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'Lophenteropneust' hypothesis refuted by collection and photos of new deep-sea hemichordates

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The deep ocean is home to a group of broad-collared hemichordates—the so-called 'lophenteropneusts'—that have been photographed gliding on the sea floor^{1–8} but have not previously been collected. It has been claimed that these worms have collar tentacles and blend morphological features of the two main hemichordate body plans, namely the tentacle-less enteropneusts and the tentacle-bearing pterobranchs. Consequently, lophenteropneusts have been invoked as missing links to suggest that the former evolved into the latter⁵. The most significant aspect of the lophenteropneust hypothesis is its prediction that the fundamental body plan within a basal phylum of deuterostomes was enteropneust-like. The assumption of such an ancestral state influences ideas about the evolution of the vertebrates from the invertebrates^{9–14}. Here we report on the first collected specimen of a broad-collared, deep-sea enteropneust and describe it as a new family, genus and species. The collar, although disproportionately broad, lacks tentacles. In addition, we find no evidence of tentacles in the available deep-sea photographs (published and unpublished) of broad-collared enteropneusts, including those formerly designated as lophenteropneusts. Thus, the lophenteropneust hypothesis was based on misinterpretation of deep-sea photographs of low quality and should no longer be used to support the idea that the enteropneust body plan is basal within the phylum Hemichordata.

The recently collected enteropneust (Figs 1a, b and 2) is described below as a new family, genus and species in the class Enteropneusta of the phylum Hemichordata.

Diagnoses. *Torquaratoridae* fam. nov.: proboscis and collar each conspicuously broader from side-to-side than in their other dimensions (anteroposterior and dorsoventral); with prominent hepatic caeca, but lacking synapticles.

Torquarator gen. nov.: diagnosis as for family.

Torquarator bullocki n. sp. Description: Living adult 70 mm long and 15 mm wide through collar (smallest length-to-width ratio

known for any adult enteropneust). Northeastern Pacific. Colour in life tan anteriorly, grading into light blue posteriorly, except where large white oocytes and dark grey gut contents show through translucent body wall. Proboscis a low dome with breadth (8 mm) conspicuously exceeding anteroposterior or dorsoventral dimensions (both about 5 mm); includes buccal diverticulum (stomochord) and proboscis skeleton with very short anterior and posterior horns; proboscis base encircled by basiepidermal nerve ring. Collar breadth (15 mm) greater than anteroposterior or dorsoventral dimensions (both about 7 mm); wide mouth at anterior end of collar opens into spacious buccal cavity; collar with midventral slit (Fig. 1b, black arrow), paired periahaemal spaces, and collar nerve cord lacking lumen. Trunk accompanied along entire length by lateral wings (sheet-like folds of body wall) and by dorsal and ventral trunk nerves. Lateral wings curling over dorsal surface of trunk in life, but retracting after fixation. Along anterior third of trunk (Fig. 1b, gt), lateral wings include several hundred separate ovaries containing oocytes of diverse sizes; largest oocytes (about 0.5 mm in diameter) white and visible through body wall (Fig. 1a, b). Pharynx (running through anterior 60% of gonadal region) dorsoventrally flattened without subdivision into respiratory region dorsally and digestive region ventrally. Several dozen pharyngeal gill slits in anteroposterior row on either side of dorsal midline with corresponding gill pores in overlying epidermis. No synapticles joining primary and secondary gill bars. Oesophagus (posterior 40% of gonadal region) subdivided into anterior and posterior zones (thin-walled, dorsoventrally flattened) separated by middle zone (thick-walled, circular in cross-section). Intestine, traversing posterior two-thirds of trunk (Fig. 1b, it) as long hepatic region anteriorly (pleated on either side by several dozen hepatic caeca with overlying epidermis closely following their contours) followed by short posterior region (lacking caeca or obvious anal sphincter). In all body regions, musculature poorly developed; epidermal mucus cells uniformly abundant.

