Deep-sea Enteropneust Fauna Of The Bering Sea

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Introduction

Acorn worms (Enteropneusta) are solitary hemichordates distributed world-wide from the littoral to hadal zone. New page in the investigation of acorn worms has begun with development of under-water photography and sampling using remotely operated vehicles (ROVs). Despite still insufficient knowledge of this taxon, the evidence is growing that deep-sea enteropneusts are a morphologically diverse group, playing an essential role in nutrient cycling and surficial bioturbation in deep-sea ecosystems. During the cruise 75 of the RV *Akademik M.A. Lavrentyev* to the Bering Sea (2016), observations were made of the deep-sea megafauna communities dominated by torquaratorid enteropneusts of an undescribed genus and species. Previously only shallow-water enteropneust *Saccoglossus mereschkowskii* (Harrimaniidae) was known from the Bering Sea. On cruises 82 (2018) and 93 (2021) of *Akademik M.A. Lavrentyev*, more photo and video records of deep-sea enteropneusts were made in the western Bering Sea. Altogether on these records we identified five species of Enteropneusta presumably of the two families, Harrimaniidae and Torquaratoridae (Table).

Materials and methods

Enteropneusts discovered on cruises of the RV *Akademik M.A. Lavrentyev* 75 (2016), 82 (2018), and 93 (2021) were photographed and videotaped *in situ* using the ROV *Comanche 18* equipped with *Canon PowerShot G5* and *Kongsberg Underwater HDTV* colour camera *OE14-502*. Specimens of **Torquaratorid-1** were sampled on the slope of the Volcanologists Massif (Fig. 1) using a manipulator of the ROV *Comanche 18* in 2016 and a slurp-gun in 2018. Details of all the collection sites see in Table.

For histological studies, the specimens of **Torquaratorid-1** were preserved in 8% regular formaldehyde buffered with seawater and stored in fixator for a year before processing. The samples were transferred in 70% ethanol and then dehydrated through increasing series of ethanol and butanol, embedded in paraplast and sectioned into sections 7 µm and 10 µm thick using a rotational microtome *Leica RM 2125RTS* (Leica Biosystems, Germany). The sections were stained with hematoxylin. Photographs of histological sections were made using the *Micmed-6* microscope (LOMO, Saint-Petersburg, Russia, 2018) with digital camera *MC-12*.

Species	Cruise, station	Coordinates	Locality	Depth, m
Torquaratorid-1 (Fig. 2A)	Lavrentyev-75 (st. 17, 18) Lavrentyev-82 (st. 9)	55.4609 N; 167.2688 E 55.3451-55.3466 N; 167.2750-167.2752 E	Northern slope of the Volcanologists Massif; southern slope of the Volcanologists Massif	1370-2470 1511-1992
Torquaratorid-2 (Fig. 2B)	Lavrentyev-75 (st. 16, 55) Lavrentyev-82 (st. 5)	55.26-55.58 N; 167.30-167.34 E	Komandorsky Graben; northern slope of the Volcanologists Massif; southern slope of the Volcanologists Massif	4278 3450-3610 3334-3931
Harrimaniidae, *Saxipendium* sp. (Fig. 2C)	Lavrentyev-82 (st. 6)	55.69 N; 167.10 E	North-western slope of the Volcanologists Massif; southern slope of the Volcanologists Massif	3391-3906 ~1930
Harrimaniid-1 (Fig. 2D)	Lavrentyev-82 (st. 14, 18, 21)	60.8343-61.1195 N; 174.3722-174.9650 E	Koryak slope of Chukotka	659-662
Harrimaniid-2 (Fig. 2E)	Lavrentyev-93 (st. 5, 6)	61.1734 N; 174.8767 E	Koryak slope of Chukotka	419-420

