

Phylum Porifera Grant, 1836

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Phylum Porifera (sponges) are metazoans united by the unique possession of choanocyte chambers, a system of afferent and efferent canals with external pores, lacking a tissue grade of construction but having a highly mobile population of cells capable of totipotency, and possessing siliceous or calcitic spicules in many (but not all) species. Four sponge classes are currently recognised, although the monophyly (and indeed the existence of the 'Phylum Porifera') has been challenged by recent molecular data and chemical evidence. Three classes have Recent species: Hexactinellida (syncytial choanoderm, discrete cells and pinacoderm, siliceous triaxone spicules, ubiquitous fibrillar collagen, mostly deeper water), Demospongiae (discrete cells, siliceous monaxon or tetraxon spicules, ubiquitous fibrillar collagen), and Calcarea (discrete cells, calcareous spicules, ubiquitous fibrillar collagen). Archaeocyatha was an important group of sessile marine organisms during the Cambrian but is now presumed extinct. It was characterized in having double-walled inverted conular growth forms with spaces between outer and inner walls filled by various skeletal structures, overall architecture of interlocking polyhedral microgranular calcite, and lacking free spicules. Within this systematics there is scope for recognition of subphyla (e.g., Demospongiae + Calcarea vs. Hexactinellida, based on cytological evidence; or Demospongiae + Hexactinellida vs. Calcarea, based on some molecular data), but this level is not applied here as the debate is still embryonic and there are still conflicting molecular data. Fossil sponges are not always easy to classify with respect to Recent taxa, with some fossilised groups such as the 'lithistids' and 'sphinctozoans' distributed within a Recent classification, but with others treated independently. Keys to the classes of Recent and fossil sponges are constructed independently to avoid presumptions of alleged phylogenetic affinities. This work describes 682 valid genera of the extant fauna (of about 1600 nominal genera) in three classes, 25 orders and 127 families; and mentions over 1000 'valid' genera amongst the fossil fauna in six 'classes', 30 orders and 245 families (although the fossil demosponge fauna is not substantially delineated in this work). Fossil 'Classes' Sphinctozoa and Stromatoporoidea are clearly polyphyletic and represent grades of construction and not phylogenetic clades.

Keywords: Porifera; Demospongiae; Calcarea; Hexactinellida; Archaeocyatha; 'Sphinctozoa'; 'Stromatoporoidea'.

DEFINITION, DIAGNOSIS, PURPOSE, SCOPE

Definition

Sessile metazoans with a differentiated inhalant and exhalant aquiferous system with external pores, in which a single layer of flagellated cells (choanocytes) pump a unidirectional water current through the body, containing a highly mobile population of cells capable of differentiating into other cell types (totipotency) and conferring a plasticity to growth form, and with siliceous or calcitic spicules present in many species.

Diagnosis

Sessile metazoans possessing inhalant and exhalant pores connected by chambers lined by choanocytes. The outside and the canals are lined by pinacocytes (exo- and endopinacocytes respectively). Water is inhaled through small pores (10–100 µm in diameter), traversing the afferent canals towards the choanocyte chamber, and is expelled through efferent canals and the larger exhalant osculum. Water currents are unidirectional, maintained by an active beating of a single layer of flagellated cells (choanocytes) usually contained within chambers. Food particles and oxygen are removed from the water by various cells, including the choanocytes. Other cells, including archaeocytes, are instrumental in transporting these respiratory and dietary products throughout the sponge body, in

addition to other functions. Cells are highly mobile, such as those that move freely within an extracellular matrix made of fibrils of collagen (the mesohyl): archaeocytes, collencytes, spiculocytes, spongocytes, glyocytes, cells with inclusions, etc. (see definitions of terms in Boury-Esnault & Rützler, 1997). Most of the cells, especially the archaeocytes, have an ability to continually evolve into several other cell types as required by the individual organism (totipotency), which provide the sponge with a plasticity for its organisation. Firmness of the sponge body is provided by (1) collagen fibrils of the mesohyl, (2) spongin fibres, and (3) an inorganic skeleton consisting of various supporting mineral elements composed of either calcium carbonate (CaCO₃) or silica (SiO₂) material (including discrete spicules, articulated or fused spicules and/or hypercalcified mineralised basal skeleton). Articulated and hypercalcified skeletons are absent in most Recent taxa, but were much more prevalent in fossil faunas ('lithistid' and 'sclerosponge' bauplans). These organic and inorganic materials are manufactured or otherwise engineered by various types of cells. Sponges have free-swimming or creeping larvae, although most groups have considerable means of asexual propagation, and all have extensive regenerative powers that appear to be vital for sustaining local populations. There are three distinct classes (Hexactinellida, Demospongiae and Calcarea), with the extinct class Archaeocyatha having suspected affinities with Demospongiae. The fossil 'classes' Sphinctozoa and Stromatoporoidea are obvious grades of construction and not phylogenetic clades (e.g., Wood, 1991a),

although distribution of the many lower taxa amongst the four well-established classes remains largely unresolved.

