are so far *D. abyssalis*, *D.* sp. iberianA and *D.* sp. langsethA (Kieneke & Zekely, 2008, current study), but from the coastal sublittoral of Scandinavia *D. phocoides* and *D. borealis* were recorded (Clausen, 1965, 2000); the only known deep-sea species of *Thaumastoderma* is so far *T. antarctica* (Kieneke, 2010), but from the seamount and island biotopes *T. moebjergi* Clausen, 2004 and *T. mediterraneum* Remane, 1927 were recorded (Clausen, 2004, Martínez et al., 2019, Todaro et al., 2019). Although the data concerning the Gastrotricha can only be regarded as highly preliminary – including the present study there are so far only three publications of deep sea plus two publications of deeper offshore gastrotrichs on species level – we can still already draw an important conclusion: the overwhelming fraction of marine gastrotrich genera that occur in shallow to deeper sublitoral sediments (mostly sand) do not occur in deep-sea sediments of bathyal to abyssal depths! And this is, in our opinion, already a strong indication that the deep sea represents indeed a barrier against long-distance dispersal of many species of marine Gastrotricha.

Table 3. Occurrences of marine genera of Gastrotricha on seamount and island biotopes and at the deep-sea bottom. Note that several more genera occur at the Norwegian coast, but, only the genus *Desmodasys* is relevant for the aim of this study.

genus	Faroe Bank[1]	Norwegian west coast[2, 3]	São Miguel (Azores)[4]	Lanzarote (Canary Islands.)[5, 6]	deep-sea[7, 8, 9]
Dactylopodola	x			x	
Dendrodasys				x	
Cephalodasys				x	
Mesodasys				x	
Lepidodasys	x		x	x	
Macrodasys			x	x	
Urodasys				x	
Crasiella			x	x	
Megadasys			x	x	
Acanthodasys			x	x	
Diplodasys	x		x	x	
Oregodasys	x		x	x	
Pseudostomella	x			x	
Ptychostomella	x			x	
Tetranchyroderma	x		x	x	
Thaumastoderma	x		x	x	x
Paraturbanella			x	x	
Turbanella			x		
Desmodasys		x			x
Xenodasys					
Neodasys				x	
Aspidiophorus				x	
Chaetonotus			x	x	
Halichaetonotus	x		x	x	
Heterolepidoderma				x	
Musellifer				x	x
Draculiciteria				x	
Heteroxenotrichula				x	
Xenotrichula				x	

Sources: 1 - Clausen (2004); 2, 3 - Clausen (1965, 2000); 4 - Arujo & Hochberg (2021); 5, 6 - Martínez et al. (2019), Todaro et al. (2019); 7, 8, 9 - Kieneke & Zekely (2008), Kieneke (2010), current study

