



Comb jellies

Zoologist **Catherine McCrohan** introduces these fascinating animals, and explains how they contribute to the debate on the evolutionary origin of the nervous system

Comb jellies (Ctenophora) are a distinct phylum of marine animals that are sparking interest among scientists because of what they might reveal about the evolution of all animals. There are around 200 known species of ctenophore, inhabiting both deep, surface and coastal waters around the world. Their common name – comb jelly – comes from their transparent, gelatinous body and possession of ‘combs’ of external cilia that are used for locomotion. Body size varies from a few millimetres to over a metre in length. Nearly all are predators, feeding on plankton, larvae, small crustaceans and other ctenophores.

Comb jellies possess a nervous system, and this is exciting researchers who want to

understand how the nervous system evolved. So far, studies of these fascinating creatures raise more questions than answers.

What do we know about ctenophores?

Many of these beautiful, ocean-living species are difficult to obtain, and to maintain and breed in the laboratory. Much of what we know about the group comes from studies of the coastal ‘sea gooseberry’ (*Pleurobrachia pileus*) and ‘sea walnut’ (*Mnemiopsis leidyi*), both of which are relatively easy to study. Further studies delving into ctenophores’ diversity, physiology and range are more limited (see Box 1).

The comb jelly body consists of two cell layers either side of a gelatinous matrix. Eight rows

Box 1 Diversity of ctenophores

There are two classes of ctenophores:

- Tentaculata possess tentacles and fall into eight orders.
 - Nuda, with no tentacles, comprise a single order.
- Within the classes and orders there is much diversity. Body shape may be rounded (e.g. *Pleurobrachia*), lobed (e.g. *Mnemiopsis*), flat or ribbon-like. Different species range from sub-zero polar seas to tropical waters of 30°C, and some thrive in low-salinity, estuarine water.

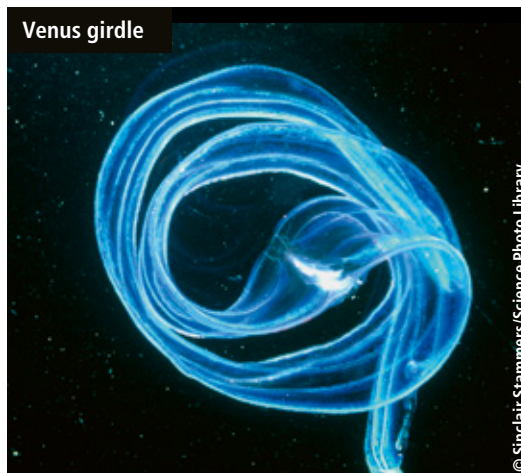
Many species show distinct adaptations. The cigar comb jelly (genus *Beroe*) belongs to the Nuda class. It has specialised cilia just inside the mouth. These are associated with a hard substance, forming hooked ‘teeth’, which are used to tear up prey as soon as it is ingested. The Venus girdle (*Cestum veneris*) is the largest comb jelly so far identified. It is ribbon-shaped – over a metre long and about 5 cm wide. In addition to beating rows of cilia, swimming is aided by waves of muscle contraction along its body.

Cigar comb jelly



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Venus girdle



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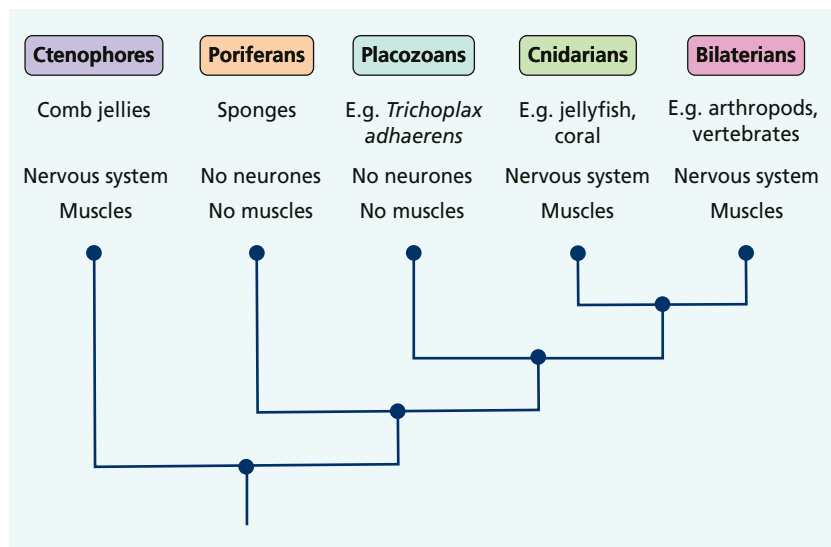


