

choanoflagellates may be the ideal reference taxon for studying metazoan origins. Like a living time capsule, they may allow us to infer the genome content and cell biology of the unicellular progenitors of Metazoa. For example, comparing choanoflagellate and metazoan genomes will reveal the minimal genetic toolkit of the first metazoan.

Pilot studies of choanoflagellate expressed genes have already uncovered homologs of a remarkable diversity of signaling and adhesion genes characteristic of Metazoa, including tyrosine kinases, cadherins and C-type lectins, extending the history of these key gene families back to the common ancestor of choanoflagellates and Metazoa. Comparisons of full genome sequences from choanoflagellates, sponges and other metazoans will provide a more complete picture of when and how important gene families evolved, the extent and impact of gene duplication and divergence, and the modes of protein- and RNA-based gene regulation available before the origin of Metazoa. Moreover, choanoflagellates provide a living system in which to study the ancient functions of genes that first evolved in unicellular organisms and today are used to mediate metazoan multicellularity.

Why are choanoflagellates important for our planet's health?

Small as they are, choanoflagellates have a huge impact on the food chain, aiding the flow of carbon from primary producers to higher trophic levels (including ourselves!). They comprise 5–40% of heterotrophic nanoflagellates and may filter between 10% and 25% of coastal surface water each day. By grazing on bacteria and detritus, choanoflagellates in turn feed their larger predators and return dissolved organic material to the water column. Both in number and feeding efficiency, choanoflagellates form a critical link in the microbial food chain that supports the global ecology.

What don't we know about choanoflagellates?

Given the potential importance of choanoflagellates to our understanding of metazoan evolution and the environment, it is remarkable how little we understand about their biology. A full accounting of a choanoflagellate genome will allow new insights into the molecular biology, physiology, ecology and evolution of these fascinating organisms. Some pressing questions about choanoflagellate biology concern how they interact with each other and their environment. Do they have sex? How do they form colonies, and why? How do choanoflagellates find, distinguish between, and capture different species of bacterial food? How is the unusual cellular architecture of choanoflagellates transmitted to each successive generation?

Is there a choanoflagellate genome project? Yes. Genome sequencing projects have been approved for two species of unicellular choanoflagellates, *Monosiga brevicollis* and *Monosiga ovata*. In addition, EST sequences for *M. brevicollis*, *M. ovata*, and a colony-forming *Proterospongia* sp. are publicly available through Genbank and ChoanoBase.

Where can I learn more about choanoflagellates?

- Searchable EST sequences:
<http://mcb.berkeley.edu/labs/king/blast/>
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Sponges

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What are sponges? Called Porifera because they are porous or 'pore bearing', sponges are animals designed around a unique body plan of canals and chambers through which they pump water to extract food. There is no centralized gut, no front or back. They lack conventional nerves and muscle, which means movement is only at the pace of the individual cell crawling. There are an estimated 15,000 sponge species living today, but only about half of them have been described and named. Their ecology and survival is often reliant upon the ability to produce unique bioactive compounds; as a result, many species are targets of natural product chemists and bioprospectors.

Are all sponges alike? Three classes of sponges have been defined, each with unique body plan features. Demosponges are cellular and most are supported by a siliceous skeleton of two- and four-rayed spicules. Hexactinellid or glass sponges have a six-rayed glass skeleton and are syncytial rather than cellular. This construction allows them to propagate action potentials over great distances. Calcareous sponges comprise less than 5% of living sponges and are characterized by a calcium carbonate skeleton and cellular organization. This is the only group in which the three grades of sponge body design – asconoid, syconoid and leuconoid – are apparent. Although systematists still use this three-class taxonomy, current phylogenetic analysis suggests that sponges could be paraphyletic, with the calcareous sponges grouping with other metazoans.

How do sponges reproduce?

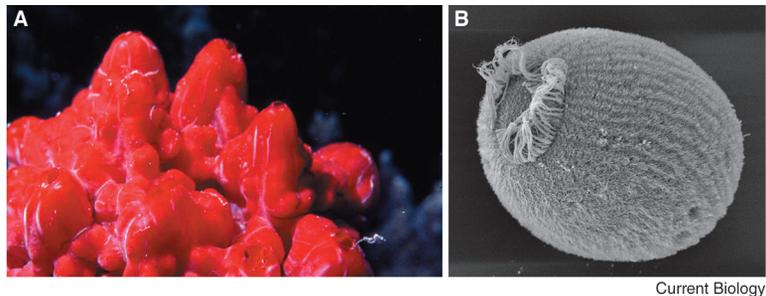
Sponges have a great array of reproductive patterns. There are no reproductive organs as such,

so gametes are derived from stem cells in the adult. Some groups are oviparous and release gametes into the sea, but far more sponges brood their eggs and embryos so that development occurs in the adult. In the latter group, embryogenesis generally gives rise to differentiated cell types that are organized by gastrulation-like processes to form a bi-layered — and in some a tri-layered — larva that is free-swimming for one to several days. Some sponges can also reproduce asexually by budding off portions of the adult body, or by sequestering cells into an overwintering cyst or gemmule.

What can sponges tell us about the evolutionary origins of multicellularity?

Similarity between the feeding cell of sponges (the choanocyte) and cells of a group of unicellular and colonial protists (choanoflagellates) suggested to early workers that sponges were examples of some of the earliest evolutionary experiments with multicellularity. Recent molecular phylogenies have confirmed that sponges are metazoans and that choanoflagellates are their nearest sister group. Because of their ancient origins, sponges have long been used as models for exploring the origin of key metazoan characteristics such as neurons, muscle and tissues. Haeckel (1872) and Metschnikoff (1874) studied sponges to determine whether germ layers are homologous in all animals, and Haeckel coined the term 'gastrula' for the ciliated larva. Wilson (1910) discovered that cells from dissociated pieces of sponge could recognize each other and reaggregate to form a new individual. If cells from two species are mixed they will sort into species-specific clumps before reforming. Evidence of self-recognition in sponges suggests this is an ancient animal trait.

Today, sponges are considered the most basal extant evolutionary lineage in the animal kingdom. While the adult sponge lacks an easily recognizable metazoan body plan, the embryo and larva



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Figure 1. External features of demosponges.

(A) A living adult demosponge. (B) Scanning electron micrograph of a demosponge larva.

have great affinities with other animals. Sponge cells move during embryogenesis in a manner akin to gastrulation, resulting in different larval cell types being patterned along an anterior-posterior axis. Recent evidence suggests that many metazoan transcription factor families are expressed during sponge embryogenesis.

Is there a sponge model system?

Few sponges live well in aquaria so it has been difficult developing sponge model systems. European and Japanese groups have pioneered use of adult formation from gemmules of the demosponges *Ephydatia* and *Spongilla*, showing the expression of homeobox and other developmental genes during formation of canals and chambers. Aggregate cultures of demosponge cells — the 'primorph' system of *Geodia* and *Suberites* — also allow for analysis of formation of the adult body plan, and many genes have been identified that are expressed during this process. Recently a tropical marine demosponge, *Reniera*, with year-round embryos and larvae has been identified and studied. Because of the clearer relationship of sponge embryos to other animals, this last model has the potential to draw sponges tighter into the metazoan fold.

Is there a sponge genome project?

Yes: the US Department of Energy Joint Genome Institute will sequence the genome of *Reniera* (<http://www.jgi.doe.gov/sequencing/why/CSP2005/reniera.html>). DNA for the project is

derived from *Reniera* larvae, which lack the diversity of prokaryotic and eukaryotic contaminants found in adult sponges. There is also a number of developmental and adult EST projects.

Where can I find out more?

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