Returning to tardigrades from the Faroe Bank, Condor Seamount and Great Meteor Seamount Plateau, the genus-level diversity of these locations sums up to 15 tardigrade genera (Kristensen & Renaud-Mornant, 1983, Hansen et al., 2001, Jørgensen & Kristensen, 2001, Hansen et al., 2003, Hansen et al., 2012, Kristensen et al., 2015, Tchesunov, 2018, Hansen & Kristensen, 2021). Among them are 5 genera (*Faroestygarctus, Higginsarctus, Rhomoarctus, Parmursa* and *Coronarctus*) that can be called "deep-sea taxa", because most of their species are known from the bathyal zone and even deeper (Kaczmarek et al., 2015). However, the species *Coronarctus dissimilis* was not present in samples from these shallow localities. *Coronarctus dissimilis* is so far recorded from the Campos Basin, Brazil, at 1300 m depth (Gomes-Júnior et al., 2020), the Newfoundland Basin at 3685 m depth (Trokhymchuk & Kieneke, 2024) and from the Cape Basin at 2981 m depth (Trokhymchuk et al., 2024). In the current study we report this species from 4163 m depth. This new record extends the range of geographic distribution of this species and enlarges the bathymetric distribution as well. All these records may indicate an amphi-Atlantic distribution of *C. dissimilis* and likewise confirm it as a true deep-sea species. But are underwater features such as the mid-oceanic ridges obstacles against the distribution of this species/genus? Comparing the anatomy of *Coronarctus* to *Tholoarctus*, which can potentially float in the water column (as mentioned in the introduction), species of *Coronarctus* doesn't have any special traits for buoyancy. On the other hand, its vermiform body and huge longitudinal muscles favor better movement in dense substrates. Comparable patterns are also known for another species of *Coronarctus*: *Coronarctus laubieri* Renaud-Mornant, 1987 was found at the Bay of Biscay abyssal plain (Renaud-Mornant, 1988), but also at the Gulf of Mexico (Romano et al., 2011), Potiguar Basin and Campos Basin, Brazil (Gomes-Júnior et al., 2020), all records also from abyssal depths. We assume that the "meiofauna paradox" affects the genus *Coronarctus* and its species less, at least in the Atlantic Ocean, a conclusion similar to that of Westheide et al. (2002). With 5 of 15 tardigrade genera that occur in both shallow sediments of island shelfs and seamount summits of the mentioned northeast Atlantic area, and also at the deep-sea bottom (see above), the ratio is less evident as in the Gastrotricha, but it is still two thirds of the genera from island shelfs and seamounts that do not occur in the deep-sea. Therefore the abyssal plains represent a severe barrier against long distance dispersal also for several genera of the Tardigrada. However, the example of *Coronarctus* demonstrates that we need to look at the level of species in order to distinguish between exclusive deep-sea and exclusive shallow-water taxa, or if species can occur in a wide range of depth layers such as *Batillipes wyedeleinorum* Bartels et al., 2024, *Angursa lingua* Bussau, 1922 or *Tholoarctus oleseni* Jørgensen et al., 2014 (see Trokhymchuk et al., 2024).

Acknowledgments

The authors are grateful to the whole scientific and nautical crews of the expedition SO280. The cruise and the related project "IceDivA" was founded by the German Federal Ministry of Education and Research (BMBF). Many thanks to Uliana Pysarenko and Jannes Lehmann for help in meiofauna sorting. This research is supported by DAAD found for R. T. This is publication number 71 that uses data from the Senckenberg am Meer Confocal Laser Scanning Microscope Facility (SGN-SaM-cLSM). The authors are grateful to Y. Kiosya for reviewing and improving the manuscript.

References

Armonies, W., Reise, K. (2000). Faunal diversity across a sandy shore. *Marine Ecology Progress Series* 196, 49-57. https://doi.org/10.3354/meps196049

Bartels, P. J., Fontoura, P., Nelson, D. R. Kaczmarek, Ł. (2024). Intertidal and shallow subtidal marine tardigrades from the British Virgin Islands with a description of a new *Batillipes* (Heterotardigrada: Batillipedidae). *Marine Biodiversity*, 54(4), 60. https://doi.org/10.1007/s12526-024-01450-8

Boetius, A., Purser, A. (2017). The Expedition PS101 of the Research Vessel POLARSTERN to the Arctic Ocean in 2016. In *Berichte zur Polar- und Meeresforschung = Reports on Polar and Marine Research* (Vol. 706, pp. 1-230). Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung. https://doi.org/10.2312/BzPM_0706_2017

Bogorov, W. G. (1927). Zur Methodik der Bearbeitung des Planktons. (Eine neue Kammer zur Bearbeitung des Zooplanktons). *Russian Hydrobiological Zhurnal*, 6, 193-198.

Brix, S., Taylor, J., George, K. H., Tewes, S., Jenssen, C., Shipboard Scientific Party. (2024). Icelandic marine Animals: Genetics and Ecology meets Diversity along latitudinal gradients in the deep sea of the Atlantic Ocean, Cruise No. SO280, 08.01.2021 - 07.02.2021, Emden (Germany) - Emden (Germany). In

SONNE-Berichte (SO280, pp. 1-36). Begutachtungspanel Forschungsschiffe. https://doi.org/10.48433/cr_so280

Bussau, C. (1992). New deep-sea Tardigrada (Arthrotardigrada, Halechiniscidae) from manganese nodule area of the eastern South Pacific. *Zoologica Scripta*, 21(1), 79-91. https://doi.org/10.1111/j.1463-6409.1992.tb00311.x