Figure 1 Proposed origin of the five animal lineages. Bilateria includes all animals that show bilateral symmetry as embryos, including vertebrates. Placozoans are simple, multicellular marine organisms, resembling ‘multicellular amoebae’

of elongated cilia – combs – extend along the body, and these beat in coordinated waves that propel and steer the body. Most species possess tentacles near the mouth, which can be retracted or extended.

Unique, multicellular structures on the tentacles, called colloblasts, are used to capture prey. A coiled filament is rapidly discharged from the colloblast, together with a sticky substance that adheres to the prey, which is then taken to the mouth. A central body cavity functions as the gut. At one end, the mouth and pharynx are controlled by muscles, allowing the comb jelly to ingest and process food. Food is digested by secreted enzymes and absorbed by nutritive cells within the epithelium that lines the cavity.

The epithelium also incorporates germ cells that produce eggs and sperm, which are released into the surrounding water prior to

fertilisation. It also contains cells that generate bioluminescence. Bioluminescence contributes to the beauty of these creatures, alongside their graceful locomotion.

Comb jellies provide a nutritious and easily digested meal for predators. These include fish, jellyfish and turtles. They are therefore an important component of the marine food web, both as a food source and by limiting populations of species whose larvae they consume. This can lead to ecological and economic impacts (see Box 2).

Ctenophore ancestry

To investigate an organism’s place in the tree of life, the best sources are the fossil record and phylogenetics. Despite their soft bodies, some fossil evidence is available, showing that animals resembling ctenophores first appeared more than 500 million years ago. But fossils cannot tell us how they arose from the last common ancestor of animals – the **animal LCA** – or when and how they diverged from other animal groups.

The main debate centres around the ancestral lineages of ctenophores and sponges (Porifera). Sponges are animals that possess neither nerves nor muscles. Based largely on morphological evidence, it was initially assumed that sponges diverged first from the ancestors of all other animals, including comb jellies. However, recent phylogenetic studies using genome sequencing suggest that ctenophores split from the animal lineage before sponges (see Figure 1). This conclusion is based on analysis of key genes and DNA sequences that place sponges closer to other animals, including vertebrates, than the ctenophores. If this is the case, then we have to explain why sponges lack many key features shared by their ‘closer’ relatives – features that are present in ctenophores.

Box 2 Ecological impacts

Research has highlighted the impact of invasive ctenophores on marine communities and fisheries.

Mnemiopsis

In the 1980s, *Mnemiopsis leidyi* was inadvertently introduced into the Black Sea, probably via shipping. It quickly established a large population that preyed on fish larvae and on the prey items of adult fish. This led to a significant reduction in fish catches. The situation was rescued by the introduction of another comb jelly, *Beroe ovata*, whose main food source is other, smaller, comb jelly species such as *Mnemiopsis*. *Mnemiopsis* numbers have declined, though they are still thriving.

