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Review

Early sponge evolution: A review and phylogenetic framework

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Abstract

Sponges are one of the critical groups in understanding the early evolution of animals. Traditional views of these relationships are currently being challenged by molecular data, but the debate has so far made little use of recent palaeontological advances that provide an independent perspective on deep sponge evolution. This review summarises the available information, particularly where the fossil record reveals extinct character combinations that directly impinge on our understanding of high-level relationships and evolutionary origins. An evolutionary outline is proposed that includes the major early fossil groups, combining the fossil record with molecular phylogenetics. The key points are as follows. (1) Crown-group sponge classes are difficult to recognise in the fossil record, with the exception of demosponges, the origins of which are now becoming clear. (2) Hexactine spicules were present in the stem lineages of Hexactinellida, Demospongiae, Silicea and probably also Calcarea and Porifera; this spicule type is not diagnostic of hexactinellids in the fossil record. (3) Reticulosans form the stem lineage of Silicea, and probably also Porifera. (4) At least some early-branching groups possessed biminerallic spicules of silica (with axial filament) combined with an outer layer of calcite secreted within an organic sheath. (5) Spicules are homologous within Silicea, but also between Silicea and Calcarea, and perhaps with Homoscleromorpha. (6) The last common ancestor of extant sponges was probably a thin-walled, hexactine-bearing sponge with bimineralic spicules. (7) The stem group of sponges included tetraradially-symmetric taxa that grade morphologically into Cambrian fossils described as ctenophores. (8) The protomonaxonid sponges are an early-branching group, probably derived from the poriferan stem lineage, and include the problematic chancelloriids as derived members of the piraniid lineage. (9) There are no definite records of Precambrian sponges: isolated hexactine-like spicules may instead be derived from radiolarians. Early sponges had mineralised skeletons and thus should have a good preservation potential: the lack of sponge fossils in Precambrian strata may be due to genuine absence of sponges. (10) In contrast to molecular clock and biomarker evidence, the fossil record indicates a basal Cambrian diversification of the main sponge lineages, and a clear relationship to ctenophore-like ancestors. Overall, the early sponge fossil record reveals a diverse suite of extinct and surprising character combinations that illustrate the origins of the major lineages; however, there are still unanswered questions that require further detailed studies of the morphology, mineralogy and structure of early sponges.

Keywords: Porifera; Chancellorida; Reticulosa; Protomonaxonida; Biomarkers; Ediacaran

Contents

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1. Introduction

Sponges are one of the key groups for understanding basal metazoan evolution, having traditionally been regarded as the most primitive living animals, both in phylogenetic topology and morphology (Bergquist, 1978; Gehling and Rigby, 1996). Recent molecular and palaeontological work has challenged this view, with a competing scenario emerging that involves secondary simplification from a cnidarian-like or ctenophore-like ancestor (e.g., Botting et al., 2014; Dunn et al., 2015; Ryan and Chiodin, 2015), although this has been both forcefully disputed (e.g., Nosenko et al., 2013; Simion et al., 2017) and supported (e.g., Whelan et al., 2015; Shen et al., 2017) by different research groups applying different analytical approaches. The debate centres on sources of error and the influence of artefacts such as long-branch attraction in the analyses, and despite confidence on both sides, the answer is not yet resolved unambiguously. Among these and other studies, however, there is now a virtual consensus that sponges form a monophyletic group, and that Silicea (Demospongiae and Hexactinellida) form one clade, probably as a sister group to Calcarea + Homoscleromorpha. The topology and branching sequence of the sponge classes, and more particularly of the Porifera and other early-branching animal phyla (Fig. 1), have critical implications for the nature of their last common ancestor and the question of how animals evolved.

Until now, the published debate has been focused almost entirely on the molecular biological evidence. Understanding the origins and derivation of the extant sponge clades is now critical to interpreting the nature of the earliest animals, but molecular work can as yet provide only limited and speculative conclusions regarding early sponge morphology and biology. There has also been a traditional assumption that the fossil record of sponges is severely limited in what information it can provide on the earliest branches, due to late-stage, independent origins of mineral skeletons (Bergquist, 1978; Reitner and Mehl, 1996), despite reviews that clearly illustrated how much evidence can be obtained from the fossil record (Pisera, 2003, 2006). Phylogenetic studies based on extant sponges have generally assumed that spicules are not homologous between the extant classes

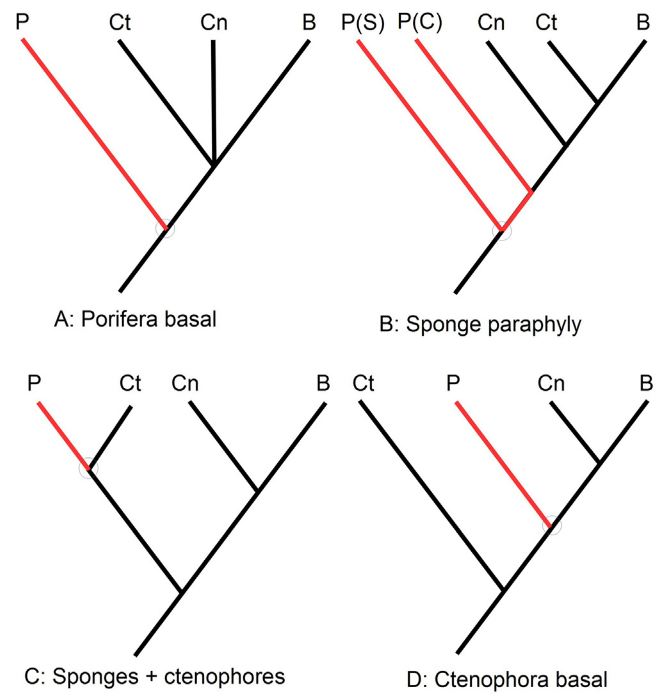

Fig. 1. Competing phylogenetic scenarios (current and recent) for sponge and other basal animal evolution; small circle marks last common ancestor between sponges and the next nearest metazoan group. The monospecific Placozoa are omitted due to further uncertainty over their position (many different published interpretations), and probable secondary simplification from a more complex ancestor of unknown nature. B: Bilateria; Cn: Cnidaria; Ct: Ctenophora; P: Porifera; P(S): Silicea; P(C): Calcarea. (A) The current standard, and traditional view, with monophyletic sponges as the basal animal group; (B) the now-outdated model of sponge paraphyly (e.g., Sperling et al., 2007), which implied that the ancestor of Eumetazoa was a sponge; (C) a rarely-encountered or lower-likelihood result of molecular phylogenies (e.g., Shen et al., 2017), but potentially supported by the fossil record (this paper); (D) the recent competing view of Ctenophora basal, in which either sponges would be secondarily simplified or nervous systems and muscles evolved at least twice.

(e.g., Manuel et al., 2003). In addition, early sponge fossils have been thought to be phylogenetically derived, for example with the assignment of Cambrian taxa to Hexactinellida, albeit the stem-group due to the differences of these taxa from living members of the class (e.g., Dohrmann et al., 2013). Both of these