Clausen, C. (1965). *Desmodasys phocoides* gen., et sp. n., family Turbanellidae (Gastrotricha Macrodasyoidea). *Sarsia*, *21*(1), 17-21. https://doi.org/10.1080/00364827.1965.10409557

Clausen, C. (2000). Gastrotricha Macrodasyida from the Tromsø region, northern Norway. *Sarsia*, 85(5-6), 357-384. https://doi.org/10.1080/00364827.2000.10414588

Cerca, J., Purschke, G., Struck, T. H. (2018). Marine connectivity dynamics: clarifying cosmopolitan distributions of marine interstitial invertebrates and the meiofauna paradox. *Marine Biology*, 165, 1-21. https://doi.org/10.1007/s00227-018-3383-2

Cerca, J., Meyer, C., Purschke, G., Struck, T. H. (2020). Delimitation of cryptic species drastically reduces the geographical ranges of marine interstitial ghost-worms (*Stygocapitella*; Annelida, Sedentaria). *Molecular Phylogenetics and Evolution*, 143, 106663.https://doi.org/10.1016/j.ympev.2019.106663

Derycke, S., Remerie, T., Backeljau, T., Vierstraete, A., Vanfleteren, J., Vincx, M., Moens, T. (2008). Phylogeography of the *Rhabditis* (*Pellioditis*) *marina* species complex: evidence for long distance dispersal, and for range expansions and restricted gene flow in the northeast Atlantic. *Molecular ecology*, 17(14), 3306-3322. https://doi.org/10.1111/j.1365-294X.2008.03846.x

Dinet, A., Vivier, M. H. (1977). Le méiobenthos abyssal du Golfe de Gascogne I. Considérations sur les données quantitatives. *Cahiers Biologie Marine*, 18, 85-97.

Fattorini, S. (2017). Endemism in historical biogeography and conservation biology: concepts and implications. *Biogeographia–The Journal of Integrative Biogeography*, 32(1). https://doi.org/10.21426/B632136433

Fontaneto, D., Plewka, M. (2021). Phylum Rotifera. In *Invertebrate Zoology* (pp. 265-278). *CRC Press*.

Gąsiorek, P. (2023). Catch me if you can, or how paradigms of tardigrade biogeography evolved from cosmopolitism to 'localism'. *Zoological Journal of the Linnean Society*, zlad191. https://doi.org/10.1093/zoolinnean/zlad191

George, K. H. (2013). Faunistic research on metazoan meiofauna from seamounts–a review. *Meiofauna marina*, 20(February), 1-32.

Giere, O. (2009). Meiofauna Taxa: A systematic account. *Meiobenthology: the microscopic motile fauna of aquatic sediments*, 103-234.

Hansen, J. G., Jørgensen, A., Kristensen, R. M. (2001). Preliminary studies of the tardigrade fauna of the Faroe Bank. *Zoologischer Anzeiger-A Journal of Comparative Zoology*, 240(3-4), 385-393. https://doi.org/10.1078/0044-5231-00046

Hansen, J.G., D'Addabbo Gallo, M. Grimaldi De Zio, S. (2003). A comparison of morphological characters within the genus *Rhomboarctus* (Tardigrada: Heterotardigrada) with the description of two new species. *Zoologischer Anzeiger - A Journal of Comparative Zoology.* 242(1), 83-96. https://doi.org/10.1078/0044-5231-00089

Hansen, J. G. (2007). The deep sea elements of the Faroe Bank tardigrade fauna with a description of two new species. *J. Limnol*, 66(1), 12-20. https://doi.org/10.4081/jlimnol.2007.s1.12

Hansen, J. G., Kristensen, R. M. Jørgensen, A. (2012). The armoured marine tardigrades (Arthrotardigrada, Tardigrada). *Scientia Danica, series B Biologica 2, The Royal Danish Academy of Sciences and Letters*, pp. 91.

Hansen, J. G., &Kristensen, R. M. (2021). A new genus and five new species of the subfamily Florarctinae (Tardigrada, Arthrotardigrada). *European Journal of Taxonomy.* 762, 149-184. https://doi.org/10.5852/ejt.2021.762.1461

Higgins, R. P., Thiel, H. (1988). Introduction to the study of meiofauna. *Smithsonian Institution Press*.

