Chapter 2
Sponges

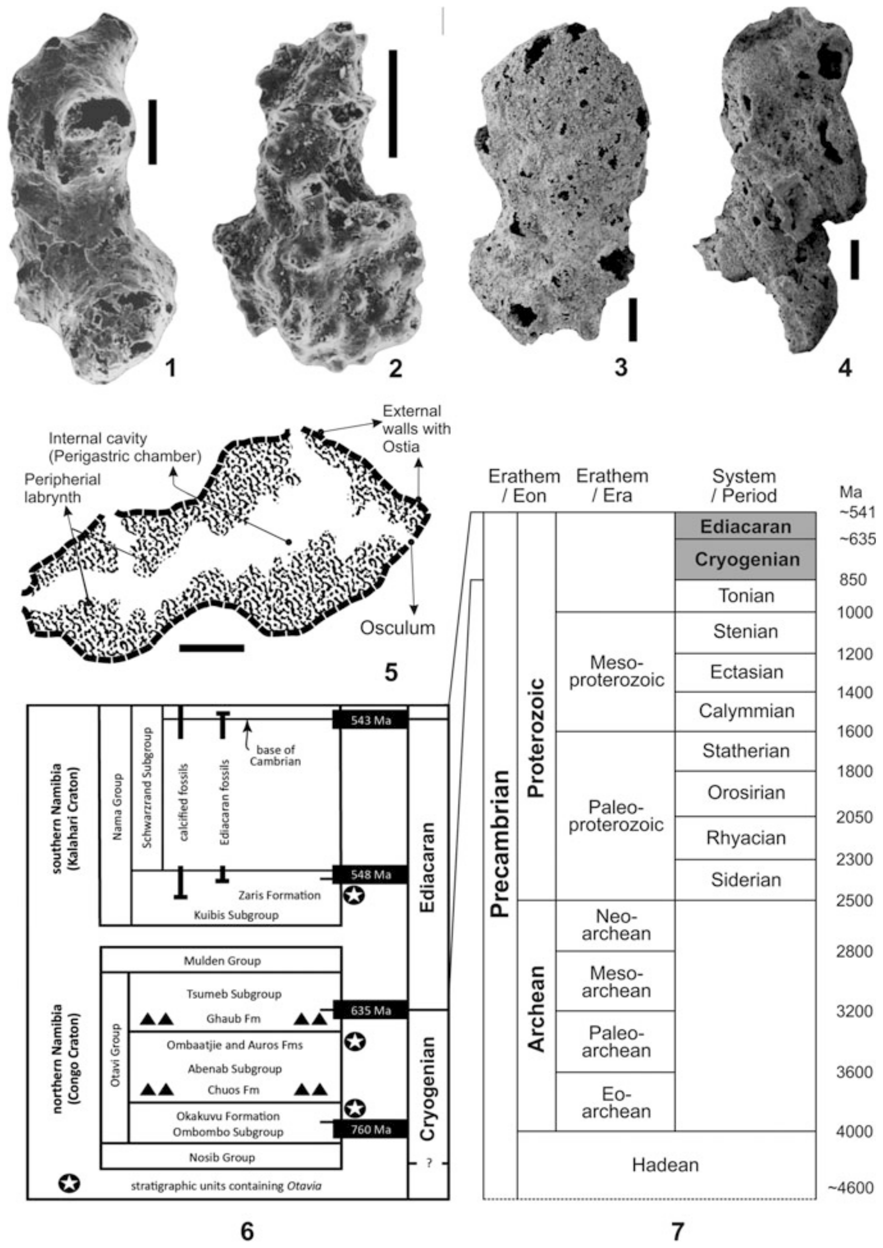
2.1 Introduction

The recent discovery of a 750 million years old sponge-like organism, *Otavia antiqua* [Fig. 2.1(1–5)], a calcareous sponge with Ca-based skeleton, from the Cryogenian–Ediacaran successions of Namibia (South Africa) makes sponges the oldest living animal (Brain et al. 2012; Maloof et al. 2010) [Fig. 2.1(6, 7)]. Their phosphatised body fossils also demonstrate a complex rigid structure [Fig. 2.1(1–5)], indicating the presence of a high level of organization, and supporting the results based on genetic sequencing and biomarkers that the first animals were sponges (Love et al. 2009; Sperling et al. 2010; Brain et al. 2012). In fact, with this discovery, the sponges are now the most basal metazoan taxon. They are also the most diverse and successful of the extant phyla, known so far (Gehling and Rigby 1996; Borchiellini et al. 2002; Philippe et al. 2009; Pick et al. 2010) (Fig. 2.1).

Sponges are invariably sessile in habit, being attached either by means of a stem or a bundle of anchoring spicules, or simply encrusting at the base (substrate). There are about 9000 living species of sponges: most are marine but few ($\sim$200 species) also inhabit freshwaters. Sponges of Class Calcarea largely inhabit shallow waters (<100 m) and are most common in intertidal habitats. Class Demospongiae that contains about 95 % of all sponge species are found at almost all depths ranging from intertidal to abyssal zones (Rigby et al. 1993).

Sponges are simple or primitive multicellular sedentary organisms that show remarkable variability in form (Fig. 2.2), size (from 1 mm to >1 m), and shape. Even among individuals of the same species, shapes vary depending largely on environmental factors such as hydrodynamics, light, and turbidity.

S. Jain, *Fundamentals of Invertebrate Palaeontology*, Springer Geology,
DOI 10.1007/978-81-322-3658-0_2


1
2
3
4
Internal cavity (Perigastric chamber)
External walls with Ostia
Peripherial labrynth
Osculum
5
southern Namibia (Kalahari Craton)
Nama Group
Schwarzrand Subgroup
calcified fossils
Ediacaran fossils
base of Cambrian
543 Ma
548 Ma
Zaris Formation
Kuibis Subgroup
northern Namibia (Congo Craton)
Mulden Group
Otavi Group
Tsumeb Subgroup
Ghaub Fm
635 Ma
Ombaatjie and Auros Fms
Abenab Subgroup
Chuos Fm
Okakuvu Formation
Ombombo Subgroup
760 Ma
Nosib Group
stratigraphic units containing Otavia
Ediacaran
Cryogenian
?
6
Erathem / Eon
Erathem / Era
System / Period
Ma
~541
Ediacaran
~635
Cryogenian
850
Tonian
1000
Stenian
1200
Meso-proterozoic
Ectasian
1400
Calymmian
1600
Statherian
1800
Orosirian
2050
Paleo-proterozoic
Rhyacian
2300
Siderian
2500
Proterozoic
Precambrian
Neo-archean
2800
Meso-archean
3200
Archean
Paleo-archean
3600
Eo-archean
4000
Hadean
~4600
7

◀ **Fig. 2.1** *Otavia antiqua*. Vertical bars measure 100 μm. *1–4* Scanning electron microscopy images of *Otavia*. Note the presence of a consistent globular to ovoid shape, external bounding surface pierced by numerous small pores and larger openings commonly forming raised mounds (particularly in Figs. 2.1 and 2.2). *5* Features of *Otavia*. Note the presence of an overall ovoid to globular shape, the external wall pierced with Ostia and the interior peripheral labyrinth surrounding an irregularly shaped internal void connected to the outside by large Oscula. *6–7* Cyrogenian and Ediacaran stratigraphy of the Neoproterozoic Otavi and Nama Groups of northern and southern Namibia (South Africa) yielding *Otavia antiqua*. Figures illustrated with permission from the South African Journal of Science (these are also free illustrations under the Creative Commons Attribution license)

2.2 Structural Features

Sponges are filter feeders where the water is pumped in through Ostia [small inhalant openings; singular: Ostium; see Fig. 2.3(1, 2)], or by the irregular beating of flagella of Choanocytes or Collar cells that bear a mobile, whip-like flagellum guarded by a cylindrical wall, the collar [Fig. 2.3(3, 4)]. The interior chambers of the sponge houses the Choanocytes [Fig. 2.3(4)]. These are responsible for the circulation of the fluid through numerous canals within the sponge body; the Osculum, the larger exhalant opening, allows for the exit of fluids [Fig. 2.3(3, 4)].

The sponges are broadly characterized by three body plans types: Ascon, Syon, and Leucon [Fig. 2.3(5–10)]; these are briefly described below.

2.2.1 Ascon Type

This is the most basic type [Fig. 2.3(5, 8)]. Such simple sponges, belonging to Class Calcarea, are usually smaller and largely radially symmetrical. They possess a typical central spongocoel lined by choanocytes, with single osculum where water exits from the spongocoel [the pseudogastric cavity; Fig. 2.3(5)]. The spongocoele opens to the outside through an excurrent pore called the Osculum. The surface has numerous pores (incurrent pores or Prosopores) that allows water to enter the sponge [Fig. 2.3 (8)]. This type of sponge represents a "flagellate chamber" and *Leucosolenia*, a living calcareous sponge, is a good example of this type of body plan.