Poriferan apomorphies

Sponges were first recognised unequivocally as being animals by Ellis (1755), Pallas (1766) and Ellis & Solander (1786), although an acrimonious debate on this topic continued for at least a century (see Lévi, 1999). They were first acknowledged as a distinct taxon within the Linnean classification, as 'Spongida', 'Spongiida' or 'Spongiae', but generally incorporated within the Protozoa (early volumes of the *Zoological Record*). It was not until the 1872 volume of the *Zoological Record* that Lütken suggested 'Spongozoa' "should probably form a class by themselves", and subsequently in 1876 were they elevated to their own section of the *Zoological Record*. Over the two centuries of earnest study the perception of sponges has evolved from suspected colonial representatives of unicellular protozoans (Clark, 1867; Saville Kent, 1880–1882), to a member of the coelenterates (Haeckel, 1872), to an intermediate taxon (Subkingdom Parazoa) (e.g., Hentschel, 1923), to a phylum lying at the base of the Metazoa (Hyman, 1940; Brien, 1967), and currently to several potential phyla of multicellular animals (e.g., Bergquist, 1985; Zrzavy *et al.*, 1998; Borchiellini *et al.*, 2001).

Their true affinities will certainly become better resolved as our technical abilities to sample the genome increase, unclouded by the myriad of phenotypic problems that currently plague sponge systematics. In the meantime, however, we continue to treat sponges (rightly or wrongly) as a monophyletic taxon, with the current definition based fundamentally on the common possession of (1) choanocytes, (2) a differentiated inhalant and exhalant aquiferous system with external pores, (3) a high cellular motility with cells capable of totipotency, and (4) presence of spicules in many species.

Recent data have already contested some of these alleged synapomorphies, with the discovery of carnivorous sponges (Vacelet & Boury-Esnault, 1995a) and some remarkable Precambrian fossils from Guizhou in southern China (Li *et al.*, 1998), both of which lack the first two synapomorphies (Vacelet, 1999a), and the last one, spicules, not universal amongst the phylum. In a theoretical context these modifications or losses to the fundamental poriferan bauplan (described as probable apomorphies by Vacelet, 1999a) are no problem, whereas they present a practical problem in clearly differentiating all putative sponges from other multicellular animals. In light of this new evidence, and in reviewing the concept of 'animality' of the Porifera, Lévi (1999) regarded the most important feature of the phylum to be their highly mobile cells and plasticity in growth form, reiterating his previous assertions (e.g., Lévi, 1970) that sponges retain a plasticity of their cellular organisation unique amongst the Metazoa. Together with their theoretical capabilities for cellular totipotency (Vacelet, 1990) these diverse cell types can be found in all organisms that we presently assign to 'sponges'. This definition has good empirical support from the cellular diversity observed in Recent species (e.g., pinacocytes, porocytes, archaeocytes, sclerocytes) also allegedly present in the Precambrian fossils from Guizhou; the cellular diversity and extremely high cellular mobility present in carnivorous species; and the incidental, but nevertheless graphic evidence that high cellular mobility is pivotal to morphogenesis, homeostasis, locomotion, and ultimately to survivorship of sponges (e.g., Fry, 1970; Bond, 1992). Perceived problems in defining Porifera may stem from our over-reliance on morphometric datasets to make taxonomic decisions, with molecular data providing increasingly important evidence to resolve

otherwise subjective taxonomic decisions based solely on morphometric data (although these molecular datasets are sometimes increasingly confounding, and in some cases clearly misleading). Nevertheless, systematics derived from genotypic data must have some corroboratory morphological support to be of any practical value. This is the purpose of this book.

