Quick guide

Ctenophores

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What are ctenophores?
Ctenophores — pronounced 'teen-o-for' or 'ten-o-for' — are more commonly known as comb jellies. They comprise a group of gelatinous zooplankton found in all the world's seas. There are about 150–200 described species; most are holopelagic (that is, they live in the open ocean), but new species continue to be discovered in blue-water and deep-sea regions. Most ctenophores are transparent or translucent, and range in size from millimeters up to two meters in length, although most are in the few centimeter range. Some of the more common animals are the sea gooseberry (genus *Pleurobrachia*), the sea walnut (genus *Mnemiopsis*) and the Venus' girdle (genus *Cestum*). Most of these beautiful and exquisite animals are not very well studied because they are either difficult to obtain or extremely delicate (or both).

Ctenophores are distinguished from all other animals by their comb rows, which are their primary means of locomotion, besides passively drifting *via* ocean currents. The word 'ctenophore' itself comes from the Greek meaning 'comb-bearer'. Each of the eight comb rows runs longitudinally down the length of the animal and is made up of individual comb plates. Each comb plate is made up of thousands of parallel linked cilia, the rhythmic and coordinated beating of which propels the ctenophore through the water. It is also because of these comb plates that ctenophores often display a colorful, rainbow-like iridescence, as the cilia in the comb plates act as diffraction gratings. Most ctenophores are also capable of bioluminescence — producing light via specialized photocytes located under the comb rows.

Their main body axis is the oral-aboral axis, which is demarcated by the mouth at one end and the apical sensory organ at the other end. They have a simple blind gut with a branching endodermal canal system. Ctenophores are also characterized by a pair of tentacles that they spread out like a web to catch zooplankton prey, such as small crustaceans and even small fish. There is even one group of ctenophores, the Beroids, which feeds on other ctenophores, and there are also a few groups that are benthic (they absorb their comb plates following embryonic development and creep along on the ocean floor). Ctenophores have a relatively complicated nervous system consisting of a peripheral nerve net and the apical sensory organ used to sense gravity, and possibly light as well. All ctenophores possess a pair of small anal pores located adjacent to the apical sensory organ thought to control osmotic pressure. They are not quite as 'simple' as one might first imagine.

How are they different from cnidarians? While comb jellies do bear a superficial resemblance to cnidarian medusae ('jellyfish') and were originally grouped with cnidarians in a clade known as the 'Coelenterata', closer inspection shows that they are quite distinct. Cnidarian medusae are said to be radially symmetrical around their oral-aboral axis, while ctenophores display a special form of biradial symmetry, with no planes of mirror symmetry but rather an infinite number of planes of rotational symmetry.

Ctenophores and cnidarians differ in their mode of locomotion. Ctenophores move through the water by beating their comb rows — they are the largest animals to move entirely by ciliary movements — but they also have a complex array of definitive muscle cells. This contrasts with cnidarian medusae, which lack individual muscle cells and move by 'pumping' pulsations of myoepithelial sheets of cells. Cnidarians have cnidocytes, or stinging cells, which penetrate and inject toxins into their prey, whereas ctenophore tentacles have distinctly different colloblasts, or sticky cells, that are used to entangle prey until they can bring them to their mouth and consume them.

Furthermore, their development and life cycle is completely different. Nearly all ctenophores are direct developing, holopelagic, and self-fertile hermaphrodites. Eggs are fertilized as they are released in the water and develop with a highly stereotyped cleavage program which in less than 24 hours gives rise to the characteristic cydippid stage, essentially a miniature adult. In contrast, cnidarians that make medusae have highly variable, biphasic, pelagio-benthic metagenic life histories. In general, medusozoans exhibit highly variable modes of embryogenesis that give rise to swimming, but non-feeding, planula larvae that metamorphose to form benthic polyps. This polyp then buds off pelagic medusae, the reproductive phase of the life cycle which make functional gametes. The ctenophore life history is much simpler in comparison.

Why do people study ctenophores?
Although historically (late 19th century) ctenophores were known as exquisite developmental material for experimental embryologists, more recently they have been in the news for their devastating ecological impact as invasive species. Their ability to grow and reproduce quickly has made at least one western Atlantic species, *Mnemiopsis leidyi*, *persona non grata* around the world. The accidental introduction of this species to European waters on multiple occasions in the past two decades led to population blooms in the Black and Caspian Seas, and more recently the North Sea, where *Mnemiopsis* was blamed for drastic declines in local fisheries. There is therefore a huge economic importance to understanding ctenophore biology to prevent or control these invasions.

Ctenophores are interesting in their own right however. Their embryos are crystal clear, which makes imaging early features of fertilization, the cell cycle and cell division possible. They are ideal systems for studying adult wound healing and regeneration; they have bioluminescent cell types, and they are capable of generating functional gametes precociously during cydippid and juvenile stages (called dissogeny).

Why are they interesting from an evolutionary point of view?
Ctenophores have always been difficult to place phylogenetically. While identifying what is or is not a ctenophore has not been so challenging, there has always

Figure 1. A ctenophore.

Oral view of a ctenophore (genus *Ocyropsis*), highlighting the two large oral lobes used for feeding and the rainbow-like iridescence caused by diffraction of light through the comb plate cilia. (Photo courtesy Mattias Ormestad.)

been contention regarding how ctenophores are related to other animals.

It has always been assumed that animal complexity was somewhat related to a group's evolutionary history. Simple sponges, which have only a dozen or so cell types, were thought to be the simplest group of animals that arose from some kind of choanoflagellate-like unicellular ancestor. Further morphological complexity, such as the evolution of true epithelial tissues, allowed the evolution of such groups as the placozoans, cnidarians, ctenophores, and subsequently the large radiation of bilaterally symmetric animals (bilaterians).

But a recent molecular study has re-examined animal phylogeny by looking at many genes from a much broader range of animal diversity. This phylogenomic study unexpectedly found high statistical support for ctenophores being the earliest branching extant animals, diverging even before sponges. While there is reason to be cautious, as limited sponge and placozoan data were available at the time of this study, these results are very exciting as they suggest an evolutionary scenario that has never been considered before.

Why does the new phylogenetic position matter? It could have a huge impact on our understanding of animal evolution. How did the first animals evolve? What morphological features were present in the first animals? Ctenophores have a definitive nervous system and muscle cells, where none have been described in sponges or placozoans, and cnidarians have a nervous system but no mesodermally derived muscle cells. If ctenophores are indeed a basally branching group, were these features lost in these more derived groups? Was the metazoan ancestor a direct developing, holopelagic animal with a stereotyped cleavage program that lived completely in the water column and never roamed the ocean floor? Or are the muscle cells, nervous system, symmetry properties, and other 'advanced' morphological features of ctenophores independently invented in their long isolated evolutionary history? Were there bottlenecks in the history of Earth in which features of stem-group ctenophores were lost (possibly a benthic or sessile stage in their life history)? Even though ctenophores may be at the base of the animal tree of life, they have been evolving on their own branch for millions of years, so how they achieved their current complexity is a very interesting area of study.

How will we know what is their correct position? Sequencing of a ctenophore genome would be very helpful in elucidating gene content, structure and gene evolution. And improved phylogenomic sampling of additional basal metazoan taxa would help to increase the resolution at these deep evolutionary nodes. In conjunction with advances in paleontology and imaging techniques of microfossils, including embryos, in the next couple of years this should provide a clearer picture of the phylogenetic relationships and morphological features of the earliest organisms on the animal branch of life.

Where can I find out more?

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