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On the molecular phylogeny of sponges (Porifera)*

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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-

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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.

Notwithstanding this comparative lag against other phyla, there is now a growing body of recent literature that reports extensive DNA data generated for Porifera, which has provided valuable insights into the molecular phylogenetics of sponges. Some of these hypotheses have corroborated morphological expectations (e.g. "Systema Porifera", Hooper & van Soest 2002a, currently the most comprehensive morphology-based supra-specific sponge classification), whereas there are still many unresolved taxa requiring more comprehensive analyses. In particular, the traditional dominance of rRNA genes for phylogenetic reconstructions has given way to the increased use of mitochondrial genes, predominantly subunit 1 of cytochrome oxidase (CO1). Mitochondrial genes provide an independent means for testing phylogenetic hypotheses based on rDNA, particularly when ribosomal gene trees contradict morphological predictions.

In this review, we summarize the current status of sponge phylogenetics. We do not repeat the recent reviews on Demospongiae (Boury-Esnault 2006), Calcarea (Manuel 2006) or Hexactinellida (Reiswig 2006; Leys *et al.* 2007) but highlight similarities and differences among the different molecular and morphological trees. We propose some priority research topics that focus on pivotal and understudied taxa, and we pinpoint new taxonomic problems that have emerged from recent molecular analyses.

The phylogenetic position of Porifera within the Metazoa

“The phylum Porifera contains those animals commonly called sponges”.

With this grossly understated definition Gribble (1998) introduces sponges to his readers, probably with the knowledge that “Porifera” and its animal entity are not commonly known to the non-scientific community. Indeed, sponges have been placed into several kingdoms over the history of their systematics, but now they doubtless belong within the Metazoa (see references below). Regarded as being among the most primitive animals, sponges are the oldest extant animal group. The first fossil demosponge records date from ca. 750 million years ago (MYA), and their bauplan is basically unchanged since the Late Cambrian (509 MYA, Reitner & Wörheide 2002). Some autapomorphies of the Metazoa (including both Porifera + Epitheliozoa / Eumetazoa) are (a) diploid multicellularity, (b) meiosis, (c) oogenesis (*one* egg cell and *three* polar bodies from one oocyte), (d) spermatogenesis (four *identical* sperm cells from one spermatocyte) and (e) the bauplan of the sperm cell itself (Ax 1995). These characters clearly differentiate sponges and other Metazoans from their assumed closest relatives, the Choanoflagellates. Molecular data have repeatedly supported the phylogenetic position of sponges within the Metazoa (e.g., Müller 1995; Rokas *et al.* 2005).

Sponges are defined by their biphasic life cycle, filter-feeding habits in combination with a sessile adult form, pinacocytes, aquiferous system, choanocytes and totipotent motile cells (e.g., Vacelet 1990; Ax 1995; Hooper & van Soest 2002). Exceptions to the classical sponge bauplan exist: some taxa lack a mineral skeleton (“keratose” sponges and *Chondrosia*, *Oscarella* and Halisarcida); there are carnivorous sponges (Cladorhizidae); and there are both recent and fossil sponges that lack choanocytes, choanocyte chambers and an aquiferous system (*Thymosiopsis*, Vacelet & Boury-Esnault 1995). These exceptions certainly contribute to the above-mentioned problems for sponge morphological systematics because primitive absence is difficult to distinguish from secondary loss.

Class–level problems in Porifera taxonomy

The extant sponge classes are relatively well–defined: Calcarea (calcareous sponges) produce extracellular limestone spicules; Hexactinellida (glass sponges) possess a syncytium of somatic cells and triaxonic silica spicules; Demospongiae produce monaxonic or tetraxonic silica spicules and/or secrete spongin (spongin B) via spongioblasts. Sclerosponges (“coralline sponges”) have a limestone basal skeleton and siliceous or calcareous spicules. They were initially regarded as a fourth class of sponges (Hartman 1969), but morphological (Soest 1984; Vacelet 1985; Reitner 1992) and molecular data (Chombard *et al.* 1997) showed their polyphyletic and predominantly demosponge origin.

Though each sponge class has been clearly defined, the phylogenetic relationships among the three classes are still largely undetermined, with several competing hypotheses: Böger (1988) divided sponges by their mineral skeleton type and differentiated Calcarea from Hexactinellida + Demospongiae (“Silicea”). Conversely, other authors regarded the syncytial tissue (“Symplasma”) of the Hexactinellida as a more discriminating characteristic and differentiated them from the non–syncytial Demospongiae + Calcarea (“Cellularia”) (Reiswig & Mackie 1983; Mehl & Reitner 1996).

Ultrastructural and molecular data provided evidence for a paraphyletic assemblage of the three classes: Woollacott & Pinto (1995) investigated the ultrastructure of choanocytes and found the flagellar bases of Calcarea to be more similar to those of diploblastic eumetazoans than to those of either Demospongiae or Hexactinellida.

The hypothesis of poriferan paraphyly has found support in various molecular analyses, although a conclusive picture has yet to emerge. Hsp70 data from Borchiellini *et al.* (1998) found sponges more derived than Cnidaria. This was in conflict to the findings of Kim *et al.* (1999), using 18S rDNA, and Medina *et al.* (2001), using 18S and 28S rDNA, who found sponges branching first, but no support for mono- or paraphyly. In the analysis of Zrzavy *et al.* (1998), based on 18S rDNA and morphology, sponges clustered paraphyletically, with siliceous sponges diverging early. Adams *et al.* (1999) used 18S rDNA data to reject sister group relationships between Calcarea and any other sponge class. Using 28S rDNA data, Lafay *et al.* (1992) provided the first molecular indication of a possible Calcarea - “Coelenterata” relationship, which was subsequently supported by Cavalier–Smith *et al.* (1996) who used 18S rDNA (see also Schütze *et al.* 1999, HSP70 data). Collins (1998, 18S rDNA) found Demospongiae and Hexactinellida at the base of the Metazoa, and positioned Calcarea as a poorly supported sister group of Ctenophora. Borchiellini *et al.* (2001, 18S rDNA) and Kruse *et al.* (1998, cPKC) displayed gene trees with Calcarea as the sister group of eumetazoans, leaving Demospongiae and Hexactinellida paraphyletic at the base of the metazoan tree, with Hexactinellida branching off first.

