

Chapter 2

Cold Biosilicification in Metazoan: Psychrophilic Glass Sponges

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2.1 Introduction

2.1.1 Early History of Glass Sponge Investigations

Deep-sea conditions from the anthropocentric viewpoint are not comfortable: dark, cold, high pressure, and different chemical composition of the water. These environments were considered not to be suitable for life in the scientific discussions of the early nineteenth century. The term ‘azoic’ characterized deep waters below 600 m, as suggested by E. Forbes in 1843. Amazingly, following previous findings of marine invertebrates by J. C. Ross and J. Hooker on the exploratory voyages of ‘Erebus’ and ‘Terror’ in 1839–1843, at depths of 1800 m, and in a series of publications by M. and G.O. Sars detailed about 100 animals at depths greater than 600 m (Gage and Tyler 1991). In 1869–1870 W. Thomson together with W.B. Carpenter organized the deep-sea cruises of ‘Lightning’ and ‘Porcupine,’ which dredged down to 4289 m (Gage and Tyler 1991). In 1872–1876, the famous circumnavigating voyage of H.M.S. ‘Challenger’ (Fig. 2.1) and expedition with the same name (supported by the GB Royal Society, the Admiralty, the Treasury, and the Parliament), with a purpose-rebuilt steam-engine which allowed trawling deep-water animals up from 5500 m, roamed the World Oceans (Fig. 2.2). The result of this expedition was a phenomenal collection of animals and a wonderful

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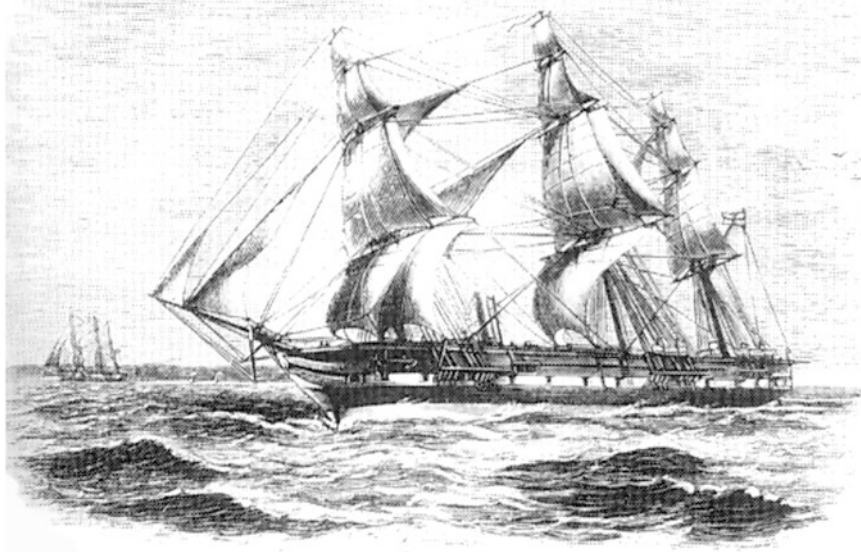


Fig. 2.1 HMS *Challenger* under sail (from Tizard et al. 1885)

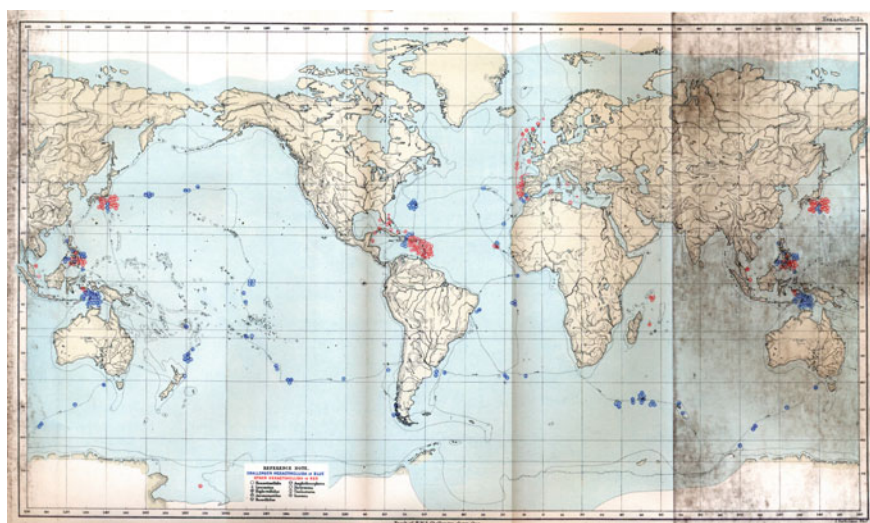


Fig. 2.2 Track of HMS *Challenger*. *Blue circles*—Hexactinellida collected by the HMS *Challenger*; *red circles*—by other expeditions (from Schulze 1887)

series entitled ‘Report on the Scientific Results.’ These publications have become the base of knowledge for most deep-water animal groups, and spurred further expeditions into the deep ocean by other countries which started analogous explorations: German: ‘Valdivia’; the US: ‘Albatross’; French: ‘Travailler,’ ‘Thalisman,’ ‘l’Hirondelle’; Dutch: ‘Siboga’; regional Japanese investigations, etc. Hence, before the ‘Challenger’ expedition, recent hexactinellid (glass) sponges were mostly known from occasional long-line catches by fishermen and sporadic dredging, such as French ‘l’Astrolabe,’ and even an earlier description of a reliable hexactinellid sponge in 1780, later assigned to the genus *Dactylocalyx* (Schulze 1887). The Challenger collection gave valid names to most of the recent genera of Hexactinellida in the publication by Schulze (1887), he also redescribed many previously known species (Fig. 2.3).

Later, in the middle of twentieth century, the situation was curiously repeated with the Ocean’s deepest areas—the deep-sea trenches with depths of more than 6000 m, as a competition between the Danish ‘Galathea’ and the USSR ‘Vityaz.’ This led to the rise of emulation of a special term for coexisting areas and faunas: hadal and ultra—abyssal (correspondingly) and a scientific discussion concerning the age and origin of this fauna.

Hexactinellids are not the only class of sponges which inhabit the depth. Demospongiae are also rather numerous in the abyss (their family Cladorhizidae, carnivorous sponges, penetrates even deeper into the ocean trenches than do the hexactinellids), and some rare calcareous sponges were also found down to 5045 m (Koltun 1970). However, the class Hexactinellida is the most numerous representative of sponges, which exceeds the other classes of Porifera in the number of specimens, biomass, and large sizes in major deep-water environments.

2.1.2 *Hexactinellida*

Hyalospongiae, Triaxonia, Symplasma, or glass sponges are a class of Porifera characterized by the presence of siliceous spicules with triaxonic (hexaradiate) symmetry or their derivatives, and with an axial filament square in cross section, as well as generally syncytial structure of the soft body: most cells are fused into giant and multinucleated structures which have no separate membrane borders. This includes a specific construction of choanocytes—a peculiar complex of branched choanocytes with a complex of collar bodies interconnected by cytoplasmic reticulate bridges, and nucleus bodies separated by specific plug junctions (Leys et al. 2007). All representatives of this sponge class are marine inhabitants, found mainly in the deep-sea with very complicated external (various body shape constructions) and internal morphology (variability of spicules and their position is amazing when compared to other Porifera) (Fig. 2.4). The amount of specific terms used in morphological descriptions is also impressive (Tabachnick and Reiswig 2002). The Hexactinellida contains more than 500 recent species allocated to about 130 genera and subgenera. Like most other sponges, hexactinellids are filter feeders which

