

Sponges: New Views of Old Animals¹SCOTT NICHOLS^{2,*} AND GERT WÖRHEIDE[†]^{*}*Department of Integrative Biology, 3060 Valley Life Sciences Building, University of California, Berkeley, California 94720*[†]*Geowissenschaftliches Zentrum der Universität Göttingen, Abt. Geobiologie, Goldschmidstr. 3, D-37077 Göttingen, Germany*

Sponges (phylum Porifera) are exclusively aquatic, sedentary, filter-feeding invertebrates, occupying essentially all benthic marine and some freshwater environments. With a worldwide fauna of at least 15,000 species (Hooper, 1994), poriferans are among the most diverse of sessile marine taxa.

Sponges diverged from other animals earlier in evolutionary history than any other known animal group, extant or extinct, with the first sponge-related record in earth history found in 1.8 billion year old sediments, based on a demosponge-specific chemofossil, 24-isopropylcholestane (McCaffrey *et al.*, 1994). The first morphological sponge fossils are known from the Early Vendian Doushantou phosphorites in China (~580 Million years ago; Li *et al.*, 1998) and the Neoproterozoic (~550 my) *Cloudina*-Reefs of southern Namibia (Reitner and Wörheide, 2002). The sponge body plan, comprising tissue-like cell associations, inhalant and exhalant canal systems, and chambers lined by flagellated choanocytes, allows for the efficient filtration of particles from the water column and is so constrained that little variation has arisen in its core components during at least 580 Ma of animal history (the fossil record of demosponges, the most diverse sponge “class” is reviewed in Reitner and Wörheide [2002]). The seemingly simple, homogeneous bauplan and morphology of sponges contrasts with their high complexity and diversity at nearly every other biological level (*e.g.*, phylogenetically, ecologically, developmentally).

This symposium was devoted to highlighting diverse aspects of poriferan biology and bringing seemingly disparate disciplines, such as paleontology, evolutionary developmental biology, ecology, population genetics, phylogeography and molecular phylogenetics together to present recent advances in our knowledge about this enigmatic phylum. It also aimed to make poriferans much more accessible as study organisms for the wider community. We feel that the papers that follow are particularly timely in light of a growing interest in sponges among non-sponge biologists due to the significance of their phylogenetic position and to their proven potential as a source for bioactive compounds for drug discovery (*e.g.*, Munro *et al.*, 1999).

A topic that is not explicitly reviewed in these symposium proceedings, but that is relevant to every area of sponge biology, is poriferan paraphyly (*e.g.*, Cavalier-Smith *et al.*, 1996) and the hypothesis that the class Calcarea and the demosponge order Homoscleromorpha are very divergent from other sponges. The available evidence, which is mainly molecular (Cavalier-Smith *et al.*, 1996; Collins, 1998; Zrzavy *et al.*, 1998; Adams *et al.*, 1999; Schütze *et al.*, 1999; Borchiellini *et al.*, 2001; Medina *et al.*, 2001; Manuel *et al.*, 2003), suggests that at least Calcarea might actually be more closely related to eumetazoans than to other sponges. The presence of a basal lamina of type IV collagen in homoscleromorphs is a potential synapomorphy shared with eumetazoans (Boute *et al.*, 1996; Borchiellini *et al.*, 2004) and might also put Homoscleromorpha in a similarly pivotal position to understand early metazoan evolution. Further confirmation of such phylogenetic relationships would support an evolutionary scenario in which the ancestor of all animals was similar to an adult sponge. Even if Porifera is determined to be monophyletic, sponges remain important to studies of early animal evolution. As the sole sister taxon to all other animals, sponges can uniquely inform us about the character states present in their last common ancestor. Furthermore, the deep phylogenetic divergences within Porifera, combined with their diverse larval types, modes of gastrulation, and reproductive strategies (reviewed in Maldonado and Bergquist, 2002), suggests that internal divergences within sponges are as old or older than divergences between other metazoan phyla (Maldonado, 2004); a proposition supported by data from the fossil record, with first occurrences of demosponges in the Late Vendian (Li *et al.*, 1998) and Hexactinellida in the Late Vendian Fontanarejo Phosphorites from Spain (Reitner, unpublished; Reitner, 2004). Comparative studies among animals (whether genomic, phylogenetic, physiological, etc.) will certainly benefit from the inclusion of a greater diversity of sponges than demanded by the traditional view of sponges as simple and biologically homogeneous.

The relevance of sponges to studies of animal evolution is highlighted in this symposium by Degnan and colleagues who use a sponge of the genus *Reniera* to illustrate how developmental genetic characteristics shared between sponges and other animals can inform us about the most recent common ancestor of all animals. The presence of numerous and diverse metazoan transcription factors in *Reniera* allows for the inference that early animals had sophisticated regulatory architecture allowing for cell differentiation and patterning in early development. Leys and Eerkes-Medrano further illustrate the im-

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portance of the study of sponge embryogenesis to our understanding of early animals by re-evaluating Haeckel's often reproduced model of gastrulation in Calcarea. They conclude that embryonic cell movements earlier than those observed by Haeckel are consistent with patterns of gastrulation in other metazoans, bringing into question the homology of early germ layers in basal metazoan phyla.

Wörheide and colleagues focus on recent advances in knowledge about sponge biodiversity, molecular ecology and phylogeography. They show that knowledge of biodiversity patterns of sponges, their historical biogeographic affinities, genetic variation and spatial patterns of this variation among sponge populations is rudimentary but that biodiversity analyses and genetic studies already revealed spatial trends not universally reflected in the distributions of other marine phyla within the Indo-West Pacific and Caribbean regions, since, at smaller spatial scales, sponges frequently form heterogeneous, spatially patchy assemblages, with no apparent latitudinal diversity gradients at larger spatial scales.

McClintock and colleagues provide an overview of the ecology of the diverse and abundant populations of sponges that border Antarctica, highlighting an unfamiliar fauna that creates habitat for other organisms, serves as a food source for spongivores, and that maintains secondary metabolite defenses against the predictions made for species living polar environments.

Walters and Pawlik follow this theme by illustrating a mechanism alternate to secondary metabolite defense that allows sponges to cope with predation pressures. They present evidence that sponges that are not chemically defended from predators can recover from injuries faster than chemically defended species; a result consistent with the hypothesis that rapid healing allows non-defended species to thrive in the presence of predation by healing at faster rates than chemically defended species.

Thacker reports on the extensive and understudied phenomenon of sponge symbioses by studying the nature of the association between different cyanobacterial symbionts and their sponge hosts. He demonstrates that species that exhibit host specificity have greater impact on the health and survival of their host than generalist species that might more frequently have commensal interactions with their hosts.

The papers resulting from this symposium highlight only a fraction of the diversity of topics being pursued in the community of sponge biologists but they should serve to illustrate to the non-specialist audience both the current state of sponge science and the relevance of sponges to the aquatic communities in which they live and to comparative studies across all Metazoa.

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