Université de Montréal

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

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Résumé

Cette étude de la famille Torquaratoridae est basée sur des descriptions morphologiques de deux nouvelles espèces, collectées dans l'Arctique canadien en 2008 et 2009 profondeur de 505 mètres et de 444 mètres Ces deux espèces représentent les premiers vers de glands décrits dans Arctique du Canada. Les nouvelles descriptions rendent le nombre total d'espèces de Torquaratoridae à neuf, elles augmentent le nombre total de Torquaratoridae à trois, pou le milieu Arctique, y compris *Coleodesmium karaensis* (Osborn et al. 2013) de l'Arctique russe, et elles augmentent les Torquaratoridae de l'Amérique du Nord à quatre, y compris *Torquarator bullocki* (Hollande Et al. 2005), du nord-est du Pacifique et *Tergivelum baldwinae* (Holland et al. 2009) du Pacifique oriental (côte californienne). La famille Torquaratoridae est différente de celle Enteropneusta en termes d'habitat, qui est épibenthique, ou à la surface des sédiments au fond de l'océan, à la dérive démersale vers de nouveaux sites d'alimentation et à des organes musculaires, vasculaires et collagènes mal développés. L'emplacement géographique de ces deux nouvelles espèces renforce l'idée que le ver du gland a une répartition mondiale dans les océans.

Mots-clés: Taxonomie, morphologie, Enteropneusta, Hemichordata, Torquaratoridae, nouveau genre, nouveau espèce, biodiversité arctique canadienne.

Summary

This study of the family Torquaratoridae is based on morphological descriptions of two new species collected from the Canadian Arctic in 2008 and 2009 at 505 meters and 444 meters depth . These two species represent the first acorn worms described from Canadian Arctic. The new descriptions bring the overall number of Torquaratoridae species to nine, increase the total number of Arctic Torquaratoridae to three including *Coleodesmium karaensis* (Osborn et al. 2013) from the Russian Arctic, and increase the North America Torquaratoridae to four including *Torquarator bullocki* (Holland et al. 2005) from the Northeast Pacific, and *Tergivelum baldwinae* (Holland et al. 2009) from the Eastern Pacific (California coast). The family Torquaratoridae is different from other Enteropneusta in terms of the habitat, which is epibenthic, or on the surface sediments at the bottom of the ocean, demersal (is an area of sea close to the benthos) drifting to new feeding sites, and poorly developed muscular, vascular and collagenous organs. The geographic location of these two new species support the idea that Torquaratoridae has a global distribution in the world's oceans.

Key words: Taxonomy, morphology, Enteropneusta, Hemichordata, Torquaratoridae, new genus, new species, Canadian Arctic biodiversity

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atr	atrial canal
bg	branchiogenital region
bc	buccal cavity
c	collar
cc	collar coelom
cs	collar septum
ct	caudal region of trunk
cts	collar-trunk septum
dg	dorsal groove
dm	dorsal mesentery
dnc	dorsal nerve cord
dv	dorsal vessel
ec	ectodermic
en	endodermis
ep	epidermis
exo	externalized ovary
g	glomerulus
ge	germinal epithelium
gb	gill bars
gl	gut lumen
ie	intestinal epidermis
m	mouth
mo	mature oocyte
n	nucleus
nfl	nerve fiber layer
np	neuropil
oo	oocytes
pc	proboscis coelom
pbf	parabranchial folds
phd	perihaemal diverticula
phl	pharyngeal lumen

pl	Plica
rd	ridges
rg	rougus
s	stomochord
sm.	smooth muscle sheet
t	typhlosole process
tc	trunk coelom
vg	ventral groove
vm	ventral mesentery
vv	ventral vessel

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1. Introduction

1.1 THE IMPORTANT OF TAXONOMY:

Canada has a history of contributions in the study of taxonomy (the processes of discovering and describing a new species) and more recently to biodiversity science and its ramifications (Lovejoy et al. 2010). This success is due to several factors, the most important is the many ecosystems in Canada, diverse funding resources, and a scientific and political will to monitor the changing biodiversity, including its loss in Canada. Canadian marine biodiversity is rich of 15,988 marine organisms, such as, (microbes, phytoplankton, fishes, zooplankton, and marine mammals) along three seas (The Arctic, the Atlantic, and the Pacific) (Archambault et al. 2010), but just 48% of canadien marine spices have been described, so there is no doubt that there are more species still undescribed and unrecorded because of several challenges that faced the taxonomic research. One of these challenges is decline the number of taxonomists who have a former training and decline the funds support for the research. However, from 2013 to today date there was a great development on taxonomy field, by increasing the formal training for the people who are interesting to taxonomy, and by enhance the funding for baseline taxonomic. Today, taxonomy science start to thrives in Canada and several programs start to address some taxonomy projects (Archambault et al. 2010). Despite this, there has been a loss of taxonomic expertise, which reflects negatively on the economy, culture, agriculture, and ecosystem. Taxonomy and biodiversity science go hand in hand. Taxonomists discover, define and classify the species unit, a fundamental level of organization in biodiversity science (Lovejoy et al. 2010). Biodiversity science is a multidisciplinary field that integrates ecology, evolutionary biology, management, agriculture and economics. It depends on the reliable definition of introduced and endemic species, functional groups, keystone species, ecological redundancy, food webs and endangered species. Each of these concepts is fundamentally dependent on taxonomy.

There are still more points should be apply in order to get the taxonomy to the required level; such as, enhance the species identification guides, which used as a resource, and also by join the biodiversity informatics with molecular techniques which result in a new tool in taxonomy (Costello et al. 2006). Depend on online publication (by emailing experts) which make the taxonomy information easy to obtain, increase the international cooperation in taxonomy research, make an access to the species by register them in the museum, and making a taxonomic revisions guides to describe and name a new species (Costello et al. 2015).

Taxonomic specimens are the most common units that comprise museum collections. Ideally each specimen will include the date, location, and some details on the ecology where the specimen was collected. This information is used in how environments change, in response to changes in landscape use, climate change (past and present) for example. Moreover, taxonomy discovers organismal modifications and innovations and therefore provide insight into the origin and evolution of species. Some of these innovations are useful to understand biochemical pathways, biomimicry, and medicine including the development of pharmaceuticals that improve human health. Today, taxonomy science is re-emerging as a more integrative science, incorporating new computational methods, genetics and molecular phylogenetic data. It has become strategic to the wise use of natural sources (Mosquin et al. 1995), including how to protect it. The taxonomic information provided here provides new insight into acorn worm biology, and the community ecology of Canada's deep sea Arctic Ocean.

1.2 THE IMPORTANCE OF HISTOLOGY:

Central to taxonomy is the practice of histology, the microscopic study of organisms, cells and tissues. Histology provides detailed knowledge of how cells, tissues and organs like the brain, the kidney, and the heart function and are arranged into body plans. Histology contributes to concepts of evolution by accumulating data on the subtle (or not so subtle) differences between sister's species, or more distantly related taxa. Here I use histological methods to define new species of acorn worms.

Species have a several definition concepts, for example; biological species are the organisms, which interbreed in the environment and natural with other members from different groups. Morphological concepts of species; characterizes a species by their anatomical criteria and body shape. Ecological concept of spices means; the organisms that described according to their natural scales, and by their react with living and nonliving aspects on their habitat. Phylogenetic definition of species is described members of organisms who have a common ancestor, a combination of specific traits, and forming a single branch in the tree of life. Species definition in taxonomy science includes and depends on the phylogenetic and morphological species concepts.

