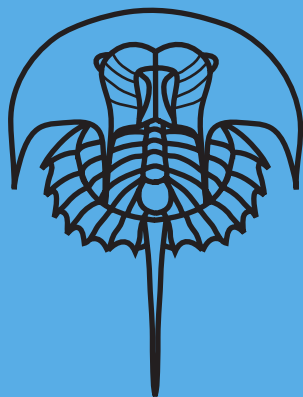




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Introduction to the Hemichordata

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PART V, SECOND REVISION, CHAPTER 1: INTRODUCTION TO THE HEMICHORDATA

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INTRODUCTION

This Second Revision of the Part V *Treatise on Invertebrate Paleontology*, dealing with the phylum Hemichordata, is a considerably extended version of the Graptolite Treatises of BULMAN (1955, 1970), which primarily covered the Graptolithina, at the time interpreted as an extinct class of the Hemichordata. With the recognition of the Graptolithina as fossil members of the Pterobranchia and the identification of the benthic colonial pterobranch *Rhabdopleura* as an extant graptolite (MITCHELL & others, 2013), the focus in this volume is extended to include the record of fossil Hemichordata and to also examine the soft-body anatomy in more detail. Zooidal anatomy is important for the interpretation of the fossil graptolites and their life style and points to the importance of modern biology in understanding the fossil record.

The two editions of BULMAN's *Treatise* (1955, 1970) have been the standard for graptolite research for seven decades, but their precursor in the *Handbuch der Paläozoologie* (BULMAN, 1938) seems to be nearly forgotten and is difficult to obtain. This volume could be regarded as the first version of the Graptolite Treatise, because it covers in a similar manner all the main aspects of graptolite taxonomy and its understanding at the time of publication and was obviously the basic source for the later versions. Unfortunately, it was published at the wrong time and in the wrong country. BULMAN (1938) established all the basic taxonomic concepts

in the volume, even introducing a number of new taxa.

BULMAN's work on the graptolites and their taxonomy in the two previous *Treatise* volumes is neither the only one nor the first attempt at a general overview of graptolites. However, most general treatments did not attain the influence and acceptance in the international scientific community, either due to the language in which they were published or the time of publication. HALL (1868) and FRECH (1897) provided an understanding of graptolite research during their times and achieved important and valuable insights. General overviews by DAWYDOFF (1948), WATERLOT (1953), MÜNCH (1952), MU and LEE (1960), and OBT (1957, 1964) had less impact due to the language barriers (published in French, German, Chinese, and Russian, respectively), but nevertheless they were important in shaping the opinions of generations of researchers.

SCOPE OF THE VOLUME

This volume is aimed at providing the most complete and up-to-date information on the fossil Hemichordata, their taxonomy, and their use in the geological sciences. The inclusion of not only the Pterobranchia (Graptolithina), but also the Enteropneusta shows our increased knowledge of the relationships of this fascinating fossil group with extant groups of organisms. This approach connects the fossil graptolites with their closest relatives, largely known from extant organisms.

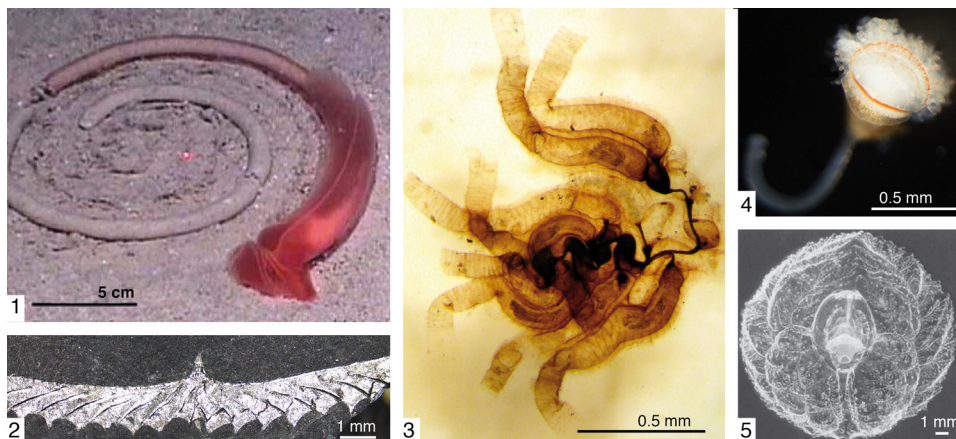


FIG. 1. Examples of the Hemichordata. 1, *Torquaratorid* enteropneust with fecal string (Holland & others, 2005, fig. 3E); 2, *Expansograptus hirundo* (SALTER, 1863), flattened tubarium, PMO 234064, Tøyen Shale, Oslo region, Norway (new); 3, *Rhabdopleura compacta* HINCKS, 1880, tubarium with zooids (Cavers, 2005, fig. 1.1); 4, *Cephalodiscus planitectus* MIYAMOTO, NISHIKAWA, & NAMIKAWA, 2020, ventral view of zooid (Miyamoto, Nishikawa, & Namikawa, 2020, fig. 2C); 5, *Planctosphaera pelagica* SPENGLER, 1932 (Hart, Miller, & Madin, 1994, fig. 1B).

