PORIFERA, CNIDARIA, AND CTENOPHORA

G. Bavestrello
Istituto di Scienze del Mare University of Ancona, Italy

M. Sarà
Dipartimeto per lo studio del Territorio e delle sue Risorse, University of Genoa, Italy

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Summary

This chapter provides information on the most primitive phyla of metazoans regarded as plants by early naturalists: Porifera, Cnidaria, and Ctenophora. Porifera (sponges) and Cnidaria (sea anemones, corals, and medusae) include numerous species, while few species of Ctenophores (jelly combs) have been described. The greater number of the species belonging to these groups is marine based, but a few families of Porifera and Cnidaria are found in fresh water. Porifera are benthic and differ from other metazoans by their lack of true nervous and muscular cells. Cnidaria show two forms, the sessile polyp and the free-swimming, planktonic medusa. They are characterized by particular cells that contain stinging capsules (cnidocysts). Ctenophora, mainly planktonic and often living in the bathyal and abyssal zones, are a small group of uncertain affinity due to a musculature independent of epithelial cells and located in the mesoglea, that has been considered to belong to a third, mesodermal layer. All the groups are involved in relevant endosymbioses with autotrophic Cyanobacteria and Zooxanthellae.

1. Introduction

Porifera, Cnidaria, and Ctenophora are the most primitive clade of metazoans. They distinguish themselves from the other metazoans by their lack of bilateral symmetry. Inside their clade, each phylum is clearly distinguished by its general features. Porifera have a cellular, rather than tissular, level of organization, without any true nervous or muscular cells. For this reason, they were generally considered to be a separate sub-kingdom of Parazoa. However, this point of view has not been confirmed by recent phylogenetic analyses. Cnidaria and Ctenophora are lumped together because of their radial organization (Radiata), and were also joined together in the taxon Coelenterata. At present, they are divided in two different phyla on the basis of the more advanced organization of Ctenophora, and on the basis of molecular data. A remarkable relationship between Porifera and Ctenophora has been shown with molecular evidence.

2. Porifera

2.1 General Remarks

Porifera represent the most primitive metazoan phylum. They are usually called sponges. They include more than 6000 described species and inhabit all seas, where they occur attached to surfaces from the intertidal zone to depths of 8500 meters or more. Few families, chiefly the Spongillidae, are found in fresh water. Unlike the other metazoans, Porifera lack true nervous and muscular cells and, therefore, are called Aneuromiaria. Their cells are not organized in true tissues and organs. Adult sponges show no conspicuous movements of body parts and are fixed to the substrate. Marine sponges frequently have small and flagellated planktonic larvae.

Early naturalists regarded sponges as plants because of their frequent branching form and their lack of obvious movement. The animal nature of sponges was reported after observation of their water currents and the movement of their openings. Sponges were then grouped with Anthozoa (Cnidarians) in Zoophyta. Later on, because of their peculiar structure, they were considered as a special subkingdom of the animal kingdom under the term Parazoa. However, recent molecular phylogenetic studies have shown the true metazoan nature of sponges and their kinship with Radiata (Coelenterates and Ctenophora).

The phylum is divided into three classes: Demospongiae, Calcarea, and Hexactinellida, with Demospongiae including more than 80% of the known species of sponges.

2.2 Importance

The soft and elastic spongin skeletal framework of some species of Demosponges has been used by ancient Greeks and Romans for household items, in bathing, to apply paint, as mops, and as substitutes for drinking vessels. During the Middle Ages, burned sponges were thought to have therapeutic effects in the treatment of various diseases. Natural sponges today are mostly used in arts and crafts, such as in pottery and jewelry making, painting, decorating, and in surgery. Synthetic sponges have largely replaced natural ones for household use. However, commercial sponges, such as *Spongia officinalis, Spongia zimocca, Spongia graminea,* and *Hippospongia communis*, are still actively harvested. The living commercial sponge is a mass of cells and fibers, its interior permeated by an intricate system of canals that open through holes of various sizes across a tough, dark brown or black skin. The commercially available sponge, that is the soft spongin skeleton, is obtained only when the body has been completely cleaned of its living cells. The harvest is done by hooking or harpooning in shallow waters, by skin diving, or by deepwater fishing. Although the most valuable sponges are found in the eastern Mediterranean area, they are also harvested off the west coast of Florida and in the Florida keys, in the West Indies, off Mexico and Belize, and, to a limited extent, off the Philippine Islands. Because of their ability to regenerate lost parts, sponges can be cultivated from small fragments. However, due to slow growth, this is not a remunerative method.

