*Intro- basics of sponges, discuss that they are likely monophyletic, hypotheses about ur-sponges (choanoflagellates or more complex organisms)*

**Introduction**

Porifera is usually described as the simplest animal phylum, as sponges are generally sessile filter-feeders which lack specialized tissues and organ systems. However, their complexity is often underestimated, as many sponges have intricate skeletons and robust immune systems, and some species of the class Homoscleromorpha may even possess true tissues (msl167).

Sponge evolution has often been conceived of as a process of increasing complexity. Researchers have noted the similarity in structure and filter-feeding strategy between single-celled choanoflagellates and sponge choanocyte cells and suggested that multicellular presponges evolved from colonies of choanoflagellates. More complex cnidarians and ctenophores could then have evolved from early sponges, and the skeletal and immune system complexity of sponges would gradually have increased as well as they transitioned from colonies into true multicellular organisms (rstb.2015.0476).

However, fossil evidence suggests some extant sponge lineages may be morphologically simpler than their most recent common ancestor. Some early fossils display radial symmetry (e.g. *Takakkawia lineata* (Walcott 1920) (add paper to github)), skeletons with many structural divisions, or spicules composed of both silica and calcium carbonate, whereas modern sponges are often asymmetrical and have skeletons composed of either silica or calcium carbonate but not both. A few sponge lineages also share traits with other eumetazoans, which may either have evolved independently, or, more probably, existed in a common ancestor and were lost by most sponge lineages (msl1167). Botting and Muir suggest that modern sponges may have evolved from ctenophore-like takakkawiids, and that the last common ancestor of porifera would have possessed a single layer of primarily hexactine biminerallic spicules (1-s2.0-S1871174X17300215-main). This contradicts hypotheses that early sponges were amorphous colonies that grew more complex over time and suggests that certain sponge classes may instead have decreased in complexity, losing one or both types of minerals from their spicules as well as the structural complexity they inherited from takakkawiids and their ctenophore-like ancestors while developing various different spicule structures.

The timing of changes in morphological complexity is unknown in many multicellular lineages, as is whether complexity changed gradually or in pulses (plant paper, also find other sources?) However, complexity scoring of extant and fossil organisms can reveal the timing and direction of past shifts in complexity. For example, Leslie et al. identified two pulses of increase in the complexity of plant reproductive structures separated by a long period of stasis by scoring the number of “geometrically distinct regions” of over 1000 extant and fossil plants ranging from the Silurian to the present. In this study we took a similar approach to analyzing the skeletal complexity of sponges, scoring the complexity of extant sponges and fossils based on the number of distinct spicule types possessed by each species. In particular we compared present and past complexity within three extant sponge classes – Hexactinellida, Calcarea, and Demospongia – to determine whether there have been any shifts in sponge complexity after the extant classes already diverged (early Cambrian and onward), or if the apparent drop in Poriferan complexity occurred early in the lineage’s history and was followed by a period of stasis or perhaps subsequent increases in complexity in one or more classes.

(discuss purpose of study, specific questions, similar studies on plant complexity)

**Methods**

The complexity of extant and fossil sponges was measured based the number of unique spicule types possessed by each species. A spicule ‘type’ was defined as a unique geometric and morphological form. Most spicule types exhibited some variation, but this variation was not used to delineate multiple spicule types unless it was discontinuous. For instance, a spicule type with size variation was not split into multiple types unless there were spicules that were morphologically similar but fell into multiple discontinuous size ranges. Spicules with the same morphology but different sizes also often occurred in different areas inside the sponge. A species’ complexity was defined as the raw number of unique spicule types it possessed, regardless of the shape of those spicules or their relative abundance. Some sponges had multiple levels of skeletal organization – for example, repeated bundles of spicules rather than individual spicules scattered throughout the body – but these levels of complexity were not measured as they are not consistently preserved in fossils; some fossils (eg an example) were only found as fragments and the original spicule organization is not known. Because some sponges do not produce microscleres when dissolved silicate concentrations are low (accurate?) and because they may not be well-preserved in fossil specimens, only megascleres were considered in the complexity measurements.

Information on types of spicules that sponge species possessed were obtained from research papers that described collected sponge specimens, which were located using OpenTree for extant sponges and PaleoDB for fossils. Usually, we deferred to the way the authors had separated spicule types when classifying the complexity of the sponges. However, when present, spicule images and size measurements were examined, and in some cases we determined that there were more or fewer morphologically distinct spicule types than the authors identified.

Objective spicule classification was difficult because not all papers described sponge spicules in as much detail as others. This was especially problematic for fossil sponges, as fossilization may not have captured the subtle differences in spicule size or geometry that is measurable in extant sponges. In some cases it was also difficult to determine whether variations in the shape and size of certain spicule types were continuous or discontinuous. For these reasons, the complexity of some modern sponges (especially Calcarea and Hexactinellida, which possess highly complex arrangements of different-sized spicules) and fossil sponges is probably underestimated. However, extant demosponges and homoscleromorphs are probably well-described because they tend to only possess a few types of spicules with little morphological variation.

Our fossil data was not evenly spread across time or across sponge classes due to difficulties in finding papers describing specimens with well-preserved spicules in every time period and every class; we also only included fossils that had complete taxonomic information on PaleoDB. We located many Cambrian, Silurian, Permian, and Neogene sponges, but there were gaps in our record during the Devonian period as well as most of the Mesozoic, except for the upper Cretaceous. However, the Mesozoic gap is consistent with known gaps in the fossil record of sponges and other marine organisms after the end-Permian event (Geological Journal - 2001). In addition most of our included fossils belonged to Demospongiae and Hexactinellida, with only a few Calcarea and no Homoscleromorpha. This is mostly consistent with the relative abundance of these sponge classes in the fossil record and their relative diversity, although our study included a disproportionate number of Hexactinellida given the greater diversity of Demospongiae. This may be due to Hexactinellids fossilizing more readily, as Demosponges often quickly disintegrate upon death and are therefore less likely to leave behind complete fossils showing the original skeletal structure and composition (i0883-1351-28-6-373).