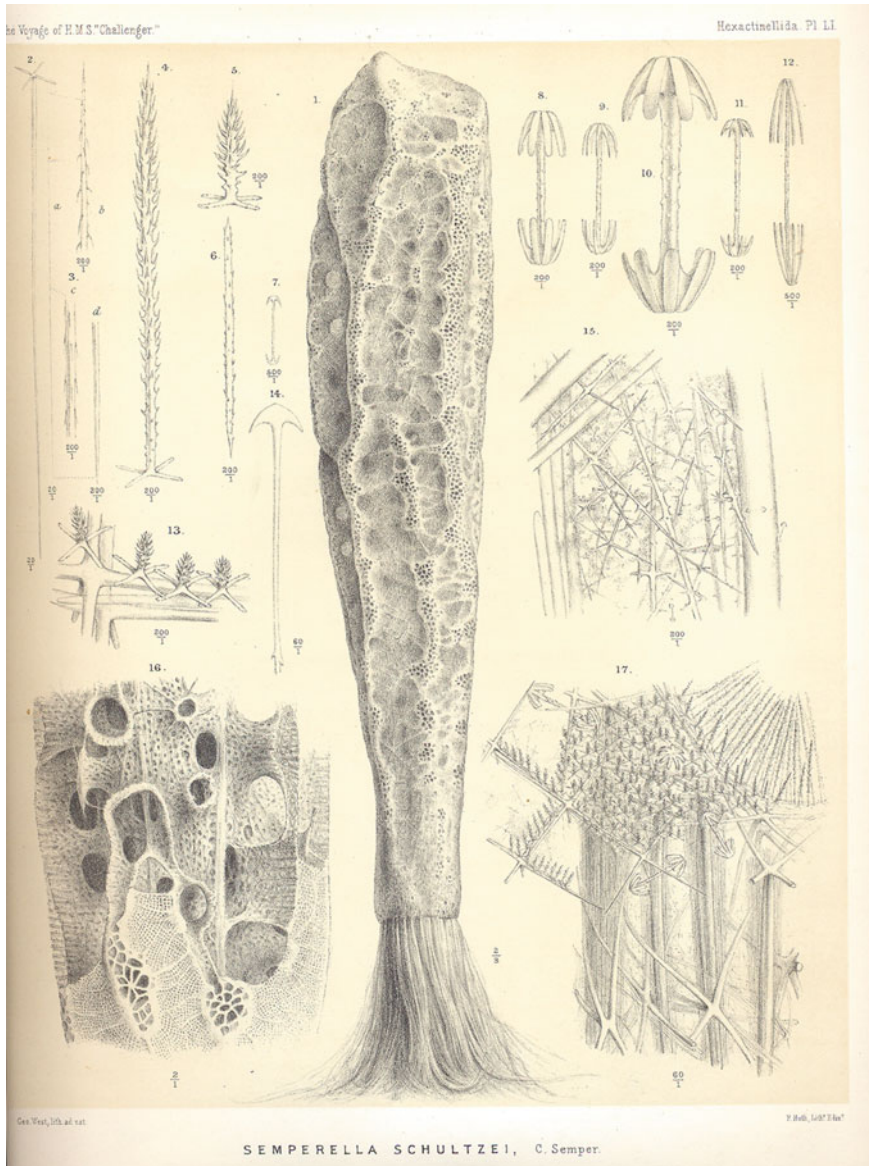


Fig. 2.3 An illustration of describing specimen (*Semperella schultzei*) and its spicules by Schulze (1887, Pl. LI)

retain small particles $<5\ \mu\text{m}$, including bacteria and dissolved organic carbon (Leys et al. 2007). While little is known concerning the enzyme kinetics of Hexactinellida (particularly at natural temperature), information on the geographic distribution of these sponges is available. Thus, we can approximately compare the hexactinellid

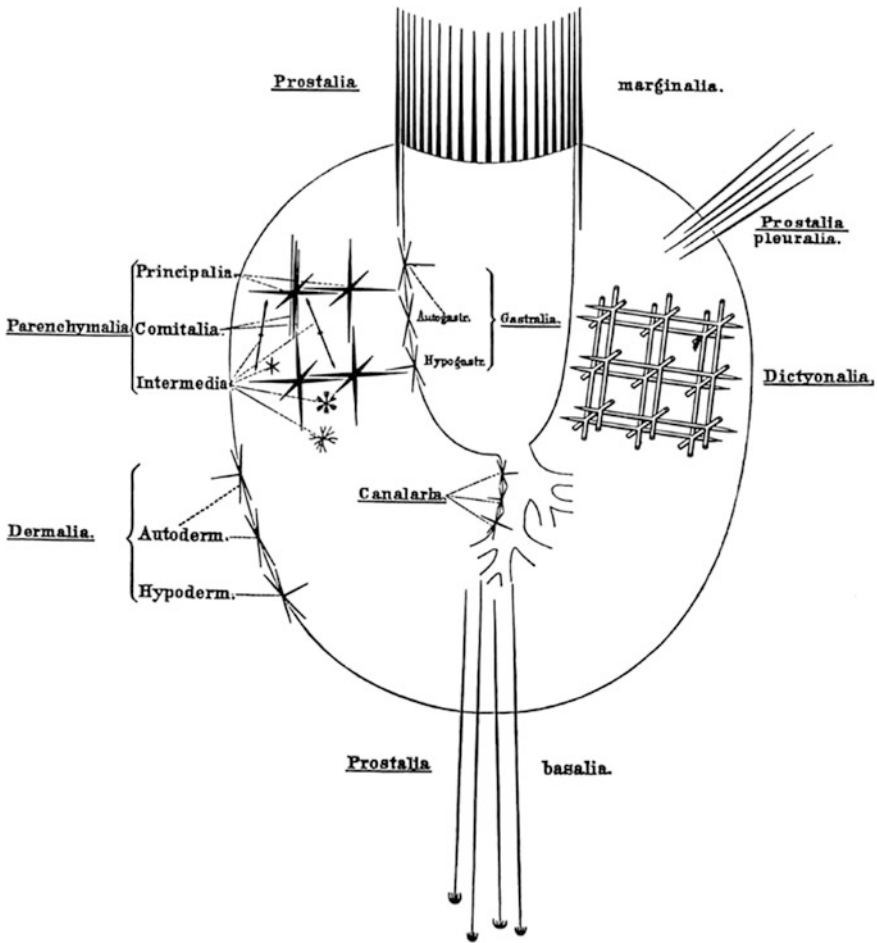


Fig. 2.4 Diagram of the arrangement of spicules in hexactinellid sponges (from Schulze 1887, 41)

distribution with the corresponding water temperatures, and with the water temperature preferences of their potential food source—bacteria. It is necessary to analyze the experimental observations taken in the laboratory where have been done on a few living representatives (collected at several of their few known shallow-water habitats) to elucidate the poorly investigated growth process of most hexactinellid species. Spicules and skeletons of hexactinellid sponges demonstrate both mechanical features of flexibility—stalks of *Hyalonema* sp. under strong water currents (Heezen et al. 1966) and rigidity—*Euplectella* aff. *aspergillum* (Aizenberg

et al. 2005), representatives of Lychniscosida (Reif et al. 1976) and the extremely rigid *Sarostegia oculata* (Ehrlich, Tabachnick, in preparation).

2.1.3 Psychrophiles

It is a fact that the dominant environment of the Earth's biosphere is cold. "The polar regions and the oceans comprise 14 and 71 % of the earth's surface, respectively. More than 90 % (by volume) of the oceans is 5 °C or colder" (Morita 1975).

Psychrophile is one of the most important parameters connected with enzyme kinetics. The most common definition of this temperature extreme is below 15 °C ("below human zone of comfort") (Rothschild and Manchinelli 2001). Following to this definition of psychrophile, we can consider all recent representatives of hexactinellid sponges to be psychrophilic. Besides, the temperature of about 15 °C and below more or less corresponds with that of waters below the permanent ocean thermocline.

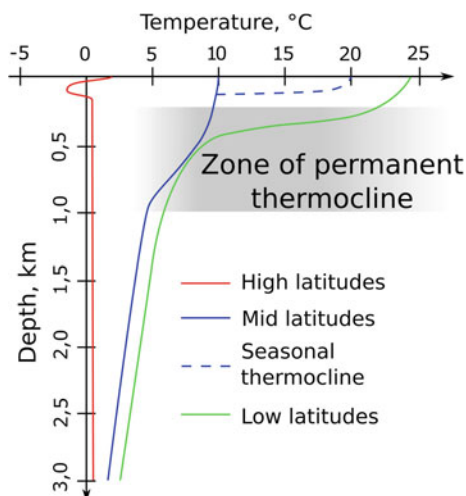
On the other hand, the life of hexactinellids is connected with potential bacteria food sources and probable bacterial infections, since hexactinellid sponges have relatively low activity of bioactive metabolites (Turk et al. 2013), especially in comparison with representatives of Demospongiae living in shallow water. Thus, bacterial psychrophile for Hexactinellida may be even more important than their own temperature optimum. Two other important borders of the psychrophile for bacteria are 0 °C (rapidly—usually 1–2 weeks—growth) (Ingraham 1958) and 5 °C (temperature optimum for some microorganisms) (Eddy 1960).