No one characteristic defines a species, but instead it is a combination of characteristics, unique to that specimen, that form the foundation of a species. In the absence of histology, we could not define new species, compare holotypes to ancient museum collections, or appreciate the morphological diversity of the phylum Hemichordata.

1.3 DIAGNOSTIC MORPHOLOGICAL CHARACTERS:

The phylum Hemichordata is comprised of three classes. The Enteropneusta are solitary worms that typically reside in the sediment, the Pterobranchia, including the graptolites (Mitchell et al. 2013) are colonial tube dwelling zooids, and the Planktospaeroidea is a monospecific class based on a larva called *Planktospaeroidea pelagica* Spengel 1932 (Hadfield and Young 1983; Hart et al. 1994). The Enteropneusta, or acorn worm is the most speciose class with almost 120 species from four families; Harrimaniidae, Spengelidae, Ptychoderidae, and Torquaratoridae. The aim of this thesis is to provide taxonomic descriptions of a two Torquaratoridae worms from the Canadian Arctic.

Acorn worms ranged between less than a millimeters to 2.5 meters in total length (Cameron & Ostiguy 2013). The body is divided into a proboscis, a collar and a trunk (Fig. 1). The muscular proboscis may be short or long depending on the species and functions in burrowing, and the collection and transport of sediment to the mouth using mucus and cilia. The collar is short and muscular and envelops the mouth and buccal cavity. It is connected to the proboscis by a stiff dorsal peduncle. The trunk includes three sections; the anterior branchiogenital region, the hepatic region and the elongate intestine. The branchial region has paired gills pores and serial gonads that differ in the positon and the extent of development depending on the genus of worm. *Glossobalanus*, for instance, has dorsolateral genital ridges, while those of *Ptychoderidae* and *Balanoglossus* form more extensive lateral ridges or ‘wings’ (Cameron & Ostiguy 2013).

The internal anatomy of the proboscis is characterized by a coelom that contains a heart-kidney-coelomic complex and a rigid stomochord. The heart compresses the blood sinus against the stomochord, which in turn forces urine through the kidney into the coelom, where it is then transported to the outside via a duct and pore. The form of this complex is rich in taxonomic characters. Particularly informative is the collagenous nuchal skeleton that underlies the stomochord and extends posteriorly through the peduncle (neck) into the collar. This Y-shaped structure gives skeletal support to the narrow neck and stomochord. In the collar it bifurcates and extends rearward, the extent depending on the genus of worm. The branchial pharynx is peanut shaped in cross section, whereby the dorsal part includes the gill pores and the ventral part is digestive. Following the branchial region is a muscular oesophagus that squeezes excess water from the mucus and food cord, before it enters the vermiform intestine (Cameron 2005).

Enteropneusts are dioecious and reproduce sexually although asexual vivipara (Gilchrist 1925) or fragmentation (Worsaae et al. 2012) have been documented. Development may be direct or indirect via a tornaria larva.

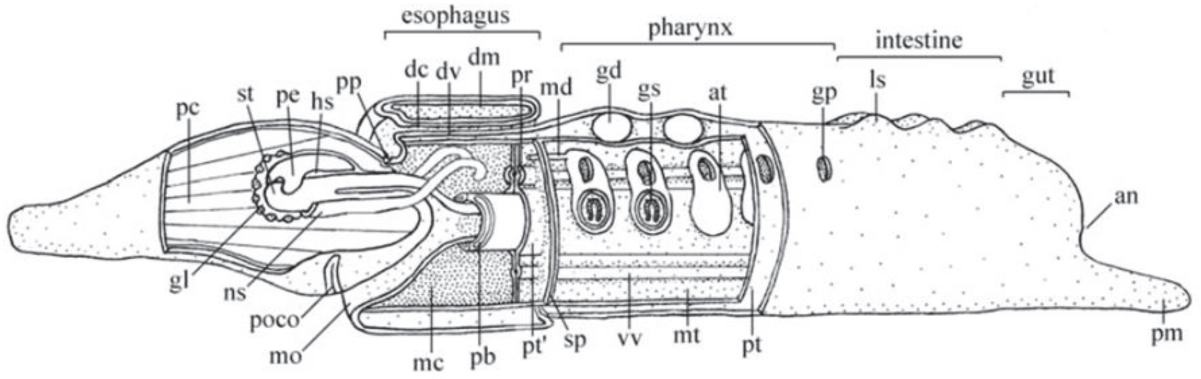

Figure 1. An illustration of a generalized enteropneust. An, anus; at, atrium; dc, dorsal nerve cord; dm, dorsal mesentery; dv, dorsal blood vessel; gd, gonad; gl, filtration glomerulus; gp, gill pore; gs, gill slit; hs, heart sinus; ls, liver sacs; mc, mesocoel; md, paired mesocoel ducts; mo, mouth; mt, metacoels; ns, Y-shaped nuchal skeleton; pb, peribuccal coeloms; pc, protocoel; pe, pericardium; pm, ventral postanal extension of the metasome; poco, preoral ciliary organ; pp, protocoel pore; pr, perihaemal coeloms; pt, somatic peritoneum; pt', visceral peritoneum; sp, septum ; st, stomochord ; vv, ventral blood vessel (from Cameron 2005).

1.4 DIAGNOSS OF THE ENTEROPNEUSTA FAMILIES:

Phylum: Hemichordata Bateson, 1885

Class: Enteropneusta Gegenbaur, 1870

Family: Harrimaniidae Spengel, 1901

This family is characterized by present of a dorsal nerve roots in the collar. The trunk doesn't have circular muscle fibers, and hepatic ceca are absent. In addition, the stomochord does not have a vermiform process. The development in this family is direct (Deland et al. 2010).

Family: Ptychoderidae Spengel, 1893

The collar contains dorsal nerve roots and the trunk does not have abdominal pores, but the lateral septa appear clearly. Hepatic caeca are usually present. In addition, the trunk has circular muscles fibers which are positioned outside of the longitudinal fibres. The stomochord does not have a vermiform process, and this family has develops indirectly via a tornaria larva (Cameron & Ostiguy 2013).

Family: Spenglidae Willey, 1899

Unlike Ptychoderidae, the stomochord of members of the Spengelidae have a vermiform process that extends anteriorly in the proboscis coelomic cavity. It is seldom that there is a dorsal nerve root arising from the collar. The trunk muscle fibre layer is positioned inside of the longitudinal fibre layer. Hepatic ceca may or may not present (Cameron & Perez 2012). The reproduction is indirect.

Family*:* Torquaratoridae Holland et al., 2005

There are seven species of Torquaratoridae. In general torquaratorids are fragile and nearly transparent animals adapted to a demersal life in the deep sea. They are characterized by a wide proboscis, and a collar that is very broad. The trunk consists of a pharynx, intestine, and prominent hepatic caeca. The collagenous gill bars and proboscis skeleton are poorly developed (Holland et al. 2009).

2. Objectives of the work

Taxonomic description of two Torquaratoridae worms from the Canadian Arctic

Here we provide a taxonomic description (Morphology description passed on the external and internal features of the body), of two new species of torquaratorid collected from the Eastern Canadian Arctic. Torquaratoridae are deep-sea animals that live on the surface of the mud. They feed on surface sediment and after defecating (Fig. 2), float to a new feeding site using demersal currents (Holland et al. 2012).

