Cycliophora

Introductory article

Reinhardt Møbjerg Kristensen, *Zoological Museum, University of Copenhagen, Denmark*

Article Contents

The cycliophorans are the recently discovered group of microscopic marine animals with an asexual and sexual life cycle. The only described species *Symbion pandora* lives on the mouth appendages of marine lobsters and have so far only been found in the Northern hemisphere. The phylogenetic position in the Animal Kingdom is still uncertain. Cycliophorans have been considered a sister group to Entoprocta and Ectoprocta or Rotifera and Acanthocephala.

Introduction

The marine Cycliophora is the most recently described phylum in the animal kingdom. Only one microscopic species, *Symbion pandora* has been described, by the Danish scientists Peter Funch and Reinhardt Møbjerg Kristensen in the journal *Nature* (14 December 1995). Investigations of mouth appendages of many decapod crustaceans worldwide resulted in the discovery of this new type of epibiont, living mainly on the setae of the mouthparts of lobsters. The type species was found on the Norway lobster, *Nephrops norvegicus*, in Scandinavian waters. Other cycliophorans were later found on mouth appendages of other lobsters such as *Homarus gammarus* and *Homarus americanus*. The cycliophorans have so far only been found on marine crustaceans from the northern hemisphere.

Basic Design and Life Styles

Cycliophorans are acoelomate metazoans with bilateral symmetry and well-differentiated cuticle. The sessile stage (**Figure 1**) is an animal with a body consisting of a ciliated buccal funnel ('head'), and ovoid trunk with U-shaped digestive system, and a stalk with a cuticular disc attaching the animal permanently to the host. The anus ('cloaca') is located outside the ciliated mouth ring close to the constriction ('neck') between buccal funnel and the trunk. The sessile animal (**Figure 2.6**) is the dominant feeding stage in a very complex life cycle. The sessile stage produces a single inner bud with a new buccal funnel and intestine; when the inner bud is fully grown it replaces the old feeding structures, and the old buccal funnel is finally cast off. Inner budding is repeated several times in the life of an individual (**Figure 2.8**).

In young large-sized sessile animals (300–450 μm long) the inner budding is coupled to the asexual formation of the mobile Pandora larva in a brood chamber (marsupium, **Figure 2.9**). A small new feeding stage develops through budding inside the rear end of the Pandora larva, when it is still in the brood chamber. The Pandora larva escapes through the cloaca or when the buccal funnel is cast off. This larva (**Figure 2.10**) is a poor swimmer and settles with head glands close to the mother individual. Soon it begins growth as described for the maternal individual, and finally it produces its own Pandora larva. This asexual part of the life cycle explains the large populations of feeding stages without males and females, as found on many lobsters.

Later in the life cycle, especially on lobsters near the end of the moulting cycle, sexually mature stages of the cycliophorans are found. Some sessile animals retract the ciliated mouth ring and stop feeding (**Figure 2.13**). Each of these feeding animals develops one dwarf male (primary male, **Figure 2.14**) in a manner similar to the development of the asexual Pandora larva. When this male leaves the brood chamber, it has only a very diffuse germinal area and lacks penile structures. It settles on a sessile individual, that is still feeding. This feeding stage will now develop a female inside the brood chamber. The female is about double the size of the primary male, and is very easy to recognize by the large single oocyte (**Figure 2.16**). The attached primary male has by internal budding developed one to three secondary males. Each secondary male has a tubular cuticular penis and a compartment with spermatozoa surrounded with a thin cuticle.

At some point internal fertilization of the egg happens inside the female, perhaps when she is still in the brood chamber, but very little is known about the sexual part of the life cycle in Cycliophora. The female with a single egg (zygote, **Figure 2.17**) then escapes from the maternal feeding stage, and after a short free existence settles on the mouthparts of the same crustacean host, but often on the palps a little away from the main population of asexual feeding animals. The female attaches in the same way as the Pandora larva, with the anterior, ventrally oriented cilia secreting the contents of numerous adhesive glands. After settling, the cilia are withdrawn and the head area forms the adhesive disc (**Figure 2.19**). The female degenerates and develops a cyst inside which a new type of larva (the chordoid larva) develops, nourished by the dying maternal cells and surrounded by the cuticular shell of the female (**Figure 2.21**).