Recently, Borchiellini *et al.* (2004) suggested that the Homoscleromorpha, traditionally assigned to Demospongiae, are not Demospongiae *sensu stricto*, although they could not resolve the correct phylogenetic relationships. Homoscleromorpha are the only group of sponges known to possess a basement membrane and therefore, true epithelia by definition (Boury-Esnault 2003; Ereskovsky *et al.* 2007). This raises the possibility that they are more closely related to Eumetazoa than to other sponges, which recently found support by molecular data (Sperling et al. 2007). Grothe (1989) speculated that Homoscleromorpha might be more closely related to Calcarea based on larval traits, and some molecular phylogenies have recently corroborated this hypothesis (Nichols 2005; Dohrmann et al., accepted). The conundrum of lower metazoan relationships–especially among the diploblast taxa Porifera, Placozoa, Cnidaria, and Ctenophora—is a continuing saga, which neither mitochondrial genome data (Haen *et al.* 2007; Wang & Lavrov 2007) nor the analysis of 50 nuclear genes (Rokas *et al.* 2005) have resolved conclusively. Much larger datasets, in terms of both taxon—and character—sampling, are probably needed to resolve (a) the relationships of Calcarea with respect to "Silicea" (Demospongiae + Hexactinellida) and Eumetazoa, and (b) the corresponding relationships of Homoscleromorpha.

Calcarea

Manuel (2006) provided an excellent recent review on the class Calcarea; and consequently this present review will discuss only more recent additions. Sponges of this class, which Manuel (2006) prefers to call

"Calcispongia", are characterized by intercellular calcium carbonate spicules, which are an autapomorphic character of this group (e.g., Ax, 1995). This morphological synapomorphy clearly defines a monophylum, which has been corroborated by ribosomal DNA data (Borchiellini *et al.* 2001; Manuel *et al.* 2003, 2004; Dohrmann *et al.* 2006). Calcarea comprises about 500 exclusively marine species occurring in all oceans (Manuel *et al.* 2002). Traditionally, Class Calcarea has been subdivided into the two subclasses Calcinea and Calcaronea based on the position of the nucleus in choanocytes and on features of spicule morphology and larval forms (Bidder 1898; Borojevic *et al.* 1990, 2000). Another feature that distinguishes the two subclasses are differences in the ratio of $\delta^{13}C$ isotopes in the spicules (Reitner 1992; Wörheide & Hooper 1999). While some authors have argued that the character states of these features in one or the other subclass might represent symplesiomorphies, rendering the respective group paraphyletic with regard to the other (e.g., Manuel *et al.* 2002), their respective monophyly is now well–supported by rDNA sequence analyses (e.g., Dohrmann *et al.*, 2006).

The existing classification within Calcinea and Calcaronea (Borojevic *et al.* 1990; Borojevic *et al.* 2000, 2002a,b,c; Vacelet *et al.* 2002a) is not based on any phylogenetic system and is primarily typologic [see Manuel (2006) for a summary]. So far, only a few studies have applied molecular systematic methods to address this problem (Manuel *et al.* 2003, 2004; Dohrmann *et al.* 2006). The outcomes of these few studies were quite disturbing to traditional taxonomic paradigms, as they revealed an apparent high level of morphological homoplasy (Manuel *et al.* 2003), and found that most supra–specific taxa are not monophyletic (Dohrmann et al. 2006). Manuel *et al.* (2003) showed, for example, that the "pharetronid" *Petrobiona massiliana* Vacelet & Lévi belongs to Baerida, instead of Lithonida, supported by the occurrence of microdiactines and pugioles (dagger–shaped tetractines). In addition, they concluded that Leucosolenida Hartman, Grantiidae Dendy and *Sycon* Risso were not monophyletic. However, taxon sample size in that study was relatively sparse, especially within Calcinea.

Dohrmann *et al.* (2006) significantly increased both character and taxon sampling, particularly in Calcinea. They confirmed that the two orders of Calcinea, Murrayonida and Clathrinida (Borojevic *et al.* 1990, 2002b; Vacelet *et al.* 2002b), were paraphyletic but agreed with previous proposals of progressive evolution, i.e., that Calcinea progressed from simple to complex forms (Borojevic *et al.* 1990; see also Manuel 2006). The Leucettidae were recovered as monophyletic, but their internal relationships were poorly resolved, pending a complete revision of that family. Although the majority of their species formed a well–supported clade, Clathrinidae (*Clathrina* + *Guancha*) was not recovered as a monophylum due to paraphyletic *Clathrina*.

Surprisingly, with respect to Calcaronea, Dohrmann *et al.* (2006) discovered an early-branching position of *Plectroninia neocaledoniense*, which belongs to the Minchinellidae (Lithonida), a group characterized by the formation of a rigid basal skeleton composed of fused spicules (Borojevic *et al.* 1990; Vacelet *et al.* 2002a). Such rigid secondary calcareous skeletons also occur in other groups of calcareous sponges (Vacelet 1991; Reitner 1992) and include *Petrobiona massiliana* (now placed in Baerida) and several species of Calcinea (see above). The inferred early-branching position of *Plectroninia* might imply that a secondary basal skeleton, composed of fused spicules, was present in the ancestor of Calcaronea [see further discussion in Dohrmann *et al.* (2006)]. The placement of *Plectroninia* also raises questions about the evolution of the aquiferous system in Calcaronea because it has a more complex leuconoid aquiferous system (see Manuel *et al.* 2004; Dohrmann *et al.* 2006). More in-depth analysis, especially with an increased taxon sampling of Minchinellidae, is needed to provide further insights. Furthermore, Heteropiidae and *Sycettusa*, Grantiidae and *Leucandra*, as well as Jenkinidae, were not recovered as monophyletic groups (Dohrmann *et al*. 2006).