Etymology. *Torquarator* derives from the Latin *torques* (collar) plus *arator* (ploughman) and refers to sediment-harvesting by the collar region. The specific name, *bullocki*, honours Professor Theodore Holmes Bullock, who published his PhD dissertation on

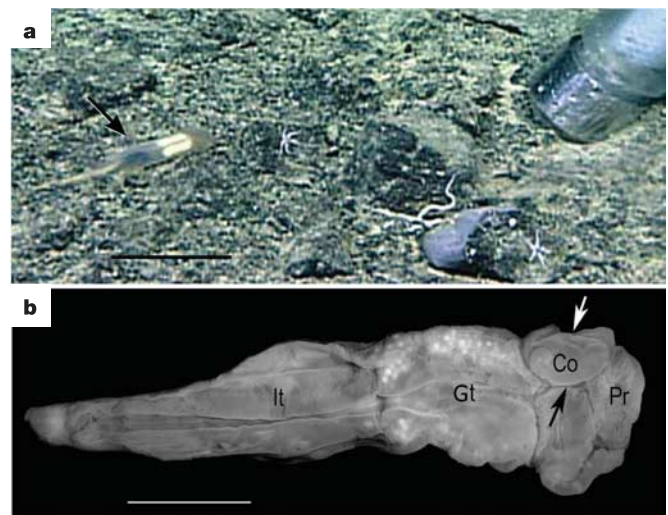


Figure 1 Holotype of *Torquarator bullocki* (Phylum Hemichordata, Class Enteropneusta). **a**, Living specimen (arrowed) crawling on deep-sea floor just before collection by a hose suction sampler (at right). Scale bar, 5 cm. **b**, Ventral view of the same specimen after collection and fixation showing the proboscis (Pr), collar (Co), gonadal trunk region (Gt) and intestinal trunk region (It); the black arrow indicates the midventral slit in the collar, and the white arrow the artefactual compression of the right side of the collar that occurred during capture and fixation. Scale bar, 1 cm.

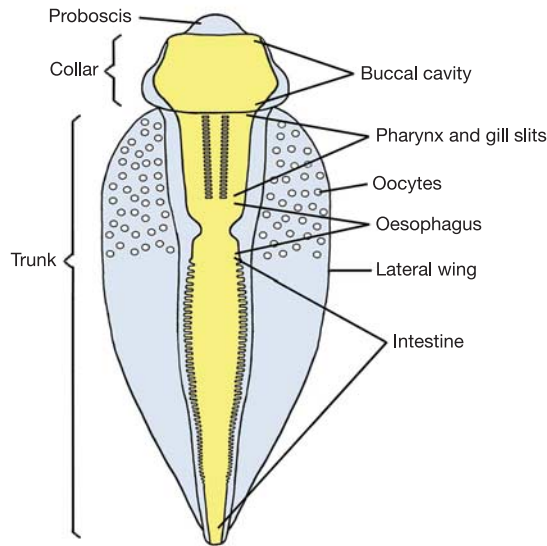


Figure 2 A diagram of *Torquarator bullocki* in dorsal view. The lateral wings are shown unfolded from the dorsal side and extended laterally to permit a clearer view of the course of the digestive tract (in yellow).

enteropneusts in 1940 and has been interested in them ever since. **Holotype.** The holotype (an adult female) was discovered on 27 July 2002, living at a depth of 1,901 m in the northeastern Pacific (42.5° N, 126.7° W) at an oxygen concentration of 1.45 ml l⁻¹, a salinity of 34.4‰, and a temperature of 2.01 °C. The living enteropneust (Fig. 1a) was videotaped for about 10 min, collected with a hose suction sampler, brought to the surface and preserved at once in 4% formalin in sea water. The fixation was appropriate for histology but precluded molecular phylogenetic study. We photographed the intact specimen and then prepared it as 20-µm serial paraffin sections stained with haematoxylin–eosin–toluidine blue.

The sectioned holotype is deposited at the Scripps Institution of Oceanography Benthic Invertebrate Collection as specimen number SIO-BICH2.