Graptolites have been used successfully in the understanding of lithostratigraphic successions, unraveling structural complexities in geology and, thus, are important biological objects enabling numerous geological interpretations, as detailed in Chapter 9 (MALETZ & VANDENBERG, 2021). LAPWORTH (1878) first used graptolites to decipher the tectonic complexities in the succession of the Moffat Series, a milestone in graptolite research (FORTEY, 1993; HAMILTON, 2001) and a first hint on the importance of graptolite research to applied geology. Graptolite fusellum has been used to determine temperature and burial histories of Paleozoic sediments (e.g., GOODARZI & NORFORD, 1985). Graptolite research, thus, goes far beyond the identification of taxa and the relative dating of successions that included graptolites as index fossils. It is not just a discipline for taxonomists and fossil collectors; the geological application of graptolites is still developing and modern data collection and database interpretations may infuse new life into graptolite research. In recent years, paleodiversity studies using graptolite faunas have become the focus of research on extinction and origination intervals in Earth's history (e.g., CRAMPTON & others, 2020).

The Enteropneusta, unfortunately, have been neglected in the past because so few fossil ones were recognized, and even the extant enteropneusts were rarely investigated in much detail. Only through the renewed interest in the Burgess Shale biota and their preservation, fossil Enteropneusta have gained more interest, and therefore new fossil taxa have been studied and described, including ones that are tubicolous (e.g., CARON, CONWAY MORRIS, & CAMERON, 2013; NANGLU, CONWAY MORRIS, & CAMERON, 2016; CAMERON, 2018) and one with tentaculate arms (NANGLU, CARON, & CAMERON, 2020), two characteristics that were previously regarded as restricted to the Pterobranchia.

FOSSIL AND EXTANT MEMBERS OF HEMICHORDATA

The recognition of fossil Hemichordata is quite difficult as these organisms in general are soft-bodied and rarely leave any trace of their existence (MALETZ, 2020). Thus, the fossil record is relatively poor. Of the three extant groups of Hemichordata (Enteropneusta, Pterobranchia, Plancto-

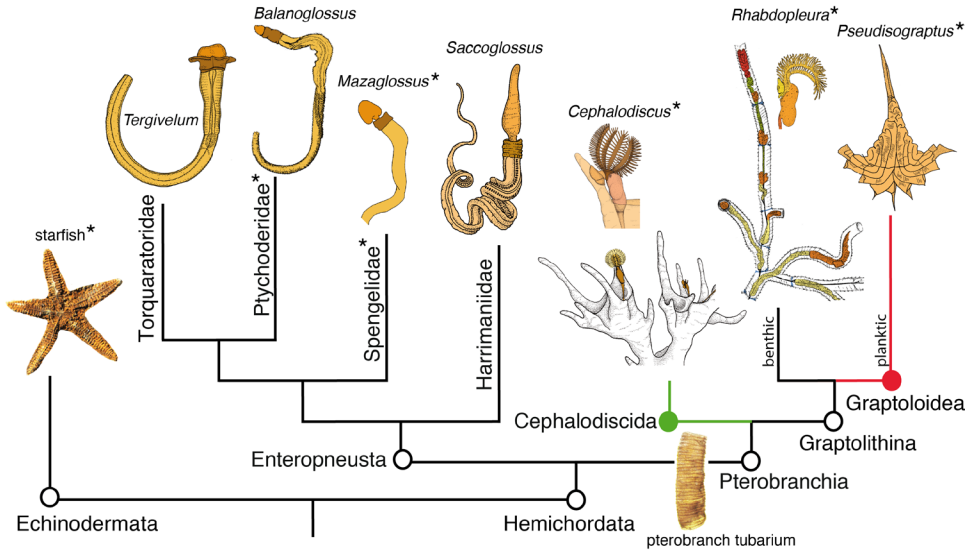


FIG. 2. Phylogenetic understanding of the Hemichordata. Taxon names with * indicate taxa known also from fossils or only from fossil material (new).

sphaeroidea), only the tube-building Pterobranchia (Fig. 1.2–1.4) are common in the fossil record due to the preservability of their organic housing, the tubarium (Fig. 1.2). The Enteropneusta (Fig. 1.1) possess a fossil record reaching back into the Middle Cambrian (CAMERON, 2018), but the Planctosphaeroidea (Fig. 1.5) are only known from a few larvae (e.g., SPENGLER 1932; HYMAN, 1959; HART, MILLER, & MADIN, 1994).

