



Canadian Journal of Zoology

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Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2017-0214.R2
Manuscript Type:	Article
Date Submitted by the Author:	09-Jun-2018
Complete List of Authors:	Jabr, Noura; Université de Montréal, Département de sciences biologiques Archambault, Philippe; Université Laval, Département de Biologie Cameron, Christopher; Université de Montréal, Sciences biologiques
Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	BIODIVERSITY < Discipline, BIOGEOGRAPHY < Discipline, TAXONOMY-SYSTEMATICS < Discipline

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Biogeography and adaptations of torquaratorid acorn worms (Hemichordata: Enteropneusta) including two new species from the Canadian Arctic

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None of the authors have any competing interests.

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Abstract

The enteropneust family Torquaratoridae, discovered in 2005 (Holland et al. 2005) has the fewest species of the four living families. It is composed of seven species that live on the cold, deep-sea floor. *Torquarator bullocki* (Holland et al. 2005) was the first species described and collected from the Northeastern Pacific. New species of Torquaratoridae were collected from the Eastern Pacific and described as *Tergivelum baldwinae* (Holland et al. 2009) and *Allapasus aurantiacus* (Holland et al. 2012). A further three species have been collected from the North Atlantic; *Yoda purpurata*, *Allapasus isidis*, and *Tergivelum cinnabarinum* (Priede et al. 2012). The latest Torquaratoridae species was collected from the Russian Arctic (Osborn et al. 2013). We add two new species to the Torquaratoridae from Baffin Bay, in the eastern Arctic of Canada. *Terminstomo arcticus* gen. and sp. nov. was collected at 505 meters depth and is characterized by lacking a heart, and a stomochord that extends from the posterior end of the proboscis through the entire length of the collar. *Allapasus fuscus* sp. nov. was collected from 444 meters depth and is characterized by a typhlosole process along the dorsal midline of the collar buccal cavity.

Key words: Acorn worm, Enteropneusta, Torquaratoridae, biogeography, deep-sea, stomochord, Canadian Arctic biodiversity.

Introduction

Species of the hemichordate class Enteropneusta, or acorn worms, are found at all latitudes from the intertidal zone to the deep-sea, living in sedimentary burrows, under rocks, among kelp holdfasts, or on the epibenthos. The fossil record includes seven species (Cameron 2016), the oldest from the Middle-Cambrian Period (Caron et al. 2013; Nanglu et al. 2016). There are 109 extant species described, from four families: Harrimaniidae (40 spp.), Spengelidae (20 spp.), Ptychoderidae (45 spp.), and Torquaratoridae (7 spp). The least understood of these is the Torquaratoridae, which was established following the remarkable discovery of *Torquarator bullocki* (Holland et al. 2005), collected from the deep-sea off the coast of Oregon. Since that time an additional six species have been described from five genera: *Allapasus* (Holland et al. 2012), *Coleodesmium* (Osborn et al. 2013), *Tergivelum* (Holland et al. 2009), *Torquarator* (Holland et al. 2005), and *Yoda* (Priede et al. 2012), all from deep waters.

Torquaratorids are exclusively found in the deep-sea, an environment characterized by low food availability, and they have several phenotypic traits that appear to be adaptations to this life (Osborn et al. 2012). Rather than living in burrows, they reside on the epibenthos where they collect food, defecate, and then drift in the demersal zone to a new feeding site where more nutrients may be found (Holland et al. 2012; Osborn et al. 2012). They are characterized by a short proboscis, and a wide collar that may have extensive 'lips'. The proboscis and collar lips function to collect sediment and transfer it to the mouth using mucus and cilia. Torquaratorids have a poorly developed (or absent) collagenous proboscis skeleton, and gill bars (Holland et al. 2005; Osborn et al. 2012). This provides them with nearly neutrally buoyancy, an adaptation to a demersal drifting (Osborn et al. 2012). They have poorly developed muscles and are delicate and often nearly transparent, though they may be coloured rose, red, or purple (Priede et al. 2012). *Allapasus* is unusual in that it burrows and the proboscis coelom has a heart, glomerulus, and stomochord that together comprise the more typical acorn worm 'proboscis complex' (Holland et al. 2012). The proboscis complex of shallow water acorn worms functions in the circulation and filtration of blood (Balser and Ruppert 1990), and its absence from torquaratorids may

be due to the poorly developed muscular system (Osborn et al. 2012) that would otherwise consume oxygen, and the delicate body that may be sufficient for gas exchange. The development of a torquaratorid has not been observed but the large egg sizes suggests direct development (Osborn et al. 2012). *Yoda purpurata* is a hermaphrodite (Priede et al. 2012), a common trait in deep-sea animals where conspecifics can be uncommon. *Coleodesmium karaensis* externally broods its embryos in small sacs that connect to the trunk by a stalk (Osborn et al. 2013).