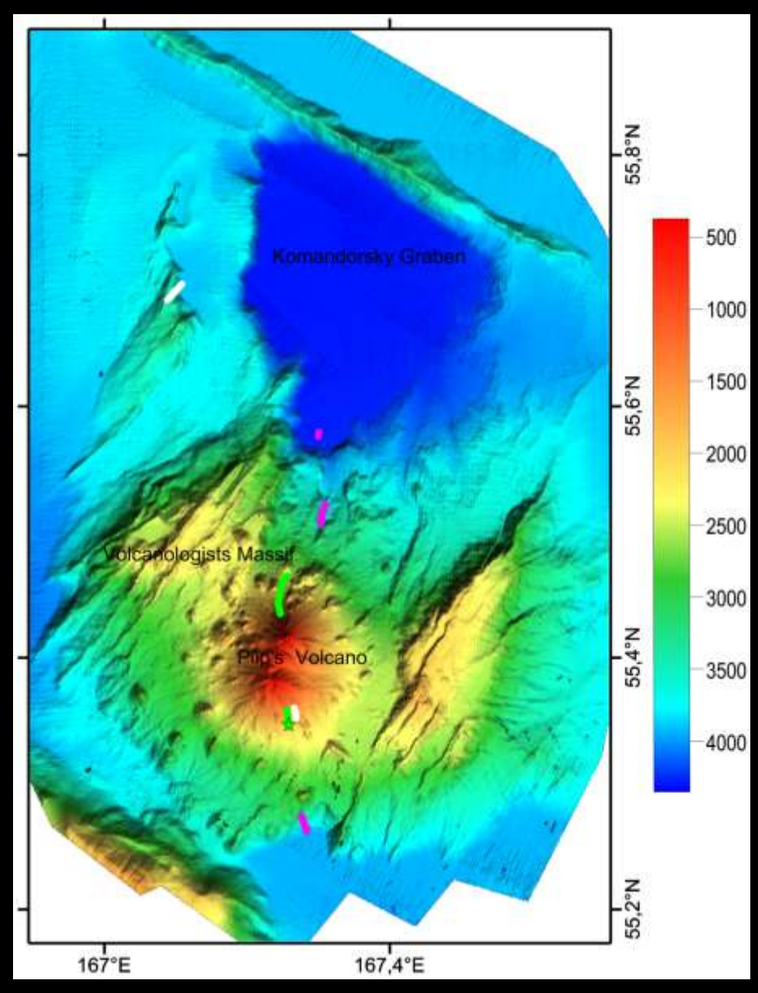


Figure 1. Distribution of deep-sea enteropneust species in the area of the Volcanologists Massif.
Green: Torquaratorid-1. Green star: type locality of Torquaratorid-1. Magenta: Torquaratorid-2. White: *Saxipendium* sp.

Results and Discussion

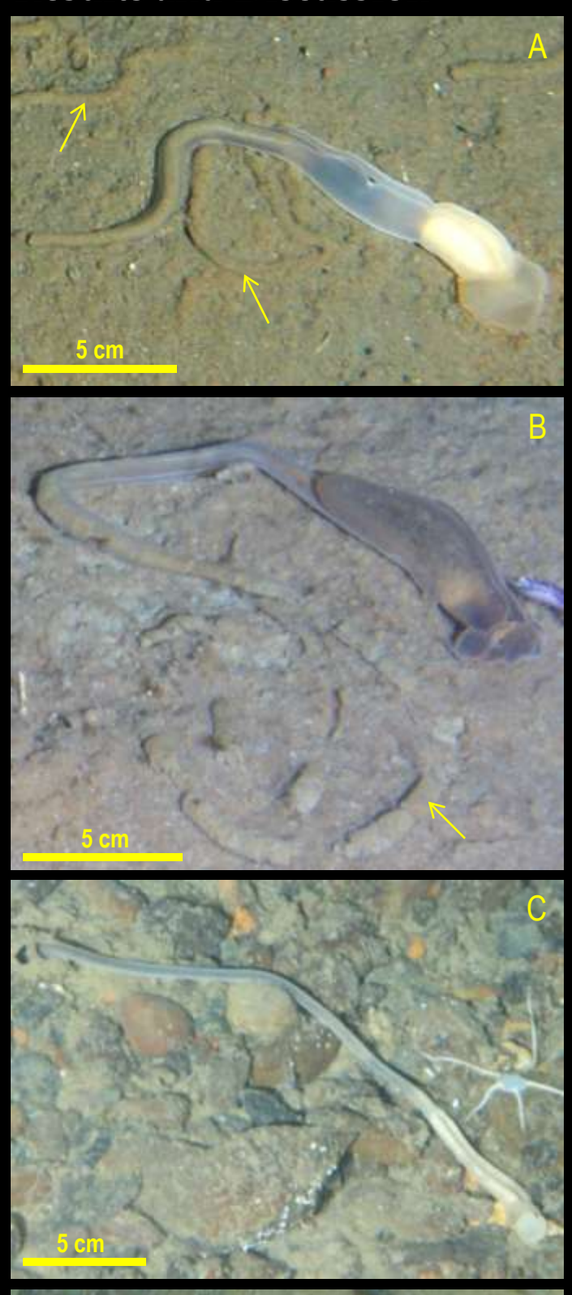


Figure 2. Deep-sea enteropneusts from the Bering Sea. (**A**) Torquaratorid-1 on soft substrate. (**B**) Torquaratorid-2 with its spiral counter-clockwise faecal trails. (**C**, **D**) Burrowing *Saxipendium* sp. (Harrimaniidae) (C), and Harrimaniid-1 (D). (**E**) Harrimaniid-2 with the trunk lightly sprinkled with sediment .