Remarks

Defining taxa of Porifera in morphological terms continues to be problematical. Fry (1970), when evaluating taxonomic contributions presented at the first symposium of international researchers held in London, remarked that sponges "*continue to enjoy a position of doubtful parentage and relationship*". Indeed, despite significant technological and conceptual advances since 1970 this uncertainty persists within the poriferan phylogeny. The definition provided here covers most but not every putative 'sponge'. For example, Cladorhizidae (Demospongiae, Poecilosclerida), a family of exclusively deep-water sponges, contains many species that lack both choanocyte chambers and a canal system, with dietary requirements provided by a strategy of carnivory evolved for living in the deep sea (Vacelet, 1999a). These species have spicule and cellular characteristics similar to other sponges – thus enabling us to recognise them as sponges in the first place – and consequently it can be said confidently that most sponges have most if not all apomorphies, and where one or more of these are absent they are subsequent evolutionary losses. The definition of Porifera is also not practical when applied to many fossil sponges or sponge-like organisms, where choanocyte chambers, the smaller afferent and efferent canals, and the morphology and structure of cells and the mesohyl are not preserved through the processes of fossilization – with the exception of the remarkable Precambrian fossils from Guizhou mentioned above (Li *et al.*, 1998), that have apparent affinities to Haplosclerida (Demospongiae) (Vacelet, 1999a). Consequently, the 'sponge nature' of fossil groups that are no longer extant in Recent faunas is a matter of circumstantial evidence and thus continually open to speculation. Our assignment of certain fossil groups to the Porifera, such as the Archaeocyatha and Heteractinida, is based on contemporary expert opinion, but it is also accepted that these opinions may change with discovery of new evidence and also the reinterpretation of existing data using new technologies.

Finally, on a cautionary note, the practical identification of sponges is fraught with pitfalls and traps due to the many losses or transformations of certain characters, especially spicule types, that are otherwise pivotal to the definition of a particular taxon. These reductions (or modifications) may confound even the best attempts to assign specimens to any reliable taxon. Fortunately, in most cases, other key characters provide clues for correct diagnoses, although sometimes these clues are very subtle. Similarly, some sponge taxa are infamous for their ability to incorporate foreign spicules and/or detritus into their skeletons, challenging the abilities of even the more experienced taxonomists to diagnose them correctly. Consequently, considerable effort has been devoted in this book to diagnose, describe and illustrate the variety of body plans and other diagnostic features used to define generic and family level taxa. Nevertheless, proceed with caution!

Current systematics

Monophyly of the Porifera. Several attempts have been made over the past 150 years to subdivide the Porifera into subphyla

and other taxa. Gray (1867a) was the first to propose such a subdivision, to differentiate 'Porifera Silicea' (later to be dubbed 'Porifera Incalcareia') from 'Porifera Calcareia' – a distinction that was maintained for many years. More recently, Reiswig & Mackie (1983), after their discovery of the syncytial nature of the choanoderm and pinacoderm of the Hexactinellida, proposed a subdivision of the Phylum into two taxa: the 'Symplasma' (containing only the class Hexactinellida) and 'Cellularia' (containing classes Demospongiae + Calcareia). This proposal was subsequently supported by Bergquist (1985), who further suggested that the Symplasma should be elevated to a separate phylum. Mehl & Reitner (1996) also supported the view of Reiswig & Mackie (1983), but pointed out the likely primitive nature of discrete cells, and accordingly they proposed a different name – 'Pinacophora' for the clade Demospongiae + Calcareia – but retained the clade Hexactinellida.

More recent molecular data using 28S ribosomal DNA (e.g., Lafay *et al.*, 1992) and 18S rDNA (e.g., Borchiellini *et al.*, 2001) were interpreted as empirical support for paraphyly within the Porifera, whereby calcareous sponges (Calcareia) appeared to be more closely related to other metazoans than to siliceous sponges (Demospongiae + Hexactinellida), showing deep radiations between these two groups. Ironically, these current state-of-the-art technical data corroborated the earliest proposal for a subdivision of the Phylum Porifera by Gray (1867a), as noted above. Siddall *et al.* (1995) and Cavalier-Smith *et al.* (1996) provided further data to support a closer relationship between calcareans and the ctenophorans than with the siliceous sponges, and Zrzavy *et al.* (1998) listed some possible synapomorphies to define a clade (Calcareia + Ctenophora + Cnidaria). These potential synapomorphies included the possible non-homology of choanocyte flagellae throughout the Porifera (with calcareans having cross-striated flagellar rootlets found in some triploblasts but not in the diploblastic siliceous sponges), and the animal-like mode of sponge embryogenesis in calcareans but not in other poriferans. They also suggested that the common possession of calcitic spicules in calcareans and anthozoans was a potential synapomorphy, but this latter hypothesis is here rejected given that these characters are non-homologous, whereby calcarean spicules are secreted extracellularly. Zrzavy *et al.* (1998), supported by Borchiellini *et al.* (2001), proposed to resurrect Johnston's (1842) taxa 'Silicispongiae' (for Demospongiae + Hexactinellida), with a potential apomorphy being the method of secretion of spicules and the ultrastructure of the sclerocytes, and 'Calcispongiae' (for Calcareia) as subphyla, or potential phyla, to reflect the alleged deep molecular divergence between these clades.

