ECOLOGY AND PALEOECOLOGY OF SPONGES

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INTRODUCTION

Sponges are ecologically different from other sessile, **epibenthic suspension feeders** in respect to the following: (1) their major food intake is from smaller particle sizes; (2) they shelter a much larger volume of **inquilines;** (3) predation pressure upon them is relatively less strong; (4) symbiotic relationships with **prokaryotes** and unicellular algae are possibly more frequent and lead, in the most highly developed instances, to bacteria-sponge entities reminiscent of lichens.

Sponges resemble corals and bryozoans, for most of them use space for a considerable distance above the sea bottom, and their mode of occupying this space is an important element of their adaptation. Competition with corals and bryozoans, therefore, is strong and is confirmed by their geologic history and present distribution. Morphologic convergence with corals and bryozoans is also strong, despite differences in food sources and feeding methods.

ECOLOGY OF SPONGES

The functional relationships of sponges with their environment center upon (1) feeding, (2) occupancy of substrate space and of the adjacent water, (3) provision of cover and camouflage to vagile benthos, and (4) provision of food to browsing carnivores. Respiration and reproduction seem less critical interactions, in that they are accomplished by modes common to most marine organisms.

FEEDING

Because digestion is intracellular (and they lack an organ for mechanical breakdown of food) sponges are limited in their use of food to the smaller end of the spectrum of particle sizes available to suspension feeders. These range from molecules through organic detritus and bacteria to the smaller protozoa and one-celled algae. Length of the **choanocyte collar** through which most food is captured is about 5 um (REISWIG, 1975). Amoebocytes of 10 um in diameter (BRIEN, 1973a) represent the upper limit on food particle size. Many one-celled organisms exceed these dimensions. Sponges do not seem to be limited in their distribution by availability of food. Particles of the size required occur in all oceanic waters, as do the sponges. Limited distributions of sponge species may be related partly to food requirements, but nothing is known at present of food-specificity in sponges. In balance, environmental factors other than food must be looked to for an explanation of the distribution of individual species.

Sponge abundance, on the other hand, seems strongly determined by food supply. For example, the area off the North Cape of Norway, where sponges constitute more than 90 percent of a locally very high absolute biomass, is beneath an area where Gulf Stream plankton are killed by Arctic waters. Other examples are the general abundance of sponges in the vicinity of coral reefs, which have a high rate of primary production, and the concentration of sponges near organic-detritus-bearing river mouths in Bermuda (DE LAUBENFELS, 1950). The abundance of sponges near the Antarctic Ross shelf ice, where algal blooms are common, can also be related to the local abundance of food.

In most of these instances successful competition for substrate space is also involved, for the sponges nearly exclude other sessile organisms. Rapid growth consequent upon a rich food supply, leading to preemption of bottom space seems to be the cause. Marginal conditions for competing species may also be involved for the two polar-water examples.

SPACE OCCUPANCY BY SPONGES

Sponges are sessile, benthic, epifaunal suspension feeders that, as a rule, project a considerable distance above the substrate. They present a large surface area of intake of food and metabolites, often by means of an elaborately branched body shape. In this they resemble colonies of bryozoans and corals and differ from brachiopods and bivalves that tap resources of the environment through relatively small areas and do not greatly increase the cross section of capture through individual growth. Such relationships have several ecological consequences. (1) Sponges take food from a considerable distance above the bottom and, thus, compete more directly with bryozoans and corals and less directly with brachiopods and bivalves. (2) An individual sponge captures quantities of food corresponding to that taken by a dense concentration of individual bivalves or brachiopods. (3) Adaptations for obtaining food by sponges is directly related to gross body shape and especially to external surface area, which in bivalves and brachiopods is related more to changes in the process or efficiency of food gathering. (4) A sponge can compete with other organisms for food through sheer growth. (5) Competition for food involves competition for space.

It is not surprising, therefore, that in the geologic past, times of sponge abundance have tended to have an inverse relationship with times of bryozoan and coral abundance. This is especially true of reef-building sponges in relation to reef-building corals. Sponges dominated reef communities in the Ordovician before corals became diverse and abundant and again in the Permian and Triassic, when rugose and tabulate corals were dying out and scleractinians were just beginning. This matter is discussed further below.

It is not surprising that sponges often have a patchy distribution. Where they are abundant they tend to occupy the substrate space to the near exclusion of other sessile epibenthos. When part of a mixed community, on the other hand, they are individually less abundant than the associated brachiopods and bivalves.

The greatest surface area for a given volume of water space occupied is achieved by a branching sponge with numerous, narrow branches. Such a shape is mechanically weak and is, therefore, most efficient in quiet water. Broadly flattened branches improve mechanical strength while maintaining much of the surface area. *Microcionia* and *Axinella* are common sponges with such shapes, as are some species of the Permian *Guadalupia* (see Fig. 85). Stouter cylindrical branches are also mechanically stronger but reduce the amount of surface area relative to internal sponge tissue unless the sponge develops a hollow tubular shape. The Pennsylvanian *Heliospongia excavata* has solid, flattened branches, while *H. ramosa* has cylindrical branches with a central cloaca, as does the later, stouter *H. vokesi.* A thin-walled tube has greater surface area relative to sponge volume but is mechanically weaker. Many such sponges as *Callyspongia* and *Mycale,* living in quieter waters, have thin-walled tubular branches.

Sponges that do not maximize surface area of food capture in the waters above the sea bottom but rather confine themselves to the space close to the sediment surface may assume mechanically stronger shapes. Simple encrusting forms can survive high wave energy. More massive shapes, including spheroidal ones, are also strong but require a more elaborate internal canal system to compensate for reduced surface area relative to internal volume. Spheroidal shapes, such as those of *Tethya, Tetilla,* and *Geodia* have complex aquiferous systems with specialized structures such as chones to regulate internal water flow. Sponges with open-cup or goblet shapes represent a compromise between mechanical strength and increased surface area of food capture.

Sponges in which rapid growth is an important element of adaptation are expected to maximize surface area of food capture. It is not surprising, therefore, to find that

Mycale has a tubular branching form, for Reiswig (1973, 1974) noted that the species of *Mycale* he studied in Jamaica is an opportunistic generalist with a high metabolic rate, high growth rate, and high reproductive rate. On the other hand, the slower growing specialist species, *Verongia gigantea* and *Tethya crypta* (Reiswig, 1973, 1974), have thick-walled goblet and spheroidal shapes, respectively. These species are adapted to protect the life of the individual sponge at the expense of slower growth (Reiswig, 1973).

Unfortunately for the paleoecologist, sponge shape alone cannot be used as a simple environmental indicator. As the above examples show, shape may relate both to mechanical efficiency and to food-getting efficiency; some species may sacrifice one for the other. Nevertheless, shape gives us a working hypothesis about the environment to be tested by independent lines of evidence. Where closely related forms have a systematic variation in shape in adjacent areas, we may accept as a possibility some form of environmental control. As an example, closely similar forms of *Guadalupia* from the same locality in the Road Canyon Formation of the west Texas Permian sometimes vary from minutely branching shapes, to flattened, subparallel branches to open cups, to cups so deep as to be nearly tubular. If mechanical efficiency alone is considered, minutely branched individuals are most effective in quiet water and open cups in rough water. Alternatively, branched forms could represent an attempt to increase food-getting efficiency under conditions of reduced supply or increased competition. In the history of the group, a minutely branched form is unusual and confined to a limited time and place, while the open-cup is most common and occurs earliest. Tubes, on the other hand, dominate in times subsequent to the Permian. Inasmuch as tubes and cups occur in reefs (presumably rough water), while the minutely branched forms occur in less clearly reefal localities (along with some cups), the quiet-water interpretation is strengthened. Likewise, evolutionary development of tubular forms may be related to increased food-getting efficiency in a relatively constant environment.

Indications of paleocurrent direction may be less equivocal. Sponges with subparallel, subhorizontal branches are usually elongate into the current, with the fastest-growing end likely to be pointed upcurrent. Flabellate vertical sheets, on the other hand, are likely to be oriented across the current.

From the point of view of efficiency of waste disposal (Bidder, 1923), sponges with oscular chimneys or narrow-mouthed, stalked goblet-shaped forms are most efficient in quiet water, while open cups are less effective. Thus, increased food-getting surfaces in quiet waters will play against decreased efficiency of waste disposal and projection. Minutely branched forms may be best in quiet water with a constant current.

ECOLOGICAL DISTRIBUTION OF SPONGES

HOLOCENE SPONGES

Environments in which Holocene sponges occur in particular abundance include the foreslopes of tropical coral reefs below the zone of maximum coral growth, i.e., from about 23 mm to about 150 m (Reiswig, 1974; Vacelet, 1981; Lewis, 1965b); rock bottoms in sheltered quiet-water lagoons behind coral reefs (Reiswig, 1973; Hay, Wiedenmayer, & Marszalek, 1970); dark caves within coral reefs (Jackson, Goreau, & Hartman, 1971; Vacelet & Vasseur, 1971b); and dark places in very shallow water such as under stones and in coastal caves (Vacelet, 1967a, 1967b, 1994; Vacelet, Boury-Esnault, & Harmelin, 1994). Sponge reefs dominated by hexactinellids have been recently reported from depths up to approximately 200 meters on the British Columbia continental shelf in Hecate Strait (Krautter & others, 2001; Conway & others, 1991, 2001). Also included in these dark environments are the abyssal plains, in general (Zenkovitch, 1963); areas adjacent to the

Antarctic shelf ice (Bullivant, 1960; Dayton, Robilliard, & Paiune, 1970); and localized patches in moderately deep water, such as off North Cape of Norway in the Barents Sea at depths of around 300 m (Zenkovitch, 1963, p. 145–146). A number of these environments are relatively dark, and various authors have suggested that sponges have generally lived in dark environments, even in the geologic past. Frequent occurrences of abundant sponges with algae in the fossil record (Finks, 1971a), however, suggest that they have also flourished in lighted environments. Bryozoans and brachiopods co-occur with sponges in present-day dark marine caves (Jackson, Goreau, & Hartman, 1971).

Another common aspect of most of these environments is a hard rock substrate. This points to two sponge requirements: a hard surface for attachment and sediment-free water. That the latter is the more important of the two is suggested by the abundance of sponges having special adaptations for attachment in soft sediments (root tufts), in environments where a soft bottom is accompanied by a low sedimentation rate, such as on the **abyssal plain.**

The following discussion summarizes those instances of clear dominance of sponges in terms of biomass, in particular ecological situations, or of restriction to particular environments. Undoubtedly many examples have been omitted through ignorance of the literature or because no clear statement was made concerning relative abundance in primary sources. The relatively recent review by Sarà and Vacelet (1973) has been particularly helpful.

Among living Monaxonida, the Poecilosclerida (sigma-bearing sponges with a fibrous skeleton of more than one type of megasclere, stylote, or oxeote) have a wide ecological distribution but are particularly characteristic of deeper waters. Two families, the Cladorhizidae and Chondrocladiidae, are confined to **bathyal,** abyssal, and **hadal** mud bottoms (Sarà & Vacelet, 1973, p. 486, 552). The deepest known occurrences of sponges of any kind are of these families. The Myxillidae and Hymedesmiidae are characteristic of bathyal hard bottoms (Sarà & Vacelet, 1973). The Mycalidae also have abyssal and hadal muddy-bottom representatives (*Abyssocladia*) and are likewise characteristic of bathyal hard bottoms (Sarà & Vacelet, 1973). The Mycalidae also have warm, shallow-water representatives that are often the dominant sponges in their respective environments, such as species of *Mycale* in coral reefs (both on the outer slope and on inner reef flats) (Reiswig, 1973; Sarà & Vacelet, 1973, p. 547) and various species of *Biemna* and *Desmacella* in mangrove swamps. Other shallow-water poecilosclerids that are locally abundant include the Microcionidae (such as *Microciona*) in temperate and tropical waters and especially the Tedaniidae (*Tedania*) in tropical waters (Hay, Wiedenmayer, & Marszalek, 1970). All the shallow-water forms are most abundant on hard bottoms, but *Biemna* may live partially buried in the mud (Sarà & Vacelet, 1973, p. 550). *Crambe* is a strong dominant in the more lighted parts of Mediterranean coastal caves (Sarà & Vacelet, 1973, p. 543).

Hadromerida (=Clavulida) (sponges with spinispires [=spirasters] and tylostyles) have some forms adapted to deep-water mud bottoms, such as the bathyal *Radiella* and abyssal to hadal members of the Polymastiidae (Sarà & Vacelet, 1973, p. 546, 552). The main center of abundance of the Hadromerida, however, is on hard bottoms or shells in shallow water, with a particular tolerance shown to brackish-water **estuarine** conditions, especially by members of the families Clionidae and Suberitidae (Sarà & Vacelet, 1973, p. 558). The Spirastrellidae are especially common in shallow-water lagoons associated with coral reefs (*Speciospongia, Anthosigmella, Spirastrella*) with specialized species found in rough-water environments (*Placospongia*) (Hay, Wiedenmayer, & Marszalek, 1970; Sarà &

Vacelet, 1973, p. 547, 561). The Hadromerida also include all the known boring sponges (Clionidae).

Axinellida (sponges with plumosely arranged styles and no microscleres) are particularly abundant in temperate waters on hard bottoms at moderate to shallow depths (Sarà & Vacelet, 1973, p. 545–546).

Halichondrida (sponges with various monaxonid megascleres, simple raphid microscleres, and a dermal specialization) include some forms particularly abundant on the inner reef flat of coral reefs (*Acanthella*) (Sarà & Vacelet, 1973, p. 547).

The Haplosclerida (sponges with oxeas, usually reticulate skeletons, and no dermal specialization) include the only freshwater sponge families (Spongillidae, Potamolepidae, and Lubomirskiidae) (Sarà & Vacelet, 1973, p. 553, 555). Occurrence of Plio-Pleistocene freshwater forms in central Japan was well documented by Matsuoka (1987), for example. In addition they include forms abundant in shallow-water lagoons associated with coral reefs (*Haliclona, Gellius)* or in strong-current areas on the reefs themselves (*Strongylophora*) (Hay, Wiedenmayer, & Marszalek, 1970; Sarà & Vacelet, 1973, p. 547, 549). *Petrosia* may be very abundant in darker parts of deeper Mediterranean caves (Sarà & Vacelet, 1973, p. 539–540).

The Lithistida as a whole are adapted by their skeletons to rough-water conditions in which they are found on coral reefs, but their main abundance is either in the totally dark parts of subreef caves and tunnels or in deeper parts of forereef slopes below the major zone of abundance of other sponges (Lewis, 1965b; Sarà & Vacelet, 1973, p. 478, 486, 544, 548).

Tetractinellida include a number of groups with characteristic environmental tolerances, on the whole tending toward deep, cold, and unlighted waters. The Theneidae (*Thenea*) are adapted to bathyal, abyssal, and hadal soft bottoms (Sarà & Vacelet, 1973, p. 486, 546, 552). The Tetillidae have a wide distribution but are extremely abundant (*Tetilla, Cinachyra*) in the Antarctic (Sarà & Vacelet, 1973, p. 551) and locally (*Craniella*) in the Arctic (off the North Cape of Norway) (Zenkovitch, 1963, p. 145–146). The Geodiidae (*Geodia*) are also common in Arctic waters, both shallow and deep (Zenkovitch, 1963, p. 145), but are found also in warmer waters and by their special, dense, dermal spiculation of sterrasters are adapted to resist shallow, rough water in general (Sarà & Vacelet, 1973, p. 561). *Geodia* is very abundant in the darkest parts of shallow Mediterranean caves (Sarà & Vacelet, 1973, p. 476). The Chondrillidae (*Chondrilla*) are very common on hard bottoms in shallow, quiet waters associated with coral-reef lagoons (Hay, Wiedenmayer, & Marszalek, 1970). In shallow-water marine caves the tetractinellids tend to occupy the semilighted parts (Sarà & Vacelet, 1973, p. 544).

The Epipolasida are especially common in warm water: in shallow protected lagoons (*Tethya*) or mangrove swamps (*Prostylissa*) (Sarà & Vacelet, 1973, p. 473, 550; Reiswig, 1973, p. 202–203).

Keratosa are another largely warm-water group (Sarà & Vacelet, 1973, p. 473). Their tough resilient skeleton adapts them to rough water (Sarà & Vacelet, 1973, p. 478). They also prefer lighted to unlighted situations, occurring at the light end of marine caves (Sarà & Vacelet, 1973, p. 544).

In shallow lagoons of coral reefs, the genera *Ircinia, Verongia,* and *Spongia* are common (Hay, Wiedenmayer, & Marszalek, 1970), and *Verongia* is also locally abundant on the upper part of the outer reef slope (Reiswig, 1973).

The Sclerospongia are also adapted by their massive skeletons to rough water but are largely confined to totally dark parts of subreef caves and tunnels or to deep but warm waters, as in the Mediterranean (Sarà

& Vacelet, 1973, p. 549–550; Jackson, Goreau, & Hartman, 1971).

The Pharetronida, among the Calcarea, have a distribution similar to the Sclerospongia (Sarà & Vacelet, 1973, p. 549–550). The non-pharetronid Calcarea are almost entirely confined to very shallow water (see chapter on Geographic and Stratigraphic Distribution, p. 276).

The Hexactinellida are dominantly cold- or deep-water forms, some groups being adapted to bathyal, abyssal, and hadal mud bottoms, others to bathyal hard bottoms. They also occur abundantly on shallower hard bottoms in the Antarctic (especially *Rosella*) (Dearborn, 1965) and with greater diversity, if not abundance, in moderately shallow tropical waters of Indonesia (see chapter on Geographic and Stratigraphic Distribution, p. 276). Hexactinellid sponges form reefs in the cold water of Hecate Strait on the continental shelf of British Columbia (Krautter & others, 2001; Conway & others, 2001).

FOSSIL SPONGES

The record of Precambrian sponges is mainly of isolated spicules from China, Iran, and elsewhere (Glaessner, 1962; Brasier, 1992; Steiner & others, 1993) and impressions of what are interpreted to be hexactinellid sponges from the Ediacaran beds of Australia (Gehling & Rigby, 1996). The *Spinther*-like *Dickinsonia* of the Ediacara fauna, if it had the specialized sponge-feeding habits of the living *Spinther,* implies the presence of its prey. By Cambrian times, however, Heteractinida, monaxonid Demospongea, and lyssacine Hexactinellida are well developed, particularly in such black shale facies as the Burgess Shale (Walcott, 1920; Rigby, 1986a), which represent quiet-water environments with much organic detritus. The Archaeocyatha appear in shallow-water limy facies at the very base of the Cambrian, often before the first trilobites. Their systematics and development have been covered in a chapter of the first revision of Part E of the *Treatise on Invertebrate Paleontology* (Hill, 1972, p. 49).

Early and Middle Cambrian true sponges are generally thin-walled, saclike forms, which is apparent both in the completely preserved whole sponges and in isolated spicules that are almost entirely two-dimensional forms such as stauractines, sexiradiates, and oxeas arranged in single layers. Early sponges appear to have been largely low, benthic forms. Tall, thin-walled Lower Cambrian sponges from Anhui Province of China, however, have been interpreted to have been high-tiering organisms (Yuan & others, 2002). By Late Cambrian time thicker-walled sponges appeared, such as *Multivasculatus* with its hexactines and the early lithistids, *Wilbernicyathus* and *Gallatinospongia.* Most of these latter sponges occur in deposits of limy shallow-water facies like that in which undoubted lithistids flourished in Ordovician times. The lithistid type of skeleton seems to have arisen as an adaptation to rough water. Not only do the interlocking zygoses provide rigidity but so does the triangular configuration of dendroclones characteristic of the first lithistids (see Anthaspidellidae), an arrangement that provides maximum resistance to deformation for a skeleton built of rodlike elements. These early lithistids are associated with shelly fossils, reefs, and algae (Toomey, 1970; Finks & Toomey, 1969). The algae provide indisputable evidence of the waters' being shallow and well lighted.

In the Early Ordovician (Canadian) the anthaspidellids are largely alone among the sponges in this environment and by Chazyan time the anthaspidellids were more diversified and were joined by sclerosponges (stromatoporoids) (Bassler, 1941; Raymond & Okulitch, 1940; Finks & Toomey, 1969; Pitcher, 1964; Church, 1974; Kapp, 1975; Wyatt, 1979). In the succeeding Black River two new lithistid groups appeared, the Astylospongiidae and the Hindiidae, as well as the sublithistid Dystactospongiidae, of axinellid or poecilosclerid affinity (Finks, 1967b, 1971a). Some thick-walled hexactinellids (Brachiospongiidae) are also associated with this environment, beginning with the

Trentonian (Beecher, 1889), as are apparently the rarer heteractinids at least as early as the Chazyan (Rigby, 1967a).

Thick-walled heteractinids (Astraeospongiidae) became common in this environment during the Silurian, along with anthaspidellids and astylospongiids in the well-known middle Silurian Gotland and Tennessee faunas (Rauff, 1893, 1894). After the Silurian the Astylospongiidae are known only from Devonian faunas in Australia (Pickett, 1969; Pickett & Rigby, 1983; Rigby, 1986b), but the rest of the elements persisted in the shallow-water sponge fauna until the end of the Paleozoic.

In the later Paleozoic, anthaspidellid lithistids were slowly replaced in abundance and diversity by their relatives and descendants, the Chiastoclonellidae and Anthracosyconidae. Likewise astraeospongiids were replaced by their descendants the wewokellids, and the brachiospongiids by their possible descendants the stiodermatids and docodermatids. The hindiids persisted with less change.

There was a drastic change in shallow-water sponge faunas beginning with the Pennsylvanian. Calcareous sponges, which had appeared in early Paleozoic assemblages (Pickett & Jell, 1983; Webby & Rigby, 1985; Rigby & Potter, 1986), became major elements in mid-Pennsylvanian times, starting in low paleolatitudes in the Tethyan realm (Des Moinesian of Kansas: Finks, 1960, 1970) and dominating shallow-water Permian and Triassic sponge faunas. These are the sphinctozoans and pharetrones. In the Mesozoic these calcareous sponges spread more widely and to higher paleolatitudes. The sphinctozoan-pharetronid association is recognizable at least as late as the Cretaceous Farringdon Sponge Gravel of England.

Rhizomorine lithistids are another important element of Mesozoic shoal-water sponge faunas. These first appear in the fossil record in the Ordovician of Australia (Rigby & Webby, 1988) but became common beginning in Carboniferous times (Visean of Scotland: Hinde, 1887b, 1888).

In addition to the shallow-water sponge fauna associated with algae and shelly facies, the Paleozoic record preserves another sponge facies associated with the quiet, if not necessarily deep, black-shale deposits and similar black limestones. They range in estimated depth from a 1-meter deep in Pennsylvanian coastal lagoon in Indiana (Zangerl & Richardson, 1963) to the 1,800-meter deep in the Permian Delaware basin (Newell & others, 1953; Newell, 1957). Earlier examples include the Cambrian Burgess Shale (Walcott, 1920; Rigby, 1986a) of British Columbia, the Wheeler Shale (Rigby, 1978) and Marjum Formation (Rigby, 1983a) of Utah, and the Ordovician Utica Shale (Walcott, 1879; Ruedemann, 1925) of New York. Thin-walled hexactinellids of the families Protospongiidae and Teganiidae are especially characteristic of the black shales. Thicker-walled relatives belonging to the family Dictyospongiidae are found in more clastic offshore deposits, such as the delta-front sandstones of the Late Devonian phases of the Catskill Delta (the Chemung glass-sponge fauna), and dark limy shales of the Mississippian of Indiana (the Crawfordsville sponge fauna) that formed the chief sources of Hall and Clarke's (1899) monograph.