2.1.4 Physical Properties of the Ocean Waters

Most experts in oceanography consider the deep-sea as starting below the edge of continental shelf (c.a. 200 m). Usually it also corresponds with the position beneath the permanent thermocline (the position varies at different locations from about 150 to 1000 m), where the temperature changes between 4 and 1 °C (exceptions are the warm Mediterranean and Red seas) (Gage and Tyler 1991) (Fig. 2.5). The lowest temperatures of ocean water is −2.2 °C in the surface and shallow water of the Antarctic Ocean (P. Dayton, personal communication).

Thus, the major biological and physical oceanographic temperature borders currently known are 15 and 4–5 °C, and the coldest seawater temperature is −2.2 °C. According to these temperature parameters, we discuss the peculiarities in the distribution of Hexactinellida.

Fig. 2.5 Generalized plot of temperature/depth of the World Ocean (adopted after Gage and Tyler 1991)



2.2 Distribution of Hexactinellida

Hexactinellid sponges inhabit all oceans and seas with normal oceanic salinity, including a few species in the high salt Red Sea. Most can be found at considerable depths.

2.2.1 Depth Distribution

The depth distribution of Hexactinellida as compared to that of the general biological depth ranges in the ocean has been the subject of several previous publications. According to de Laubenfels (1955), the modern Hexactinellida live generally at depths below 1000 m, and only in the Antarctic they are found at less than 100 m. Since that time, findings of hexactinellids at 100 m depth and shallower have become rather numerous. It is well known that fossil representatives of Hexactinellida inhabited shallower depths, apparently both past and present members are tolerant toward warm temperatures (Reid 1968). In Late Mesozoic times, the deep-water temperatures are considered to have been higher than in the recent oceans, up to about 13–17 °C (Lowenstam 1964), which corresponds to recent shallow-water findings of some hexactinellids. The present low deep-water temperatures are due to the climatic cooling that took place after the warm Cretaceous epoch. Vacelet (1988) divided the Hexactinellida into two principal groups: those with rigid skeleton—mainly bathyal, and those with loose spicular skeleton—bathyal-abyssal inhabitants. Tabachnick (1994) analyzed the vertical distribution of the Hexactinellida according to data in the literature. The maximum occurrences of both species and genera of these sponges is at 500–1000 m.

However, another taxonomic diversity parameter (number of species/number of genera) shows two maxima. The most significant maximum corresponds to the former one, whereas the second is at 3500–4500 m. Comparable results are obtained by analysis of the abundance (ca. 11000) specimens collected at different depth intervals (at each 100 m) (Fig. 2.6) and stored in different museums: The Natural History Museum, London, The United Kingdom; Institute of Oceanology of the Russian Academy of Sciences, Moscow, Russian Federation; Muséum national d'Histoire naturelle, Paris, France; Museu Nacional, Rio de Janeiro, Brazil; Musée Océanographique de Monaco, Monaco; South African Museum, Capetown, Republic of South Africa; Station Marine d'Endoume, Marseille, France; Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; Western Australian Museum, Perth, Australia; Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russian Federation; Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam, The Netherlands; Zoologisches Museum für Hamburg, Hamburg, Germany; Zoologisches Museum für Naturkunde an der Universität Humboldt zu Berlin, Berlin, Germany; Zoological Museum, University of Bergen, Norway). Thus, Hexactinellida are most abundant at 200–1500 m depths, and have another maximum at 4000–5000 m depths. The first maximum corresponds to the upper bathyal, and the second is at the intermediate

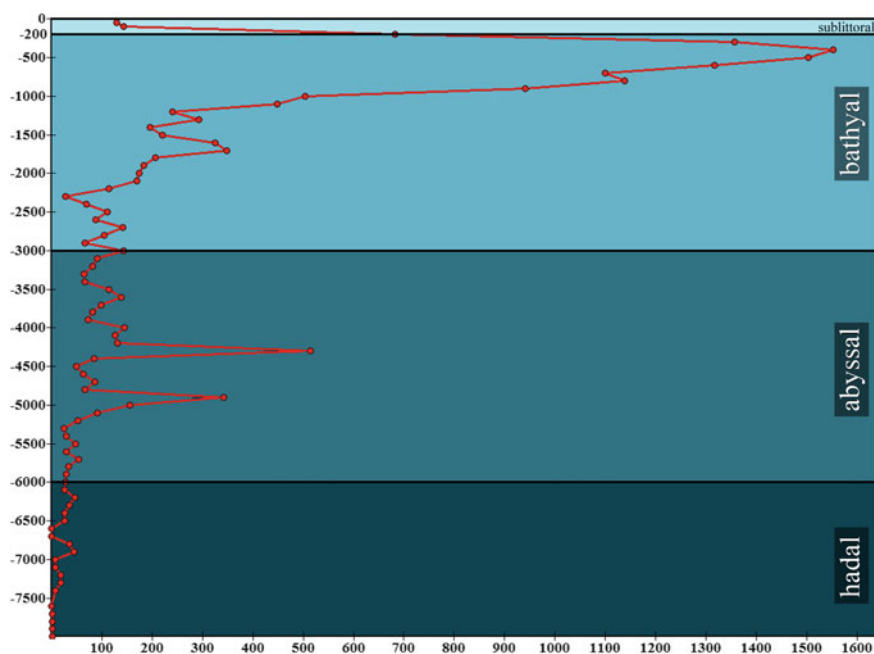


Fig. 2.6 Plot of the abundance (ca. 11,000) specimens of hexactinellid sponges collected at different depth intervals (at each 100 m) stored in different museums

abyssal depth. Most of these findings were made by trawls, and surely the specimens from the rocky substrata are underrepresented in the collections; a great disproportion is undoubtedly present in the sampling of the deepest abyssal to hadal waters. Nevertheless, we suggest that the tendency of this scheme reflects a certain depth preferences in the distribution of hexactinellid sponges.

Sublittoral (0–200 m). The sublittoral zone comprises 7.6 % of the entire World Oceans. It corresponds to the geomorphologic continental shelf zone, whose border is at about 200 m depth. The faunistic sublittoral zone does not necessarily correspond with the continental shelf. In some areas, such as the Antarctic region, this zone may extend down to depths of 500–800 m.

Sublittoral shallow water (<40–50 m). The shallow-water locations of hexactinellids at depths accessible for scuba-diving exploration are very rare, and only a few representatives of this sponge class inhabit them. All these areas are characterized by cold waters. These shallow-water locations have become very important, since they yield material for laboratory experiments (see the section below) and more or less long-term observations. This is true, e.g., for the Antarctic McMurdo Sound, where growth and reproduction rates of the hexactinellid species, *Anoxycalyx* (*Scolymastra*) *joubini*, *Rossella nuda* and *Rossella racovitzae*, were monitored for 22 years (Dayton et al. 2013). This area is known for its extremely cold waters -1.8 to -2.2 °C (Dayton, personal communication).

At shallow depths in the coastal waters of British Columbia (S-W Canada) four species were reported: *Aphrocallistes vastus* >10 m (Austin 1999); *Heterochone calyx* >25 m (Reiswig 1979); *Acanthascus* (*Rhabdocalyptus*) *dawsoni* >10 m (Austin 1999); *Acanthascus* (*Staurocalyptus*) *dowlingi* (Mackie 1979) >30 m. The water temperature is 9.5–11.5 °C (Kahn et al. 2015).

