ENCYCLOPEDIA OF EARTH SCIENCES, VOLUME XV

The ENCYCLOPEDIA *of* BEACHES AND COASTAL ENVIRONMENTS

EDITED BY

Maurice L. Schwartz

Western Washington University

Hutchinson Ross Publishing Company

Stroudsburg, Pennsylvania

Devonian, as well as five orders of living "true ferns." The latter group is represented by abundant fossils dating back to the Carboniferous period. The great majority of living ferns belong to the Filicales order, divided into 14 or more families containing about 170 genera, with nearly 9000 species (Scagel et al., 1965).

Fern leaves are typically in the form of large, feathery fronds that bear spore cases (sporangia) on the under surfaces. In a few genera spores are borne on specialized stalks believed to be reduced fronds. The stem may be very small, sometimes existing only as an underground rhizome, but in the tropical tree ferns the stem is enlarged to form a tall columnar trunk. Reproduction involves alternation of generations between a sexual gametophyte stage and an asexual sporophyte phase. The gametophyte consists of a tiny green platelike *prothallium* connected to the soil by hairlike roots. The prothallium bears two types of sexual organs, male *antheridia* and female *archegonia.* Unlike flowering plants and conifers, the fertilized germ cell does not develop into a seed; instead, the embryo grows into the familiar fern plant. This asexual form matures and produces spores, which are then released to develop into a new generation of prothallia. Fertilization only occurs when the archegonia is surrounded by a film of water. Thus ferns are most commonly found in moist habitats. Some varieties are capable of vegetative reproduction, such as by fragmentation.

Polypodiophyta are particularly abundant in the wet tropics, and constitute an important part of the flora of rain forests. Many species are herbaceous, but the range of habitats is quite diverse, and ferns occur as mosslike fronds, climbers, creepers, and tree- and shrublike forms. A few of the Filicales and the Marsiliales occur as partially submerged aquatic plants, while the Salviniales are found as small, free-floating plants on ponds and lakes. These aquatic ferns commonly have wide geographic distribution because waterfowl ingest their spores. Most terrestrial Polypodiophyta have only regional distribution, but some species have widely disjunct ranges because of wind dispersal of their spores. For example, the bracken fern (*Polypodium aquilinum*) is an agressive cosmopolitan weed (Smith, 1955). A few ferns live in arid regions, and at least one species is adapted to dry portions of salt marshes. Ferns of warm regions remain evergreen, but in cool temperate localities the plants die down during the winter, though the roots remain alive and produce new foliage in the spring.

LOUIS CUTTER WHEELER*
GEORGE MUSTOE

References

Scagel, R. F.; Bandoni, R. J.; Rouse, G. E.; Schofield, W. B.; Stein, J. R.; and Taylor, T. M. V.. 1965. *An Evolutionary Survey of the Plant Kingdom.* Belmont, Calif.: Wadsworth Publishing Co., 658p.

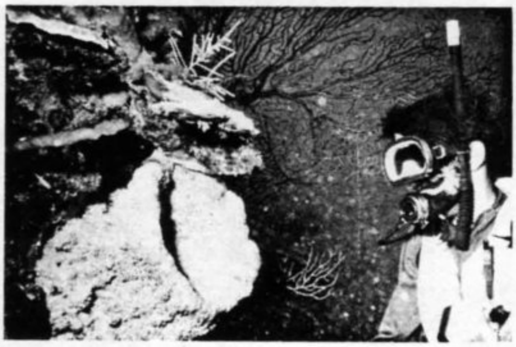
Smith, G. M., 1955. *Cryptogamic Botany,* vol. 2, *Bryophytes and Pteridophytes.* New York: McGraw-Hill, 399p.