In the Pennsylvanian, *Stioderma* occurs in shallow-water facies; in the Permian it occurs in both deep and shallow water, as do many lithistids (Finks, 1960). It is possible that the brachiospongiids were facultative occupiers of deeper water at times of greater competition for shallow-water space, such as in the Permian with its proliferation of shallow-water Calcarea. In this they parallel the Permian lithistids; although the lithistids seem to have been sturdier competitors with their principal abundance in shallow water, both within the Texas basin and also outside it, throughout the Cordilleran shelf, and in Arctic Canada and Spitsbergen. In Timor an exclusively lithistid fauna (so far as now known, see Gerth, 1927) of archaic aspect (almost entirely anthaspidellids) is of uncertain facies; the associated fauna of echinoderms and corals (also partly archaic) suggests shallow water. The peculiar nature of this fauna may be a reflection of a high paleolatitude as part of the Australian plate, then much nearer the south pole. (The Permian outcrops are tectonically isolated and need not be part of the same plate or plates as the rest of Timor.) In general the lithistids dominate Permian sponge faunas of high paleolatitudes.

The reef facies is a special development of the shallow-water fauna. Sponges have been an element of reef faunas from Ordovician times up to the present day. Their relative abundance has varied. In general, they were important elements in construction of reefs at times when corals were less prevalent in the world faunas. In Early Ordovician (Canadian) time, reefs were formed of anthaspidellid lithistids and calcareous algae (Toomey, 1970; Rigby, 1971; Church, 1974; Wyatt, 1979). By Chazyan time they were joined by stromatoporoids (sclerosponges), bryozoans, and the first tabulate corals. In the Chazy Group of the Lake Champlain area, the relative abundance of these reef builders varies from one reef mound to its neighbor, at the same horizon, suggesting a competitive relationship among these elements (Pitcher, 1964; Finks & Toomey, 1969; Toomey & Finks, 1969; Kapp, 1975).

In reefs of the Silurian, lithistid sponges were already a distinctly subordinate element, present only in early stages of reef succession (Lowenstam, 1957). Tabulate corals and bryozoans are distinctly dominant in Silurian reefs. By Devonian time, rugose and tabulate corals formed reefs by themselves (Coeymans and Onondaga formations, see Oliver, 1951, 1956) or largely by themselves (Playford & Lowry, 1966; Playford, 1967), although sponges do occur as moderately abundant elements in the reefs of Western Australia (Rigby, 1986b). Stromatoporoids are among the major reef constituents in the Upper Devonian of Alberta (Fischbuch, 1970). After the Devonian, however, stromatoporoids become rare, but bryozoans reappear, forming reefs with algae in the Permian of Germany (Mägdefrau, 1933). In the great Permian reefs of Texas, they are joined by sphinctozoans and pharetronid calcareous sponges (Newell & others, 1953; Newell, 1957; Finks, 1960; Pray & Esteban, 1977; Yurewicz, 1977a, 1977b, Rigby & Senowbari-Daryan, 1996b; Rigby, Senowbari-Daryan, & Liu, 1998). This reappearance of sponges coincides with the noticeable decline of tabulate and rugose corals, which became, respectively, nearly and totally extinct by the end of the Permian. The scleractinian corals that replaced them as dominant reef builders in Mesozoic and later times did not appear until the mid-Triassic and did not enter significantly into reefs until the upper successional stages of Upper Triassic reefs in the Alps (Sieber, 1937; Flügel, 1981; Schäfer & Senowbari-Daryan, 1981; Senowbari-Daryan, Schäfer, & Abate, 1982; Flügel & Stanley, 1984; Reid & Ginsburg, 1986). Most earlier Triassic reefs, as well as Late Triassic Tethyan-type reefs on the southern Yukon in North America (Senowbari-Daryan & Reid, 1987), are built by a sphinctozoan-pharetronid sponge fauna almost identical to that of the Permian reefs. The cryptostome bryozoan and specialized strophomenid brachiopod elements present in Permian reefs, however, have become extinct; they were replaced by hydrozoan and possible sclerosponge (spongiomorph) elements. Calcareous algae were still important.

An ecologic succession in the Upper Triassic reefs was worked out by Sieber (1937) and included in a paper that deserves to be better known, for it seems to be the first paper in which ecologic succession was documented from the fossil record. This succession predicts strikingly the future development of Mesozoic reef faunas. Examination of succession in Silurian reefs (Lowenstam, 1957; Nicol, 1962) and Ordovician reefs (Toomey & Finks, 1969; Church, 1974; Wyatt, 1979) shows a similar predictive power. This can be understood if the assumption is made that the relative competitive relationships between organisms is the principal determinant of ecologic succession rather than a change in water depth as is often assumed. A documented reef succession at a moment in time can then be used as an experimental text of relative competitive relationships between these organisms at that juncture in the history of the earth.

Alpine Upper Triassic reefs began as patches of crinoids on a seabed bearing an epifaunal pelecypod interreef fauna. These crinoid-rich areas provided a harder substrate suitable for the attachment of the sphinctozoan and pharetronid calcisponges that built much of the rest of the reef mass. Toward the top of the reef mound, scleractinian corals appear, increasing in abundance relative to the sponges and ultimately almost crowding them out completely. According to SIEBER (1937) this process was repeated in each reef mound at more than one level. Such a succession has also been documented for Permian reefs in China (FAN, RIGBY, & QI, 1990).

In Ordovician reefs of the Chazy Group (PITCHER, 1964; FINKS & TOOMEY, 1969; TOOMEY & FINKS, 1969; CHURCH, 1974) lithistid sponges are replaced upward in most reef mounds by either stromatoporoids or tabulate corals (*Eofletcheria, Billingsaria*), which are the two groups that dominate the subsequent Silurian reefs. Likewise, in the Silurian reefs of the Niagaran beds (LOWENSTAM, 1957; NICOL, 1962) lithistids are minor elements that appear very early in the succession and die out upward, while stromatoporoids, tabulates, and rugose corals attain their greatest abundance at the top of the reef. It is precisely these three groups that dominate reef structures in the succeeding Devonian (OLIVER, 1956; FISCHBUCH, 1970; PLAYFORD, 1967).

Ecologic succession in Jurassic reefs has been best documented from the Oxfordian of Germany (GWINNER, 1958, 1968, 1976; GAILLARD, 1983). In these reefs, pharetronid sponges are still an important element; sphinctozoans, which became extinct in the Cretaceous, are less so. Nevertheless, they are subordinate to scleractinians from the reef beginning and become less abundant in higher parts of the reef. Sponges are particularly characteristic of the reef-flank fauna.

In the Upper Jurassic of Germany there are also reeflike structures built of siliceous sponges, principally hexactinellids (ROLL, 1934). This was, thus, the second time since the Ordovician that siliceous sponges formed moundlike masses, for Triassic sponge mounds have been described recently from China in the Sichuan Province (WU & ZHANG, 1982). These mounds have been interpreted as deep-water structures formed by sponges that trapped mud moved along the sea floor; thus they are a different sort of community from the shallow-water coral reef and are analogous to the deep-water coral banks described by TEICHERT (1958).

The coral reef community, as it is known today, with scleractinians and hydrozoans as the dominant frame builders with calcareous algae as binders, was already present by Cretaceous time. As far as sponges go, sphinctozoans died out gradually during the Cretaceous (FINKS, 1967b) and likewise diminished in the reefs. The pharetronids were still more abundant in Cretaceous coral reefs than in present ones. Although the Cretaceous was the period of acme for pharetronids, lithistids, and hexactinellids in the world history of sponges, nevertheless, the pharetronids were not as abundant in coral reefs of the Cretaceous as in the non-reef environments. By Holocene time, pharetronids and the sclerosponges became minor constituents of coral reefs and are largely confined to caves and passages under reefs (JACKSON, GOREAU, & HARTMAN, 1971; SARÀ & VACELET, 1973), where they may be locally abundant.

Although many non-lithistid demosponges are abundant in the vicinity of present-day reefs, they are most numerous away from the reef, either in back-reef lagoons or on fore-reef slopes (e.g., REISWIG, 1973). Lithistids tend to attain maximum abundance in deeper waters of the fore-reef slope. LEWIS (1965b) studied the ecology of the deeper water adjacent to coral reefs of Barbados and recognized a sponge-coral community between 50 and 150 meters depth, just below the active coral reef. He also recognized a coelenterate-mollusc-echinoderm community between 100 and 300 meters depth, where massive, upright lithistids replace the branching and encrusting non-lithistids of the higher sponge-coral zone. A corresponding concentration of lithistids was noted in deeper waters adjacent to the calcareous-sponge reefs of the Texas Permian (FINKS, 1960). For a discussion of possible origins of deep-sea and hadal sponge faunas, which may postdate the Cretaceous, see the chapter on Geographic and Stratigraphic Distribution (p. 275).

Where sponges are very abundant and conditions are favorable for their preservation, sedimentary deposits consisting almost entirely of sponge spicules may form. Such **spiculites** seem to be formed from spicules of siliceous sponges. They may be cemented with silica probably remobilized from the spicules themselves to form bedded chert, but they are also known with calcareous or argillaceous matrix. Spiculites are known in the fossil record from the Lower Cambrian. They have almost certainly formed in more than one environment and must be interpreted in terms of abundance of sponges rather than a particular environment. They are forming today on the coast of Antarctica at depths between 50 and 400 meters (DEARBORN, 1965). Spiculites in the basin facies of the Texas Permian may have accumulated in water as deep as 1,800 meters (NEWELL & others, 1953; NEWELL, 1957). On the other hand, some appear to have formed in shallow, nearshore environments, such as the chert of the Permian Phosphoria Formation (YOCHELSON, 1968) that intertongues with nearshore sandstone and shoal-water carbonates. A particularly instructive example was reported by CAVAROC and FERM (1968) from the Pennsylvanian of West Virginia and adjacent states. Spiculitic cherts, such as the Kanawha Flint, pass laterally within 5 to 10 miles into seat-earth and coal beds across an intermediate belt of brachiopod-bearing siltstone and shale. CAVAROC and FERM noted an absence of such spiculites where a wide belt of brackish-water beds separates the coal from normal marine faunas and concluded that the sponges were abundant where normal-marine waters closely approached the shoreline. They suggested that abundant silica from the weathering of the seat-earth provided a favorable environment for siliceous sponges. Abundant organic detritus from the coal-swamp, however, is also a likely cause of sponge proliferation.

SILICA AND SPONGE ECOLOGY

For such planktonic organisms with siliceous skeletons as radiolaria and diatoms, silica is a limiting element because surface waters of the oceans are almost totally depleted in dissolved silica through the activities of these organisms (BROECKER, 1974, p. 7). Siliceous sponges, which are the only benthic silica-secreting organisms of any importance, are not so limited because the rain of planktonic skeletal silica, as well as terrigenous silica in sediments, keeps bottom waters well supplied. Nevertheless, all ocean water is strongly undersaturated in silica (BROECKER, 1974, p. 33), and lateral variation in dissolved silica may have an effect on distribution of sponges. In the present deep sea, silica content of bottom water increases from the Atlantic to the Antarctic to the Indian to the Pacific Oceans, so that the Pacific bottom water has five times the silica concentration of the North Atlantic bottom water, as a consequence of bottom water circulation proceeding in this direction (BROECKER, 1974, p. 23). It is of interest to note that Monaxonida dominate the Atlantic deep-sea sponge fauna, the Lyssacinosa that of the Antarctic, and Hexactinosa-Lychniscosa that of the Pacific (see chapter on Geographic and Stratigraphic Distribution, p. 275). If their distribution is controlled by dissolved silica concentration, the fact that the Monaxonida reached an early peak in the Ordovician (Dystactospongiidae, Anthaspidellidae), the Lyssacinosa-Reticulosa somewhat later in the Devonian to Permian, and the Hexactinosa-Lychniscosa not appearing until the Triassic and peaking in the Cretaceous suggests a possible progressive increase in dissolved silica of the oceans. Inasmuch as the Cretaceous diversity peak of the Hexactinosa-Lychniscosa was greater than their present diversity, a post-Cretaceous decrease in dissolved silica is also suggested. Obviously other explanations are possible.

INFAUNAL SPONGES

Sponges are predominantly epifaunal organisms. Nevertheless, a substantial number of species live almost completely buried in loose sediment or in hard substrates. Those living in hard substrates include not only the well-known boring sponges but also those that occupy borings made by other organisms, including other sponges. Those living in soft sediment are less well known but are of particular interest to the paleontologist because it may be difficult to differentiate such a sponge from a spicule-filled burrow or from a concretion when encountered in the rock. Similar problems may be caused by the many epifaunal sponges that incorporate substantial quantities of sediment in their bodies.

Living sponges that characteristically grow buried in sand include species of the poecilosclerid genera *Biemna, Pellina, Siphonodictyon,* and *Ichnodonax* and the hadromerid genus *Anthosigmella* (DE LAUBENFELS, 1936, p. 66; 1954, p. 112, 167, 201; RÜTZLER, 1974, p. 13; WIEDENMEYER, 1974). The buried part of the sponge is either a ramifying, rhizomelike mass (*Anthosigmella, Ichonodonax*) or a massive, cakelike structure (*Biemna, Pellina, Siphonodictyon*), with oscular chimneys that rise from buried parts to the sediment surface. All the above are known from coral sand in shallow water; sometimes the sand is mixed with organic-rich mud, often near mangroves. Sand may be incorporated in the base of some of these sponges (*Anthosigmella, Biemna*) (RÜTZLER, 1974, p. 13).

Fossil sponges with similar habits are less easy to recognize. A species of a pharetronid calcisponge *Virgola* from the Permian of Texas was buried at least partially in shelly sand during life. The lower parts of the ramifying mass incorporated shell hash continuous with that of the surrounding matrix, as is clearly shown when the silicified matrix and sponge were etched from limestone.

Boring sponges, which live infaunally in excavations of their own making in solid calcium carbonate substrates such as shells, coral skeletons, and lithified limestone, are known in both fossil and recent examples. They are an important cause of erosion of living coral reefs. (In this discussion, the term boring is used for sponges that excavate solid substrates, and the term burrowing for those that displace unconsolidated substrates. The term **interstitial** may be used for those that occupy only **interstices** between grains of unconsolidated sediments; these are also known as cementing sponges (RÜTZLER, 1965a). In addition to the living genera *Cliona* and *Cliothosa,* RÜTZLER (1973) has shown that the living poecilosclerid (adociid) *Siphonodictdyon* and the hadromerids (spirastrellids) *Anthosigmella* and *Spheciospongia* also bore by the same process. Besides those known definitely to bore, the tetraxonid *Samus* occupies or shares borings presumed to have been produced by another sponge (DE LAUBENFELS, 1954, p. 132).

Borings of *Cliona* have a ramifying, anastomosing pattern of tubular galleries of small diameter and more or less uniform spacing; often small, globular spaces are connected by finer tubules. Frequent openings to the surface are present. Some fossil examples have been referred to the genus *Entobia* PORTLOCK, 1843, understood as applying to borings rather than to the organism that produced them (Bromley, 1970). The record of such borings goes back to the Lower Cambrian (Kobluk, 1981a) and Ordovician (Kobluk, 1981b) where carbonate chips associated with borings have the distinctive scalloped surfaces of clionid-produced debris. The Devonian *Clionoides* and similar Paleozoic branching borings in shells are less likely to have been produced by sponges. The characteristically concavely chipped inner surface of borings produced by sponges is visible with scanning electron microscope and offers a possible means of identifying fossil sponge borings. The chips themselves form an appreciable component of the sediment in the vicinity of boring sponges. They may be identified by their characteristic shape when isolated but recognizing them may not be possible in lithified sediment. Their sizes range from 15 to 94 µm (Rützler & Rieger, 1973, p. 159). Presence of tylostyles or spinispires in a fossil boring is strong although not conclusive evidence of their production by sponges but would not identify them as those of *Cliona* because other hadromerids also bore. It is of interest to note that most of the sponges that live buried in sand belong to families that include the non-clionid boring sponges (Adociidae, Spirastrellidae). It is apparent that the boring habit is related to a general infaunal adaptation and that either burrowing led to boring or vice versa. Many of the infaunal sponges live in the intertidal zone and are thereby enabled to support exposure at low tide (Sarà & Vacelet, 1973, p. 487).

An interstitial habit is related to the burrowing habit in soft substrates and occurs where the sponge occupies and completely fills interspaces between clastic grains. This habit, in turn, grades into the condition in which the sponge incorporates sediment into its body while remaining above the sediment surface. The two modes of life are difficult to separate in a fossil. Interstitial sponges cement and at least temporarily stabilize loose clastic sediments. Living interstitial sponges include species of the keratose genus *Ircinia,* the poecilosclerids *Hiattrochota* and *Tedania,* and the tetraxonid *Geodia* (de Laubenfels, 1954, p. 124, 127–129; Rützler, 1965a, p. 291).

SPONGES INCORPORATING SAND IN THEIR BODIES

Foreign material in a sponge may be of accidental origin, but in a large number of genera the presence of foreign material and its localization in the sponge seems characteristic of the taxon. Most species of Keratosa incorporate sand in their spongin fibers, frequently only in the larger ascending fibers (in the Dictyoceratida). In addition, many species have the entire ectosome or cortex more or less heavily charged with sand; this is particularly characteristic of the genus *Phyllospongia,* but it occurs in many other genera of the Spongiidae. Other keratose genera have the whole endosome more or less filled with grains and clumps of sand, sometimes to the point where protoplasm of the sponge seems like a cement for the sand. The genus *Dysidea* is particularly characterized by large amounts of sand, a circumstance that does not prevent the sponge from assuming a characteristic external shape. In all these instances, spicules of other sponges, often broken, may be included with the inorganic and other bioclastic debris. Spicules and debris may be both siliceous and calcareous.

The Keratosa may be thought of as using sand in place of spicules, but in other demosponges with proper spicules, sand may also occur in large quantities. In the Haplosclerida sand may be incorporated in spicule tracts of some species (e.g., species of *Callyspongia, Iotrochota*) or in the ectosome (*Desmopsamma*). The Poecilosclerida may include many species that incorporate sand, usually in the endosome. One group, sometimes united in the family Psammascidae de Laubenfels, comprises species in which the great bulk of the body is made of sand, along with the sponge's own spicules. Some species of Hadromerida incorporate notable quantities of sand; they belong to the families Suberitidae and Spirastrellidae. Table 6 lists notable recent genera that include sand-bearing species.

Occasional foreign bodies are as common in fossil sponges as in Holocene ones. More thoroughgoing studies of incorporation of sand into fossil sponges have not been published (Table 6).

PREDATION ON SPONGES

Although sponges have comparatively few predators, a considerable number of animals are specialized predators on them, and many others of more generalized feeding habits include sponges in their diets. Among the specialized predators of sponges, the aberrant polychaete annelid *Spinther* is of interest because of its resemblance to the late Precambrian organism *Dickinsonia.* Many species of *Spinther* have the color of the sponge species on which they feed and live (MacGinitie & MacGinitie, 1968). The related and equally aberrant *Euphrosyne* is also specialized for living and feeding on sponges (Ushakov, 1955). Species of *Haplosyllis* and *Typosyllis* are parasitic inquilines of sponges, especially dictyoceratid Keratosa (Reiswig, 1973; Ushakov, 1955) as are some eunicids (Ushakov, 1955). In addition, suspension-feeding spionids have been reported to be opportunistic feeders on the larvae of *Microciona* and *Ophilitaspongia* (Bergquist & Sinclair, 1968).

Among the gastropods, many species of dorid nudibranchs are specialized feeders on particular species of demosponges, which they mimic in color, while others, somewhat less specialized, bestow their attentions on more than one type of sponge (see Table 7 for details).

Among the echinoderms, a number of asteroids are specialized or occasional predators of sponges (see Table 7): *Henricia sanquinolenta* and *Echinaster sepositus* are specialized predators of sponges and prefer species of *Mycale, Ficulina,* and *Hymeniacidon* (Vasserot, 1961). Reiswig (1973) reported that the echinoids *Eucidaris tribuloidea, Lytechinus variegatus,* and *Tripneustes ventricosus* are major predators on *Tethya crypta* in Jamaica.

Among the arthropods, the larvae of the neuropteran fly *Sisyra* and one stage in the life cycle of the mite *Unionicola* are specialized feeders on freshwater sponges (Sarà & Vacelet, 1973). The decapod crustacean *Typton spongicola* appears to be a parasitic inquiline of sponges (Hunt, 1925; Balss, 1927).

Several species of the bony fish *Pomacanthus, Holacanthus, Cantherhines, Acanthostracion,* and *Chaetodipterus* seem to subsist largely on various demosponges, while other genera and species feed more occasionally on sponges (Bakus, 1964; Randall & Hartman, 1968; Sarà & Vacelet, 1973; Wulff, 1994). The hawksbill turtle, *Eretmochelys imbricata,* is also known to be an active sponge browser (Meylan, 1990).

In general, specialized predators of sponges seem to belong to small, restricted groups in various phyla, and it must be admitted that many of them, such as the nudibranchs and pomacanthid fish, are of late origin, despite the possible Precambrian existence of spintherids.

OTHER ORGANISMS IN SPONGES

Living sponges normally play host to a great number of epibiotic and endobiotic commensals. In some instances the relationship is a regular association. When the sponge and a sessile commensal modify one another's growth, the association provides a powerful tool for determining the constituent elements of the local organism community among fossils. Cross associations among species from a single locality can yield a substantial list of coexisting species (16 genera of 5 phyla from one Permian locality, Finks, 1960, p. 30).

So many organisms are associated with sponges that a list would include most of the phyla of animals. Only a few will be mentioned here. Annelids and crustacea are

TABLE 6. Sand-bearing sponges and sponges submerged in sand (new).

