

OTHER INVERTEBRATE TAXA

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Summary

This chapter provides information on several smaller groups of animals. Mesozoa are probably derived and simplified forms. They include the commensal Rhombozoa from the kidney of cephalopods and the parasitic Orthonectida. *Xenoturbella bocki* is another animal that lacks characteristics that indicate a relationship to one certain group. Kamptozoa (Entoprocta) and Sipunculida are spiralian taxa related to mollusks or annelids. Tardigrades and onychophorans are both related to arthropods. Arrow worms (Chaetognatha) are of unresolved phylogenetic relationships. They are an important element of plankton. The two last groups, Tentaculata and Hemichordata are probably not monophyletic. Tentaculata, which include the shelled brachiopods, the (mostly) colonial bryozoans and the worm-like phoronids, may either be related to deuterostomes or be spiralian. The two hemichordate taxa, Enteropneusta and Pterobranchia, are deuterostomes. Enteropneusts are burrowers in sediment, while pterobranchs are small colonial filter feeders.

1. Introduction

This article describes a variety of animal groups. To present a rough guideline, it will be convenient to start with a brief outline of metazoan phylogeny. It is generally agreed that Porifera branch off first, followed by the Cnidaria and then by a small taxon, Ctenophora. All remaining metazoans have a bilateral symmetry and are therefore called Bilateria. Among Bilateria, there is debate over the two highest ranked sister taxa. There is a taxon, Deuterostomia, including vertebrates, echinoderms, and some other groups. The sister taxa of deuterostomes may be found among tentaculates (Phoronida, Bryozoa, Brachiopoda), although this is not supported by molecular data (see *Tentaculata, or Lophophorata*). If tentaculate taxa are closely related to Deuterostomia, then this whole clade is named Radialia. The other clade is synonymously called Gastroneuralia or Protostomia. Among Gastroneuralia, Nematelminthes and Spiralia are sister taxa. Spiralia include platyhelminthes as a basal taxon and Trochozoa (spiralian with a trochophore larva) as more derived taxon.

The chapter starts with the enigmatic parasitic taxa Rhombozoa and Orthonectida, followed by *Xenoturbella bocki*, another animal for which a wide variety of phylogenetic hypotheses is available. Kamptozoa (Entoprocta) and Sipunculida are members of the Trochozoa. Two taxa, Tardigrada and Onychophora, are closely related to Euarthropoda. The chaetognaths are again of uncertain relationship. The three taxa Phoronida, Bryozoa, and Brachiopoda are often united as Tentaculata, but this taxon may be paraphyletic. The phylogenetic position of the tentaculates is also highly debated. Finally, two deuterostome taxa are presented that are often united as Hemichordata: Pterobranchia and Enteropneusta.

Important characteristics in the division of large taxa among Metazoa are the cleavage pattern and the further embryonic development (the fate of the blastopore). The structure of body cavities is also often referred to as a phylogenetically important structure. The primary mode of cleavage is radial, while spiral cleavage is derived. In spirally cleaving eggs, spindles become obliquely oriented and new cells are therefore given off slightly displaced in comparison with the mother cell. Radial cleavage is present, for example, in Porifera, Cnidaria, Deuterostomia, Tentaculata, and some other taxa, while spiral cleavage is hypothesized as a unique evolutionary development characteristic for the taxon Spiralia. During further development, a hollow ball is formed. Parts of the cells invaginate, leaving a pore at the outside, the blastopore. This is a generalized scheme, and many deviations are known. The further fate of the blastopore may be to become either the mouth or the anus of the adult. The primary mode is to become the mouth opening (although originally there is only one opening, with the function of both mouth and anus). In Deuterostomia the blastopore becomes the anus, and the mouth is a secondary, new structure. It should be mentioned that deuterostomy evolved sometimes in parallel among non-deuterostome (protostome) animals.

Body cavities are either completely absent (in many small taxa: acoelomate), are lined by extracellular material (primary body cavity), or by a cellular epithelium (secondary body cavity or coelom). An extracellular matrix (ECM) either surrounds cells (such as

muscle cells) or is an attachment layer for cells (such as the basal lamina for epithelial cells). If fluid is secreted into clefts in this ECM, large spaces may result that are then bordered by ECM. Primary body cavities and a coelom may coexist; for example, the blood vascular system and the coelom in annelids. Evolutionary scenarios starting with an acoelomate condition and reaching a coelom over an intermediate primary body cavity (pseudocoelom) are probably oversimplistic. Many so-called pseudocoelomate taxa are in reality acoelomate. The distribution of coeloms is patchy, and a multiple evolution of the coelom cannot be excluded (this is, for example, supported by the structure of excretory organs connected to the coelom, the metanephridia). Therefore, body cavities may be of minor phylogenetic importance.