One species—*Oopsacas minuta*—inhabits the shallow waters of the Mediterranean Sea >6 m at 13.8–17 °C. The first shallow-water finding was in the Trois Pépés cave off La Ciotat (France), which turned out to be of unique construction—unlike other caves it is descending and located in an upwelling current zone. In the summer season its cool water (>15 m at 13.8–14 °C) is covered by the seasonal local thermocline (the main seasonal thermocline outside the cave is situated about 40 m deeper) (Boury-Esnault et al. 1993) (Fig. 2.7). Later this species was detected in several Adriatic caves, which are also of descending types, and even shallower occurrences of *O. minuta* in complete darkness (>6 m, at 15–17 °C) were also found (Bakran-Petricoli et al. 2007).

Sublittoral deep water (40–200 m). The sublittoral fauna of Hexactinellida may notably reach the upper zones, nevertheless this fauna is poorly investigated nearly everywhere. Two areas from this zone could be considered to be more or less well known: the S-E seashore of Canada (British Columbia shallow-water reefs—see below) and the Atlantic sector of Antarctica where temperatures in the sublittoral zone range between -1.9 and $+14$ °C. As the Antarctic shelf is a hotspot for large glass sponges of the family Rossellidae, particularly numerous in depths at or less than 200 m, it is well suited for in vivo experiments and long-term ROV-observations, e.g., of recolonization, growth, and reproduction rates, similar

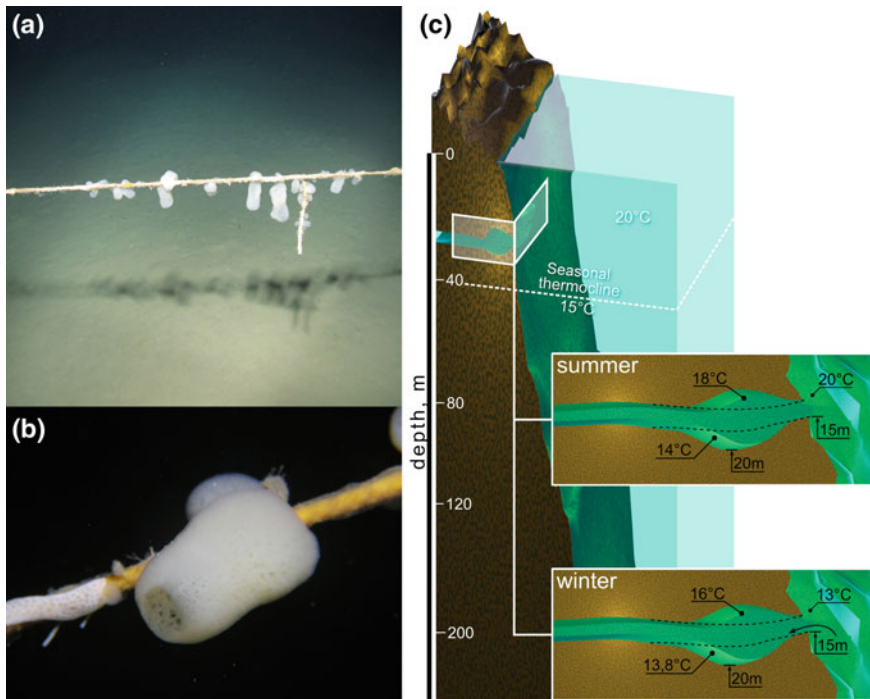


Fig. 2.7 **a, b** *Oopsisacas minuta* settled on artificial substratum (wire) in the Trois Pépés cave off La Ciotat (France) (courtesy of T. Pérez). **c** Scheme of the cave Trois Pépés shows its unique peculiarities during winter and summer seasons (adopted after Boury-Esnault et al. 1993)

to what was done at the former Larsen AB ice-shelf of the western Weddell Sea near the Antarctic Peninsula (Fillinger et al. 2013).

Bathyal (200–3000 m). This zone comprises 14.5 % of the space of the World Ocean; the water temperature of the bathyal zone is 0.5–4 °C, sometimes up to 12 °C. It contains the richest fauna of Hexactinellida. Palaeontological evidence indicates that this was the origin of, at least, the so-called dictyonine hexactinellids (with a rigid framework of dictyonal strands in their main skeleton) in the Late Mesozoic Tethyan fauna (Reid 1967). As in many other marine animals, the diversity hotspot of Hexactinellida is in the Indo-West Pacific. Its fauna shows close relationships of hexactinellid sponge taxa between West and East Atlantic regions (Tabachnick 1994).

The Indo-West-Pacific area considered to be the most well investigated and is the Sagami Sea (Pacific seashore of Japan). A number of pioneer studies on hexactinellid sponges caught by long line fishery were published by Ijima (1901, 1902, 1903, 1904), Topsent (1928), and later by Okada (1925, 1928), Ijima and Okada (1938). The total list of hexactinellid taxa from this area comprises about 28 genera-subgenera with 55 species and subspecies (from which 47 species/subspecies were described as new to science and 30 are still considered

endemic of the Sagami Sea). Only four representatives of this fauna were registered in both sublittoral and bathyal zones, while the other are known to exclusively inhabit the bathyal zone.

Other areas are still poorly investigated. Hexactinellid sponges from the Indonesian archipelago are known mostly from the Netherlands 'Siboga' expedition in the beginning of twentieth century (Ijima 1927).

Abyssal (3000–6000 m). Abyssal planes cover 77.1 % of the World Oceans and more than 50 % of the entire Earth surface. Water temperatures in the abyssal are about 0–4 °C. Pelagic fine-grained sediments (mainly clay and silt) are the most common substrata in this environment, but some areas offer larger amounts of hard substrates, such as ice-berg drop stones or fields of poly-metallic nodules. The abyssal zone is very poorly investigated due to the technical challenge and expenses connected with this time-consuming and costly research. Hexactinellid sponges inhabiting this area show obvious adaptations for the life on soft substrata, such as basal stalks with root tufts of long anchorage spicules (Tabachnick 1991). The number of families and genera of hexactinellid inhabiting the abyssal planes is rather low compared to the bathyal: Hyalonematidae: *Hyalonema*—the most diverse genus within the hexactinellids; Euplectellidae—*Holascus*, *Malacosaccus*, *Acoelocalyx*, *Docosaccus*, some *Euplectella*; Rossellidae—some representatives of *Bathydorus*, *Calycosoma*, *Lanugonychia*, *Caulophacus* (the representatives of the latter genera require some stones or peduncles of elder specimens (*Caulophacus*) for initial fixation). Unfortunately, it is unknown how the larva of hexactinellid sponges capable of inhabiting soft sediment settle to start their sessile life, as well as what their initial stages look like. All genera mentioned above are stenobathic, and their representatives could be found in the bathyal and sublittoral zones, as well as in the abyss. Since these species, like most Hexactinellida, are known only by rare, often unique findings, the endemism of the abyssal hexactinellid fauna is reported as high 76 % (Tabachnick 1994). One of the most important expeditions explored the abyssal areas—the Danish 'Galathea' expedition 1950–1952—included only 16 abyssal stations with representatives of Hexactinellida from all over the World, and about half of all species collected were new ones (Lévi 1964). It is therefore not possible to claim any abyssal plane or any local area as being well investigated given this current state of research.

Hadal or Ultraabyssal (>6000 m). This area is small, compared to the shallower zones, about 1.5 % of the World Ocean—its temperate is stable about 3 °C, sometimes –0.3 to 4.5 °C (Belyaev 1972). The hadal fauna of hexactinellid sponges is not rich, more common here are rare and small representatives of carnivorous Demospongiae, the Cladorhizidae, e.g., *Asbestopluma*. Nevertheless, several dense aggregations of Hexactinellids were described from the Kuril–Kamchatka Trench: *Hyalonema apertum* captured at depths between 6272 and 6282 m (Koltun 1970). The fauna of sponges from the hadal zone can be assumed to originate from the abyssal one, as it is rather poor in species and shows no generic endemics at all. The deepest representative of hexactinellid sponges are *Bathydorus* sp.—from the Central Pacific (6800–7300 m depth), and *Caulophacus*

sp.—together with *Malacosaccus* sp. from the Antarctic South Sandwich Trench (depth 6875–6766 m) (original data).

The most investigated abyssal area is the Kuril–Kamchatka Trench. Only four representatives of hexactinellid sponges were described from this trench. They all were previously known from shallower depths (Koltun 1970; Downey and Janussen 2014).