Hummon, W. D. (1969). *Musellifer sublitoralis*, a new genus and species of Gastrotricha from the San Juan Archipelago, Washington. *Transactions of the American Microscopical Society*, 88(2), 282-286. https://doi.org/10.2307/3224502

Hummon, W.D., ed. 2001-2010. Global Distribution of Marine Gastrotricha (at http://www.gastrotricha.unimore.it/checklist.htm)

Ingels, J., Valdes, Y., Pontes, L. P., Silva, A. C., Neres, P. F., Corrêa, G. V., ... dos Santos, G. A. (2020). Meiofauna life on loggerhead sea turtles-diversely structured abundance and biodiversity hotspots that challenge the meiofauna paradox. *Diversity*, *12*(5), 203. https://doi.org/10.3390/d12050203

Jørgensen, A., Kristensen, R. M. (2001). A new tanarctid arthrotardigrade with buoyant bodies. *Zoologischer Anzeiger-A Journal of Comparative Zoology*, *240*(3-4), 425-439. https://doi.org/10.1078/0044-5231-00051

Jørgensen, A., Boesgaard, T. M., Møbjerg, N. Kristensen, R. M. (2014) The tardigrade fauna of Australian marine caves: With descriptions of nine new species of Arthrotardigrada. *Zootaxa*, 3802(4), 401-433. https://doi.org/10.1078/0044-5231-00033

Jörger, K. M., Norenburg, J. L., Wilson, N. G., Schrödl, M. (2012). Barcoding against a paradox? Combined molecular species delineations reveal multiple cryptic lineages in elusive meiofaunal sea slugs. *BMC evolutionary biology*, 12, 1-18. https://doi.org/10.1186/1471-2148-12-245

Kaczmarek, Ł., Bartels, P. J., Roszkowska, M., Nelson, D. R. (2015). The zoogeography of marine Tardigrada. *Zootaxa*, *4037*(1), 1-189. https://doi.org/10.11646/zootaxa.4037.1.1

Kånneby, T., Atherton, S., Hochberg, R. (2014). Two new species of *Musellifer* (Gastrotricha: Chaetonotida) from Florida and Tobago and the systematic placement of the genus within Paucitubulatina. *Marine Biology Research*, *10*(10), 983-995. https://doi.org/10.1080/17451000.2013.872797

Kieneke, A. (2010). A new species of *Thaumastoderma* (Gastrotricha: Macrodasyida) from the Antarctic deep sea with a phylogenetic analysis of the whole genus. *Journal of the Marine Biological Association of the United Kingdom*, *90*(3), 575-584. https://doi.org/10.1017/S002531540900085X

Kieneke, A., Zekely, J. (2008). *Desmodasys abyssalis* sp. nov.— first record of a deep-sea gastrotrich from hydrothermal vents. *Marine Biodiversity Records*, 1, e88. https://doi.org/10.1017/S1755267207008950

Kieneke, A., Münter, L. Riemann, O. (2020): Gastrotricha. In: Schmidt-Rhaesa, A. (ed.): Guide to the Identification of Marine Meiofauna, *Verlag Dr. Friedrich Pfeil*, München, pp. 104-163.

Kieneke, A. Brix, S. (2021). IceDivA (SO280) Eine Tiefseeexpedition zur Vernetzung langjähriger Messdaten und Proben (*GfBS newsletter* 39). 39, 16-23.

Kolicka, M. (2016). Gastrotrichs in bromeliads—newly recorded *Chaetonotus* (*Hystricochaetonotus*) *furcatus* Kisielewski, 1991 (Chaetonotida) from the Łódź Palm House. *Zoosystema*, *38*(1), 141-155. https://doi.org/10.5252/z2016n1a5

Kreuzinger-Janik, B., Majdi, N., Traunspurger, W. (2021). Distribution and diversity of meiofauna along an aquatic-terrestrial moss ecotone. *Nematology*, *23*(6), 695-714. https://doi.org/10.1163/15685411-bja10070

Kristensen, R. M., Renaud-Mornant, J. (1983). Existence d'Arthrotardigrades semi-benthiques de genres nouveaux de la sous-famille des Styraconyxinae subfam. nov. *Cahiers de Biologie marine*, 24, 337-353.

