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Chapter One - Deep Phylogeny and Evolution of Sponges (Phylum Porifera)

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Abstract

Sponges (phylum Porifera) are a diverse taxon of benthic aquatic animals of great ecological, commercial, and biopharmaceutical importance. They are arguably the earliest-branching metazoan taxon, and therefore, they have great significance in the reconstruction of early metazoan evolution. Yet, the phylogeny and systematics of sponges are to some extent still unresolved, and there is an on-going debate about the exact branching pattern of their main clades and their relationships to the other non-bilaterian animals. Here, we review the current state of the deep phylogeny of sponges. Several studies have suggested that sponges are paraphyletic. However, based on recent phylogenomic analyses, we suggest that the phylum Porifera could well be monophyletic, in accordance with cladistic analyses based on morphology. This finding has many implications for the evolutionary interpretation of early animal traits and sponge development. We further review the contribution that mitochondrial genes and genomes have made to sponge phylogenetics and explore the current state of the molecular phylogenies of the four main sponge lineages (Classes), that is, <u>Demospongiae</u>, <u>Hexactinellida</u>, <u>Calcarea</u>, and <u>Homoscleromorpha</u>, in detail. While classical systematic systems are largely congruent with molecular phylogenies in the class <u>Hexactinellida</u> and in certain parts of <u>Demospongiae</u> and Homoscleromorpha, the high degree of incongruence in the class Calcarea still represents a challenge. We highlight future areas of research to fill existing gaps in our knowledge. By reviewing sponge development in an evolutionary and phylogenetic context, we support previous suggestions that sponge larvae share traits and complexity with eumetazoans and that the simple sedentary adult lifestyle of sponges probably reflects some degree of secondary simplification. In summary, while deep sponge phylogenetics has made many advances in the past years, considerable efforts are still required to achieve a comprehensive understanding of the relationships among and within the main sponge lineages to fully appreciate the evolution of this extraordinary metazoan phylum.

Introduction

Sponges are sessile aquatic organisms that inhabit most marine and many freshwater habitats. Adult sponges are of large ecological importance as, for example, filter-feeders and bioeroders (Bell, 2008) and have considerable

commercial/biopharmaceutical value (Faulkner, 2002). Their systematics, phylogeny, evolution, and taxonomy have often been proven difficult to reconstruct because many sponges possess only a few systematically/phylogenetically informative morphological characters, and some skeletal traits, which for a long time served as the sole basis for sponge systematics, are prone to homoplasies (reviewed in Erpenbeck and Wörheide, 2007) and relatively variable as a function of local environmental conditions (Maldonado *et al.*, 1999). Nevertheless, significant progress has been achieved in recent years (e.g. Cárdenas et al., 2009, Cárdenas et al., 2011, Dohrmann et al., 2011, Dohrmann et al., 2012, Morrow et al., 2012, Voigt, 2012b).

Because of their early-branching position in the animal tree of life (Philippe et al., 2009, Pick et al., 2010), sponges are instrumental in the on-going efforts to better understand the main trajectories of early animal evolution and to decipher the paleogenomics of the last common ancestor of animals (Taylor *et al.*, 2007). Additionally, other non-bilaterian taxa (i.e. Placozoa, Cnidaria, and Ctenophora) and their relationships to each other and to the Bilateria have gained substantial interest as they are of great importance for understanding the evolution of key metazoan traits (Miller, 2009). The statement "*Nothing in biology makes sense except in the light of (a) phylogeny*" (modified after Dobzhansky, 1973) is especially true for the non-bilaterian part of the animal tree of life.

This review is intended to summarize the current state of the debate on the phylogenetic relationships within and among the main sponge lineages and their relationships to other non-bilaterian animals. Erpenbeck and Wörheide (2007) reviewed the then current status of the molecular phylogeny of sponges. They concluded with the statement that "*Coming years will bring the science of sponge systematics closer to its long-awaited goal of a fully consistent phylogeny*". Since then, numerous phylogenies have been published, and the reconstruction of deep-level animal relationships has shifted from the analyses of single or a small number of genes to phylogenomic approaches analyzing dozens to hundreds of genes (e.g. Hejnol et al., 2009, Philippe et al., 2009) and complete mitochondrial genomes (e.g. Lavrov *et al.*, 2008)—we might now ask the question: are we there yet?