	Taxon	Appropriate species number	Habitat
Mesozoa	Rhombozoa	70	commensal
	Orthonectida	30	parasitic
	Xenoturbellida	1	marine
	Kamptozoa	150	marine, freshwater
	Sipunculida	160	marine
	Tardigrada	600	marine, freshwater, terrestrial
	Onychophora	160	terrestrial
	Chaetognatha	120	marine
Tentaculata	Phoronida	15	marine
	Bryozoa	4500	marine, freshwater
	Brachiopoda	350	marine
Hemichordata	Pterobranchia	15	marine
	Enteropneusta	70	marine

Table 1. Summary of species numbers and habitats

2. Mesozoa

Mesozoa are a heterogeneous group comprising the two taxa Rhombozoa and Orthonectida. Both are parasites or commensals, are more or less simple in organization, but are complex in the mode of reproduction. Originally they were considered as intermediate between protozoans and metazoans (therefore Mesozoa), but several characteristics hint at them being real metazoans that probably were reduced during their parasitic history. The placement among metazoans is not clear. Neither morphological nor molecular data have produced a well-supported hypothesis. It only seems probable that Mesozoa is not a monophyletic taxon.

2.1. Rhombozoa

About 70 species of Rhombozoa known are all small animals (1 mm to 2 mm) composed of fewer than 40 cells. They live in the kidney of benthic cephalopods, probably not as parasites, but as commensals that do not negatively affect their host. In contrast, they may support the excretion of ammonia by acidification of the urine. There are two subgroups: Dicyemida with the majority of species, and Heterocyemidae with two species. The following data refer to the Dicyemida.

Dicyemida are composed of one long central cell, the axial cell, and surrounding jacket cells. Within the axial cell are 1 to 100 small reproductive cells (axoblasts) which either develop directly into an adult (via a so-called vermiform stage) or form oocytes and spermatozoa. This sexual phase is induced when population densities within the kidney become high. Fertilization and early development of the larva (the infusoriform larva) take place within the axial cell. The infusoriform larva leaves the axial cell and the host. It is composed of 37 to 39 cells, including two conspicuous apical cells at the anterior end. The mode of infection is not completely clear: larvae have been found in the stomach of cephalopods and later in the digestive gland, but how they reach the kidney is unknown.

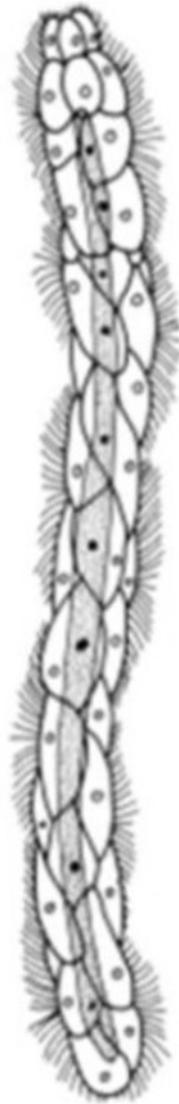


Figure 1. Generalized scheme of a dicyemid rhombozoan with internal axial cell and peripheral jacket cells (drawing after several authors)

2.2. Orthonectida

Orthonectida are extremely small animals (about 100 μ m) which are composed of 240 cells to 260 cells. About 30 species are known. They live intracellularly in several invertebrate taxa such as free-living platyhelminthes, annelids, mollusks, or echinoderms. Hosts are severely affected by hypertrophy of cells (e.g., muscle cells) and corresponding damage to the gonads.

Sexual stages of orthonectids have an epithelial layer of ciliated cells that surround a central mass of gametes. A cuticle, a sensory organ, and probably muscle cells are present. The male attaches to the female and transfers sperm; the fertilization is internal. The zygote develops into a free-swimming larva that infects new hosts. The outer

ciliated cells are shed, and the internal cells scatter and infect host cells. The parasitic stage is called the plasmodium. It reproduces through fragmentation and at some point develops into the sexual forms.

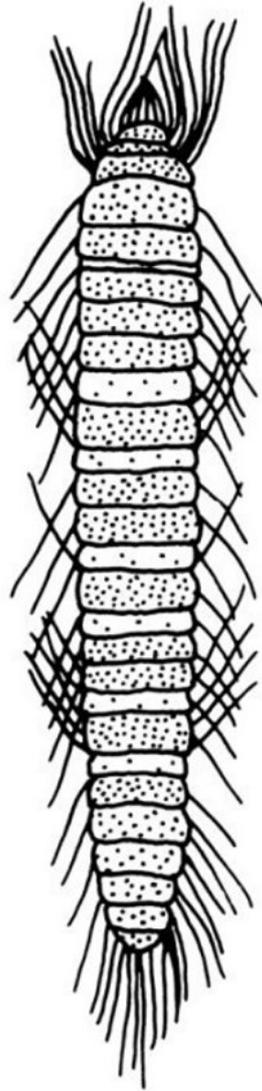


Figure 2. Male of the orthonectid *Ciliocincta sabellariae* (drawing after Ax 1995)

3. *Xenoturbellida* (*Xenoturbella* Bocki)

The species *Xenoturbella bocki* lives on muddy sea sediments in the Skagerrak and the Irish Sea. It has a more or less simple body organization, with an epidermis rich in glands, a plexus-like nervous system, and musculature underlying the epidermis and surrounding the sac-like intestine. An anus is not present. The mouth opens ventrally in the mid-region of the body. Characteristic is a ciliated transverse furrow in about the middle of the animal and a statocyst on the anterior end.