This family has a minimal proboscis skeleton, which makes its body delicate. The proboscis and the collar are broad. The hepatic caeca are prominent, and there are no synapticles bridging primary to secondary gill bars, which are poorly developed. There are seven species in the family that differ in the extent of soft body parts, skeletal elements and body colour. One of the specimens is not brightly pigmented like many torquaratorids, but it has a small dome shaped proboscis. The proboscis of *Allapasus aurantiacus* n. gen. n. sp. is small and dome shaped, and the colour is not dramatic, so I have closely examine slides of this species. *A. aurantiacus* is the only torquaratorids with a complete proboscis complex including a heart, glomerulus, coelom and stomochord, and the collar is wider than long. The muscles of the proboscis and collar are more developed than other species. The pharynx is located in the trunk, and paired lateral wings present extend the full length of the lateral trunk (Holland et al. 2012) (Fig. 3). The species of torquaratorid from the Russian Arctic, *Coleodesmium karaensis* is a close relative to this specimen, though unusual in that its collar nerve cord is ensheathed in a tubular part of the proboscis skeleton, its bright colour, and it broods embryos in the lateral wings (Osborn et al. 2013).

Figure 2. Torquaratoridae evacuate the gut onto the sea floor, often leaving fecal castings in a characteristic pattern, before drifting in the demersal zone to another feeding location (from Osborn et al. 2011).

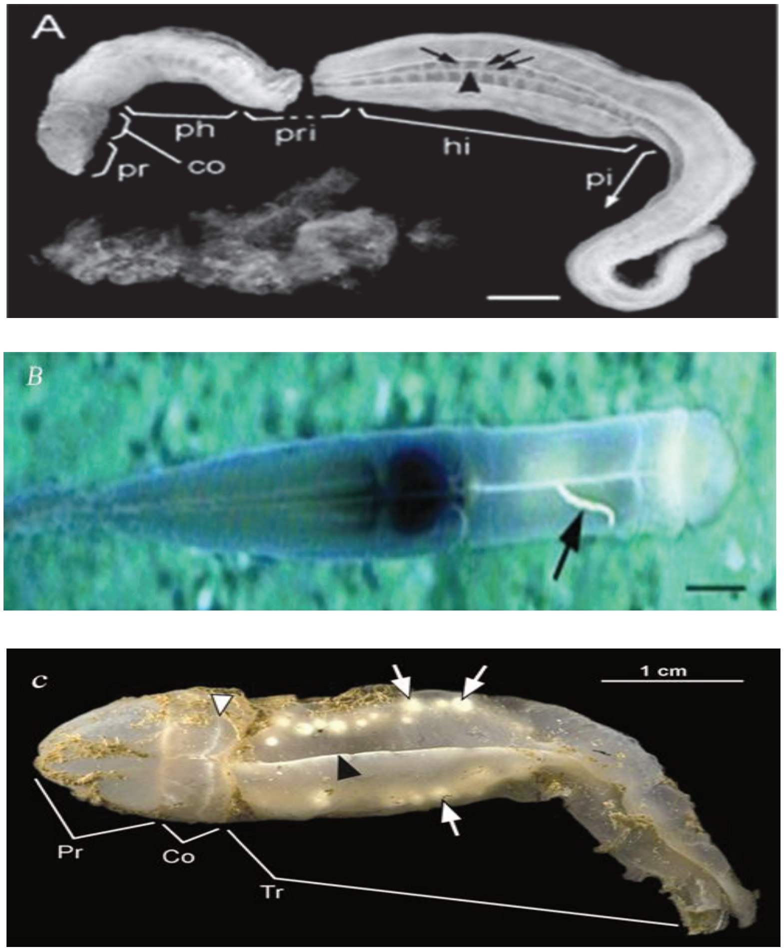

Figure 3. (A) *Allapasus aurantiacus*, and (B) *Allapasus isidis*. Pr, proboscis; co, collar; ph, pharynx; pri, prehepatic intestine; hi, hepatic intestine; pi, posthepatic intestine. (from Holland et al. 2012 & Priede et al. 2012), (C) *Coleodesmium karaensis* Torquaratoridae from the Kara Sea (Russian Arctic) a dorsal view of the living holotype, showing: pr, proboscis; co, collar; and tr, trunk posterior part missing; the white arrowhead indicates the transverse stripe o the collar; the black arrowhead indicates the mid-dorsal apposition of the left and right lateral wings accompanying the trunk; and the white arrows indicate large oocytes or embryos visible through the translucent body wall. Scal bar = 1 cm (from Osborn et al.2013)

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

ABSTRACT

The enteropneust family Torquaratoridae is the smallest family of enteropneust, comprised of individuals that live on the cold, deep-sea floor of Ocean. Seven species of Torquaratoridae have been described from several locations in the global oceans. *Torquarator bullocki* was the first species described and was collected from the Northeastern Pacific at 1901 meters depth (Holland et al. 2005). A new species of Torquaratoridae was collected from the Eastern Pacific from 4 km depth and described as *Tergivelum baldwinae* (Holland et al. 2009). *Allapasus aurantiacus* also gathered from the Eastern Pacific from depth ranged from 2,900 to 3,500 m depth (Holland et al. 2012). A further three species have been discovered, collected and described from the North Atlantic *Yoda purpurata*, *Allapasus isidis*, and *Tergivelum cinnabarinum* (Priede et al. 2012). The newest Torquaratoridae genus and species was collected from the Russian Arctic, Kara Sea from 350 m depth (Osborn et al. 2013). In this paper, we added two new species to the Torquaratoridae family from the Western Arctic, were collected from Baffin Bay. One species *Terminstomo arcticus* gen. & sp. nov. was collected at 505 m depth is characterized by a lack of a heart, and a stomochord that extends from the posterior end of the proboscis through the entire length of the collar. The second species *Allapasus fuscus* sp. nov. collected from 444 meters depth and is characterized by a typhlosole process along the dorsal midline of the collar buccal cavity. A map of the collection location, a dichotomous key to the six Torquaratoridae genera, and a table of diagnostic characters for the existing and new species are provided.

Key words: Taxonomy, Enteropneusta, Torquaratoridae, stomochord, new species, dichotomous key, 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 is scant, but dates back to the Cambrian period (Caron et al. 2013; Cameron 2016; Nanglu et al. 2016). There are 109 extant species described from four families: Harrimaniidae (40 spp.), Spengelidae (20 spp.), Ptychoderidae (42 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 of the coast of California. Since that time an additional six species have been described from five genera: *Allapasus* (Holland et al. 2012), *Coleodesmium* (Osborn et al. 2013), *Yoda* (Priede et al. 2012), *Torquarator* (Holland et al. 2005), and *Tergivelum* (Holland et al. 2009), 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. 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 ressources may be found. They are characterized by a short proboscis, and a wide collar that usually has 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. 2012). This provides them with nearly neutrally buoyancy, an adaptation to a demersal drifting (Priede et al. 2012). They have poorly developed muscles and are delicate and often nearly transparent, though they may be rose, red, or purple in color (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’. In shallow water worms the proboscis complex functions in the circulation and filtration of blood (Balser and Ruppert 1990) and its absence in torquaratorids may be due to the poorly developed muscular system (Osborn et al. 2011) 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 (Holland 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 western Arctic. We also provide a table of the morphological characters that define each of the seven species, and a dichotomous key to the Torquaratoridae genera.

MATERIAL AND METHODS

The details of the two speciments are given, for each respective species, in the treatments below. They were collected by Heike Link onboard the CCGS Amundsen. Specimens were fixed in formalin and shipped back 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.