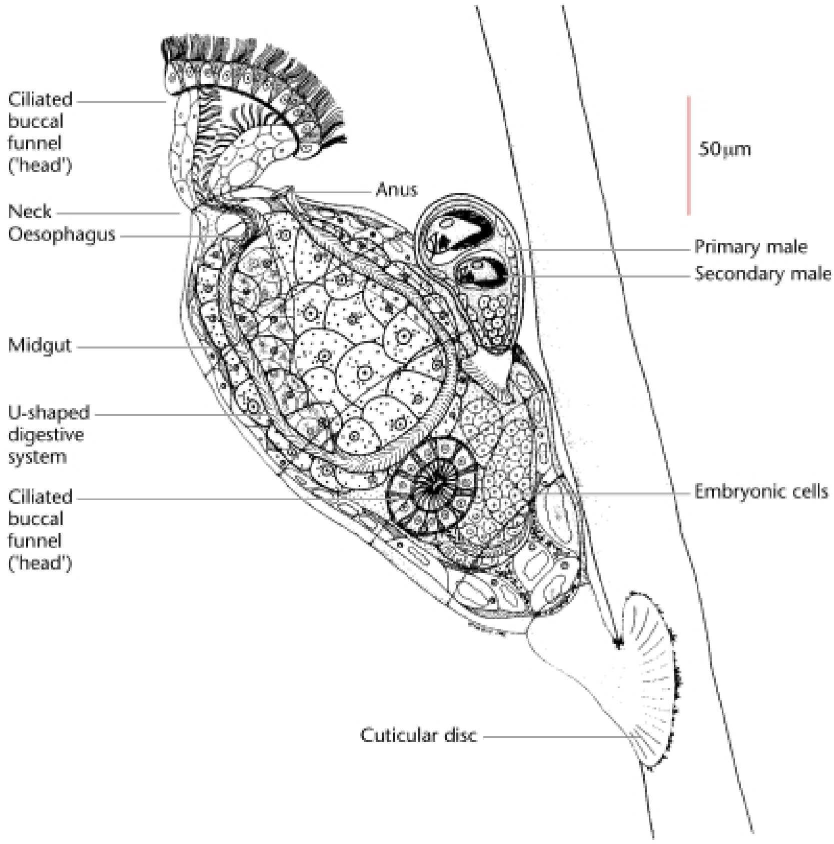

Figure 1 The holotype and allotype of *Symbion pandora* from Norway lobster *Nephrops norvegicus*. The holotype is an asexual feeding stage attached to a seta of the lobster. The allotype is a primary male with two secondary males inside. (Modified from Funch and Kristensen 1997, drawn by Stine Elle).

The chordoid larva is named after a mesodermal chordoid structure composed of 40–50 stacked muscle cells (**Figure 3**). This chordoid larva hatches with the head first (**Figure 2.22**). It is equipped with an extensive ventral locomotory ciliation, a pair of protonephridia, and numerous adhesive glands. The motile chordoid larva is a much better swimmer than the Pandora larva, and it is thought to be a dispersal stage for the cycliophorans (**Figure 2.23**). It settles on a new crustacean host (**Figure 2.1**), and after metamorphosis it becomes the sessile stage with an inner bud (**Figure 2.3**). This bud develops into the feeding stage initiating the asexual life cycle.

Phylogeny

In the classic descriptions of triploblastic animals three body cavity designs exist: acoelomate, pseudocoelomate and coelomate. According to this concept cycliophorans are acoelomate and should be placed close to Platyhelminthes. However, new ultrastructural research shows that the classic description of the body condition in the Protostomia does not have great value. Several scientists now suggest that such terms should be avoided. When the new phylum Cycliophora was established, striking similarities to some aschelminthes ('pseudocoelomate') groups were found, for example the ultrastructure of the cuticle of *Symbion pandora* is similar to that found in some Nematoda, Nematomorpha and Gastrotricha. The chordoid larva of *S. pandora* shows that the mesodermal chordoid structure resembles similar tissue found in *Chordodasys*, a genus of Gastrotricha. Other features superficially resemble rotifers. The precise phylogenetic relationship is unclear, but Entoprocta may be the strongest candidate to be the sister group of Cycliophora, and similarities (bud generation and brood chamber) to the coelomate Ectoprocta are also apparent.

The introduction of molecular data to the phylogenetic discussion of animal affinities has provided a new tool for resolving the problem of whether entoprocts are related to rotifers or to ectoprocts. Comparative anatomy using the most modern ultrastructural techniques has not yielded a consensus on this. The discovery of Cycliophora presented