All extant Hemichordata share a tripartite body plan of their worm-like soft-bodied organization as a characteristic feature. Modern taxa investigated with DNA analysis indicate a phylogenetic position of the Hemichordata as a sister group to the echinoderms (e.g., HALANYCH, 1996; CANNON & others, 2009; LI & others, 2019) (Fig. 2). The extant Pterobranchia may have evolved from an enteropneust-like ancestor through a reduction in size and morphological complexity, a colonial or pseudocolonial life style, and development of the colony zooids through asexual budding (CAMERON, GAREY, & SWALLA, 2000). Interestingly, a miniaturization also occurs in enteropneusts (e.g., *Meioglossus* WORSAAE & others, 2012).

Phylum HEMICHORDATA Bateson, 1885

[Hemichordata BATESON, 1885, p. 111; *nom. transl. ex class* Hemichordata BATESON, 1885, p. 111, HYMAN, 1959, p. 74]
[=Klasse Helminthomorpha GROBBEN, 1908, p. 505, non Helminthomorpha POCOCK, 1887 (Diplopoda, millipedes); =subphylum Stomochordata DAWYDOFF, 1948, p. 367]

Hemichordate synapomorphies include a tripartite body; a muscular-secretory-locomotory preoral organ (enteropneust proboscis or pterobranch cephalic shield) that encloses a heart–kidney coelomic complex, including a stomochord; a collar with paired valved mesocoel ducts and pores; and a trunk that includes a ventral post-anal extension of the metacoels (enteropneust juvenile tail or pterobranch stalk). *Cambrian, Terreneuvian (Fortunian)–Holocene* (extant); worldwide.

BATESON (1885) introduced the term Hemichordata for the Enteropneusta, but it was FOWLER (1892, p. 132) who revised the Hemichordata to also include the colonial Pterobranchia. The status of the Planctosphaeroidea in the Hemichordata is still uncertain (see p. 6). The Hemichordata are comparable to the Helminthomorpha of GROBBEN (1908, p. 505), who included the

Enteropneusta and Pterobranchia. SPENGLER (1932, p. 26) included *Planctosphaera* as a third class in the Helminthomorpha. The Helminthomorpha GROBBEN, 1908 has commonly been used in German literature and may easily be confused with the Helminthomorpha POCKOCK, 1887, a clade of millipedes.

The Hemichordata range in length from less than one millimeter (WORSAAE & others, 2012) to more than two meters. Of the living hemichordates, the Enteropneusta are the most well known members. For a detailed look at Enteropneusta, see Chapter 2 (CAMERON, 2018). They are benthic marine worms that are distributed from the shallow intertidal zone to the deep sea and appear not to be limited by temperature barriers. They are usually infaunal elements, but deep-water enteropneusts include epibenthic demersal drifters (OSBORN & others, 2012). The enteropneust *Saxipendium coronatum* WOODWICK & SENSENBAUGH, 1985 is known to congregate on rock surfaces near hydrothermal vents.

Uncertainty about the relationships of the Hemichordata has been present since the first enteropneust was discovered in 1821 and was thought to be an atypical holothurian (ESCHSCHOLTZ, 1825). HYMAN (1959) provided a thorough historical treatment of early hemichordate classifications. KOWALEWSKY (1866) provided the first anatomical study of an acorn worm including the discovery of pharyngeal openings that aligned the Enteropneusta with the Chordata. METSCHNIKOFF (1869) found that the tornaria larva was an enteropneust rather than an asteroid larva, adding weight to the echinoderm and enteropneust relationship. Then, BATESON (1885) placed a subphylum Hemichordata in the phylum Chordata based on the presence of a notochord, the central nervous system, and the gill slits. This position was protested by SPENGLER (1893) and subsequently abandoned by the German, French, and American treatises on invertebrates, namely VAN DER HORST (1939), DAWYDOFF (1948), and HYMAN

(1959). The similarities and close relationship of the hemichordates to the echinoderms was the predominant view for the latter half of the twentieth century, although the common ancestor remained contentious. On one side, BATHER (1900) referred to the dipleurula larva, a name introduced by SEMON (1888), as a common ancestor. The larva shared features of the enteropneust tornaria or asteroid auricularia. It was soft, bilaterally symmetric with a ventral mouth, apical organ, ciliated bands, and three pairs of coelomic sacs that were arranged on either side of the gut (GISLÉN, 1930), referred to as the protocoele, mesocoele, and metacoele. The protocoele opened to the exterior by a ciliated duct and pore. The hypothesis that this dipleurula elongated to become the ancestral chordate animal (GARSTANG, 1928) gained acceptance.