The exceptional breadth of the proboscis and collar distinguish the Torquaratoridae from all other enteropneust families (Ptychoderidae, Spengelidae, Harrimaniidae and Saxipendiidae^{15,16}). Analysis of additional characters shows that the Torquaratoridae does not simply represent a previously recognized family with the collar adaptively broadened to facilitate the gathering of deep-sea sediments. Whereas the Torquaratoridae and the Ptychoderidae differ from all other enteropneusts in having prominent hepatic caeca, the former family differs from the latter in lacking synapticles. The family-level status of additional broad-collared deep-sea enteropneusts (Fig. 3, Table 1) remains undetermined until they can be collected.

When observed alive, the holotype of *T. bullocki* was gliding smoothly forwards at about 5 mm min⁻¹, the movement presumably mediated by the coordinated beating of epidermal cilia. While crawling, the worm did not leave behind an obvious fecal trail on the ocean floor, although other deep-living enteropneusts often produce such trails in a meandering (Fig. 3a) and/or spiral pattern (Fig. 3b, e). The ventral (mouth) side was oriented towards a hard substratum of fragmented volcanic glass covered with a very thin layer of soft sediment. The poorly developed body muscles of *T. bullocki* indicate that this species cannot burrow, but it might periodically swim or float above the bottom, as has been observed for another wide-collared deep-sea enteropneust⁸.

The oocyte size and the gut contents permit some inferences about aspects of the reproductive and feeding biology, respectively. It is likely that *T. bullocki*, as is typical of other deep-sea invertebrates with ripe oocytes on the order of 0.5 mm in diameter, produces larvae that are lecithotrophic and develop directly¹⁷. The contents of the intestine include finely granular material, long filamentous bacteria, sponge spicules, holothurian ossicles, diatoms, coccolithophores and benthic foraminiferans. The foraminiferans contain remnants of cytoplasm and may, with the bacteria, constitute a significant energy source for the enteropneust. In addition, the

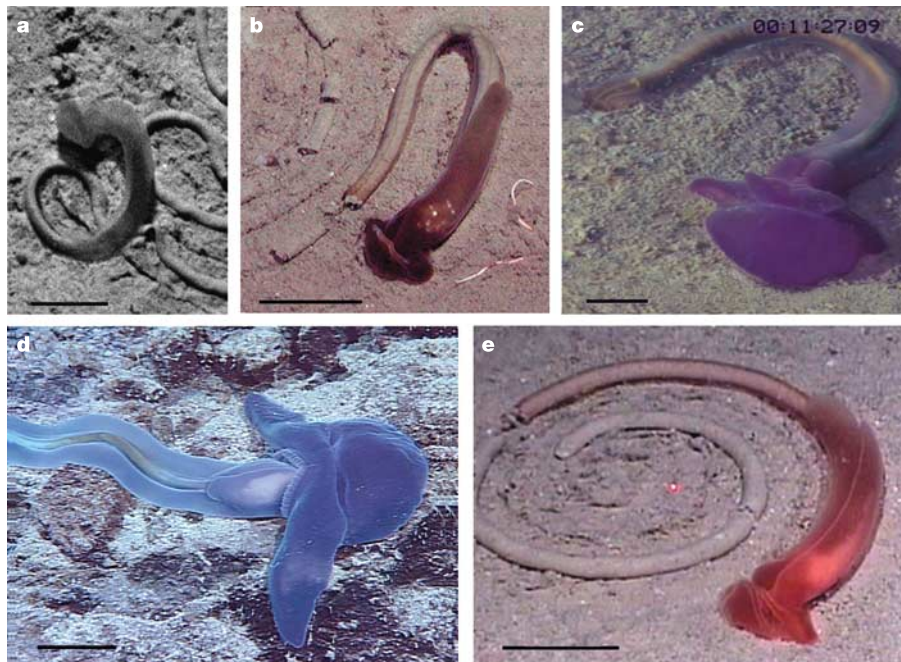


Figure 3 Deep-sea photographs of broad-collared enteropneusts not yet collected and described (depths, longitudes and latitudes are given in Table 1). **a, b**, Western Pacific (**a**) and Eastern Pacific (**b**) forms, with low dome-shaped proboscis and moderately broad collar. **c**, North Atlantic form with high dome-shaped proboscis and moderately broad

collar extended posterodorsally by two conspicuous lobes. **d**, Mid-Pacific form with high dome-shaped proboscis and very broad collar. **e**, A second North Atlantic form with small shield-shaped proboscis and moderately broad collar. Scale bar, 1 cm (**a, c**); 5 cm (**b, d, e**).

