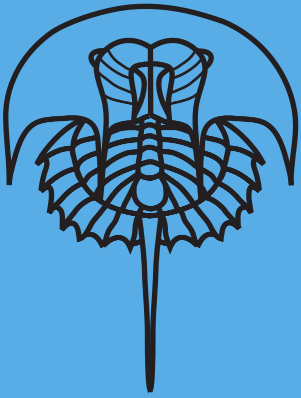

# TREATISE ONLINE

## Number 109

# Part V, Second Revision, Chapter 2: Class Enteropneusta: Introduction, Morphology, Life Habits, Systematic Descriptions, and Future Research

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2018

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

# PART V, SECOND REVISION, CHAPTER 2: CLASS ENTEROPNEUSTA: INTRODUCTION, MORPHOLOGY, LIFE HABITS, SYSTEMATIC DESCRIPTIONS, AND FUTURE RESEARCH

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## Class ENTEROPNEUSTA Gegenbaur, 1870

[*nom. correct.* Haeckel, 1879, p. 469 *pro* Enteropneusti Gegenbaur, 1870, p. 158]

Free living, solitary, worms ranging from lengths of less than a millimeter to 1.5 meters; entirely marine; body tripartite, with proboscis, collar, and trunk; proboscis coelom contains heart-kidney-stomochord complex; preoral ciliary organ posterior-ventral; collagenous Y-shaped nuchal skeleton extends from proboscis through neck before bifurcating into paired horns in collar; paired dorsal perihaemal coeloms associated with collar dorsal blood vessel; anterior trunk pharynx perforated with paired gill slits that connect via atria to external gill pores; mesocoel ducts connect collar coeloms to first pair of gill pores atria; larvae possess locomotory ciliated band (telotroch), and when tornaria present, apical plate retractor muscle. *Cambrian (Miaolingian, Wuliuan)–Holocene* (extant): worldwide.

The class Enteropneusta is differentiated among four living families: the Harrimaniidae, Spengelidae, Ptychoderidae, and Torquaratoridae, based in large part on the structure of the heart-kidney coelomic complex, gills, gonads, liver sacs, and diverticula of the coelomic compartments. The modern families are a crown group clade with respect to the Cambrian fossil stem group, which includes *Oesia disjuncta* and *Spartobranchus tenuis* (see p. 12).

## MORPHOLOGY

The acorn worm body is arranged into an anterior proboscis, a collar, and a posterior trunk (Fig. 1). Body length can vary from less than a millimeter (Worsaae & others, 2012) to 1.5 meters (Spengel, 1893). The proboscis is muscular and its epidermis replete with sensory, ciliated, and glandular cells (Benito & Pardos, 1997). Acorn worms deposit-feed by trapping sediment in mucus and transporting it to the mouth with cilia. A pre-oral ciliary organ on the posterior proboscis (Brambel & Cole, 1939) (Fig. 2.1) directs the food-laden mucous thread into the mouth (Gonzalez & Cameron, 2009). The proboscis coelom contains a turgid stomochord (Fig. 1, Fig. 2.2a), an anterior projection of the dorsal collar buccal cavity that consists of vacuolated cells arranged around a central ciliated cavity and encapsulated in a collagen sheath (Welsch & Storch, 1970). The result is a rigid structure against which the pericardium (heart) compresses the intervening blood sinus so that urine can be forced across the glomerulus (kidney) into the proboscis coelom (Balser & Ruppert, 1990). The stomochord is not a homolog of the chordate notochord (Satoh & others, 2014). The right protocoelom is small or absent, and the left coelom is dominant and extends a ciliated duct, which is lined with nephridia (mesothelial monociliated podocytes and myocytes) to the exterior via

Cameron, Christopher B. 2018. Part V, Second Revision, Chapter 2: Class Enteropneusta: Introduction, morphology, life habits, systematic descriptions, and future research. Treatise Online 109:1–22, 8 fig.

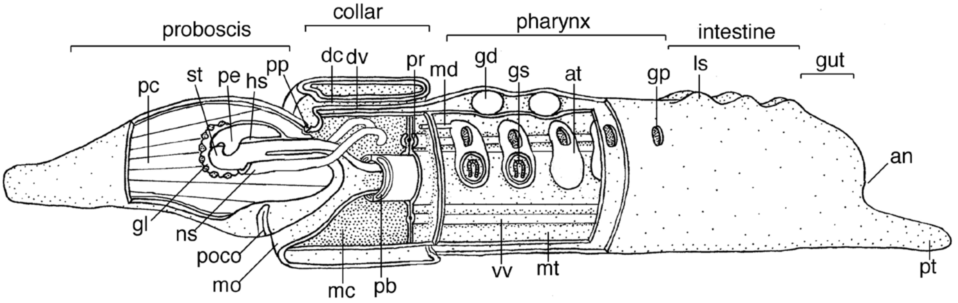


FIG. 1. Illustration of a generalized morphology of an enteropneust. Anus (*an*), atrium (*at*), dorsal nerve cord (*dc*), dorsal blood vessel (*dv*), gonad (*gd*), filtration glomerulus (*gl*), gill pore (*gp*), gill slit (*gs*), heart sinus (*hs*), liver sacs (*ls*), mesocoel (*mc*), paired mesocoel ducts (*md*), mouth (*mo*), metacoels (*mt*), Y-shaped nuchal skeleton (*ns*), peribuccal coeloms (*pb*), protocoel (*pc*), pericardium (*pe*), ventral post-anal tail (*pt*), preoral ciliary organ (*poco*), urinary pore (*pp*), perihaemal coeloms (*pr*), stomochord (*st*), and ventral blood vessel (*vv*) (adapted from Cameron 2005, fig. 1).

a left dorsal lateral urinary, proboscis pore (RUPPERT & BALSER, 1986) (Fig. 1). There is extensive inter- and intraspecific variation in the form of this proboscis heart-kidney-coelom complex (DELAND & others, 2010). The stomochord is supported ventrally by a collagenous Y-shaped nuchal skeleton (Fig. 1, Fig. 2.2a–b). The skeleton extends posteriorly through the neck and bifurcates into paired horns in the collar (SPENGEL, 1893; HORST, 1939; EZHOVA & MALAKHOV, 2009).

The collar lip forms the mouth anteriorly, and its interior is the buccal cavity (Fig. 1). In some species, the anterior lip is muscular and flexible, adept at guiding sediment laden strings of mucus from the proboscis into the mouth or rejecting them over the lip and onto the collar. The collar epidermis is usually differentiated into histologically distinct zones of transverse bands of numerous gland cells and dense bands of cilia (BENITO & PARDOS, 1997; HORST, 1939), with distinct mucin and glycoprotein secretory patterns (SIMAKOV & others, 2015). The acorn worm nervous system is an epidermal plexus with two longitudinal intraepidermal nerve cords in the trunk and a neurulated cord in the collar (BULLOCK, 1940; KNIGHT-JONES, 1953). Sensory cells, ganglion cells, interneuronal junctions, and motor innervation are arranged diffusely (BULLOCK, 1940; BENITO & PARDOS, 1997). The collar cord is intraepithelial even where the epithelium containing the nerves becomes internalized, and most commonly has paired, parallel, and discontinuous lacuna that are lined with cilia. There is no central nervous system. The collar cord is a simple conduction pathway (CAMERON & MACKIE, 1996) and is aligned with the perihaemal muscles, suggesting a role in the rapid contraction of the proboscis (RUPPERT, 2005). This cord is unlike the hollow, neuroepithelium found in the rays of echinoderms, or the hollow, neural tube of chordates (BULLOCK, 1940; CAMERON & MACKIE, 1996; RUPPERT, 2005). Paired diverticula of the trunk coeloms, called perihaemal and peribuccal coeloms, project anteriorly into the collar (Fig. 1). Paired mesocoel ducts connect the collar coeloms to the first pair of gill pore atria in the anterior trunk (Fig. 1).