Cross-references: *Biotic Zonation; Coastal Ecology, Research Methods; Coastal Flora.*

*Deceased

PORIFERA

Sponges (phylum Porifera) are sessile aquatic Metazoa of simple organization (Figs. 1, 2). They are filter feeders and pump water by means of characteristic flagellated cells (choanocytes) (Fig. 3), which are usually arranged to form small spherical chambers scattered throughout the body. Water enters a sponge through small pores (ostia) and leaves through larger openings (oscula) that are connected to



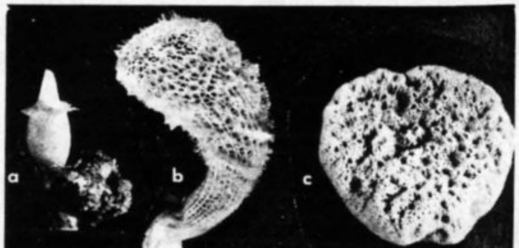


FIGURE 2. Representatives of the major sponge classes: *a. Sycon* sp. (Calcispongea) × 1.7; *b. Euplectella* sp. (Hyalospongea) × 0.3; *c. Spongia* sp. (Demospongea) × 0.4.

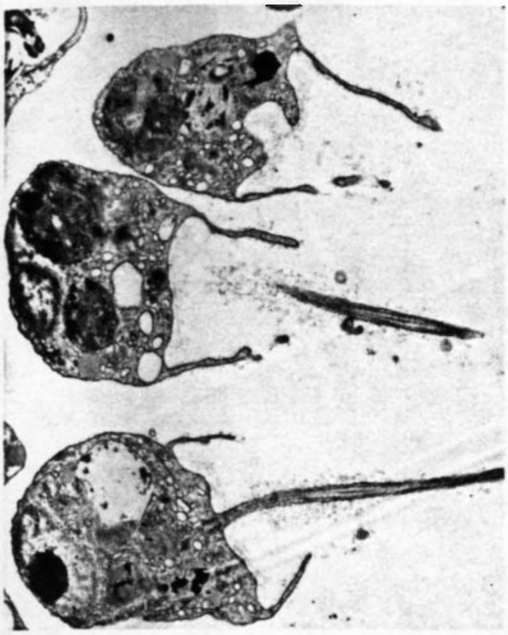


FIGURE 3. Portion of flagellated chamber lined with choanocytes (*Gelliodes* sp., Demospongea) × 7500 (transmission electron photomicrograph).

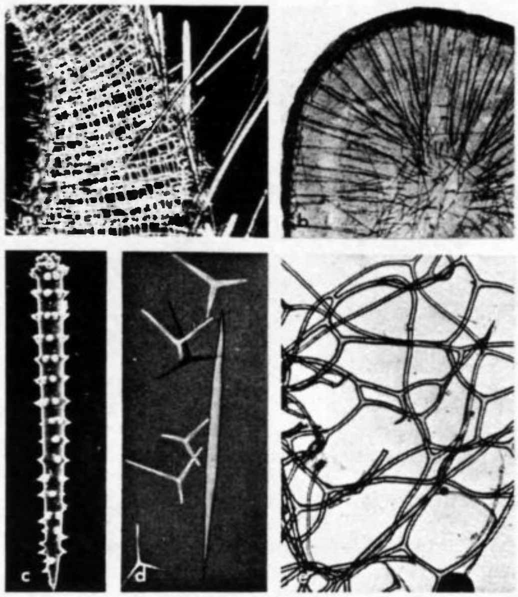


FIGURE 4. Sponge skeletons. *a.* Cross section through the body wall of *Sycon* sp. (Calcispongea); lattice of tri- and tetraradiate calcareous spicules, some large monactins protruding, × 27.5 (polarized light). *b.* Cross section through hemispherical *Stelletta* sp. (Demospongea); radial arrangement of silicious megascleres, × 27.5. *c.* Silicious spicule (acanthosty) of *Agelas* sp. (Demospongea) × 275 (scanning electron micrograph). *d.* Calcareous spicules of *Sycon* sp. (Calcispongea); monactin tri- and tetraradiates, × 68.8 (semipolarized light). *e.* Spongin fibers of *Spongia* sp. (Demospongea).