Torquaratorid-1: Large animals reaching 17 cm in length (Fig. 2A). Semitransparent. Proboscis, collar, and intestinal part of trunk are colorless. Gonads are white, light yellow, cream, or light brown. Hepatic region is light blue. Proboscis is short, dome-like. Slender proboscis stalk is absent; proboscis adjoins widely to collar on the dorsal side. Two lateral collar lips and additional midventral lip. Lateral wings arch over the dorsal surface of the trunk; each wing is subdivided by a transverse constriction into anterior genital segment and posterior hepatic segment.

Axial proboscis complex (or "heart-kidney") comprises pericardial coelomic sac, glomerulus, and buccal diverticulum (Fig.4). Stalk skeleton is represented by two plates. Buccal cavity is absent. Collar has two symmetric coelomoducts and coelomopores, which open directly into the exterior (Fig. 3). Full description of a new genus and new species is in press.

Bathyal epibenthic surface-dweller, almost motionless or slowly crawling along the seafloor collecting surface deposit using the wide collar lips. Mainly associated with soft sediments, this species was also found on the hard substrate. Based on our observations, this species occurred in habitats with sediment cover varying from 30 to 70%. Apparently, these acorn worms are able to feed on a thin coating of sediment on the rocks. The faecal trails on the seafloor were mainly meandering (Fig. 2A, arrows), very rarely a combination of meandering and switchback patterns; spirals were never recorded. The species formed dense population with up to 12 specimens per $1m^{-2}$ dominating the soft-sediment community at the depths 1765–2290 m on the slope of the Volcanologists Massif (Fig. 1).

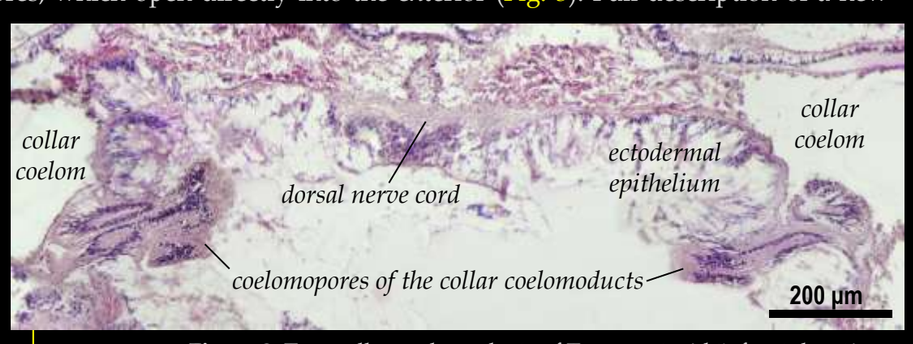
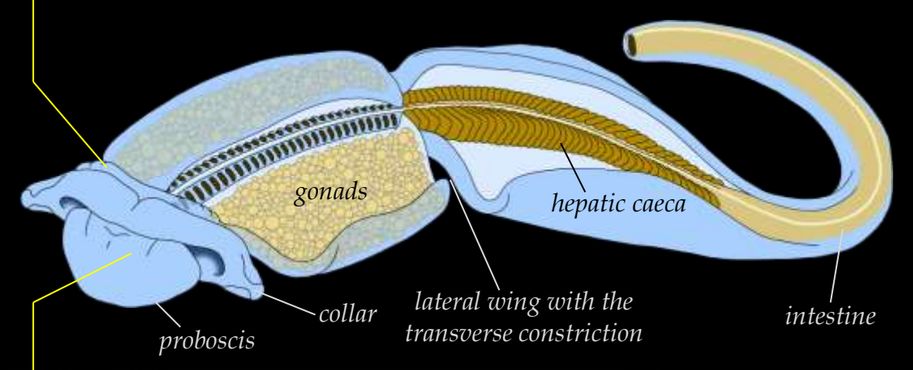


Figure 3. Two collar coelomoducts of Torquaratorid-1; frontal section.