Xenoturbella bocki has been assigned to diverse taxa such as acoel flatworms (Platyhelminthes) and enteropneusts. Recently, it has been hypothesized as the sister group of all bilaterian animals or, due to the analysis of the 18S rDNA gene, as a highly

derived mollusk, is closely related to its prey species, bivalves of the taxon *Nucula*.

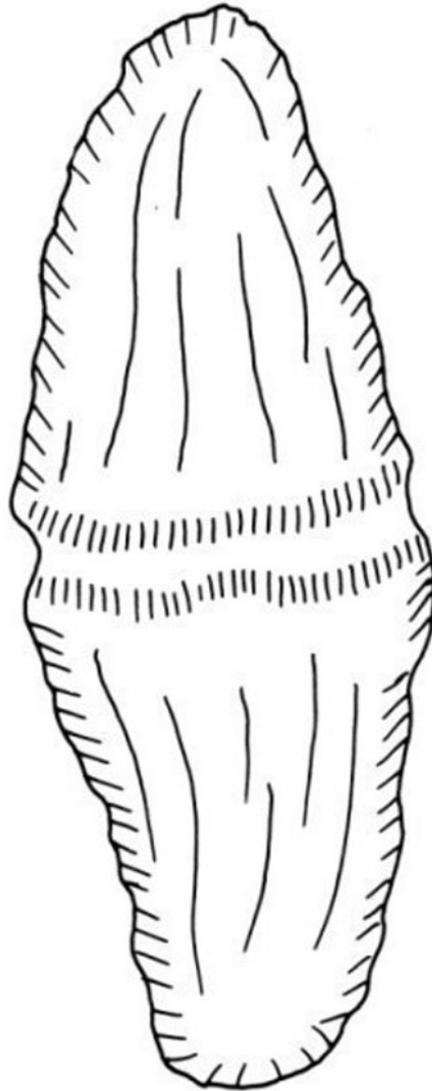


Figure 3. *Xenoturbella bocki* (drawing after Ax (1995))

4. Kamptozoa (Entoprocta)

With one exception (*Urnatella gracilis*), Kamptozoa are marine animals. They do not exceed 7 mm in size. The body consists of a stalk that is attached to hard sediments or other animals, and a calyx which carries all organs and a tentacular crown. With these tentacles, kamptozoans filter particles from the water. About one-third of all kamptozoans known to date form colonies. They occur in coastal regions worldwide.

The tentacles surround a central area containing mouth and anus (therefore *Entoprocta*). Consequently, the intestine is U-shaped. Food particles are filtered from the water by cilia on the tentacles, enclosed in mucus and transported by ciliary action toward the mouth opening. The anus is situated on a small papilla. Thereby the danger of feces

getting into the current containing nutrients is minimized.

Some groups of kamptozoans are hermaphrodites and others are dioecious. The oocytes are fertilized within the ovary, and eggs are kept in a special, pocket-like fold of the epidermis until the larval stage. A larva from the trochophore-type is free-swimming only for a few days, then attaches to substratum, and finally metamorphoses into the adult. Asexual reproduction is possible, with buds from the calyx. In colonies, specimens are connected by stolons. Some genera with abundant species are *Loxosomella*, *Pedicellina*, and *Barentsia*.

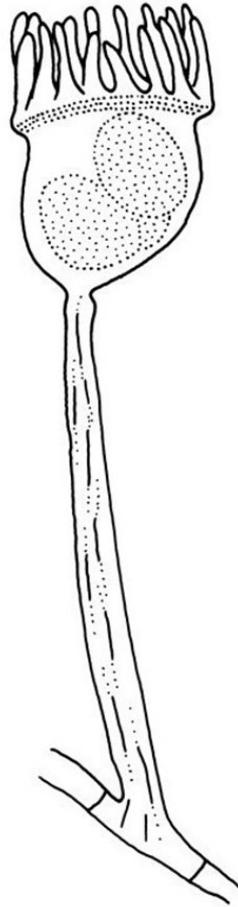


Figure 4. The kamptozoan *Pedicellina nutans* (drawing after Nielsen 1989)

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Biographical Sketch

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