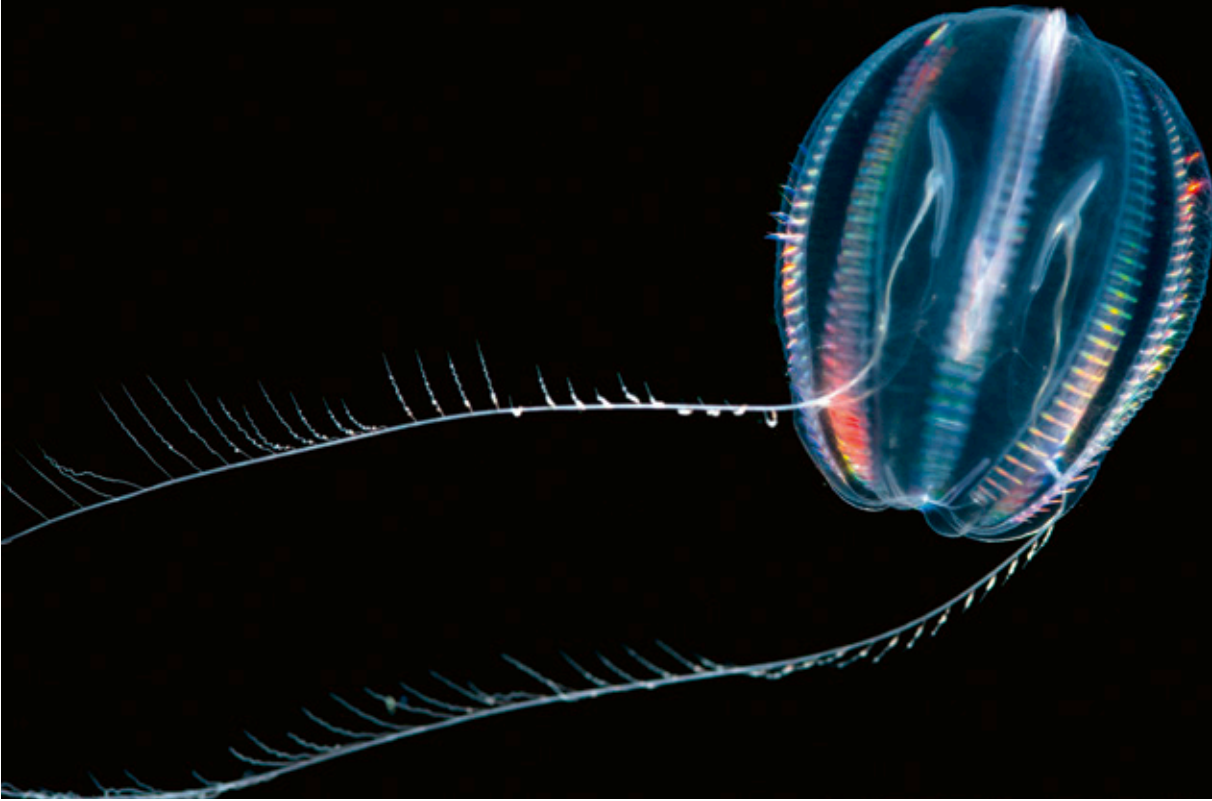
Pleurobrachia

In India, scientists have investigated the effects of ‘swarms’ of *Pleurobrachia* in the Bay of Bengal. They found that the presence of high densities of comb jellies – swarms – depended on a variety of factors, such as temperature and salinity, which vary across the Bay. Swarms of *Pleurobrachia* can reach a density of 6000 individuals per cubic meter.

Once a swarm develops, the comb jellies have a dramatic effect on the composition of the phytoplankton. This has knock-on effects on local fisheries. The variety of fish species caught in swarm areas has much lower economic value, whereas those from non-swarm areas provide commercially important species.

Sea gooseberry, *Pleurobrachia*

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The phylogeny debate has not yet been settled. One part of the problem is that genomic data for ctenophores is based on just a few species. We cannot be sure that these represent the phylum as a whole. Indeed, they could be specialist outliers – other ctenophore species may be better representatives of the group.

An unusual nervous system

Predators need a fast and effective nervous system. They must be able to detect their prey using sense organs, and to move fast to catch it. They may also need to detect and evade predators. Comb jellies do not have a brain. Instead, the nervous system comprises a 'nerve net' – a connected network of neurones distributed over the entire body, enabling fast coordination throughout the body. Possession of a nerve net is not unique. Other animals, such as sea urchins and starfish, rely on a nerve net, with little or no concentration of nerve cells into a rudimentary brain.

