Ctenophora

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Introductory article

The Ctenophora are a small group of marine invertebrates most of whom have eight longitudinal rows of fused macrocilia, called comb rows, which they use to propel themselves through the water.

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Basic Design

Ctenophores constitute a small phylum of invertebrate animals. The name of the phylum, which is Greek for 'comb bearer', provides an immediate clue to their identification. Most ctenophores have eight longitudinal rows of fused macrocilia, called comb rows, which are used to propel the animals through the water. In fact, they are the largest organisms that use cilia for propulsion. Ctenophores have an extremely simple body plan, and were once joined with the phylum Cnidaria into a single phylum called the Coelenterata, because of this simplicity (**Figure 1**). They are, in contrast to cnidarians, biradially rather than radially symmetrical. Ctenophores have an outer skin, the ectodermal layer, separated from the inner skin, the endodermal layer, by a poorly differentiated gelatinous layer of varying thickness, called the mesogloea. Ctenophores have a digestive system consisting of mouth, stomodaeum and infundibulum, from which radiate various canals which provide nutrition to the body. Like the Cnidaria, they lack an anus, and undigested material is voided through the mouth. Food is captured with macrocilia, or with paired tentacles or structures elaborated from the body surface, which are equipped with adhesive cells called colloblasts. Colloblasts are unique to ctenophores. The digestive system and tentacular apparatus are used to define the morphology of ctenophores. The mouth defines the oral pole, and one imaginary major plane of symmetry is defined by the stomodaeum, which is usually flattened, and called the stomodaeal plane. A second major plane is called the tentacular plane, because it passes through the bases of the two tentacles. Therefore, the four comb rows that pass adjacent to the plane of the stomodaeum are called the substomodaeal comb rows, and the four comb rows that pass adjacent to the tentacle bases are called the subtentacular comb rows.

The sensory apparatus of ctenophores is very simple. The most prominent sensory structure is the statocyst, which lies at or slightly beneath the aboral pole. This structure is supported by four macrocilia, and modulates the beating of the combs in the comb rows. Many ctenophores are sensitive to light and mechanical stimuli, but appear to have no specific organs to detect them. Indeed, ctenophores have been described as being at the tissue, rather than the organ, grade of construction.

Most ctenophores are simultaneous hermaphrodites, capable of self-fertilization, but members of one genus, *Ocyropsis*, have separate sexes. Only members of the Platyctenida have been reported to be capable of asexual reproduction. Further, although some platyctenids have brood pouches, most ctenophores have external fertilization, with development occurring in the plankton.

Diversity and Life Styles

All ctenophores that are presently known are predators. They are restricted to the marine environment, with the greatest diversity in the open sea. Most ctenophores are strongly bioluminescent. The phylum is a small one, and is divided into two classes, primarily based on differences in development: the Tentaculata and the Nuda.

The vast majority of ctenophores belong to the first class, which is divided into several orders. All members of this class pass through a developmental stage resembling the Cydippida and thus all have paired tentacles, at least at some stage in their development. The orders familiar to most people are the Cydippida, the Lobata, the Platyctenida and the Cestida. Cydippids are planktonic and usually small, ranging in size from a few millimetres to tens of centimetres. They feed on a wide variety of prey, ranging from small crustaceans to fish. Perhaps the best-known cydippid is *Pleurobrachia pileus*, the sea gooseberry, which becomes extremely common in the North Sea in spring, and is often found on beaches, looking like small, transparent golf balls. Lobates are also planktonic, and are characterized by (usually) large structures at the oral pole, the oral lobes, which are used to capture prey. Perhaps the best known lobate is *Mnemiopsis leidyi*, which was recently accidentally introduced into the Black Sea, causing considerable damage to the fisheries. Lobates are usually larger than cydippids, ranging in size from one centimetre to over a metre. Platyctenids are the only benthic group of ctenophores, and are generally small and cryptic, so that they are often mistaken for flatworms, since most species lack comb rows. They are often brightly coloured, mimicking the coloration of their specific substrates. Cestids are long and ribbon-shaped, ranging in size from a few centimetres to over a metre, and the best known species is *Cestum veneris*, commonly called the