the choanocyte chambers by an incurrent and excurrent canal system. Most sponges have a skeleton of mineral (calcium carbonate, silicic acid) or organic (*spongin*) nature (Fig. 4), which is of great taxonomic importance. The skeleton supports a body that can be a mere crust a few millimeters in size or an irregular broad mass reaching 2–3 m in diameter. Sponges can assume a variety of shapes, including vases, tubes, and treelike branching rods. Every color of the spectrum, even some fluorescence, can be displayed by shallow-water sponges. The great plasticity in internal organization and the coordination of physiological events support the present view that sponges are individuals rather than colonies. Approximately 5000 species are known. Representatives of the phylum occur in all seas, depths, and climatic zones. The Spongillidae is the largest of the three families that occur in freshwater.

Evolution and Fossil Record

There are similarities between sponge choanocytes and certain choanoflagellates. *Proterospongia* is a colonial choanoflagellate but not acceptable as a transitory stage. Sponges are probably derived from flagellates that were also ancestors to choanoflagellates. Fossil sponges without fused mineral skeletons are generally poorly preserved. The first certain records are Hyalospongea from the Lower Cambrian. Demospongea appeared in the Middle Cambrian Period; Calcispongea not before the Devonian Period. Chert and flint are rocks that may be entirely composed of sponge *spicules.*

Classification

The principal criteria for separating the four classes of Porifera (Demospongea, Hyalospongea, Calcispongea, Sclerospongea) are the mineral composition and symmetry conditions in the skeleton. The largest class and the only one with quantitative importance in recent coastal environments are the Demospongea. The orders and families of this class are distinguished by structural features of the skeleton (major spicule types and spongin fibers) and by certain cytological and embryological characteristics. For the identification of genera and species the type, shape and size of spicules, details of the spongin meshwork, shape and pigmentation of individuals, consistency, surface structures, and arrangement and size of oscula and ostia are of great importance.

The Role of Sponges in Coastal Environments

Geographic Distribution and Depth. The continental shelves of tropical seas are particularly rich in sponges. The Indo-West Pacific, Central Pacific, and West Indian regions are distinct faunal provinces. The northeastern coasts of South America, the northwestern coasts of Africa, and the Pacific coasts of Central America and California have affinities with the West Indies. The Mediterranean Sea has subtropical character with elements from the Red Sea. The Arctic Ocean has mainly a fauna of boreal Atlantic and Pacific species. The Antarctic is rich in sponges with many endemic species. The upper limit of depth distribution is the lower intertidal. Sponges can not survive desiccation, but some can grow under rocks or algal cover or in tide pools in the littoral zone. They can be abundant in the shallow zone of photophilous algae, but there they are often restricted to areas of low light levels (for example, to caves in the Mediterranean). Highest quantitative values can be obtained in the zone of sciaphilous algae 30–100m.

Habitats. Because all adult sponges are sessile, they depend on the availability of solid substrates. They occur in great abundance on artificial structures—fouling on buoys, pilings, harbor walls. Mangrove roots and sea grass rhizomes are colonized unless they are intertidal. Rocky coasts, coral reefs, and all other hard substrate formations show almost invariably rich sponge populations. Some species connect pieces of gravel, thus creating new habitats in high energy environments. Certain sponges grow on protected soft bottoms if small substrate fragments for initial settlement are available; others can develop root structures for stabilization.