Masson’s trichrome, Heidenhain’s iron alum hematoxylin or Mallory’s triple stains were used. 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 fucshin for five minutes, then to phosphotungstic / phosphomolybdic acid solution for five minutes, and finally to aniline blue solution for five minutes.

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.

RESULTS

SYSTEMATICS

Phylum Hemichordata Bateson, 1885.

Class Enteropneusta Gegenbaur, 1870.

Family Torquaratoridae Holland et al., 2005.

Diagnosis: The family is defined by a broad, short, and dome shaped proboscis, and wide collar. Their bodies are weak, soft, and semitransparent with length range from 2 cm to 26 cm. Torquaratoridae individuals have a poorly developed muscular system, proboscis skeleton and gill bars. 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 & 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. 5A-C, 6A-K)

Material examined. Holotype, comprising 81 slides of one complete female specimen. The specimen was collected 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 4).The substrate was mud and sand. The specimen was photographed on the deep-ocean floor, with the proboscis extended up into the water (Figure 5A).It broke into two fragments during the collection process (Figure 5B).

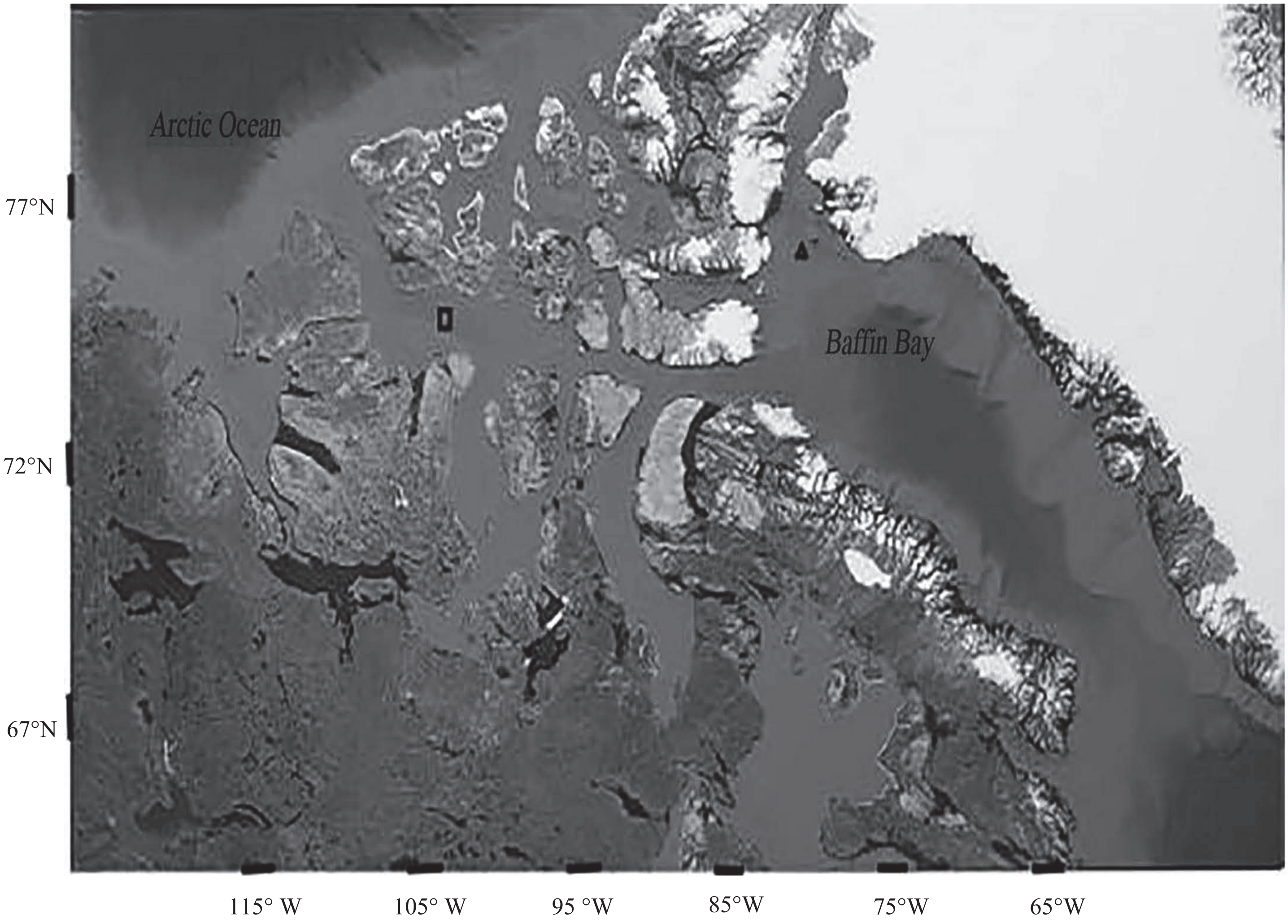

Figure 4. A map of the Canadian Arctic showing the collection locations of *Terminstomo arcticus* (square) (505 m depth), *Allapasus fuscus* (triangle) (444 m depth).

External features (Fig.5 A-C): The total length of the body measured after fixation is 22.1 mm. The proboscis is 3.2 mm long by 5.1 mm wide with a dome shape and a small ventral groove; the collar is 3 mm long by 5.4 mm wide. The trunk is 15.9 mm long. The living holotype color is transparent white anteriorly. The intestine is visible through the body wall and is dark brown.

Paired dorso-lateral ridges (Figure 5A), project from the anterior third of the trunk and some dozen oocytes were seen.

Approximately ten pairs of gill pores occur between the lateral ridges and the dorsal midline (Figure 5C). 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 5A).

Internal features (Fig. 6A-K): The proboscis epidermis has dark staining and glandular cells, below which is a fine subepithelial nervous layer. Connective tissue and sparse muscle fibers occupy the entire proboscis coelom. There is no empty protocoelom. Muscle cells are diffusely and evenly distributed in the proboscis coelom but for a concentration at the center of the proboscis coelom (Figure 6A). 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 6B, 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 6D). 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. A dorsal neurolated cord runs the length of the dorsal collar and under it are paired perihaemal diverticula, which are anterior projections of the trunk coeloms. The septum of the right perihaemal diverticula extends from the right diverticula and connects with the nerve fiber layer of the external wall of the collar (Figure 6D), 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 perihaemal diverticula mesenteries (Figure 6E). The main cavity in *Terminstomo arcticus* is the buccal cavity. In contrast to *Allapasus aurantiacus*, *Terminstomo* arcticus 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 were found in the collar (Figure 6E).

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 continued into the trunk, and is underlined by a dorsal vessel (Figure 6F). 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 6G). Approximately ten pairs of gill pores open to the exterior via the atrial canals (Figure 6G, H). Collagenous gill bars are poorly developed, 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 epidermis at this level of the trunk has a shallow groove that, in transverse section, gives the epidermis an arch shape, and the ventral vessels are well developed in this site (Figure 6G).

The holotype is female. Ovaries are located in the paired dorsal-lateral ridges and open via pores on their proximal sides (Figure 6H). The presence of mature and immature oocytes suggests asynchronous oogenesis. The oocyte of Enteropneusta in general has three main layers (i.e., coelomic epithelium, basement membrane & germinal epithelium) (Hadfield, 1975). A nucleus and nucleolus were present in some oocytes; the largest oocytes had a diameter of approximately

203 µm (Figure 6I). 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. 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 in this site is thin (10 µm) (Figure 6J). The deep ventral groove of the epidermis continues to this level of the trunk (Figure 6K).