Here we add to the seven species already described, an additional two new species, including one new genus, from the eastern Arctic Ocean of Canada. We also provide a table of the morphological characters that define each of the seven species (Table 1).

Material and Methods

Torquaratorid acorn worms are relatively difficult to collect, unlike most of their shallow-living relatives. Here we describe two new species of torquaratorid, each based on a single and only specimen. The two specimens were collected by Heike Link onboard the CCGS Amundsen. Each specimen was photographed in situ using a ROV (ArcticNet and CCGS Amundsen) equipped with a Typhoon colour camera, and then collected using an Ursnel box core. Specimens were fixed in formalin and shipped to the Université de Montréal, Canada for histology. Specimens were dehydrated, paraffin embedded, trimmed and sectioned at 10-12 μm , mounted onto slides, dewaxed and rehydrated, stained, and photographed on a compound or dissecting microscope. The staining steps included placing slides for fifteen minutes in Bouin's solution at 56 degrees Celsius, then Weigert's Iron Hematoxylin for five minutes, then Biebrich scarlet-acid fuchsin for five minutes, then phosphotungstic / phosphomolybdic acid solution for five minutes, and finally to aniline blue solution for five minutes.

The sectioned and stained specimens were viewed with an Olympus SZX16 stereomicroscope, or an Olympus BX51 compound microscope. Select sections were photographed with a Q Imaging Retiga-2000R digital camera using Q Capture Pro software by Q Imaging.

Systematics

Phylum Hemichordata Bateson, 1885.

Class Enteropneusta Gegenbaur, 1870.

Family Torquaratoridae Holland et al., 2005.

Diagnosis. (Osborn et al. 2012) amended the diagnosis of the family Torquaratoridae to accommodate the increased diversity and to reflect the molecular phylogeny. The proboscis skeleton is absent or reduced to a small medial plate. The adult stomochord is either absent or separated from the buccal cavity of the collar (Osborn et al. 2012). To this we add a broad, short, and dome shaped proboscis, and wide collar. Their bodies are fragile, and semitransparent. The muscular system, and gill bars are poorly developed. Only *Torquarator bullocki* has proboscis horns, or crurae (Holland et al. 2005). Coelomopores have not been found. The sexes are separated except for *Yoda purpurata* which is a hermaphrodite (Priede et al. 2012).

Remarks. Species of all five genera included in this family, namely: *Allapasus*, *Coleodesmium*, *Yoda*, *Torquarator*, and *Tergivelum* are found exclusively in the deep-sea.

Genus *Terminstomo* n. gen.

Type species. *Terminstomo arcticus*, n. sp. JABR and CAMERON

Diagnosis. There is a ventral groove in the proboscis, the stomochord terminates in the posterior proboscis. The proboscis had poorly developed muscles, and lacks a proboscis skeleton, a heart, and blood sinus. The gill bars are poorly developed, as are the circulatory, and muscular systems. There is a deep groove in the posterior, ventral trunk.

Remarks. The genus is monotypic for *T. arcticus* n. sp., which is fully described below. The genus name derives from the Latin word *Termin* meaning “limit” and “*stomo*”, which is an abbreviation for ‘stomochord’. This name refers to the limited appearance of the stomochord in the proboscis region.

Type species. *Terminstomo arcticus* n. gen. et n. sp.

(Figures. 2A-C, 3A-K)

Material examined. Holotype USNM #, comprising 81 slides of one complete female specimen. The specimen was collected using an Ursnel box core from Viscount Melville Sound, Beaufort Sea, Baffin Bay, Canada at station 308, ArcticNet-CSSF the position was 74° 6.244'N; 108° 52.578'W, from 505 meters depth, on October 20, 2009 (Figure 1). The substrate was mud and sand. The specimen was photographed on the deep-ocean floor, with the proboscis extended up into the water (Figure 2A). It broke into two fragments during the collection (Figure 2B).