Kristensen, R. M., Sørensen, M. V., Hansen, J. G., Zeppilli, D. (2015). A new species of *Neostygarctus* (Arthrotardigrada) from the Condor Seamount in the Azores, Northeast Atlantic. *Marine Biodiversity*, 45, 453-467. https://doi.org/10.1007/s12526-015-0323-y

Leasi, F., Todaro, M. A. (2008). The muscular system of *Musellifer delamarei* (Renaud-Mornant, 1968) and other chaetonotidans with implications for the phylogeny and systematization of the Paucitubulatina (Gastrotricha). *Biological Journal of the Linnean Society*, 94(2), 379-398. https://doi.org/10.1111/j.1095-8312.2008.00974.x

Leasi, F., Todaro, M. A. (2010). The gastrotrich community of a north Adriatic Sea site, with a redescription of *Musellifer profundus* (Chaetonotida: Muselliferidae). *Journal of the Marine Biological Association of the United Kingdom*, 90(4), 645-653. https://doi.org/10.1017/S0025315409991068

Magpali, L., Machado, D. R., Araújo, T. Q., Garraffoni, A. R. (2021). Long distance dispersal and pseudo-cryptic species in Gastrotricha: first description of a new species (Chaetonotida, Chaetonotidae, *Polymerurus*) from an oceanic island with volcanic rocks. *European journal of taxonomy*, 746, 62-93. https://doi.org/10.5852/ejt.2021.746.1319

Martínez, A., Eckert, E.M., Artois, T.,Careddu, G., Casu,M., Curini-Galletti, M., Gazale, V., Gobert, S., Ivanenko , V.N., Jondelius, U., Marzano, M., Pesole, G., Zanello, A., M. Todaro, A., Fontaneto, D. (2020): Human access impacts biodiversity of microscopic animals in sandy beaches. *Communications Biology* 3, 175. https://doi.org/10.1038/s42003-020-0912-6

Minowa, A. K., Kieneke, A., Campos, A., Balsamo, M., Guidi, L., Araújo, T. Q. Garraffoni, A. R. S. New branch of the Tree of Life of Gastrotrich: Establishment of a new genus for limno-terrestrial species. *Zoological Journal of the Linnean Society.* (under revision)

Nelson, D. R., Guidetti, R., Rebecchi, L. (2015). Phylum tardigrada. In *Thorp and Covich's Freshwater invertebrates* (pp. 347-380). Academic Press.

Radziejewska, T., Gruzka, P., Rokicka-Praxmajer, J. (2006): A home away from home: a meiobenthic assemblage in a ship's ballast water tank sediment. *Oceanologia*, 48, 259–265.

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., ... Vecchione, M. (2010). Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences*, 7(9), 2851-2899. https://doi.org/10.5194/bg-7-2851-2010

Rao, G. C., Clausen, C. (1970). *Planodasys marginalis* gen. et sp. nov. and Planodasyidae fam. nov.(Gastotricha Magrodasyoidea). *Sarsia*, 42(1), 73-82. https://doi.org/10.1080/00364827.1970.10411164

Remane, A. (1925). Organisation und systematische Stellung der aberranten Gastrotrichen. *Verhandlungen der deutschen zoologischen Gesellschaft*, 30, 121-128.

Remane A. (1927). Beiträge zur Systematik der Süsswassergastrotrichen. *Zoologische Jahrbücher. Abteilung für Systematik*. 53(12), 269-320.

Remane, A. (1926). Morphologie und Verwandtschaftsbeziehungen der aberranten Gastrotrichen I. *Zeitschrift für Morphologie und Ökologie der Tiere*, 625-754.

Renaud-Mornant, J. (1968). Présence du genre *Polymerurus* en milieu marin, description de deux espèces nouvelles (Gastrotricha, Chaetonotoidae). *Pubblicazioni della Stazione Zoologica di Napoli*. 36,141 – 51.