2.2.2 Syon Type

This is made up of a group of several flagellate chambers of the Ascon type around an Excurrent canal [or Apochete; the pseudogastric cavity; see Fig. 2.3(6)]. The excurrent pores lead into this and it empties to the outside through an Apopore (or Osculum). In simple terms, the body wall folds to form secondary choanocyte chambers, which then empties into the spongocoel through a system of canals

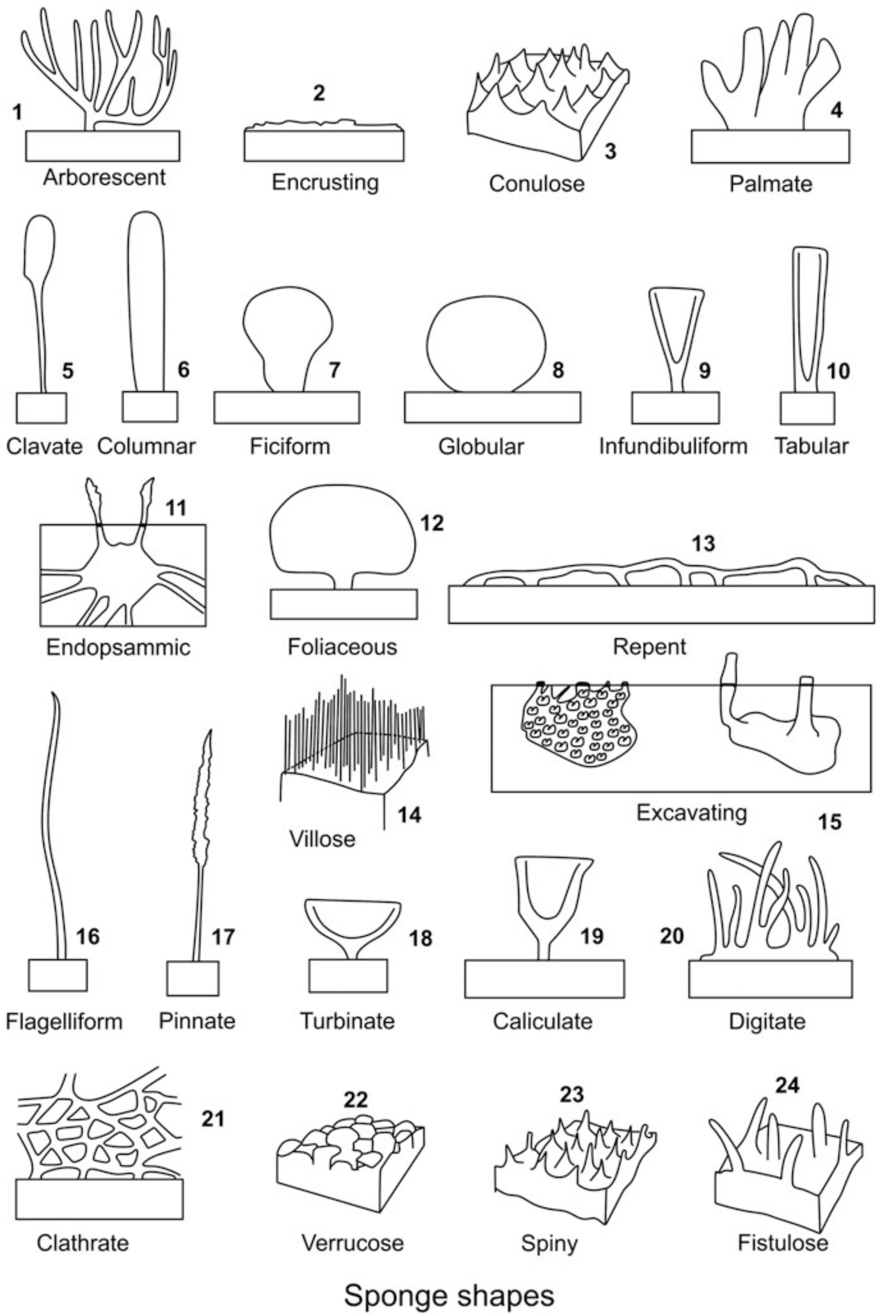
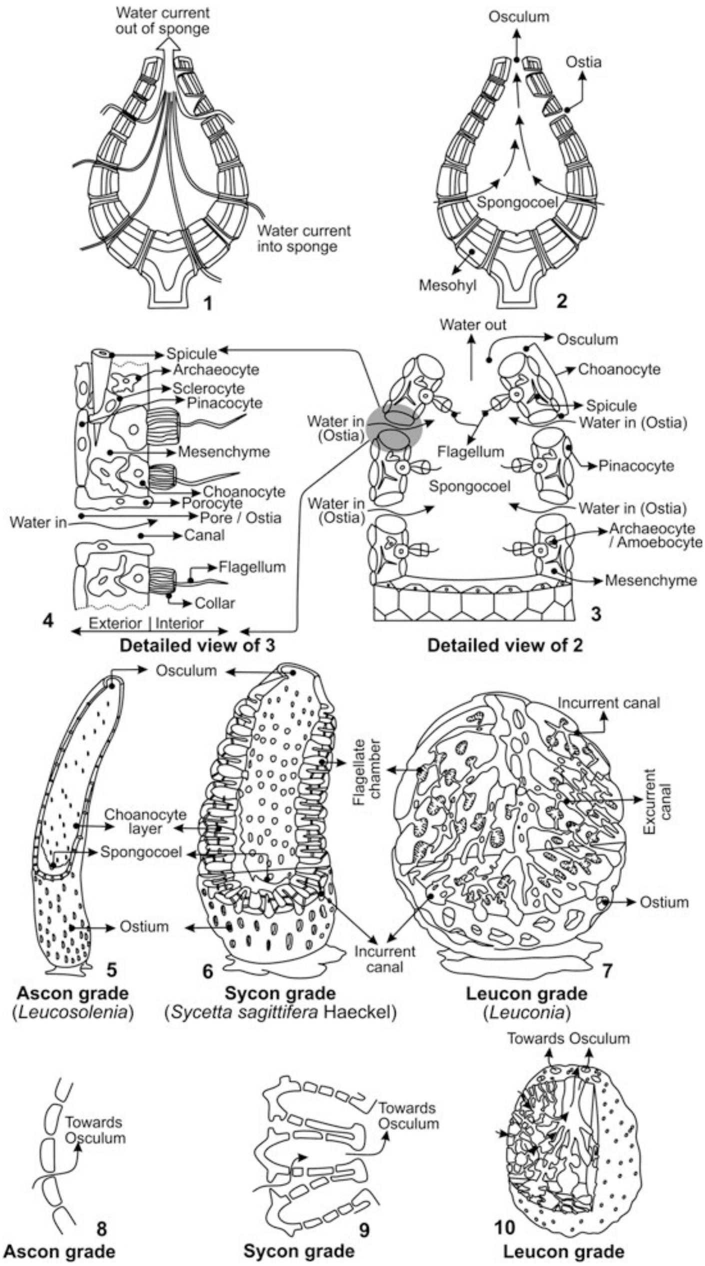


Fig. 2.2 Shape variability in sponges


Water current out of sponge
Water current into sponge
1
Osculum
Ostia
Spongocoel
Mesohyl
2
Spicule
Archaeocyte
Sclerocyte
Pinacocyte
Mesenchyme
Choanocyte
Porocyte
Pore / Ostia
Water in
Canal
Flagellum
Collar
4
Exterior | Interior
Detailed view of 3
Water out
Osculum
Choanocyte
Spicule
Water in (Ostia)
Water in (Ostia)
Flagellum
Pinacocyte
Spongocoel
Water in (Ostia)
Water in (Ostia)
Archaeocyte / Amoebocyte
Mesenchyme
3
Detailed view of 2
Osculum
Choanocyte layer
Spongocoel
Ostium
Flagellate chamber
Incurrent canal
Excurrent canal
Ostium
Incurrent canal
5
Ascon grade
(Leucosolenia)
6
Sycon grade
(Sycetta sagittifera Haeckel)
7
Leucon grade
(Leuconia)
Towards Osculum
Towards Osculum
Towards Osculum
8
Ascon grade
9
Sycon grade
10
Leucon grade

◀ **Fig. 2.3** Sponge canal systems. *1–2* Water enters the Spongocoel through the incurrent pores or Ostia and passes out through the Osculum. *3* The flagellated collar has withdrawn to small, radial chambers, each of which communicates to the Spongocoel. *3* The small chambers lined with collar cells are deeply embedded in Mesenchyme and connected by intricately branched incurrent and excurrent canals. *5–10* Major structural types of sponges (modified from Boardman et al. 1992). *5* Ascon type—a single flagellate chamber lined by a layer of choanocytes (choanosome). *6* Sycon type—several independent flagellate chambers opening directly into the Pseudogastric cavity (spongocoele). *7* Leucon type—several sycon structures with a system of pores connected by canals, and with incurrent canals leading toward flagellate chambers and then through excurrent canals and pores emptying into the cloaca. *Arrows* indicate the direction of water circulation. *8–10* Cross sections of body walls of three structural types. *5* and *8* *Leucosolenia* Bowerbank; *6* and *9* *Sycetta sagittifera* Haeckel; *7* and *10* *Leuconia* Grant

[Fig. 2.3(9)]. Many calcareous sponges have such a plan of construction such as the recent *Sycetta sagittifera* Haeckel.

2.2.3 Leucon Type (or Rhagon Type)

This emerges from the merging of several Sycon units. The excurrent canals or apopores open into a pseudogastric cavity (or Cloaca) which empties to the outside, through a true osculum [Fig. 2.3(7, 10)]. The presence of a dermis and/or cortex in certain syconoid forms and in all leuconoid forms consequently entails the development of a complex network of incurrent canals (or prosochetes) between the incurrent pores (prosopores), which are open to the outside and that empty into the flagellate chambers through the prosopyles. These are homologous to the incurrent pores of the basic asconoid forms. All species of Demospongiae, and most of Calcarea, have a Leuconoid plan of construction. The Recent calcareous sponge *Leuconia* is a good example of this type of body plan.

2.3 Cell Terminology

The cell terminology used to describe the sponge body plan (see also Boury-Esnault and Rützler 1997) is briefly given below and illustrated Fig. 2.3.