External features. Total body length after fixation 22.1 mm. Proboscis 3.2 mm long by 5.1 mm wide, dome shaped with small ventral groove. Collar 3 mm long by 5.4 mm wide. Trunk 15.9 mm long. The living holotype colour transparent to white anteriorly. Intestine visible through the body wall, dark pigmented throughout its length. Paired dorso-lateral ridges (Figure 2A), project from anterior third of the trunk, containing a dozen oocytes. Approximately ten pairs of gill pores occurred between the lateral ridges and the dorsal midline (Figure 2C). The living holotype was photographed on the deep-ocean floor with the proboscis projected into the water column, which illustrates a surface-dwelling habit (Figure 2A).

Internal features. Proboscis epidermis with dark staining secretory and light staining glandular cells, over a fine subepithelial nervous layer. Connective tissue and sparse muscle fibers occupy the entire proboscis coelom. There is no open protocelom. Muscle cells are diffusely and evenly distributed in the proboscis coelom but for a concentration at the center of the proboscis (Figure 3A). Where the proboscis meets the collar there is a thickening of the nervous fiber layer, a poorly developed stomochord, a small glomerulus, and a posterior neuropil (Figure 3B, C). Strikingly, the stomochord in *Terminstomo arcticus* only projects anteriorly into the neck (posterior of the proboscis), and extends posteriorly to almost the mid-dorsal collar, which is a distinguishing feature of this genus. The nerve

fiber layer under the stomochord is thicker than the remainder, measuring 50 μm , and the stomochord lacks a lumen (Figure 3D). No heart or blood sinus was detected. The circulatory system is poorly developed.

The collar coelom is spacious and the muscle fibers are diffuse with no peribuccal diverticula of the trunk coeloms. A dorsal nerve cord runs the length of the dorsal collar and under it are paired periaemal diverticula, which are anterior projections of the trunk coeloms. The septum of the right periaemal diverticula of the trunk coelom extends from the right diverticula and connects with the nerve fiber layer of the external wall of the collar (Figure 3D), but this septum disappears suddenly in the mid-collar in conjunction with the disappearance of the stomochord. A dorsal vessel is at places found between the periaemal diverticula mesenteries (Figure 3E). The main cavity in *Terminstomo arcticus* is the buccal cavity. In contrast to *Allaparus aurantiacus*, *Terminstomo arcticus* it lacks a proboscis skeleton that separates the stomochord from the buccal cavity (Holland et al. 2012). Neither a peribuccal vessel nor sacculations of the racemose organ were found in the collar (Figure 3E).

The trunk coeloms are spacious, almost completely lacking muscle, and are separated into left and right cavities by dorsal and ventral mesenteries. The dorsal collar nerve cord continues into the trunk, and is underlined by a dorsal vessel (Figure 3F). A very long right collar-trunk septum runs at this level of the trunk with no evidence of a left collar-trunk septum; this septum runs from the dorsal nerve layer to the ventral nerve layer (Figure 3G). Approximately ten pairs of gill pores open to the exterior via the atrial canals (Figure 3G, H). Collagenous gill bars are poorly developed, and because of this the pharyngeal lumen is not divided into dorsal branchial and ventral digestive regions. At this level of the trunk the paired dorso-lateral ridges project from either side of the body wall along with the dorsal mesentery, which demarcates the dorsal vessels. The ventral midline of the ectodermis at this level of the trunk has a shallow groove that, in transverse section, gives the dermis an arch shape, and the ventral vessels are well developed in this site (Figure 3G).

The holotype is female. Ovaries are located in the paired dorsal-lateral ridges and open via pores on their proximal sides (Figure 3H). The presence of mature and immature oocytes indicates asynchronous oogenesis. The ovaries of Enteropneusta in general have three main layers (i.e., coelomic epithelium, basement membrane and germinal epithelium) (Hadfield 1975). A nucleus and nucleolus were present in some oocytes; the largest oocytes had a diameter of approximately 203 μm (Figure 3I). Ovaries continue posteriorly to the middle of the intestinal region in conjunction with the ridges.

The posterior intestinal trunk at the level of the hepatic region was damaged on collection, but there was no evidence of hepatic sacs. The intestinal wall is rugose and the gut lumen has brown contents that appeared to be fine sediment of suspended flocculent material. The dorsal and ventral mesentery extend to the end of the trunk with prominent dorsal and ventral vessels in between, the nerve fiber layer of trunk at this site is thin (10 μm) (Figure 3J). The deep ventral groove of the epidermis continues to this level of the trunk (Figure 3K).