Table 1 Photographs of broad-collared, deep-sea (>1,500-m) enteropneusts

Designation	Quality of photo	Depth (m)	Location
Enteropneust ¹	High	4,735	30° S 177° W
Organism ²	Low	3,786	15° N 58° W
Organism ²	Low	3,681	10° N 92° W
No designation ³	Low	2,907	70° S 125° W
Enteropneust ⁴	Low	2,018	31° S 114° E
Enteropneust ⁴	Low	6,725	15° S 175° W
Lophenteropneust ⁵	Low	8,259	6° S 152° E
Lophenteropneust ⁵	Low	8,254	12° S 166° E
Lophenteropneust ⁶	Medium	5,160	12° N 159° W
Enteropneust ⁷	Medium	5,099	14° N 127° W
Enteropneust ⁸	Low	2,040	21° S 167° E
Enteropneust (Fig. 3a)	High	1,670	46° S 174° E
Enteropneust (Fig. 3b)*	High	2,715	43° N 127° W
Enteropneust (Fig. 3c)	High	3,000	53° N 35° W
Enteropneust (Fig. 3d)†	High	3,036	19° N 156° W
Enteropneust (Fig. 3e)	High	2,355	53° N 35° W

The table describes previously published photographs and those in Fig. 3; it omits deep-living enteropneusts with collars approximately circular in cross-section (*Saxipendium coronatum*¹⁶, *Glandiceps abyssicola*²² and undescribed^{23–25}). *Six similar-looking enteropneusts were photographed on different dates at 36° N 123° W at depths between 3,200 and 3,498 m. †A similar-looking enteropneust was photographed at 34° N 121° W at a depth of 1,960 m.

pharynx contained four acol flatworms, evidently commensals, each about 1 mm long, and the post-hepatic intestine contained two intact harpacticoid copepods, possibly also commensals.

From an evolutionary point of view, our most significant finding is that the conspicuous width of the collar of *T. bullocki* is not due to the presence of tentacles. This species is therefore certainly not a lophenteropneust in the sense intended by Lemche⁵. This raises the question as to whether any of the enteropneusts visible in deep-sea photographs are actually lophenteropneusts. We therefore examined all of the photographic evidence, both published and unpublished (Fig. 3, Table 1). We found that photographs of low to moderate quality are inadequate to demonstrate the presence or absence of collar tentacles. Conversely, none of the high-resolution photographs with the potential to resolve collar tentacles ever showed such structures. Additionally, one observer in a submersible, who obtained a close view (but no photographs) of deep-sea enteropneusts, saw no tentacles¹⁸. In sum, there is no evidence that lophenteropneusts exist as originally described. They can be removed from the list of provocative evolutionary intermediates (although the evolutionary model they engendered—namely enteropneusts giving rise to pterobranchs—might still turn out to have merit on other grounds¹⁴). Although the lophenteropneust hypothesis resulted from a misinterpretation of low-resolution photographs, it has been a valuable stimulus for research on deep-sea hemichordates^{19–21}. □

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Ancient co-speciation of simian foamy viruses and primates

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Although parasite–host co-speciation is a long-held hypothesis, convincing evidence for long-term co-speciation remains elusive, largely because of small numbers of hosts and parasites studied and uncertainty over rates of evolutionary change^{1–5}. Co-speciation is especially rare in RNA viruses, in which cross-species transfer is the dominant mode of evolution^{6–9}. Simian foamy viruses (SFVs) are ubiquitous, non-pathogenic retroviruses that infect all primates^{10,11}. Here we test the co-speciation

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