2.3.1 **Archaeocyte (Amoebocyte)**: These are cells in the Mesenchyme (=Mesohyl). They possess pseudopods that are used for processing food and distributing it to other cells

2.3.2 **Choanocyte (Collar Cell)**: These cells line the inner cavity of the sponge. The flagellum enables the organism to obtain nutrients and oxygen by processing the flowing water

2.3.3 **Flagellum**: A whip-like structure of the choanocyte cell that moves, pushing water (containing nutrients) through the sponge

2.3.4 Mesenchyme (Mesohyl): A gelatinous layer between the outer body of the organism and the spongocoel (the inner cavity = pseudogastric cavity)
2.3.5 Osculum (Plural = Oscula): Large openings that allow the water to flow out of the organism
2.3.6 Pinacocyte (Epidermis): These are the thin, flattened cells of the epidermis (a layer of cells that covers the outer surface of the sponge)
2.3.7 Porocytes: These are cells with pores located all over the sponge body; the water flows into the sponge through them
2.3.8 Spicule: Located in the mesenchyme, these sharp spikes made of calcium carbonate, form the "skeleton" of most sponges
2.3.9 Spongocoel (Cloaca): It is the central, open cavity through which water flows

2.4 Skeleton

The internal skeleton of sponge which supports its soft parts (tissues) is either made of organic fibers or mineralized needle-like or multirayed spicules, or a combination of both (Bergquist 1998) (see Fig. 2.4). The spicules are distributed throughout the sponge's soft tissue or intertwined, and sometimes fused, into a rigid skeleton that facilitates their fossilization, sometimes even preserving the original shape (Uriz et al. 2003). The group's excellent geological record is largely due to its mineralized skeleton (both calcareous and siliceous). Hence, the discussion below on spicule is largely about the calcareous and siliceous types and of Class Desmospongea.

2.4.1 Spicules

The composition spicules is opaline silica or crystalline to microgranular calcium carbonate, although, no sponge will secrete both materials at the same time. Thus, the presence of a skeleton and its corresponding structure provides a first basic subdivision—sponges without a skeleton and sponges with a calcareous, collagenous, or siliceous skeleton.

Hence, sponge classification is based on the nature, shape, and the interrelationships of spicules (see also Butler 1962; De Vos et al. 1992; Uriz et al. 2003; Dohrmann et al. 2012). Their composition further enables differentiation wherein Calcarea, Archaeocyatha, and Sclerospongiae contain calcium carbonate as layered, granular to crystalline aragonite or calcite. In Sclerospongiae and the hypercalcified sponges in two subclasses of the Demospongea have intermixed siliceous and carbonate skeletal elements.

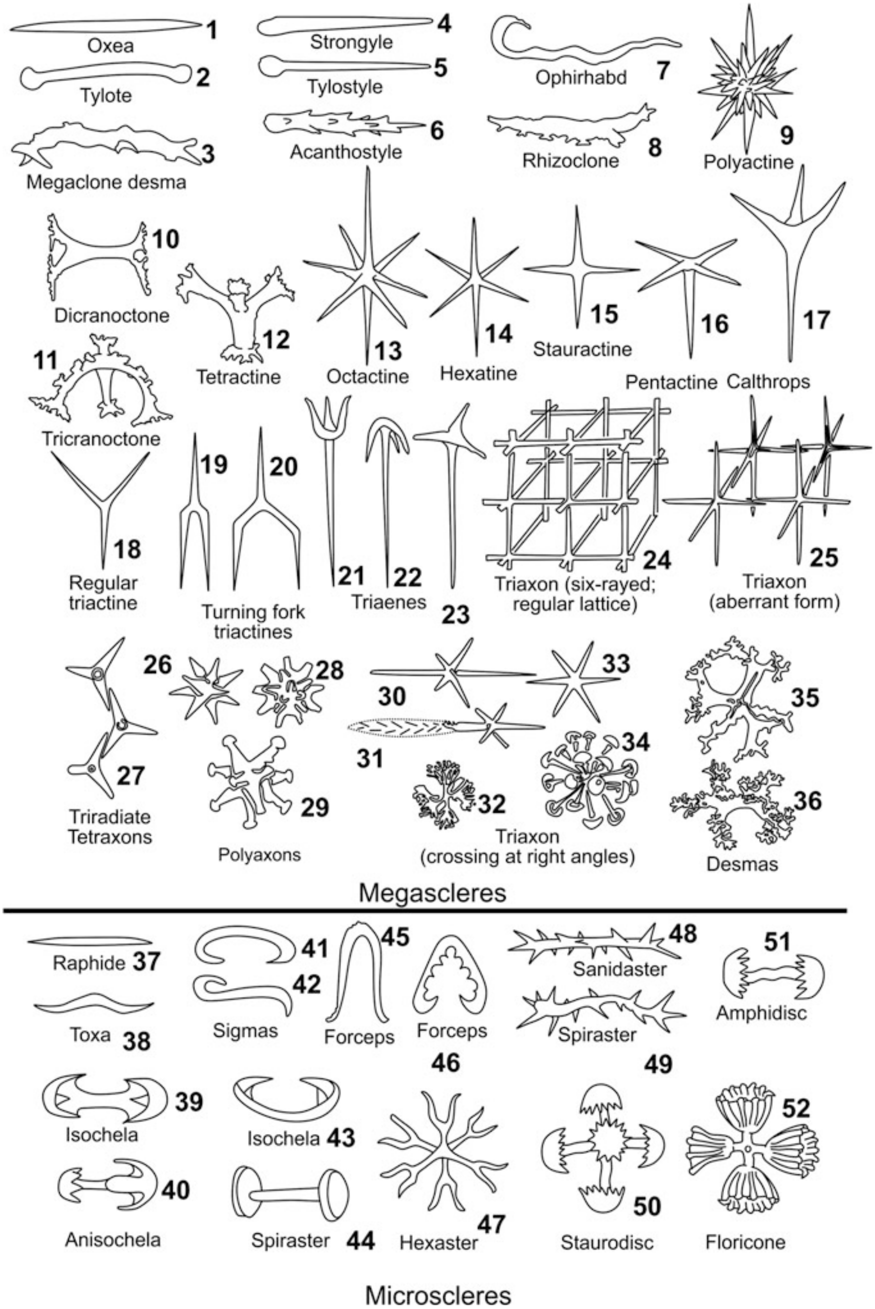


Fig. 2.4 Spicules. The sponge soft parts are supported by internal skeletons made of organic fibers, mineralized needle-like or multirayed spicules, or a combination of fibers and spicules. These are distributed throughout the soft tissue or intertwined, and sometimes fused, into a truly rigid skeleton which facilitates their fossilization. This mineralized skeleton makes up most of the geological record for the group

2.4.2 *Spicule Size and Nomenclature*

Both the spicule size and numbers of rays (axes) enable categorization. However, a single sponge may possess different kinds of spicules, and the same kind of spicule may also occur in several sponges.

Broadly, spicules are of two types: the large ones that make the skeletal framework are called the Megascleres [Fig. 2.4(1–36)] and the smaller ones, the Microscleres [Fig. 2.4(37–52)]. These are irregularly distributed and always form only an accessory element of the skeleton. The microscleres measure <100 μm and megascleres >300 μm (see also Wang et al. 2009). Therefore, the size of megascleres extends over 4–5 orders of magnitude; the microscleres are much more uniform in size. The largest known natural silica structure, the 3 m long Giant Basal spicule is of the recent hexactinellid sponge *Monorhaphis chuni* (Schulze). The diameter of megascleres commonly varies between 3 and 30 μm (De Laubenfels 1955) but can grow up to 12 mm (Levi et al. 1989). The spicules are secreted by specialized mobile cells (the archaeocyte/amoebocytes) within the mesenchyme [Fig. 2.3(4)].

Names for the general categories of spicules are formed by adding a numerical prefix, mono- (=one), di- (=two), tri- (=three), and tetra- (=four), to the word “axon” when the number of axes composing the spicule is referred to, or to the word “actine” when the number of rays is referred to. In the latter case additional prefixes pent- (=five) or hex- (=six) may occur. A rod-shaped spicule pointed at both ends is called a monaxonid diactine; if pointed at one end and rounded at the other, it is monactine. Tetraxonid and triaxonid spicules also occur, as do tetractine and hexactine spicules. Among calcitic spicules (as in class Calcarea), triactines and tetractines have three or four rays, respectively. The calcareous tetractines with eight rays (=Octactines) are characteristic of Heteractinida, a Palaeozoic class. The polyactines or polyaxons, or sphaeractines are those that possess multiple rays and axes of growth. All these terms refer to the larger spicules of sponges, that is, the megascleres that make up the primary framework of the skeleton [Fig. 2.4(1–36)].