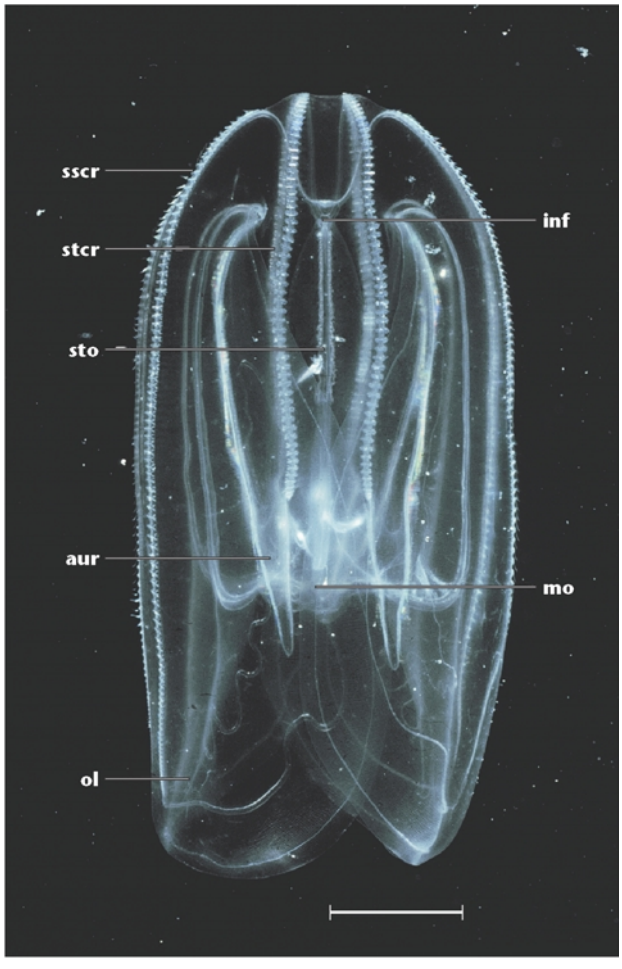

Figure 1 The lobate ctenophore, *Mnemiopsis leidyi*, illustrating the body plan of ctenophores. Bar, 1 cm. Abbreviations: aur, auricle; inf, infundibulum; mo, mouth; ol, oral lobe; sto, stomodaeum; sscr, substomodaeal comb row; stcr, subtentacular comb row.

Venus' girdle. They are planktonic, have the eight comb rows reduced to four, and feed on small prey.

The second class, the Nuda, contains primarily members of the genus *Beroe*, which completely lack tentacles in all stages of development. In further contrast to other ctenophores, species in this group use fused macrocilia, rather than colloblasts, for the capture of prey. Members of this group range in size from a few centimetres to tens of centimetres, and prey on other gelatinous organisms, such as other ctenophores and salps.

Fossil History and Phylogeny

Since ctenophores are gelatinous, their fossil record is extremely limited. Several organisms from the Palaeozoic Era have been described as ctenophores. Some of these resemble modern ctenophores, but others diverge widely from any presently known species. It is not clear at this stage whether or not these organisms should be placed in the phylum Ctenophora.

The phylum that is most closely related to the Ctenophora is not presently known. Ctenophores superficially resemble the Cnidaria, but these similarities are primarily based on features lacking in both groups, such as a developed mesoderm, an anus and well-developed organs. It has also been suggested that ctenophores arose from the Platyhelminthes, but few support such a view today. Molecular studies have thus far failed to elucidate their relationships with other phyla.

Within the Ctenophora, evolutionary relationships are not completely understood. Within the class Tentaculata, the orders Lobata and Cestida appear to be monophyletic, since each order has developed unique and characteristic structures. Although members of both orders have larvae that resemble adult cydippids, it is not clear how closely related the two orders are. It is very likely that the Cydippida and Platyctenida are polyphyletic. Since the class Nuda is small, homogeneous and restricted to only a handful of genera, it is very likely to be monophyletic.

Further Reading

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