To date, the few molecular studies (Manuel *et al*. 2003, 2004; Dohrmann *et al*. 2006) and the one cladistic analysis of morphological characters of Calcarea (Manuel *et al.* 2003) have raised more questions than they have solved, with the most significant result being the extreme discrepancy between the rDNA analyses and the traditional, typological classification scheme. To better comprehend the evolution of Calcarea, much more comprehensive taxon sampling, especially in previously un- or under-sampled taxa like Minchinellidae, as well as the inclusion of additional molecular markers is needed. In addition, more in-depth and systematic molecular analysis of large genera, such as *Sycon*, *Leucetta* and *Clathrina,* is required in order to test existing systematic hypotheses based on morphological traits [e.g., Klautau & Valentine (2003) for *Clathrina*].

Hexactinellida

Excellent recent reviews on the systematics and biology of glass sponges (class Hexactinellida) have been written by Reiswig (2006) and Leys *et al.* (2007). This present review will provide only a brief overview and some more recent additions.

Hexactinellids are exclusively marine and are now restricted mainly to deep–water habitats, with only a few exceptions (see Leys *et al.* 2007). First described from the late Neoproterozoic (e.g., Brasier *et al.* 1997), no significant changes to their bauplan have occurred since then, though distinct Paleozoic and Mesozoic forms can be distinguished (Mehl 1992, 1996). They reached their peak diversity in the late Cretaceous (Mehl, 1992), but they had already contributed significantly to reef–building in the Jurassic (Tethys Sea; e.g., Leinfelder *et al.* 1994). About 500 extant species are currently described. The monophyly of Hexactinellida is well-established based on their unique triaxonic spicule symmetry and syncytial tissue organization (see Leys *et al.* 2007). The first molecular phylogenetic analysis to test this hypothesis will be published soon (Dohrmann *et al.*, accepted). As in the case of Calcarea, the classification system within Hexactinellida is rather typologic and not based on explicit phylogenetic systematic analysis.

It is now generally accepted that Hexactinellida is divided into the two subclasses Amphidiscophora Schulze and Hexasterophora Schulze (Reiswig 2002). The forthcoming analysis of Dohrmann *et al.* (accepted) will show that the molecular phylogeny is largely consistent with previous morphological classifications and the morphology–based phylogeny proposed by Mehl (1992), as well as with results from a computerized cladistic analysis of morphological data. This agreement between molecular systematics and morphological data is surprising given the discrepancies observed for the other two sponge classes. The congruence of molecules and morphology in Hexactinellida probably results from the greater number of more differentiated morphological characters. However, the biological reasons for this elevated morphological complexity in Hexactinellida remain enigmatic.

Demosponges (sensu stricto)

Demosponge higher phylogeny

In the past decade molecular data was able to shed new light on the morphological classifications. Boury-Esnault (2006) recently reviewed this evolution of demosponge research and described the transition from morphology to genomics. It is evident that different data sets, analytical methods and interpretations produced many different classifications over the past decades (see Erpenbeck 2004 for an overview).

Borchiellini *et al.* (2004), reconstructed one of the first comprehensive demosponge order–level phylogenies based on 18S and 28S rDNA. Their gene tree made a valuable contribution to the relationships between selected representatives of all orders. However, the number of sequences analyzed for this study was relatively low, given the diversity of sponges and the uncertain monophyly of many orders. Studies that drew on a larger taxon set are generally in agreement with this work, but provide a better impression of demosponge complexity, including the para- and polyphyly of many morphologically well-defined taxa (e.g., Nichols 2005; Holmes & Blanch 2007). All these first comprehensive studies supported the notion, dating back 20 years, to abandon the historic demosponge subclasses "Ceractinomorpha" and "Tetractinomorpha," which were primarily based on reproductive features (see the Halichondrida section below).

In combination with the frequent, mostly subtaxon-based phylogenies, we can assemble a more comprehensive picture of the phylogeny of demosponges, though we are limited by the fact that many molecular analyses utilize the same genes and sequences, and comprehensive mitochondrial data are still scarce.

In most molecular phylogenies, sponges without a mineral skeleton are among the first branching Demospongiae (Borchiellini *et al.* 2004; Addis & Peterson 2005; Nichols 2005; Schmitt *et al.* 2005; Holmes & Blanch 2007; Redmond *et al.* 2007, all rDNA). The orders Dictyoceratida and Dendroceratida possess a skeleton consisting of organic (spongin) fibres without endogenous mineral components. [It should be noted that the sphinctozoan Dictyoceratida, *Vaceletia*, does possess a secondary calcareous skeleton, as discussed below.] Both orders are in a sister group relationship (Borchiellini *et al.* 2004: clade "G1" "Keratosa"; Addis & Peterson 2005; Schmitt *et al.* 2005, all rDNA).

Similarly, Verongida and Chondrosida are closely related, as evident from both ribosomal data (Borchiellini *et al.* 2004: clade "G2" "Myxospongiae"; Addis & Peterson 2005; Nichols 2005; Schmitt *et al.* 2005; Holmes & Blanch 2007; Redmond *et al.* 2007; all rDNA) and mitochondrial data (Nichols 2005; Rot *et al.* 2006; Erpenbeck *et al.* in press –a). These taxa contain some genera that *do* possess mineral elements or no skeleton at all. In addition, Verongida and Chondrosida cluster with the skeleton-lacking Halisarcida (Borchiellini *et al.* 2004, 28S rDNA). However, current molecular data cannot resolve whether "Keratosa" and "Myxospongiae" are sister taxa, as suggested by 18S rDNA, or whether they are paraphyletic with "Keratosa" branching first, as suggested by 28S rDNA (but with low support).