Remarks. The internal features of the present form are distinct from the other seven species of Torquaratoridae, in the presence or absence of some features. *Terminstomo* shares with *Allapasus* and *Coleodesmium* a stomochord and glomerulus. The glomerulus of *Allapasus*, *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 that the stomochord is not separated from the gut by a skeleton. The stomochord of *Terminstomo* is unusual in that its most anterior end is in the posterior proboscis. From here it extends posteriorly to the mid-collar. The stomochord of *Allapasus* and *Coleodesmium* extends further anteriorly, and in *Allapasus* it is separated from the gut by a proboscis skeleton. Two characteristics of *Allapasus* that are absent from *Terminstomo* are paired peribuccal vessels in the lateral sides of the collar, and sacculations of a racemose that project downward into the buccal cavity. The pharyngeal lumen of *Allapasus* 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* lack the externalized epidermal pouches of *Allapasus* and 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.

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:

- The presence of 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 the 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.

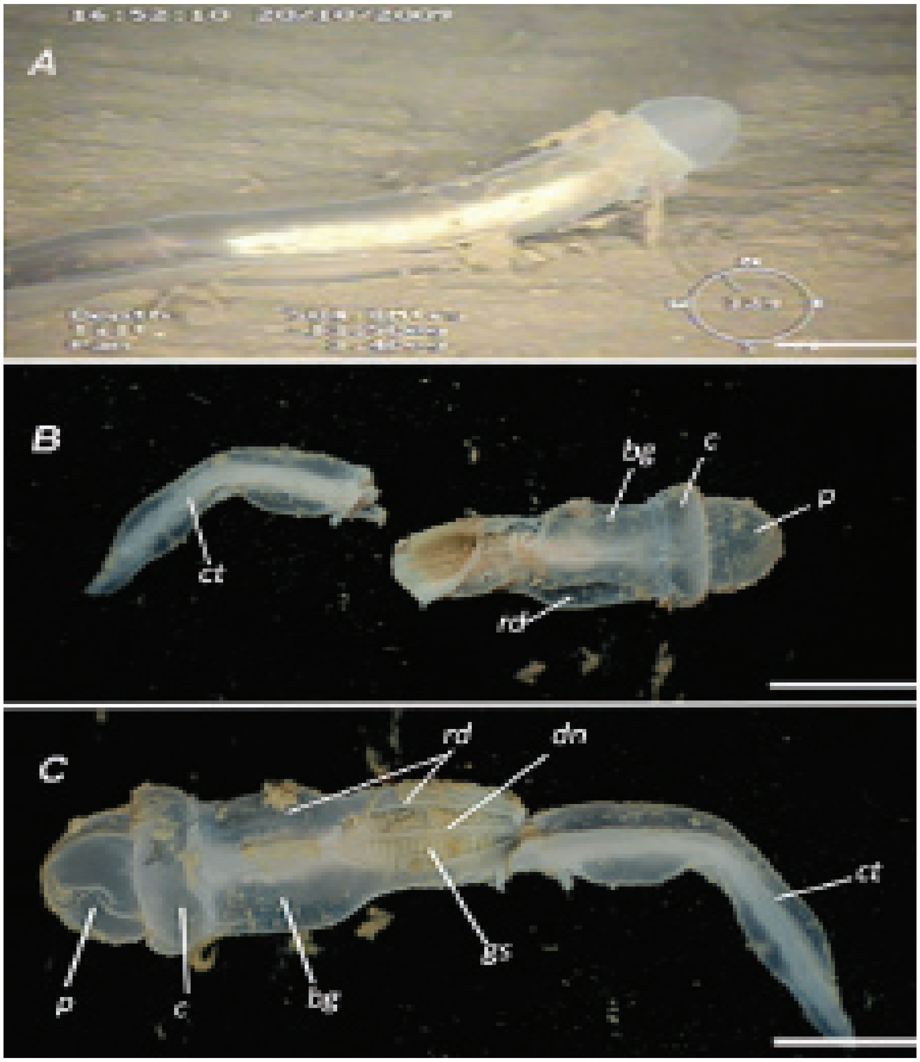

Figure 5. (A) Photograph of a living specimen of *Terminstomo arcticus* n. gen., n. sp. on the deep-ocean floor in lateral view. (B) The holotype was broken into two fragments. (C) The holotype after fixation. Abbreviations: bg, branchiogenital region of trunk; c, collar; ct, caudal region of trunk; dn, dorsal nerve cord; gs, gills; p, proboscis; rd, ridges. Scale bars: 1 cm.(photographed by Pilots: L. Michaud, & P. Massot).