TAXON	LOCATION OF SAND	REFERENCE
KERATOSA		
Aplysilla	whole sponge	de Laubenfels, 1954
Aulena	ectosome	de Laubenfels, 1954
Cacospongia	fibers	de Laubenfels 1954; Vacelet & Vasseur, 1971b
Druinella	fibers	de Laubenfels, 1954
Dysidea	fibers, endosome, ectosome	de Laubenfels, 1936, 1954; Hechtel, 1965
Euryspongia	fibers, ectosome	de Laubenfels, 1954
Heteronema	fibers	de Laubenfels, 1954
Hippiospongia	fibers, ectosome	de Laubenfels, 1954
Hircinia	fibers, ectosome	de Laubenfels, 1954
Ianthella	endosome	de Laubenfels, 1954
Ircinia	fibers, ectosome	de Laubenfels, 1954
Oligieras	fibers, ectosome, endosome	de Laubenfels, 1954
Phyllospongia	fibers, ectosome	de Laubenfels, 1954; Vacelet & Vasseur, 1971b
Polyfibrospongia	fibers	de Laubenfels, 1954
Spongia	fibers	de Laubenfels, 1954
Thorectopsamma	fibers, ectosome	de Laubenfels, 1954
Trypespongia	ectosome	de Laubenfels, 1954
HAPLOSCLERIDA		
Callyspongia	ectosome of cloaca	de Laubenfels, 1936, 1954
Desmapsamma	ectosome	de Laubenfels, 1954; Hechtel, 1965
Fibula	buried in sand	de Laubenfels, 1936
Iotrochota	fibers	de Laubenfels, 1954
Protphlitaspongia	ectosome	de Laubenfels, 1954
Rhizochalina	ectosome	de Laubenfels, 1954; Vacelet & Vasseur, 1971b
POECILOSCLERIDA		
Biemna	sand in base, sponge buried	Rützler, 1974
Clathriopsamma	endosome	de Laubenfels, 1954; Vacelet & Vasseur, 1971b
Didiscus	choanosome	de Laubenfels, 1954; Vacelet & Vasseur, 1971b
Hiattrochota	interstitial	de Laubenfels, 1954
Holopsamma	whole sponge	de Laubenfels, 1936
Ichnodonax	no sand in sponge, although buried	de Laubenfels, 1954
Iotrochopsamma	whole sponge	de Laubenfels, 1954
Lissodendroyx	endosome	de Laubenfels, 1954
Meriamium	endosome, tracts	de Laubenfels, 1936
Mycale	endosome	de Laubenfels, 1954
Myrmekioderma	ectosome	de Laubenfels, 1954
Pellina	endosome	de Laubenfels, 1936
Psammascus	whole sponge, especially ectosome	de Laubenfels, 1936, 1954
Psammolchela		de Laubenfels, 1936
Psammodoryx		de Laubenfels, 1936
Psammopemma		de Laubenfels, 1936
Psammotoxa		de Laubenfels, 1936
Stylotrichophora	tracts	de Laubenfels, 1954
Tedania	interstitial	de Laubenfels, 1954
Siphonodictyon	bores in coral skeleton or buries in sand	Rützler, 1974; Vacelet & Vasseur, 1971b
Tedaniopsamma	choanosome	de Laubenfels, 1954
Thalysias	ectosome	de Laubenfels, 1954
HALICHONDRIDA		
Raphisia	endosome?, whole sponge?	de Laubenfels, 1954
HADROMERIDA		
Aaplos	endosome	de Laubenfels, 1954
Anthosigmella	sand in base, sponge buried	Rützler, 1974
Cliona	bores in shells, corals, and limestone	de Laubenfels, 1936
Laxosuberites	ectosome	de Laubenfels, 1954; Vacelet & Vasseur, 1971b
Spheciospongia	sand in pits on surface	de Laubenfels, 1936
Spirastella	whole sponge, interstitial	de Laubenfels, 1936, 1954
Terpios	endosome	de Laubenfels, 1954
CARNOSA		
Samus	lives in *Cliona* borings	de Laubenfels, 1936

frequent endobionts. Many crabs of the superfamily Oxrhyncha invest themselves with living sponges, along with other benthonic organisms, presumably as camouflage (MacGinitie & MacGinitie, 1968). More specific is the association between hermit crabs (Paguridae) and species of *Suberites.* The sponge overgrows the gastropod shell in which the crab lives, extending beyond it and providing the growing crab with an ever-expanding home. The original shell apparently dissolves, leaving an external mold within the sponge.

Another specific association is that of the thin-shelled oyster *Ostrea permollis* that occurs only within the sponge *Steletta grubii* (Forbes, 1964). The oyster has a direct inhalant opening to the surface of the sponge but makes use of the sponge's exhalant system for its own exhalant stream. Several species of the scallop *Chlamys* are regularly coated with specific sponges. *Chlamys hericius* and *C. hindsii* of the Puget Sound area are coated on their upper valves with *Myxilla parasitica* or *Mycale adhaerens* (MacGinitie & MacGinitie, 1968). The sponges apparently occur preferentially or exclusively on this substrate. In New Zealand, *Chlamys diefenbachi* develops spines only when encrusted by a sponge (unidentified), which is its most common condition (Beu, 1965). The *Chlamys* is completely enclosed by the sponge. Terebratuloid brachiopods have also been found coated with sponges during life (G. A. Cooper, personal communication, 1955).

Among the coelenterates, the scyphozoan *Stephanoscyphus* goes through one state of its life cycle embedded in various sponges (Sarà & Vacelet, 1973). If the conulariids are scyphozoans, this association may have considerable antiquity, for Permian conulariids have been found embedded in several species of lithistid and calcareous sponges (Finks, 1955, 1960). The hydroid *Dupurena halterata* lives imbedded in suberitids (Sarà & Vacelet, 1973).

Other probable commensal associations known from both living and fossil sponges include ophiuroids from as far back as the Devonian (Clarke, 1912, 1921) and pleurotomarian archaeogastropods from as far back as the Pennsylvanian (Batten, 1958; Finks, 1960), both occurring in the cloacae of various large sponges.

Many microorganisms inhabit living sponges, but it is not always possible to tell whether they are commensal, symbiotic, or parasitic. There are four groups, however, where a symbiotic relationship seems likely. These are zoochlorellae (unicellular Chlorophyceae) in freshwater spongillids; zooxanthelae (unicellular Chrysophyta) in some marine demosponges; cyanophyta in other marine demosponges; and bacteria in both demosponges and calcisponges (Sarà & Vacelet, 1973). The symbioses with prokaryotes are of particular interest.

Sponges are the only metazoans that have a symbiosis with blue-green algae. Likewise, the extent to which symbiotic bacteria participate in the bulk of some sponges has no parallel among other organisms. The established great antiquity of prokaryotes suggests the possibility of great antiquity of the sponges and of the symbioses between them.

The symbiotic bacteria (*Pseudomonas* sp. and *Aeromonas* sp.) of the keratose sponge *Verongia cavernicola* regularly constitute 38 percent of the tissue volume of the individual sponge. By comparison, cells of the sponge constitute only 21 percent, the remainder (41 percent) being intercellular substance (mesogloea) (Sarà & Vacelet, 1973). Although the same species of bacteria are capable of living outside the sponge, they have special morphological features when they are within the sponge (thicker cell walls); and when the sponge dies, the bacteria also die. The sponge appears to crop constantly its population of bacteria by -**phagocytosis,** using them as a food source and maintaining constant population density. This confirms the symbiotic nature of the association (Sarà & Vacelet, 1973). The same authors noted that similar large symbiotic bacteria populations occur in many other demosponges, not only among Keratosa but also in tetractinellids. It also

TABLE 7. Predators, their degree of specialization, and sponge taxa with which they interact (new).

PREDATOR	SPONGE	DEGREE OF SPECIALIZATION	REFERENCE
Mollusca, Gastropoda, Opisthobranchia			
Doris sp.	*Halichondrida panacea*	specialist (mimics color of sponge)	Sarà & Vacelet, 1973
Rosanna rubicund	*Microciona coccinea* *Ophilitaspongia soriata* *Holoplocamium neozelanicum*	specialist	Ayling, 1968
Rosanna pulchra	orange-red sponge	specialist (mimics color of sponge)	MacGinitie & MacGinitie, 1968
Peltodoris atromaculata	*Petrosia ficiformis*	specialist	MacGinitie & MacGinitie, 1968
Tylodina fungina	*Verongia thiona*	major predator	MacGinitie & MacGinitie, 1968
Tylodina perversa	*Verongia aerophoba*	specialist (mimics color of sponge)	Sarà & Vacelet, 1973
Glossodoris tricolor	*Cacospongia scalaris*	specialist	Sarà & Vacelet, 1973
Archidoris stellifera	*Stylotella*	specialist	Morton, 1967
Archidoris pseudoargus	*Halichondrida*	specialist	Morton, 1967
Archidoris britannica	various demosponges	specialist on demosponges but not a particular species	Sarà & Vacelet, 1973
Prosobranchia			
Lamellaria orbiculata	*Lissodendoryx noxiosa*	major predator	MacGinitie & MacGinitie, 1968
Fissurellidae, including			
Emarginula conica, E. crassa, E. reticulata	sponges, especially monaxonida	specialist	Graham, 1971; Fretter & Graham, 1976a
Puncturella noachina	sponges	specialist	Graham, 1971
Diodora apertura	sponges, especially *Halichondrida* and *Hymeniacidon*	specialist	Fretter & Graham, 1976a
Cerithiopsis tubercularis	*Halichondrida, Hymeniacideon, Grantia*	specialist	Fretter & Graham, 1976a
Triphora perversa	*Halicondria, Hymeniacidon*	specialist	Fretter & Graham, 1976a
Drupe ricina	sponges and holothurians	nonspecialist	Wu S. K., 1965
Patella	various sponges	occasional nonspecialist	Sarà & Vacelet, 1973
Theodoxus	green protophytes; sponges	nonspecialist	Fretter & Graham, 1976a
Littorina	various sponges	occasional nonspecialist	Sarà & Vacelet, 1973
Cypraea friendi, C. venusta, C. marginata Citeres, C. cervus	sponges	specialist	Wilson & Gillette, 1971; Taylor & Wells, 1975
Polyplacophora			
Placiphorella velata	various sponges	occasional nonspecialist	MacGinitie & MacGinitie, 1968
chitons	various sponges	occasional nonspecialist	MacGinitie & MacGinitie, 1968; Sarà & Vacelet, 1973

Annelida, Polychaeta			
Haplosyllis spongicola	*Verongia gigantea* and other dictyoceratids	parasitic inquiline	Reiswig, 1973; Ushakov, 1955
Typosyllis sclerolaema	sponges	parasitic inquiline	Ushakov, 1955
a polychaete	*Ianthella ardia*	?	Sarà & Vacelet, 1973
spionid polychaetes	larvae of *Microciona* and *Ophilitaspongia*	occasional but temporary major predator (suspension feeder)	Bergquist & Sinclair, 1968
Spinther citrinus	yellow sponges	specialist (mimics color of sponge)	MacGinitie & MacGinitie, 1968
Spinther spp. (all spp.)	sponges	specialist	Ushakov, 1955
Euphrosyne spp.	sponges	feeds mainly on sponges (parasitic inquiline)	Ushakov, 1955
some Eunisids	sponges	parasitic inquiline	Ushakov, 1955
Arthropoda, Crustacea, Decapoda			
Typton spongicola	?	specialist? (parasitic inquiline)	Hunt, 1925; Balss, 1927 (*fide* Sarà & Vacelet, 1973)
Cammarus	spongillids	occasional?	Sarà & Vacelet, 1973
deep water Mediterranean prawns	sponges	occasional	Sarà & Vacelet, 1973
Copepoda			
copepods	sponges	?	Sarà & Vacelet, 1973
Insecta, Neuroptera			
Sisyra larvae	spongillids	specialist (major predator)	Killian, 1964 (*fide* Reiswig, 1973); Sara & Vacelet, 1973
Arachnida, Acarina			
Unionicola	spongillids	specialist (part of life cycle)	Sarà & Vacelet, 1973
Echinodermata, Asteroidea			
4 spp. of asteroids	Antarctic sponges *Rosella* and other lyssacines	major predator	Dayton, Robilliard, & Paiune, 1970; *fide* Reiswig, 1973; Sarà & Vacelet, 1973
Asterina gibbosa	sponges	major predator	MacGinitie & MacGinitie, 1968
Patiria miniata	*Myxilla noxiosa*	occasional	MacGinitie & MacGinitie, 1968
Henricia sanguinolenta	*Mycale, Ficulina, Hymeniacidon*	specialist	MacGinitie & MacGinitie, 1968; Vasserot, 1961 (*fide* Sarà & Vacelet, 1973)
Echinaster sepositus	*Mycale, Ficulina, Hymeniacidon*	specialist	MacGinitie & MacGinitie, 1968; Vasserot, 1961 (*fide* Sarà & Vacelet, 1973)
Pteraster tessellatus	sponges	occasional	MacGinitie & MacGinitie, 1968
Echinoidea			
Eucidaris tribuloides	*Tethya crypta*	major predator	Reiswig, 1973
Lytechinus variegatus	*Tethya crypta*	major predator	Reiswig, 1973
Tripneustes ventricosus	*Tethya crypta*	major predator	Reiswig, 1973

occurs among Calcarea (*Leuconia* and *Clathrina*), although the bacteria are of a different type (spiral form).

Symbiotic cyanophytes are also widespread among sponges, sometimes lending their blue-green color to the sponge. As with the bacteria, the algae are phagocytosed by the sponge (Sarà & Vacelet, 1973). Multicellular algae also occur in symbiotic association with sponges. Some Keratosa use the algal filaments as partial or total replacement for their own skeletal fibers (Sarà & Vacelet, 1973), for example the alga *Jania* in the sponge *Dysidea fragilis. Gellius cymiformis* is so intertwined with its algal symbiont *Ceratodictyon spongiosum* that the form of the ensemble is controlled by the alga (Sarà & Vacelet, 1973). It would seem likely that such associations with macroscopic algae would be recognizable in the fossil record, although I do not know of any such that have been reported.

SUBSTRATE

It is widely stated in various ecologic discussions that many sponge species are confined to particular substrates. This is obviously of great paleoecological interest. Unfortunately, the species are rarely identified, and it is not possible to make useful generalizations.

LIGHT

Many sponge species require light for symbiotic algae or for other clearly understood reasons. Sarà and Vacelet (1973) summarized much information on the distribution of sponges in marine caves, where light intensity seems to be a principal control. The living sclerosponges, as well as many pharetronids and lithistids, are more abundant in the totally dark parts of such caves than elsewhere. It has been speculated that lack of competition from the light-requiring and faster-growing reef corals and comparable sessile benthos are the chief reasons for the limitations of these sponges in dark environments.

SALINITY

The vast majority of sponges require full marine salinity for survival. Nevertheless, some monaxonid demosponges are adapted to brackish or fresh water. The Spongillidae and Potamolepidae are specialized freshwater dwellers. Some species of clionids (Clavulina: Hadromerida) and some other marine monaxonids are tolerant of estuarine conditions (Hartman, 1958b).

TEMPERATURE

Some taxonomic groups of varying levels in the hierarchy are confined to warmer waters, such as the Keratosa. Information on higher categories is summarized in the chapter on Geographic and Stratigraphic Distribution (p. 275), but for genera and species few useful generalizations can be made. Many genera and certainly higher taxa have an extremely wide range of temperature tolerance, although individual species are probably restricted more narrowly.

EVOLUTION AND ECOLOGIC HISTORY OF SPONGES DURING PALEOZOIC TIMES

Robert M. Finks

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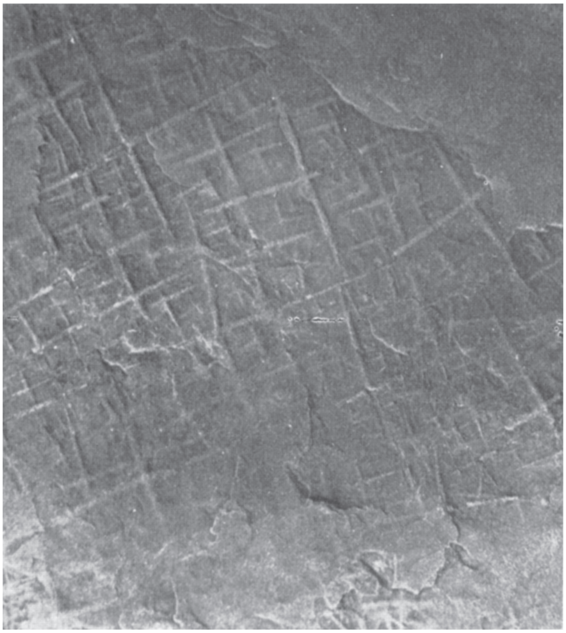
The best sample of earliest sponge faunas is that of the Middle Cambrian Burgess Shale of western Canada, although it is not the earliest record of sponges. Impressions of what are interpreted as hexactinellid sponges have been reported from the Neoproterozoic Ediacaran beds of Australia (Gehling & Rigby, 1996). Isolated spicules have been reported from probably equivalent beds from the Yangtze Gorge area of China (Steiner & others, 1993); hexactines and monaxons have been reported from the Neoproterozoic of India by Tiwari, Pant, and Tewari (2000); and monaxons have been described from late Precambrian rocks from northern Iran (Brasier, 1992). The earliest known body fossils of Early Cambrian sponges are those described by Steiner and others (1993) from the lowermost Cambrian Niutitang Formation in northern Hunan Province, China. No major types have been recovered from Precambrian or Lower Cambrian strata that are not also represented in the Burgess Shale. Three major classes of the phylum Porifera were already present in the Early Cambrian: the Hexactinellida, Heteractinida, and Demospongea (Rigby, 1986a, 1987b).

The hexactinellids (*Protospongia*) and at least some of the heteractinids (*Eiffelia*) and demosponges (*Leptomitus*) of the Burgess Shale (Walcott, 1920) are extremely thinly walled, saclike sponges in which the spicules form essentially a single layer (Fig. 109). Rays of principal spicules are paratangential to the body wall of the sponge. Such a skeleton could not have supported a thick-walled sponge, and among the hexactinellids, there would have been no mesogloea for support either. Thus, these early hexactinellids of the *Protospongia* type may have had an asconoid structure, a possibility strengthened by the fact that embryos of living hexactinellids are asconoid and have a monolayered spiculation of stauractines like that of *Protospongia.* Although the earliest hexactinellids may have been asconoid, they are nearly all thick walled and presumably leuconoid from the Ordovician onward.

All Early Cambrian hexactinellids are of the *Protospongia* type, or consist of isolated stauractines. The first hexactines, implying a thicker body wall, appear in the Middle Cambrian, although it was not until the discovery of the Late Cambrian *Multivasculatus* that a coherent skeleton of hexactines was known as a fossil (Fig. 110). If the earliest hexactinellids were asconoid, it took about a third of Cambrian time, say 30 million years, to develop a leuconoid hydraulic system. Among the hexactinellids, possible asconoid *Protospongia* type forms persisted into the Ordovician, where they are found in black-shale facies.

The earliest demosponges from Lower Cambrian rocks in Vermont and Pennsylvania and from the Middle Cambrian Burgess Shale are thin-walled, tubular forms but obviously thick enough to have been of leuconoid architecture. In view of the fact that living demosponge embryos develop a leuconoid canal system directly, members of this class may never have had asconoid or syconoid forms.

Spiculation of the Burgess Shale demosponges generally consists almost entirely of oxeas. They are arranged either in an isodictyal net, with mesh spaces as wide as one spicule length or in ramifying, subparallel, anastomosing tracts in which fascicles of oxeas may have a slightly plumose arrangement (Walcott, 1920; Rigby, 1986a). Both types of organization occur in the genus *Hazelia* (Fig. 111). It is likely that spongin held the spicules together. Tangential or perpendicular oxeas supporting a dermal



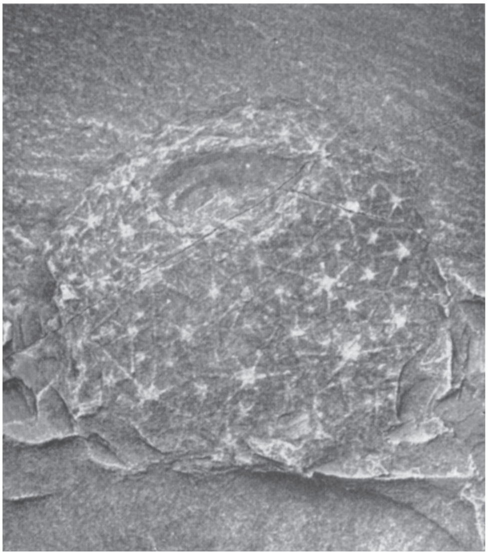


FIG. 109. *1, Eiffelia globosa* WALCOTT, 1920, syntype, USNM 66522; *2, Protospongia hicksi* HINDE (WALCOTT, 1920), hypotype, Burgess Shale at its type locality near Field, British Columbia, Canada, USNM 66502, ×3 (Finks, 1970).

membrane may have been present in some forms, but no specialized spicules are known.

The demosponges were the first group to undergo a major expansion or adaptive radiation in the Ordovician. Perhaps arising from such Middle Cambrian genera as *Rankenella* or *Capsospongia* (KRUSE, 1983; RIGBY, 1986a) or the Late Cambrian *Wilburnicyathus* and *Gallatinospongia* but certainly appearing by the Early Ordovician *Archaeoscyphia,* the lithistid family Anthaspidellidae expanded to some seventeen de-

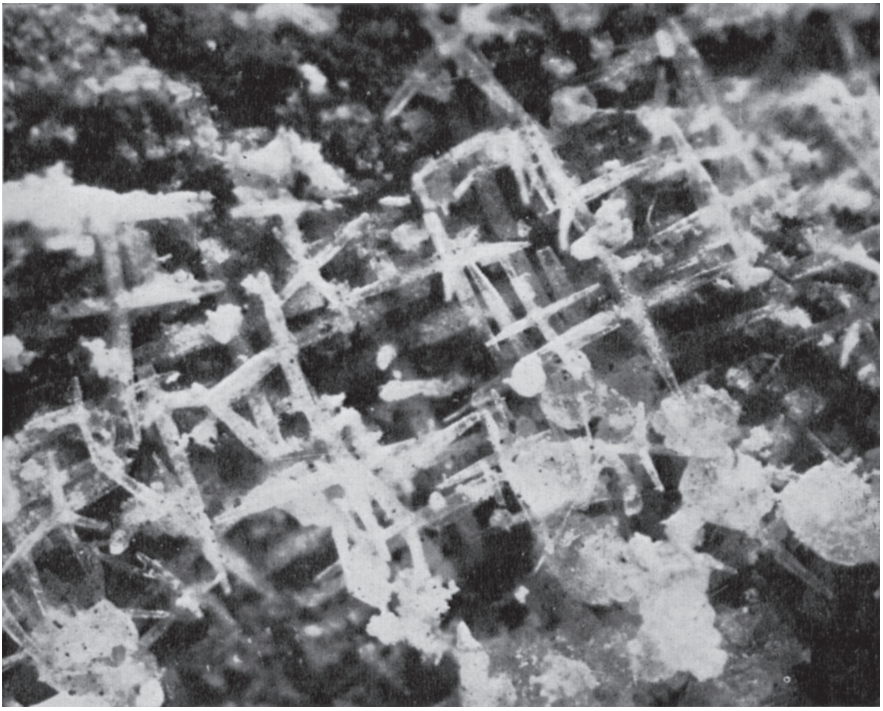


FIG. 110. *Multivasculatus ovatus* HOWELL & VAN HOUTEN, hypotype, USNM 163626, Windfall Formation, Eureka, Nevada, USA, ×30 (Finks, 1970).

scribed genera in lower Middle Ordovician rocks (Llanvirn–Llandeilo). The skeleton is essentially an isodictyal net of the sort seen in the Cambrian *Hazelia* in which constituent monaxons have developed terminal zygoses. Sponges of the family participated in the building of Lower (Arenig) and Middle (Llanvirn) Ordovician reefs and occur elsewhere in shallow-water, shelly facies. The lithistid modification is undoubtedly adaptive for such an environment, conferring strength and resistance against mechanical disruption in rough water. It may indeed be that the availability of such niches gave direction to this branch of demosponge evolution. Adaptive radiation was cut short in the later Ordovician, as was the participation of lithistid sponges in reefs, although the family persisted into the Permian. The rhizomorine type of lithistid skeleton, in which zygoses develop along the sides as well as at the ends of spicules, also appeared in the Ordovician (*Warrigalia, Taplowia, Boonderooia, Nipterella*).

By the later Middle Ordovician (Caradoc, Trentonian) at least three other major types of demosponges evolved and constituted three separate lineages that continued into later times. One of these lineages is represented by *Saccospongia* and related dystactospongiids, with skeletons built of subparallel plumose bundles of styles coated with monocrepid desmoids. Very similar structures are present in living sublithistid Sigmatosclerophora and a direct line of descent is quite possible (FINKS, 1967a). One could even see the Cambrian roots of this lineage in a form like *Hazelia palmata* or *Hazelia dignata* (WALCOTT, 1920; RIGBY, 1986a).