The more derived demosponge orders comprise taxa with more-or-less complex mineral skeletal structures, and the phylogenetic hypotheses about them often lack unequivocal support. Here, marine species of the paraphyletic "Haplosclerida" (*i.e.*, Petrosina and Haplosclerina) branch off first in many gene trees, followed by their freshwater relatives (Spongillina) (Borchiellini *et al.* 2004, 18S rDNA; Holmes & Blanch 2007, 28S rDNA; Rot *et al.* 2006, CO1, marine species only). However, marine haplosclerid taxa frequently display long branches in ribosomal and mitochondrial phylogenies (Erpenbeck *et al.* 2004; 2007c) and are therefore prone to cause artifacts in phylogenetic reconstructions (see section on Haplosclerida below for further information). The relationship among the remaining demosponge groups remains largely speculative because major orders have been found to be non-monophyletic in molecular analyses. Nevertheless, several well-defined and partially supported clades crystallize out of the different gene trees, one of which combines Astrophorida and Spirophorida. Representatives of both orders cluster together in most ribosomal and mitochondrial phylogenies (e.g., Vacelet *et al.* 2000; Borchiellini *et al.* 2004: "Tetractinellida"; Addis & Peterson 2005; Nichols 2005; Holmes & Blanch 2007; Redmond *et al.* 2007; Erpenbeck *et al.* in press–a; Itskovich *et al.* in press.)
Morphologically, the "Tetractinellida" possess tetractine spicules that distinguish them from the remaining taxa, which comprise the orders Agelasida, Halichondrida, Hadromerida and Poecilosclerida. The latter three orders are probably polyphyletic (see their respective chapters below). Several gene trees display an unsupported sister group relationship between "Tetractinellida" and the agelasid, halichondrid, hadromerid, and poecilosclerid taxa (Borchiellini *et al.* 2004; Addis & Peterson 2005; Erpenbeck *et al.* 2004, 2005; Nichols 2005; Redmond *et al.* 2007; Kober & Nichols in press; Itskovich *et al.* in press). Some suggest close phylogenetic relationships between poecilosclerid (s.s.) and hadromerid taxa (discussed below).

"Lithistid" demosponges are a polyphyletic group that contains 13 extant families (Pisera & Lévi 2002). The polyphyly of this group has been known for a long time (see Pisera & Lévi 2002) as demonstrated also by molecular analysis (e.g., Kelly-Borges & Pomponi 1994). For example, several "lithistid" taxa cluster with the Astrophorida / Spirophorida (Tetractinellida) group: *Aciulites* sp. ("lithistid" family Scleritodermidae), *Theonella* and *Discodermia* ("lithistid" family Theonellidae), and *Corallistes* ("lithistid" family Corallistidae) (Addis & Peterson 2005; Nichols 2005; Itskovich *et al.* in press). We will therefore refrain from a separate "Lithistida" section but will instead discuss the phylogenetic position of lithistid taxa together with the other taxa with which they cluster.

In the following sections, we will summarize the phylogenetic status of the demosponge orders *sensu* Hooper & van Soest (2002a).

Spirophorida

Tetillidae is the only family within Spirophorida that has been included in molecular phylogenies. This is presumably due to the encrusting or excavating habit of the other two families, Samidae and Spirasigmidae, which makes them both more difficult to collect and prone to contamination. Therefore monophyly of the Spirophorida, although morphologically supported by sigmaspire microscleres, has yet to be confirmed by molecular studies. The Tetillidae *Tetilla* and *Cinachyrella* cluster monophyletically (e.g. Nichols 2005; Redmond *et al.* 2007).

Astrophorida

Astrophorida comprises five families (excluding lithistid families and *Lamellomorpha*). Ancorinidae and Geodiidae are thus far the only taxa included in comprehensive molecular taxon sets, and they cluster monophyletically (e.g., Nichols 2005, 28S rDNA and CO1). The 28S tree of Nichols (2005) comprises six astrophorid genera. Four of them are identified as Ancorinidae, but they do not form a monophyletic group with respect to Geodiidae (*Geodia*). Support values in this study are low, and the sixth sequence, a putative *Lamellomorpha*, is placed *incertae sedis* in the Astrophorida because of morphological similarities to Ancorinidae and Pachastrellidae in addition to families of other orders (Hooper & Maldonado 2002).

A more detailed analysis on the Astrophorida relationships and morphological character stability (Chombard *et al.* 1998) underlined the problems of distinguishing between primary absence of morphological characters and their secondary loss. The families analyzed—Calthropellidae, Ancorinidae and Geodiidae—share the possession of euasters. With Pachastrellidae they share calthrops–like megascleres (van Soest & Hooper 2002a). The gene tree displays the Pachastrellidae *Poecillastra compressa* branching off first from the Spirophorida outgroup, but the study identifies neither Ancorinidae (*Penares* and *Stryphnus*) nor Geodiidae (*Pachymastia* and *Erylus*) as monophyletic. Sequences of the lithistid genera *Discodermia* and *Corallistes* cluster inside the non–lithistid astrophorids (see also Vacelet *et al.* 2000).

Chondrosida

The four genera of the order Chondrosida have not yet been identified as monophyletic in molecular trees. Ribosomal data could not unite *Chondrosia* with *Chondrilla, Thymosia* and *Thymosiopsis* (Borchiellini *et al.* 2004; but see also Vacelet *et al.* 2000 for monophyletic Chondrosida without *Chondrilla* sequence). 28S rDNA sequences of partly unidentified Chondrosida cluster paraphyletically (Nichols 2005), and mitochondrial data for *Chondrosia* and *Chondrilla* could not support their monophyly either (Erpenbeck *et al.* in press–a).

Hadromerida

Hadromerida comprise sponges morphologically very diverse in terms of spicules and skeletal shape. They were the subjects of the first molecular phylogeny of sponges (Kelly–Borges *et al.* 1991), but their gene trees were constructed with notoriously few representative taxa. Borchiellini *et al.* (2004) employed a single Suberitidae as hadromerid representative, which is only one extreme of the hadromerid taxonomic spectrum. In contrast, the gene trees of Nichols (2005) originated out of a Hadromerida analysis, which consequently contained a more representative taxon set. In his study, Hadromerida are polyphyletic and closely related to monophyletic Poecilosclerida.

