# Acoels

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***What are acoels?*** Acoels are small (less than 15 mm) soft-bodied, unsegmented worms. They live only in marine habitats and are found in all the world's oceans. They constitute their own clade 'Acoela', in which there are approximately 370 species. The name 'acoel' refers to their lack of a gut cavity as well as a coelomic cavity. Furthermore, they lack other features, such as a through gut as well as excretory and vascular systems. Instead, these animals have only a mouth opening on the underside and a syncytial digestive system, in which they digest unicellular algae or other prey.

***What do they look like?*** At first sight, the most prominent feature of these completely ciliated worms is the single gravity sensing organ, or statocyst, located at the anterior end of the animal (Figure 1). In some species, strings of ripe oocytes are also clearly visible. Some species have two or four 'eyes' that are each composed of only two cells — one pigment cell and one receptor cell — the simplest known eyes in the animal kingdom. Their nervous system consists of a 'brain' considered to be a nerve ring in the area of the statocyst. From this 'brain', between three and six pairs of nerve cords extend to the posterior tip of the body. Despite considerable variation between species, this still represents one of the simplest nervous systems found in bilateral animals. Taken together, acoels are among the simplest free living bilaterians.

***How do acoels 'do it'?*** Acoels are hermaphroditic and nearly all species reproduce sexually by mating and — somewhat unusual for marine animals — internal fertilization. They can often be male, female or sequentially hermaphroditic, first male, then female. Despite having very few organs, acoels have a highly developed copulatory apparatus, which varies a lot between species and has been traditionally used for classification. The copulation of hermaphrodites is mutual, such that each partner transfers its sperm to the other. This 'allosperm' is then stored in some species in a female organ called a 'seminal bursa' until the eggs are ready to be fertilized. Acoel spermatozoa are very unusual in that they have two flagella, a feature only found in one other animal group. More dramatically, some species mate by hypodermic impregnation in which one animal directly injects sperm into the body of another, and the sperm then migrates to the bursa.

***Interesting, and how do they produce offspring?*** While in some acoels the fertilized eggs are released through the mouth — as jellyfish and corals do — a few species have developed a special opening — a female gonopore — through which the oocytes are released. All acoels possess a male gonopore, through which the sperm are released. Eggs are laid in clusters embedded in jelly. Developing acoel embryos show an unusual cleavage pattern, called 'duet cleavage', which is unique among the bilaterians. It is a stereotyped cleavage program, which allows tracing back the expression of developmental genes to individual blastomeres with known cell fate. Acoels hatch as miniature worms, without an intervening larval stage. Besides sexual reproduction, acoel worms of the genus *Convolutriloba* can reproduce asexually by either budding off parts of their body or dividing by fission, a process linked to the capacity for regeneration. This regenerative capacity can be explained by the proliferation of unique stem cells called 'neoblasts'. Another mode of vegetative reproduction is seen in the species *Paratomella rubra*, which forms chains of smaller animals that bud off at the posterior end ('paratomy').

***Where do they live?*** Most acoels live in marine habitats, in tropical and temperate zones, as well as polar regions. They are often 'interstitial', meaning they live between sand grains or gravel on beaches and on the sea bottom, forming part of the benthic meiofauna. Some species, such as *Hofstenia miamia*, live on submerged mangrove leaves and roots. Most acoels are free-living, but can also live as commensals — a type of non parasitic interaction — on or in other marine invertebrates. Acoels of the genera *Waminoa* and *Convolutriloba* live on corals and are often found reproducing successfully in tropical reef aquaria. Yet other