Two types, rather different from the foregoing, also first appeared at this time, namely *Hindia* and *Astylospongia.* The first is built of concentric shells of tripodal

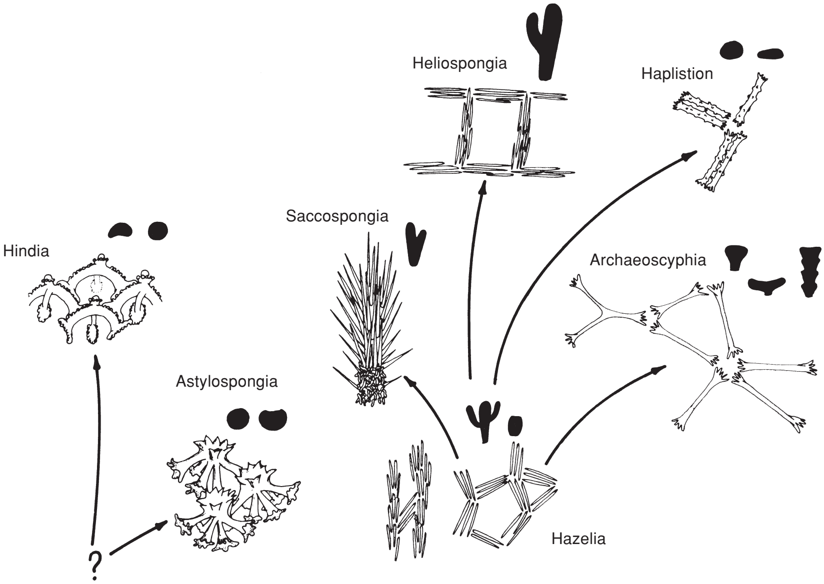


FIG. 111. Principal types of skeletal nets among Paleozoic demosponges showing postulated relationships; forms of whole sponges shown in silhouette (Finks, 1970).

spicules, the second of a three-dimensional net of hexapodal spicules. Both have, in addition, radial and tangential oxeas that probably supported a dermal membrane (Fig. 112). Both evolved into Mesozoic and later forms (Dicranocladina and Sphaerocladina, respectively) that possess tetraxonid dermalia and astrose microscleres.

At this juncture in demosponge history it seems not unreasonable to recognize the already differentiated roots of the Calvaxinellida and Ceractinomorpha, represented by *Saccospongia* and its nonlithistid relatives, and at least some of the roots of the Tetractinomorpha, e.g., the hindiids and astylospongiids (Fig. 113).

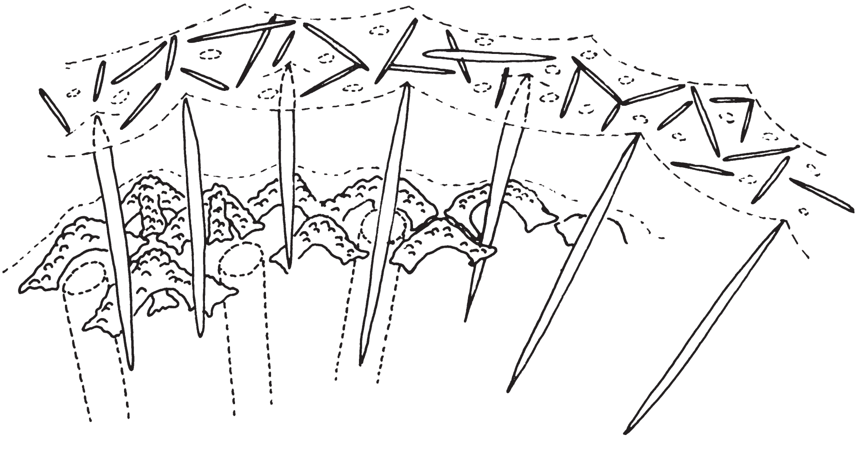


FIG. 112. Skeleton of family Hindiidae shown in its postulated relationship to dermal membrane, subdermal space, and choanosome with its radial canals; outlines of flesh *dotted* (Finks, 1970).

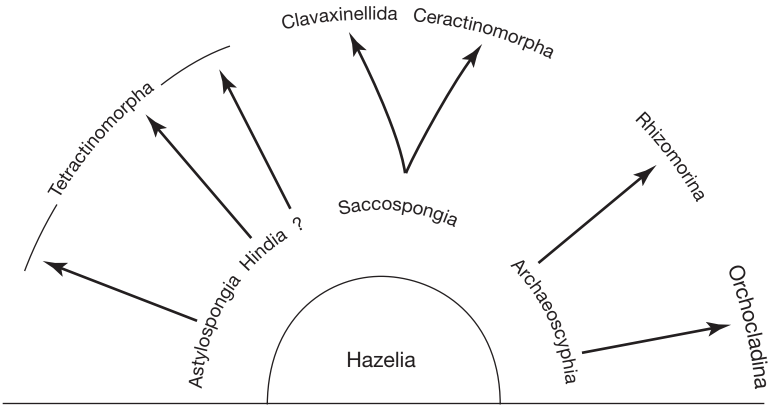


FIG. 113. Postulated lines of descent of living demosponge taxa from Cambrian and Ordovician genera and their relatives (Finks, 1970).

Work by HARTMAN and GOREAU (1966) has strongly suggested that at least some of the Paleozoic Stromatoporoidea were ancestors of the living aberrant, lime-secreting demosponges *Ceratoporella, Astrosclera,* and *Merlia.* If so, this line of sponge evolution diverged early, for the first stromatoporoids appeared in the Cambrian. Furthermore, they predate, by far, any forms that have been referred, even remotely, to the Calcarea (except for the Heteractinida and the Archaeocyatha). The Stromatoporoidea, it

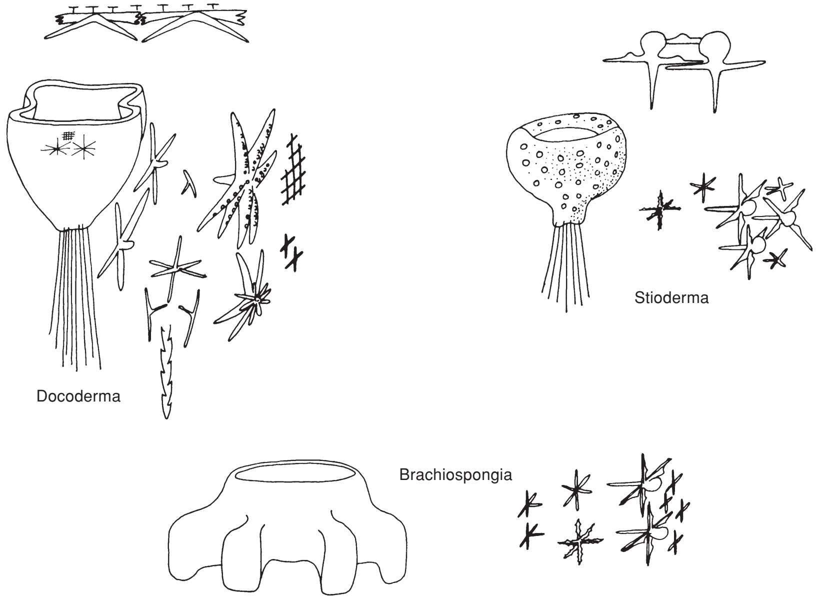


FIG. 114. Paleozoic hexactinellids related to *Brachiospongia; Brachiospongia* is of Ordovician age, *Stioderma* is of Carboniferous and Permian ages, and *Docoderma* is of Permian age; spicular skeleton is shown in exploded view, outside of sponge to right; above *Docoderma* and *Stioderma* are side views of dermal layer showing manner of joining of hypodermalia and autodermalia; scale variable (Finks, 1970).

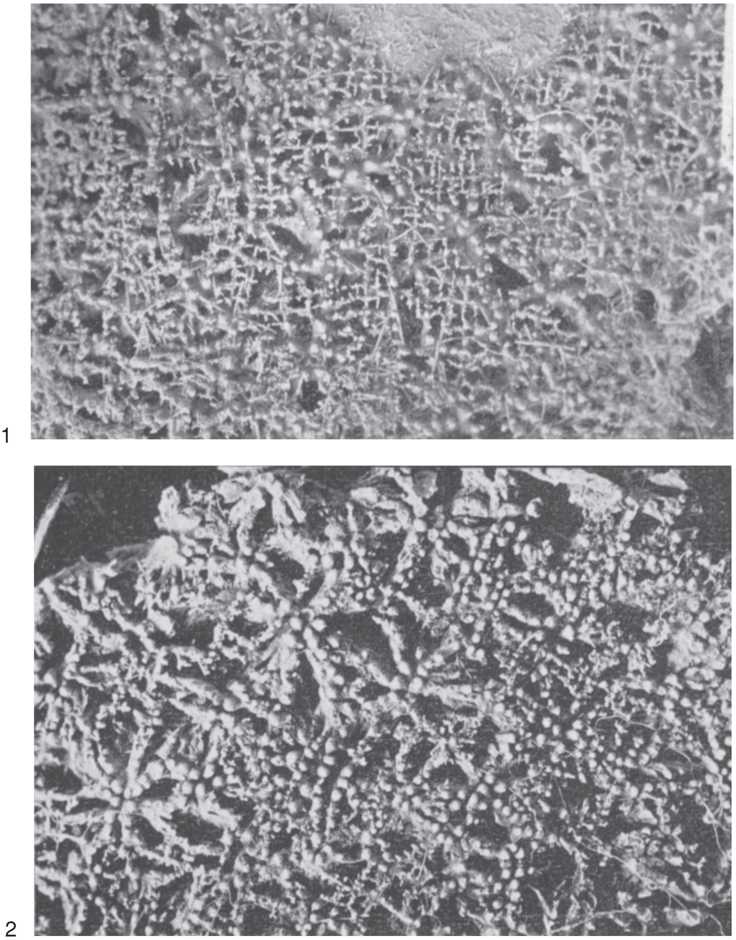


FIG. 115. *Docoderma rigidum* FINKS, 1960, showing fusion of hypodermal and autodermal spicules; *1,* outer surface of fused hypodermal spicules; *2,* another part of same specimen in which fused autodermalia overlie hypodermalia; holotype, USNM 127659, Road Canyon Formation, Permian, Word Ranch, Glass Mountains, Texas, USA, ×5 (Finks, 1970).

may be noted, had their acme of development in the Silurian and Devonian, at which time they and the rugose and tabulate corals were the chief reef-building animals.

The mid-Ordovician also marked the first appearance of an advanced hexactinellid *Brachiospongia* (Fig. 114), which has specialized, large, hypodermal spicules, covered by smaller autodermalia. Its body wall is much thicker than that of any of the known Cambrian sponges, and its spicules lack the regular parallel orientation of the Cambrian forms. Silurian forms such as *Oncosella* may have continued this line, and a late Paleozoic form (*Stioderma*) has a remarkably similar complement of spicules, especially in the form of the hypodermalia and the interior spinose hexactines. Other Permian forms such as *Docoderma* have a similar construction. In apparent late Paleozoic end members of this lineage, hypodermalia and autodermalia tended to fuse in the adult sponges, forming a rigid skeleton (Fig. 115). *Docoderma* developed interlocking processes on hypodermal spicules, a function parallel to the skeleton of the lithistid demosponges

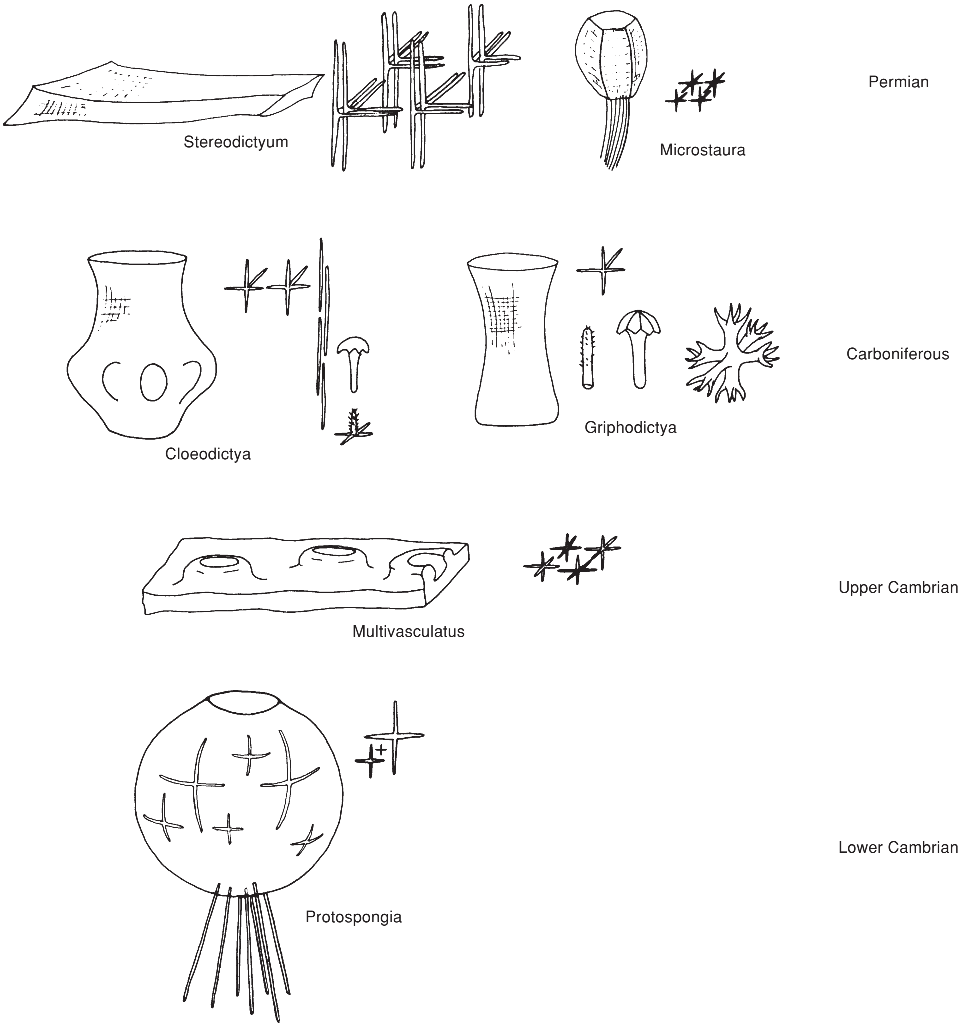


Fig. 116. Paleozoic hexactinellids showing variants of simple, parallel, spicule arrangement characteristic of *Protospongia,* from which they may have descended; geologic periods are shown along side, scale variable; two spicules on far right beside each Carboniferous dictyosponge are microscleres, approximately ×3,000 (Finks, 1970).

and apparently unique among the hexactinellids (see Finks, 1960).

The Ordovician record also contains the beginnings of a second hexactinellid lineage springing directly from the Cambrian *Protospongia* (Fig. 116). *Cyathophycus* of the Ordovician is like a thicker-walled *Protospongia* and is not too different from the simplest of the Devonian dictyosponges, namely *Dictyospongia* itself (see Hall & Clarke, 1899). In this line of development the spiculation remains that of simple hexactines and their derivatives, in parallel orientation without enlarged hypodermalia. The structural type and presumed lineage can be traced through to the Permian *Microstaura,* with a curious thick-walled offshoot, *Stereodictyum.* The dictyonine type of rigid net, which first appeared in the Devonian, could have been derived from this lineage, and the presence of hexasters in a Carboniferous dictyosponge (*Griphodictya* Hall

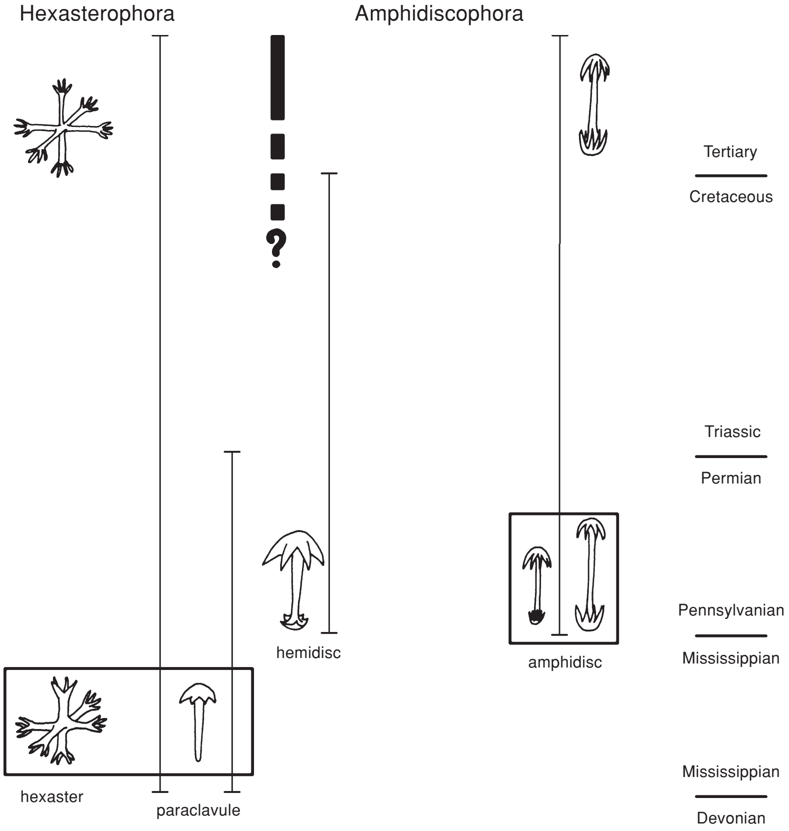


FIG. 117. Ranges of diagnostic microscleres in class Hexactinellida; two spicules enclosed by a rectangle occur in same specimen (Finks, 1970).

& CLARKE, 1899) does not invalidate this hypothesis.

The Paleozoic history of hexactinellid microscleres is worth noting, inasmuch as the classification of living hexactinellids is based on the mutual exclusion of hexasters and amphidiscs. In addition to hexasters, *Griphodictya* possesses paraclavules, as do several other dictyosponge genera. Paraclavules are shaped like one-ended amphidiscs. Unequal-ended amphidiscs, called hemidiscs, are known as isolated spicules from the Cretaceous (ORTMANN, 1912; SCHRAMMEN, 1924a). True amphidiscs are known almost as early as hexasters, having been reported from the Upper Carboniferous (*Uralonema,* LIBROVICH, 1929). KLING and REIF (1969) reported two Late Carboniferous species, one bearing amphidiscs, the other bearing hemidiscs. At least one of the amphidiscs they described is slightly unequal ended (Fig. 117). The graded series paraclavule-hemidisc-amphidisc and the occurrence of paraclavules with hexasters suggest that the Hexasterophora and Amphidiscophora could have diverged from a common stock during the Paleozoic and that they could be the sole survivors of a number of early lineages in some of which both hexasters and amphidiscs could have occurred together.

The Heteractinida, in their relatively modest history, trend in general toward increasing complexity and diversity of the spicules (Fig. 118). The main line of heteractinid evolution seems to start with the

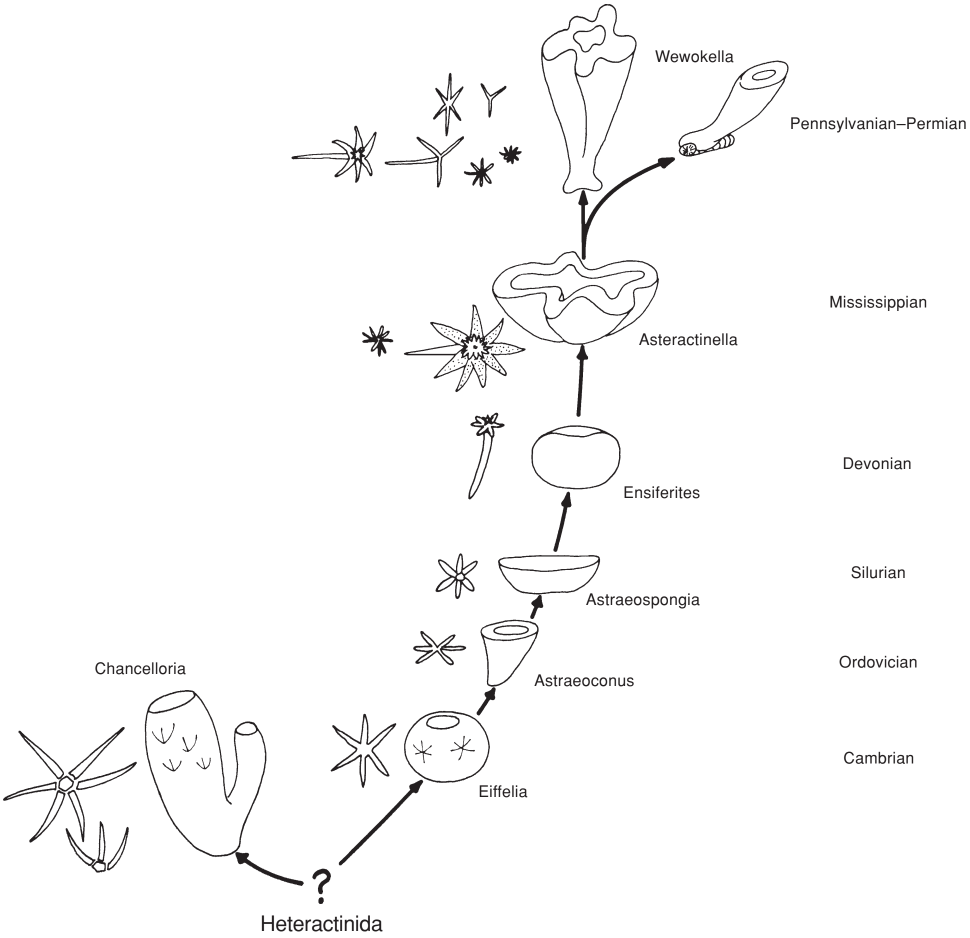


FIG. 118. Evolution of Heteractinida; geologic periods indicated along right side; spicule complements shown to left of each sponge; scale variable (Finks, 1970).

Cambrian *Eiffelia.* The symmetrical, two-dimensional sexiradiates of *Eiffelia* continued in the Ordovician thicker-walled sponge *Astraeoconus* (RIETSCHEL, 1968), but in the Silurian and Devonian *Astraeospongium,* short proximal and distal rays may be developed. The Devonian *Ensiferites* (REIMANN, 1945b) has a greatly enlarged proximal ray, and the distal ray may have dissolved into a rosette of short branches. The Early Carboniferous *Asteractinella,* described by VANDERCAMMEN (1950), continued this trend with spicules having recurved, umbrella-like paratangential rays, often more than six in number and bearing a distal rosette or tubercles, to which was added a new type of spicule, the globular polyactine. The later Carboniferous *Wewokella* and the Carboniferous-Permian *Regispongia* have essentially the same types of spicules as *Asteractinella,* but the paratangential rays of the principal spicules are often reduced to three in *Wewokella.* Simple triradiates and sexiradiates are also present.