Torquaratorid-2: Large animal reaching 18 cm in length, transparent, with signs of violet colouring and with a short proboscis and well-developed lateral collar lips (Fig. 2B). Lateral wings are devoid of the constriction and arch over the anterior region of the trunk.

Abyssal epibenthic surface-dweller with a spiral counter-clockwise pattern of faecal trails (Fig. 2B, arrow). The species was quite common on soft sediments at depths 3334–4277 m (Fig. 1), but did not reach high population densities.



***Saxipendium* sp. (Harrimaniidae)**: Quite long, about 20 cm, animals with well-contractile proboscis and narrow collar (Fig. 2C). Proboscis, collar and anterior trunk are of a yellowish colour, the posterior trunk is light violet.

This bathyal-abyssal species was observed on sedimented hard substrates. It was not recorded on purely soft sediment without stones. Animals were often recorded with their posterior parts buried in sediment accumulated between rocks or in caverns, with anterior parts exposed on the substratum. These enteropneusts are able to quickly retract into holes in sediment or caverns. The species was observed in the abyssal, at depths 3334–3931 m with population density reaching 4 specimens per $1m^{-2}$. Occasionally the species was seen in the bathyal (<3000 m) on hard substrate on the southern slope of the Volcanologists Massif co-occurring with **Torquaratorid-1** (Fig. 1).

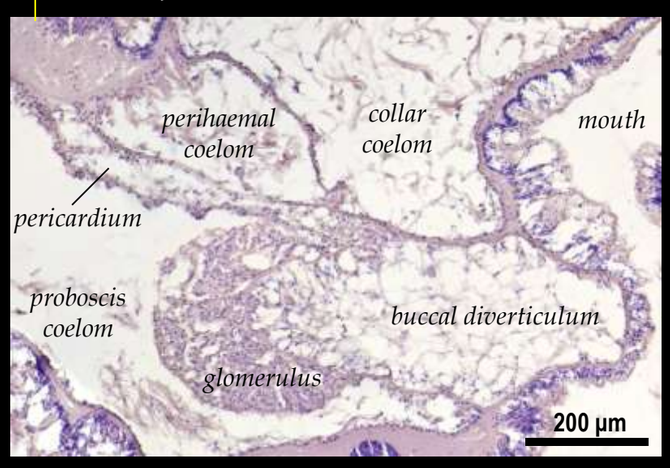


Figure 4. "Heart-kidney", or axial proboscis complex of Torquaratorid-1; sagittal section.

Harrimaniid-1: Proboscis, narrow collar and anterior trunk are of a red colour (Fig. 2D), the colour of posterior trunk is unknown.

The specimens were recorded in the upper bathyal zone on the Koryak slope in the vicinity of the methane seepages, at the depths about 660 m. The species was usually observed with its posterior body part buried in soft sediment sometimes close to areas of bacterial mat.

Harrimaniid-2: Proboscis and narrow collar on the surface of the substrate are red (Fig. 2E) and trunk lightly sprinkled with sediment is white (Fig. 2E, arrow).

This upper-bathyal species was also recorded near the methane seep of the Koryak slope. The photos of the red proboscis and collar exposed from the soft sediment were very fuzzy; however, on the video, one entire specimen was seen drifting in water with near-bottom currents. The species is occurring in very closely geographically located areas with **Harrimaniid-1**, but at the depths 419–420 m.

Torquaratorid-1 allows clarifying the diagnosis of the family Torquaratoridae. In addition to characters previously known for the family (the translucent body, poorly developed musculature, reduction of stalk skeleton, absence of proboscis coelomoduct and coelomopore, presence of lateral extensions of the collar and prominent hepatic caeca), **Torquaratorid-1** demonstrates several new features: the collar coelomoducts, the axial complex with pericardial coelom and a stalk skeleton comprising two plates. Some of the characters are shared with other families of Enteropneusta, including the axial complex with the pericardial coelom and developed glomerulus as a heamocoelic mesh between the coelomic tubules, the paired collar coelomoducts and coelomopores. Also, one character in **Torquaratorid-1** is shared with other class of the phylum Hemichordata, Graptolithoidea – the opening of the collar coelomopores directly into the exterior. This morphological condition makes **Torquaratorid-1** an important link for understanding the evolution of Hemichordata and Deuterostomia.

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