The acorn worm trunk bears middorsal and midventral longitudinal grooves that correspond to the location of longitudinal nerves and blood vessels (PARDOS & BENITO, 1990) (Fig. 1). The dorsal and ventral nerve cords are connected anteriorly by a circumpharyngeal ring (BULLOCK, 1940; KAUL-STREHLOW & others, 2015). The ventral cord is the fastest conducting cord due to its proximity to the large ventral longitudinal muscles (PICKENS, 1970; CAMERON & MACKIE, 1996). The trunk is differentiated into regions along its length that correspond to the specializations of the gut. The anterior region bears paired dorsolateral series of gills, followed by an esophagus, and an intestine that terminates at an anus (Fig. 1). The gill slits, demarcated by a series of M-shaped collagenous gill bars, are connected to the outside pores by atrial cavities, akin to those of cephalochordates. The ciliated bars pump water through the pharynx, slits, and pores, removing food particles from suspension (Cameron, 2002a; Gonzalez & Cameron, 2009). Support for the hypothesis that gills are a deuterostome plesiomorphy are shared patterns of genes expressed during gill and pharynx development and the organization of these genes in synteny in acorn worms and vertebrates (Gillis, Fritzenwanker, & Lowe, 2012; Simakov & others, 2015). The food and mucus are then transported down the gill bars to the ventral gut, concentrated into a mucous food cord, and then transported posteriorly through the esophagus. Iodine$^{125}$ binding experiments suggests that an endostyle function may reside in the entire pharyngeal lining of Enteropneusta, and in *Schizocardium* Spengel, 1893, an epibranchial ridge is organized into zones of cells, reminiscent of the chordate endostyle (Ruppert, Cameron, & Frick, 1999; Ruppert, 2005; see also Satoh & others, 2014) (Fig. 2.3). The muscular esophagus functions to eliminate excess water from the food cord as it passes to the intestine. Anteriorly, the intestine is usually darkly pigmented. It is a simple tube except in *Schizocardium* and the family Ptychoderidae, in which it develops dorsally projecting rows of hepatic sacs, presumably to deal with a diet of heavy sediment. Gonads occur along the pharyngeal region, and in the family Ptychoderidae, they develop in external paired longitudinal ridges or wings. A few species have a curious pygochord structure in the posterior ventral trunk that Willey (1899) suggested may be a homolog to the chordate notochord. It is comprised of vacuolated cells positioned between the posterior ventral trunk mesenteries (Willey, 1899; Spengel, 1903; Uribe & Larrain, 1992; Miyamoto & Saito, 2007) or intestine (Horst, 1939). Punnett (1906) suggested that the structure may be a vestigial collateral intestine, which may instead function to support the fragile trunk as it projects from the burrow to eject fecal sediment. Distinct protuberances characterize the epidermis of the acorn worm trunk. These are formed by secretory and sclerocyte cells that occlude extracellular spaces, where microscopic calcium carbonate ossicles develop. In *Ptychodera* (Fig. 2.4a) and *Saccoglossus* (Fig. 2.4b), the ossicles form a polycrystalline aggregate of laminar layers, with perforations that are comparable to the echinoderm stereome (Cameron & Bishop, 2012). The functions of the pygochord, and the ossicles are unknown.

## DEVELOPMENT AND REPRODUCTION

The sexes are separated except for *Yoda purpurata* Priede & others, 2012 which is a hermaphrodite (see Priede & others, 2012). Fertilization is external (Burdon-Jones 1951; Lowe & others 2004) although vivipary is known for *Xenopleura vivipara* Gilchrist, 1925, and the deep-sea *Coleodesmium karaensis* Osborn & others, 2013, which broods their embryos in sacs that connect to a gonadal wing by a narrow stock (Osborn & others, 2013). In most species, eggs are released in a jelly coating that breaks down following fertilization (Colwin & Colwin, 1954). All subsequent development occurs in the seawater. Cleavage is holoblastic, radial, and more or less equal. Cell fates and axis specifications are in most respects similar to that of an echinoderm (Henry, Tagawa, & Martindale, 2001). A coeloblastula is followed by gastrulation by invagination. The blastopore is located posteriorly but closes before a new anus and mouth are formed (Burdon-Jones, 1952; Colwin & Colwin, 1953). The fertilization envelope weakens and ruptures, releasing ciliated, swimming embryos by late gastrula. The organization of the coelomic sacs is comparable to echinoderms. The ambulacrarian coeloms are organized anterior to posterior as

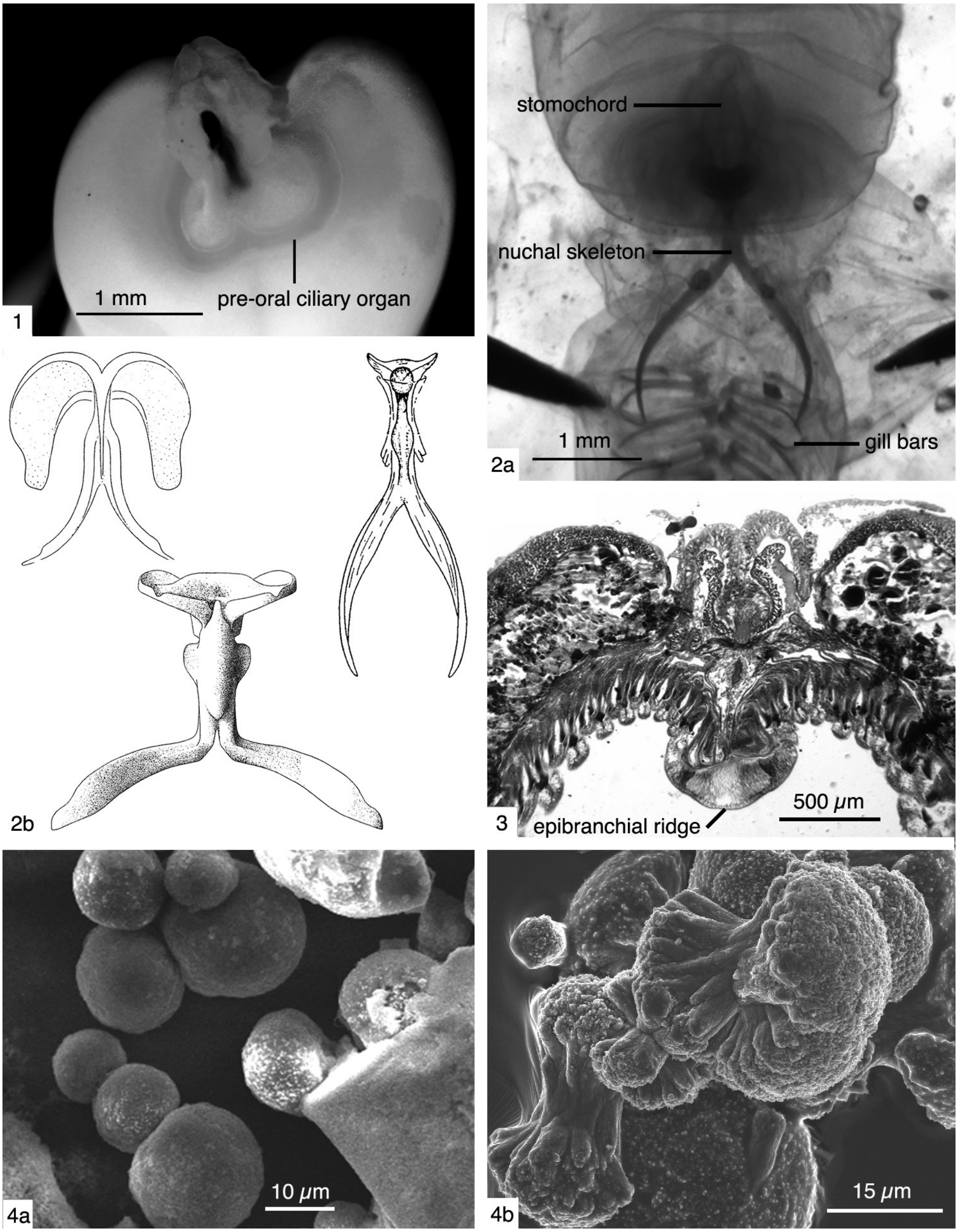


Fig. 2. Acorn worm anatomy. *1,* Pre-oral ciliary organ of *Protoglossus graveolens* Giray & King, 1996; *2a,* stomochord, nuchal skeleton, and gill bars of *P. graveolens; 2b,* illustrations of nuchal skeletons, in clockwise order, *Protoglossus koehleri* (Caullery & Mesnil, 1900), *Saccoglossus ruber* Tattersall, 1905, and *Balanoglossus hydrocephalus* Horst, 1940; *3,* epibranchial ridge of *Schizocardium peruvianum* Spengel, 1893; *4a,* ossicles of *Ptychodera flava* var. Eschscholtz, 1825, Galapagos; *4b,* ossicles of *Saccoglossus bromophenolosus* King, Giray, & Kornfield, 1994 (all, new).