Remarks. The internal features of the present form are distinct from the other seven species of Torquaratoridae, in the presence or absence of features. *Terminstomo* shares with *Allaparus* and *Coleodesmium* a stomochord and glomerulus. The glomerulus of *Allaparus*, *Coleodesmium*, and *Terminstomo* is positioned against the stomochord rather than associated with an apparent blood sinus (Holland et al. 2012). The blood sinus of *Terminstomo* is absent, as is a heart and a proboscis skeleton. The absence of a proboscis skeleton means there is no skeletal keel supporting the ventral side of the stomochord. The stomochord of *Terminstomo* is unusual in that its most anterior extends only into the posterior proboscis, and posteriorly it extends to the mid-collar. The stomochord of *Allaparus* and *Coleodesmium* extends further anteriorly, and in *Allaparus* it is separated from the gut by a proboscis skeleton. Two characteristics of *Allaparus* that are absent from *Terminstomo* are paired peribuccal vessels in the lateral sides of the collar, and sacculations of a racemose organ that project downward into the buccal cavity. The pharyngeal lumen of *Allaparus* is also divided into a ventral digestive and dorsal branchial regions. *Terminstomo* has lateral ridges with ovaries that extend into the intestinal

region of the trunk. The oocytes of *Terminstomo* are not enclosed in the externalized epidermal pouches of *Allapasus*, and it is not an external brooder like *Coleodesmium*. *Terminstomo* has a deep ventral groove in the epidermis of the intestinal region and the ventral and dorsal mesenteries of the trunk are well developed.

Etymology The species name, *arcticus*, derives from Latinized adjective 'Arctic', where the holotype was sampled. *Terminstomo arcticus* n. gen., n. sp. is unique from other Torquaratoridae genera by a combination of the following characters:

- A ventral groove in the proboscis.
- A stomochord that projects from the mid-dorsal collar terminating anteriorly in the neck.
- Poorly developed proboscis muscles.
- Absence of a proboscis skeleton.
- Absence of a heart and blood sinus.
- The pharyngeal lumen is not divided into dorsal branchial, and ventral digestive regions.
- Poorly develop of gill bars, circulatory, and muscular systems.
- A deep ventral groove in the posterior intestinal trunk.

***Allaparus fuscus* n. genus, n. sp.** JABR and CAMERON

(Figures 4, 5A-G)

Etymology of the specific name. *Fuscus* is a Latin adjective meaning dark brown, in reference to the colour of the body.

Material Examined. Holotype USNM #, comprising 82 slides of one complete female specimen. Collector Ms. Heike Link using an Ursnel box core on September 14, 2008, deployed from the deck of the CCSG Amundsen, at station 108, 76°16.20000'N, 074°35.64000'W, in 444 meters depth (Figure 1). This location is a biodiversity hotspot and area of high benthic boundary fluxes of oxygen located in central Baffin Bay (Link et al. 2013). The specimen was fixed in formalin.

External features. Total body length after fixation 29.2 mm long (Figure 4). Proboscis 3.2 mm long by 3.1 mm wide, dome-shape with a small dorsal groove. Collar 2.8 mm long by 3.5 mm wide. Trunk 23.2 mm long by 5.1 mm wide in the pharyngeal region, and 2.2 mm wide in the intestinal region. The living specimen dark brown. Transparent epidermis. Dorsal nerve cord visible through the epithelium of the dorsal midline of the collar. Paired dorsal lateral ridges extend from the anterior trunk to the end of the pharyngeal region, and housed the ovaries. The ridges formed an envelope around large, cream coloured, external oocytes that were attached by a stalk. About nine pairs of gill pores occurred on either side of the dorsal midline of the trunk.

Internal features. The epidermis of the proboscis is thickest in the mid-dorsal groove. The proboscis coelom is full of connective tissue including abundant, dispersed muscle fibers, except for anteriorly where the muscle cells form a concentrated muscle mass (Figure 5A). The proboscis lacks an open coelomic cavity, a pericardial sac, and a blood sinus. The anterior end of the stomochord extends into the posterior region of the proboscis, and is flanked by a small glomerulus (Figure 5B). A collagenous sheath surrounds the stomochord and in the posterior collar it thickens and becomes conjoined with the basal lamina of the proboscis neck, where it is also thick. The subepidermal nerve plexus is also thick in

this region. There is no proboscis skeleton. A thin septum separates the proboscis and collar coeloms (Figure 5B).