2.4.2.1 Megascleres

Broadly, these siliceous skeletal elements are resolvable into a few fundamental types (Fig. 2.4), such as the following:

2.4.2.1.1 Uniaxial spicules or Monaxons. Straight or bent, smooth, prickly or knotty, bevelled, sharpened or truncated needles, rods, hooks, clasps, pins, and anchors (amphidisc). They almost always contain an axial canal, which may be either entirely sealed up, or open at one or at both ends

2.4.2.1.2 Tetraxial spicules or Tetraxons. The normal form is characterized by four equal rays intersecting like the bisectrices of the plane angles of a regular tetrahedron. Triaxial forms result from the occasional abortion of one of the rays. One of the rays may become elongated or otherwise modified so as to form anchors (triaens) with three simple or furcate hooks. Three of the rays may be numerously divided or foliately expanded so as to produce forms resembling thumb-tacks (trichotriaens, phyllotriaens; atrophy of the fourth ray in the last-named form reduces the spicule to a delicate silicious disk. A peculiar forking of the shaft gives rise to candelabras or amphitriaens, while other modifications may produce umbel-like spicules, etc. Certain skeletal elements of the Lithistids may be regarded as irregular tetraxons (desmas), in which the extremities of the four rays are prolonged in knotty, root-like excrescences

2.4.2.1.3 Hexactinellid spicules (Hexactins or Triaxons). The groundform is an axial cross with six equal arms intersecting at right angles like the axes of a regular octahedron. Atrophy of one or more of the rays may result in pentaxial, tetraxial, triaxial, or even nail-shaped forms, without their real character becoming entirely obliterated. Bifurcation or other modifications of a number or all of the rays produce those exquisite siliceous structures so characteristic of the group Hexadinellida, which resemble candelabras, double-headed anchors, fir trees, pitchforks, rosettes, etc. The fusion of juxtaposed hexactins produces more or less symmetrical latticeworks with cubical interstices. Anaxile or polyaxile bodies of spherical, cylindrical, stellate, or discoidal shape, which are not derivable from either of the three ground forms, occur in only a few varieties of recent and fossil siliceous sponges

2.4.2.2 Microscleres

The Microscleres [Fig. 2.4(37–52)] are small-sized spicules that provide a dermal armor at the surface, strengthen the ground substance of the cortex or mesenchyme, or may reinforce the pinacoderm that line the canals. Many kinds of microscleres occur in Demosponges and Hexactinellids and are given names of Latin or Greek origin to describe their shapes [Fig. 2.4(37–52)]. The Microscleres, due to their low preservational potential through geological time, are of minor use in paleontology.

2.5 Classification

The fossil sponges are traditionally classified on the following three parameters: composition and forms of spicules, canal systems, and structural grades. Recently, a more balanced multicharacter approach is taken in which spicules, skeletal structure, soft parts, and life history characteristics are included resulting in three unchallenged classes: Calcarea, Hexactinellida, and Demospongea (see also Hooper

1991; Van Soest 1991; Clarkson 1993; Van Soest et al. 1994; Hooper and Wiedenmayer 1994; Hooper and Van Soest 2002) and the fourth Archaeocyatha (contentious) (Table 2.1; Fig. 2.5). To the established three, Chaetetids and Stromatoporoids (Sclerospongia) have recently been included, making them five (see Table 2.1).

Table 2.1 Traditionally, five classes have been recognized in the phylum, including the Calcarea, Demospongea, and Hexactinellida

Class	Subclass	Order	Age range
Calcarea Bowerbank 1864			**Cambrian-Holocene**
	Calcinea Bidder, 1898		?Precambrian, Cambrian-Holocene
		Clathrinida Hartman, 1958	Holocene
		Murrayonida Vacelet, 1981	?Precambrian, Cambrian-Holocene
	Calcaronea Bidder, 1898		?Cambrian,? Triassic, Jurassic-Holocene
		Leucosoleniida Hartman, 1958	Holocene
		Sycettida Bidder, 1898	Holocene
		Sphaerocoeliida Vacelet, 1977	Cretaceous
		Lithonida Doederlein, 1892	Jurassic-Holocene
Demospongea Sollas, 1875			**Precambrian-Holocene**
	Clavaxinellida Lévi, 1956		Precambrian-Holocene
	Choristida Sollas, 1880		Late Ordovician-Holocene
	Tetractinomorpha, Lévi, 1953		Middle Ordovician-Holocene
	Ceractinomorpha Lévi, 1953		Middle Cambrian, Middle-Late Ordovician, ? Pennsylvanian, Holocene
	Lithistida Schmidt, 1870		Cambrian-Holocene
Hexactinellida Schmidt, 1870			**Precambrian-Holocene**
	Amphidiscophora Schulze, 1887		Precambrian-Holocene
		Amphidiscosa Schrammen, 1924	Ordovician-Holocene
		Reticulosa Reid, 1958	Precambrian-Upper Permian

(continued)

Table 2.1 (continued)

Class	Subclass	Order	Age range
		Hemidiscosa Schrammen, 1924	Late Pennsylvanian-Cretaceous
		Hexasterophora Schulze, 1887	Ordovician-Holocene
		Lyssacinosa Zittel, 1877	Ordovician-Holocene
		Hexactinosa Schrammen, 1903	Permian-Holocene
		Lychniscosa Schrammen, 1903	Upper Triassic-Holocene
Heteractinida de Laubenfels, 1955			**Lower Cambrian-Lower Permian**
		Octactinellida Hinde, 1887	Early Cambrian-Lower Permian
		?Hetairacyathida Bedford and Bedford, 1937	Early Cambrian
?Sclerospongiae			**Cambrian-Holocene**
	Chaetetids and Stromatoporoids		

To these have recently been added Chaetetids and Stromatoporoids (Sclerospongia) (see text above for further explanation)

However, as simple as it seems, the classification of the Porifera is still largely based on morphological characters, spicules, and fibers. But, with recent molecular studies, discrepancies between the results of morphological and molecular analysis are increasingly becoming common and hence, new tools are needed to weigh the competing results.

Representative examples of fossil sponges through time are illustrated in Figs. 2.6, 2.7, 2.8, 2.9, 2.10, and 2.11, and the classes are briefly discussed below (Figs. 2.12 and 2.13).

2.5.1 Class Calcarea Bowerbank (Calcispongia or Calcareous Sponges)

This class includes sponges with calcareous skeletal elements that lack both silica and spongin. Skeleton is characterized by the range from three-rayed spicules of calcite or aragonite, to those with rigid skeletons of fused polygonal elements or imbricate calcitic plates. Their present day analog is exclusively marine and commonly found in shallow tropical environments.

Calcarea have a worldwide distribution. Their structure is of the leucon type but, in contrast to the other classes, of the sycon and ascon types (see Fig. 2.3 for types). Three types of spicules are found in virtually all species: monaxon diactinal; triaxon

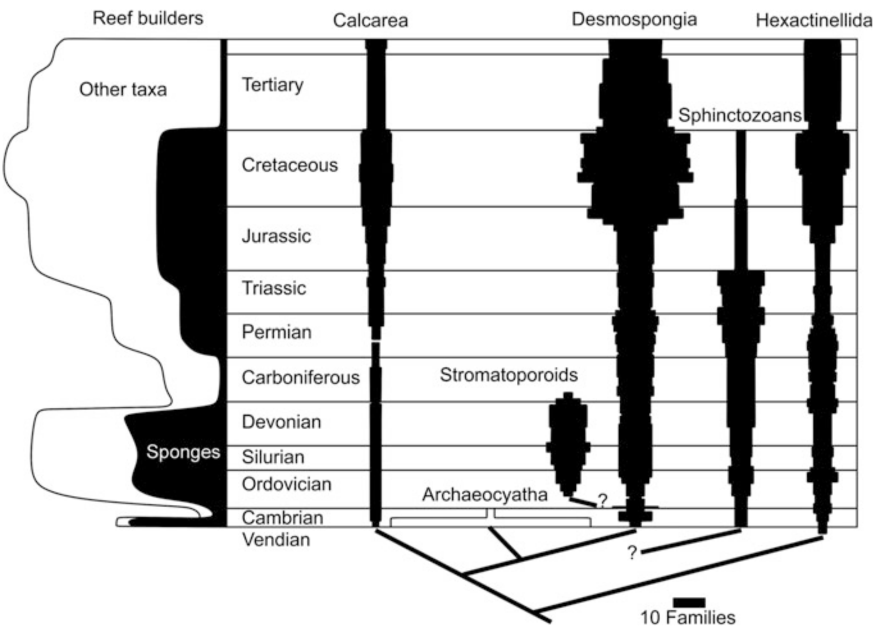


Fig. 2.5 Simplified classification of sponges. Traditionally, five classes have been recognized in the phylum, including the Calcarea, Hexactinellida, and Demospongea (see also Table 2.1). To these have recently been added Chaetetids and Stromatoporoids (Sclerospongia). Fossil "sphinctozoan" ("chambered sponges") families for which calcarean or demosponge affinities cannot be determined are known from the Cambrian to the Cretaceous. Calcarea is the smallest class with 860 species (9 % of the total sponges) (Fig. 2.5). This has exclusively calcareous skeletal material and are predominantly whitish and small, and of fragile consistency. The second class (600 species or 6 %) is the Hexactinellida ("glass sponges"), have siliceous skeletons built of hexaradiate spicules. These occur predominantly in deep oceanic habitats. The third and by far the most diverse class (8400 species or 85 %) are the Demospongiae. Their skeletons are built of siliceous spicules of various forms (but not hexaradiate) and are often cemented together with a keratinous protein called Spongin

triactinal with the rays arranged at an angle of 120° in the same plane of symmetry (triod) or in different planes (tripod); and a particular type in the shape of a tuning fork called "pharetron" (see also Fig. 2.4).

Some consider Heteractinida (Early Cambrian to Early Permian) as a class but most assign it as an order of Calcarea. Heteractinida is characterized by a skeleton made of large calcareous octactine spicules [Fig. 2.4(13)]. This is one of the only two classes of sponges to have become extinct. Examples of Class Calcarea illustrated here include the following: *Girtyocoelia typica* King, *Girtyocoelia beedei* (Girty), *Maeandrostia kansasensis* Girty, *Girtyocoelia dunbari* King, *Cotyliscus ewersi* King, *Amblysiphonella prosseri* Clarke, *Cystauletes mammilosus* King, *Barroisia anastomans* (Mantell), *Stellispongia glomerata* (Quenstedt), and *Corynella quenstedti* Zittel.