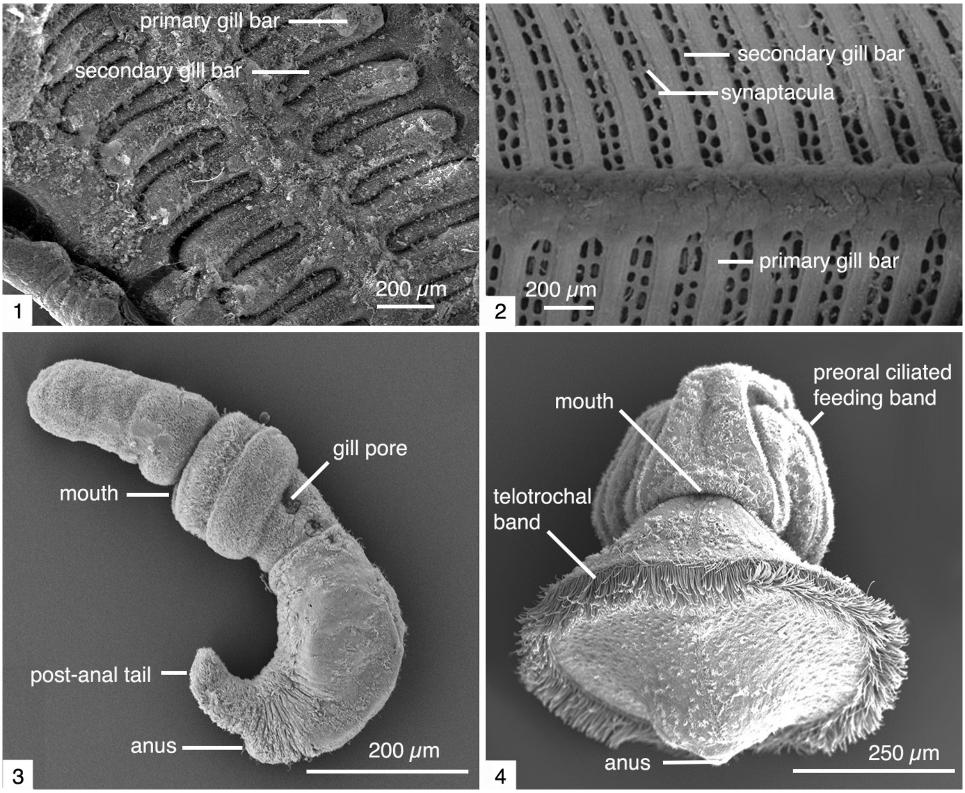


FIG. 3. SEM photos of details. *1,* gill region of *Harrimania planktophilus* CAMERON, 2002b; *2,* gill region of *Ptychodera* sp.; *3, Saccoglossus kowalevskii* AGASSIZ, 1873 at the three-gill pore stage, showing a typical harrimaniid juvenile post-anal tail; *4,* posteriofrontal view of a tornaria larva of *Schizocardium* sp., showing the swimming telotrochal band (all, new).

paired protocoel, mesocoels, and metacoels (CRAWFORD & CHIA, 1978). They develop as independent pouches from the archenteron by enterocoely (KAUL-STREHLOW & STACH, 2013). Reports of schizocoely have not been substantiated (HADFIELD, 1975). GEMMILL (1914) provides a thorough comparative study of coelomogenesis in the asteroid (starfish), *Asterias rubens* LINNAEUS, 1758 and an enteropneust (summarized in CAMERON, 2005).

Harrimaniid worms (e.g., *Saccoglossus*) develop from a large, yolky egg to a ciliated, non-feeding larva with a telotrochal band and apical tuft that allows for a brief swimming and exploratory period (COLWIN & COLWIN, 1953). Following settlement, the juvenile worm has a ciliated, adhesive, post-anal tail (Fig. 3.3) that allows for rapid forward and reverse locomotion, adhesion, and release (BURDON-JONES, 1952; BURDON-JONES 1956; CAMERON, 2002b; STACH & KAUL, 2011) that may be a homolog to the pterobranch stalk (BURDON-JONES, 1952; HYMAN, 1959; LESTER, 1985; CAMERON, 2005). Ptychoderid worms (e.g., *Ptychodera*) shed small transparent eggs. Development is rapid and indirect via a tornaria larva that resembles an echinoderm auricularia (MORGAN, 1891; GEMMILL, 1914; GISLÉN, 1930; TAGAWA & others, 1998; URATA & YAMAGUCHI, 2004) (Fig. 3.4). These diplurula larvae are delicate and transparent with a preoral ciliated feeding band (Fig. 3.4) that creates an upstream feeding current using monociliated cells (MORGAN, 1891;

Strathmann & Bonar, 1976), and a perioral ciliated band that manipulates and conveys food into the esophagus (Lacalli & Gilmour, 2001). The free-swimming, feeding tornaria are able to turn due to a band of multiciliated cells that comprise the locomotory telotroch (Fig. 3.4), an acorn worm innovation. The tornaria apical plate retractor muscle (and associated coughing behavior) (Morgan, 1891) is another acorn worm larval apomorphy. Tornaria may persist in the plankton for months before metamorphosis and settlement to a suitable juvenile worm habitat. The larval body elongates differentiating the three body regions and organs. The larval apical tuft, nervous system, and feeding band are lost, followed by the telotroch band. The gills develop as out-pockets of the gut that open to the exterior by paired dorsolateral pores. Nothing is known of torquaratorid development, but the exceptionally large egg size (Osborn & others, 2012; Priede & others, 2012) hints that development is direct, via a loss of a feeding tornaria, parallel to the ontological loss of the larva in the line to modern harrimaniids.

Asexual reproduction by fragmentation is widespread among enteropneusts, including ptychoderids (Gilchrist, 1923; Packard, 1968; Miyamoto & Saito, 2010; Humphreys & others, 2010), a spengelid (Urata, Iwasaki, & Ohtsuka, 2012), and the minute harrimaniid *Meioglossus psammophilus* Worsaae & others, 2012, which lacks males and reproduces by paratomy. Regeneration is particularly well developed in the ptychoderids, a group especially susceptible to breakage due to their larger and fragile bodies. The posterior fragments are particularly good at regeneration, although some experimentally bisected animals can regenerate new individuals from both anterior and posterior fragments (Willey, 1899; Dawydoff, 1909, 1948; Rao, 1955; Tweedell, 1961; Packard, 1968; Petersen & Ditadi, 1971; Rychel & Swalla, 2009; Humphreys & others, 2010; Miyamoto & Saito, 2010). The cells that participate in blastema formation and morphogenesis during regeneration have not been identified (Rychel & Swalla, 2009; Miyamoto & Saito, 2010).

## LIFE HABITS

Acorn worms are exclusively marine and usually burrow into the sand or mud or are associated with the underside of rocks, although species have also been found entangled in kelp holdfasts (Ritter, 1900). To burrow, they penetrate the sediment using muscular peristaltic contractions of the proboscis and transport the sediment using the ciliated epidermis of the proboscis and collar. Burrow structure varies greatly. They may be Y-shaped, with one arm forming a feeding funnel (Duncan, 1987), U-shaped (Rao, 1954), coiled (Burdon-Jones, 1950) (Fig. 4.1), sinuous, irregular (Brambel & Goodhart, 1941; Knight-Jones, 1953), poorly defined (Burdon-Jones, 1956) or absent for animals that occupy interstitial spaces (Cameron, 2002b; Worsaae & others, 2012). Most acorn worms form mucus-lined burrows (Fig. 4.1) that smell of haloindols or brominated phenols (Higa, Fujiyama, & Scheuer, 1980; Giray & King, 1997; Woodin, Walla, & Lincoln, 1987). In the absence of a burrow or in response to stress, a mucous tube may be produced (Burdon-Jones, 1952; Halanych & others, 2013). The antibiotic properties of the phenols stabilize the sediment around the burrow (Cedhagen & Hansson, 2013) and likely repel predators, such as gastropods on the coasts of Japan and South Carolina that have been known to nip the tail from defecating ptychoderids (K. Tagawa, E. E. Ruppert, personal communications). *Saxipendium* Woodwick & Sensenbaugh, 1985 cling to rocky outcroppings near hydrothermal vents (Woodwick & Sensenbaugh, 1985), and members of the deep-sea family Torquaratoridae reside on the seafloor.