Physicochemical Factors. These always act in combination and cannot be isolated entirely. Temperature influences the geographic and bathymetric distribution, the growth rate of individuals and of spicules, and the time of reproduction. Light controls the distribution within small areas. It favors growth of plants that are competing for substrate but also of algal symbionts that are an important food source for some sponge species. Light gradients in shallow caves can generate population sequences similar to those that occur with depth, only on a smaller scale. Hydrodynamic conditions influence the growth form of sponges and interact with sediments. Fine sediment in stagnant water can have a smothering effect; coarse sediments in agitated environments act as an abrasive. Sufficient water exchange is important also for food transport. The prevailing water movement determines the stability of small substrates. Substrate inclination influences light conditions and exposure to sedimentation. Most sponges are adapted to normal ocean salinity. Only a few (for example, suberitid and clionid) species have invaded brackish water. Silicon is one of the most important mineral substances. Its presence controls the size and number of spicules. Other minerals promote the growth of microorganisms that are needed for food.

Biological Interactions. Under suitable conditions intensive competition for space can develop among sponges and between sponges and other sedentary organisms. Fast-growing incrusting species can be successful competitors by overgrowing and killing their neighbors—other sponges, corals, and bryozoans (Fig. 5). Many cases of epibiosis are also known where sponges grow on other organisms (e.g. on algae, on sponges, on majid, dromiid, and pagurid crustaceans) without harming them, and even protecting them (Fig. 6*a*). On the other hand, sponges can serve as substrate for settlers like algae, hydroids, zoanthids, barnacles and bryozoans (Fig. 6*b*). Some species, particularly those with a large interior canal system (for example, of the genera *Hippospongia, Ircinia, Spheciospongia*) can harbor a wealth of endobiotic associates, mostly polychaetes, nematodes, and crustaceans (Fig. 6*c*). With a few exceptions this relationship is inquilinistic and the sponge host is not harmed. An association of great nutritional advantage to sponges is the symbiosis with bacteria and unicellular algae (Fig. 6*d*). Bacteria and Cyanophycea occur in great quantities in a variety of Demospongea species. Dinoflagellates (Zooxanthellae) are known only from some clionid species. Preda-

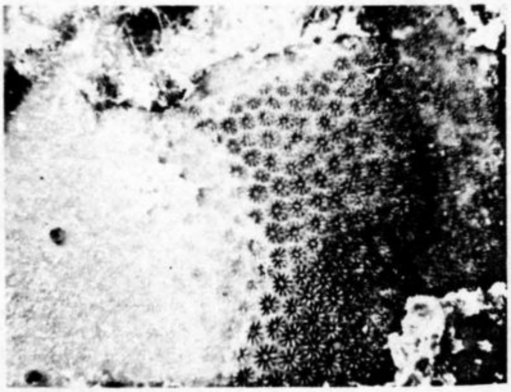


FIGURE 5. Spatial competition. Sponge (*Cliona* sp., left, two oscular openings visible) taking over live coral (*Montastrea* sp., right), × 1.