GROBBEN (1923) put forward the hypothesis that the echinoderms are derived from the pterobranchs. The ancestor was similar to *Cephalodiscus* M'INTOSH, 1882 in that it had five pairs of arms with tentacles. The cephalic shield was comparable in position to the attachment pit of the crinoid and asteroid larvae that was drawn out to become a stalk. Most people regarded the pterobranchs as more primitive than enteropneusts because of their simple nervous system. The echinoderms then would have evolved by the extension of the protocoele (echinoderm hydrocoele) into multiple arms. The protocoele opened to the exterior by a pore. The digestive tract was comprised of an esophagus, stomach, and intestine and curved to open into an anus on the anterior ventral side. This ancestor metamorphosed into an echinoderm with the right protocoele and five arms diminished, and the body attained a circular disk-like shape. The remaining arms radiated in five directions to form the echinoderm rays. JEFFRIES (1986) developed a similar calcichordate hypothesis whereby the echinoderms and the chordates evolved from a pterobranch-like ancestor that had fallen over and then elaborated one side. The prevailing hypotheses of the

twentieth century was that pterobranchs were either basal deuterostomes (GEE, 1996; NIELSEN, SCHARF, & EIBYE-JACOBSEN, 1996) or plesiomorphic hemichordates (HYMAN, 1959; BARRINGTON, 1965).

The GUTMANN (1981) hypothesis posits that the ancestral deuterostome, based on a functional-mechanical analysis, was a metameric, coelomate worm-like animal with complex body muscles that formed the basis of a hydrostatic skeleton. The sequence of morphological changes leading to the chordate ancestor was, in chronological order, the appearance of a notochord, the dorsal hollow nerve cord, the post-anal tail, and the branchial basket. This primitive chordate would have been most like a lancelet. From here, the enteropneusts lost the notochord, dorsal nerve cord, and segmented condition and developed a muscular burrowing proboscis. The collar originated to prevent water from exiting the mouth. Pterobranchs then arose from this acorn worm by a reduction in the branchial basket and an elaboration of the collar into arms and tentacles, and finally, the appearance of the tubarium. By this hypothesis, echinoderms arose from the pterobranch-like ancestor by specializing for sessile life, developing feeding tentacles and losing the branchial basket.

The twenty-first century saw the dawn of a new hypothesis, that the common ancestor to the deuterostomes was an enteropneust-like worm with chordate-like gills (CAMERON, GAREY, & SWALLA, 2000). This worm hypothesis was further elaborated by CAMERON (2002b, 2005), who stated that the ancestral deuterostome was a benthic vermiform organism with a terminal mouth and anus and a pharynx perforated with gill slits bordered by gill bars of collagen used in filter feeding (CAMERON, 2002b). This organism possessed a simple nerve plexus with little sign of regionalization. The enteropneust collar cord is not a homologue of the chordate dorsal nerve cord. It had a cluster of vacuolated cells with myofilaments, expanded extracellular matrix, and extracellular spaces developed from the middorsal

wall of the archenteron that provided the foundation for the independent evolution of the chordate notochord and enteropneust stomochord. Iodotyrosine was produced in cells lining the gut, but these cells had not yet coalesced into an endostyle. It is not known if this animal had trimeric or metameric coeloms, but the ancestor probably had well-developed circular and longitudinal muscles (CAMERON, 2005). On the branch to the Ambulacraria, the dipleurula larva appeared. The first echinoderm adult was bilaterally symmetric (RAHMAN & others, 2015) and may have possessed echinoderm-like ossicles (CAMERON & BISHOP, 2012) and gill slits (e.g., *Jaekelocarpus* KOLATA, FREST & MAPES, 1991, see DOMINGUEZ, JACOBSON, & JEFFRIES, 2002). The first pterobranchs then, similarly evolved from an acorn worm-like ancestor.