Hadromerid families

Kober & Nichols (in press) used full-length 18S and 28S rDNA sequences to re-analyse the phylogenetic positions of the poecilosclerid/hadromerid clade and the relationships among hadromerids. Focusing only on hadromerid and poecilosclerid sequences and excluding sequences of other taxa, their refined analysis supports the initial molecular hypothesis of paraphyletic Hadromerida with Polymastiidae branching off first (see Nichols 2005; Holmes & Blanch 2007; see also Kelly-Borges *et al.* 1991). Furthermore, the analysis supports a Tethyidae + Hemiasterellidae clade with a monogeneric Timeidae in a sister group relationship and a Clionaidae + Spirastrellidae clade with Placospongiidae as sister group. Morphologically, members of the families Clionaidae and Spirastrellidae share similar spiraster microscleres, and families Tethyidae and Hemiasterellidae—and the closely related family Timeidae—share asterose microscleres (Kober & Nichols, in press).

Suberitidae

Among the paraphyletic Hadromerida as determined by Kober & Nichols (in press), Suberitidae sequences are recovered in a single clade among several non-suberitids (e.g., *Hemiasterella*). In addition, ribosomal DNA (in particular 28S rDNA) repeatedly groups Halichondriidae (order Halichondrida) with Suberitidae (Chombard & Boury-Esnault 1999; McCormack & Kelly 2002; Erpenbeck *et al.* 2004, 2005). Recently this constellation could be supported by mitochondrial data (CO1, Erpenbeck *et al.* in press–a, see also the Halichondrida section).

Poecilosclerida

Comprising some 25 families and 129 genera, Poecilosclerida is the largest order of demosponges (Hooper & van Soest, 2002b). Despite its obviously important position among the demosponges, poecilosclerida monophyly and internal phylogenetic relationships have received little attention in molecular studies. While poecilosclerid species are occasionally included in population analyses (e.g., Duran *et al.* 2004), higher phylogenies are lacking. Morphologically, Poecilosclerida is regarded as a well-defined monophylum, particularly because most of its genera possess characteristic chelae microscleres. Other, non-chelae-bearing taxa such as Raspailiidae or Desmacellidae are assigned to Poecilosclerida because of similarities in skeletal arrangement and spiculation other than chelae (see Hooper & van Soest, 2002 for details). Nevertheless, many important demosponge gene trees do not comprise a representative set of chelae-lacking poecilosclerid taxa and consequently resolve their (few) Poecilosclerida sequences as monophyletic (Borchiellini *et al.* 2004; Nichols 2005; Holmes & Blanch 2007; Redmond *et al.* 2007). In contrast, a recent CO1 analysis (Erpenbeck *et al.* in press–a) finds that the chelae-lacking taxa *Ectyoplasia ferox* (Raspailiidae), *Pandaros acanthifolium* (Microcionidae) and *Neofibularia nolitangere* (Desmacellidae) are unrelated to chelae-bearing Poecilosclerida. Instead, their sequences cluster with other taxa of ambiguous ordinal classification, such as *Ptilocaulis* (Halichondrida: Axinellidae, see Halichondrida section below). A reciprocal analysis of the internal relationships in Raspailiidae supports this outcome; the chelae-bearing Poecilosclerida are unrelated to the chelae–lacking Raspailiidae (Erpenbeck *et al.* in press–b). The analyses of Rot *et al.* (2006, COI) did not recover chelae–lacking Poecilosclerida as monophyletic because *Negombata* (Podospongiidae) forms a sister group with *Axinella* (order Halichondrida) instead of *Biemna* (Desmacellidae, n.b.: support is low). On the other hand, *Tedania* (Poecilosclerida: Tedaniidae) is a chelae-lacking Poecilosclerida, but it *does* cluster with the chelae–bearing species in 28S and CO1 analyses. For this genus, a secondary loss of chelae can be assumed. We can conclude that chelae-bearing Poecilosclerida form a monophyletic clade but do not necessarily share a common ancestor with several non-chelae subtaxa, such as Raspailiidae.

Poecilosclerida suborders

The suborders Mycalina, Microcionina and Myxillina have not been recovered within the monophyletic, chelae-bearing Poecilosclerida, as predicted from their morphology (Hooper & van Soest 2002b). Although Borchiellini *et al.* (2004, 18S rDNA) found that the two Myxillina taxa *Phorbas* and *Crella* form a monophylum as a sister group to the monophyletic Mycalina and Microcionina representative (*Mycale* resp. *Microciona*), subsequent analyses, in particular those involving additional Myxillina, do not retrieve monophyletic suborders (Nichols 2005). These relationships should probably be treated with caution in light of the low support values calculated for the phylogenetic tree. This large and important demosponge order clearly requires more thorough molecular analysis.

Raspailiidae

The relationships of this poecilosclerid family have recently been analyzed with molecular data. First, 28S rDNA (Erpenbeck *et al.* 2007b) confirms morphological evidence (van Soest *et al.* 2006) that Sollasellidae, previously assigned *incertae sedis* in the Hadromerida, is in fact a raspailiid taxon. Internal raspailiid analyses show that *Raspailia* (s.s.), *Eurypon*, *Sollasella* and *Aulospongus* form a Raspailiinae clade. Some *Raspailia* subgenera, in particular *R.* (*Parasyringella*), are not retrieved monophyletically. *Trikentrion* falls into the Thrinacophorinae and not the Cyamoninae as earlier hypothesized. On the other hand, axinellid (Halichondrida) genera *Ptilocaulis* and *Reniochalina* cluster with Raspailiidae and are distant from the other Axinellidae (Erpenbeck *et al.* in press–b).