The Calcarea in the strict sense (that is, excluding the Archaeocyatha, Aphrosalpingoidea, Heteractinida, and Stromatoporoidea) appeared later in the record than

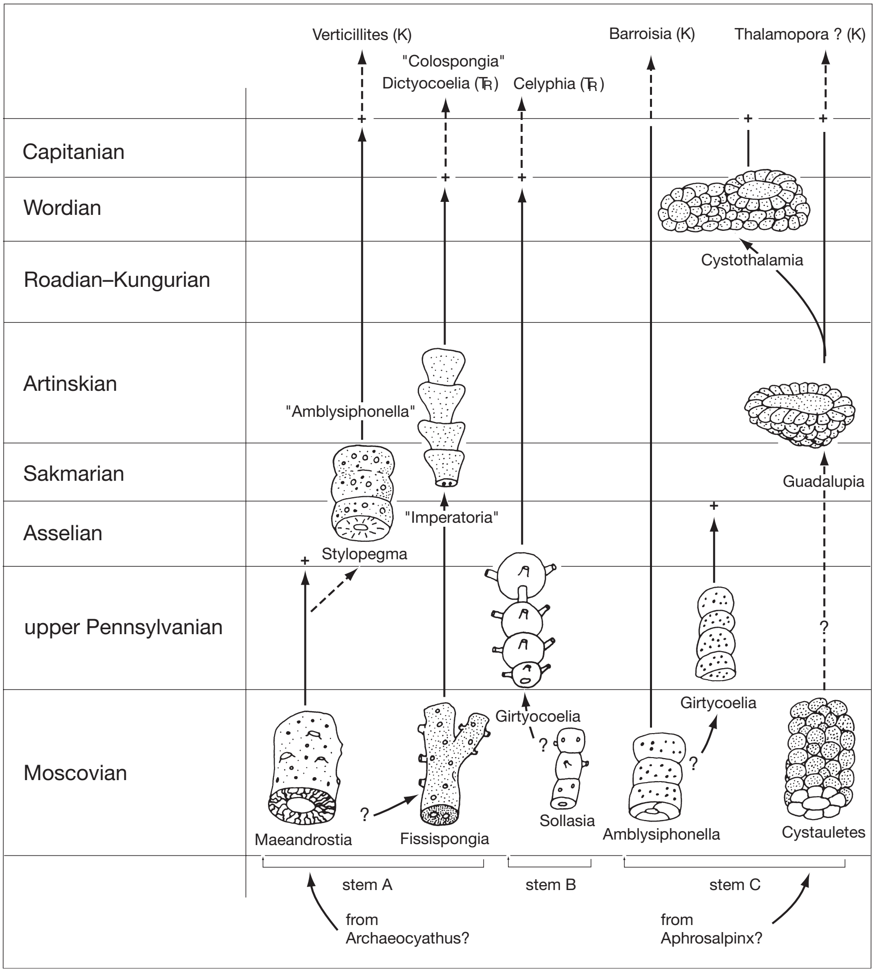


FIG. 119. Postulated lineages among Late Paleozoic Sphinctozoa from Carboniferous until their extinction; relative scale of sponge drawings is approximately uniform (Finks, 1970).

other classes of sponges. The Devonian *Protoleucon* (BOLKHOVITINOVA, 1923) is not clearly a calcareous sponge. The isolated triradiates and tetraradiates from the Lower Carboniferous described as *Peronidella sparse* by HINDE (1888) may belong to the Calcarea and, if so, are the oldest described spicules of the class, although affinity to the Heteractinida cannot be excluded.

The Sphinctozoa have an undoubted appearance in the Ordovician of Australia (WEBBY & RIGBY, 1985) and North America (RIGBY & POTTER, 1986) but have only a limited record until the Middle Carboniferous of Spain (Bashkirian) and North America (Des Moinesian, Moscovian) (STEINMANN, 1882; BARROIS, 1882; FINKS, 1960). Among these early Sphinctozoa (Fig. 118–119) are three major structural types: (1) those built of porous-walled chambers containing internal solid partitions (*Amblysiphonella, Sebargassia, Girtycoelia, Cystauletes*); (2) those built of imperforate-walled, hollow chambers with a small number of spoutlike openings (*Sollasia, Girtyocoelia*); and (3) those containing

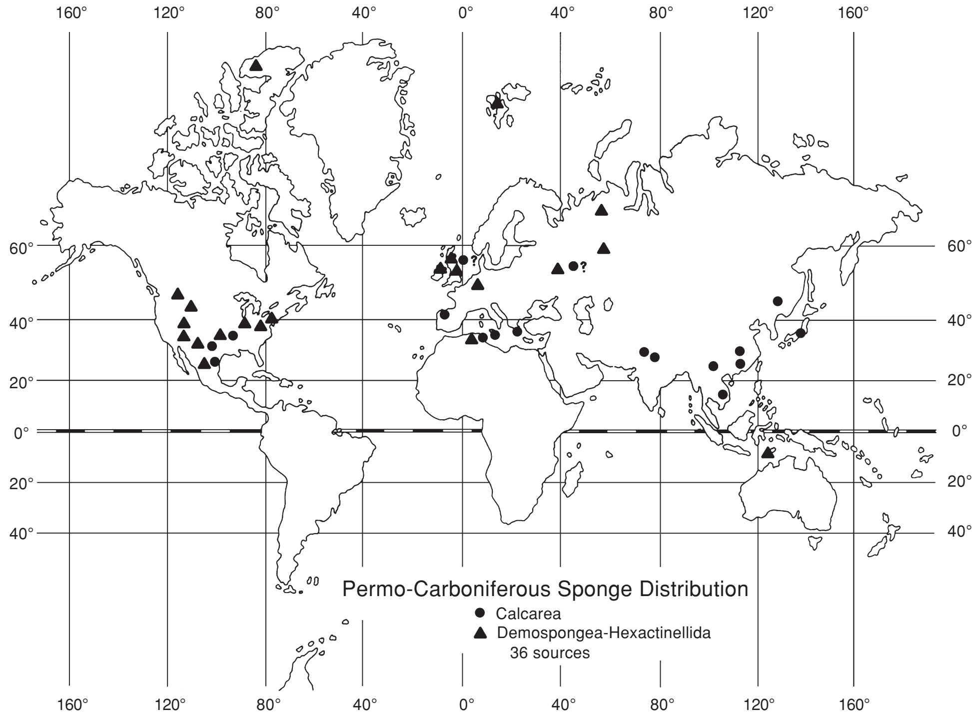


FIG. 120. Geographic distribution of reported occurrences of known Calcarea, Hexactinellida, and Demospongea from Carboniferous and Permian rocks; some localities close to each other have been combined (Finks, 1970).

coarsely perforate dermal and cloacal walls (*Maeandrostia, Fissispongia*). Because in Texas and elsewhere each of the structural types can be traced through continuously developing lineages into the Permian and possibly beyond, they may represent three basic evolutionary stocks among the Sphinctozoa. They appear suddenly in the record, and there is no trace of their prior divergence from a common ancestor. It is worth noting, however, that *Maeandrostia* has an overall structure very much like that of Early Cambrian *Archaeocyathus,* and *Cystauletes* is not too different from that of Silurian-Devonian *Aphrosalpinx.*

The earliest Pharetronida appear to be two genera that enter the record in the Lower Permian (Lenox Hills, Sakmarian) of Texas. Other genera appeared in the Permian in several parts of the world, and the group expanded into the Mesozoic. The Calcarea were active in reef building in Permian time and continued so into the Triassic.

The late Paleozoic Calcarea (Fig. 120) have a more concentrated geographic distribution than the siliceous sponges that could be termed Tethyan. This may have resulted from climatic control and perhaps also from a center of origin.

All the classes of sponges have had at least some representatives that lived in shallow water during the Paleozoic. This can be seen from a list of those groups that have been associated with algae, that is, with the euphotic zone, or with reefs that reveal evidence of having grown in rough water, such as accumulations of talus (Fig. 121). Persistent environmental preferences of some groups of sponges, however, can be demonstrated by noting their association with specific types of sediment. Also, associations of

	occurring with	
period	algae	reefs
Permian	Hexactinellida Demospongea Heteractinida Calcarea	Hexactinellida Demospongea Calcarea
Carboniferous	Hexactinellida Demospongea Heteractinida Calcarea	Hexactinellida Demospongea
Devonian	Hexactinellida Demospongea? Receptaculitida	Hexactinellida Demospongea? Heteractinida? Receptaculitida
Silurian	Hexactinellida? Demospongea? Heteractinida Receptaculitida	Demospongea Heteractinida Receptaculitida
Ordovician	Hexactinellida Demospongea Receptaculitida	Hexactinellida? Demospongea Receptaculitida
Cambrian	Archaeocyatha	Archaeocyatha

FIG. 121. Shallow-water sponges of each period as shown by occurrences with algae or reefs; *question marks* indicate uncertainty as to reality of association in life (Finks, 1970).

sponges characteristic of specific environments can be traced through time, and changes in the composition of these associations can be noted (Fig. 122).

One such environment is quiet water, identifiable by fine-grained sediment and other geologic criteria. This environment has been the special province of the siliceous sponges (Hexactinellida, Demospongea). Abundant occurrences of Paleozoic hexactinellids are almost always in such sediments, although sporadic occurrences in rougher waters and even in reefs are known. Quiet water is not necessarily deep; where depth can be estimated, estimates range from 500 meters in the basin facies of the Texas Permian (NEWELL & others, 1953; NEWELL, 1957) to 1 m in the Late Carboniferous coastal lagoon represented by a black shale overlying a coal bed (ZANGERL & RICHARDSON, 1963). Black shales form a distinct subgroup within this environment and were the special home of thin-walled, delicate hexactinellids of persistently primitive type.

A different environment of agitated, shallow water with relatively little suspended sediment, identified by deposits built largely of whole or fragmented, coarse skeletal debris, is commonly designated the shelly facies. It has a characteristic sponge fauna from the Ordovician on. Lithistid demosponges and heteractinids are particularly characteristic of this facies, as are the stromatoporoids. In the Ordovician record, anthaspidellid lithistids are particularly dominant among the sponges of this facies. In the Silurian and Devonian record the facies is marked by the presence of hindiid lithistids and the astraeospongiid heteractinids, accompanied in the Silurian by another lithistid group, the astylospongiids. In

period	quiet water	shelly facies	reef builders
Permian	demosponges hexactinellids	Sphinctozoa Pharetronida Chiastoclonellidae Heliospongiidae* Wewokellidae* Rhizomorina Hindiidae (Hexactinellida)	Sphinctozoa Pharetronida
Carboniferous	demosponges hexactinellids	Sphinctozoa Wewokellidae Heliospongiidae (Rhizomorina) (Hexactinellida)	
Devonian	demosponges hexactinellids	Stromatoporoidea Hindiidae Astraeospongiidae Receptaculitida (Hexactinellida)	Stromatoporoidea
Silurian	demosponges hexactinellids	Stromatoporoidea Astylospongiidae Astraeospongiidae Hindiidae (Hexactinellida?)	Stromatoporoidea
Ordovician	demosponges hexactinellids	Stromatoporoidea Anthaspidellidae Hindiidae Dystactospongiidae Astylospongiidae Receptaculitida (Hexactinellida?)	Stromatoporoidea Anthaspidellidae Receptaculitida
Cambrian	demosponges hexactinellids heteractinids	Archaeocyatha Stromatoporoidea	Archaeocyatha

FIG. 122. Sponge taxa associated with three types of environments in different periods; under shelly facies and reef builders, taxa arranged in approximate order of abundance, with most abundant on top; those in *parentheses* are minor elements; *asterisks* indicate extinction before end of period; *question marks* indicate uncertainty as to reality of association (Finks, 1970).

the later Paleozoic, stromatoporoids dropped out. The astraeospongiids evolved into the wewokellids. New demosponge groups became abundant, especially the Heliospongiidae, and Calcarea appeared in force, first the Sphinctozoa, then the pharetronids. The rigid or heavy skeletons of all these groups are undoubtedly adapted to rough water. It should be noted that some of the lithistids of this facies may also be abundant in the quiet-water facies, but not the Calcarea, Heteractinida, and Stromatoporoidea.

Reefs form a special environment that may be regarded as an offshoot of the environment in which the shelly facies accumulated. When sponges participate in reef building, they are represented consistently by groups that are most abundant in the shelly facies. The times of greatest sponge participation in reefs are the Ordovician and the Permian. When principal reef-building organisms are listed by periods (Fig. 123), it is evident that corals (Tabulata and Rugosa) dominated the reefs during the intervening periods, a time that coincided with their

period	reef builders
Permian	algae Sphinctozoa* pharetronids* Bryozoa hydrocorallines?
Carboniferous	corals algae
Devonian	corals stromatoporoids algae
Silurian	corals stromatoporoids Bryozoa algae?
Ordovician	Bryozoa stromatoporoids algae demosponges* corals Receptaculitida
Cambrian	Archaeocyatha algae
Pre-Cambrian	algae

FIG. 123. Principal reef-building organisms in each period of Paleozoic, listed in approximate order of abundance under each period, with most abundant organisms at top; *asterisks* indicate sponges; *question marks* indicate uncertainty of identification of organisms (Finks, 1970).

general peaks of abundance and diversity. In the reef environment, corals were apparently competitively superior to sponges, with the exception of the stromatoporoids that appear to have been the competitive equals of the corals. Because sponges and corals do not use the same food sources (suspension feeding versus carnivorous macrophagy), the food supply was unlikely to have been a factor in either successful or unsuccessful competition. Bryozoans appear to have been the competitive equals of some sponges but also inferior to the corals. That these various groups competed with each other is suggested by the tendency for approximately contemporaneous reefs in the same area to be dominated by one or the other of the reef-building groups, as described for the Ordovician by PITCHER (1964).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

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HOLOCENE DISTRIBUTIONS

Sponges are almost exclusively marine, except two freshwater families, the Spongillidae and the closely related Lubomirskiidae of Lake Baikal, both members of the class Demospongea. At the level of classes sponge distribution is cosmopolitan, extending from the Arctic Ocean on the north to the Antarctic Continent on the south and occupying all oceans. At the ordinal level some groups are restricted. The Lychniscosa of the class Hexactinellida appear to be restricted to low latitudes; 11° N to 26° N in the Atlantic and 11° S to 6° N in the Indo-Pacific. The Lithistida of the class Demospongea are restricted to low and middle latitudes: 10° S to 42° N in the Atlantic and 40° S to 35° N in the Indo-Pacific. The Pharetrones in the class Calcarea occur in the Indo-Pacific between latitudes 33° S and 34° N. In the Atlantic region only one species is known and there is also one from the Mediterranean (39° N to 44° N). The three latter groups are relatively uncommon and their true distribution may be greater than that cited; the paucity of reports on South Atlantic sponges is almost certainly a contributing factor to the lack of records in that area. Nevertheless, the limited distribution must be real and reflects a contraction from their Cretaceous distribution. At the level of families and lower categories, distribution may be even more restricted, although there are many cosmopolitan genera in all three major classes of the phylum.

BATHYMETRY

Depth distributions of various groups of living sponges have been used to interpret water depths of deposits of fossil sponges (e.g., Oakley, 1938; Wagner, 1963). Since the publication of the Challenger Reports (Poléjaeff, 1884; Ridley & Dendy, 1887; Schulze, 1887a; Sollas, 1888) the major classes have been recognized as having maximum abundances at different depths, although with strongly overlapping ranges. Figure 124, adapted from Nestler (1961), shows the relative diversity of the major classes of sponges at various depths. It is based on an earlier compilation (Walther, 1893–1894) but is not seriously changed by later data. It seems worthwhile to review, at least in a preliminary way, the bathymetric data now available to provide a frame of reference for further paleoecologic interpretation.

The accompanying charts (Fig. 125–129) show depth distributions of each major order recognized in this volume. The total range of each group is plotted against latitude, because the latter parameter is correlated to some extent with temperature. Depths for Indo-Pacific occurrences have been plotted separately from those for the Atlantic-Arctic-Mediterranean systems to allow some control over effects of provincial faunal differences. Only the major monographs and such smaller reports as yield extremes in depth and latitude were consulted, and of these effort focused only on those that were relatively easily used. Despite these limitations, most of the available data have been gathered, and it is likely that patterns displayed reflect true distributions of most sponges. It is possible that new or missed data may extend greatly the extremes for the less common groups.

Use of total range is more appropriate to the usual sort of paleontological work, although knowledge of maximum abundance would provide a sharper tool. The nature of paleontological samples is generally too limited to provide secure data on abundance, but simple presence or absence can be interpreted in connection with the charts herein.

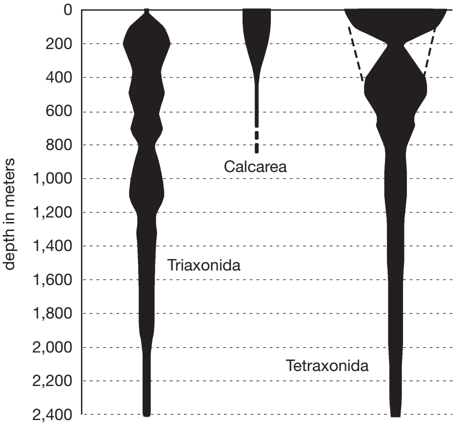

Fig. 124. Relative diversity of major classes of living sponges at various depths in modern oceans (Nestler, 1961).

Assessment of the present distribution of abundance also involves problems of sampling.

The class Calcarea retains its former reputation for a dominantly shallow-water distribution, in general being confined to depths less than 600 m and occurring as shallowly as low tide level (Fig. 125). Recent work (Koltun, 1964; Borojevic & Graat-Kleeton, 1965), however, has extended the extreme range of deep-sea species from the Arctic to 3,800 m. In the equatorial regions there are few reports below 200 m; whether this is due to deficiencies of sampling or to some other cause is not clear. The Pharetronida range from 5 to 25 m in the Mediterranean (all in poorly lighted caves and hollows) and from 5 to 430 m in the Indo-Pacific.

The class Hexactinellida has a different pattern for each of its subgroups (Fig. 126–127). The deepest record of any sponge is an as yet unidentified hexactinellid from the Kurile-Kamchatka Trench at 8,610 m (Vinogradov, 1958, p. 87). The subclass Amphidiscophora is everywhere confined to depths below 200 m. Maximum recorded depth is 7,000 m (*Hyalonema* from Kermadec Trench, Lévi, 1964, p. 83). Their total latitudinal extent is from the Arctic (80° N) to the vicinity of Antarctica. The upper limit of depth distribution does not rise with increasing latitude (as does that of the Lyssacinosa), suggesting that more is involved than simple temperature control.

Of the subclass Hexasterophora, the Lyssacinosa have upper and lower depth limits that tend to rise toward the poles, suggesting a temperature control of distribution. The pattern is best shown in the Atlantic-Arctic (Fig. 126), with a range of 800 to 5,900 m near the equator, rising to about 70 to 3,000 m at the Arctic end (70° to 80° N) and 50 to 4,000 at the southern end (50° to 60° S). In the Indo-Pacific (Fig. 127) the corresponding figures are 110 to 5,000 m near the equator, 130 to 1,200 m at 55° N, and 50 to 600 m at 72° S. The deepest record is at 32° S where *Caulophacus* has been taken from 7,000 m in the Kermadec trench (Lévi, 1964, p. 83). The northern end is truncated somewhat arbitrarily by inclusion of the Arctic with the Atlantic (with which it has the most open connection and to which it belongs faunistically (see Hentschel, 1929, p. 1012); the southern end is more significant with Lyssacinosa occurring on the Antarctic shelf, often beneath shelf ice. It may be argued that the lower limit is controlled by bathymetry of the ocean floor, but the upper limit is not controlled and yet shows a significant rise.

The Hexactinosa are almost completely absent from water shallower than 100 m, but a few occurrences in equatorial regions record them as shallow as 10 to 40 m. Their latitudinal distribution extends, again, from Arctic to Antarctic regions. The maximum depth record is a *Farrea* from 6,860 m in the Kurile-Kamchatka trench (Vinogradov, 1958, p. 87). The Hexactinosa are common elements in the only known living hexactinosan sponge reefs recently discovered on the continental shelf of British Columbia in Hecate Strait, in water up to 200 m deep (Krautter & others, 2001; Conway & others, 2001). A variety of lyssacinosan sponges also occur in the reefs.

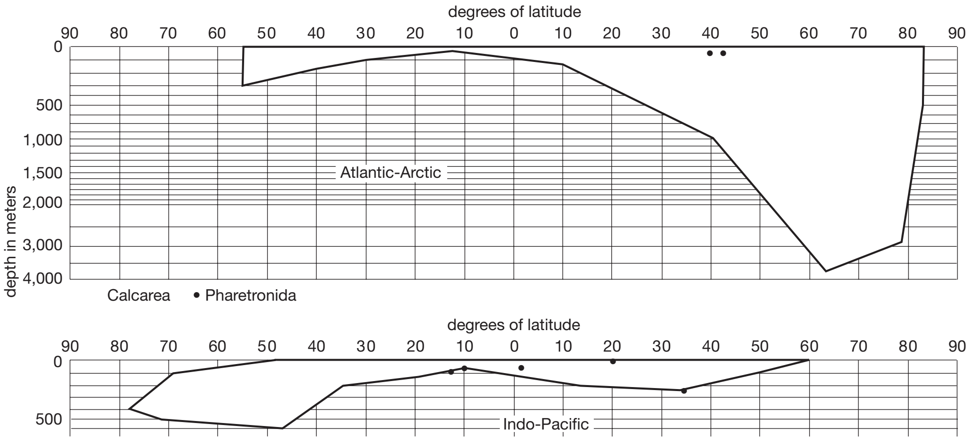

FIG. 125. Distribution of Calcarea, including the Pharetronida, showing depth and latitudinal occurrences in the Atlantic-Arctic Ocean, above, and the Indo-Pacific Ocean, below (new).

The Lychniscosa have the most restricted distribution in the class. They are confined entirely to low latitudes and to moderate depths. In the Atlantic they occur between 11° N and 26° N at depths between 200 and 700 m. In the Indo-Pacific they occur between 11° S and 6° N at depths between 80 and 600 m. The latitudinal restriction may be related to a temperature requirement, the bathymetric restriction perhaps to some form of competitive exclusion that seems to keep all living Hexactinellids out of shallowest water.

The class Demospongea, which includes the great majority of living sponge species, also has noteworthy differences in distribution between the orders recognized here (Fig. 128–129). Representatives of all orders have been reported at the very shallowest depths, low tide, or even slightly above it. The Monaxonida have the deepest range, extending to 7,000 m (*Asbestopluma hadalis* LÉVI, 1964, from the Kermadec trench); they appear to be the only demosponges to populate the deep sea below about 4,200 m. They also include the only freshwater

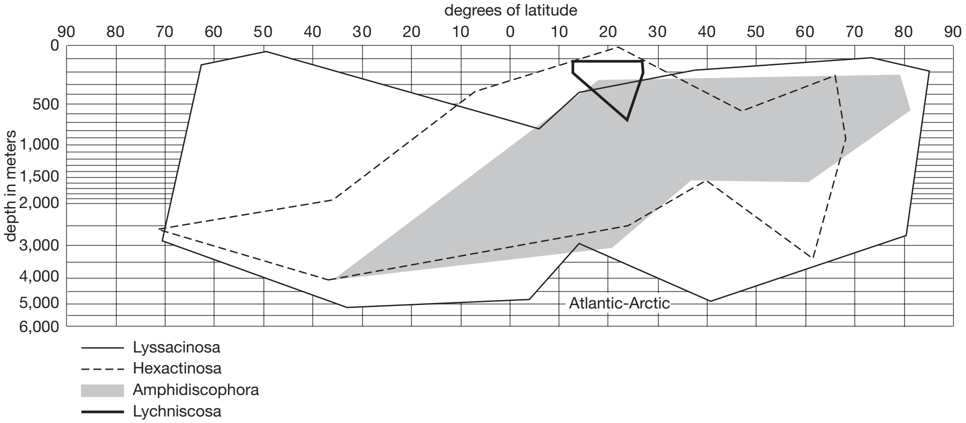

FIG. 126. Distribution of orders of hexactinellid sponges showing depth and latitudinal occurrences in the Atlantic-Arctic Ocean (new).