The discovery of two Cambrian Burgess Shale enteropneust fossils that are tubicolous (CAMERON, 2018), and another with arms and tentacles (NANGLU, CARON, & CAMERON, 2020) suggest that these traits originated before the pterobranchs. The major innovations of pterobranchs then are coloniality and a reduction in size that resulted in the loss of the gill skeleton, branchiomic nephridia, and three pairs of coelomic diverticula; the periaermal, peripharyngeal, and peribuccal coeloms (CAMERON, 2005). The hypothesis that the ancestor to the deuterostomes was an enteropneust-like worm is supported by morphological and molecular phylogenetic trees (CAMERON, 2005; CANNON & others, 2009), molecular development (LOWE, 2021), and comparative genomics (SIMAKOV & others, 2015). An important caveat to this hypothesis, which points to fruitful future avenues of research, is the almost total absence of pterobranch molecular developmental studies (SATO & others, 2009) and the absence of a pterobranch genome.

The preservation of the Hemichordata (see Chapter 5; MALETZ, 2018) as fossils depends strongly on the type of sediments in which they are embedded and the

environmental conditions in these sediments (MALETZ, 2020). In general, indications of the organic soft-tissue of organisms is only preserved under very special conditions and can be found in rare Lagerstätten, such as the Burgess Shale of British Columbia, the Chengjiang fauna of China (CAMERON, 2018) and the Mazon Creek fauna of North America (CAMERON, 2016). The fossil record of the Pterobranchia is extensive, as is seen by the common occurrence of graptolite tubaria in Paleozoic sediments, but does not include any identifiable organically preserved zooids (MALETZ, 2020; RAMÍREZ-GUERRERO & CAMERON, 2021).

Class PLANCTOSPHAEROIDEA van der Horst, 1936

[Planctosphaeroidea VAN DER HORST, 1936, p. 612]

The species *Planctosphaera pelagica* SPENGLER, 1932 is based on a large, spherical larva that may exceed 25 mm in diameter and is the sole member of the monotypic class Planctosphaeroidea VAN DER HORST, 1936. The surface is laced with paired and ramified food grooves lined by two continuous ciliated bands used in filter feeding (HART, MILLER, & MADIN, 1994). The viscera are clearly visible through the jelly interior and include a mouth that is located internal to paired stomodeal canals, followed by an esophagus, stomach, and intestine with a terminal anus. It has a triangular shaped protocoel with a posterior extending duct and pore. A muscle strand connects the protocoel with an apical nerve plate, and from the other two corners paired horns extend anteriorly along the stomach. Paired mesocoels and metacoels are located on either side of the intestine. Except for the paired stomodeal canals to the mouth and the horns of the protocoel, all of these features are present in enteropneust tornaria. Other apomorphies include a ventral depression that extends into the larva as paired boot-shaped diverticula positioned on either side of the intestine and posterior stomach.

Planctosphaera SPENGLER, 1932, p. 4 [**P. pelagica*; OD].
Hypertrophied, spherical tornaria-type larva with

bilateral symmetry; gut system U-shaped; mouth and anus close together on ventral side; surface covered by a complex ciliated band; internal organs occupy only a small part of the whole sphere. Extant: Atlantic and Pacific Oceans (no known fossil record).—Fig. 1.5. **P. pelagica* SPENGLER, Bermuda, western Atlantic Ocean (Hart, Miller, & Madin, 1994, fig. 1B).

The taxonomic and phylogenetic affinities of *Planctosphaera pelagica* are not clear but its morphology is like that of enteropneust tornaria (SPENGLER, 1932; VAN DER HORST, 1936) and its deep-water collection localities suggest that it may be a hypertrophied tornaria that has not undergone metamorphosis due to absence of a settlement cue (HADFIELD & YOUNG, 1983). HADFIELD (1975) and HALANYCH, TASSIA, and CANNON (2018) regarded the taxon as the giant larva of a deep-water enteropneust, thus, probably of the Torquaratoridae.

A few specimens of *Planctosphaera pelagica* were collected from deep-water trawls in the Bay of Biscay (SPENGLER, 1932; DAMAS & STIASNY, 1961) and other regions of the Atlantic Ocean (see SCHELTEMA, 1970, fig. 1), but it is also known from shallow water adjacent to Bermuda (HART, MILLER, & NADIN, 1994). Specimens from the Pacific Ocean are from a depth of 75–500 m near O'ahu in the Hawaiian islands (HADFIELD & YOUNG, 1983). SCHELTEMA (1970) suggested this was a warm-water species due to the biogeographic distribution of the few known specimens. HADFIELD and YOUNG (1983) suggested a worldwide distribution of this organism probably originating from abyssal depths. HART, MILLER, and MADIN (1994) described suspension feeding of a single living larva from surface waters near Bermuda in the western Atlantic Ocean.

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