Choanoflagellates

FS07030

Leadbeater, B. & Kelly, M (2001).
Evolution of animals – choanoflagellates and sponges.
Water and Atmosphere Online. 9 (2): 9-11.

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Evolution of animals – choanoflagellates and sponges

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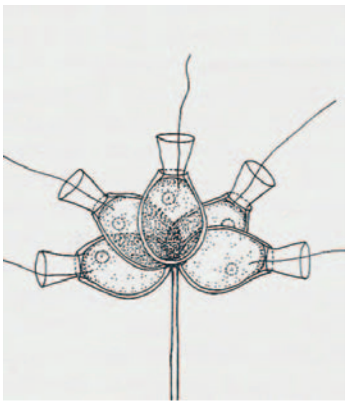
One aim of biodiversity studies is to work out how different kinds of plants and animals are related to each other – all of which is part of the much bigger story of evolution.



Drawing of a spherical colonial choanoflagellate Sphaeroeca lackeyi. *Individual cell bodies are 10 µm long.*

THE NINETEENTH CENTURY was rich in scientific achievements. Possibly the most important of these to biology was the establishment of evolutionary theory. Darwin's five-year voyage on board the *Beagle* (1831–36) and his subsequent publication of "The Origin of Species" (1859) promoted a fundamental explanation of how animals and plants had evolved. The main idea was that all life had a common origin and that complex multicellular animals and plants were derived from single-celled creatures. This set biologists in search of so-called missing links between the major living groups of animals and plants. The search led to the discovery of "living fossils" – remnant species of much larger groups of animals or plants which had previously dominated life on earth.

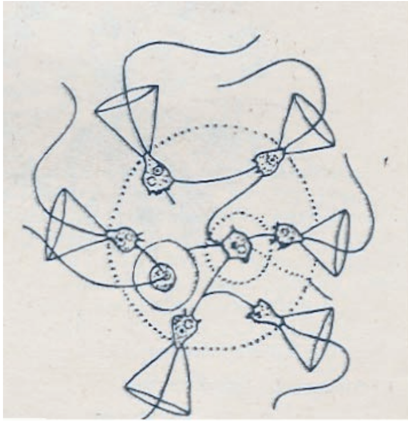
Over 140 years on, the origin of **animals** is still elusive, even with the recent great advances in microscopy and molecular techniques. However, one important link – between unicellular and multicellular animals – has been debated over that whole period.

It was first suggested towards the end of the nineteenth century that a group of non-pigmented **flagellates**, the choanoflagellates, might be linked to the sponges, a multicellular animal group. The reason for suggesting this link was that the choanoflagellate cell bears a remarkable resemblance to the so-called choanocyte cells of sponges.

What is a choanoflagellate?

The term choanoflagellate literally means collared flagellate. This is an apt name to describe an ovoid-to-spherical cell with a single, forwardly directed **flagellum** surrounded by an inverted cone-shaped collar of 30–40 tentacles. The flagellum beats with a base-to-tip undulation that creates a forwardly directed current of water. Particles, especially bacteria, are then sifted from the water by the collar. Many kinds of choanoflagellates attach to a surface with a stalk.

Choanoflagellates are present in almost all aquatic habitats. They are bacteriovores – feeding mainly on bacteria. They are a major component of the so-called microbial loop in foodwebs, where their role is to feed on bacteria and to release inorganic nutrients back into the water.



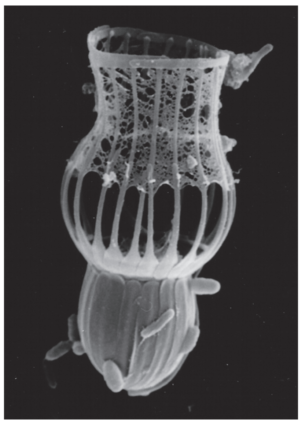
Drawing of a stalked colonial choanoflagellate Codosiga botrytis. *One cell body is 10 µm long.*

In appearance, choanoflagellates are quite unlike any other group of flagellates. In fact, their nearest relatives may be parasitic single-celled animals that don't have flagella at all.

Stalks, baskets and flagella

Choanoflagellate cells are distinctive and very easy to recognise. But the material covering the cell varies considerably from species to species. This variation gives clues about evolution within the choanoflagellates and is probably responsible for their wide distribution.

The importance of the cell covering is partly explained by the function of the flagellum: it is used for feeding. If the cell is not attached to a surface, the beating flagellum propels the cell through the water, and feeding efficiency is much reduced. So most cell coverings serve to attach the cell to something. Many cell coverings are made of organic material and come in different shapes – small cups, long vases, long stalks. Some species are colonial with stalks arranged like fingers. Others without stalks form a colony in which the movements created by the flagella are cancelled out as each cell attempts to move in a different direction.



Scanning electron micrograph of the basket-like lorica of Diplotheca costata *(approximately 12 µm long).*

Whole mount of a choanocyte from a freshwater sponge. Note the single anterior flagellum and the collar of thread-like tentacles. Cell body is approximately 6 µm.

Perhaps the most remarkable feature of some choanoflagellates is their covering (or lorica) of silica strips, rather like matchsticks. The strips are arranged in a characteristic basket-like pattern. Each species has a particular lorica shape and composition.

Surrounding a cell with a basket creates drag, which counteracts the movement caused by the flagellum. A large basket of very thin silica strips can cancel out movement altogether, and at the same time help the cell to remain suspended in the water. So these baskets have enabled choanoflagellates to extend their habitat range to the open ocean.