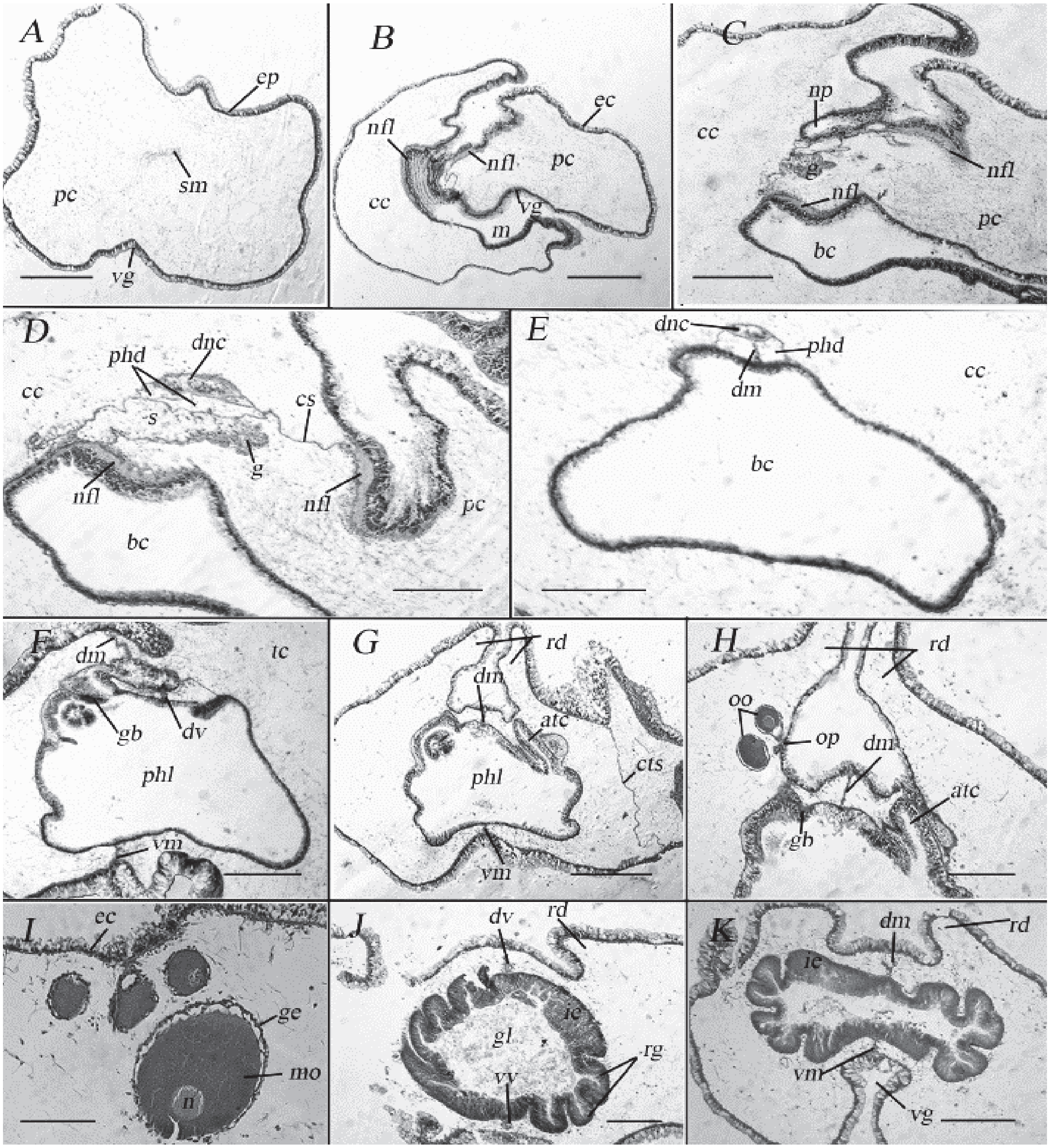

Figure 6. Light micrographs of transverse sections of *Terminstomo arcticus*. n. gen., n. sp. (A) Cross section in the anterior end of the proboscis showing a central sheet of connective tissue and muscles. (B) Proboscis showing the ventral groove, and the conjunction point between the proboscis and the collar. (C) Fuses between the proboscis and the collar forming the posterior neuropil and glomerulus. (D) Posterior of the proboscis and anterior of the collar showing the proboscis complex and the collar septum. (E) Posterior in the collar showing the appearance of the buccal cavity, perihaemal diverticula, and dorsal nerve cord. (F) Anterior trunk showing unseparated pharyngeal lumen. (G) Branchiogenital region of trunk with left and right lateral ridges arising from it, right collar-trunk septum, and gill pores. (H), Oocytes attached the ectodermal of the ridges. (I) The largest mature oocyte with nucleus. (J) Anterior

intestinal region of the trunk showing gut lumen, dorsal and ventral vessels, and shrinking of the 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, perihaemal 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 µm; B, C = 600 µm; D, E, H, J = 1000 µm; I = 150 µm; K = 450 µm.

***Allapasus fuscus* n. genus, n. sp.** JABR & CAMERON

(Figures 7, 8A-G)

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

Material Examined. Holotype, 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 4). 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 (Fig.7): Whole animal with a dark brown body, 29.2 mm long (Figure 7). The proboscis is 3.2 mm long by 3.1 mm wide and is dome-shape with a small dorsal groove. The collar is 2.8 mm long by 3.5 mm wide. The epidermis is transparent and the dorsal nerve cord can be seen in the dorsal midline of the collar. The trunk is 23.2 mm long by 5.1 mm wide in the pharyngeal region and 2.2 mm wide in the intestinal region. A pair of dorsal lateral ridges extend from the anterior trunk to the end of the pharyngeal region and houses the ovaries. The ridges form an envelope around some large externally located oocytes that are a cream color. About nine pairs of gill pores were counted on either side of the dorsal midline of the trunk.

Internal features (Fig. 8 A-G): 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 8A). 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. 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 8B).

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 the paired extensions of the trunk coeloms, the perihaemal diverticula, which form mesenteries between them that envelop a dorsal blood vessel. There are no peribuccal diverticula. 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 8C). 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 8C, 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 8E). 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 the ridges and are most abundant near to the inner (proximal) faces of the ridges (Figure 8F). Externalized ovaries attach to the inner face of the ridge epidermis by a thin stalk (Figure 8F), the largest oocytes diameter is approximately 950 μm. 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 8G). 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 *Allapasus*, and can be distinguished from them by the absence of some characters and the presence others. *A. fuscus* is brown in color whereas *Allapasus aurantiacus* is light orange and *Allapasus isidis* is light yellow (Holland et al. 2012; Priede et al. 2012).

Allapasus fuscus is different from the other two species in that the protocoel is absent, and the stomochord is not separated from the main gut via a proboscis skeleton. In the collar, no peribuccal vessels can be 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 is annelids (i.e., earthworms) and echinoderms provides skeleton support, and an increased surface area for the absorption of nutrients.

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

The defining characters of *Allapasus fuscus* are:

- The protocoel in the proboscis is absent.
- The stomochord is not separated from the main gut because of absent of the proboscis skeleton.
- A typhlosole process extending from the dorsal buccal cavity, resulting in a T-shape in transverse section.
- The peribuccal vessels are absent.
- No externally projecting hepatic sacculations in the collar.

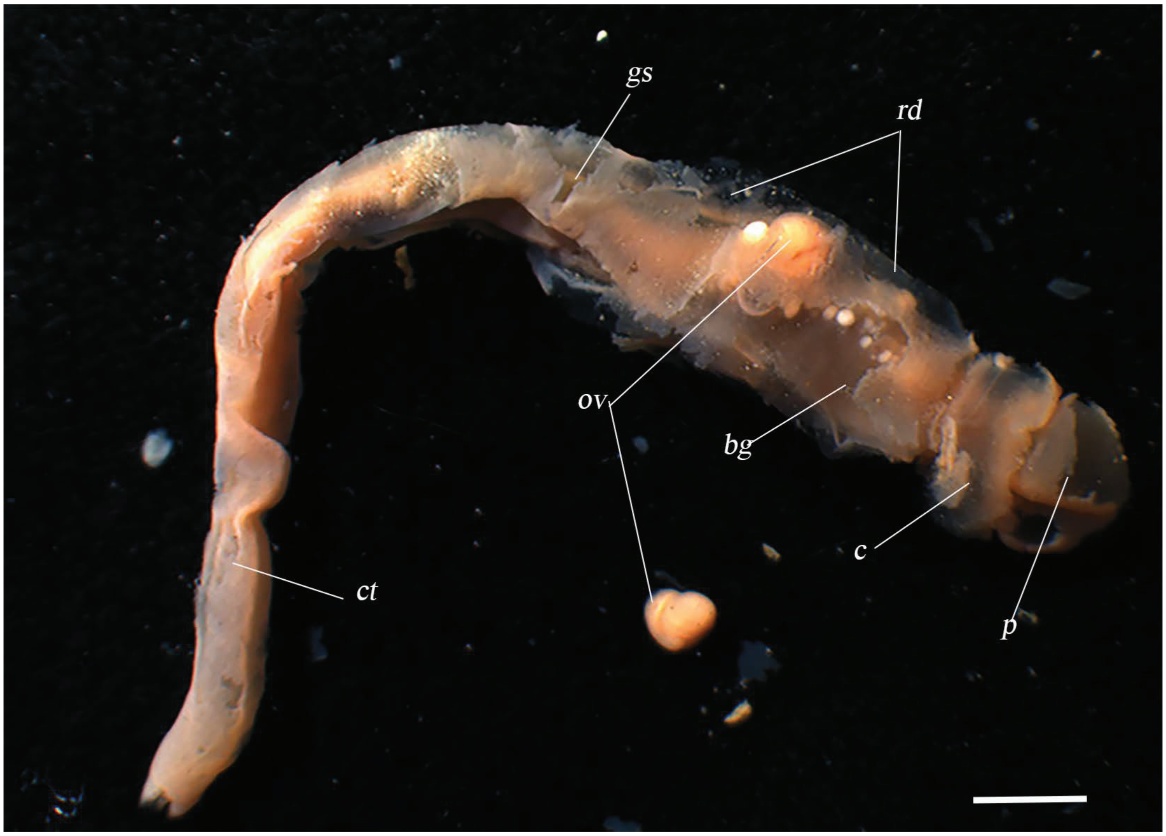

Figure 7. (A) Photograph of a fixation specimen of *Allapasus fuscus* n. sp. from the Eastern Canadian Arctic. Abbreviations: bg, branchiogenital region of trunk; c, collar; ct, caudal region of trunk; gs, gills; ov, ovaries; p, proboscis; rd, ridges. Scale bars: 0.5 cm. (photographed by Jabr, N at Cameron lab).