An anterior nerve pore is found under the anterior midline of the collar. The dorsal cord has a hollow continuous lumen and under it are paired extensions of the trunk coeloms, the perihæmal diverticula, the mesenteries of which envelop a dorsal blood vessel. There are no peribuccal diverticula of the trunk coeloms. The stomochord extends through the anterior half of the collar. Anteriorly the buccal cavity is T-shaped in transverse section, and the lateral arms of the 'T' curl ventrally (Figure 5C). There is a well-developed typhlosole process, which is an elaboration of the ventral surface of the collar cavity into the collar lumen. A deep mid-ventral groove runs through the posterior half of the collar and into the trunk. The dorsal vessel runs the length of the collar, whereas the anterior end of the ventral one is found in the mid-pharynx region of trunk (Figure 5C, D, and E).

A septum demarcates the collar coelom from the trunk coelom. The left and right trunk coeloms are separated by dorsal and ventral mesenteries throughout the length of the trunk. The pharyngeal lumen is partially divided by paired parabranchial ridges into a dorsal branchial and a ventral digestive pharynx (Figure 5E). The collagen of the gill bars is poorly developed. There are approximately nine pairs of gill atria that connect the internal gill slits to the external gill pores. There is a thickening of the subepithelial nerve plexus both dorsally and ventrally that forms the trunk nerve cords. Ovaries are located in paired, dorso-lateral ridges of the trunk and are most abundant near to the inner (proximal) faces of the ridges (Figure 5F). Externalized ovaries attach to the inner face of the ridge epidermis by a thin stalk (Figure 5F). The largest oocyte is approximately 950 µm in diameter. The ovaries extend posteriorly to the anterior end of the intestinal region, ending with the terminal end of the lateral ridges. The intestinal gut epithelium is thick and plicated, and the gut lumen is full of fine particles and mucus (Figure 5G). There are no externally projecting hepatic sacculations.

Remarks. *Allapasus* genus is characterized by a very well developed muscular proboscis and collar. The stomochord is separated from the main gut of the digestive lumen by the proboscis skeleton (Holland et

al. 2012). The pharyngeal lumen is divided by the parabranchial ridge into a ventral digestive region and a dorsal branchial region (Holland et al. 2012). This new species shares some features with the previous two species of *Allaparus*, and can be distinguished from them by the absence of some characters and the presence others. *A. fuscus* is brown in colour whereas *Allaparus aurantiacus* is light orange and *Allaparus isidis* is light yellow (Holland et al. 2012; Priede et al. 2012).

Allaparus fuscus is different from the other two species in that the protoceol is absent, and the stomochord is not separated from the main gut via a proboscis skeleton. In the collar, no peribuccal vessels were found. There are no externally projecting hepatic sacculations. Lastly, there is a typhlosole process in the dorsal buccal cavity, a feature unique to this species. The typhlosole process in annelids (i.e., earthworms) and echinoderms provides skeleton support, and an increased surface area for the absorption of nutrients.

Allaparus fuscus, shares with *Allaparus aurantiacus*, and *Allaparus isidis* parabranchial ridges that divide the pharyngeal region into a ventral digestive region and a dorsal branchial region, and externalized ovaries.

Etymology The species name, *fuscus*, derives from Latinized adjective 'brown', the colour of the holotype. The defining characters of *Allaparus fuscus* are:

- The proboscis protoceol is absent.
- The stomochord is not separated from the main gut, due to the lack of a proboscis skeleton.
- A typhlosole process extends from the dorsal buccal cavity, resulting in a T-shape in transverse section.
- Peribuccal vessels are absent.
- No externally projecting hepatic sacculations in the collar.

Discussion

Enteropneusts are one of the abundant macro-fauna residing on the surface of several deep-sea territories (Anderson et al. 2011; Jones et al. 2013). Three species have been collected from pools of sediment on the Northern mid-Atlantic ridge including *Yoda purpurata*, *Tergivelum cinnabarinum*, and *Allaparus isidis* (Jones et al. 2013). Their lengths range between 12 and 26 centimeters (Osborn et al. 2012; Priede et al. 2012; Jones et al. 2013). This video survey recorded 92 individual *Tergivelum cinnabarinum* and found that it was most abundant in the northern section, 273 individuals of *Yoda purpurata* that had a higher density in the southern section, and one *Allaparus isidis* in the southwest (Jones et al. 2013). More polar species include *Coleodesmium karaensis* (Osborn et al. 2013) from the Kara Sea in the Russian Arctic. Others not described, but identified based on DNA sequences of worm fragments include one from Iceland, and two from the Ross Shelf Antarctica, collected between 732 and 531 meters depth (Cannon et al. 2013). Two additional species have been photographed between 531 and 1111 meters depth along the West Antarctic Peninsula shelf and adjacent fjords and on the Ross Sea shelf (Halanych et al. 2013). We add to this list of polar species two additional species, *Terminstomo arcticus* and *Allaparus fuscus*, from the eastern Arctic of Canada.