Podospongiidae

CO1 sequence analyses places *Negombata* and *Diacarnus* in a monophyletic group (Erpenbeck et al., unpublished CO1 data). Podospongiidae are classified as Mycalina *incertae sedis* based on an interpretation that the protorhabd of spinorhabds is sigmoid and potentially a sigmancistra derivative (Kelly & Samaai 2002). Molecular analyses find Podospongiidae clustering not with Mycalina but with other suborders instead (Nichols 2005; Schmitt *et al.* 2005; Rot *et al.* 2006; Itskovich *et al.* in press).

Haplosclerida

Haplosclerida is evolutionary a very diverse and successful demosponge group (van Soest & Hooper 2002c). Its definition comprises all freshwater sponges (Spongillina) as well as several marine members, all of which share striking skeletal similarities (van Soest & Hooper 2002c for details). Initial gene trees derived from molecular analyses repeatedly rejected a sister group relationship between freshwater sponges and any marine haplosclerid sponge taxon (Nichols 2005, 18S and 28S rDNA; Addis & Peterson 2005, 18S rDNA). However, these studies were carried out with only one freshwater sponge sequence or only one marine sponge sequence. Comprehensive analyses with more representative taxon sets corroborated the non-monophyletic entity of marine and freshwater Haplosclerida (Redmond *et al.* 2007; Itskovich *et al.* in press).

The lithistid *Vetulina* (Vetulinidae) clusters with haploscerid taxa; in particular, it clusters close to freshwater sponges (Addis & Peterson 2005; Itskovich *et al.* in press, 18S rDNA). Nevertheless, a haplosclerid affinity of *Vetulina* lacks any morphological support. Elucidating the phylogenetic position of this genus will require additional analysis.

Spongillina (freshwater sponges)

The monophyly of freshwater sponges has been addressed and shown in several gene trees (Itskovich *et al.* 1999; Schröder et al. 2003; Addis & Peterson 2005, 18S rDNA, also CO1; Itskovich *et al*. 2006 (all lacking representative marine haplosclerid taxa); Redmond *et al.* 2007, 18S rDNA; Itskovich *et al.* in press, 18S rDNA and CO1). The nominal family Spongillidae is apparently non-monophyletic (Itskovich *et al.* 1999; Addis & Peterson 2005; Redmond *et al*. 2007, Meixner *et al*. 2007). Its genus *Ephydatia*, a Spongillina genus widespread particularly in the Northern Hemisphere (Manconi & Pronzato 2002) forms a monophyletic clade with the Lake Baikal endemic Lubomirskiidae and the monophyly of the latter has been tested by several publications (see Schröder et al. 2003, CO1 and tubulin-intron; Addis & Peterson 2005, 18S rDNA and ITS; Itskovich *et al.* 2006; but see also Itskovich *et al.* 1999 and in press; Meixner *et al.* 2007). In several of those analyses, The Metaniidae *Corvomeyenia* mostly branches off at the base from other Spongillina (Addis & Peterson 2005; Meixner *et al*. 2007, Itskovich *et al.* in press). Malawispongiidae are polyphyletic and the position of the tropical Potamolepidae, *Echinospongilla*, remains unresolved (Meixner *et al.* 2007, Itskovich *et al.* in press).

Marine Haplosclerida

The molecular evolution of the marine Haplosclerida appears to be somewhat enigmatic. This is particularly noteworthy because *Amphimedon queenslandica,* the target species of the sponge genome project, is a member of this order. Haplosclerid ribosomal genes display a different secondary structure and an elevated substitution rate compared to the other demosponge orders (Erpenbeck *et al.* 2004). Among other peculiarities, the mitochondrion of *Amphimedon queenslandica* lacks *atp9,* and it is unknown whether other Haplosclerida share this loss (Erpenbeck *et al.* 2007c).

Most molecular phylogenies support the monophyly of marine Haplosclerida but fail to recover most families and their two suborders Haplosclerina and Petrosina as monophyletic (McCormack 2002; Erpenbeck *et al.* 2004; Redmond *et al.* 2007). Several genera, in particular the species-rich *Haliclona* (Chalinidae) and *Callyspongia* (Callyspongiidae), are not recovered as monophyletic at all and form mixed clades. Some mitochondrial markers, such as CO1, do not support the monophyly of marine Haplosclerida at the nucleotide level (Erpenbeck *et al.* in press–a), but many of the clades converge when their amino acid sequences are compared (Erpenbeck, pers. obs.).

Halichondrida

The order Halichondrida obtained from classical (morphological) analyses occupies a pivotal position in demosponge phylogeny. Working independently, van Soest (1984) and Hooper (1984) pointed out inconsistencies in the current classifications of Poecilosclerida and Axinellida, respectively. After the introduction of cladistic character analyses in sponge systematics (van Soest 1990), both authors independently concluded that the division of demosponges into the subclasses Ceractinomorpha and Tetractinomorpha is unparsimonious and artificial. They suggested re-merging the order "Axinellida" (formerly Tetractinomorpha) with Halichondrida (formerly Ceractinomorpha). The Halichondrida now comprise five families (van Soest & Hooper 2002d), but their monophyly has not been determined by studies using multiple data sets (see Erpenbeck 2004 for more details). On the contrary, different lines of evidence support the polyphyletic nature of this important taxon. The first evidence of halichondrid non–monophyly came from the 28S rDNA data of Lafay *et al.* (1992) and the biochemical data of Braekman *et al.* (1992). Both studies showed a close relationship between Agelasida and Axinellidae. More recently, these findings have been corroborated using additional, independent markers (e.g., Erpenbeck *et al.* 2006).

Furthermore, 28S rDNA studies consistently suggest a close relationship between Halichondriidae and Suberitidae (Hadromerida) (e.g., Chombard & Boury-Esnault 1999), and these studies have recently been corroborated by mitochondrial (CO1) data (Erpenbeck *et al.* in press–a). A Halichondriidae + Suberitidae taxon may be accepted in the future.