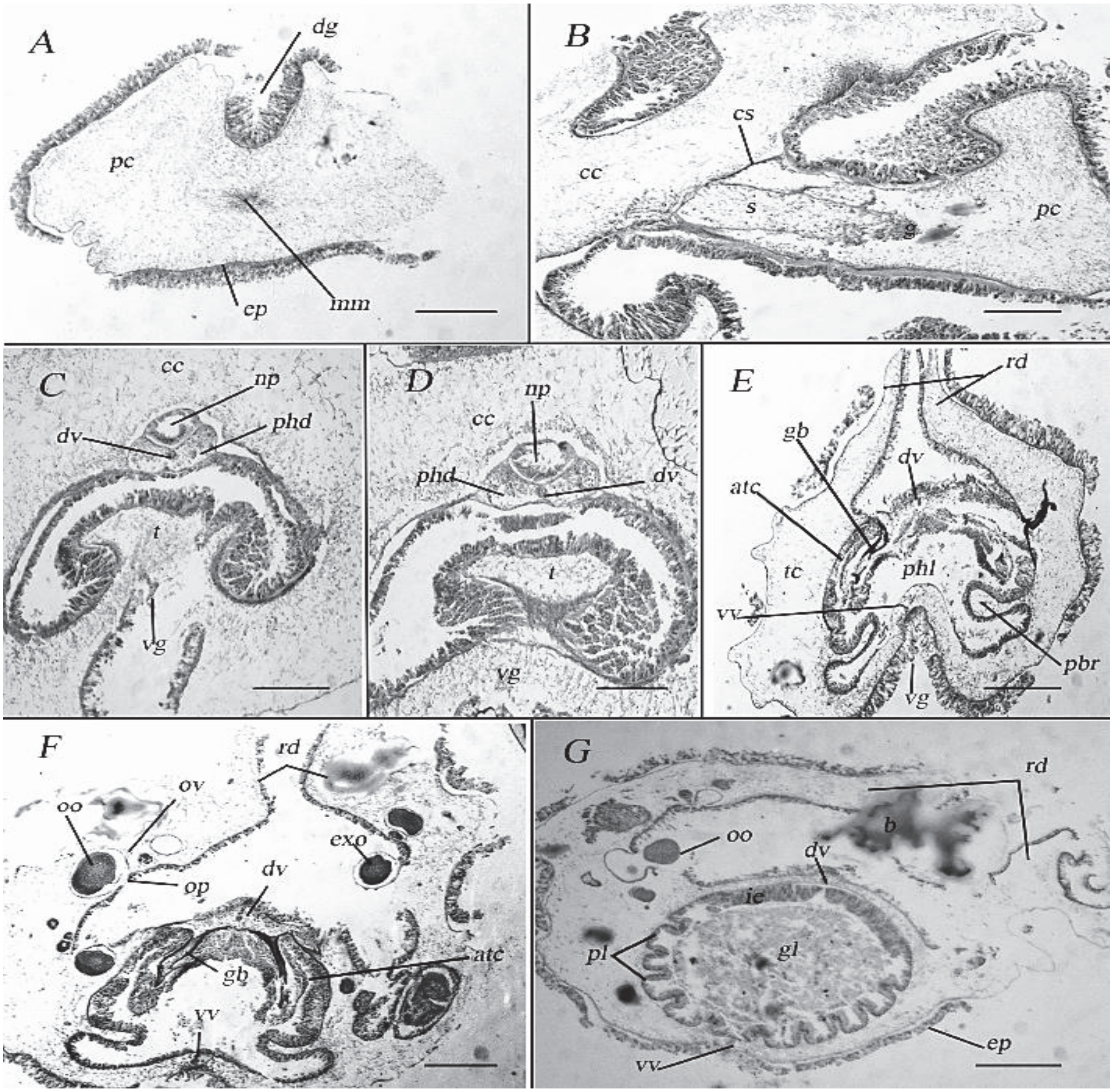

Figure 8. Light micrographs of transverse sections of *Allapasus fuscus* n. sp.: (A) Proboscis with a central sheet of muscles. (B) Posterior part of the proboscis and anterior part of the collar showing the proboscis complex. (C) Mid-collar showing the beginning of the typhlosole process. (D) Mid-collar 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 cleome; 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, perihaemal 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 μm; B= 500 μm; C, F= 1000 μm; D, G= 450 μm; E= 400 μm.

DISCUSSION

Enteropneusts are one of the abundant mega-faunal in several deep sea surface; such as, Australian continental margins and Mid-Atlantic ridge (Anderson et al. 2011; Jones et al. 2013). In the Atlantic, torquaratorids are abundant on the Northern Mid-Atlantic Ridge, three species have been collected from pools of sediment on the Northern Ridge including *Yoda purpurata, Tergivelum cinnabarinum*, and *Allapasus isidis* (Jones et al. 2013). Their length ranged between 12 to 26 centimeters (Osborn et al. 2011; Priede et al. 2012; & Jones et al. 2013). A video survey of the Mid-Atlantic Ridge 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 *Allapasus 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). An Antarctic worm, clearly identified as a torquaratorid based on its wide lips, and a mucous tube which secreted by worm and attached to the body (Halanych et al. 2013). We add to this list a two additional species, *Terminstomo arcticus* and *Allapasus fuscus* from the Western Arctic.

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,) *Allapasus aurantiacus* (Holland et al. 2012), and *Tergivelum baldwinae* (Holland et al. 2009) and (Osborn et al. 2011).

Additional undescribed species are found near Hawaii, Oregon, the Gulf of California, and southern Washington states (Osborn et al. 2011). 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 other 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. 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, but their abundance may suggest that bioturbation caused by feeding and fecal deposition may enhance the benthic micro faunal biodiversity in the deep sea (Jones et al. 2013).

The torquaratorid *Allapasus aurantiacus* is unusual in that it lives in burrow (Osborn et al. 2013, Holland et al. 2012), 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 (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. 2013). 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 be a demersal drifter (Figure 5A).

One of the most notable adaptations of torquaratorids, including *Allapasus fuscus* is the reduction in collagenous structures. *Allapasus fuscus* lacks a proboscis skeleton and the gill bars are poorly developed. This morphology may also 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 nuchal skeleton of acorn worms passes from the proboscis through a ridged neck to the collar, providing skeletal support in muscular burrowing species. The absence of a nuchal skeleton in torquaratorids may be interpreted as a loss, correlated with the abandonment of a burrowing life style. Torquaratoridae is the smallest family of Enteropneusta, and our two new species are the first torquaratoridae that observed, photographed, and collected from the Canadian Arctic, and so we have increased the number of Arctic torquaratoridae to three, and the North America torquaratoridae to four that include the first torquaratoridae genus and species that collected and described by Holland in 2005 Torquarator bullocki. Despite this addition to the value of biodiversity of Canadian water, but we still lack the knowledge of marine biodiversity in Canada's water, which is riche of living marine resources and organisms along three oceans. Canada's oceans face numerous threats, including climate change, overfishing, eutrophication, introduced species, habitat destruction, and chemical loading, and more effort need to be done to obtain a complete baseline of Canadian marine biodiversity of all undiscovered species (Archambault et al. 2010).