Torquaratorids are also abundant in the deep Pacific. Three species have been collected adjacent to Washington, Oregon, and California, including *Torquarator bullocki* (Holland et al. 2005) *Allaparus aurantiacus* (Holland et al. 2012), and *Tergivelum baldwinae* (Holland et al. 2009; Osborn et al. 2012). Additional undescribed species are found near Hawaii, Washington, Oregon, and the Gulf of California (Osborn et al. 2012). They are commonly captured by video on the east (259-2260 meters depth) and west (641-4827 meters depth) Australian continental margins (Anderson et al. 2011). Several additional distinct forms have been photographed by submersibles in the Pacific and Atlantic but not collected, and others have been collected but have yet to receive a formal taxonomic description (Holland et al. 2009; Jones et al. 2013). In general, Torquaratorids appear to be common in the deep-sea, across a wide range of environments, frequently identified when remotely operated vehicles are deployed to survey the epibenthos. Their apparent ubiquity and abundance suggests that the small

taxonomic sample taken to date likely under-represents the actual diversity of torquaratorids. The ecology of torquaratorids is poorly known. (Jones et al. 2013) suggests bioturbation caused by feeding and fecal deposition of torquaratorids may enhance the benthic micro faunal biodiversity in the deep-sea.

The torquaratorid *Allaparus aurantiacus* is unusual in that it burrows beneath the surface (Holland et al. 2012; Osborn et al. 2013), whereas the remaining torquaratorids are instead epibenthic, surface deposit feeders. Their presence is sometimes made apparent by the presence of fecal casts that they deposit on the sea-bed, and that form distinct clockwise or counter-clockwise shaped spirals (Smith et al. 2005; Jones et al. 2013). After voiding the gut, the worms then drift into the demersal zone, a short distance above the sea-floor (Osborn et al. 2012). The drifting of *Tergivelum baldwinae* is assisted by strings of secreted mucus that act as a parachute, lifting and drifting the worm to a new feeding site, where some nutrients might be found (Holland et al. 2009). We did not observe fecal castings or demersal drifting, but the epibenthic location and upward position of the proboscis in *Terminstomo arcticus* suggests that it may also be a demersal drifter (Figure 2A).

One of the most notable adaptations of torquaratorids, including *Allaparus fuscus* is the reduction of collagenous structures. *Allaparus fuscus* lacks a proboscis skeleton and the gill bars are poorly developed. This morphology may be adaptations to demersal drifting, analogous to the loss of bone in deep-sea pelagic fish, which enables the fish to maintain nearly neutral buoyancy (David and Anthony 1997). The proboscis skeleton of shallow water, burrowing, acorn worms provides skeletal support between a muscular proboscis and the collar. It is located under the stomochord, a turgid structure that antagonizes the pericardial sac as it compresses the blood in the blood sinus, for ultrafiltration through the glomerulus (Balser and Ruppert 1990). The absence of a proboscis skeleton in torquaratorids may be interpreted as a loss, correlated with the abandonment of a burrowing life style and a poorly developed circulatory system.

Torquaratoridae are currently the least speciose family of Enteropneusta, though new species are being discovered at a rapid pace. Here we describe two new species, the first acorn worms observed, photographed, and collected from the Canadian Arctic. Species, and their abundance, are the basic indicators of biodiversity. Canada has the longest coastline of any country. Its oceans are home to the bulk of its animal biodiversity and resources, but are also the least known, especially in the Arctic Ocean. This ocean is under increased pressure from climate change, overfishing, eutrophication, shipping and introduced species, habitat destruction, and chemical loading (Archambault et al. 2010). More concerted effort is needed to have a basic baseline of its marine biodiversity during this historical period of rapid change.

AKNOWLEDGEMENTS

We would like to thank the following people for their contribution to the specimen's collection: Ms. Heike Link, the ROV pilots L. Michaud and P. Massot. We also thank Madam Pelletier Louise for her histology advice. We thank the officers and crew of the CCGS 'Amundsen' and the ArcticNet scientific and technical personnel for support onboard. Work was supported by ArcticNet, Canadian Healthy Ocean Network (CHONe) and Natural Sciences and Engineering Research Council of Canada.

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Tables

Table 1. Comparison of external and internal features of the species of the family Torquaratoridae. Characters from previously described species were obtained from the literature. Question marks indicate when a character state is unknown.