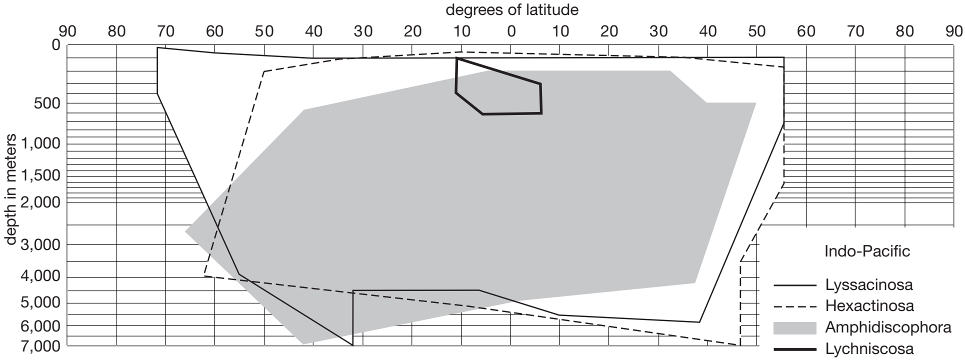

FIG. 127. Distribution of orders of hexactinellid sponges showing depth and latitudinal occurrences in the Indo-Pacific Ocean (new).

sponges. The Keratosa, which appear to be most closely related to the Monaxonida (and especially to the sigma-bearing forms that comprise most of the deep-sea monaxonids), on the other hand, are the most limited in depth. They are not known below 2,000 m, and most of them not below 200 m. The Choristida extend down to 4,160 m (*Sphinctrella horrida* SCHMIDT from the Azores, TOPSENT, 1913). The Lithistida range from 110 to 2,200 m in the Atlantic and 0 to 1,300 m in the Indo-Pacific, being the group most restricted in depth after the Keratosa. The lithistids are also the only demosponge order to have a latitudinal restriction. They are confined in the Indo-Pacific between 40° S and 35° N (Fig. 128). In the Atlantic they range from 10° S to 42° N (Fig. 129), although one report of *Macandrewia azorica* from about 60° N was given by SOLLAS, 1888. Temperature may limit the distribution of the lithistids.

Considering the phylum as a whole, the monaxonid demosponges (or more precisely the order Cornacuspongida of LENDENFELD and other authors) have been the most adaptable. They include most living sponge species; are the only ones to live in fresh water; and range more deeply in the sea than any other sponges except amphidiscophoran

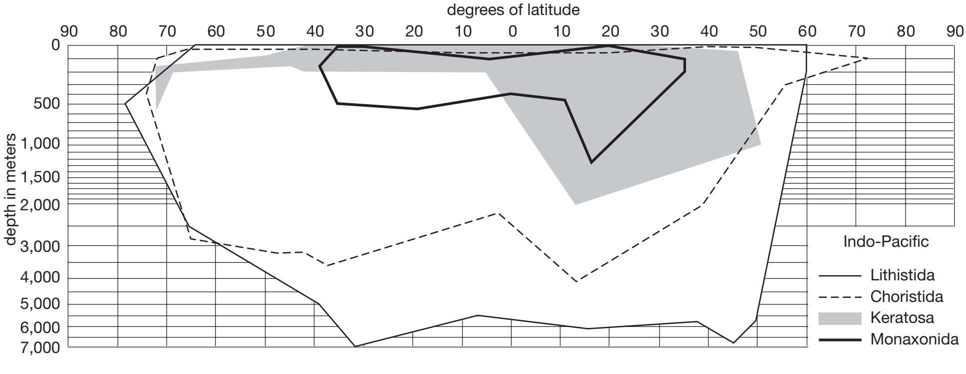

FIG. 128. Distribution of orders of demosponges showing depth and latitudinal occurrences in the Indo-Pacific Ocean (new).

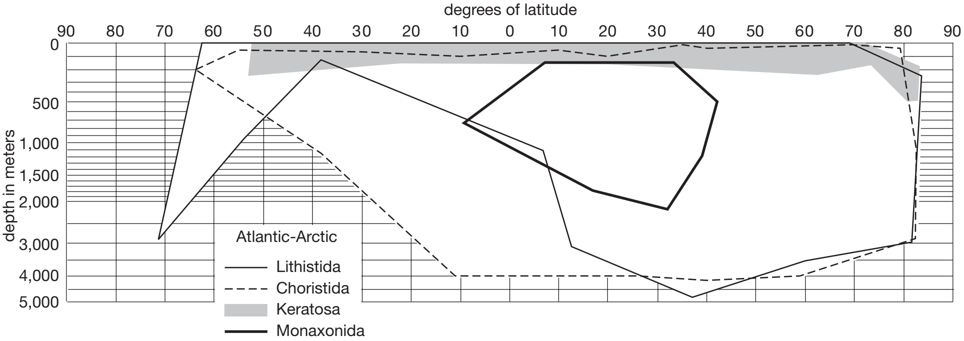

FIG. 129. Distribution of orders of demosponges showing depth and latitudinal occurrences in the Atlantic-Arctic Ocean (new).

Hexactinellida. Their microscleres include the most complex and asymmetrical ones, have the greatest development of spongin, and are characterized by a sort of ovoviviparity or incubated larval stage. The class Hexactinellida, with its low-efficiency hydraulic system, is largely excluded from present shallow waters, possibly because of competition related to feeding. In the Mesozoic and Paleozoic this restriction was much less noticeable. The class Calcarea is largely excluded from deeper waters, possibly because of increased solubility of calcium carbonate at greater depths. Three archaic groups, one from each class, are restricted to low latitudes: the Lithistida, the Lychniscosa, and the Pharetrones. Their present restriction seems to be most readily explained by limited tolerance to low temperatures. Because these groups might be characterized as those with the most massive skeletons, the postulated intolerance to low temperature may be related to a higher metabolic rate. Their greater diversity, abundance, and geographic distribution in Mesozoic times may have resulted from a warmer world climate.

VINOGRADOV (1958) reviewed records of sponge species occurring at depths below 2,000 m (abyssal and hadal zones) and identified two well-defined depths at which there is a major turnover in species (Fig. 130–131). That is, at these depths there is a strong maximum in both the number of species that appear for the first time at this depth and in the number of species that disappear. Overlapping of ranges leads also to a maximum in the total number of species at that depth (Table 8).

For sponges as a whole and for Hexactinellida alone (Fig. 130), the upper maximum is at 2,500 to 3,000 m and the lower at 4,000 to 4,500 m. The upper maximum for the Demospongea alone (Fig. 131) is slightly higher (2,000 to 2,500 m) and the lower maximum for the Choristida (“Tetraxonida”) alone is likewise higher (3,500 to 4,000 m). The differences reflect the smaller number of specifically abyssal and hadal species among the demosponges; the lower maximum for choristids is scarcely above the lower limit of their distribution. It is not clear what critical factors determine the two depths of faunal turnover. VINOGRADOV (1958) found corresponding changes in many other groups of animals.

ORIGIN OF THE ABYSSAL SPONGE FAUNA

Sponges form an important element of populations on the sea floor below 2,000 m. Over vast areas of the abyssal plain of the central Pacific, well below 3,000 m, sponges have constituted more than 50 percent of trawl catches (SOKOLOVA, 1964; and Fig. 132 herein). Nevertheless, very few genera

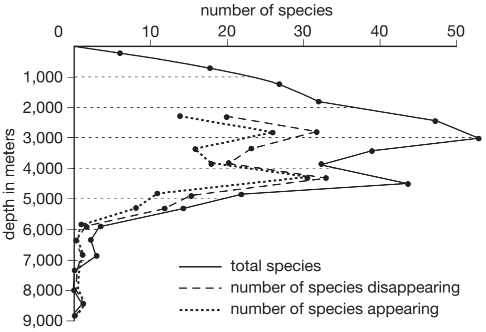

FIG. 130. Numbers of species of Hexactinellida, per depth, in modern oceans, and numbers of species appearing and disappearing at particular depths (Vinogradov, 1958).

are confined to abyssal depths, most abyssal sponges being eurybathic genera. On the assumption that stenobathic abyssal genera originated as adaptations to the abyssal environment, their first appearance in the fossil record should give a minimal age for the origin of that environment, and the numbers of species in each genus living today should provide a minimal rate for evolution of the genera. Following is a list taken from the compilation of LÉVI (1964) of stenobathic abyssal genera with more than one living species, which is in essential agreement with the similar data of VINOGRADOV (1958). Their geologic range is also added.

Class Demospongea
  Order Monaxonida
    Cladorhiza 14 living spp. (*?Eocene–Holocene*)
    Asbestopluma 6 spp. (*Holocene*)
    Chondrocladia 10 living spp. (*?Eocene–Holocene*)
    Esperiopsis 3 living spp. (*?Eocene–Holocene*)
  Order Choristida
    Thenea 12 spp. (*Holocene*)
Class Hexactinellida
  Order Amphidiscophora
    Hyalonema 1 living sp. (*?Eocene–Holocene*)
    Oonema 11 spp. (*Holocene*)
    Prionema 4 spp. (*Holocene*)
    Leptonema 9 spp. (*Holocene*)
  Order Hexasterophora
    Suborder Lyssacinosa
      Holascus 10 spp. (*Holocene*)
      Malacosaccus 6 spp. (*Holocene*)
      Caulophacus 15 living spp. (*?Eocene–Holocene*)

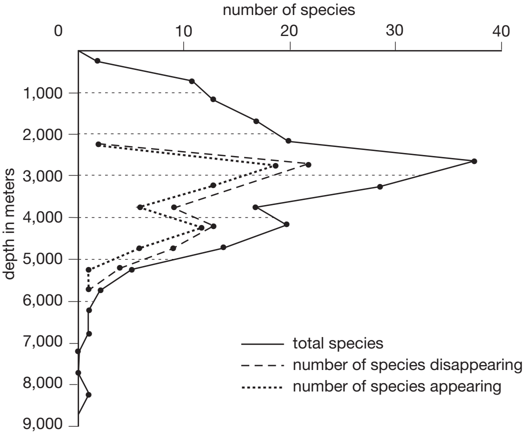

FIG. 131. Numbers of species of Demospongea, per depth, in modern oceans, and numbers of species appearing and disappearing at particular depths (Vinogradov, 1958).

Table 8. Depth ranges of various taxa of sponges (new).

GROUP	UPPER MAXIMUM			
		Number of species		
	Depth (in m)	Total	Appearing	Disappearing
Triaxonida (Hexactinellida)	2,500–3,000	38	18	22
Tetraxonida (approx=Choristida)	2,000–2,500	ND	ND	ND
Cornacuspongida (approx=Monaxonida)	2,000–2,500	ND	ND	ND
Total sponges	2,500–3,000	55	26	32

GROUP	LOWER MAXIMUM			
		Number of species		
	Depth (in m)	Total	Appearing	Disappearing
Triaxonida (Hexactinellida)	4,000–4,500	20	12	13
Tetraxonida (approx=Choristida)	3,500–4,000	ND	ND	ND
Cornacuspongida (approx=Monaxonida)	4,000–4,500	ND	ND	ND
Total sponges	4,000–4,500	45	32	33

Unfortunately the first Eocene records of *Cladorhiza, Chondrocladia, Esperiopsis, Hyalonema,* and *Caulophacus* are from from a paper by Hinde and Holmes (1892) on Eocene sponges from Oamaru, Otago, New Zealand, in which identifications were made on the basis of isolated spicules, mainly microscleres. At that time, shape of individual spicules was considered to be more characteristic of particular genera than has turned out to be so. Consequently we cannot rely on these, the only fossil records of the genera involved. Nevertheless, we can assert for the first four Eocene genera, on the basis of the microscleres described, that reasonably close relatives were present, as they were also in the Cretaceous (Zittel, 1876; Schrammen, 1910, 1912).

Even if these stenobathic abyssal genera were actually present in the Eocene, they were associated in the fauna described by Hinde and Holmes (1892) with spicules of lithistids that are today entirely excluded from the abyssal fauna. The same is true of the Cretaceous chalk. Therefore, the known Cretaceous and early Tertiary sponge faunas that have the closest affinities to the living abyssal fauna appear to be of a shallower water nature, possibly within the bathyal zone. If the abyssal sponge fauna had not already originated at this time, a matrix for it was at least present in the bathyal fauna; and differentiation of abyssal adaptations may conceivably date from the early Tertiary.

Indeed, in present seas, in addition to living stenobathic abyssal forms, there are several eurybathic genera whose main centers of development are in the bathyal or even sublittoral zone but which have wholly or partly abyssal species. Included are several Hexactinosa of the class Hexactinellida, namely *Eurete, Farrea, Aphrocallistes, Bathyxiphus, Auloplax, Chonelasma,* and *Aulocalyx* (Lévi, 1964). Of these seven genera, the first five are known from the Upper Cretaceous. The same is true of the lyssacinosan *Regadrella* (Reid, 1958a). Many more genera of Demospongea with abyssal representatives were listed by Lévi (1964), but they are almost all unknown as fossils. Two that are recognizable by characteristic spicules are *Latrunculia* and *Geodia,* and these are both present in the New Zealand

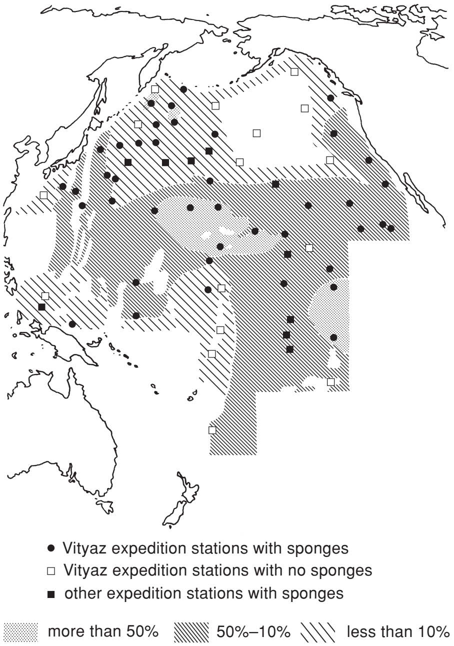

FIG. 132. Distribution of sponges as a percentage of trawl catches from central and northern Pacific Ocean (Sokolova, 1964).

Eocene deposit described by HINDE and HOLMES (1892). *Geodia* is also known from the Cretaceous (HURCEWICZ, 1966) and *Geodia*-like sterrasters as far back as the Upper Jurassic *Rhaxella* (HINDE, 1890). Thus, several of the eurybathic generic elements of the present abyssal sponge fauna can be traced back at least to the early Tertiary or Cretaceous.

An analysis of genera of abyssal sponges given by LÉVI (1964) is presented in Table 9 (Calcarea from KOLTUN, 1964, and BOROJEVIC & GRAAT-KLEETON, 1965).

The small number of exclusively abyssal genera may have resulted from a relatively recent origin of the fauna (and the environment). Or it may reflect the uniformity or the extreme nature of the environment or both. The greater percentage of exclusively abyssal Hexactinellid genera may indicate the deeper water focus of development of this class.

HISTORY OF DEPTH DISTRIBUTIONS

To trace depth distributions of sponges into the geologic past we must start with fixed points of reference that are known with the greatest certainty and from these build an interlocking net of evidence. Identification of the shallow-water environment seems to be the most securely founded and the one that can be determined within the narrowest limits. Among indicators of shallow water, the presence of benthic calcareous algae is least subject to alternative interpretations and determines depth most precisely.

Algae must have light for photosynthesis, and the depth of light penetration sufficient for photosynthesis is known in modern seas to extend from the surface down to a maximum of about 200 m. The Rhodophyceae, which are able to use the more penetrating shorter wavelengths of light, occur down to this depth in clear waters of low latitudes, where light penetration is greatest owing to the high angle of incidence (POLUNIN, 1960, p. 513, 530). At higher latitudes and in more turbid waters, maximum depths may be considerably less. The lower limit of "the more abundant attached plants" is only about 40 to 60 m (POLUNIN, 1960, p. 512). Consequently fossil sponges directly associated with sessile algae must have lived at depths no greater than 200 m and probably no greater than 100 m (assuming no radical changes in insolation). It should be noted that these are limits and that the greatest abundance of algae is commonly within 20 m of the surface (EMERY, TRACY, & LADD, 1954); fossil sponges associated with large numbers of algae may have lived in very shallow water indeed.

A somewhat more equivocal criterion of shallow water environment is occurrence in or upon a fossil reef. Such a structure, when surrounded by an aureole of talus beds that clearly interfinger with the reef mass, must have formed in water shallow enough for wave action to break up the fabric of the reef while it was actively growing. It is difficult to place a numerical value upon a maximum depth for such an occurrence since it depends both on the force of the waves and on the construction of the reef. The mere occurrence of a reef structure, in the sense of a solid mass of autochthonous skeletal material that stood above the sea floor, does not guarantee shallow depth, for deep-water coral reefs are known from present seas and have sponges as members of the associated fauna (TEICHERT, 1958). Present-day tropical scleractinian-algal-foraminiferal reefs are limited to depths shallower than about 30 m because of limits on the algae and symbiotic zooxanthellae of the corals (WELLS, 1957). There is no secure basis for assuming that fossil reefs formed by organisms other than Scleractinia were confined to the same depths. Most fossil reefs, however, contain substantial quantities of calcareous algae and, thus, must have been limited to the photic zone as discussed above.

Lithologic criteria of shallow-water deposition include oolites, which form in water turbulent enough to suspend the ooliths while they received their successive coatings of calcium carbonate. Other criteria are of much more sporadic occurrence, although they may furnish quite precise indications of depths; an example is a limestone-boulder conglomerate of Miocene age deposited in localized depressions on a surface of unconformity and in which the boulders are extensively bored by various lithophages, including *Cliona* (RADWANSKI, 1964).

Finally, we may seek corroborative evidence from the sponges themselves. Three groups that are common as fossils have a present distribution confined to shallow and intermediate water depths. These are the Calcarea (0 to 600 m, rarely to 3,800 m), the Lithistida (0 to 2,200 m), and the Lychniscosa (80 to 700 m). At least some of the Calcarea have been associated with both algae and reefs continuously since the Permian. The Lithistida also have a nearly continuous association with algae and reefs since their first significant appearance in the Ordovician. They are also associated with both Calcarea and Lychniscosa since the first appearance of these groups. The Lychniscosa participated in construction of reefs in the Upper Jurassic, although associated with Calcarea and Lithistids, and may not be associated with algae. This would be in line with their present exclusion from waters shallower than 80 m. It is also in line with the conclusion of ROLL (1934) that talus associated with the German Jurassic sponge reefs was formed from later erosion of the dead reef following a fall in sea level. He based his conclusion on the fact that no binding organisms were present, the sponges merely serving as sediment traps; thus the living reef surface was not solid enough to be broken up by wave action. He discounted reports of algae by SCHRAMMEN (1924b). It should be noted that REID (1958b, p. 265) reported specimens of the Upper Cretaceous lychniscosan *Rhizopoterion tubiforme* to have healed breakage during life, presumably broken by rough water.

The Calcarea, Lithistida, and Heteractinida have had shallow-water representatives essentially throughout their history. The Amphidiscophora, on the contrary, have not been clearly associated with shallow water, although as early as the Pennsylvanian and as late as the Eocene they have been associated with lithistids (not necessarily shallow-water ones but probably not abyssal ones). The Lyssacinosa or Reticulosa have had shallow-water representatives at

TABLE 9. Distribution of abyssal genera of sponges (new).

Group	Abyssal genera	Exclusively abyssal genera	Present %
Demospongea	68	6	8.8
Monaxonida	58	5	8.6
Choristida	10	1	10.0
Hexactinellida	44	10	22.7
Amphidiscophora	14	4	28.6
Hexasterophora	30	6	20.0
Lyssacinosa	23	6	26.1
Hexactinosa	7	0	0.0
Lychniscosa	0	0	0.0
Calcarea	2	0	0.0

least from Devonian to Permian times but only doubtfully earlier (Precambrian to Silurian) or later (Triassic to Holocene). The Hexactinosa and Lychniscosa are associated with oolites and reefs in Jurassic deposits and with Calcarea and Lithistida in Cretaceous ones, but never or rarely with algae and possibly, therefore, never or rarely occurring in shallowest water. The Monaxonida have very shallow-water representatives at least as early as the Permian (probably earlier, but isolated monaxons cannot be assigned with certainty) and have freshwater representatives (Spongillidae) from the Jurassic on (NALETOV, 1961; HINDE, 1890). The Choristida have shallow-water representatives as early as their first appearance in the Mississippian.

Here and there we catch glimpses of more detailed patterns of distribution. In the Upper Cretaceous of northern France and Belgium a transgressive, shoreward conglomeratic facies is dominated by the lithistid group Rhizomorina with subordinate Sphaerocladina. A more seaward, quartz-sandy facies is dominated by Tetracladina, a limy-argillaceous facies by Hexactinosa, and the chalk by Lychniscosa (DEFRETIN-LEFRANC, 1961). Dominance is expressed both in variety of species and in number of individuals. It is apparent that the pattern is, in part, a reflection of bathymetry, but other environmental factors may be involved, most obviously the nature of the sediment substrate. For example, lithistids of the conglomeratic facies are encrusting forms that coat the boulders of the conglomerate (DEFRETIN-LEFRANC, 1961).

Contemporaneous beds of Northern Ireland discussed by REID (1958b, p. 261) differ in some respects because the glauconitic sandstone facies does not contain a rich development of tetractinellid Demospongea and because the chalk facies Hexactinosa and Lychniscosa of the chalk facies appear to occur in equal variety. REID (1958b, p. 264) suggested that nonbathymetric factors are involved in the distribution of Hexactinellida, inasmuch as Mesozoic Hexactinellida are predominant in calcareous sediments but are absent or rare in clays, such as in the Lias, that seems to have been deposited in similarly deep water. NESTLER (1961) noted the presence of the Pharetronid calcisponge *Porosphaera* accompanying Lychniscosa and Hexactinosa of the latest Cretaceous chalk of northern Germany (island of Rügen). Because modern Pharetronida range from 5 to 430 m; and, as REID (1958b) pointed out, modern Hexactinellida have as great a variety and abundance at 200 m as at any greater depth, a depth of the sponge-bearing chalk of 200 to 400 m accords with present day distributions.

Although the pharetronid Calcarea occur sporadically in facies where lithistids and hexactinellids dominate, their greatest development in the Cretaceous is in the glauconitic or greensand facies, but only very locally, as at the famous occurrences of Faringdon, England (Aptian), and Essen, Germany (Cenomanian). There they dominate to the virtual exclusion of other sponges. These are usually considered to represent very shallow-water, nearshore deposits, either formed in a rough-water environment or washed into offshore depressions from a rough-water source area (CASEY, 1961).

The Cretaceous bathymetric scheme can be traced back into the Jurassic (GAILLARD, 1983). WAGNER (1963) cited a coral reef from the upper Malm of Germany in which numerous silicisponges are present, namely, Hexactinosa, Rhizomorina, and Tetracladina. One layer in this reef, however, contains a large number of pharetronid calcisponges together with abundant encrusting calcareous algae that are notably absent from most of the reef. The association of Calcarea with algae makes a bathymetric explanation of the sponge distribution likely. In coral reefs of identical age and from the same general region that were described by FRENTZEN (1932), algae, Calcarea, and silicisponges (Rhizomorina and Sphaerocladina) occur together in the reef, and Calcarea dominate the talus fauna. In this seemingly shallower-water reef it is noteworthy that Hexactinellida and Tetracladina are absent from the sponge fauna, while the Rhizomorina and Sphaerocladina remain, the very silicisponges that are characteristic of the shallowest water in the Cretaceous (DEFRETIN-LEFRANC, 1961). In reefs of the lower Malm of the same region, corals and algae are absent; and the reef fabric is composed of Hexactinellid (Hexactinosa and Lychniscosa) with very subordinate numbers of Calcarea (DORN, 1932). Both the absence of algae and the presence of the Cretaceous deeper-water sponge fauna is consistent with a deeper-water site for these earlier reefs. The same conclusion about bathymetry was reached by ROLL (1934) from an independent line of reasoning, namely that the lack of binding organisms in the reef implies that the living reef could not have been wave resistant and therefore must have grown below the zone of rough water.