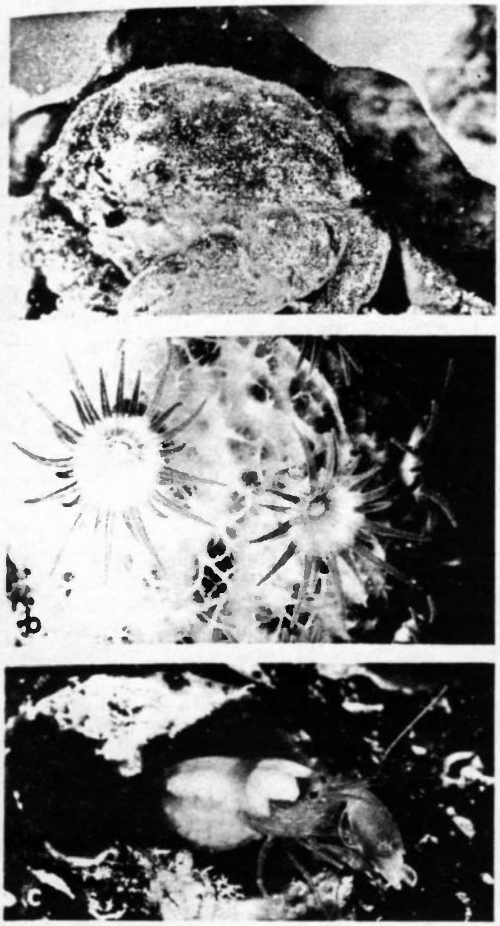


FIGURE 6. Symbiosis. *a*. Crab (*Dromia* sp.) carrying *Chondrosia* sp., × 0.7 (photo: K. Sanved). *b*. Zoanthid (*Parazoanthus* sp.) on *Gelliodes* sp., × 6. *c*. Shrimp (*Synalpheus* sp.) inside *Verongula* sp., × 0.8 (photo: K. Sanved). *d*. Bacteria and unicellular blue-green algae intercellular in *Verongula* sp.; one alga being engulfed by the large sponge cell, some vacuoles contain debris of previously digested symbionts, × 14,000 (transmission electron photomicrograph).

tors sometimes control the growth and distribution of sponge populations. Among these are endobiotic polychaetes and crustaceans, epibiotic mollusks (Nudibranchia) and several associated and nonassociated species of asteroid echinoderms and fishes.

Pollution. Since sponges function as powerful filter pumps, they could potentially purify water from bacteria and other filter organisms. However, they are sensitive to pollutants, and only a few species survive in eutrophicated water.

Commercial Sponges. Softness and absorbency have made the cleaned spongin skeletons of keratose species (genera *Spongia, Hippospongia*) a desired article for the household and for art and industry since antiquity. Sponge fishing centers were once located in the eastern Mediterranean, on the west coast of Florida and in the Bahamas. Because of overexploitation, disease, and introduction of plastic products, this industry has steadily declined during the past three decades. Attempts to cultivate sponges under controlled conditions were successful on a small scale but never gained commerical importance.

Bioerosion. A number of sponges, most of them belonging to the family Clionidae, are able to excavate limestone and to live in cavities or galleries formed by that activity. Water exchange is maintained through ostia and oscula, which are located on ectosomal papillae or incrustations at the surface of the substrate. Some species can reach a free, massive "gamma" stage after the available limestone support has been used up. The excavation is accomplished by special cell processes that free calcium carbonate fragments by etching around them. These chips are expelled through the sponge osculum, and form an important constituent of the mud-size fraction of many coastal sediments. An average clionid sponge population can erode as much as 250 gr of calcium carbonate per m^2/year. Excavating sponges cause most of the framework destruction in deep coral reefs (that is, below wave action). Clionid sponges have long been considered a pest in oyster cultures, where they erode the shells of the bivalves until the muscle supports break. Cultures in brackish water are safe; in other areas the sponge growth can be controlled by periodic exposures to low salinity.

Literature

A bibliography of early works, up to 1913, was presented by Vosmaer (1928). Later publications are listed in the continuing *Zoological Record*, published by the Zoological Society of London. The data summarized in the present article are found in greater detail in handbook contributions such as Hentschel (1923), Hyman (1940), Laubenfels (1955), Brien et al. (1973), and Bergquist (1978); and in symposium volumes edited by Fry (1970), Boardman, Cheetham, and Oliver (1973), Harrison and Cowden (1976), and Levi and Boury-Esnault (1979). The most recent summary presentations and some research papers that are particularly relevant to coastal ecology are by Reiswig (1973), Fell (1974), Rützler (1975, 1976, 1978), and Wiedenmayer (1977).

KLAUS RUETZLER

References

Bergquist, P. R., 1978. *Sponges*. Berkeley: University of California Press, 268p.

Boardman, R. S.; Cheetham, A. H.; and Oliver, W. A., Jr., eds., 1973. *Animal Colonies, Development and Function*. Stroudsburg, Pa.: Dowden, Hutchinson & Ross, 603p.

Brien, P.; Lévi, C.; Sarà, M.; Tuzet, O.; and Vacelet, J., 1973. Spongiaires, *in* P. P. Grassé, ed., *Traité de Zoologie*, vol. 3. Paris: Masson et Cie, 716p.