Sponges have many compounds unknown in other animals. Some of these have been shown to have antibiotic and antitumoral properties. Intense research is currently in progress on this subject by many laboratories all over the world. However, basic scientific research is being done on the primitive organization of sponges. One field of investigation is free cell behavior, characterized by motile properties and cell dedifferentiation. Another is coordination systems, in the absence of nervous cells. As a matter of fact, sponges usually contract when handled or removed from water, while their oscula can close under various stressful conditions. A primitive system of coordination, with a likely chemical nature, seems to exist, and electrical impulses are assumed to be propagated over long distances, especially in Hexactinellids, which have a syncytial organization. Through the movement and coordination of their loose cells, sponges are also capable of small displacements on the substrate, of the order of cm per day. On the other hand, sponges are provided with an elaborate immune system that is in contrast with the plasticity of their organization and protects the self from non-self intrusion. However, sponges show outstanding morphogenetic and ecological plasticity with exceptional regenerative capabilities. A promising research field is looking at association with other organisms, especially bacteria. Endosymbioses produce relevant effects on the morphology, physiology, and ecology of sponges. The occurrence in sponges of homeobox and other genes similar to those present in higher animals, such as mammals, but with different functions, indicate that they are also interesting for molecular biology study.

Figure 1. Growth forms in marine sponges.
Top: the calcarean Ascandra falcata and the tubulose demosponges Agelas oroides and Aplysina cavernicola. Center: the massive Petrosia ficiformis, Chondrilla nucula and Chondrosia reniformis. Bottom: the papillae of the boring sponge Cliona celata, the encrusting Spirastrella cunctatrix showing the main excurrent canals and the tree-like Axinella verrucosa (courtesy of C. Cerrano)

Porifera are important components of many benthic communities such as those living in marine caves, coralligenous formations, coral reefs, and on the Antarctic shelf. In food webs, they play a role as filter feeders of the most minute planktonic fraction, such as bacteria. Other important ecological roles are related to the substrate. This may be covered, outcompeting other organisms, incorporated, bored (by sponges of the

Clionidae family), or cemented. Sponges are relevant in the geodynamic cycle of construction and destruction of rocky coasts. Porifera are also important as hosts of several commensal or symbiotic animals, algae, and bacteria. Particularly relevant are endosymbioses with Cyanobacteria and Zooxanthellae in marine sponges and with Zoochlorellae in fresh water sponges.

2.3 Form and Function

2.3.1 Size and Shape

Most sponges, often crust-like or cushion-like, are a few centimeters in size, but some are less than a centimeter. Others, shaped like vases, tubes or branches, may be one to two meters tall, with broad, round masses up to one or two meters in diameter. Size within a species may vary with age, environmental conditions, and food supply.

The external appearance of sponges is highly variable. Many are shapeless or amorphous masses that form thin incrustations or are cushion-shaped. Others may appear bushy, tree-like with finger-like projections, or have tubular, cup, fan or spherical shapes. Hexactinellids are erect, often cylindrical with a stalk-like base. Shape may change, to a certain extent, also within the same species, owing to the high degree of plasticity in sponges.

2.3.2. Color, Consistency, and Surface

Color among sponges is variable and frequently bright, ranging from red, yellow, and orange to violet, and occasionally black. Most Calcarea are white. Some sponges (e.g., Spongillidae) are often greenish, because green algae live in a symbiotic relationship within them, while other marine sponges are violet or pinkish, because they harbor symbiotic Cyanobacteria.

Another variable character in sponges is consistency, which may range from the soft and viscous state of some encrusting species, to the stone-like quality of the genus *Petrosia* and of Sclerospongiae.

The surface of a sponge may be smooth, velvety, or rough with protruding skeletal elements called spicules, or conulose (i.e. provided with protrusions called conuli, papillae, or tubercles).

2.3.3. Water Current System

Porifera are very primitive animals in that they lack well-defined organs to carry out their various functions. The most important structure is the system of canals and chambers, called the water current system, through which water circulates to bring food and oxygen, to excrete catabolites, and to carry gametes in oviparous sponges, and larvae in viviparous ones.

The essential elements of the water current system include a high number of microscopic pores, or ostia, through which water enters the sponge (incurrent system), the choanocytes, or collar cells, which are flagellated cells that capture food, and one or few macroscopic oscula, openings through which water is expelled (excurrent system). Three types of water current systems of increasingly complex structure—ascon, sycon, and leucon—may be distinguished, depending on the arrangement of choanocytes and the development of canals. The simplest, or ascon, type, found only in certain primitive genera of Calcarea, is characterized by an arrangement of choanocytes around a central cavity that directly communicates with the osculum. The walls of these sponges are perforated by pores, which are actually openings through cells (porocytes). The sycon type of water current system, found also in Calcarea, is characterized by choanocytes that surround finger-like projections, called radial canals, of the sponge wall. In the leucon type, which is found in the more advanced Calcarea and in all Demospongiae and Hexactinellids, radial canals are replaced by numerous, small, flagellated chambers in which the choanocytes are located. Water enters the microscopic pores found among the cells (pinacocytes) that line the outer surface of the sponge. After passing through a system of incurrent canals and cavities, also lined with pinacocytes, it reaches the choanocyte chambers, entering and leaving them through openings called prosopyles and apopyles, respectively. The water is then expelled through the osculum after passing through a system of excurrent canals and cavities lined with pinacocytes. During the development of many sponges, a simpler water current system (rhagon) precedes the leucon type.