In the Triassic, records of siliceous sponges are too few for any bathymetric patterns to emerge, but abundant sphinctozoans and pharetronid Calcarea associated with algae are locally present as reef builders, and almost certainly lived in a shallow-water environment (SIEBER, 1937; FLÜGEL, 1981; SCHÄFER & SENOWBARI-DARYAN, 1981). Similar reefs of shallow and somewhat deeper environments also occur in Upper Triassic rocks of the southern Yukon (REID & GINSBURG, 1986; SENOWBARI-DARYAN & REID, 1987). The absence of siliceous sponges from these reefs is consistent with the same type of depth zonation seen in younger rocks.

The calcareous sponges of the Triassic provide a link with the Permian, for the same general fauna of demosponge sphinctozoans and Pharetronida is found in reefs and associated with algae (NEWELL & others, 1953; FINKS, 1971a). The Permian reefs of Texas, however, contain also subordinate numbers of Lithistida (Rhizomorina, Orchocladina, Eutaxicladina), Monaxonida (Heliospongiidae), Heteractinida, and two genera of lyssacine Hexactinellida. The lyssacines are a Paleozoic shallow-water element seen here for the first time, as are the exclusively Paleozoic groups, Heteractinida, Orchocladina, and Eutaxicladina. The same tendency for a bathymetric separation of Calcarea and siliceous sponges is nevertheless present. A basin facies of dark limestones in front of or marginal to the reefs contains a fauna dominated by siliceous sponges, in which there is a great proliferation of species of lyssacine and reticulosid hexactinellids at some localities (FINKS, 1960).

There is independent stratigraphic evidence that the basin lithofacies, in general, was deposited in water significantly deeper than that of the reefs. In the upper Guadalupian Stage the depth of water in the basin may have attained a maximum of about 545 m below the reef's surface, although it was apparently less during most of the Permian (NEWELL & others, 1953; NEWELL, 1957). In the vicinity of some patch reefs an autochthonous fauna of reef-type Calcarea has been collected in proximity to a rich basin-type fauna (FINKS, 1960, p. 33). This suggests that the bathymetric difference was not always large and that such factors as water agitation or nature of the sea bottom may have controlled distribution. The lithistids are common to both facies.

Beyond this point it becomes difficult to follow the thread. The presence of hexactinellids in lagoonal black shale above a Pennsylvanian coal seam (ZANGERL & RICHARDSON, 1963) and in Devonian reefs (LECOMPTE, 1936) reveals a persistent shallow-water strain in this group.

The most comprehensive data from the middle Paleozoic come from the middle Silurian reefs of Illinois (LOWENSTAM, 1948, 1957). Here we find the germ of later patterns. Sphaerocladines (*Astylospongia, Palaeomanon*), eutaxicladines (*Hindia*), and heteractinids (*Astylospongia*) occur in the interreef beds and in the lower levels of reefs. *Hindia* and *Astraeospongia* persist longer to midlevels of the growing reefs and, therefore, are considered to have been more tolerant of shallow water. In the rough-water stage of the mature reef their place is taken by the algal Receptaculitida (*Ischadites*). They are the bathymetric equivalents of the later Calcarea.

Still farther back, in mid-Ordovician (Chazy) times, orchocladine lithistids (*Zittelella*) are associated with algae in reefs, while lophophytous hexactinellids occupy the somewhat deeper water around them (Pitcher, 1964, and field observations of RMF, 1968). Here indeed is the earliest example of the persistent bathymetric separation of lithistids and hexactinellids. Earlier than this, secure data on relative bathymetry are not available, although one of the earliest lithistids, the Lower Ordovician *Archaeoscyphia,* is associated with algae in shallow-water deposits in the El Paso region of Texas and New Mexico (Toomey & Nitecki, 1979).

HOLOCENE SPONGE FAUNAL PROVINCES

Most living sponge genera are cosmopolitan or at least widely distributed in the world's oceans. Most species, on the other hand, are provincial. Arctic (Hentschel, 1929) and Antarctic (Burton, 1932) sponge faunas each have characteristic species, and their faunas appear to have differentiated out of faunas of the middle latitudes of neighboring seas. Burton (1932) pointed out that Antarctic species of the monaxonid sponges *Tedania* and *Iophon* appear to be more specialized relatives of lower-latitude species. Hentschel (1929) noted that the Arctic fauna has 60 percent of its species in common with the fauna of the North Atlantic, with which the Arctic Ocean is in open communication, while it has only 8.3 percent in common with the North Pacific, where the narrow Bering Strait (or at times in the past, a land bridge) forms a barrier. Opposite sides of the Atlantic appear to have different faunal assemblages (Burton, 1934), with those of the European-African side (including the Mediterranean) more closely related to that of the Arctic. The cooler marine climate of the east side of ocean basins, as a result of the upwelling of deeper waters brought about by the circulation pattern of surface currents, may account for this distribution. The Arctic monaxonid *Stylocordyla borealis,* on the other hand, has a deep-water distribution down the east coast of North America to the West Indies. Burton (1934) suggested that the deeper currents may distribute this species.

The Caribbean area forms a distinct province with a proliferation of species. It is related to a Brazilian province on the south and both of them to the vast Indo-Pacific province, whose center of species proliferation is in the Indonesian-Malayan region (Sollas, 1888). These three provinces form a nearly continuous circumtropical belt and undoubtedly owe their resemblances to common climatic conditions. Burton (1934) called attention to the similarity of Keratosa in the Caribbean and in coastal regions of northern Australia. This is perhaps not surprising inasmuch as both areas are on the western sides of ocean basins, where warm currents begin to turn poleward. The horseshoe crab *Limulus* is a well-known example of a genus with a similarly disjunct distribution in climatically analogous areas.

Sollas (1888) recognized, in addition, three temperate zone provinces in the southern hemisphere, associated with the three main continental masses, namely, a South African, a South Australian, and a Patagonian province. A separate Magellanic province occupies the cool-water antiboreal region of the southern end of South America.

Lithistids are most diversified in the Caribbean and Indo-Pacific provinces (Sollas, 1888). Data from the HMS *Challenger* expedition (Sollas, 1888) show that the Atlantic has fewer species of siliceous sponges than the Indo-Antarctic and the Pacific; the

TABLE 10. Numbers of species of deep-sea sponges (data from Lévi, 1964; new).

	ANTARCTIC	ARCTIC	ATLANTIC	INDIAN	PACIFIC	TOTAL*
Choristida	0	0	14	5	5	24
Monaxonida	4	12	75	15	23	114
Lyssacinosa	15	1	18	17	23	66
Hexactinosa	2	0	10	2	3	16
Amphidiscophora	1	0	4	14	41	61
Total	22	13	121	53	95	281

* Each species is counted only once.

Indo-Antarctic has a somewhat greater variety of Hexactinellida and Monaxonida than the Pacific; and the Pacific has a greater variety of Choristida and Lithistida than the Indo-Antarctic.

Deep-sea sponges have a rather different pattern. LÉVI (1964) compiled records of all species reported to that time from depths below 2,000 m. A summary of his data are presented in Table 10.

The Arctic deep-sea sponge fauna is dominated by Monaxonida, while that of Antarctica by Lyssacinosa. The Monaxonida also dominate the Atlantic deep-sea fauna, having four times as many deep-sea species as the next most diversified group, the Lyssacinosa. The Monaxonida are also much more diversified in the Atlantic deep sea than in either the Indian or Pacific deep sea or than in the Indian and Pacific together. The Choristida, Hexactinosa, and Amphidiscophora are virtually absent from the polar deep sea. The Hexactinosa are much more abundant in the Atlantic deep sea, having very few deep-sea species in the Indian or Pacific Oceans. The reverse is true of the Amphidiscophora, which have few species in the Atlantic but many more in the Indian and Pacific. The Amphidiscophora are by far the most diversified element of the Pacific deep-sea fauna. The Lyssacinosa are the most evenly distributed, except for their virtual absence from the Arctic.

The Lyssacinosa appear to have a southern center of distribution, spreading northward into all three seas, perhaps with Antarctic bottom water. The deep-sea Monaxonida, by contrast, appear to have a more northerly focus or perhaps an Atlantic one and dominate the interconnected bottom waters of the Atlantic and Arctic. The Amphidiscophora appear to have their center of distribution in the lower latitudes of the Pacific, perhaps the eastern part, to judge from most of the records (LÉVI, 1964). The Choristida and Hexactinosa are also mainly lower-latitude forms and not especially diversified in deep water. In general the bottom sponge fauna of the Pacific is mainly hexactinellid, especially amphidiscophoran; the Atlantic fauna is mainly monaxonid. As expected, faunas near the poles have less diversity than ones from lower latitudes; since we are dealing with deep-sea forms, these differences must be due to factors other than temperature or light. It is perhaps unexpected that the Atlantic has greater diversity of deep-water sponges than the other oceans, especially in view of the smaller diversity of its shallow-water sponges (SOLLAS, 1888).

GEOGRAPHIC DISTRIBUTION IN THE PAST

Provincial faunas probably existed in the past, but the limited distribution of rich sponge faunas in the fossil record makes it difficult to delineate such provinces. Sporadic examples show that contemporaneous local faunas often differ at the species level. It is obvious, for example, when studying collections from the rich middle Silurian sponge faunas of Tennessee and Gotland that although both faunas are dominated by the lithistid family Astylospongiidae, the specimens from Gotland are more robust and differ in details of surface ornamentations from those of Tennessee (see also RAUFF, 1894). On a more restricted geographic scale, a few genera of sponges out of a large fauna appear to have specific differences on opposite sides of the Delaware basin (approximately 60 km apart) in Leonardian beds of the west Texas Permian (FINKS, 1960). Local differences in environment or slight differences in time may account for these examples, rather than the separate evolution of isolated populations.

The tying of some sponge faunas to specific lithofacies and therefore to specific environments is frequently demonstrable in the fossil record. Their geographic distribution as preserved, however, may indicate only the chance preservation of the appropriate lithofacies and not the original pattern of their distribution. In the Upper Cretaceous, Hexactinellida are almost entirely confined to calcareous facies, while Calcarea dominate in sandy or glauconitic facies (REID, 1958b). In Europe, their distributions are related to the form of the advancing Upper Cretaceous sea, and a rich fauna is developed in both facies. Yet there is a possible wider pattern involved here, which is difficult to identify as to cause. The Atlantic Coastal Plain of North America contains an extensive series of sandy and glauconitic beds and the Gulf Coastal Plain a well-developed chalk facies, both being contemporaneous with the Santonian to Maastrichtian sponge-rich beds of Europe. Yet sponges are seemingly extremely rare throughout this vast region except for the calcisponge *Porosphaera* in the Gulf Coast chalk. Those sponges that do occur can be referred to European genera. There may be here the shadowy outline of some large geographic pattern, as yet impossible to delineate.

In the Permian, however, a truly global pattern occurs. The Calcarea and calcareous sphinctozoans are confined largely to the Tethyan realm (RIGBY & SENOWBARI-DARYAN, 1995). Abundant sponges occur at many localities at higher paleolatitudes outside the Tethyan realm, in the northern Laurentian-European realm or in the southern Indo-Australian realm, but there the sponges are entirely siliceous. The same pattern seems to be present in the preceding Carboniferous Period, although the number of localities available is fewer. A climatic zonation is clearly indicated by this pattern. Inasmuch as the Carboniferous was also a time of great diversification of the calcareous sponges, it is tempting to see the distribution as a reflection of their focus of origin. In view of the rapidity with which living sponge faunas are known to migrate, however, it is likely that these calcareous sponges would have spread to the limits of the available congenial environments within less than a geological period.

In the Triassic the Calcarea were more widely distributed than in the preceding two periods. One may argue that the distribution results merely from the distribution of shallow-water deposits because the Calcarea have always been concentrated in shallow waters. It is not possible to refute entirely this point of view because depth control on most of the exclusively siliceous sponge deposits is lacking, but at least one of them, the Park City Formation of the Wyoming Permian, appears to be of shallow-water origin (FINKS, YOCHELSON, & SHELDON, 1961). It is worth noting that the Permian and Triassic mark the acme of the Sphinctozoa and that both they and the Pharetronida are sufficiently dominant in shallow-water faunas during these periods that they are important reef builders. It is also worth noting that the geographic expansion of the calcareous sponges between the Permian and the Triassic may be related to the reduction of competition.

Siliceous sponges are almost completely absent from Triassic deposits, although they occur abundantly with calcisponges before the Late Permian extinctions. This cannot be weighed too heavily, however, because in the subsequent Jurassic and Cretaceous the

Calcarea not only lived together again with siliceous sponges but the Pharetronida also attained their greatest diversity. Perhaps world environmental conditions in the Triassic were more marginal than before or after and favored Calcarea over siliceous sponges. It is obvious that the calcareous sphinctozoan sponges survived and indeed thrived in environmental conditions that caused extinction of archaic Paleozoic groups during the later Permian. If the Permian geographic distribution of the calcareous sponges indicates a tropical adaptation, the adverse conditions could have been related to high temperatures.

PRECAMBRIAN

Sponges are known to occur in upper Proterozoic sequences from Mongolia, China, India, and Australia, but their discoveries have been reported only recently, and their record is so scattered and incomplete that suggestion of faunal provinces is impossible at this time.

Precambrian demosponges were reported from Vendian beds by LI, CHEN, and HUA (1998) from central Guizhou (South China), where small fossils have skeletons of siliceous monaxial spicules that are randomly oriented. These small fossils are mostly globular, with a few that are tubular, and reportedly have preserved evidence of former soft parts in the phosphatic replacements. Other possibly Vendian spicules have been reported by TIWARI, PANT, and TEWARI (2000) from the Lesser Himalayas, northern India, where isolated hexactines have been observed in the Gangolihat Dolomite.

Somewhat younger unequivocal hexactines were reported by BRASIER, GREEN, and SHIELDS (1997) from beds of late Ediacaran age from Mongolia. Other hexactinellid spicules have been reported from late Proterozoic Ediacaran beds from China by STEINER and others (1993). Complete skeletons of possible hexactinellid sponges were described by GEHLING and RIGBY (1996) from Ediacaran beds of South Australia, but identification of hexactines in the moldic preservation of these latter sponges was not possible.

CAMBRIAN

Cambrian sponge faunas are almost entirely Hexactinellida, Heteractinida, and Monaxonida and are widely distributed in broad outlines, cosmopolitan. Few entire sponges have been preserved, and regional differences cannot be identified. Isolated stauractines, pentactines, and hexactines are widespread in dark limestones of Middle and Late Cambrian age in North America (PALMER, personal communication, 1966). Several genera have been described from the Burgess Shale (WALCOTT, 1920; RIGBY, 1986a) that are not known elsewhere, but it is hardly possible to state that such a distribution represents an endemic development (WALCOTT, 1920).

ORDOVICIAN

Some Ordovician genera have a worldwide distribution, such as the Lower Ordovician orchocladine lithistid *Archaeoscyphia* known from all over North America (TOOMEY, 1964; TOOMEY & NITECKI, 1979; JOHNS, 1994; CARRERA & RIGBY, 1999), Argentina (BERESI & RIGBY, 1993; CARRERA & RIGBY, 1999), northern Europe (HACHT & RHEBERGEN, 1997; VAN KEMPEN, 1978; RHEBERGEN & others, 2001), Australia (RIGBY & WEBBY, 1988), and China (GRABAU, 1932; LIU & others, 1997). In North America the lithistid Orchocladina are the dominant element in the sponge faunas at most localities with abundant sponges (Antelope Valley Limestone, Nevada; Pogonip Group, Utah; Platteville Limestone, Illinois; Crown Point Limestone, New York). Possible endemism may be shown by the Nevada and Utah faunas (JOHNS, 1994), which contain several genera not known elsewhere, along with other genera that are more widespread, and by the abundance of Dystactospongiidae (Demospongea) in north-central United States

(Tennessee to Minnesota). Since the hexactinellid *Brachiospongia* occurs in the central United States and in Scotland, however, much more will have to be known about Ordovician sponges before conclusions can be drawn concerning provincial faunas. Hexactinellida are most abundant in black shales (Utica, Little Métis), the orchocladines may have lived in reefs (New York, Texas, Utah, and Nevada).

SILURIAN

The lithistid Astylospongiidae and Hindiidae and the heteractinid Astraeospongiidae seem to dominate Silurian centers of sponge abundance. Possible provincial differences between North America and Sweden have been discussed above. The North American astylospongiids and astraeospongiids appear to have their maximum abundance in a somewhat deeper-water facies between and outside of reefs (Lowenstam, 1957). Diverse assemblages of orchocladine, megamorine, and rhizomorine lithistid sponges occur with astylospongiids and hindiids in middle Silurian slope to basin assemblages in Arctic Canada (Rigby & Chatterton, 1989) and in the Northwest Territories of northwestern Canada (Rigby & Chatterton, 1999).

DEVONIAN

Although sporadic occurrences of heteractinids (Astraeospongiidae) and lithistids (Hindiidae) are widespread in limy facies, as for example in the reefs of the Canning basin in western Australia (Rigby, 1986b), the most diversified and widespread sponges are Hexactinellida of the family Dictyospongiidae. These are known from many parts of the world (Europe, Africa, North America) and occur mainly but not exclusively in sandstone. The well-known fauna from the Upper Devonian of New York (Hall & Clarke, 1899) contains many genera not known elsewhere and may represent an endemic development, as do the largely undescribed Devonian sponge faunas from Poland (Rigby, Racki, & Wrzolek, 1982; Rigby, Wrzolek, & Racki, 2001).

CARBONIFEROUS

The Carboniferous was marked by the first emergence of geographic patterns of distributions on a global scale, as discussed above. The calcareous sphinctozoan demosponges expanded in the late Paleozoic part of their record, as seen in the Upper Carboniferous in south-central United States, Spain, and Manchuria. Bashkirian representatives are known from Spain, and a Tethyan origin of later lineages is possible. They are not known from any of the many sponge-bearing localities to the north of the Tethyan belt, and since this pattern persists into the Permian, it indicates a genuine geographic restriction. Carboniferous siliceous sponges are mainly reticulosid Hexactinellida, rhizomorine and orchocladine Lithistida, and isolated spicules of the first Choristida. There is also a variety of Heteractinida that follow the distribution of the siliceous sponges and locally may be quite abundant. All these sponges occur with the sphinctozoans in the south-central United States, so the restricted distribution is mainly on the part of the later sponges.

PERMIAN

The Permian had a tremendous development of sphinctozoan demosponges along with the first Pharetronida. They are locally abundant in a belt that runs from the Mediterranean area including Tunisia, through the Himalayan region, southeast Asia, southern China, and Japan. They are also very well developed in south-central United States and northern Mexico. Outside these areas they are completely absent, although numerous Lithistida occur at many localities to the north (northern Rocky Mountains, Arctic Canada, Spitsbergen, Ural Mountains). There is less control in the southern hemisphere (Rigby & Senowbari-Daryan, 1995), but a rich lithistid fauna occurs in Timor. Siliceous sponges are associated with the calcareous sphinctozoans in Mexico, USA (Texas), and Tunisia. There is some indication of endemism among the calcisponges, for there is a great proliferation of the Guadalupiidae in Texas that are not common elsewhere, as well as several individual genera of sphinctozoans or Pharetronida that are confined to Texas, Sicily, Tunisia, or China. *Amblysiphonella,* on the other hand, is found everywhere that calcisponges occur. Endemism also seems to occur among the lithistids, with a variety of quite different genera of Orchocladina in Timor and Texas. A diversified lyssacine hexactinellid fauna is also known from the dark limestone facies of Texas that has not been recognized elsewhere. On the other hand cosmopolitan genera of lithistids, such as the eutaxicladine *Scheiia* and the rhizomorine *Haplistion,* occur almost wherever there are siliceous sponges. It is noteworthy that the sphinctozoans, along with other Demospongea and a few Pharetronida, participated in construction of reefs in Texas, China, and Tunisia, a habit that was continued into the Triassic.

TRIASSIC

Very sporadic occurrences of Hexactinellida are known from the Triassic, including the earliest representatives of the Hexactinosa (Anisian) and Lychniscosa (Carnian). Lithistida appear to be completely absent from published records. This paucity of silicisponges is striking when compared with the abundance of the calcareous sphinctozoans and Pharetronida, which continued their Permian abundance and diversity, in some instances even being assigned to Permian genera. The continuity of calcisponges contrasts with the sharp break in silicisponges, where nearly all the Paleozoic families were extinguished at the end of the Permian, and where the forms that straggle back into the record, in the later Triassic and Jurassic, belong mostly to new orders. The Calcarea extend their geographic distribution beyond that of the Permian. In addition to the rich Alpine European faunas, diverse Upper Triassic sphinctozoan faunas have been described by BOIKO, BELYAEVA, and ZHURAVLEVA (1991) from the Caucasus and Pamir regions of Russia, Tajikistan, and the far-eastern part of Russia. New Triassic faunas of calcareous sponges from central Iran have also been reported by SENOWBARI-DARYAN, SEYED-EMAMI, and AGHANABATI (1997). Calcareous sponges have also been found in Upper Triassic patch reefs in the Yukon Territory of western Canada (SENOWBARI-DARYAN & REID, 1987) and in at least two places in Indonesia. One of these latter places is Timor, which is of particular interest because calcareous sponges have not been recognized in the Permian section, although a rich fauna of archaic lithistids was developed. Another place to which the calcareous sponges extended their range is Peru. Marine Lower Permian faunas are known from Peru (NEWELL, CHRONIC, & ROBERTS, 1948), and they have considerable affinity to the contemporary faunas of Texas. Lower Permian sponges are not known from Peru, however, although Triassic ones are.

The Triassic sphinctozoans appear to have a decided development of provincial faunas, Peru, USA (Nevada), and the Canada (Yukon) forming one province, the Alps another, and Indonesia a third. The American province is more distinctive than the other two, although all three differ at the generic level as originally described. The Alpine and Indonesian faunas also have more continuity with the preceding Permian fauna and contain several Permian genera.

JURASSIC

Jurassic sponges are known almost entirely from Europe, where a rich fauna is developed in the limy beds, especially in the oolites of England, the Jurassic of France, and the Malm of Germany (GAILLARD, 1983). All the modern orders are present, some for the first time. No geographic patterns of distribution can be recognized in this small area save those imposed by bathymetry, discussed elsewhere above (p. 283). In the Jurassic the first record of the invasion of fresh water by sponges occurs also. Spongillidae occur in the Purbeck beds of England (Hinde, 1893b), in the region of Lake Baikal in Siberia (Naletov, 1961), and in the Morrison Formation of Colorado in the western United States (Dunagan, 1999). A record of Hexactinosa from Australia suggests the probable worldwide distribution of many sponges in the Jurassic despite the paucity of records.

CRETACEOUS

The Cretaceous appears to have been the peak of diversity of the phylum as a whole and of each of the three living classes individually. Yet this great richness is known to us almost entirely from the chalk facies and greensand facies of Europe. Contemporaneous facies in North America and elsewhere have not been nearly so productive. Part of this may be due to the longer history of intensive paleontological work in Europe, but it must reflect surely a real pattern of distribution as well. If the cause of the pattern is environmental, its nature is not apparent in the lithology of the sediments. No provincial patterns are apparent from the data; on the contrary there seems to be an essential uniformity.

The most significant feature of Cretaceous distribution is the presence at high latitudes in northern Europe of such groups as the Lychniscosa, Lithistida, and Pharetronida, which are today confined to lower latitudes (tropical in the instance of the Lychniscosa). Because the relative position of poles and continents was close to the present arrangement by the Late Cretaceous according to most interpretations, the distribution suggests either a warmer climate or greater tolerances on the part of the sponges. Because many of the sponges are of living genera and because the same expanded distribution of present warm climate types are shown by many other marine animals and land plants, the first alternative seems more likely.