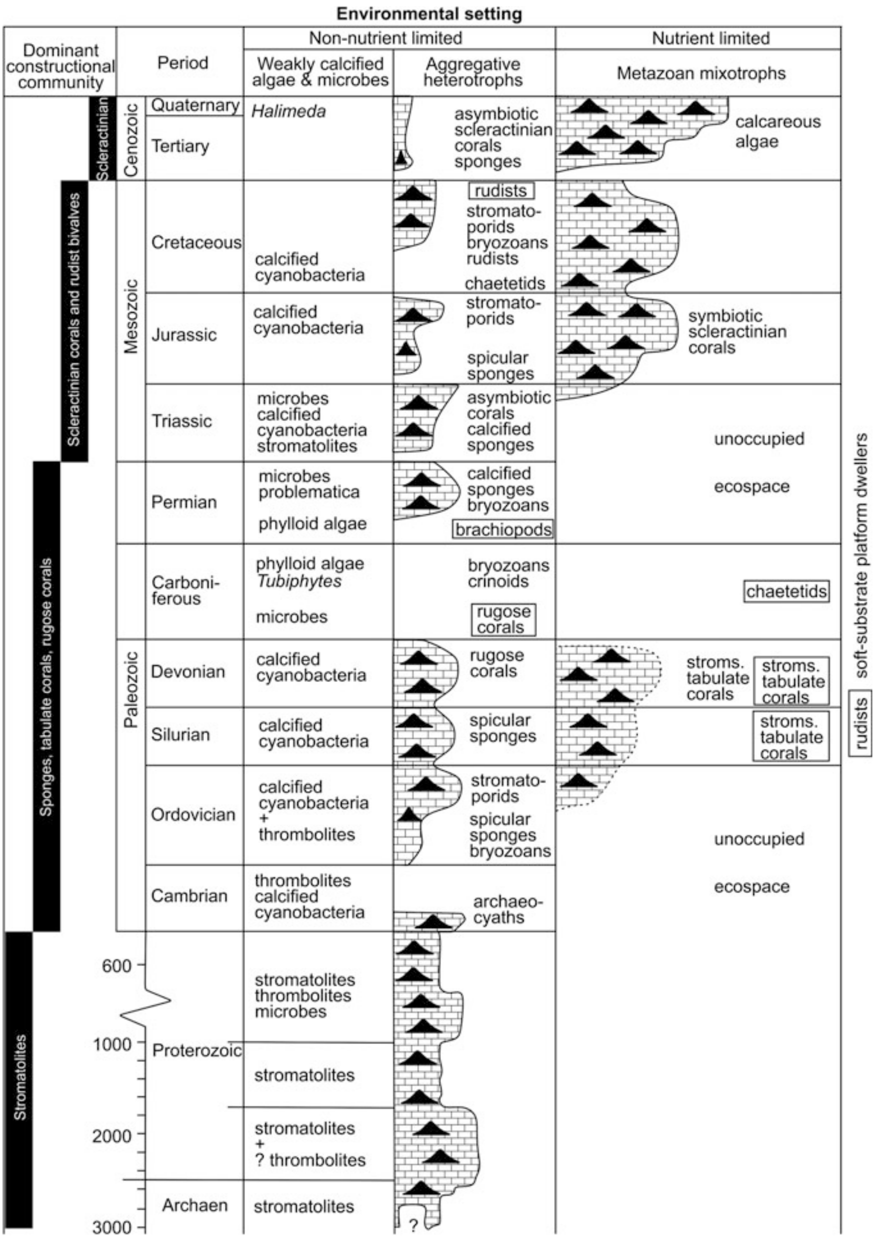


Fig. 2.6 Sponge reef builders across ages. A simplified diagram of the contribution of sponges in reef building through time is shown in Fig. 2.5

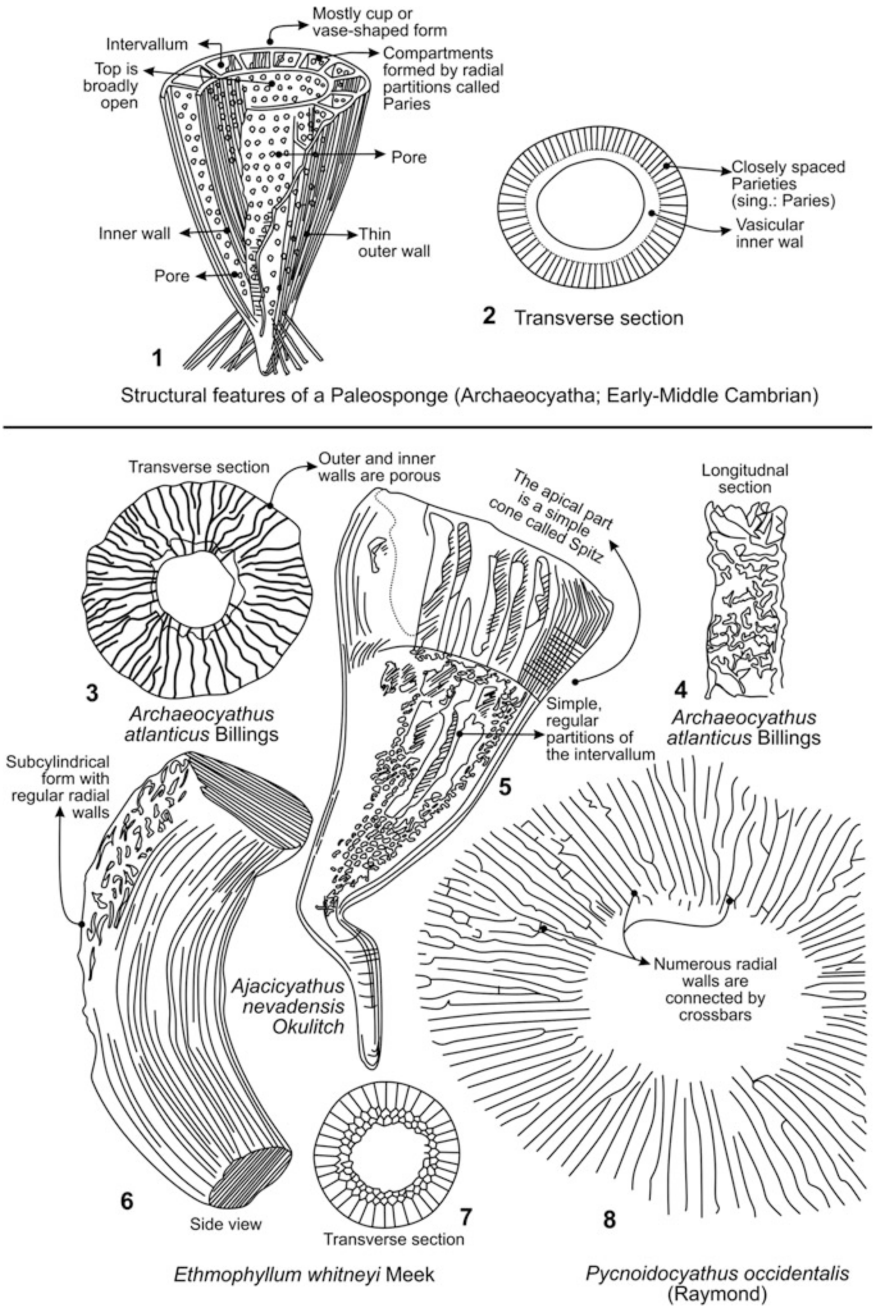


Fig. 2.7 Paleosponge (Archaeocyaths) and their major distinguishing characters. *1–2*: Structural features of a Paleosponge (Early-Middle Cambrian)

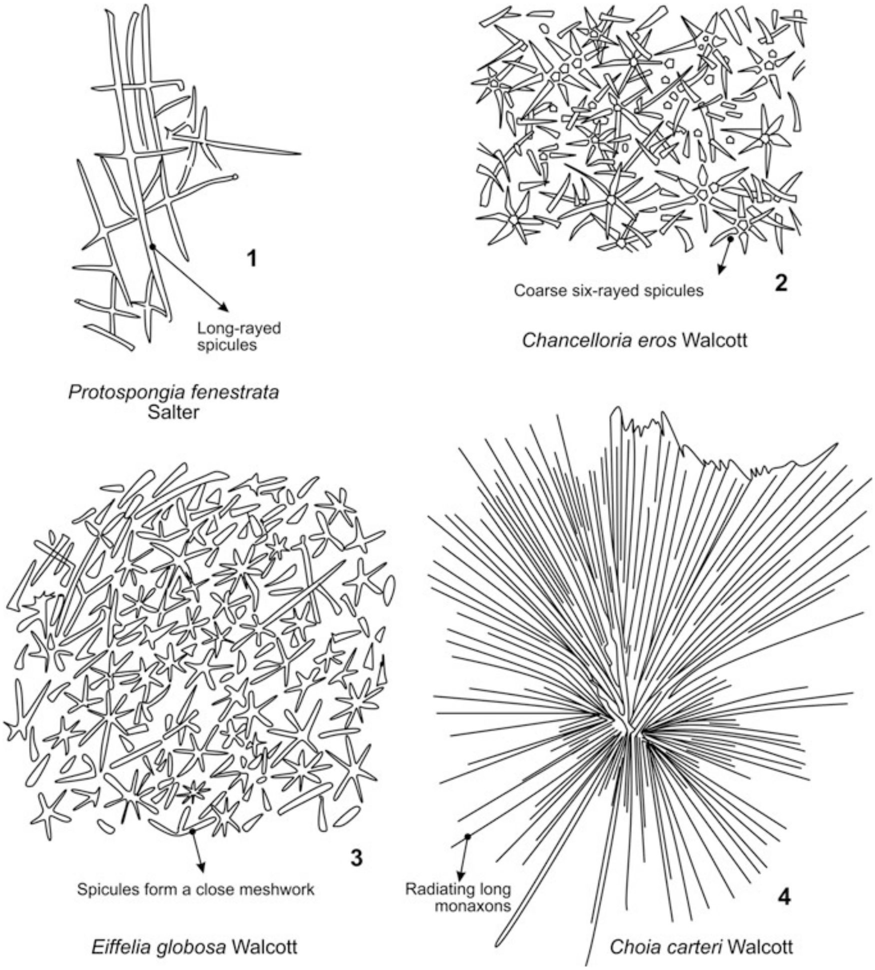


Fig. 2.8 Representative Middle Cambrian (Burgess Shales) sponges, British Columbia, Canada, and their major distinguishing characters