These data conflict with earlier phylogenetic hypotheses that support the monophyly of Porifera (e.g., Reitner & Mehl, 1996). Furthermore, a recent investigation of new full-length 28S and 18S rDNA sequences (Medina *et al.*, 2001), including re-examination of some previously published sequences by these authors, found very strong support for the clade (Demospongiae + Hexactinellida), for which they used the later name of Silicea Gray, 1867a. They did not, however, find conclusive or statistically significant support for poriferan paraphyly, or resolve the position of the Calcareia within the phylum, suggesting that earlier conclusions about 'Phylum Calcispongiae' must be interpreted cautiously for the time being, including any inferred relationships of the Calcareia with the Eumetazoa. These findings also suggest that these genetic markers (18S and 28S rDNA) might not be the most appropriate to resolve this specific question of calcarean relationships. Consequently, we prefer, at this juncture of uncertainty, to avoid the issue of potential

paraphyly within the Porifera altogether, and thus sidestep any proposal to rearrange the classification of its established classes until the matter has been more satisfactorily resolved. Nevertheless, it is predictable that escalating molecular evidence based on multiple gene sequences will soon approach a satisfactory resolution to answer the question whether 'sponges' are monophyletic or paraphyletic. For the present we propose that these data are still contentious phylogenetic hypotheses, lacking substantial corroboratory support from other genes, whereby only a few taxa have been analysed thus far, and only incomplete (single gene sequences) have contributed to potential phylogenies. These divergences of opinion have, and probably always will occur throughout sponge systematics, and it is important for the young reader to understand that science is always progressing, and that there is NO absolute truth – even in a huge volume like this.

Phylogenetic 'Clades' versus 'Grades' of construction. Hartman (1969, 1979), after his re-discovery of the sponge nature of the so-called coralline sponges (sponges with solid limestone 'hypercalcified' basal skeletons), proposed a fourth class of Porifera, 'Sclerospongiae'. However, subsequent investigations (e.g., Vacelet, 1985) clearly showed that solid limestone skeletons have been developed independently in several unrelated lines of demosponges. 'Sclerosponges', or coralline sponges, or hypercalcified sponges, are here treated at the level of families included in various orders of which the majority of families do not possess the solid limestone skeleton. Similarly, possession of basal skeletons composed of desmas ('lithistids', previously assigned to order Lithistida), or different grades of skeletal construction (e.g., 'sphinctozoans' in class Sphinctozoa, 'stromatoporoids' in class Stromatoporoidea) also remain contentious (e.g., Wood, 1991a), with present indications suggesting that these features are homeoplastic and their indicated taxa are polyphyletic – with the similar consequence that, where possible from other corroboratory evidence (e.g., geometry of free spicules), these taxa are distributed amongst the established classes and orders of Porifera. Achieving this task completely, however, remains elusive and hence the systematics of Porifera is still largely unresolved at higher levels of classification. For this reason the *Systema Porifera* project has deliberately focussed on the intermediate taxa (families, genera), and includes the higher taxa (suborders, orders, and above) only to provide an 'indicative context' to these more practical units of classification. Resolving the higher systematics of sponges is clearly beyond the capabilities of this present book or morphometric data alone.

Scope

For the purpose of this project the Phylum Porifera is subdivided into three (unchallenged) Recent classes, with a fourth, apparently exclusive fossil class (Archaeocyatha) included – the latter showing possible affinities to the Demospongiae based on studies of immune responses and peculiar budding types (Debrenne & Zhuravlev, 1994). Due to diagenetic changes in fossil sponges and the frequent loss of vital spicule components – particularly free spicule types that are often useful as 'systematic indicators' – it is impossible to key out fossil and Recent taxa using a single key. Thus, we treat fossil and Recent specimens separately here.