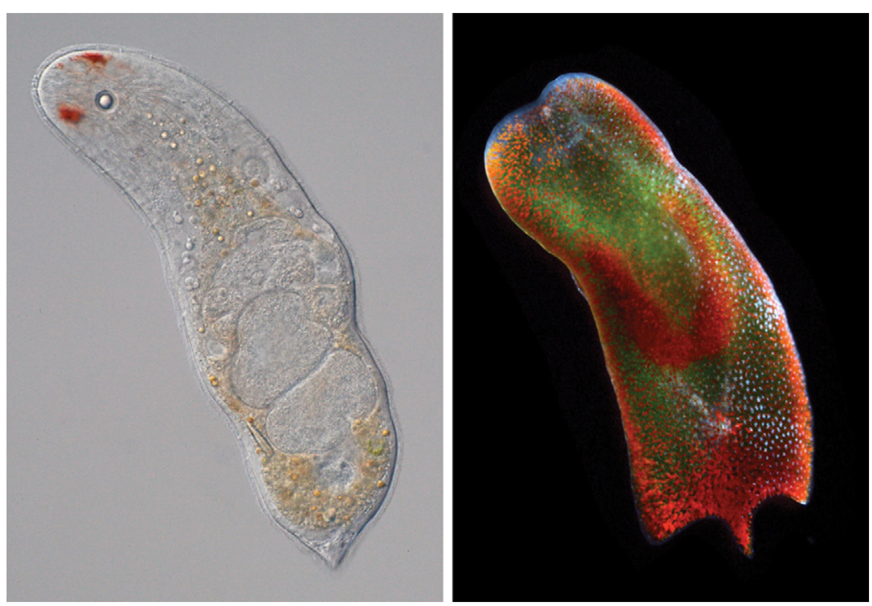

Figure 1. Two species of acoel.

Left panel: The acoel *Notocelis gullmarensis* (photo by Ulf Jondelius) is 800 micron in length. The statocyst is visible between the red eye fields and two large egg cells can be seen in the lower half. Right panel: *Convolutriloba longifissura* (photo by Eric Roettinger). The green body colour of the adult comes from algal symbionts integrated in its skin. The red stripes in the middle of the body of this 3 mm long worm indicate mature oocytes.

species have been described as pelagic, i.e. living freely in the water column. As is often the case with poorly studied microscopic animals, there probably remains a large number of undescribed acoel species, and possibly lifestyles.

***Why are some acoels known as 'plant-animals'?*** The acoel groups Convolutidae and Sagittiferidae live in symbiosis with unicellular algae (Figure 1). The acoel *Symsagittifera roscoffensis*, for instance, can be found in dense, spinach green mats in the intertidal zone on the beaches of southern England and northern France. *Symsagittifera* forms a symbiosis with the alga *Platymonas convolutae*. *Symsagittifera* acoels are born colourless and acquire the free-living flagellated algae from the surrounding sea water three days after hatching. This symbiosis is obligate: as adults, the worms stop feeding and are entirely dependent on light and algal photosynthetic products. Animals which are kept free of algae after hatching do not survive. After ingestion, *Platymonas* algae migrate below the epidermis of the animal, establish themselves extracellularly, change shape and lose their flagella, theca and eyespot. *Symsagittifera* worms, in turn, come up to the surface to bask in the bright midday light. In *Convolutriloba longifissura* (Figure 1), symbiosis is also obligate but the worms also continue to feed. Symbioses of this kind are of particular interest as they are a source of evolutionary novelty and have in the past contributed to the evolution of major lineages, and to the exchange of genetic material between host and symbiont.

***What are acoels related to?*** Acoels were until recently thought to belong to the flatworms or 'Platyhelminthes', which also include parasitic tapeworms and trematodes, because their gross anatomy looks very similar. New evidence now shows that not all so-called 'flatworms' belong to one group. Instead, molecular studies clearly show that the acoels fall outside the major group of flatworms and originated before the last common ancestor of all the bilaterally symmetrical animals. The remaining flatworms are related to other, morphologically more complex animals, such as annelids and molluscs. Acoels are thus of particular interest, as they represent a primitively simple branch at the base of the bilaterian tree of life. Another small group of flatworms, the nemertodermatids, are considered a sister group of the acoels and together they form the 'Acoelomorpha'.