	<i>Terminstomo arcticus</i> *	<i>Allaparus fuscus</i> *	<i>Allaparus Isidis</i> ¹	<i>Allaparus aurantiacus</i> ²	<i>Coleodesmium karaensis</i> ³	<i>Yoda purpurata</i> ⁴	<i>Torquarator bullocki</i> ⁵	<i>Tergivelum cinnabarinum</i> ⁶	<i>Tergivelum baldwinae</i> ⁷
Living holotype length	2.21 cm	2.92 cm	13 cm	26 cm and 18 cm (after fixation)	6.3 cm	12 cm	7 cm	12 cm	9-28 cm
Living holotype colour	Transparent, white anterior gut, dark pigmented intestine	Dark brown	Light yellow	Light orange (anterior), and light Beige (posterior)	Translucent (translucent)	Dark reddish purple	Tan (anterior) Light blue (posterior)	Cinnabar (anterior), light orange (posterior)	Dark brown (anterior), Beige (posterior)
Proboscis shape	Dome	Short dome	Dome	Pointed dome	Dome	Smooth Dome	Low dome	Dome	Shallow rounded dome
Proboscis length	0.32 cm	0.32 cm	?	0.6 cm Fixation	0.9 cm	2 cm	0.5 cm	?	?
Proboscis Width	0.51 cm	0.31 cm	?	1 cm Fixation	1.2 cm	3.5 cm	0.8 cm	?	?
Proboscis groove	Yes,ventral	Yes,dorsal	Yes,ventral	Yes,ventral	Yes,dorsal and ventral	No	No	No	No
Presence and shape of skeleton	No	No	Yes,plate-like	Yes,plate (nearly verticle)	Yes,tubular	No	Yes,reduced, short horn ant. And post.	No	No
Anterior and posterior proboscis skeleton horns	No	No	No	No	No	No	Yes,short	No	No

*New species; 1. Priede et al. 2012; 2. Holland et al. 2012; 3. Osborn et al. 2013; 4. Priede et al. 2012; 5. Holland et al. 2005; 6. Priede et al. 2012; 7. Holland et al. 2009.

Table 1. Continued

	<i>Terminstomo arcticus</i> *	<i>Allapapus fuscus</i> *	<i>Allapapus Isidis</i> ¹	<i>Allapapus aurantiacus</i> ²	<i>Coleodesmium karaensis</i> ³	<i>Yoda purpurata</i> ⁴	<i>Torquarator bullocki</i> ⁵	<i>Tergivelum cinnabarinum</i> ⁶	<i>Tergivelum baldwinae</i> ⁷
Collar length	0.3cm	0.28 cm	?	0.5 cm (anterior-posterior), 0.6 cm (dorsal-ventral), fixation 0.35 cm	0.5 cm	0.5 cm	0.7 cm	?	9 cm
Collar width	0.54 cm	0.35 cm	?	1 cm fixation	1.4 cm	6 cm	1.5 cm	?	2cm
Stomochord	Yes	Yes	Yes	Yes	Yes	No	Yes	No	No
Buccal cavity	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes
Perihaemal Coelom	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes
Trunk length	1.59 cm	2.32 cm	?	17 cm (anterior-posterior), 0.5 cm (dorsal-ventral),	4.8 cm	14.5 cm	?	?	?
Trunk width	?Damaged	0.51 cm anterior. 0.22 cm posterior	?	1 cm (1.4 cm in hepatic intestine)	1.3 cm	0.7 cm	?	?	?
Glomerulus	Yes	Yes	Yes	Yes	Yes	No	No	No	No
Heart	No	No	Yes	Yes	?	No	No	No	No
Coelomopores	No	No	No	No	No	No	?	?	?
Sex	Separated	Separated	Separated	Separated	Separated	Hermaphrodites	Separated	Separated	Separated
Distinctive Characters	Stomochord terminates in posterior proboscis, deep ventral groove in posterior intestinal region of trunk	Typhlosole process in the collar, external Ovaries	Externalized ovaries	Externalized ovaries	Proboscis skeleton has tubular component ensheathing the collar that has transverse opaque stripe, external brooded embryos.	Hermaphrodite, lacks hepatic sacs, lateral lips, nuchal skeleton protuberance of collar	Anterior and posterior horns of the proboscis skeleton	Back veils, paired buccal muscles	Back veils, laterodorsal fossa in the proboscis, paired buccal muscles.