In the present work Recent sponges are distributed amongst three classes, seven subclasses, 25 orders (one herein abandoned), 127 families and 682 valid genera (with over 1600 nominal genera

(‘available names’, but here considered to be junior synonyms), plus approximately 500 other invalid (‘unavailable’) names). Treatment of the fossil fauna is far less comprehensive and less critical, with six ‘classes’, 30 orders, 245 families and 998 ‘valid’ genera mentioned, although fossil demosponges in particular are not substantially delineated in this work, awaiting a more comprehensive

treatment in the forthcoming revision of the *Treatise on Invertebrate Paleontology* (J.K. Rigby *et al.*, editors).

Further reading

Brien *et al.*, 1973; Bergquist, 1978; Hartman, 1982.

KEY TO RECENT PORIFERA

- (1) Mineral skeleton absent **Demospongiae**
 Mineral skeleton includes a ‘hypercalcified’ basal skeleton of solid limestone 2
 Mineral skeleton consisting of discrete spicules 3
- (2) Soft parts contain siliceous spicules **Demospongiae**
 Soft parts contain calcareous spicules (test with acid) **Calcarea**
- (3) Spicules siliceous, the larger ones are triaxone/hexactine (six-rayed), occurring both individually and fused together **Hexactinellida**
 Spicules siliceous, the larger ones are tetraxone or monaxone **Demospongiae**
 Spicules calcareous (test with acid), usually triactine or tetractine **Calcarea**

KEY TO FOSSIL PORIFERA AND ‘SPONGIOMORPHS’

Key to the classes of fossil Porifera and sponge-like fossils

Preservation of sponges depends upon processes of fossilisation (generally restricted to the hard body parts), and taphonomy (compaction, dislocation of skeleton, diagenetic modifications). Consequently, a key to the fossil fauna differs in its approach and format to that of the living fauna.

Isolated spicules in sediments

- Siliceous spicules: stauractines, pentactines, hexactines **Hexactinellida**
 Monaxones **Demospongiae** [since Precambrian]
 Monaxones, tetractines, rare dermal spicules **Demospongiae** [since Cambrian]
 Calcareous: polyactines **Calcarea** (Heteractinida, extinct group) [since Cambrian]

Complete (or almost complete) bodies

- By early phosphatisation: cellular sponge structures and embryos? **Demospongiae** [Late Sinian, China]
 In lagerstätten
- (1) Cast of? **Hexactinellida** [Precambrian of Ediacara]
 (2) With siliceous hexactine spicules in bundles or distinguishable bodies **Hexactinellida** [Lower Cambrian of Chengjiang, Middle Cambrian of Burgess Shales]
 (3) With siliceous tetractine spicules **Demospongiae** [Lower Cambrian of Shansha, Greenland, Middle Cambrian of Burgess Shales]
 (4) With polyactine calcareous spicules **Calcarea** [Middle Cambrian Burgess Shales]

Massive spicular skeleton

- With six-rayed siliceous spicules **Hexactinellida**
 With tetraxone/monaxone siliceous spicules **Demospongiae**
 With trimeral symmetric calcareous spicules **Calcarea**

Perforate calcareous skeleton consisting of uniform interlocked polyhedral microgranular calcite **Archaeocyatha**

‘Hypercalcified’ basal skeleton of solid limestone (aragonitic or calcitic)

- With or without embedded siliceous spicules **Demospongiae**
 With or without embedded calcareous spicules **Calcarea**

'Spongiomorphs'

The systematic position of problematic organisms with calcified skeletons, Recent as well as ancient groups, has long been disputed. Poriferan affinities are now generally admitted. But the discovery of hypercalcified 'living fossils' and the re-evaluation of the systematic value of architectural patterns demonstrate that 'Sphinctozoa' (successive chambers), 'Stromatoporoidea' (laminae and pillar mesh-like coenosteum) and 'Chaetetidae' ('Tabulata') (calicles) represent grades of organisation rather than systematic clades and are present in the different classes of sponges. Systematic position within classes depends upon presence or absence of 'normal' sponge systematic characters. (Refer to chapters on: Class Archaeocyatha, Fossil Demospongiae, 'Class Stromatoporoidea', Fossil 'Sphinctozoa', Order Heteractinida).