Renaud-Mornant, J. (1988). Développement postembryonnaire du Tardigrade abyssal *Coronarctus laubieri* Renaud-Mornant, J. (1987) (Tardigrada, Heterotardigrada). *Bulletin du Muséum national d'histoire naturelle. Section A, Zoologie, biologie et écologie animales*, *10*(2), 327-345. https://doi.org/10.5962/p.292211

Renaud-Mornant, J. (1987). Bathyal and abyssal Coronarctidae (Tardigrada), descriptions of new species and phylogenetical significance. *In: R. Bertolani, editor. Biology of Tardigrades. Selected Symposia and Monographs U.Z.I., 1. Mucchi, Modena, Italy,* 93–101.

Romano Iii, F., Gallo, M., D'Addabbo, R., Accogli, G., Baguley, J., Montagna, P. (2011). Deep-sea tardigrades in the northern Gulf of Mexico with a description of a new species of Coronarctidae (Tardigrada: Arthrotardigrada), *Coronarctus mexicus*. *Journal of Zoological Systematics and Evolutionary Research*, 49, 48-52. https://doi.org/10.1111/j.1439-0469.2010.00597.x

Santos, E., Veiga, P., Rubal, M., Bartels, P. J., da Rocha, C. M. Fontoura, P. (2019). *Batillipes pennaki* Marcus, 1946 (Arthrotardigrada: Batillipedidae): deciphering a species complex. *Zootaxa*, 4648(3), zootaxa-4648. https://doi.org/10.11646/zootaxa.4648.3.9

Sergeeva, N., Ürkmez, D., Todaro, M. A. (2019). Significant occurrence of *Musellifer profundus* Vivier, 1974 (Gastrotricha, Chaetonotida) in the Black Sea. *Check List*, *15*(1), 219-224. https://doi.org/10.15560/15.1.219

Shimabukuro, M., Zeppilli, D., Leduc, D., Wenzhöfer, F., Berg, P., Rowden, A. A., Glud, R. N. (2022). Intra- and inter-spatial variability of meiofauna in hadal trenches is linked to microbial activity and food availability. *Scientific reports*, *12*(1), 4338. https://doi.org/10.1038/s41598-022-08088-1

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. *Nature Methods*, 9, 676–682. https://doi.org/10.1038/nmeth.2019

Thiel, H. (1975). The size structure of the deep-sea benthos. *Integrationale Revevue der gesamten Hydrobiologie*. 60, 575–606

Todaro, M. A. D., Hummon, W. D. (2008). An overview and a dichotomous key to genera of the phylum Gastrotricha. *Meiofauna Marina*, *16*, 3-20.

Traunspurger, W., Majdi, N. (2017). Meiofauna. In: *Methods in Stream Ecology, Volume 1* (pp. 273-295). Academic Press.

Trokhymchuk, R., Kieneke, A. (2024). Novel distribution records of marine Tardigrada from abyssal sediments of the Northwest Atlantic Ocean. *Organisms Diversity & Evolution*, 1-16. https://doi.org/10.1007/s13127-024-00641-2

Trokhymchuk, R., Schmidt-Rhaesa, A., Utevsky, S., Kristensen, R. M., Kieneke, A. (2024) Towards a better understanding of deep-sea tardigrade biogeography: numerous new records and a new species from the Southern Ocean. *Zootaxa*, 5543(1), 1-39. https://doi.org/10.11646/zootaxa.5543.1.1

Tchesunov, A. V. (2018). A new tardigrade species of the genus *Neostygarctus* Grimaldi de Zio et al., 1982 (Tardigrada, Arthrotardigrada) from the Great Meteor Seamount, Northeast Atlantic. *European Journal of Taxonomy*, (479). https://doi.org/10.5852/ejt.2018.479

Vincx, M., Bett, B. J., Dinet, A., Ferrero, T., Gooday, A. J., Lambshead, P. J. D., ... Vanreusel, A. (1994). Meiobenthos of the deep Northeast Atlantic. In: *Advances in Marine Biology* (Vol. 30, pp. 1-88). Academic Press. https://doi.org/10.1016/S0065-2881(08)60061-9

Westheide, W., Haß-Cordes, E., Krabusch, M., Müller, M. (2003). *Ctenodrilus serratus* (Polychaeta: Ctenodrilidae) is a truly amphi-Atlantic meiofauna species–evidence from molecular data. *Marine Biology*, 142, 637-642. https://doi.org/10.1007/s00227-002-0960-0

Zeppilli, D., Bongiorni, L., Cattaneo, A., Danovaro, R., Santos, R. S. (2013). Meiofauna assemblages of the Condor Seamount (North-East Atlantic Ocean) and adjacent deep-sea sediments. *Deep Sea Research Part II: Topical Studies in Oceanography*, 98, 87-100 https://doi.org/10.1016/j.dsr2.2013.08.009.