2.5.2 Class Demospongea Sollas

The Demosponges are a dominant, heterogeneous group, characterized by varied shapes, canal patterns, and spicule shapes (and their inter-relationships). There are several thousand known living species and about 500 fossil genera. They mainly inhabit shallow marine niches and are the only known living and fossil freshwater sponges. Their structure is Leucon type [Fig. 2.3(7, 10)]. They usually possess a skeleton made up entirely or partly of organic spongin fibers (with a poor paleontological record), siliceous spicules, or mixed spongin, and siliceous spicules (with a much better preservational geological record). Diversity of shapes and

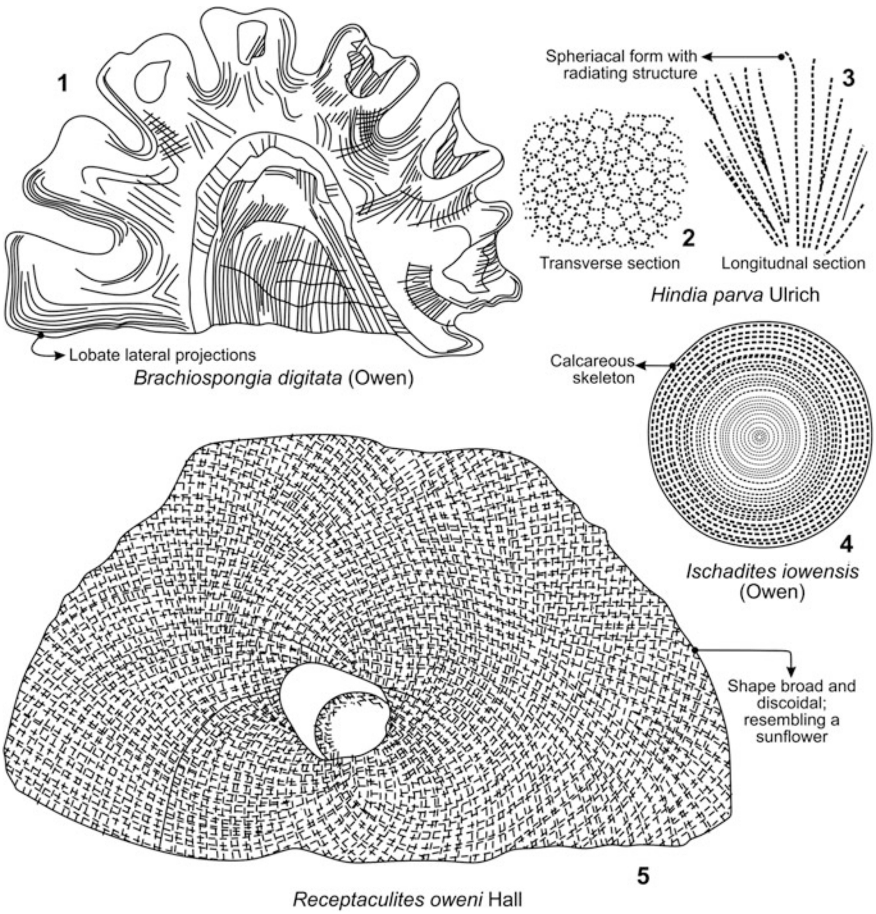


Fig. 2.9 Representative Middle Ordovician sponges and their major distinguishing characters

skeletal structures is huge (Fig. 2.2). The skeletons are composed either of spongin fibers or with siliceous spicules. These are usually divided into larger megascleres and smaller microscleres. Spicules of the class range from loose monaxons to tetractines whose rays do not join at right angles or to irregular root-like forms (Fig. 2.4). Their skeleton is composed of particular spicules or desmas, which are formed by the complex deposition of silica on an original megasclere (as "mortar") [Fig. 2.4(35, 36)]. The spicules are diactinal or tetractinal and are recognizable from the axial canals. Among Demosponges, Order Lithistida is the dominant fossil group, due to their higher preservational potential; their skeleton is made up of spicules fused together to form a rigid network, making them "as hard as rock," as their name implies.

Examples of Class Demospongea illustrated here include the following: *Protospongia fenestrata* Salter, *Chancelloria eros* Walcott, *Eiffelia globosa*

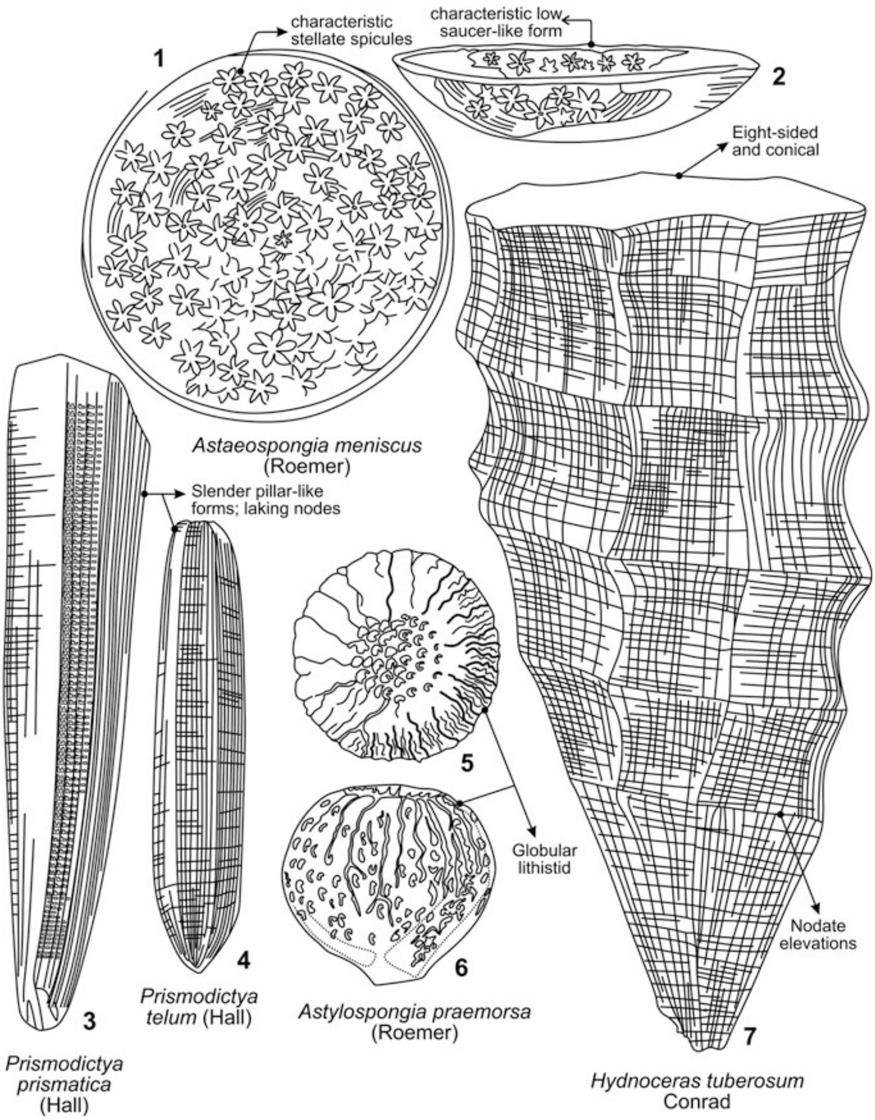


Fig. 2.10 Representative Late Ordovician-Late Devonian sponges and their major distinguishing characters

Walcott, *Brachiospongia digitata* (Owen), *Astaeospongia meniscus* (Roemer), *Prismodictya telum* (Hall), *Prismodictya prismatica* (Hall), *Hydnoceras tuberosum* Conrad, *Titusvillia drakei* Caster, *Ventriculites striatus* Smith, *Coscinopora infundibuliformis* Goldfuss, and *Coeleptychium agaricoides* Goldfuss.