2.2.2 *Some Peculiarities About Hexactinellid Sponges are Connected with Specific Geological Conditions*

Submarine ridges: banks, mountains, and mounting chains. Underwater rises usually have rich fauna due to the local upwelling of nutrient-rich waters. Hexactinellid sponges commonly represent a large part of the benthic fauna on these landscapes.

The banks are located in the sublittoral zone. An interesting fact is the occurrence of the hexactinellid species, *Vazella pourtalesi*, known for a long time by several findings of small specimens off Florida and in the central Atlantic (Tabachnick 2002). Recently larger sizes of this sponge were found to be dominant at the rate of tons per trawl on the banks of Nova Scotia (E Canada) (Fuller 2002; Reiswig 2004).

Underwater mountains and mid-oceanic ridges are located in the deeper (bathyal) zone. Hexactinellid sponges are often the most prominent macrobenthos in these areas due to their large individual size.

The hexactinellid fauna from the Magellan Mountains (NE of Indonesia) are among the best known (Tabachnick 1988; Tabachnick et al. 2011). The total number of Hexactinellida is 17 species and 13 subspecies, which were new to science (Fig. 2.8).

The Mid-Atlantic Mountain Chains are the best investigated of all (Tabachnick et al. 2008, 2013; Lopes et al. 2013). From there 28 species of Hexactinellida were registered, and 14 turned out to be new.

Hydrothermal vents and cold seeps. Dense aggregations of hexactinellids in the close vicinity of hydrothermal vents are unknown; moreover, they seem to avoid these areas. The description of *Caulophacus cyanae* from the East Pacific Ridge in the zone of ‘strong hydrothermal’ influence (Boury-Esnault et al. 1988) is not convincing. It is very likely that the local aggregations of these sponges are located far from the hydrothermal zone. It is also unknown, whether or not the bacteria or organics, which are the main food source of these animals, are actually of hydrothermal origin (the easily proved fact by isotopic analysis of the sponge body).

The occurrence of a few *Hyalonema* sp. around probable cold seeps in the N Atlantic was observed during a Norwegian expedition (unpublished data). Unfortunately, these sponges were not collected, as required for their further and detailed identification and description.

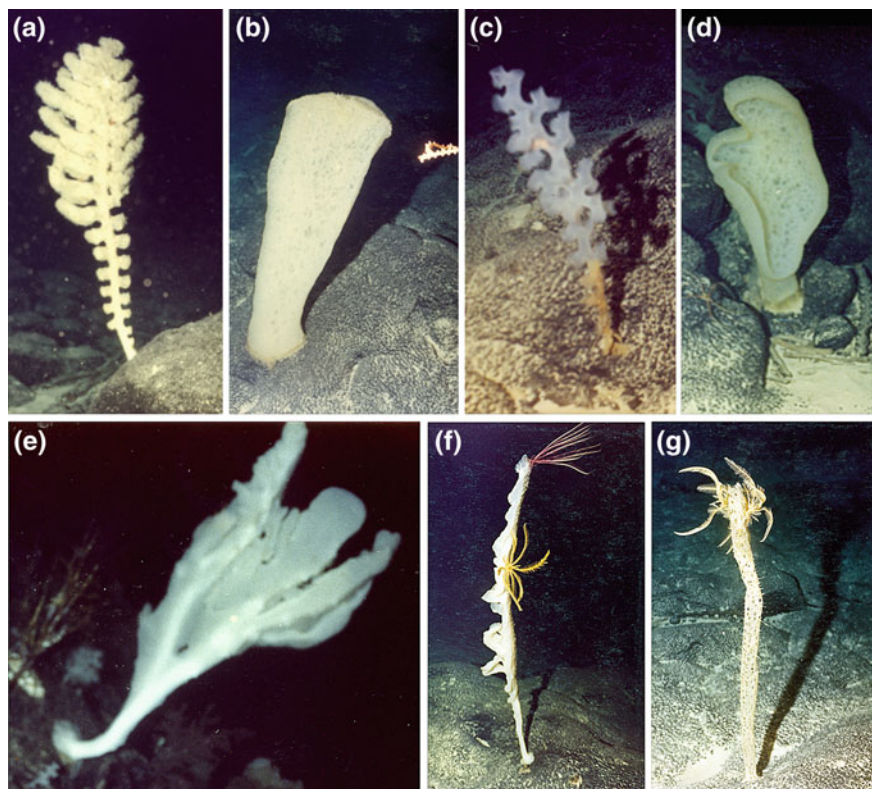


Fig. 2.8 Hexactinellida from the Magellan Mountains photos (RV *Academic Mstyslav Keldysh*—9, submersible *Piscies VII* and *XI*). **a** *Aspidoscopulia* sp., 1600 m. **b** *Semperella alba*, 1494 m. **c** *Farrea occa polyclavula*, 1980 m. **d** *Poliopogon amadou pacifica*, 1570 m. **e**, **f** *Tretopleura styloformis*, 1520 and 1600 m. **g** *Walteria leucarti longina*, 1660 m

2.3 Areas with Dense Aggregations of Hexactinellida

Many areas with relatively dense aggregations of hexactinellid sponges are known. Usually these are local aggregations which may be found everywhere in the above mentioned vertical zones. Commonly they are connected with local changes of the relief, e.g., borders of sharp protruding edges, or changes of the relief where local water currents and turbulences are more or less permanent and strong, which facilitates passive filtration (Rice et al. 1990). Another possible cause of dense aggregations is asexual reproduction, although only few poorly convincing confirmations exist of this type of reproduction within the Hexactinellida [e.g., *Anoxycalyx* (*Scolymastra*) *joubini* on the Antarctic shelf (Dayton et al. 2013)].

Hexactinellida as environmental converters. Hexactinellid sponges, particularly when they occur in dense aggregations, significantly influence the bottom landscapes. One possibility is concerning the lysscinosan sponges with skeletons of

loose spicules: after death of the sponge these spicules may be deposited as part of the bottom sediment. In recent depositions they are called spicule mats, in fossil sedimentary rocks they are known as spiculites or biostromes (Brückner 2006; Brückner and Janussen 2005). Another possibility concerns the hexactinellids with dictyonal rigid skeletons (representatives Hexactinosida and Lychniscosida), which are not destroyed after the death of the sponge and serve as substrata for future generations of sponges and other sessile animals. Such constructions are common as fossil reefs, especially in geological formations of the Mesozoic. However, they are rarely present also in more recent marine environments where they constitute large bioherms or reefs (Krautter et al. 2001, and below). Recent sponges with other types of fused massive skeletons, such as Aulocalycoidea, Fieldingida, and Lychniscosida, are very rare, and not known to form dense aggregations [only the latter are known to be numerous in the Mesozoic fossil record (Krautter 2002)].

2.3.1 Recent Hexactinellid Reefs

Shallow-water reefs of the British Columbia (S-E seashore of Canada). In 1987–1988, during the geophysical investigations off E-S Canada seashore; in Queen Charlotte Sound and Hecate Strait; several reefs, in summary about 700 km² at 140–240 m depth, were discovered. The investigation with the submersible (Conway et al. 1991, 2001) showed that they are inhabited by 6 species of Hexactinellida, of which the most important ones belong to the Hexactinosida (sponges with rigid dictyonal skeleton)—*Heterochone calyx* (Fig. 2.9) and *Aphrocallistes vastus*, sometimes together with *Farrea occa*. These skeletons are not destroyed after the death of the sponges, only loose spicules including the microscleres disappear from the main dictyonal framework. Thus, unlike sponges constructed by loose spicules (Lyssaacinosida and Amphidiscosida), the dead skeletons of *H. calyx* and *A. vastus* (which only partly sink into the mud) stay rigid and provide substrates above the muddy sediments for the successful settlement of larvae of new generations of these sponges and other animals as base for the future reefal growth. Later, similar reefs were found in Strait of Georgia at depths of 150–190 m (Conway 2004) and water temperature of 6–7 °C (Conway et al. 2005); 9.5–10 °C (Kahn et al. 2015). The living sponges form a layer of 1–2 m in thickness at the upper part of these reefs, their dead parts form the lower 5–8 m, and sometimes up to 21 m thickness of the total reefal construction. The age of such constructions is estimated to 6000–9000 years (Conway et al. 2001).