Detailed comparison of the ctenophore nervous system with that of other animals involves study of their genes, neural cell types, and neurone-to-neurone communication, including identifying chemical signalling molecules, such as neurotransmitters. Researchers have found that the nervous system of comb jellies differs in a number of fundamental ways

from those of other animals. In contrast, most of the key neural components are shared by all other animals that possess a nervous system.

The ctenophore nervous system comprises several different cell types. These include sensory cells that respond to mechanical and light stimuli, as well as neurones that connect with muscles. Sensory cells are concentrated in an aboral organ at the opposite end of the body to the mouth, and are also located all over the body. The aboral organ contains a statocyst that can monitor the position and orientation of the body.

It has not yet been possible to determine whether ctenophore neurones generate action potentials – that is, whether they are **excitable**. However, they do express genes that code for voltage-gated ion channels, which we know to be necessary for action potential generation. In addition, the comb jelly's rapid behavioural responses to sensory stimuli point to fast action potential transmission through the nerve net. Their muscle cells are excitable, leading to contraction.

Synapses are present in ctenophores, in particular between nerves and muscles, and between sensory cells and the nerve net. However, they differ in morphology from the synapses of other animals, and it is not known exactly how they work. Many neurotransmitters that we are familiar with from other animals,

such as acetylcholine, are not found in ctenophores. Instead, they appear to possess a unique set of neurochemicals. However, one important neurotransmitter present in all animals – glutamate – is also widely used in ctenophores, in particular at synapses between nerve and muscle cells.

Most neurones within the ctenophore nerve net are not linked by synapses. Instead, they form a **syncytium** – individual nerve cells anastomose (fuse) with their neighbours, forming a continuous ‘web’ of cytoplasm with many nuclei, a feature unique to the ctenophore nervous system.

Did the nervous system evolve more than once?

The existence of unique cellular and molecular features in the nervous system of ctenophores, together with their phylogenetic position, raise the possibility that it evolved completely independently from that of other animals, including humans. This would explain why sponges, our closer relatives, do not possess a nervous system. The nervous system of all animals except ctenophores would have evolved after the sponges split onto a separate branch (see Figure 1). But the nervous system of any animal is highly complex and organised, both structurally and functionally. Is it likely, or even possible, that it could have evolved twice? Despite obvious differences, ctenophore nervous systems also share features with other animals, pointing to a common origin. However, these could represent an example of **convergent evolution**.

An alternative hypothesis is that the last common ancestor of all living animals possessed cellular components – possibly even neurones – that were the precursor of all nervous systems, including that of ctenophores. In this scenario, the sponges would have lost these components. As sessile filter feeders, sponges can be considered to have a passive lifestyle – waiting for opportunities to come their way. It is possible



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that a nervous system was unnecessary for the successful survival of sponge ancestors. This is in sharp contrast to ctenophores, which are active predators.

So, how did nervous systems evolve? The jury is still out. Only by studying the outlier – ctenophores – will we come any closer to an answer. Nervous systems are essential for rapid and effective interaction with the environment, enabling animals to move purposefully, find prey and mates, and avoid predators. Possession of a nervous system provides a critical advantage to all but a few animals, such as sponges. The question of whether the nervous system evolved only once, or more than once, is key to our quest to fully understand our evolutionary ancestry and, indeed, the potential capacity of convergent evolution.

TERMS EXPLAINED

Animal LCA The last common ancestor from which all animal phyla evolved. It lived around 600 million years ago.

Convergent evolution Evolution of similar traits in unrelated species whose common ancestor did not possess the trait.

Excitable Excitable cells are those that can generate all-or-nothing action potentials.

Syncytium A cell with multiple nuclei and continuous cytoplasm, formed by fusion of many cells.

RESOURCES

More about ctenophores:

<https://tinyurl.com/Ctenophores-video>

How two injured comb jellies can fuse into a single entity: <https://tinyurl.com/comb-jellies-fuse>

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