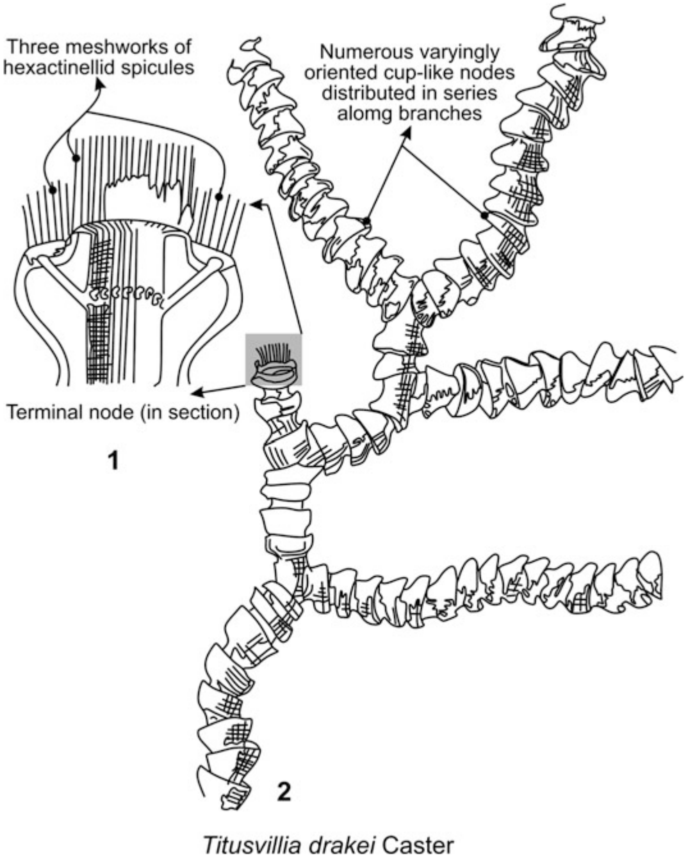


Fig. 2.11 Representative Early Mississippian sponge and their major distinguishing characters

2.5.3 *Class Hexactinellida Schmidt (Hyalosponges or "Glass Sponges")*

The siliceous hexactine spicules [Fig. 2.4(14)] characterize the skeleton of this exclusively marine class. In modern day seas, the Hexactinellida commonly inhabit on seafloors, from depths ranging from 200 to 2000 m, although many species have been reported from lower bathyal depths also (up to 4000 m).

In contrast to the demosponges, the hexactinellids form a homogeneous group of a simple leucon type with a large pseudogastric cavity of the sycon type [Fig. 2.3 (7–10)]. Their megascleres are characterized by rays arranged at right angles from a point of divergence. They build triaxon—hexaradiate spicules (i.e., the three axes of

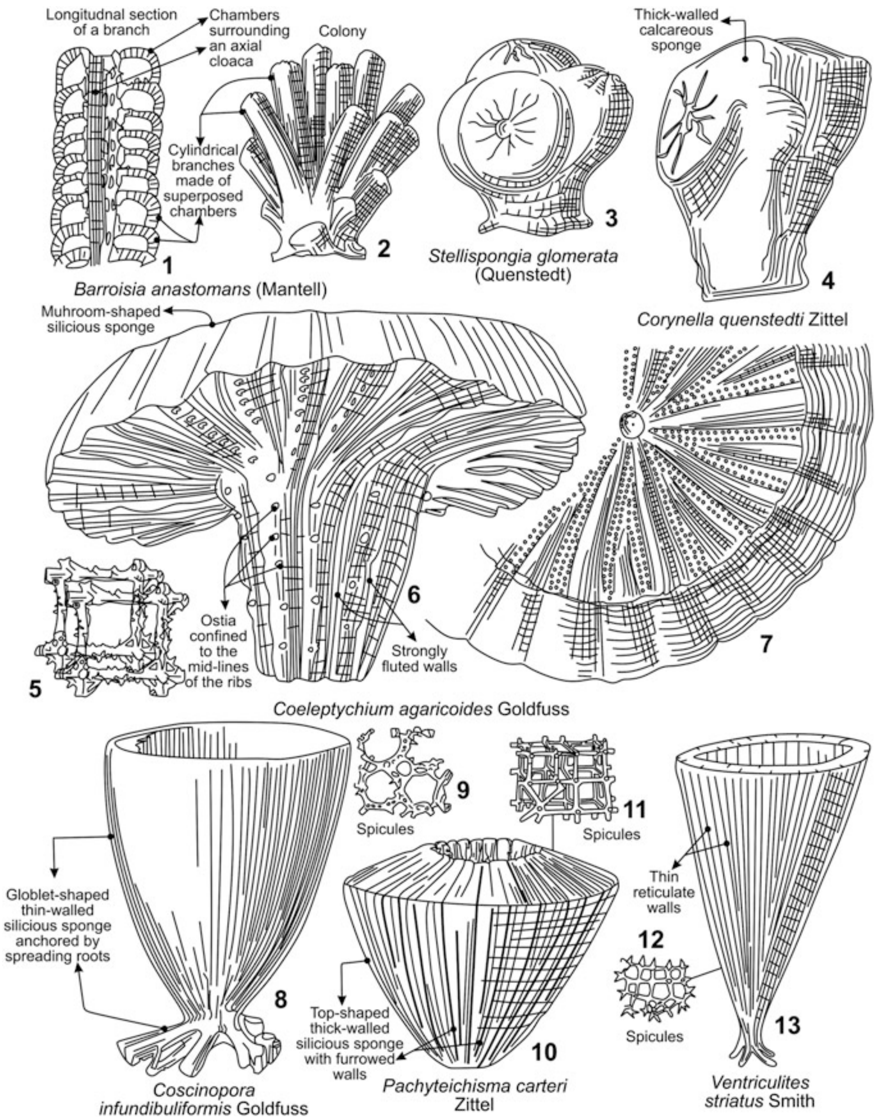


Fig. 2.12 Representative Early Cretaceous-Late Jurassic sponges and their major distinguishing characters

the spicules intersect at right angles) (Fig. 2.4). The triaxon hexactinal spicule, sometimes considered as the basic type, is characteristic only of the dictyids (with the hexactinellid family), and other types may be dominant in other species. A tetraxon spicule with the four rays lying in the same plane (also known as stauractinal) is a common type. There are also pentactinal (five), hexactinal

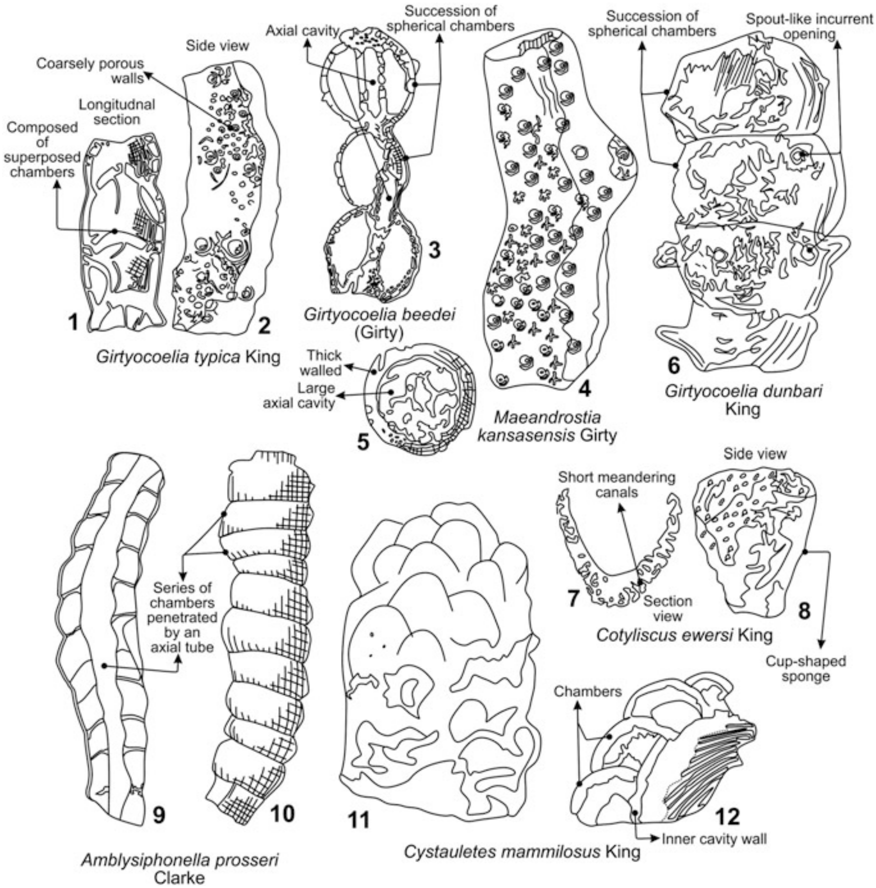


Fig. 2.13 Representative Late Pennsylvanian-Permian sponges and their major distinguishing characters

(six) and octactinal (eight) types, and even polyactinal spicules with more than eight rays. The heteractinids, with a skeleton made up essentially from polyactinal spicules assimilated into megascleres (Fig. 2.4). Hexactinellids lack any calcareous or spongin components in the skeleton.

2.5.4 Class Sclerospongiae

Class Sclerospongiae was proposed to include a few living sponges. It was introduced fairly recently to cover some recent "relict" sponges, and two fossil groups usually placed with the Coelenterata: the Stromatopora, historically compared to the hydrozoans, and the Chaetetids, sometimes also placed among the hydrozoans or, more frequently, with Tabulata (Corals; Chap. 9).

Stromatoporoids possess a laminated calcareous skeleton that is perforated by astrorhizal canals, and the living animal is thought to have occupied essentially only the upper surface. They have domal, tabular, branching, or bulbous growth forms.

The Chaetetids were shallow-water marine organisms. Their growth form, skeletal structure, and the rare occurrence of spicules indicate a strong relationship to other Sclerosponges. They have compound skeletons that range from plate-like or domed to columnar and are composed of clustered narrow tubes, or calicles, that are less than 1 mm in diameter and commonly polygonal to irregular in cross-section.

The Stromatoporoida exhibit greater diversity, and during the Devonian, and were among the main builders of the earliest bioherms (see Fig. 2.6) (see also Maldonado et al. 1999; Mueller 2003). Chaetetids, on the other hand, were important and abundant reef builders during the Paleozoic (Suchy and West 2001; May 2008).