Section snippets

Higher-Level Non-bilaterian Relationships

In recent years, several contradicting hypotheses about higher-level non-bilaterian relationships have been published (reviewed by Edgecombe et al., 2011, Philippe et al., 2011). Conflicting results among studies addressing non-bilaterian relationships are not completely unexpected because such studies attempt to reconstruct cladogenetic events that occurred hundreds of millions of years ago (Ma), possibly as early as the Cryogenian (~650Ma, Peterson et al., 2008, Erwin et al., 2011). Resolving ...

Mitochondrial DNA in Sponge Phylogenetics

Mitochondria—the energy-producing organelles present in most eukaryotic cells—contain their own genome (mtgenome or mtDNA), which is separate from that of the nucleus. For technical and historical reasons, mtDNA has been one of the favourite molecular markers in animal phylogenetic, population genetic, and biogeographic studies as it provides convenient access to a set of orthologous genes with few or no introns, little or no recombination, usually uniparental inheritance, and high...

Introduction to Demospongiae

Demosponges inhabit most aquatic habitats, including all oceans from the intertidal to the abyss, from the tropics to the polar seas, and (almost) all types of freshwater habitats. This diversity in habitats is reflected in their taxonomic

diversity. Demosponges are by far the most diverse group of Porifera, comprising about 85% of all extant sponge species.

Demosponges comprise cellular (i.e. not syncytial) Porifera possessing spongin (sometimes greatly reduced) whose mineral skeleton (if...

Introduction to Hexactinellida

Hexactinellida (glass sponges) are exclusively marine and siliceous sponges largely restricted to the deep sea, with a few notable exceptions, such as massive glass sponge reefs found in SCUBA-accessible depths off the Canadian west coast (e.g. Conway et al., 2001, Krautter et al., 2001, Cook et al., 2008) and population of sublittoral caves in the Mediterranean by one species (*Oopsacas minuta*: Vacelet et al., 1994, Bakran-Petricioli et al., 2007). Currently, 623 extant species are considered...

Introduction to Homoscleromorpha

Homoscleromorpha is a small group of marine sponges (<100 described species), the monophyly of which is well accepted on the basis of their general organization and the shared features of their cytology and embryology. Their affinities to other sponges, however, are less clear and have recently been questioned. Traditionally, homoscleromorph sponges were considered as a family or a suborder of the subclass Tetractinellida of the class Demospongiae mainly due to the shared presence of siliceous...

Introduction to Calcarea

Calcareous sponges (Class Calcarea) include about 675 accepted extant species (Van Soest *et al.*, 2011), which are exclusively marine. They occur mostly in shallow waters; only a few species are known from the deep sea (for an overview see, e.g. Rapp *et al.*, 2011). In contrast to the intracellularly formed siliceous spicules found in the other sponge classes, Calcarea are characterized by calcium carbonate spicules that are excreted to the extracellular space (Manuel et al., 2002, Sethmann and...

The Evolution of Sponge Development

With a phylogeny mostly based on molecular markers that are independent of morphological characters, it is now possible to map traits, trace their origin, and define shared ancestral features of Porifera and, more generally, Metazoa. In particular, the analysis of development in a phylogenetic framework may identify some of the key innovations that accompanied the origin of the Metazoa. The use of embryonic development to reconstruct early animal evolution dates back to Haeckel's Gastraea...

Conclusions and Outlook

Based on the discussion in this chapter, it is clear that deep sponge phylogenetics has come a long way in recent years. Large-scale phylogenomic analyses have so far rejected the hypothesis that sponges are paraphyletic; instead, several studies are consistent with the notion of monophyletic Porifera. It has also become clear from evolutionary developmental studies of sponges that sponge larvae share traits and complexity with eumetazoans and that the simple sedentary adult lifestyle of...

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...The earliest currently confirmed sponge fossils are earliest Cambrian (Fortunian) in age (Chang et al., 2017, 2019), and keratosans are preserved in Early (Luo et al., 2020) and Middle Cambrian Burgess Shale-type biotas (Botting et al., 2013; Ehrlich et al., 2013; Yang et al., 2017). Although many uncertainties remain (Antcliffe et al., 2014; Botting and Muir, 2018; Nettersheim et al., 2019), biomarker (Love et al., 2009; Sperling and Stockey, 2018) and phylogenetic (Wörheide et al., 2012) studies suggest the likelihood that sponges were extant in the Neoproterozoic. Present-day sponges harbor diverse inter- and intracellular symbiotic microbes (Rützler, 1990, 2012; Reitner, 1993; Rodriguez-Marconi et al., 2015) that can constitute a significant proportion of body mass (Hentschel et al., 2006), in some cases up to 40% (Taylor et al., 2007)....

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