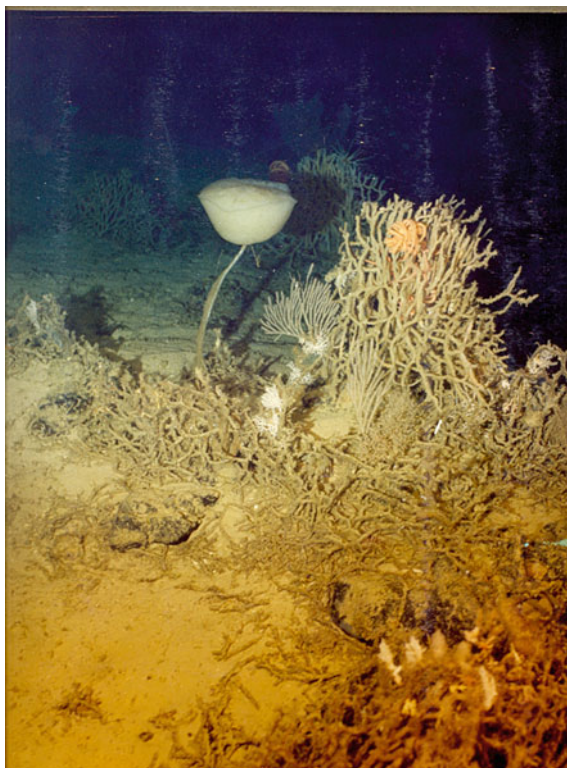
Recently Larkin et al. (2009) and Marliave et al. (2011) described shallow water dense aggregations (“sponge gardens”) at 30 m depth from the fjord Howe Sound and off Texada Island (S British Columbia), as well as deeper (70–100 m) bioherms constructed by a single species of the Hexactinosida: *Aphrocallistes vastus*.



Fig. 2.9 Shallow-water reef of the S British Columbia, likely *Heterochone calyx* 70–170 m (courtesy of S. Leys, A. Kahn and ROPOS.com)

Deep-water reefs of hexactinellid sponges. A newly found deep-water reef construction from the Mount Error Guyot were observed during the R.V. ‘Academic Mstyslav Keldysh’ 7 voyage in 1984 from the submersible ‘Pisces.’ Unfortunately the collected specimen was lost and only photos of the bioherm constructions are available. They show notable masses of dead and living mass-occurring organisms situated on the slope of the Guyot on mixed sandy and rocky substrata at 1200–1820 m depth, including details of a bioherm, several square meters in area and about 1 m high (above the substratum). The reef constructors are identified based on the external shape as belonging to the genus *Sarostegia* (Fig. 2.10), a monotypic genus with single species *S. oculata* Topsent (1904) (Porifera, Hexactinellida, Hexasterophora, Hexactinosida, Farreidae). The body of these sponges consists of thin (2–5 mm in the upper parts and about 10 mm in diameter at base) dichotomous branching, and anastomosing skeletal protusions (Fig. 2.11). Two similar representatives of Hexactinellida from another family, the Tretodictyidae, are known to have a similar body form: *Sclerothamnus* and *Sclerothamnopsis*. The first genus possesses numerous widened rings situated along the branches; the second genus shows great variation of the branches, and in any case anastomosing is rare in both of these genera. Another criterion of differentiation among possible genera of Hexactinellida is their geographical distribution. *Sclerothamnus* and *Sclerothamnopsis* inhabit the Pacific Ocean (a new species, not

Fig. 2.10 Deep-water reef of *Sarostegia oculata* from the Mount Error Guyot, RV *Academic Mstyslav Keldysh* —7, submersible *Pisces*, 1200–1820 m. A large pedonculate Hexactinellida is a representative of the family Euplectellidae, subfamily Bolosominae



yet described, of the latter genus is known from the Indian Ocean, off Madagascar). *Sarostegia oculata* is widely distributed in the N and W part of the Indian Ocean as well as in the Atlantic Ocean of the Cap Verde Islands and off the coast of Brasil. *S. oculata* inhabits depths from 256 to 1900 m (according to literature data and data of the recently collected material (Fig. 2.12). The Mount Error Guyot distribution corresponds to both depth and spatial distribution of this species, which we consider as an indirect confirmation of its identification according to the photos. Certainly, the scale of these reefs is not as impressive as Canadian ones, and they are much smaller than the deep-water coral reefs of *Lophelia* form at more considerable depths (Fosså et al. 2002).

2.3.2 *Spicule Mats*

First reports on such substrata came from fishermen's stories in the Barents Sea when the bottom fish-trawls came up full of large amounts of silica sponge spicules

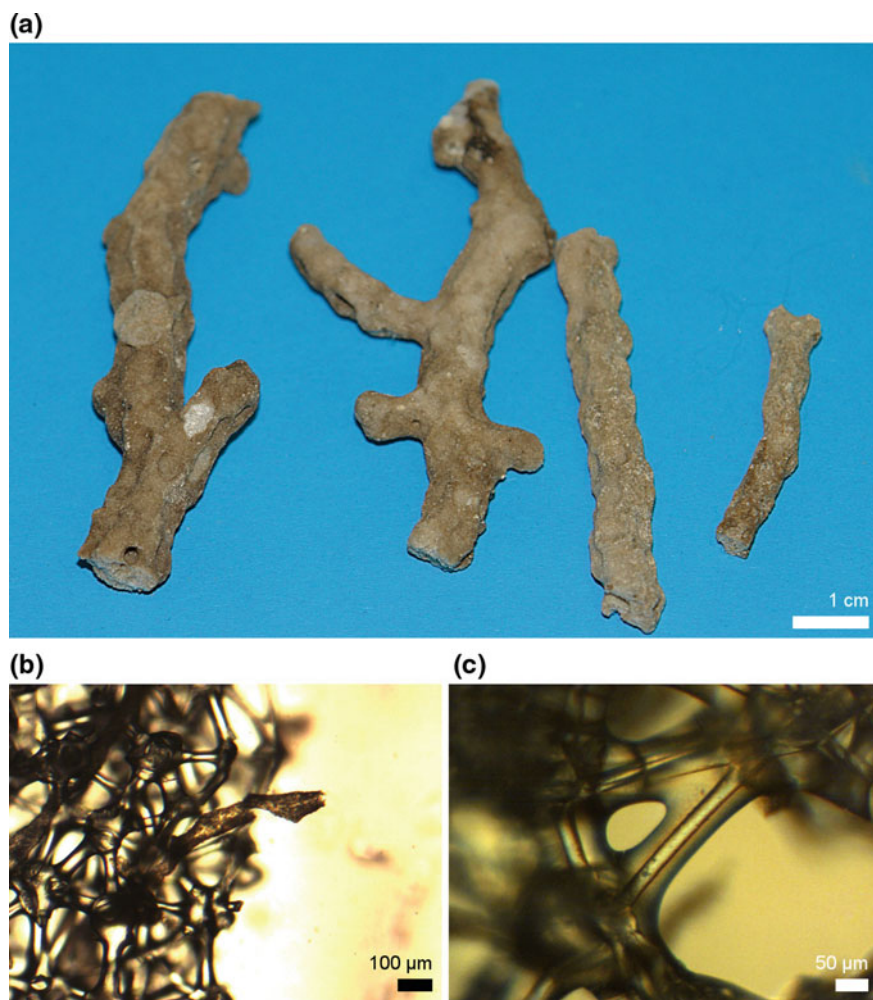


Fig. 2.11 The skeleton of *S. oculata* (a) is made of massive glassy network with well developed channel system (b, c)

produced by representatives of Demospongiae (Koltun, personal communication). Meanwhile, occurrences of analogous substrata produced by hexactinellid sponges are also known. The most famous are the extensive large areas of the Antarctic shelf covered by spicules of dead specimens from various species of the Southern Ocean endemic genera *Rossella* and *Scolymastra* (Gutt et al. 2013).