4. Conclusion

4.1 MORPHOLOGY:

Terminstomo arcticus is described here as a new genus and species. It is close to the two previous described genus *Allapasus* and *Coleodesmium* by sharing some internal features; such as the presence of a stomochord and glomerulus. *Terminstomo* is distinguished from *Allapasus* and *Coleodesmium* by the absence of proboscis skeleton and a stomochord that does not separate from the main gut. The stomochord moreover terminates in the neck, rather than the proboscis. The second new species *Allapasus fuscus* has a unique structure in the collar region called the typhlosole process. This process emerges downward from the dorsal buccal cavity, which gives the cavity a T-shape in transvers section, similar to that of an earth worm. The three *Allapasus* species have in common a pharyngeal lumen that is divided into a ventral digestive and dorsal branchial region by parabranchial ridges. They also have externalized ovaries that attached to the lateral ridges via thin stalks.

4.2 BEHAVIOUR:

Shallow water acorn worms typically burrow into soft substrates forming temporary or permanent tubes (Smith et al 2005), though some are known to live on the underside of rocks or in kelp holdfasts (Cameron 2005). Some feed from within the confines of the burrow, others extend the proboscis from the burrow to surface deposit feed, and Glandiceps hacksi extends the body from the opening of the borrow (Urata et al. 2012). Deep water torquaratorids do not burrow with one exception; *Allapasus aurantiacus* (Holland et al. 2012). Instead they rest on the sea floor to feed, deposit a fecal casting, and drift to a new feeding site (Priede et al. 2012). This behaviour might explain why the family has a weak muscular system in the proboscis and the collar, and poorly developed collagenous structures (Y-shaped nuchal skeleton and gill bars). Some enteropneust families have direct development (Harrimaniidae), and some have indirect development via a tornaria larva (Ptychoderidae and Spenglidae). The development in Torquaratoridae is unknown, but the large egg size suggest direct development. Torquaratoridae have some unique reproductive adaptations: *Yoda purpurata* (Priede et al. 2012), is a hermaphrodite, members of the genus *Allapasus* have externalized ovaries (*Allapasus aurantiacus* Holland et al. 2012 and *Allapasus fuscus* current study), and *Coleodesmium karaensis* (Osborn etal. 2013) broods the embryos inside sacs on the worms lateral flaps. The reason for these adaptations is unknown.

This study has provided us a great chance to evaluate features that used to distinguish Torquaratoridae species. The generic diagnoses and dichotomous key of the family and its genera are a useful way to define the species and are most likely to be stable. Present and absent of the proboscis complex including the stomochord and the proboscis skeleton, the development of the gonads, collagen, circular and muscular system were the most common and important points that we focused on it during the classification process. Large size of the oocytes of *Terminstomo arcticus* 203 µm, and 950 µm of *Allapasus fuscus* support the belief that torquaratorids that may have a direct development (Holland et al. 2012). This study has showed that some Torquaratoridae species have characters which are unique and distinctive for enteropneusta and Hemichordata, such as, the typhlosole process that extends along the buccal cavity of the collar in the *Allapasus fuscus.* However*,* there remain many characters believe to be diagnostic of the Torquaratoridae family, in the future we hope there will be more collect, improve, and enhance in the taxonomy of this family. Because with the low number of samples, we lost many new and unique features.

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APPENDIX

Table I. 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.

	Terminstomo arcticus*	***Allapasus fuscus****	***Allapasus Isidis*[1]**	***Allapasus aurantiacus*[2]**	***Coleodesmium karaensis*[3]**	***Yoda purpurata*[4]**	***Torquarator bullocki*[5]**	***Tergivelum cinnabarinum*[6]**	***Tergivelum baldwinae*[7]**
Living holotype length	2.21 cm	2.92 cm	13 cm	26 cm & 18 cm (after fixation)	6.3 cm	12 cm	7 cm	12 cm	9-28 cm
Living holotype color	Transparent White	Dark brown	Light yellow	Light orange (anterior) , & light Beige (posterior)	Translucent & lightly lavender Color	Dark reddish purple	Tan (anterior), light blue (posterior)	Cinnabar (anterior), light orange (posterior)	Dark brown (anterior), Beige (posterior)
Proboscis shape	Dome	Short dome	?	Dome	Dome	Smooth Dome	Low dome	?	Shallow rounded dome
Proboscis length	0.32 cm	0.32 cm	?	0.6 cm Fixation	0.9 cm	2 cm	?	?	?
Proboscis width	0.51 cm	0.31 cm	?	1 cm Fixation	1.2 cm	3.5 cm	0.8 cm	?	?
Proboscis groove	Ventral	Dorsal	Ventral	Ventral	Dorsal & ventral	?	?	?	?
Proboscis muscles	Poorly Developed	?	Radially	Radially	Loose mesh partly horizontal	Diffuse	Poorly developed	?	?
Presence & shape of skeleton	No	No	Plate-like	Plate (nearly vertical)	Plate-like	No	Yes	No	No
Anterior & posterior horns	No	No	?	No	No	?	Yes	?	?

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

Table I. Continued.

	Terminstomo arcticus*	***Allapasus fuscus****	***Allapasus Isidis[1]***	***Allapasus aurantiacus[2]***	***Coleodesmium karaensis[3]***	***Yoda purpurata[4]***	***Torquarator bullocki[5]***	***Tergivelum cinnabarinum[6]***	***Tergivelum baldwinae[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	?	?	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, full of vacuolated cells & no detectable lumen	Yes, full of vacuolated cells	Full of vacuolated cells	No	Yes	No	No
Buccal cavity	Yes	Yes	Yes	Yes	Yes	?	Yes	Yes	Yes
Perihaemal Coelom	Yes	Yes	Yes	Yes	Yes	?	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	?	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
Heart	No	No	Yes	Yes	?	No	?	No	No
Number of gill pores	10	9	?	?	Two dozen	?	?	?	30
Coelomopores	No	No	No	No	No	No	?	?	?
Sex	Separated	Separated	Separated	Separated	Separated	Hermaphrodites	Separated	Separated	Separated
Distinctive Characters	A stomochord that terminates in the posterior proboscis	Typhlosole process in the collar & externalized ovaries	Externalized ovaries	Externalized ovaries	Proboscis skeleton has a tubular component ensheathing the collar that has transverse opaque stripe.	No	Anterior & posterior horns	Back veils & right-left buccal muscles.	Back veils & Laterodorsal Fossa in the Proboscis & Right-left buccal muscles.

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

Table II. A dichotomous key to the genera of family Torquaratoridae.

1 A stomochord, glomerulus, and heart are present; externalized ovaries observed; the stomochord separated from the main gut of digestive lumen via the proboscis skeleton-- *Allapasus*

- A stomochord and glomerulus are present, but the heart is absent------------------- 2

2 Part of the proboscis skeleton is a tubular sheath around the collar cord. Externally brooded embryos-- *Coleodesmium*.

3 A proboscis skeleton with a short anterior and posterior horns. A collar with a midventral slit-- *Torquarator*

- The proboscis has a laterodorsal fossa (is a depression or a cavity in the lateral dorsal side of proboscis--- 5

4 Hermaphrodite; lateral lips; nuchal protuberance; lateroventral folds----------------- *Yoda*

5 The trunk has two conspicuous flaps or ‘back veils’ and right-left buccal muscles- *Tergivelum*

6 A stomochord that extends from the mid-dorsal collar anteriorly to the neck; deep ventral groove in the posterior intestinal region of the trunk--------------------------- *Terminstomo*