***Why are acoels interesting from an evolutionary perspective?*** A puzzling question in animal evolution is what the last common ancestor of all bilaterally symmetrical animals, or 'Urbilateria' might have looked like. Did this animal already have complex morphological traits, such as segments, a body cavity, a through gut and a centralized nervous system — similar to, say, annelid worms — or was it, rather, a small unsegmented marine worm with a very simple body plan, such as an acoel? In 1882, Ludwig von Graff already considered acoels as possibly representing the bilaterian ancestor. However, all extant animals feature a mix of ancestral characters — primitive traits inherited from the ancestor — and derived characters — traits which have been more recently evolved, and were not present in the common ancestor. Thus, strictly speaking, there can be no such thing as a 'living fossil', and one cannot really say if the Urbilateria looked like an acoel or not. Instead, what is likely to be ancestral or derived has to be inferred from comparisons between extant animals. For instance, many features of bilaterians that are absent from acoels are also missing in cnidarians, such as a through gut, a centralized nervous system and nephridia. It is thus parsimonious to assume that the lack of these features may indeed be ancestral for the acoels.

***Sounds as if they are worthwhile studying?*** Before they were moved to their new, important phylogenetic position at the base of the bilaterian tree of life, research on acoels was focused mainly on their stem cell system and their ability to regenerate large parts of their body as well as on the algal symbiosis. Due to their phylogenetic position, many aspects of acoel biology gain significance. Their morphological and developmental features make them an excellent proxy for reconstructing the bilaterian ancestor, as well as the nature of specific cell–cell interactions in this ancestor. The primitive immune system of acoels may also help explain the evolutionary roots of more complex immune systems, including that of humans. Acoels will inevitably receive a lot of attention by biologists in the future. There are as yet no genome projects of acoels, but large collections of expressed sequence tags have been generated and used in phylogenomic studies. With the development of new sequencing technologies, we will surely have genome sequences from several easily cultured acoel species, such as the *Convolutriloba* species, *Isodiametra pulchra* and *S. roscoffensis.* These genomes will provide deeper insights into the evolutionary roots of genome organization and the role of developmental gene networks in the evolution of most organ systems.

***Where can I find out more?***

Gschwentner, R., Ladurner, P., Nimeth, K., and Rieger, R. (2001). Stem cells in a basal bilaterian. S-phase and mitotic cells in Convolutriloba longifissura (Acoela, Platyhelminthes). Cell Tiss. Res. *304*, 401–409.

Hejnol, A., and Martindale, M.Q. (2008). Acoel development indicates the independent evolution of the bilaterian mouth and anus. Nature *456*, 382–386.

Henry, J.Q., Martindale, M.Q., and Boyer, B.C. (2000). The unique developmental program of the acoel flatworm, Neochildia fusca. Dev. Biol. *220*, 285–295.

Keeble, F. (1910). Plant-Animals: A Study in Symbiosis. (London: Cambridge University Press.)

Raikova, O.I., Reuter, M., and Justine, J-L. (2001). Contributions to the phylogeny and systematics of the Acoelomorpha. In Interrelationships of the Platyhelminthes, ed. D.T.J. Littlewood, and R.A. Bray. (London: Taylor & Francis), pp. 13–23.

Rieger, R., Tyler, S., Smith, J.P.S., and Rieger, G.E. (1991). Turbellaria. In Microscopic Anatomy of Invertebrates: Platyhelminthes and Nemertea ed. F.W. Harrison, and B.J. Bogitsh. (New York: Wiley.) vol. 2, pp. 7–140.

Ruiz-Trillo, I., Paps, J., Loukota, M., Ribera, C., Jondelius, U., Baguñá, J., and Riutort, M. (2002). A phylogenetic analysis of myosin heavy chain type II sequences corroborates that Acoela and Nemertodermatida are basal bilaterians. Proc. Natl. Acad. Sci. USA *99*, 11246–11251.

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