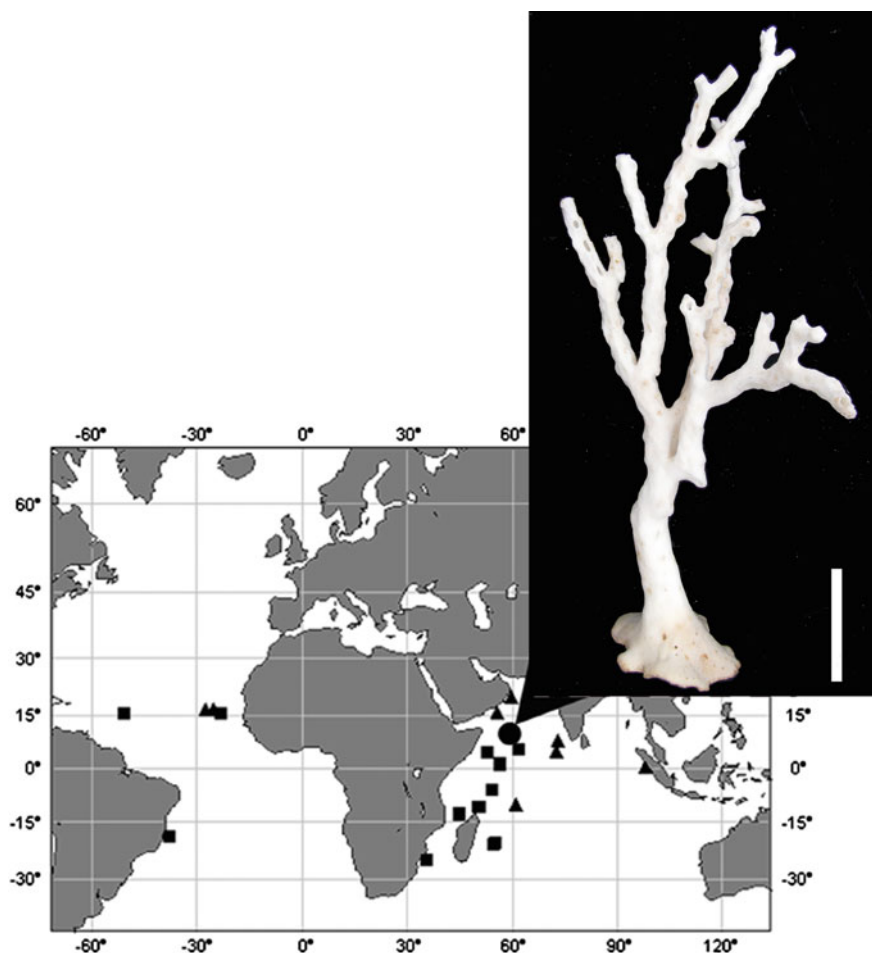


Fig. 2.12 Distribution of *S. oculata*. Triangle—previous (literature) data, square—new data, circle—data from the underwater photo. *Sarostegia oculata* on the photo—a specimen collected by the trawl (scale 30 mm)

Pheronema carpenteri (Hexactinellida, Amphidiscophorida) occurs in dense aggregations in the Porcupine Seabight, SW of Ireland, at 1000–1300 m depth, water temperature 4–10 °C. The spicule mats constitute about one-third part of the entire bottom surface (Bett et al. 1992). As observed in photos (Fig. 2.13), most specimens of these sponges are surrounded by spicule mats. Thus, their recruitment strategy is similar to that known from reefs, where the settlement of larvae is facilitated by the presence of corresponding substrata originated from sponges.

Fig. 2.13 Spicule mats and numerous sponges *Pheronema carpenteri* settled on it from the Reykjanes ridge south of Iceland, RV *Academic Mstyslav Keldysh*—28, submersible *Mir*, 1011–1078 m. A single tubular sponge—*Asconema* sp.



2.4 Cultivation of Hexactinellids in the Laboratory Under Psychrofile Conditions

Marine ranching of sponges is, principally, subject to great scientific and industrial interest based on their typically quite unique secondary metabolites. Consequently, reports on cultivation techniques with glass sponges are very intriguing. To summarize, all specimens for investigations on living Hexactinellida were collected from a few shallow-water locations, and were investigated in the laboratories situated closely to places of their occurrences. Such experiments are possible during a restricted time after capture.

Rhabdocalyptus dawsoni (Rossellidae) collected off the Bamfield Marine Station (S-W Canada), at 13 °C in less than 18 m depth (Leys et al. 2004), were used for: reaggregation of syncytia and cells (Pavans de Ceccatty 1982). The estimation of conductivity was observed at 11 °C (Mackie et al. 1983), and at 10 °C (Leys et al. 1999). Pumping activity of this species was observed at 7–12 °C (Leys et al. 2006) and cultivation of sponge tissues at 10 °C (Wyeth et al. 1996). *Rhabdocalyptus dawsoni* and *Aphrocallistes vastus* (Hexactinosida) from 130 to 170 m depth were cultured for experiments at temperatures of 9–13 °C (Yahel et al. 2007).

Oopsacas minuta (Rossellidae) specimens collected from the submarine cave near La Ciotat were kept at 13 °C at the Station Marine d'Endume (Marseille) for some short-term experiments with particle retention (Perez 1996); embryogenesis observations were performed at 12 °C (Leys et al. 2006).

The only experiments examining temperature effects on the speed of propagation were done on *Rhabdocalyptus dawsoni* (Leys and Meech 2006). The propagation was maximal at 10 °C and showed a linearly decreasing correlation with temperatures above and below the maximum. This points to temperature as being one of the most important factors affecting the distribution of hexactinellids, which has species specificity.

Thus all laboratory experiments on living hexactinellid sponges were performed with shallow-water representatives at temperatures between 9 and 13 °C. So far, temperatures above this level are found to be fatal for all Hexactinellida.

2.5 Observations on Growth and Death of Hexactinellida

There is information concerning the rates of biosilicification in sponges habituating under psychrophilic conditions remains lacking. First estimates of hexactinellid growth rates were made in the Antarctic, where sponges from three rossellid species were monitored over a 10 years period (Dayton 1979). Large specimens of two species, *Rossella nuda* and *Anoxycalyx (Scolymastra) joubini*, showed only minute growth; while the smaller specimens of the third species *Rossella racovitzae* showed notably faster growth with 100–300 % increases in volume. These observations indicate that the size of individual hexactinellid sponges is limited even in those genera with non-rigid skeletons; which were the subject of the above study. Similar observations were noted later for *Rhabdocalyptus dawsoni* off Vancouver Island (Leys and Louzon 1998). Notable vertical growth, 1–3 cm/year, was observed for *Aphrocallistes vastus* in the Canadian sponge reefs (Austin 2003). Recent observations in the former Larsen Ice-shelf area, Antarctic Weddell Sea, showed rapid growth and colonization of *Rossella* sp. to become one of the dominant taxa within 5 years, both by abundance and biomass (the latter increased 2–3 times) (Fillinger et al. 2013).

In some hexactinellids with loose, nonrigid skeletons, like Lyssacinosida and Amphidiscophorida, secondary silica depositions may take place between the larger spicules (this is true for *Euplectella aspergillum*, *Walteria flemmingii* and others) (Schulze 1887). The cementation within lyssacinosid skeleton starts from the base of the sponge. In many representatives this takes place only in the basal parts (such as the basidictyonal plate described from *Acanthascus (Staurocalyptus) glaber* Ijima 1904), or it involves particularly the stalk in pedunculate Rossellidae and Euplectellidae (e.g. the genera *Caulophacus*, *Bolosoma*) (Ijima 1903). In such cases, further growth seems to become impossible. Moreover, usually only adult sponges are represented in collections while the juveniles with loose or partly cemented microcleres are very rare, probably because of their rarity in nature and/or rapid growth before adult size.

Amphidiscophora never have rigid skeletons or fused spicules, but observations on collected specimens indicate that the possibility to add new basalia is restricted to a certain growth stage (unpublished observations). At later stages, the sponge can elongate the basal anchorage spicules in its proximal part. As seen in many Hyalonematidae, the proximal part of the stalk is then situated inside the body. The distal parts, which lack tissues, protrude from the base of the body and are partly exposed to the surrounding sea water, and partly embedded in the substrata. Hexactinellida, whose principal skeletons are rigid and constructed of initially fused macroscleres (Hexactinosida—dictyonal strands; Fildingida and Lychniscosida—initially fused hexactinic spicules; probably Aulocalycida with fusion of hexactin spicules immediately after formation) are capable of marginal (oscular) growth by adding additional layers of fused megascleres throughout the lifetime of the sponge while the living tissue is present around these spicules.