A link to sponge choanocytes?

Sponges consist of a series of internal chambers lined with choanocytes (choano = collar; cyte = cell). Like choanoflagellates, each choanocyte bears a collar of tentacles surrounding a single anterior flagellum. Undulation of the flagella of thousands of choanocytes creates a current of water that is drawn in from outside the animal, passes through the internal chambers and is expelled through an exhalant opening. Choanocytes are responsible for transporting oxygen-rich water to the internal cavity of the sponge and for bringing food particles, particularly bacteria, to the surface of the collars where they can be ingested.

Thus, choanoflagellates and sponge choanocytes are remarkably similar. The resemblance is also striking in many detailed ultrastructural features. But does such similarity imply an evolutionary link between the two groups of organisms? And why should this particular evolutionary link be so important?

The debate about sponges

The first recorded mention of a possible evolutionary link between the choanoflagellates and sponges dates back to the mid-nineteenth century. Dujardin (1841), a French biologist who was interested in protozoa and their evolution, suggested that sponges were colonial **Infusoria** – the term then in use to describe microscopic organisms. However, after introduction of the term **Protozoa** by the German biologist Golfuss (1817) and the subsequent exclusive use of this term by another German scientist von Siebold (1845) for singled-celled organisms, sponges came to be seen as the critical link between the Protozoa and more complex animals.

Haeckel, a controversial German biologist and polymath of the nineteenth century, argued that sponges should be included within the **Metazoa**, which according to his concept of evolution included all "higher animals". Nevertheless, Haeckel did not consider the sponges to be in the direct line of animal evolution – a position he reserved for the coelenterates – but as a curious side branch to the main line of animal evolution.

Haeckel's views were hotly challenged by a contemporary British protozoologist, Saville-Kent (1880), who considered that the sponges were colonial Protozoa derived directly from the choanoflagellates on account of the similarity in collared cells. Kent was so persuaded by his view

Definitions *(of terms in bold in the text)*

Animal A eukaryotic organism that obtains its nutrition by the ingestion of complex organic prey. (Eukaryotes have cells that contain discrete organelles like a nucleus.) Animals range from single cells to the most complex mammals, including humans.

Coelenterates A phylum of the **Metazoa** which are aquatic and have a single body cavity. They include the jellyfish and Hydra.

Flagellum (plural: flagella) A whip-like undulatory appendage used for locomotion in single cells, and on multicellular organisms for creating currents of water.

Flagellate A single cell bearing one or more flagella. Most flagellates are motile for at least part of their life cycle.

Infusoria Literally means infusion animals: microscopic organisms that grow in organic infusions. This term does not have a precise scientific meaning and is not generally used nowadays.

Metazoa A subkingdom of the Animal Kingdom comprising multicellular animals having two or more tissue layers.

Phylogenetic tree A "tree-like" illustration showing possible evolutionary relationships between organisms

Protozoa Single-celled organisms. Now considered to be a very diverse grouping of organisms, including single-celled plants, animals and fungi.

18s r-RNA gene The gene that codes for the small eukaryotic ribosomal subunit. This structure occurs in all eukarytotic cells; the gene shows sufficient variation and conservativeness to be useful for determining "long-distance" evolutionary relationships.

References

Cavalier-Smith, T. (2000). Flagellate megaevolution: the basis for eukaryote diversification. *Systematics 59*: 361–391. [Special volume on The flagellates edited by B.S.C. Leadbeater and J.C. Green]

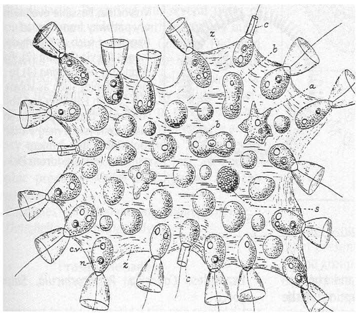
Darwin, C. (1859). On the origin of species. John Murray, London.

Dujardin, F. (1841). Histoire Naturelle des Zoophytes. Infusoires. Roret, Paris.

Golfuss, G.A. (1817). Uber die Entwicklungsstufen des Thieres. Leonard Schrag, Nuremberg.

Saville-Kent, W. (1880–82). A manual of the infusoria. Vols 1–3. David Bogue, London.

Siebold, C.T.E. von (1845). Lehrbuch ver vergleichenden Anatomie der Wirbellossen Thiere. *In*: Lehrbuch der Vergleichenden Anataomie (eds: C.T.E. von Siebold and H. Stannius. von Veit, Berlin.



Drawing of Proterospongia haeckeli, *which Kent (1880–82) considered to be a missing link between choanoflagellates and sponges. Colony is 40–50 µm wide.*

that when he eventually discovered a colonial choanoflagellate he called it *Proterospongia* (protero = primitive or original) in the belief that it was the "missing link" between choanoflagellates and sponges.

Since this time it has remained conventional wisdom that the choanoflagellates and sponges are closely related and that either this line of evolution or an offspring gave rise to the Metazoa and the remainder of the Animal Kingdom.

Recent developments

Apart from electron microscopy, the great contribution of the twentieth century to our understanding of evolutionary relationships has come from molecular genetic analysis. In particular, sequencing of the **18s rRNA** gene has provided us with valuable data on which to construct **phylogenetic tree**s. The information to date would appear to indicate that animals almost certainly evolved from a choanoflagellate ancestor (Cavalier-Smith 2000) and that the choano-flagellates and sponges are probably sister groups with a common ancestor. ■

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