Enteropneusta are mucociliary feeders, that collect their food particles on the proboscis with abundant mucin and glycoprotein secretions and transport them to

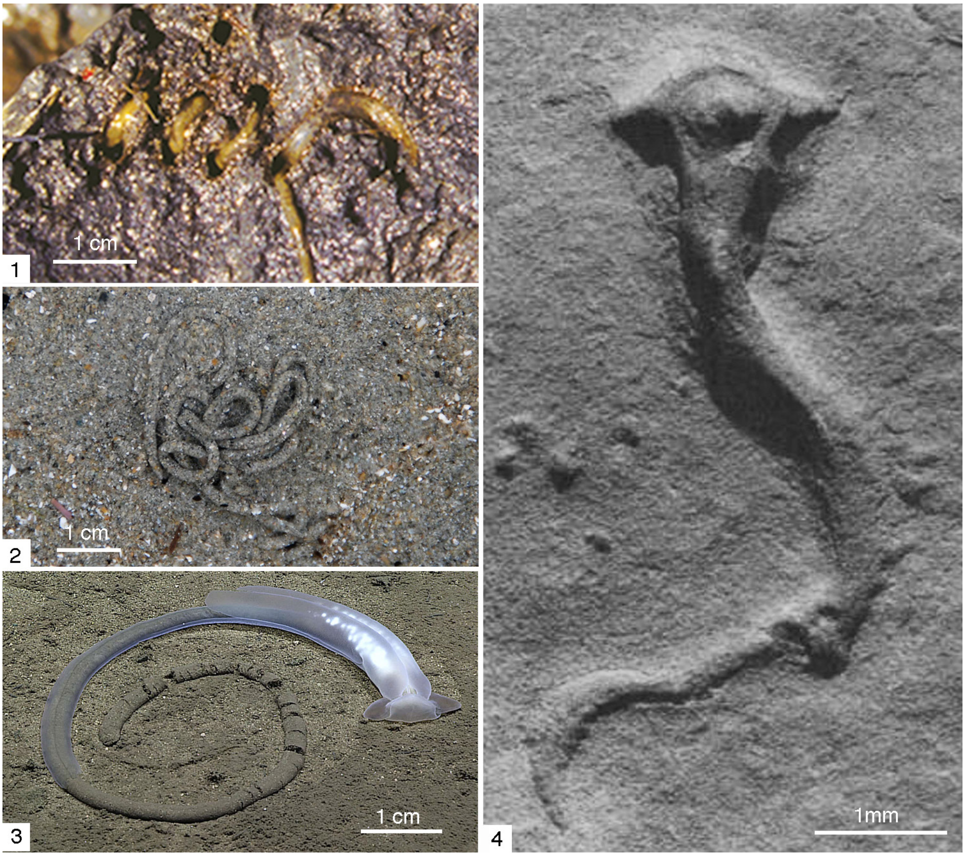


Fig. 4. Enteropneust traces. *1,* Helical-shaped burrow of *Saccoglossus bromophenolosus* King, Giray, & Kornfield, 1994, Willapa Bay, Washington, USA, exposing the brominated lining of the burrow (new, photo, M. K. Gingras); *2,* fecal casting of *Saccoglossus pusillus* Ritter, 1902 (new); *3,* fecal trail of *Tergivelum* sp? (photo courtesy of NOAA Office of Ocean Exploration and Research); *4,* resting trace of torquaratorid enteropneust (Twitchett, 1996, fig. 2.1).

the mouth with cilia (Barrington, 1940; Knight-Jones, 1953; Burdon-Jones, 1962; Thomas, 1972). Many are facultative filter feeders that pump water into the mouth, then through the pharynx and gills slits using cilia that line the gill bars (Barrington, 1940; Knight-Jones, 1953; Burdon-Jones, 1962; Cameron, 2002a; Gonzalez & Cameron, 2009). Balanoglossids ingest copious amounts of sand, in some cases forming feeding funnels at the mouth of the burrow system. *Saccoglossus* extend a long proboscis from the burrow to exploit surface sediments and marine snow, sometimes forming feeding rosettes. To defecate, the worm protrudes its posterior from the burrow system and ejects the fecal casting with rapid force. These surface castings are often the best clue that acorn worms reside below the sediment surface (Fig. 4.2).

Torquaratorids have evolved several unique traits for life in the deep sea. Most notably, they are often brightly colored and, rather than residing in burrows, they are epibenthic deposit feeders (Fig. 4.3). The collar of many species is elongated into lips that are used to collect and transport sediment to the mouth (Holland & others, 2005; Osborn & others, 2012; Priede & others, 2012). Their castings form tightly wound spiral coils to wandering, switchback loops on the sea floor (Bourne & Heezen

1965; SMITH, HOLLAND, & RUHL, 2005) (Fig. 4.3). Trace fossils may provide some indirect evidence of acorn worms in the fossil record. See MALETZ (2014) for a review of trace fossils with possible enteropneust affinities, including ones of a spiral form. Many typical meandering deep-water trace fossils (e.g., graphoglyptid traces, *Nereites* ichnofacies) may be explained as mucus-coated fecal casts produced by enteropneusts. The gut contents act as ballast, and when voided, the worms may drift through the demersal zone (SMITH, HOLLAND, & RUHL, 2005; OSBORN & others, 2012; HOLLAND, KUHNZ, & OSBORN, 2012). This adaptation allows for economical, long-distance movements to a new feeding site in an environment where food is typically heterogeneous and limited (OSBORN & others, 2012; JONES & others, 2013).

Two species of *Glandicepts* SPENGEL, 1893 from the west Pacific swim by flattening the trunk in a dorsoventral aspect, and then undulate and turn as the worm ascends to the sea surface (SPENGEL, 1909; YOSHIMATU & NISHIKAWA, 1999; URATA, IWASAKI, & OHTSUKA, 2012). This behaviour does not appear to be coordinated with spawning (URATA, IWASAKI & OHTSUKA, 2012). An unusual feature of some ptychoderids is their ability to produce light upon stimulation (KUWANO, 1902; CROZIER, 1917; HARVEY, 1926; RAO, 1954). This luminescence is neurally mediated and appears to be intracellular, though luminous slime is also produced (BAXTER & PICKENS, 1964). The role of swimming and bioluminescence in acorn worms is unknown.

## EVOLUTION

The embryologist BATESON (1884, 1885) studied the direct-developing acorn worm *Saccoglossus kowalevskii* AGASSIZ, 1873 and found the notochord, gill slits, collar nerve cord, and mesoblast development comparable to amphioxus, and so regarded enteropneusts are sister to chordates. Earlier, METSCHNIKOFF (1869) studied the development of the genus *Balanoglossus* DELLE CHIAIE, 1829 and noted many similarities of the tornaria to echinoderm larvae, so regarded hemichordates as sister taxon to echinoderms, a superphyletic group that he called Ambulacraria. With the advent of modern cladistics and phylogenetic methods, early phylogenies were consistent with these early ideas that envisioned the deuterostome ancestor as either a sessile tentaculate filter-feeding organism similar to a pterobranch (ROMER, 1967), or to a diplurula larva (GARSTANG, 1928). This dichotomy, and the polyphyletic relationship of enteropneusts (as sister to chordates) and pterobranchs (allied with echinoderms), persisted for nearly a century (GEE, 1996; HOLLAND, HOLLAND, & HOLLAND, 2015; LOWE & others, 2015; SATOH, 2016; PETERSON & EERNISSE, 2016). These hypotheses have fallen out of favor, replaced by the hypothesis that the deuterostome ancestor was a free-living worm with a pharynx perforated with gill slits, used in filter feeding—similar to a modern enteropneust (e.g., CAMERON, SWALLA, & GAREY, 2000; CAMERON, 2002b; LOWE & others, 2015; SATOH, 2016). This hypothesis is consistent with an extensive morphological phylogeny for hemichordates (CAMERON, 2005) and current molecular phylogenies, which regard Enteropneusta and Pterobranchia as sister taxa and the monophyletic Hemichordata as sister to the Echinodermata, together forming the Ambulacraria (Fig. 5) (WINCHELL & others, 2002; PETERSON & others, 2013; CANNON & others, 2014; TELFORD & others, 2014; SIMAKOV & others, 2015).