Нові знахідки глибоководних Gastrotricha і Tardigrada в Іберійському та Канарському басейнах (північно-східна Атлантика) з коментарями щодо складу абісальної мейофауни та парадоксу мейофауни

Р. Трохимчук, А. Кінеке

“Парадокс мейофауни” пов’язаний з амфіокеанічним або навіть космополітичним поширенням видів цієї екологічної групи, а саме морської мейофауни, в противагу їх слабкому потенціалу розселення. Розв’язання цього парадоксу включає, з одного боку, знахідки комплексів генетично різних, але морфологічно криптичних видів із значно обмеженими ареалами; а з іншого – дослідження “оселищ-сходинок”, таких як шельфові зони океанічних островів і вершини підводних гір. Такі біотопи поділяють великі дистанції, наприклад, від одного континенту до іншого, на більш короткі проміжки. Однак тоді слід виключити можливе поширення “мілководної мейофауни” просто через зростання популяції та розширення ареалу на абісальних рівнинах Світового океану. Для того, щоб перевірити, чи можуть абісальні рівнини бути бар’єром для розселення певних таксонів морської мейофауни, ми дослідили склад мейофауни з шести проб (станцій) під час експедиції R/V Sonne IceDivA (SO280) в Іберійському та Канарському басейнах з абісальних глибин (4904 - 5485 м). Домінантними таксонами в усіх пробах були нематоди (13.0 - 97.7 ос./см^2) та копеподи (0.4 - 9.6 ос./см^2); анеліди, кіноринхи і остракоди мали меншу щільність. Відмічено три види гастротрих (*Desmodasys* sp. iberianA, *Desmodasys* sp. langsethA, *Musellifer* sp. iberianA (*Musellifer* aff. *tridentatus*)) та один тихохід (*Coronarctus dissimilis*), які дослідили з використанням світлової мікроскопії (ДІК та КЛСМ) а також СЕМ. Всі представлені гастротрихи, ймовірно, належать до нових та досі не описаних видів. Ареал *Coronarctus dissimilis* розширено до Іберійського басейну та глибини в 4163 м (банка Джозефіна). Ця знахідка може свідчити на користь потенційного амфіатлантичного поширення виду. Ми порівняли наші дані з іншими дослідженнями підводних гір, океанічних островів та з глибоководдя і прийшли до висновку, що абісальні рівнини є значним бар’єром на шляху поширення на великі відстані для більшості родів (і видів) гастротрих, а також для певної частини родів тихоходів.

Ключові слова: *Атлантичний океан, біорізноманіття, біогеографія, глибоке море, Desmodasys, Musellifer, Coronarctus*

Цитування: *Trokhymchuk R., Kieneke A. 2024. New records of deep-sea Gastrotricha and Tardigrada from Iberian and Canary Basins (Northeast Atlantic) with comments on abyssal meiofauna composition and the meiofauna paradox. Вісник Харківського національного університету імені В.Н.Каразіна. Серія «Біологія», 43, с. 66-84. https://doi.org/10.26565/2075-5457-2024-43-6*

Про авторів:
Трохимчук Р. – Харківський національний університет імені В.Н. Каразіна, майдан Свободи, 4, 61022, Харків, Україна; Німецький центр досліджень морського біорізноманіття (DZMB), Зенкенберг ам Меєр, Зюдштранд 44, 26382, Вільгельмсгафен, Німеччина; rtrokhymchuk@gmail.com; https://orcid.org/0000-0001-9570-0226
Кінеке А. – Німецький центр досліджень морського біорізноманіття (DZMB), Зенкенберг ам Меєр, Зюдштранд 44, 26382, Вільгельмсгафен, Німеччина; alexander.kieneke@senckenberg.de; https://orcid.org/0000-0001-8180-2483

Подано до редакції: 05.09.2024 / Прорецензовано: 16.10.2024 / Прийнято до друку: 18.10.2024