



On the molecular phylogeny of sponges (Porifera)*

DIRK ERPENBECK and GERT WÖRHEIDE¹

Courant Research Center Geobiology, Georg-August-Universität Göttingen, Goldschmidtstr. 3, 37077 Göttingen, Germany & Biodiversity Program, Queensland Museum, 4101 South Brisbane, Queensland, Australia

¹ Corresponding author. Email: gert.woerheide@geo.uni-goettingen.de

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Abstract

In the past decade molecular genetic markers have been introduced for research on the evolution and systematics of sponges. Historically, sponges have been difficult to classify due to lack of complex characters with the result that hypothesised phylogenetic relationships for various sponge taxa have changed rapidly over the past few years. Here, we summarize the current status of systematic and phylogenetic hypotheses proposed for sponges. We discuss the relation-

ships among the three classes, Calcarea (calcareous sponges), Hexactinellida (glass sponges) and Demospongiae, as well as those among the members within each class. While molecular phylogenies of hexactinellids corroborate previous morphological hypotheses, phylogenetic hypotheses based on rDNA sequence analyses in Calcarea largely conflict with the previous, typological classifications. Many demosponge taxa have only recently been shown to be para- or polyphyletic and thus their new clades and other phylogenetic relationships have only now begun to be tested using current molecular approaches.

Key words: Porifera, Demospongiae, Hexactinellida, Calcarea, systematics, molecular phylogeny

Introduction

“While I pass with my spongiological work the columns of Hercules, I am facing a task which, to its full extent, can only be performed with the strength of a hero.”

O.E. Schmidt 1870, second chapter, preface

Oskar Schmidt (Schmidt 1870) describes in these few words the difficulties he experienced during his work on the systematics of sponges. More than a century later, many issues in sponge systematics and phylogeny have been resolved, but ambiguities remain. Schmidt and his fellow sponge taxonomists up through the present have been challenged by the primitive bauplan of their study subjects, which often lacks any obvious or truly informative phenotypic characters. Such morphological characters are necessary for an unambiguous classification using, for example, the cladistic framework that was developed approximately 60 years ago (Hennig 1950).

Sponge systematics has traditionally been based almost entirely on skeletal traits and, in particular, on the skeleton's mineral elements, the spicules. However, spicule complexity and information content is limited. Spicule morphogenesis and evolution have been studied extensively (see Dendy 1921; Jones 1997; Uriz *et al.* 2003), but the results have contributed only marginally towards solving problems of the sponge classification. Other various morphological characters—such as shape, surface, texture or colour—depend on microhabitat conditions or season (e.g., Jones 1984) or are present *in situ* only. The suitability of cytological features for sponge systematics has been examined (Boury-Esnault *et al.* 1994), and, while successfully resolving a few higher taxa, these characters still appear insufficient to address broader phylogenetic questions. Morphological traits of sponges have been shown to be frequently plagued by homoplasies (e.g. Manuel *et al.* 2003) that impede cladistic analyses, such that additional and/or alternative non-morphological characters are in demand.

Biochemical compounds were suggested as an alternative to morphological characters in sponge systematics (e.g., Bergquist 1978, 1979), and certainly the quantity and resolution of chemotaxonomic data on sponges have increased significantly in the contemporary literature (see reviews in van Soest & Braekman 1999; Erpenbeck & van Soest 2007) although over the past couple of years this literature has decreased, due to apparent difficulties in identifying the actual producers (sponge or symbiont), homologization of pathways and experimental difficulties, and most significantly the comparative ease in obtaining nucleic acid data compared to other potential datasets (e.g. Kelly-Borges *et al.* 1991).

Theoretically, DNA analysis provides a considerable amount of additional phylogenetic information to be obtained with less effort than other methods. Despite this, molecular methods took a relatively long time to be established in sponge research as compared to many other metazoan phyla. Although sponges are recognised as a pivotal phylum for understanding metazoan evolution and remain of great interest in the biotechnology sector because they produce a greater number of (currently novel) bioactive compounds than any other metazoan phyla, comparatively little is understood about their molecular evolution. Only a few sponge mitochondrial genomes have been published, and so far these do not cover all classes. Moreover, the first sponge genome (based on the species *Amphimedon queenslandica* Hooper & Van Soest 2006) still awaits publication.