The class Enteropneusta consists of three major clades, one comprised of the three families Ptychoderidae, Torquaratoridae, and Spengelidae; the monophyletic Harrimaniidae (OSBORN & others, 2012; CANNON & others, 2014); and the stem group Cambrian fossils (Fig. 5). According to a molecular clock estimate based on the genomes of *Ptychodera flava* and *Saccoglossus kowalevskii*, the three-family clade and Harrimaniidae clade diverged 373 million years ago (SIMAKOV & others, 2015). Among

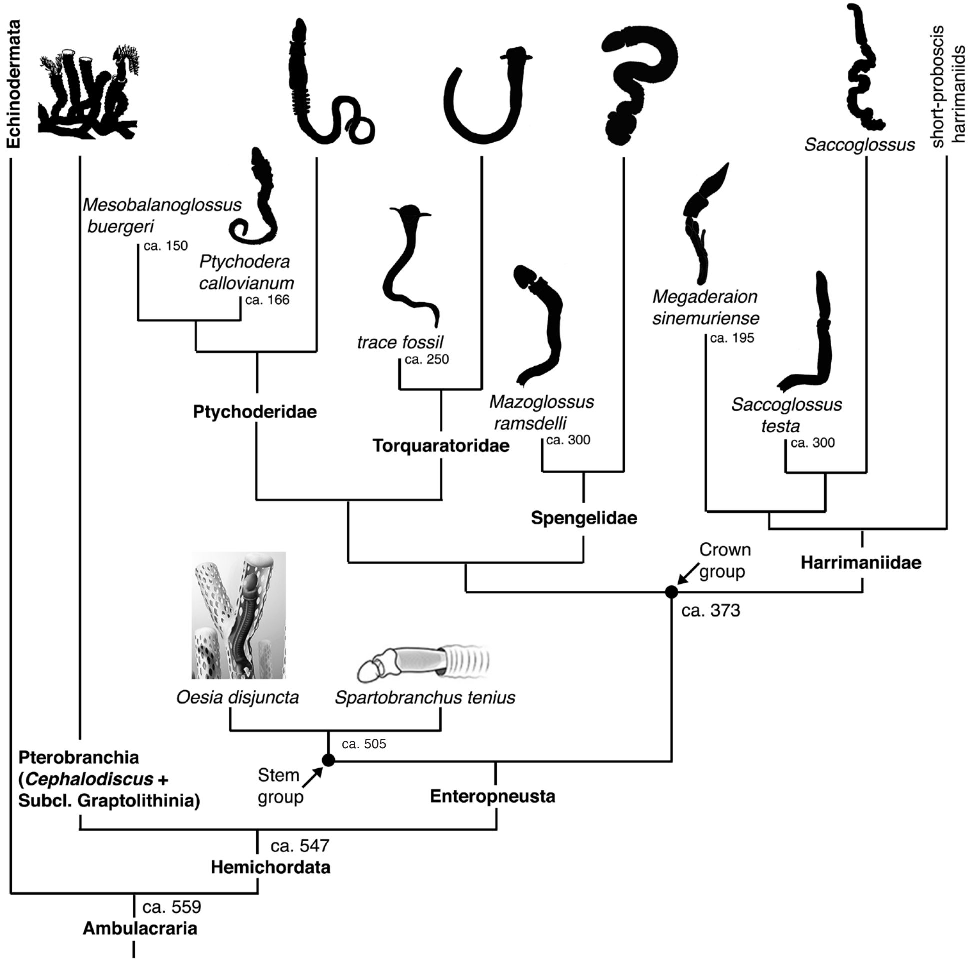


FIG. 5. Phylogenetic tree of acorn worms. The age of each fossil is provided in millions of years, and the stratigraphic details are provided in the text. Neither the tree branch lengths nor the worm silhouettes are to scale. The age of the Ambulacraria, Hemichordata, and crown group are molecular clock estimates from SIMAKOV & others (2015) (adapted from Cameron, 2016).

the larger three-family clade, Spengelidae is sister to the Ptychoderidae + Torquaratoridae (CAMERON, 2005; OSBORN & others, 2012; CANNON & others, 2014). OSBORN and others (2012), sequenced 25 torquaratorids and found them to be a monophyletic sister group to the Ptychoderidae. Based on two unidentified specimens, CANNON and others (2014) suggested that the Torquaratoridae are nested within the family Ptychoderidae (i.e., ptychoderid paraphyly). Torquaratorids have several unique morphological adaptations to life in the deep sea (see family diagnoses, below) that are absent from ptychoderids. Interestingly, these adaptations did not evolve by parallelism in the deep-sea acorn worms *Glandiceps abyssicola* SPENGEL, 1893 (Spengelidae) (HOLLAND & others, 2013), *Ritteria* DELAND & others, 2010, nor *Saxipendium* (Harrimaniidae) (DELAND & others, 2010; HOLLAND, OSBORN, & KUHNZ 2012).

The family Harrimaniidae is monophyletic and sister to the three-family clade (Fig. 5). Within the Harrimaniidae there are three clades that differ in the arrangements of their proboscis musculature (Deland & others, 2010). *Saxipendium*, a genus previously assigned to the monospecific family Saxipendidae, has been reclassified as a harrimaniid based in part on the shared presence of diffusely arranged proboscis musculature with *Mesoglossus* Deland & others, 2010 and *Ritteria*. The proboscis muscles of *Saccoglossus* are arranged in concentric rings, whereas radially arranged muscles are the ancestral acorn worm state (Deland & others, 2010).

The three-family clade and Harrimaniidae clade, inclusive of their fossil species, together comprise the crown Enteropneusta and diverged from a common ancestor about 373 million years ago (Fig. 5). Neither clade can be regarded as ancestral or derived. Each of the clades (as well as each family and species) exhibits ancestral and derived traits, though in general, the evolution of harrimaniids is characterized by losses of tornaria larval traits, whereas that of ptychoderids is characterized by gains of adult complexity. Harrimaniidae develop via a swimming, non-feeding, ciliated larva that swims with a telochrochal ciliated band—an acorn worm innovation. The harrimaniid larval telotroch suggests that the tornaria larva was lost in this family.

The modern families are a crown group clade with respect to the Cambrian fossil stem group, which includes *Oesia disjuncta* and *Spartobranchus tenuis* (Fig. 5). These 505 million-year-old fossils then, are the closest representatives of the ancestral acorn worm condition, and in most respects, they have a harrimaniid-like body plan. The Cambrian fossils lack hepatic sacs, genital wings, and synaptaculae that bridge the primary and secondary gill bars that characterize ptychoderids and the spengelids *Spengelia* Willey, 1898 and *Schizocardium*—this trait then, evolved by parallelism in Cephalochordata (Figs. 3.1–3.2). Tubes are unique to stem enteropneusts. Those of *Oesia disjuncta* are fibrous (Fig. 6.1) and those of *Spartobranchus tenuis* sometimes branch (Fig. 6.2). Dozens of the *O. disjuncta* and approximately one-quarter of the *S. tenuis* specimens are associated with tubes, suggesting a facultative tubicolous habit (Caron, Conway Morris, & Cameron, 2013; Nanglu & others, 2016). The tubes are interpreted as a homolog to pterobranch tubes, abandoned on the internode branch to the crown enteropneust clade.