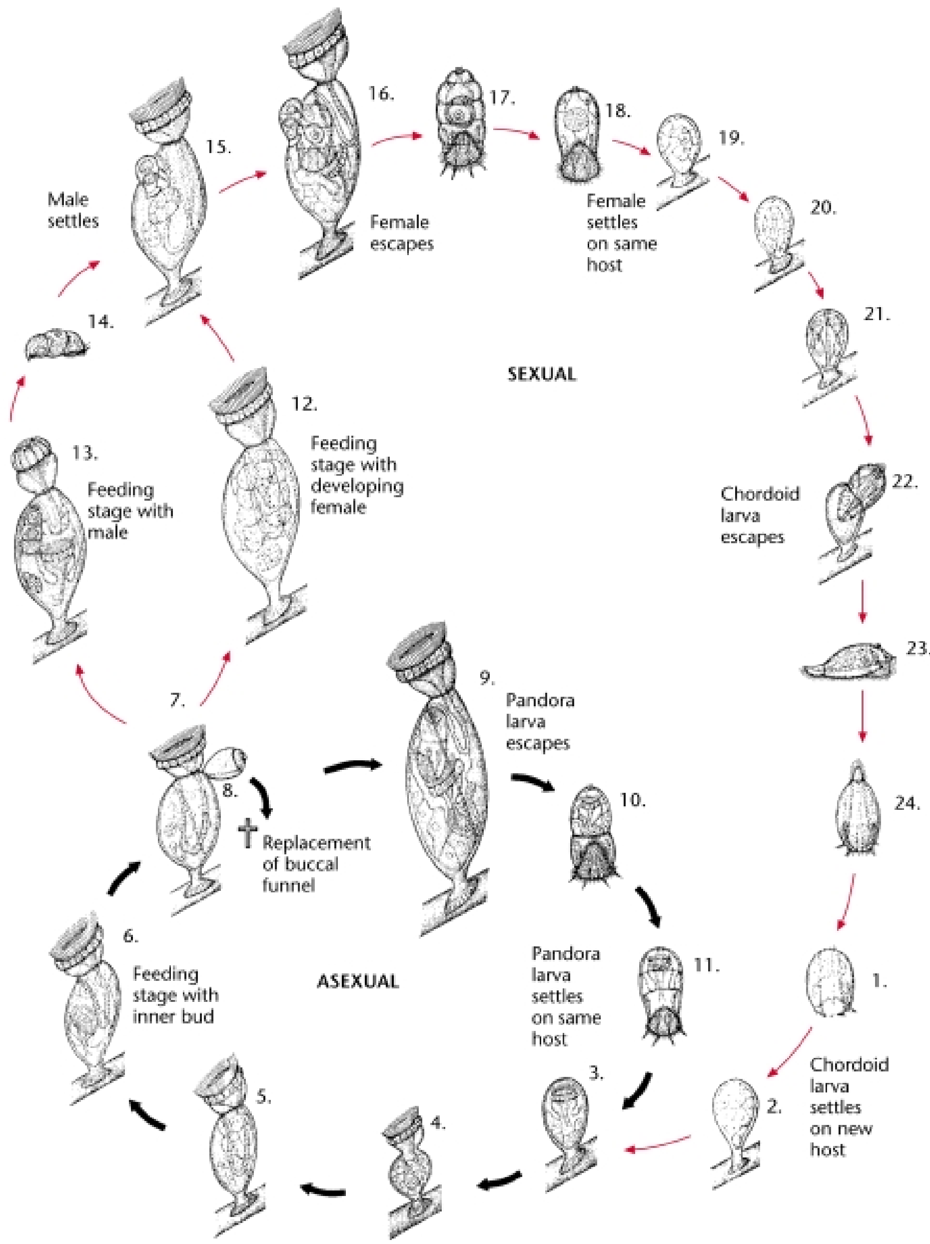

Figure 2 The proposed life cycle of *Symbion pandora* (numbers in the figure refer to those used in the text). The dominant stages in the life cycle are the feeding stages (4–9, 12–13, 15–16), so named because they are the only stages with a digestive tract. The feeding stage is attached to the mouthparts of the host with an acellular stalk and adhesive disc. The trunk contains a U-shaped gut, and basal to this undifferentiated cells continually produce internal buds. These buds develop into new feeding structures and other organs (5–6). Eventually a feeding stage also produces a Pandora larva asexually (9). Later, feeding stages switch to production of a primary male (13) or a sexually mature female (16). The Pandora larva (9), primary male (13), and female (16) are developed inside the feeding stages in a brood chamber. They are all short-lived and do not possess a gut. The Pandora larva develops a juvenile feeding stage from budding cells, while inside the feeding stage (9). A fully developed Pandora larva escapes from its maternal feeding stage (10), settles somewhere on the mouthparts of the lobster (11), and a new feeding stage develops from buds (4). When the primary male escapes (14), it seeks a feeding stage and attaches permanently (15). Some primary male organs then degenerate, but budding cells inside develop into several new individuals, tiny sexually mature males. Eventually a female develops inside the feeding stage (16). The female develops a single oocyte, while inside the feeding stage. This oocyte is fertilized either by hypodermic insemination, during release of the female or just after the release. Free females have a zygote inside (17) and later a 4-cell embryo may be observed (18). The female then settles on the mouthparts (19), degenerates and an embryo develops to a chordoid larva (19–21). The chordoid larva escapes from the old cuticle of the female (22), seeks an appropriate site on the mouthparts of a lobster, settles (1), degenerates (2), except for budding cells posteriorly, which develop into a new feeding stage (2–4). (Modified from Funch and Kristensen 1995; published in *Nature* **378**: 711–714.)