Halichondrida families

Sequences of almost all molecularly investigated Halichondriidae cluster together in the Halichondriidae (+Suberitidae) clade, which corroborates their close genealogical relationship predicted from morphology (Erpenbeck & van Soest 2002). The genus *Axinyssa* is the only exception, and it clusters distantly; it is also lacking one of the most characteristic features of Halichondriidae: the tangential ectosomal skeleton (Erpenbeck et al. 2005).

The family Dictyonellidae was defined in order to cope with taxa of the revised Halichondrida sensu van Soest *et al.* (1990). It is based entirely on the absence of characters and therefore tends to include unrelated taxa, as has been revealed by molecular data of independent genes. There is presently no molecular evidence to uphold this family. Members of this family are scattered over the phylogenetic trees, and sequences of the nominal genus *Dictyonella* do not cluster in the vicinity of Halichondriidae (e.g., Nichols 2005; Erpenbeck *et al.* 2005).

Axinellidae are also polyphyletic in molecular phylogenies. The nominal genus *Axinella* cannot be recovered monophyletically (Alvarez *et al.* 2002). In all molecular phylogenies reconstructed to date, *Reniochalina*, *Ptilocaulis* and *Phakellia* cluster distantly but with a close relationship to Raspailiidae (see Poecilosclerida sections above, Holmes & Blanch 2007, 28S rDNA; Erpenbeck *et al.* in press–a, –b, 28S rDNA and CO1).

Too few taxa of the families Heteroxyidae and Bubaridae have been sequenced to draw conclusions about their phylogeny.

Agelasida

The sister group relationship of the families Astroscleridae *s.s.* and Agelasidae has been shown repeatedly using molecular (Chombard *et al.*, 1997; Alvarez *et al.*, 2000, Nichols 2005) and biochemical data (reviewed in Wörheide 1998). A close relationship to halichondrid taxa (*Axinella*, *Stylissa*) has been documented with independent molecular data sets (see the Halichondrida section).

Recent gene trees also favour a close relationship between some Raspailiidae (Poecilosclerida) with Axinellidae and Agelasida. For example, 28S rDNA sequences of *Amphinomia* are almost identical with their agelasid counterparts (Erpenbeck *et al.* in press–b). In addition, CO1 data found *Eurypon* (order Poecilosclerida) and *Prosuberites laughlini* (formally *Eurypon laughlini*) as a sister group to Agelasida and Axinellidae (Nichols 2005; Itskovich *et al.* in press). Until quite recently Agelasidae was considered a poecilosclerid taxon by most authors, defined in the older literature simply as comprising Poecilosclerida with echinating spicules (van Soest & Hooper 2002b). However, molecular data with a more representative taxon sampling could not confirm close relationships between Raspailiidae *s.s.* and Agelasida (Erpenbeck *et al.* 2007b and in press–b).

Preliminary molecular results on the internal relationships of Agelasida, especially Agelasidae, have been shown by Parra-Velandia *et al.* (2006).

Verongida

The monophyly of this biochemically interesting order has been demonstrated in a few gene trees (e.g. Borchiellini *et al.* 2004; Nichols 2005; Holmes & Blanch 2007; Redmond *et al.* 2007). Within Aplysinidae, ribosomal data (Schmitt *et al.* 2005, 18S; Erwin & Thacker 2007, ITS) and mitochondrial data (Erpenbeck *et al.* in press–a) indicate a closer relationship of *Aplysina* and *Verongula* with respect to *Aiolochroia*. However, when a more representative verongid taxon set is used, the entity of the family Aplysinidae is not supported as the monogeneric Pseudoceratinidae (*Pseudoceratina*) forms a sister group with *Verongula* (Erwin & Thacker 2007). *Pseudoceratina* sequences appear problematic in several gene trees and additional data and re–determination of voucher material will have to confirm the phylogenetic position of this genus (Nichols 2005; Erwin & Thacker 2007). Furthermore, *Aiolochroia* clusters with Ianthellidae (*Ianthella*) and Aplysinellidae (*Aplysinella*), which form a sister group and split first in ITS sequence phylogenies (Erwin & Thacker 2007), but support values are rather low. Monophyly of the families Ianthellidae and Aplysinellidae must still be verified with molecular markers. ITS data also recognize *Aplysina aerophoba* as sister group to *A. fulva*, *A. cauliformis* and *A. fistularis* (Schmitt *et al.* 2005; Erwin & Thacker 2007).

Dictyoceratida

Monophyly of dictyoceratid sequences has been demonstrated in most gene trees (Borchiellini *et al.* 2004; Nichols 2005; Holmes & Blanch 2007; Redmond *et al.* 2007; Kober & Nichols in press). However, only a few publications provide insight into the internal phylogenetic relationships of the Dictyoceratida. Redmond *et al.* (2007) find *Ircinia* and *Spongia* in a sister group relationship with Dysideidae splitting at the base. Dysideidae (*Dysidea* and *Pleraplysilla*) are paraphyletic in 18S rDNA reconstructions (Addis & Peterson 2005, see also Borchiellini *et al.* 2004, 28S rDNA).

Preliminary results of a comprehensive phylogenetic analysis of "keratose sponges" indicate a monophyletic clustering of Irciniidae (*Sarcotragus* and *Ircinia*) and also the thorectid subfamily Phyllospongiinae

(*Phyllospongia*, *Carteriospongia* and *Strepsichordaia*; Erpenbeck *et al.* 2007a, 28S rDNA). Molecular data on multiple genes also show that *Vaceletia*, the only extant representative of the polyphyletic group "Sphinctozoa" and a member of the order Verticillitida (Vacelet, 2002), is in fact a dictyoceratid sponge (Wörheide *et al*. 2006).

Dendroceratida

A monophyletic relationship between *Darwinella* and *Aplysilla* has been demonstrated by Borchiellini *et al.* (2004) using 28S rDNA. The preliminary analyses of Erpenbeck *et al.* (2007a) found the same for *Aplysilla* and *Chelonaplysilla*; in addition, this study found that a taxonomically unverified *Acanthodenrilla* sequence clustered distantly. To our knowledge no detailed molecular phylogenies of dendroceratid taxa have yet been published.