It is reported that rossellid sponges can rapidly regenerate small amounts of damage from predators (Dayton 1979), but to the best of our knowledge, no reliable data about the natural death of hexactinellids has been ever published. So far, the process of natural mortal degradation can be reconstructed only based on museum specimens. This process is suggested to be different in sponges with lophophytous type of fixation (sponges, which fixing themselves to the substrate by a tuft of basal spicules). These are all Amphidiscophora (*Hyalonema*, *Monorhaphis*, *Pheronema*, etc.) and some nonrigid Hexasterophora, Lyssacinosida (for instance *Rossella* and most *Euplectella* species). Young specimens have the capacity to add new basal spicules, while in the larger specimens this process has ceased. It is easy to imagine that the continuous growth of the upper living part of the sponge body without any possibility to increase or change its basal part responsible for fixation may lead to the collapse, or detachment, of the entire specimen with mortal consequence. Most of the rigid Hexasterophora have a basiphytous fixation [usually by a basidictyonal plate or rhizophytous rootlike structures, Reid (1964)] to a hard substrate. Common observations on large specimens in the collections show that in most cases, unlike lophophytous sponges, the dictyonal sponge has no living tissue at all at its basal part. The incapacity of enlarging and reinforcing the basal part of the body may lead to breakage and death of the specimen. An important fact is that the Hexactinosida are known to act as reef builders, and also others have a capacity to strengthen their fixation by additional secondary points of fixation. As can be observed on the hexactinellid skeletons' preserved fossil sponge reefal constructions, this mechanism was much more common in the past, e.g., in the Jurassic sponge reefs.

2.6 Biosilicification in Hexactinellids

The mesohyl is a primitive type of connective tissue specific only for the phylogenetically original Metazoa—notably sponges. It is very variable and may include dead elements, such as fibrils (of collagen, spongin and/or chitin), rigid skeletal elements (spicules) as well as living elements: amoeboid cells (amoebocytes),

multinucleate trabecular syncytia, and scleroblasts located between dermal and choacocytes layers. Evolutionary the mesohyl is one of the oldest and most original tissue types. In Hexactinellida the mesohyl is known to contain collagen (Mackie et al. 1983), but no spongin, and spicules besides some cellular elements. Its functional role is very important: Support of the main trabecular multinucleate syncytium, which can be also regarded as a mesohyl component, as well as the multinucleate scleroblasts producing the spicules. The study of spicule formation processes (biosilicification) in hexactinellid sponges includes three different methodological approaches.

One is histological, descriptive, and offers interpretation of mineralization process on spicules observed under the TEM microscopy by analysis of ultrathin soft body sections. This process is described in several recent publications and generally it is reported to be similar in Demospongiae and in Hexactinellida, both sponge classes with siliceous spicules (Weisenfels and Lanschoff 1977; Boury-Esnault et al. 1994). The silica deposition begins around the initial axial filament inside a vacuole—silica deposition space (Leys et al. 2007) with specific membrane—silicoblast of a special cell—scleroblast (silicoblast). The only difference between Hexactinellida and Demospongiae is the spicule formation by giant multinucleate sclerocytes (sclerocyncytia) in hexactinellids (Mackie and Singlar 1983). An exception is cell (scleroblast not sclerocyncytial) formation of spicules in some hexactinellids juveniles (Leys 2003). The spicule can be enlarged by two ways: in length by growth at the outer ends, usually when the axial canal is opened, and in thickness or by secondary fusion of several spicules by deposition of additional concentric layers of silica. It is suggested that silicic acid penetrates in numerous vesicles into a silica deposition space around the spicule where the amorphous silica is deposited as nanospheres or nanoparticles (Cha et al. 1999; Aizenberg et al. 2004).

The other approach emphasizes the specific enzymatic model—including the activity of so-called silicateins—which are entirely (or mostly) connected with the organic axial filament (Cha et al. 1999). This method is based on hydrofluoric weak acid treatment of spicules for demineralization, which under cold temperature are transformed to be soft enough for preservation of some organic material, including silicateins (Müller et al. 2007). Generally, silicateins belong to a specific class of enzymes—cathepsins. A weakness of this model is the fact that it is very difficult to imagine how the silicateins from the centrally located axial filament forms silica layers on the outer surface of the spicule. For instance, the single basal spicule of *Monorhaphis* can reach up to 3 m in length and about 1 cm in diameter. If we imagine that the axial canal is opened at the outer ends of the spicule, silicateins should move at least 1.5 m to reach the middle of the spicule. On the other hand the spicule thin section shows many concentric layers of the deposited silica (Lévi et al. 1989). It is unknown whether the silicateins have the capacity to penetrate these numerous layers of amorphous silica, which are up to 5 mm in thickness (as it is the case in *Monorhaphis*), or if they penetrate through some sparsely distributed channels within the concentric layers. It is equally difficult to imagine this scheme for the smaller hexactinellid spicules. This enzymatic theory requires a kind of long distance induction of activity which currently has not been observed or

documented. Nevertheless, it was shown in vitro at standard conditions of 20 °C that the process of the silica polymerization under the influence of silicateins does take place (Cha et al. 1999). However, it is very questionable if this reaction also takes place under psychrophilic conditions, in which all hexactinellids and some Antarctic species of Demospongiae inhabit.

The latest approach is connected with findings of organic matrix inside sponge silica spicules (different from the axial filament which organic nature has long been known) after solution and dissociation (usually long-term) using NaOH. The organic remnants of the spicule after dissociation of the amorphous silica were found to be various: collagen is found in basal spicules of *Hyalonema sieboldi* (Ehrlich et al. 2006), *Monorhaphis chuni* (Ehrlich et al. 2008a, 2010), and α -chitin was documented in *Farrea occa* (Ehrlich et al. 2007), *Euplectella aspergillum* (Ehrlich and Worch 2007), *Rossella fibulata* (Ehrlich et al. 2008b). The both types of organic matrix are considered to be templates for amorphous silica biomineralization, and chitin also serves as a template for multi-phase biomineralization of both silica and crystalline aragonite (Ehrlich 2013). Both types of mineralization are known from Verongida sponges, but that from *Caulophacus* (Hexactinellida) is found to include minute calcitic reinforcements of the silica joints (Ehrlich et al. 2011). Experimental silicification of colloidal chitin (Ehrlich and Worch 2007) and *Rossella fibulata* (Ehrlich et al. 2008a) was performed at room temperature, the collagen (from *Chondrosia reniformis* Demospongiae origin) silica mineralization was created at 20 °C (Heinemann et al. 2007).

Silicoblast or sclerocyncytia likely produce organic matrix simultaneously with silica deposition (chitin or collagen not mineralized by silica have not been found in the spicules by TEM investigations). In contrast to the traditional interpretation of silicateins, the silica acid is now considered to have a catalytic activity in sugar polymerization reactions (Lambert et al. 2010), or even to cause canalization of sugar polymerization reactions (Boutlerow's formose reaction) which lead to uniformity of final products (Markov 2010). It is possible that proteins such as silicateins (as well as collagen and chitin) do not have a direct enzymatic function in the spicule formation, but that they may play another role—a structural or mechanical function. Thus, silicateins may play a part in the formation only of the initial silica coat around the axial filament, and later the role of main spicule growth—elongation and thickening may be performed by secretion of collagen or chitin. In any case, silicatein activity in silica deposition, as well as collagen, during the chitin matrix mineralization should be investigated under experimental psychrophilic conditions as this corresponds to the natural environment of all Hexactinellida and many representatives of Demospongiae.

2.7 Conclusions

All hexactinellid sponges are unquestionably psychrophilic, inhabitants of marine zones with temperature below 15 °C, and commonly dwell in deep-water (below 200 m) with rather cold conditions. They are an important component of the

macrobenthos, sometimes forming dense aggregations and even large reef constructions with major influence upon the environmental conditions.

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