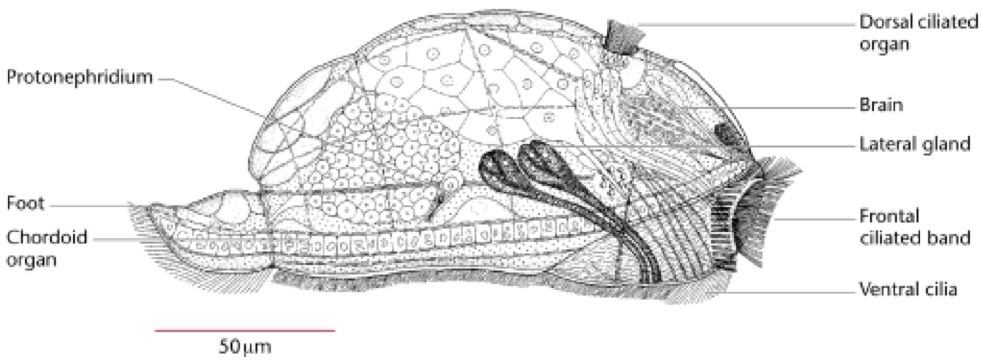

Figure 3 Free chordoid larva of *Symbion pandora*. Lateral view. The dorsal side has a uniform cuticle, except for the anterior part on top of the brain forming a rigid hood and the dorsal ciliated organ. The ventral side has cilia and several outlets of glands. The chordoid organ, composed of 50 stacked muscle cells, runs through the whole length of the larva. (Modified from Funch 1996, drawn by Stine Elle.)

a new dilemma: are cycliophorans related to rotifers or entoprocts/ectoprocts, or are cycliophorans merely neotenic entoprocts that have reduced the tentacular crown when they formed a commensalistic life cycle?

The new 18S rRNA data advocates a close relationship between Rotifera–Acanthocephala and Cycliophora and there is no evidence for the theory that cycliophorans are neotenic entoprocts. The morphological implications of a close relationship between rotifers and cycliophorans have until now been overlooked and further ultrastructural research is still needed, but the following morphological support can be given. In sessile rotifers (Collothecea) the digestive tract is curved (U-shaped) and the anus is located close to the coronal projections, but always outside the corona. The digestive tract is U-shaped in both entoprocts and cycliophorans, but in entoprocts the anus is located inside the tentacular crown. In cycliophorans the anus is located in the neck region outside the buccal funnel similar to sessile rotifers. The rotifers have a pharyngeal mastax with trophi, but it is in the process of degeneration in the collothecacean rotifers. The cycliophorans have no trace of a mastax, but could have lost it by reduction. If Acanthocephala is a subtaxon of Rotifera (as many scientists today believe) the mastax can clearly be secondarily lost in rotifers.

The life cycle is extremely complex in Cycliophora including two types of feeding stage and two types of larva. A similar complex life cycle is not seen in Rotifera, but if acanthocephalans (having several larval stages including acanthor larva, acanthella and cystocanth stage) are only parasitic bdelloid rotifers then the differences are not so large.

Conclusion

The cycliophorans are a recently discovered group of animals that have been considered as a sister group to Entoprocta or Entoprocta/Ectoprocta. New molecular data (18S rRNA) show that Cycliophora have affinities to Rotifera/Acanthocephala. Cycliophora have several striking similarities with sessile collothecacean rotifers.

Further Reading

Funch P (1996) The chordoid larva of *Symbion pandora* (Cycliophora) is a modified Trochophora. *Journal of Morphology* **230**: 231–263.

Funch P and Kristensen RM (1995) Cycliophora is a new phylum with affinities to Entoprocta and Ectoprocta. *Nature* **378**: 711–714.

Funch P and Kristensen RM (1997) Cycliophora. In: Harrison FW and Woollacott RM (eds) *Microscopic Anatomy of Invertebrates 13: Lophophorates, Entoprocta and Cycliophora*, pp. 409–474. New York: Wiley-Liss.

Hyman LH (1951) *The Invertebrates. Volume 3: Acanthocephala, Aschelminthes and Entoprocta. The Pseudocoelomate Bilateria.* New York: McGraw-Hill.

Nielsen C (1995) *Animal Evolution. Interrelationships of the Living Phyla.* Oxford: Oxford University Press.

Winnepenninckx BMH, Backeljau T and Kristensen RM (1998) Relations of the new phylum Cycliophora. *Nature* **393**: 636–638.