Outlook

We have summarized the current status of sponge molecular phylogeny in Figure 1.

Most of the analyses have been based on ribosomal DNA sequences and supplemented in some cases with CO1 data. A comprehensive analysis of demosponge relationships based on complete mitochondrial genomes appears forthcoming (see Lavrov *et al.* 2006). A consistent topology reconstructed from ribosomal and full mitochondrial genome sequences would provide overwhelming support for the current molecular view on sponge evolution, but the details for many clades will still need to be resolved. For demosponges in particular, the relationships among poecilosclerid, haplosclerid, halichondrid and hadromerid taxa will require analyses of several independent genes and will have to include a far larger taxon set than previously analysed to accommodate the new clades recovered to date.

As the number of phylogenies has increased, discrepancies between mitochondrial and nuclear gene trees have decreased. Certainly, new data facilitate identification of erroneous species determinations. Moreover, the use of additional and, in particular, longer sequences helps to identify paralogous (e.g., pseudogene) sequences, which might be responsible for topological discrepancies (Erpenbeck *et al.* 2006 and unpublished data).

We would like to point out that our review comprises a molecular view on the phylogeny of sponges. The discrepancies between the molecular phylogenies and the morphological classification especially in Demospongiae and Calcarea (e.g. Hooper & van Soest 2002) remain remarkable. A lot of gene trees, reconstructed from a variety of markers, cannot be explained without assuming a large amount of homoplasies in morphological characters. Certainly, the simplicity of sponge morphological characters triggers classification on such homoplasies, but we have to admit that, although DNA evolution appears better understandable due to sophisticated substitution models, several molecular gene trees clearly require more insight into molecular evolution. It remains to hope that soon a robust phylogeny will facilitate the comprehensive understanding of sponge morphological (and molecular) character evolution. Coming years will bring the science of sponge systematics closer to its long–awaited goal of a fully consistent phylogeny.

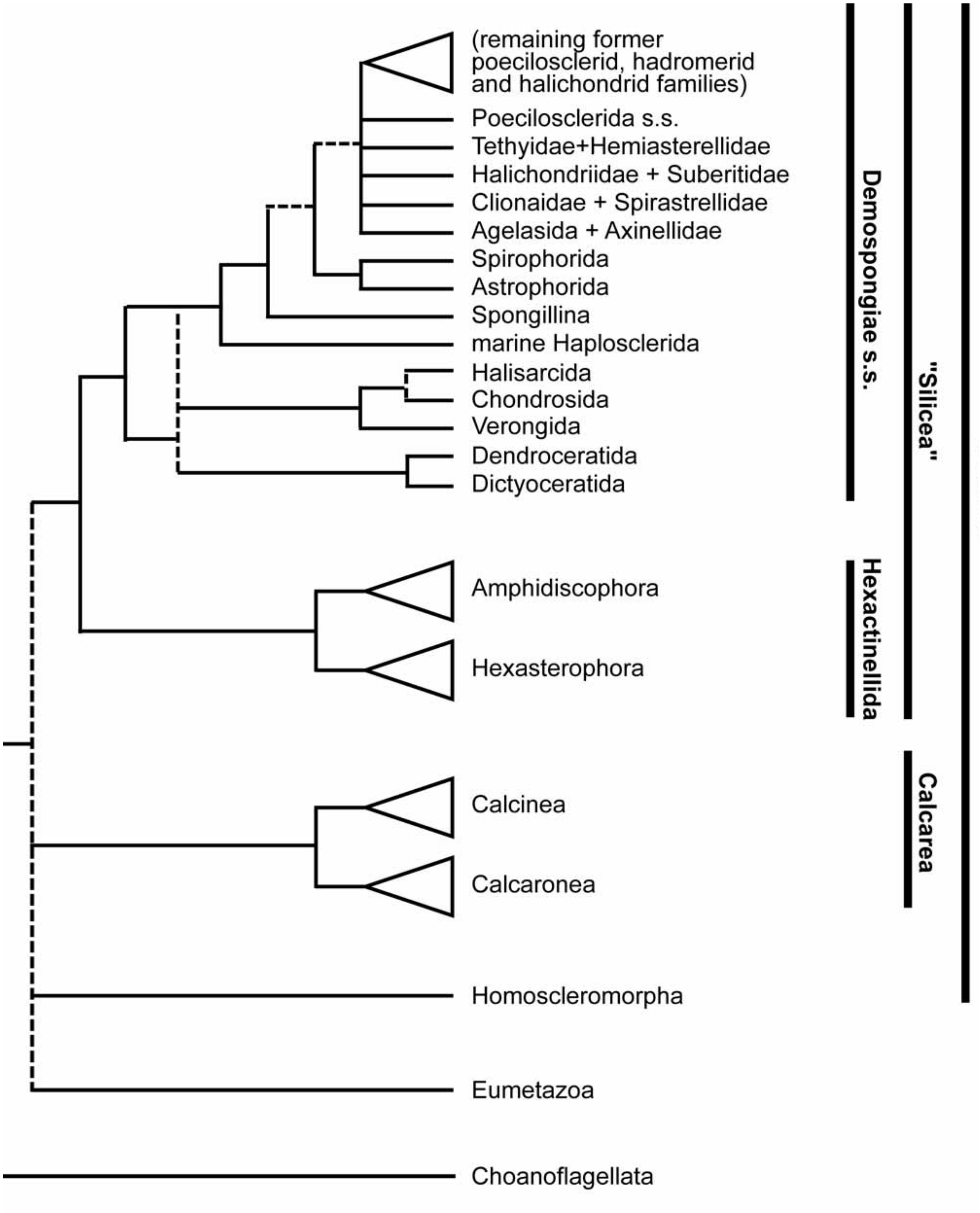

FIGURE 1: Summarized view on the current knowledge of molecular phylogenetic relationships of sponges as discussed in the text. Dashed lines indicate branches of particularly uncertain molecular hypotheses.

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