2.5.5 Archaeocyatha

The Archaeocyaths (Fig. 2.12) are an extinct class of the phylum Porifera, close to the living Demospongiae (Debrenne 2007; Debrenne and Vacelet 1984). They are sessile, benthic, and filter feeders. They lived only in environments with restricted temperatures (stenothermal), salinity (stenohaline), and depth (stenobathic; 20–30 m). The archaeocyathans have been recorded from low latitudes during the Cambrian such as in Antarctica, Australia, China, Kazakhstan, Siberia, and North America. This latitudinal distribution is similar to that of modern colonial corals that inhabit warm shallow seas.

Typically, the archaeocyathan skeleton is solitary conical to branching [Fig. 2.12 (1)]. The central cavity of the organism is surrounded by a porous inner wall followed by a cavity called Intervallum and then outside it, a thin porous outer wall [Fig. 2.12(1)]. The Intervallum is divided into longitudinal openings by radial septa that acts as a bridge between the two porous walls [Fig. 2.12(1)]. At the base, root-like attachment structures occur that also act as holdfasts [Fig. 2.12(1)]. Various body forms have been reported from simple (single-walled) to more complex thalamid chambered forms. Rare are branched colonial forms with moderately complex walls (fan-shaped and bowl-shaped genera).

The Archaeocyaths were the oldest of the calcified sponges, and the first metazoans to build reefs (in association with calcimicrobes; see Fig. 2.6), are characteristic fossils used for the biozonation of the first, pre-trilobitic Cambrian stage (Tommotian) (Kerner et al. 2012).

The Archaeocyaths appeared close to the base of the Cambrian and became extinct by Middle Cambrian. The Cambrian Archaeocyathan occurrences can be broadly grouped into two associations—the Early Cambrian sponges from China, and the Middle Cambrian sponges in North America (mainly from the Canadian British Columbia and American Utah) (see also Carrera and Botting 2008). These first metazoan reef formers were relatively abundant during the Early Cambrian, from where over 300 genera have been described. The first subdivision of a stage based on archaeocyaths was established on the Siberian Platform (Zhuravleva 1960). Morocco, western Europe, Australia, and Canada have since provided regional scales, which allow stratigraphic comparisons that parallel trilobites biozones or replace them when necessary.

Appendix A gives the list of illustrated specimens mentioning the chapter number, species name, age, and locality along with its figure number within the chapter.

References

Bergquist, P. 1998. Porifera. In *Invertebrate zoology*, ed. D. Anderson, 10–27. USA: Oxford University Press.

Boardman, R.S., Cheetham, A.H. and A.J. Rowell. eds. 1992. Fossil invertebrates. Wiley, New York.

Borchiellini, C., M. Manuel, E. Alivon, N. Boury-Esnault, J. Vacelet, and Y. Le Parco. 2002. Sponge paraphyly and the origin of Metazoa. *Journal of Evolutionary Biology* 14(1): 171–179.

Boury-Esnault, N., and K. Rützler. 1997. Thesaurus of sponge morphology. *Smithsonian Contributions to Zoology* 596: 1–55.

Brain, C.K., Prave, A.R., Hoffmann, K.H. et al. 2012. The first animals: ca. 760-million-year-old sponge-like fossils from Namibia. South Africa Journal of Science 108(1/2), Art. #658. 10.4102/sajs.v108i1/2.658.

Butler, P. 1962. Morphologic classification of sponge spicules, with descriptions of siliceous spicules from the Lower Ordovician Bellefonte Dolomite in central Pennsylvania. Journal of Paleontology, 191–200.

Carrera, M.G., and J.P. Botting. 2008. Evolutionary history of Cambrian spiculate sponges: implications for the Cambrian evolutionary fauna. *Palaios* 23: 124–138.

Clarkson, E.N.K. 1993. *Invertebrate palaeontology and evolution*. London: Chapman and Hall. 434 p.

De Laubenfels, M. 1955. Porifera. *Treatise on Invertebrate paleontology*, 21–112. Lawrence: Geological Society of America and University of Kansas Press.

De Vos, L., Ruetzler, K., Boury-Esnault, N., Donadey, C. and J. Vacelet. 1992. Atlas of sponge morphology. Atlas de morphologie des Èponges. Washington and London: Smithsonian Institution Press.

Debrenne, F. and J. Vacelet. 1984. Archaeocyatha: is the sponge model consistent with their structural organization? In 4th international symposium on fossil Cnidaria, New York, 358–369.

Debrenne, F. 2007. Lower Cambrian archaeocyathan bioconstructions. *Comptes Rendus Palevol, Paris* 6(1–2): 5–19.

Dohrmann, M., C. Göcke, D. Jannussen, J. Reitner, C. Lüter, et al. 2012. Systematics and spicule evolution in dictyonal sponges (Hexactinellida: Sceptrulophora) with description of two new species. *Zoological Journal of the Linnean Society* 163: 1003–1025.

Gehling, J.G., and J.K. Rigby. 1996. Long expected sponges from the neoproterozoic ediacara fauna of South Australia. *Journal of Paleontology* 2: 185–195.

Hooper, J.N.A. 1991. Revision of the family Raspailiidae (Porifera: Demospongiae), with description of Australian species. Invertebr. Taxon. 5(6): 1179–1418.

Hooper, J.N.A. and R.W.M. Van Soest. 2002. Systema Porifera. A Guide to the Classification of Sponges. Kluwer Academic/Plenum Publishers, New York, (2 vols.) 1708 p.

Hooper, J.N.A., and F. Wiedenmayer. 1994. Porifera. In Zoological catalogue of Australia, edited by Wells, A., Vol. 12, 1–620.

Kerner, A., Vignes-Lebbe, R. and F. Debrenne. 2012. Computer-aided identification of the Archaeocyatha genera now available online. Carnets de Géologie / Notebooks on Geology, Brest, Letter 2011/02 (CG2011_L02), pp. 99–102.

Levi, C., Barton, J., Guillemet, C., Bras, E., Lehuede, P. 1989. A remarkably strong natural glassy rod: the anchoring spicule of theMonorhaphis sponge. Journal of Materials Science Letters 8: 337–339.

Love, G. D., Grosjean, E., Stalvies, C., et al. 2009. Fossil steroids record the appearance of Demospongiae during the Cryogenian period. Nature 457: 718–722.

Maldonado, M., Carmona, M.G., Uriz, M.J. and A. Cruzado. 1999. Decline in Mesozoic reef-building sponges explained by silicon limitation. Nature 401: 785–788.

Maloof, A., Rose, C., Beach, R., Samuels, B., Calmet, C., Erwin, D., Poirier, G., Yao, N., and F. Simons. 2010. Possible animal-body fossils in pre-Marinoan limestones from South Australia. Nature Geoscience. doi:10.1038/ngeo934.

May, A. 2008. Corals (Anthozoa, Tabulata and Rugosa) and chaetetids (Porifera) from the Devonian of the Semara area (Morocco) at the Museo Geominero (Madrid, Spain) and their biogeographic significance: Bulletin dell'Institut Scientifique Rabat, Section Sciences de la Terre 30: 1–12.

Muller, W.E.G. 2003. Sponges (Porifera), Springer, Berlin, 258 p.

Philippe, H., Derelle, R., Lopez, P., et al. 2009. Phylogenomics revives traditional views on deep animal relationships. Current Biology 19: 706–712.

Pick, K.S., Philippe, H., Schreiber, F., et al. 2010. Improved phylogenomic taxon sampling noticeably affects nonbilaterian relationships. Molecular Biology Evolution 27: 1983–1987.

Rigby, J.K., Budd, G.E., Wood, R.A., and F. Debrenne. 1993. Porifera. In The fossil, record edited by Benton, M.J., Vol. 2, 71–99. Chapman and Hall, London.

Sperling, E. A., Robinson, J. M., Pisani, D., and K.J. Peterson. 2010. Where's the glass? Biomarkers, molecular clocks, and microRNAs suggest a 200-Mry missing Precambrian fossil record of siliceous-sponge spicules. Geobiology 8: 24–36.

Suchy, D.R., and R.R. West. 2001. Chaetetid buildups in a Westphalian (Desmoinesian) cyclothem in Southeastern Kansas: Palaios 16(5): 425–443.

Uriz, M., Turon, X., Becerro, M., and G. Agell. 2003. Siliceous spicules and skeleton frameworks in sponges: origin, diversity, ultrastructural patterns, and biological functions. Microscopy Research and Technique 62: 279–378.

Van Soest, R.W.M. 1991. Demosponge Higher Taxa Classification Re-Examined. In J. Reitner, H. Keupp (eds), Fossil and Recent Sponges. Springer-Verlag, Berlin, Heidelberg: 54–71.

Van Soest, R.W.M., Van Kempen, T.M.G., and J.-C. Braekman, eds. 1994. Sponges in time and space. In Proceedings of the 4th international sponge symposium, 515 p. Balkema: Rotterdam.

Wang, X., Schroder, H., and W. Muller. 2009. Giant siliceous spicules from the deep-sea glass sponge *Monorhaphis chuni*. International Review of Cell and Molecular Biology 273: 69–184.

Zhuravleva, I.T. 1960. Arkheotsiaty Sibirskoy Platformy (Archaeocyaths of the Siberian Platform). Akademiya Nauk SSSR, Moscow, 344 p.

http://www.springer.com/978-81-322-3656-6

Fundamentals of Invertebrate Palaeontology
Macrofossils
Jain, S.
2017, XI, 405 p. 209 illus., Hardcover
ISBN: 978-81-322-3656-6