*New species; 1. Priede et al. 2012; 2. Holland et al.2012; 3. Osborn et al. 2013; 4. Priede et al.2012; 5. Holland et al. 2005; 6. Priede et al. 2012; 7. Holland et al. 2009.

Figure captions

Figure 1. A map of the eastern Arctic of Canada showing the collection locations of *Terminstomo arcticus* (square) (505 m depth), *Allapapus fuscus* (triangle) (444 m depth).

Figure 2. (A) Photograph of a living specimen of *Terminstomo arcticus* n. gen., n. sp. on the deep-ocean floor in lateral view (photographed by Pilots: L. Michaud, and P. Massot). (B) The holotype was broken into two fragments. (C) The holotype after fixation. Abbreviations: bg, branchiogenital region of trunk; c, collar; ct, caudal region of trunk; dn, dorsal nerve cord; gs, gills; p, proboscis; rd, ridges. Scale bars: 1 cm.

Figure 3. Light micrographs of transverse sections of *Terminstomo arcticus*. n. gen., n. sp. A, Cross section of the anterior end of the proboscis showing diffuse muscles and a central sheet of connective tissue and the ventral groove. B, Proboscis showing the conjunction point between the proboscis and the collar. C, The posterior neuropil and glomerulus. D, The posterior proboscis and anterior collar interface showing the stomochord, glomerulus and dorsal nerve cord. E, The posterior collar showing the buccal cavity, periahaemal diverticula, and dorsal nerve cord. F, Anterior trunk showing the pharyngeal lumen, a vestigial gill bar, dorsal and ventral mesenteries. G, Branchiogenital region of trunk with left and right dorso-lateral ridges, right collar-trunk septum, and an atrial canal. H, Oocytes connected to the external dorso-lateral ridges via a duct and pore. I, The largest mature oocyte with nucleus. J, Anterior intestinal region of the trunk showing gut lumen, dorsal and ventral vessels, and reduced posterior ridges. K, Caudal region of the trunk showing very deep ventral groove. Abbreviation: atc, atria canal; bc, buccal cavity; cc, collar coelom; cs, collar septum; cts, collar-trunk septum; dm, dorsal mesentery; dnc, dorsal nerve cord; dv, dorsal vessel; ec, ectodermic; ep, epidermis; en, endodermis; g, glomerulus; ge, germinal epithelium; gb, gill bars; gl, gut lumen; ie, intestinal endodermis; m, mouth; mo, mature oocyte; n, nucleus; nfl, nerve fiber layer; np, neuropil; oo, oocytes; pc, proboscis coelom; phd, periahaemal diverticula; phl, pharyngeal lumen; rd, ridges; sm, smooth muscles sheet; tc, trunk coelom; vg, ventral groove; vm, ventral mesentery; vv, ventral vessel. Scale bars: A, G = 400 μ m; B, C = 600 μ m; D, E, H, J = 1000 μ m; I = 150 μ m; K = 450 μ m.

Figure 4. Photograph of a fixed specimen of *Allapapus fuscus* n. sp. from the eastern Arctic of Canada. Abbreviations: bg, branchiogenital region of trunk; c, collar; ct, caudal region of trunk; gs, gills; ov, ovaries; p, proboscis; rd, ridges. Scale bars: 0.5 cm.

Figure 5. Light micrographs of transverse sections of *Allapapus fuscus* n. sp.: A, Proboscis with a central sheet of muscles. B, Posterior part of the proboscis and anterior part of the collar showing the proboscis complex. C, Mid-collar showing the beginning of the typhlosole process. D, Mid-collar showing the complete of the typhlosole process and formed of buccal cavity. E, Pharyngeal region of the trunk. F, Genital region of the trunk showing the oocytes, gill bars, and externalized ovary. G, Intestinal region of the trunk. Abbreviations: atc, atria canal; b, blood; cc, collar coelom; cs, collar septum; dg, dorsal groove; dv, dorsal vessel; ep, epidermis; exo, externalized ovary; ie, intestine; g, glomerulus; gb, gill bars; gl, gut lumen; mm, muscle mass; np, neuropil; oo, oocytes; op, ovary pores; ov, ovary; pc, proboscis coelom; pbr, parabranchial ridge; phd, periahaemal diverticula; phl, pharyngeal lumen; pl, plica; rd, ridges; s, stomochord; t, typhlosole process; tc, trunk coelom; vg, ventral groove; vv, ventral vessel. Scale bars: A, H=600 μ m; B= 500 μ m; C, F= 1000 μ m; D, G= 450 μ m; E= 400 μ m.