## PALEONTOLOGY

Fossils of the soft-bodied enteropneusts are rare and typically occur in Konservat-Lagerstätten. The oldest of these are the Cambrian fossils *Oesia disjuncta* and *Spartobranchus tenuis* from the Burgess Shales of British Columbia, Canada, and date to about 505 million years ago. *O. disjuncta* is abundant in the Raymond Quarry and the Marble Canyon Quarry (Fig. 7,*2*). Its body is dominated by a broad and long pharynx that extends to nearly the posterior end of the animal. There is no appreciable intestine. A few of the specimens show what appears to be a posterior grasping appendage. Based on these unusual traits, Nanglu and others (2016), speculated that it may be a basal hemichordate, but here it is allied with *S. tenuis* in the stem Enteropneusta, with which it shares tubes and a similar age. *O. disjuncta* occupied tubes that were formerly classified as the algae *Margaretia* Walcott, 1931. The tubes are cosmopolitan, composed of woven fibers that form a sediment anchor basally and project into the water column (Fig. 6.1). The large pharynx, tube-dwelling habit, and lack of sediment in the gut suggest it was an epibenthic filter feeder. *S. tenuis,* from the Walcott Quarry, has a body plan that resembles that of a modern harrimaniid worm, including an extensive pharynx followed by a vermiform, unembellished intestine (Fig. 7,*1a–c*). It occupied infaunal tubes that could tear, though fibers are not apparent. The discovery of a torquaratorid inside a mucous tube has led to the idea that *S. tenuis* was a member of the family Torquaratoridae (Halanych & others, 2013; Cannon & others, 2014). This idea is rejected because *S. tenuis* lacks all diagnostic torquaratorid traits, mucus does not fossilize

(Nanglu, Caron, & Cameron, 2015), and the Cambrian fossils predate the origin of the crown enteropneusts (Simakov & others, 2015). *S. tenuis* was probably a facultative filter and deposit feeder. The tubes of Cambrian acorn worms provide evidence of a link to the tubarium of pterobranchs, including graptolites (Caron, Conway Morris, & Cameron, 2013; Nanglu & others, 2016).

Following the Cambrian, over 200 million years passed before the next fossil acorn worms appeared in the Carboniferous, and after the divergence of the modern families, at about 373 million years ago (Simakov & others, 2015). Though a precarious exercise, the Carboniferous, Triassic, and Jurassic acorn worms have been assigned to the four modern families: Harrimaniidae, Spengelidae, Ptychoderidae, and the deep-sea Torquaratoridae (Cameron, 2016). *Mazoglossus ramsdelli* (see Bardack, 1985, 1997; Maletz, 2014) and *Saccoglossus testa* Cameron, 2016 are from the Mazon Creek fauna, Illinois, USA (~307–309 million years ago). *M. ramsdelli* (see p. 13) has a wide anterior trunk suggesting a well-developed pharynx (Fig. 8,*3*). Gill pores are reported (Bardack, 1985), but having viewed all of the specimens to date, the present author was unable to detect them. The enlarged gonadal-branchial region and absence of gonadal wings suggest it was a member of the family Spengelidae (Cameron, 2016). The two *S. testa* specimens, also from Mazon Creek, are located next to each other in a single concretion (Fig. 8,*1*). They possess a long proboscis and therefore likely represent a re-emergence to surface deposit feeding. The proboscis of living saccoglossids are aposomatically colored—usually orange, red, or peach—and chemically defended. The Mazon Creek fauna is replete with predators including horseshoe crabs, sea scorpions, crustaceans, a shark, and the Tully monster (McCoy & others, 2016; Sallan & others, 2017), so chemical defense and aposomatic colors may have evolved as early as *S. testa* (Cameron, 2016).

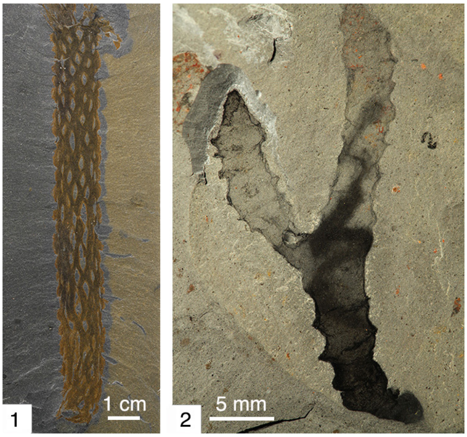


Fig. 6. Tubes of Cambrian fossil acorn worms. *1,* spirally arranged pores perforate the tube of *Oesia disjuncta* Walcott, 1911, ROM 63716 (Nanglu & others, 2016, fig. 4a); *2,* branching tubes of *Spartobranchus tenuis* (Walcott, 1911), ROM 57170 (Caron, Conway Morris, & Cameron, 2013, fig. 2f).

The next evidence of an acorn worm is a resting trace fossil from the Lower Triassic Werfen Formation of northern Italy (Twitchett, 1996) (Fig. 4.4). It has collar lips that extend laterally and a pharynx that narrows posteriorly, characteristic of the Torquaratoridae, a family of surface-dwelling, pelagic deep-sea acorn worms (Holland & others, 2005; Priede & others, 2012). *Megaderaion sinemuriense* (see p. 13) is from the Sinemurian (Lower Jurassic) strata of Osteno, northern Italy (Fig. 8,*2*). It is a single, small (2 cm) specimen that lacks gonadal wings, hepatic sacs, and an enlarged branchial region, characteristic of the family Harrimaniidae. It resembles *Mesoglossus,* a harrimaniid worm with a medium-long proboscis (Deland & others, 2010).

*Ptychodera callovianum* (Alessandrello, Bracchi, & Riou, 2004) was a ptychoderid (Fig. 8,*4*), from the Lower Callovian (Middle Jurassic) of La Voulte-sur-Rhone, France. The youngest fossil is *Mesobalanoglossus buergeri* (see p. 14) from the lower Tithonian (Upper Jurassic) Solnhofen Limestones, southern Germany (Fig. 8,*5*). It is assigned to Ptychoderidae due to its length (68.8 cm) and enlarged genital wings, but the proboscis preservation is poor and the presence of bristles in the pharynx (Frickhinger, 1999) suggest that it was not an acorn worm.

This chapter limits its systematic section to seven genera with fossil evidence—two from the stem group, and five from the crown group. The excluded genera are only known from extant species. What we understand at this point, based on the pattern of appearance of these seven fossil acorn worm species, is: (1) the evolution of acorn worms is characterized by an evolutionary stasis—the harrimaniid body plan of *Spartobranchus tenuis* appears in the Cambrian and persists to this day in the Harrimaniidae, including *Saccoglossus* (Fig. 5); (2) this body plan was followed by that of a spengelid in *Mazoglossus ramsdelli* from the Pennsylvanian (Bardack, 1997) and then by a torquaratorid, characterized by collar lips, in a Lower Triassic trace fossil (Twitchett, 1996); and (3) the complex ptychoderid body plan appeared last in *Ptychodera callovianum* from the Upper Jurassic (Alessandrello, Bracchi, & Riou, 2004; Cameron, 2016) (Fig. 5).

## STEM GROUP TAXA

The stem group enteropneusts include tube-dwelling taxa with a vermiform body that consists of a proboscis, a collar, and a trunk with a pharynx framed by multiple, paired, circumferential gill bars and slits.

**Oesia** Walcott, 1911, p. 132 [**O. disjuncta;* OD] Tripartite body with proboscis, collar, and trunk; trunk unusual, possessing extensive pharynx and lacking esophagus and intestine; posterior grasping appendage; tubes, fibrous with spirally arranged openings. *Cambrian (Miaolingian, Wuliuan,* Bathyuriscus–Elrathia *Biozones):* Canada.——Fig. 7,*2.* **O. disjunta*, USNM 57630, lectotype (selected by Szaniawski, 2005, p. 2), one of three specimens illustrated by Walcott (1911), Burgess Shale, Walcott Quarry, British Columbia, Canada (new, photo by J.-B. Caron).

**Spartobranchus** Caron, Conway Morris, & Cameron, 2013, p. 503 [**Ottoia tenuis* Walcott, 1911, p. 130; OD]. Vermiform, maximum length 10 cm; body comprised of short proboscis, collar, pharyngeal area with up to 40 pairs of gill and tongue bars; elongate posterior trunk ending in bulbous unit; gut straight, anus terminal; approximately one-quarter of specimens associated with tube of organic walls; tube varies from straight, completely circular, to helicoidal, and sometimes branching; no more than one individual per tube has been observed. *Cambrian (Miaolingian, Wuliuan,* Bathyuriscus–Elrathia *Biozones):* Canada.——Fig. 7,*1a–c.* **S. tenuis (*Walcott); *1a–b,* USNM 108494, lectotype (selected by Caron, Conway Morris, & Cameron, 2013, supplement 1, from a small number of specimens supposedly collected by Walcott [1911] who described, but never illustrated *Ottoia tenuis* and the whereabouts of his material is unknown), specimen missing proboscis and terminal portion of trunk; *1a,* part, direct light; *1b,* counterpart, polarized light; *1c,* complete specimen, ROM 62123 (Caron, Conway Morris, & Cameron, 2013, fig. 1).