Fell, P. E., 1974. Porifera, *in* A. C. Giese and J. S. Pearse, eds., *Reproduction of Marine Invertebrates*, vol. 1. New York: Academic Press, 1-125.

Fry, W. G., ed., 1970. *The Biology of the Porifera*. London: Academic Press, Zoological Society of London Symp. No. 25, 512p.

Harrison, F. W., and Cowden, R. R., eds., 1976. *Aspects of Sponge Biology*. New York: Academic Press, 354p.

Hentschel, E., 1923. Porifera, *in* W. Kükenthal and T. Krumbach, eds., *Handbuch der Zoologie*, vol. 1. Berlin: Walter de Gruyter and Co., 295-418.

Hyman, L. H., 1940. *The Invertebrates: Protozoa through Ctenophora*. New York: McGraw-Hill, 726p.

Laubenfels, M. W. de, 1955. Porifera, *in* R. C. Moore, ed., *Treatise on Invertebrate Paleontology*, Part E. New York: Geological Society of America, 21-112.

Lévi, C., and Boury-Esnault, N., eds., 1979. *Biologie des Spongiaires*. Paris: Centre National de la Recherche Scientifique, 533p.

Reiswig, H. M., 1973. Population dynamics of three Jamaican Demospongiae, *Bull. Marine Sci.* 23, 191-226.

Rützler, K., 1975. The role of burrowing sponges in bioerosion, *Oecologia* 19, 203-216.

Rützler, K., 1976. Ecology of Tunisian commercial sponges, *Tethys* 7, 249-264.

Rützler, K., 1978. Sponges in coral reefs, *in* D. R. Stoddard and R. E. Johannes, eds., *Coral Reefs: Research Methods*. Paris: UNESCO, 299-313.

Vosmaer, G. C. J., 1928. *Bibliography of Sponges, 1551-1913*. Cambridge: Cambridge University Press, 234p.

Wiedenmayer, F., 1977. *Shallow-Water Sponges of the Western Bahamas*. Basel and Stuttgart: Birkhäuser, 287p.

Cross-references: *Algal Mats and Stromatolites; Biotic Zonation; Coastal Fauna; Coastal Waters Habitat; Coral Reef Coasts; Coral Reef Habitat; Mangrove Coasts; Organism-Sediment Relationship.*

POSTGLACIAL REBOUND

Postglacial rebound is a special case of *isostatic adjustment*, which is the vertical displacement of the earth's surface due to removal or buildup of loads on or near the earth's surface. In the general isostatic case, the earth's outer layers are viewed as behaving hydrostatically, as though they were floating on some compensation layer within the earth's *mantle*. Thus, any given column of the earth's outer layers tends to be in equilibrium so that it rises to a height proportionate to its mean density. If this equilibrium is disrupted by load additions or subtractions so that the mean density is altered, a given column will tend to move vertically in proportion to the density change until equilibrium is restored. In practice, only large scale changes (that is, sedimentary buildup of large deltas, water buildup in large reservoirs) have produced measurable displacements.

Postglacial rebound refers specifically to the vertical rise in a land surface caused by the removal of glacial and/or glacial water masses from it, such as occurred with the melting of the late Pleistocene ice sheets (Andrews, 1974, 1975). Rebound from this latest deglaciation has aggregated in excess of 300 m in some areas and continues at maximum rates of up to 1 cm/yr.

In general, if a glacier is in existence long enough to cause the earth's surface beneath it to be depressed into equilibrium, the total amount of rebound to be expected from the melting of the ice is proportionate to the thickness of ice removed, in a ratio nearly equal to the density of ice and the density of the earth at the compensation level (approximately 1:3). Such relationships can be used to estimate ice thicknesses if rebound amounts are known, or reversed to estimate rebound amounts if ice thicknesses can be determined.