TERTIARY

The Tertiary record of the Porifera is less abundant but more widely dispersed. The presence of Lychniscosa in the Eocene of northern Europe suggests the persistence of warmer conditions there than those of today. Paleocene pharetronids in Denmark and Eocene lithistids in Europe and New Zealand point to the same conclusion. Beyond this, little pattern emerges from the scanty data. In the Lake Baikal region, the endemic, still-living, freshwater sponges, *Lubomirskia* and *Baicalospongia* have been identified in sediments possibly as early as the Paleogene and certainly by the Miocene (Naletov, 1961).

DETERMINANTS OF SPONGE DISTRIBUTION

The distribution of any organism is determined by both positive and negative factors. Negative factors are (1) physical and chemical conditions that inhibit metabolism of the organism, and (2) competition from other organisms that preempt metabolites and space or that create unfavorable physical and chemical conditions. Positive factors are (1) presence of appropriate food species or other sources of energy and (2) presence of other organisms that facilitate metabolism, either through direct symbiotic relationships or through favorably modifying the physicochemical environment.

Limits of geographical distribution are set mainly by limiting physical and chemical conditions and by the availability of food or energy. In the instance of suspension-feeders such as sponges, the availability of food is a minor factor in limiting distribution, for usable suspended particles are available almost everywhere in the aquatic environment. Therefore, mainly physicochemical conditions limit the latitudinal and bathymetric distribution of sponges. Abundance, on the other hand, is determined by both optimum physicochemical and food conditions and by interactions with other organisms. Symbioses do not play a vital role in sponges, and local areas of abundance are probably determined by absence of competition as well as by optimum conditions.

It is well known that sponges tend to have a spotty distribution with local areas of great abundance. This is evident in the fossil record where some formations and localities are crowded with sponges (e.g., the Ordovician Antelope Valley Limestone of Nevada, USA; the Devonian Chemung sandstones of New York, USA: the Permian limestones of west Texas, USA; the Cretaceous Faringdon sponge gravel of England; and the Upper Cretaceous chalk facies of northwestern Europe). Such a spotty distribution occurs also in present seas.

A particularly instructive example is a large patch of Demospongea on the bottom of the Barents Sea, north of the North Cape of Norway, where the sponges constitute as much as 95 to 98 percent of the total biomass of the benthos (Zenkovitch, 1963, p. 145–146 and fig. 56). The sponges *Geodia barretti, Craniella cranium,* and *Thenea maricata* lie free on a mainly sandy bottom at 150 to 350 m depth and occur in such numbers that they seriously interfere with operations of fishing vessels. The biomass of this community, which averages 351 g/m^2 but locally reaches 5,000 to 6,000 g/m^2, is considerably higher than that of any other bottom community in the Barents Sea (the next highest averages 221 g/m^2, see Zenkovitch, 1963, fig. 56, reproduced herein as Fig. 133). The high biomass of the sponge-dominated community relative to those of the surrounding communities implies an optimum food supply. Manteufel (1938) has suggested that debris from the warm-water plankton brought in by the Gulf Stream and killed by the cold waters at the entrance to the Barents Sea may be the source of this food. Nevertheless, the fact that it is sponges rather than some other suspension-feeding organisms that take advantage of this food supply implies that some other factor is also involved that favors the sponges.

The absence of competition might be a reasonable explanation and is consistent with the following data. The sponge *Geodia barretti* was considered by Blacker (1965) to be an indicator of Atlantic water and presently attains the northernmost limit of its distribution, so far as the vicinity of Spitsbergen goes, along the west coast of West Spitsbergen. A recent compilation of water temperatures (Schröder, 1963) at a depth of 200 m in the North Atlantic, which is the approximate depth of occurrence of *Geodia barretti* off both Spitsbergen and North Cape, shows that the average temperature is approximately the same in the two localities, namely around 3° C. Furthermore, distribution of *Geodia barretti* appears to be controlled by temperature, because it has extended its range in the last few decades from south of Spitsbergen northward along its entire west coast, consequent to worldwide warming of the climate (Blacker, 1965). Since *Geodia barretti* is at the northern limit of its range at this temperature near Spitsbergen, it seems likely that it is also near the limit of its range near North Cape. Thus the abundance of *Geodia barretti* off North Cape is not likely to be due to optimum physical conditions, but rather to be in spite of the physical conditions. As pointed out above, an optimum food supply will not account for development of sponges to the virtual exclusion of other suspension feeders it must be the reduced viability of possible competitors in that environment that has permitted sponge numbers to expand so profusely, so close to the limits of their own temperature tolerances. Indeed, it may be the possession of a slight edge over competitors in a marginal environment that determines the abundant occurrence of sponges elsewhere, such as in the Antarctic. Such an explanation may account for many of the sponge concentrations in the fossil record as well.

One aspect of the food supply should be pointed out, however, for the food of sponges may differ from that of most suspension feeders. It has been shown (Madri & others, 1967) that sponges can consume great quantities of bacteria, and that prosopyles of flagellated chambers of most demosponges are scarcely large enough to

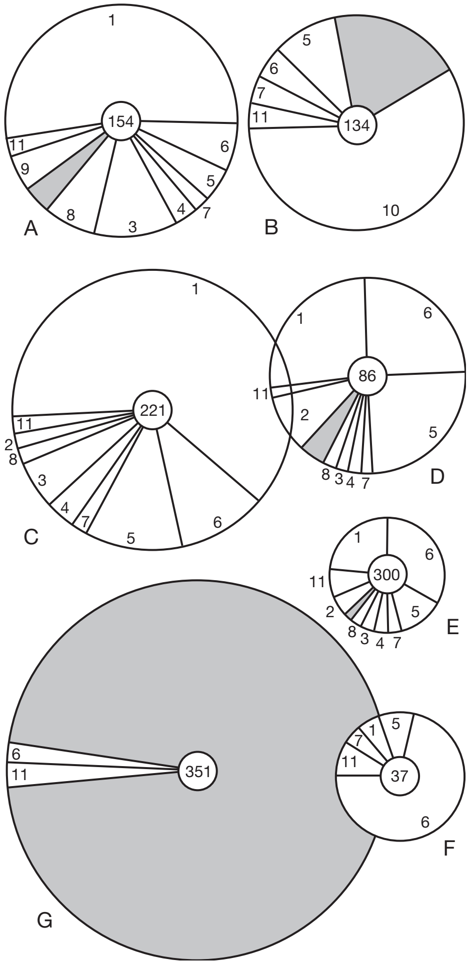

FIG. 133. Graphs showing composition of bottom faunas from seven localities in Barents Sea; *A,* Eastern (littoral); *B,* Northern (deep water); *C,* Eastern (medium depths); *D,* Central; *E,* Northern (littoral); *F,* Waldheimia-Brisaster; *G,* Porifera; *1,* Lamellibranchiata; *2,* Gephyrea; *3,* Crustacea; *4,* Coelenterata; *5,* Polychaeta; *6,* Echinodermata; *7,* Sipunculoidea; *8,* Gastropoda; *9,* Tunicata; *10,* Brachiopoda; *11,* Varia; *shaded,* Porifera; *numbers* in center circles refer to biomass in terms of g/m^2 (Zenkovitch, 1963).

admit a larger organism (see chapter on Physiology, p. 201 herein). Sponges are also capable of absorbing directly dissolved amino acids (Efremova, 1965).

Data are apparently unavailable on bacterial content of waters near North Cape, but an abundance of bacteria and dissolved organic matter, if it occurs, would explain the concentrations of sponges near the outlets of rivers. de Laubenfels (1958) has suggested this explanation for the concentrations of sponges near river mouths in Bermuda as well as for the concentration near the west coast of Florida.

Sponges in general are concentrated in two main environments of present seas, one in the sublittoral environment immediately adjacent to the land and the other in centers of ocean basins. Such a distribution is shown in Figure 134, a map of the northwestern Pacific by Filatova and Barsanova (1964). A survey of the Pacific as a whole (Sokolova, 1964) shows that in the center of the Pacific basin, sponges form more than 50 percent by weight of trawl catches. This focus of their relative abundance lies within a larger zone in which more than 50 percent by weight of trawl catches is composed of suspension feeders (Fig. 135). Detritus feeders and carnivores dominate a zone outside of this, closer to the land masses but still in deep water. It is apparent that in the center of the Pacific the organic matter available to benthic animals is chiefly in the form of suspended particles and that under such conditions sponges tend to become abundant. It appears, furthermore, that their concentration in the center of the suspension-feeder zone implies a greater ability to survive on lower concentrations of suspended matter than other suspension feeders and that they may thrive here because competition is reduced. This interpretation assumes that the concentric pattern indicates a gradient of decreasing particle density toward the center of the oceanic area, an assumption supported by figures for plankton productivity, which are 0.2 g dry organic matter/m^2/day in the open Pacific, versus 3.2 g for shallow, inshore waters (Odum, 1959). The sponges in question consist of the taxonomically rather limited abyssal fauna, mainly Amphidiscophora. It should be noted that total biomass of benthos in the central ocean area is very much less (by a factor of 10^5) than in the coastal zone (0.010 g/m^2 versus 1,000–5,000 g/m^2, Zenkovitch, 1963, p.

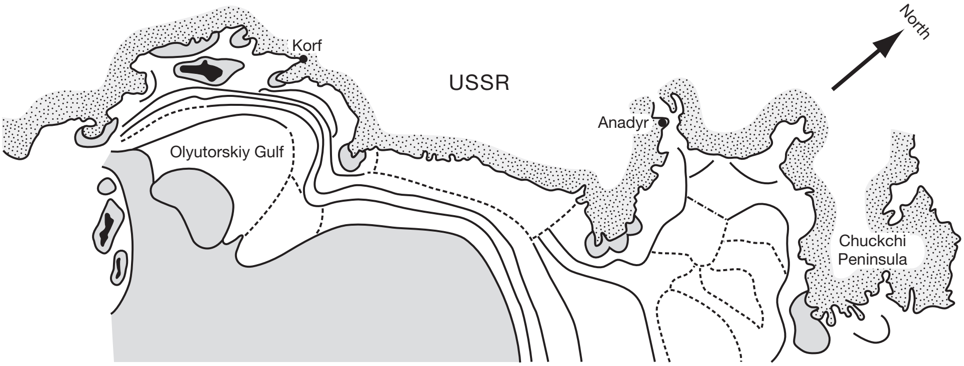

FIG. 134. Distribution of modern modern sponges concentrated in sublittoral environments adjacent to the Russian shore and in separated northwestern Pacific Ocean basin (Filatova & Barsanova, 1964).

723). Abundance of sponges in the coastal zone is probably related to the general abundance of food.

The Hexactinellida are most abundant today in deeper or colder waters. Their very open canal system and flagellated chambers provide lower hydraulic efficiency than that of most other sponges and seemingly require the passage of large quantities of water through the body at a slow rate (BIDDER, 1923; JØRGENSEN, 1955, 1966; see also chapter on Physiology, p. 201, herein). This implies a lower rate of metabolism than other sponges, which is already lower than that of most other animals (see chapter on Physiology, p. 203, herein). As mentioned above, their present distribution may reflect their ability to survive under conditions that are adverse for suspension feeders with higher metabolic rates. Their past distribution seems to have been in warmer and shallower waters, but it is tempting to speculate whether their times and places of abundance even then may have been relatively poor in suspended particles, sufficiently so to give them an advantage over suspension feeders with higher food requirements.

The Calcarea seem always to have been most abundant in the photic zone or a little below it. The greater solubility of calcium carbonate in colder water may be a limiting factor in relation to their calcium metabolism, although the existence of abyssal Arctic species shows that this can be circumvented if it is indeed operative. It is possible that the key to their distribution lies in their larval ecology, possibly involving a phototropic element, but knowledge on this point is insufficient to decide the question.

Distribution of Demospongea has been so wide and their apparent adaptability so great that any generalization about controls of distribution would have to be made at the level of species and genus. It is apparent that their tolerance of reduced salinity is greater than that of other sponges. Besides including the only freshwater sponges, several species are tolerant of brackish water. For example, *Cliona truitti* occurs in brackish waters with a salinity range as low as 10 to 16‰, whereas the marine species *C. celata* rarely lives in waters with a salinity below 25‰ (HARTMAN, 1958b). The Demospongea also include abyssal species that range as deeply as any of the Hexactinellida.

As for determining factors in the formation of faunal provinces, historical factors of isolation and connection are sometimes invoked, but in view of the radical changes in climate during the Pleistocene and the rapidity with which faunal boundaries can shift, this must be done with caution. BLACKER (1965) pointed out that the Atlantic fauna, including the sponge *Geodia barretti,* has spread northward for a distance of nearly 200 km along the west coast of

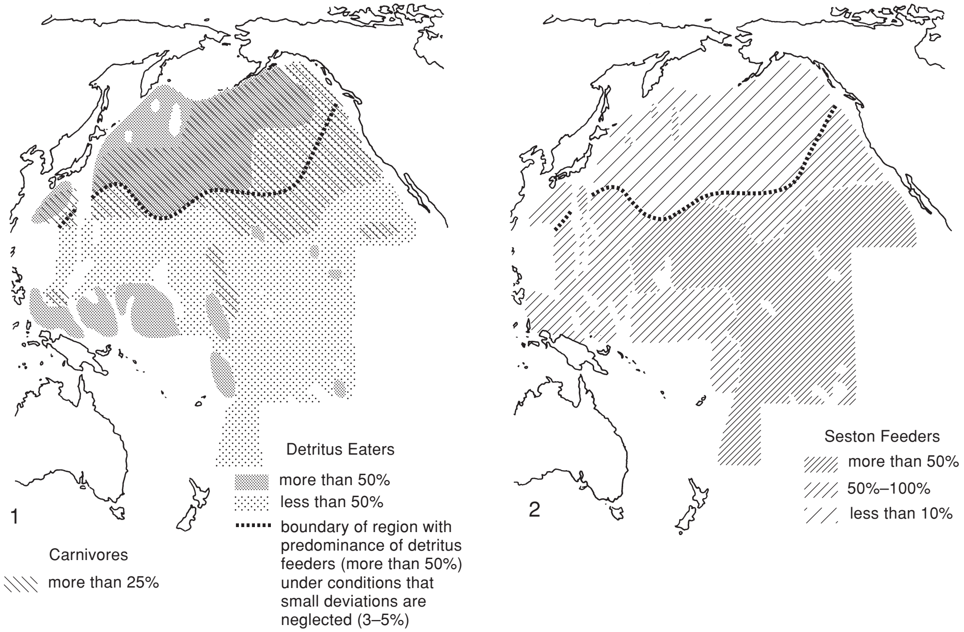

FIG. 135. Composition of trawl catches, by percentage weight, in northern and central Pacific basin; sponges make up more than fifty percent of suspension feeders in the central Pacific basin; *1,* detritus feeders; *2,* seston, or suspension, feeders (Sokolova, 1964).

Spitsbergen during the past few decades, presumably as a result of climatic warming, and replaced the Arctic fauna to as far north at 79°. *Geodia barretti* and other Atlantic-water indicators were not present at all along the west coast of Spitsbergen, as recorded in reports of oceanographic expeditions from 1878 to 1931, but were present in reports of expeditions made between 1949 and 1959. Inasmuch as the temperature changes in recent decades are very much less than those that accompanied glacial periods, fluctuations of faunal boundaries in the past must have covered much wider areas. Consequently there must have been considerable opportunity for mixing of latitudinally separate faunas, at least in the two major ocean basins. The present provinces may be largely climatically determined. Nevertheless, there is a degree of endemism in the Arctic and Antarctic (HENTSCHEL, 1929) and on the two sides of the North Atlantic (BURTON, 1934), which suggests that propagation of many faunal elements is coastal and that the open ocean may serve as a barrier.

TECHNIQUES OF STUDY

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INTRODUCTION

Observations of fossil sponges include such matters as spacing, density, diversity, life position, and orientation to be determined in the field; and growth form, size and arrangement of pores and canals, form of skeletal net, and form, size, and arrangement of spicules to be determined in the laboratory. The soft parts best studied in living sponges by histological and cytological techniques, can be studied as well in a limited way through skeletal correlates (e.g., the presence of spicules that normally support a dermal membrane, or skeletal canals that correspond to known structures of the aquiferous system); but much is lost, especially in the study of sponges whose skeletons fall part after death. The analysis of organic molecules concentrated in the vicinity of sponge fossils has not so far been published.

FIELD OBSERVATIONS

Where large bedding surfaces or a laterally extensive vertical section of a single bed are exposed, and sponges are sufficiently numerous, one can estimate the proportion of each species to the total fauna and their volume per unit area of sea bottom (biovolume of WALKER & BAMBACH, 1974). Both estimates can be obtained simultaneously by the -linear-transect method; that is by stretching a line or a series of lines in a grid pattern over the bedding surface (or along it in a section) and measuring the linear intercept of each species. When converted to a percentage, this is proportional to their basal area or to their volume. This is also true of point counts of their occurrences at intersections of a regular grid. Illustrations of these techniques were given by AGER (1963, fig. 14.3, 14.7, 14.8).

A test of spatial dispersion (that is, clumped, random, or even distributions) can be made by counting numbers of specimens in each square of a grid and testing its fit to a Poisson distribution. Many even more sophisticated distribution functions have also been developed in recent years. Detailed mapping of extensive bedding surfaces to show occurrence of larger patches of sponges can be used in favorable exposures. Gridded data can be subjected to many other statistical techniques, for example, trend-surface analysis of sponge size (for specimens clearly in place) to determine patterns of environmental conditions).

Orientations of oscules or of branches of sponges in life position are always worth recording, as a significant common orientation may indicate current directions (oscules tend to face down current and flabellate branches across current) (BIDDER, 1923; WARBURTON, 1960). Methods of determining statistical parameters of orientation data were given by REYMENT (1971). When feasible, it is desirable to record stratigraphic top and a compass orientation of each specimen collected.

Where well preserved, sponges should be collected as completely as possible with enough of the surrounding matrix to insure that such delicate, outlying structures as root tufts, dermal spicules, and prostalia have been included. Because sponges are irregular and complex in outline, care is necessary to see that the entire specimen has been removed.

LABORATORY STUDY

PREPARATION

Special problems in preparation of sponges arise from the fact that their surfaces are often irregular, and as a result mechanical separation from the matrix is not easy. Dermal spicules are often unattached to the rest of the skeleton and are delicate. If the sponge is siliceous or silicified and the matrix is a carbonate, the sponge may be freed by etching with acid. Where large numbers of specimens are to be processed or large blocks contain a mixed fauna, a less careful technique may be tolerated; but there is the risk of losing loose spicules or delicate structures. If specimens are unusually complete, rare, or delicate, as with lyssacine hexactinellids or nonlithistid demosponges, great care in using this method can be very rewarding.

The less careful method of processing is as follows. Completely cover the base of the limestone block containing the siliceous fossils with moderately viscous cellulose lacquer, continuing the coating about halfway up the sides of the block. This will prevent the acid from undermining the block, which would cause crushing of the fossils in the lower part. Then place the block in an acid-proof vat on a tray of acid-proof screening (fiberglass or plastic), just cover the block with water, and add an equal amount or half this amount of concentrated hydrochloric acid (technical grade will do). Adding a small amount of surfactant to the water will prevent the formation of foam and reduce the violence of the bubbling. Use of a weaker organic acid, such as acetic acid or formic acid will cause less violent bubbling, which is desirable if spicules are delicate, but it will lengthen the time required. (In such instances, however, it is better to use the more careful technique described below.) If the matrix is partly argillaceous, it will be necessary to wash gently the etched surface of the block with water from time to time to lay bare fresh matrix. If bubbling stops before the fossils are freed, more acid must be added, but it may be desirable to leave a delicate specimen only partly freed from the matrix. After etching is complete, neutralize any remaining acid with sodium carbonate and remove the screening with the contained fossils to a container through which a gentle current of water is made to flow for a period of several hours. After a thorough rinse, the fossils may be air dried or dried in an oven at low temperature.

For delicate or rare sponge specimens it is desirable to etch them separately. The acid may be applied with a brush or dripped, washing immediately with a dropperful of water and repeating until as much of the specimen as necessary is freed. If the spicular net shows signs of disintegrating, polystyrene dissolved in xylene, acetone, or some other thin lacquer may be applied to it with a small brush before proceeding further with the etching. The polystyrene solution should not be so thick that it obscures the spicules. Areas of matrix may be blocked off in the same way to prevent undermining by the acid. As unattached spicules appear they may be removed after their position has been noted.

A delicate specimen, completely freed from matrix by whatever method, may be strengthened by dipping in a very thin solution of polystyrene in xylene or acetone, or if extremely delicate, by spraying with clear acrylic resin obtainable in aerosol cans.

Calcareous specimens in a soft argillaceous or limy matrix or siliceous specimens in a soft, noncalcareous matrix are best prepared mechanically. An air-abrasive machine (e.g., that produced by S.S. White & Company) using powdered dolomite abrasive may work in some instances, but delicate spicules are frequently abraded or blown away. Using sharpened needles (dissecting needles or sewing needles in a pin vise) or dental drills permits the greatest control, but even the finest needles or burrs are often too coarse for a fine spicular net.

In the study of sponges without a rigid skeletal net or of sponges that do not differ chemically or mechanically from the enclosing matrix, polished sections, acetate peels (if calcareous), and thin sections are the only means of study. One section should be in an axial or sagittal plane, if such exists, and another at right angles to the axis; but the choice of orientations may need to be varied according to the often complex form of the sponge. Tangential sections at various points on the outer and inner surfaces may be needed to show the distribution of pores and of skeletal material in a surficial layer. Sections tangent to internal structures, such as canals and spiculo-fibers, may also be needed.

EXAMINATION AND DOCUMENTATION

In addition to the qualitative description of external form, patterns of skeletal canals on the interior, patterns of skeletal pores on exterior and cloacal surfaces, forms of spicules, localization of spicules, patterns of spicular arrangements, and microstructure of aspicular parts of the skeleton (sclerosome), there are also quantitative data that may be determined. These include size distributions of pores, canal diameters, spicule lengths, spicule-ray thickness, skeletal mesh spacing, thickness of trabeculae or spiculo-fibers, thickness of cortex, size of micro-ornament on spicules, and size of spherulites or other microelements of sclerosome. The extent to which statistical treatment of these measures is done depends on the purpose of the study, but for usual taxonomic purposes range, mean or mode, and possibly standard deviation are sufficient. Down to the generic level, shapes and patterns of distribution of morphologic features are sufficient for taxonomic discrimination.

For both study and illustration of spicules and of the microstructure of sclerosome, the scanning-electron microscope is the instrument of choice. The production of photographic stereopairs is relatively easy by rotating the specimen. Unfortunately the use of the instrument and the preparation of specimens is expensive and time consuming. For the study and photography of thin-sections and acetate peels, a biological microscope with high magnification (400X) and good optics is indispensable. For ordinary study of whole specimens, especially to examine the spicular network in three dimensions, a binocular microscope of considerable range of magnification (from 5X to 100X) is essential, preferably mounted on a beam with swiveling capabilities so as to permit the positioning of large, irregular sponges. Photography through such a microscope, with the camera replacing the eyepiece, usually gives better results than the use of close-up lenses on the camera. Careful adjustment of lighting and coating of the specimen with sublimated ammonium chloride often bring out fine spicular detail. Photography of specimens in black shale while they are submerged in xylene or water will often bring out good detail, but it should be done in a ventilated hood because of the poisonous nature of the xylene vapors.