## CROWN GROUP TAXA

### Family HARRIMANIIDAE
### Spengel, 1901

[Harrimaniidae Spengel, 1901, p. 215]

Simple morphology, largely characterized by features it lacks; no dorsal collar nerve roots arising from the collar nerve cord; gills lack synaptaculae that bridge primary and secondary gill bars; trunk lacks hepatic sacs, circular muscle fibers, and lateral septa, only dorsal and ventral septa present; intestinal pores only rarely present; posterior projecting horns of Y-shaped proboscis skeleton extend at least to middle of collar; proboscis longitudinal musculature may be arranged diffusely, in radial plates, or in concentric rings; development via short-lived, non-feeding larvae that become juveniles with adhesive post-anal tail. *Carboniferous (Pennsylvanian, Moscovian)–Holocene* (extant): worldwide.

The Harrimanidae comprises ten living genera, including one (*Saxipendium* Woodwick & Sensenbaugh, 1985) that was previously assigned to its own family (Deland & others, 2010; Worsaae & others, 2012). *Saccoglossus* is the most speciose and familiar genus (Cameron, Deland, & Bullock, 2010). Its proboscis longitudinal musculature is arranged in concentric rings, while other genera may be arranged diffusely (e.g., *Mesoglossus*), or in radial plates (e.g., *Protoglossus* Horst, 1939).

**Saccoglossus** Schimkewitsch, 1892, p. 2 [**Balanoglossus mereschkowskii* Wagner, 1885, p. 46; OD] [=*Balanoglossus* (*Dolichoglossus*) Spengel, 1893,

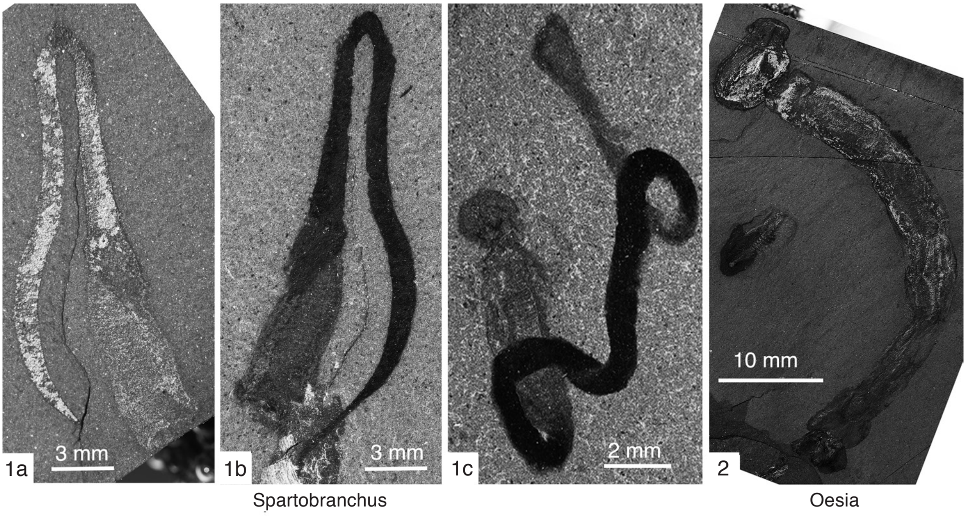


Fig. 7. Stem group Enteropneusta (p. 12).

p. 360 (type, *D. kowalewskii* Agassiz, 1873, SD Spengel, 1901, p. 215)]. Proboscis long; longitudinal muscle fibers of proboscis arranged in several concentric rings; middorsal longitudinal groove may be present; collar usually very short compared to proboscis; dorsal interbranchial genital ridges and dorsal gonads absent but lateral extrabranchial genital ridges may be present; intestinal pores often present; perihaemal cavities always present; peribuccal cavities usually present. [Many species favor quiet muddy-sandy flats not far from the mouth of a bay, living in semi-permanent and helical-shaped burrows and throwing up low conical mounds of quasi-spiral fecal castings. See Cameron, Deland, & Bullock, 2010; also see Fig 4.2.]——Fig. 8,*1. S. testa* Cameron, 2016, holotype, FMNH PE 45216, one of two counterparts (new).

**Megaderaion** Arduini, Pinna, & Teruzzi, 1981, p. 105 [**M. sinemuriense;* OD]. Elongate worm divided into elongate, rounded, and ogival proboscis; collar wider than long, tapering trunk; single specimen small (2 cm) lacking gonadal wings, hepatic sacs, and enlarged branchial region, characteristic of family Harrimaniidae; resembles *Mesoglossus,* with medium-long proboscis. [See Deland & others, 2010.] *Lower Jurassic (Sinemurian,* Coroniceras bucklandi *Biozone):* Italy.——Fig. 8,*2. *M. sinemuriense*, holotype, i751 (Museo Civico di Storia Naturale di Milano) (Arduini, Pinna, & Teruzzi, 1981, fig. 1).

### Family SPENGELIDAE Willey, 1899

[Spengelidae Willey, 1899, p. 239] [=Glandicipitidae Spengel, 1901, p. 215]

Anterior vermiform process of stomochord present in all members; skeletal horns usually extend over whole length of collar; dorsal nerve roots arising from collar nerve cord rare; lateral septum absent; hepatic caeca and synapticula may or may not be present; circular muscle fiber layer positioned inside longitudinal muscle layer in trunk. *Carboniferous (Pennsylvanian, Moscovian)–Holocene* (extant): worldwide.

In the cases where development has been documented, Spengelidae species have a tornaria larva (Cameron & Perez, 2012). The family includes four living genera (see Horst, 1939; Cameron & Perez, 2012). Cameron (2016) referred *Mazoglossus ramsdelli* to the family Spengelidae, thus, extending an extant enteropneust family to include a Carboniferous fossil species.

**Mazoglossus** Bardack, 1997, p. 89 [**M. ramsdelli;* OD] Small (specimens less than 10 cm total length); recognizable as an enteropneust by outline shape of proboscis, collar, and trunk. Illinois, USA.——Fig. 8,*3. *M. ramsdelli*, FMNH PE 23053, one of two counterparts, complete specimen (adapted from Cameron, 2016, fig. 2C).

### Family PTYCHODERIDAE Spengel, 1893

[Ptychoderidae Spengel, 1893, p. 359] [=Balanoglossidae Willey, 1899, p. 239]

Lateral septa in trunk; invariable absence of abdominal pores; lack of vermiform process of stomochord; dorsal nerve roots in collar present; skeletal horns rarely reach beyond anterior half of collar; synapticulae form bridges between primary and secondary gill bars in pharynx, hepatic caeca usually present; dorsolateral ciliated grooves in abdominal part of alimentary canal; circular muscle fibers in trunk, usually outside the longitudinal fibers; development occurs through typical tornaria larva [See CAMERON & OSTIGUY, 2013, p. 144.] *Middle Jurassic (Callovian)–Holocene* (extant): worldwide.

Ptychoderidae includes four extant genera, including the familiar *Balanoglossus*. *Mesobalanoglossus* is here included in the Ptychoderidae. CAMERON (2016) referred the Upper Jurassic *Megaderaion callovianum* ALESSANDERELLO, BRACCHI, & RIOU, 2004 to the Ptychoderidae. The species is here included in the genus *Ptychodera*.

**Ptychodera** ESCHSCHOLTZ, 1825, p. 740 [**P. flava;* M]. As for family, except gill pores open by long slits, whereas those of *Balanoglossus* open by small pores.——FIG. 8,*4. P. callovianum* (ALESSANDRELLO, BRACCHI & RIOU, 2004), MNHN L.P.M.-B. 48352, holotype.

**Mesobalanoglossus** BECHLY & FRICKHINGER in FRICKHINGER, 1999, p. 77 [**M. buergeri;* OD] Single specimen, 68.8 centimeters long, with diminutive proboscis, collar, and long trunk with bristles interpreted as gill bars; trunk tapers posteriorly, anterior wide part interpreted as gonadal wings. *Upper Jurassic (Lower Tithonian,* Hybonoticeras hybonotum *Biozone):* Germany. ——FIG. 8,*5. *M. buergeri,* holotype (Bechly & Frickhinger in Frickhinger, 1999, fig. 144).

### Family TORQUARATORIDAE Holland & others, 2005

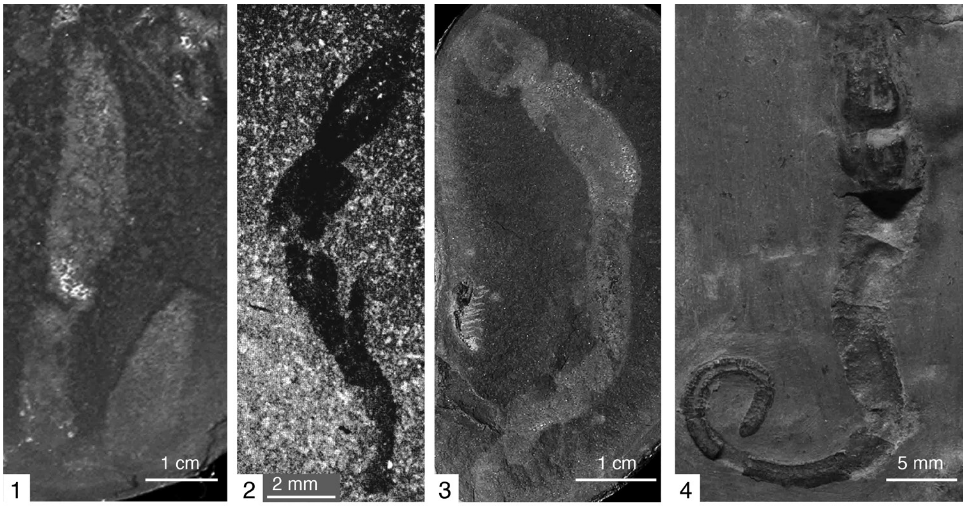
[Torquaratoridae HOLLAND & others, 2005, p. 374]

Proboscis broad, short, dome shaped; collar wide, usually embellished with lateral lips; body semi-transparent, frequently brightly colored; muscular system poorly developed; collagenous proboscis skeleton and gill bars greatly reduced; proboscis skeletal horns absent from all species but *Torquarator bullocki* (HOLLAND & others, 2005). *Lower Triassic (upper Olenekian)–Holocene* (extant): worldwide.

The family Torquaratoridae is exclusive to the deep sea (HOLLAND & others, 2005, 2009; HOLLAND, KUHNZ, & OSBORN, 2012). There are five genera (JABR, ARCHAMBAULT, & CAMERON, in press). Fossil specimens of the Torquaratoridae are unknown, but a single resting trace from the Lower Triassic (Olenekian) Werfen Formation of northern Italy (TWITCHETT, 1996) shows, through its characteristic shape, the presence of the family in the Mesozoic (see Fig. 4.4).

## FUTURE RESEARCH

In the intervening years since the first edition of this chapter (BULMAN, 1970) in which only a short note on the Enteropneusta appeared, 22 new, living enteropneust species have been described, and with it, their zoogeographic range better appreciated (see especially, CAMERON, DELAND, & BULLOCK, 2010), particularly with respect to their abundance in the deep sea (OSBORN & others, 2012; PRIED & others, 2012; CANNON, SWALLA, & HALANYCH, 2013). While fossil enteropneusts were unknown to BULMAN (1970), here we show that seven fossil acorn worm species extend from the Jurassic to the Cambrian periods. Fine details of cellular ultrastructure (see especially PARDOS & BENITO, 1990) have been brought into the light, contributing to a better appreciation of the functional morphology of the group. Surprising observations have been made on their life habits. Interest in the molecular developmental of the group has revealed body plan patterns conserved with their common ancestor, chordates (LOWE & others, 2003; LOWE & others, 2006). The current phylogeny is robust, with broad taxonomic sampling (CANNON & others, 2014), with the exception of the family Spengelidae. The genomes of *Saccoglossus kowalevskii* and *Ptychodera flava* have been sequenced, providing a tremendous resource for future investigations (TAGAWA, 2016; SIMAKOV & others, 2015). The conserved linkage, or micro-synteny, of transcription factors involved in gill development have been revealed (GILLIS, FRITZENWANKER, & LOWE 2012; SIMAKOV & others, 2015). Similar studies on other organ systems will come, and higher levels of conserved linkages, or



Saccoglossus Megaderaion Mazoglossus Ptychodera

Mesobalanoglossus

FIG. 8. Harrimaniidae (*1–2*), Spengelidae (*3*), Ptychoderidae (*4–5*). (p. 12–14).

macro-synteny, may be expected. The genes involved in the biosynthesis and degradation of the sialic acid molecule, a deuterostome synapomorphy (CAMERON, 2005), includes nine that arrived as transposons from a prokaryote or protist donor (SIMAKOV & others, 2015). In their review of the development of the group, KAUL-STREHLOW and RÖTTINGER (2015) stressed a need for more investigations on the development of the nervous and muscular systems, and I would add to that the coelomic, reproductive, and immune systems. There is a single paper on the immunodefense of the group (TASSIA, WHELAN, & HALANYCH, 2017). Interest in acorn worm biology has grown—affirmed by the 1st International Hemichordate Meeting, Hopkins Marine Station at Stanford University, December 2016—and the future looks bright.

Future fruitful avenues of research may include: (1) A more extensive sampling of South America, Africa, Asia, as well as deep water where many species remain to be found. (2) The burrow shape of acorn worms varies tremendously and there seems to be some genus-specific patterns. The fossil record of burrow trace fossils is rich (Bromley, 1996; Seilacher, 2007; Gingras & others, 2008), and may provide some insight on the origin of modern acorn worm genera. Horst (1940) suggested that an enteropneust similar to *Saccoglossus* is responsible for the spiraling trace fossil, *Gyrolithes.* This, as well as changes to burrow structure—depending on season or sediment parameters—should be explored. (3) Intensive sampling of many individuals within a species is needed to assess the amount of interspecific variation, in the structure of the heart-kidney coelomic process, the collagenous gill bars and nuchal skeleton, the ossicles, as well as developmental genes—since variation is what selection works on. Such studies are rare, the most comprehensive study being that of the many *Ptychodera flava* variants from the Indian Ocean (Punnett, 1906). (4) Do closely related species have similar developmental processes—as might be expected—or is the variation substantive, as we have seen from the direct developer *Saccogossus kowalevskii*, to the tornaria of *Schizocardium californicum* (see Gonzalez, Uhlinger, & Lowe, 2017)? Experimental molecular developmental approaches that include gene knock-down (Tagawa, 2016), RNAi, CRISPR, and single-cell sequencing (Klein & others, 2015), will provide more robust and nuanced tests of homology. (5) Nearly nothing is known of the post-juvenile development of acorn worms, but the powerful potential of these investigations is that the ontological development can be compared with the paleontological equivalents, particularly with the Cambrian forms that are abundant and show exquisite details of extracellular matrix structures, including gill bars and tubes. (6) Nothing is written on the quantitative genetics, the population-based studies of continuously varying characters, nor how these characters respond to selection. (7) Slight more is known about the neural physiology (Pickens, 1970; Cameron & Mackie, 1996), and respiratory physiology of acorn worms (Azariah, Ismail, & Najib, 1975; Ditadi, Mendes, & Bianconcini, 1997). Is the physiological role of the gill slits respiratory as the name Enteropneusta—Greek for gut-breathing—implies, or is the primary role of the acorn worm gills in ammonia exchange or acid-base regulation? Even less is known of embryonic and larval physiology and behavior.

## ABBREVIATIONS FOR MUSEUM REPOSITORIES

**BSPGM**: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany
**FMNH PE**: Field Museum, Chicago, Illinois, USA
**i751:** Museo Civico di Storia Naturale di Milano, Italy
**ROM:** Royal Ontario Museum, Toronto, Canada
**USNM:** United States National Museum of Natural History, Washington, D. C., USA
**MNHN:** Muséum National d'Histoire Naturelle, Paris, France

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