2.3.4. Cell Types

Sponges lack a well-defined organization of tissues. Single layers of cells line the outer surface of the body and internal cavities; other cells, both motile and fixed, and fibers occur in an amorphous substance (mesohyl), gelatinous in nature. Cell types are different from those of other animals. They may be scattered or gathered, or may form layers or membranes inside the sponge. They have a remarkable ability to migrate and to transform from one cell type to another. Three main types of cells may be distinguished: choanocytes, archaeocytes, and pinacocytes-collencytes.
The choanocytes, which line choanocyte chambers or cavities, are provided with a flagellum, which is surrounded by a collar composed of cytoplasm. The main function of the flagellum is to produce the water current, whereas the collar is responsible for capturing food particles. Choanocytes may transform into gametes, especially sperm.

The archaeocytes, which are scattered in the mesohyl, have a remarkable potential to transform into different cell types. Some persist without specializing, thus forming an embryonic reserve from which other cell types may be derived; others become specialized in carrying out particular functions. One transformation is in amebocytes, motile amoeboid cells that are important for regeneration purposes and in the transportation of food particles throughout the sponge body. They may carry granules consisting of various substances and may take different names, such as spherulous cells, or thesocytes. Archaeocytes may transform into gametes, especially eggs.

Pinacocytes form the pinacoderm, a single cell layer found on the body surface and lining the canals. In Calcarea, the outer surface of the body also contains porocytes, flattened cells that contain the pores needed to let the water into the sponge.

Collencytes, found in the mesohyl, are elongated cells that often form a net in the cytoplasm with a support function. The sponge mesohyl, more or less rich in collagen fibers, contains other types of cells. Lophocytes, with long cytoplasmic processes at one end, giving them the appearance of a comet, secrete collagen fibers (spongin) with a skeletal function. Sclerocytes produce the calcareous or siliceous spicules of the skeleton. Myocytes are elongated and contractile cells, which may control the expansion and contraction of oscules; they may occur in rows and are considered as representative of a primitive conduction and contractile system that in sponges replaces the nervous and muscular systems present in other animals.

2.3.5. Skeleton

The skeleton of sponges is of great taxonomic significance. It may be mineral in nature (calcareous or siliceous) or composed of scleroproteins (spongin).

The mineral skeleton is mostly formed of units called spicules, either scattered throughout the sponge or united to form fibers. Spicules are classified as megascleres, with a support function, and microscleres, with a protection function and also aiding in the support function.

Calcareous spicules, characteristic of Calcarea, are mainly composed of calcium carbonate in its crystalline forms of calcite and aragonite. Calcareous spicules may have one axis (monoaxons) that is usually pointed at both ends; these spicules are called oxeas. Triaxons have three rays and are called triacts; tetraxons have four rays and are called tetracts. Siliceous spicules, found in Demospongiae and in Hexactinellids, are essentially made of hydrated silicic acid in an amorphous, opaline form. Proteinaceous organic matter, called spiculine, forms an axial fiber. The characteristic spicules of Hexactinellida are triaxon forms, with three orthogonal axes, and then six rays, which are called hexactines. Spicules are connected in a continuous network and, after the death of the sponge and the loss of its soft parts, the remaining skeleton acquires a delicate glass texture, as in the Venus basket *Euplectella*, which is used as an ornamental object. Bundles of large spicules form stalks that allow members of Hexactinellida to attach to the deep water, muddy bottoms in which they generally live. In the genus *Monoraphis*, the stalk is one enormous spicule that may reach a length of two or three meters and a thickness of approximately one centimeter. Siliceous spicules of Demospongiae, consisting of both megascleres and microscleres, have an enormous variety of forms and, consequently, a rich terminology. Megascleres may be monaxons, triaxons, and tetraxons; microscleres may be star-shaped (asters), sometimes with reduced or missing rays, and with other specialized shapes (sigmas, toxas, chelas, anchoras, and so on).

A few orders of Demospongiae lack skeletons. In some orders, a type of collagen (spongin) cements spicules in bundles or meshes, thereby increasing the elastic nature of the skeleton. In other orders, spongin fibers make up the entire skeleton. In commercial sponges, spongin fibers are particularly soft and elastic because they lack inclusions (grains of sand, fragments of spicules) that are present in other horny sponges. Some specialized, massive skeleton types are found in groups of great paleontological value, by now represented only by a limited number of Calcarea or Demospongiae species.

They consist of an amorphous mass of calcium carbonate to which calcareous (Pharethronida) or siliceous spicules (Sclerospongiae) are associated, while in polyphyletic Lithistida, they are built by fused siliceous spicules (desmas). The extinct Archaeocyatha—now considered to be sponges—had a massive continuous calcareous skeleton.

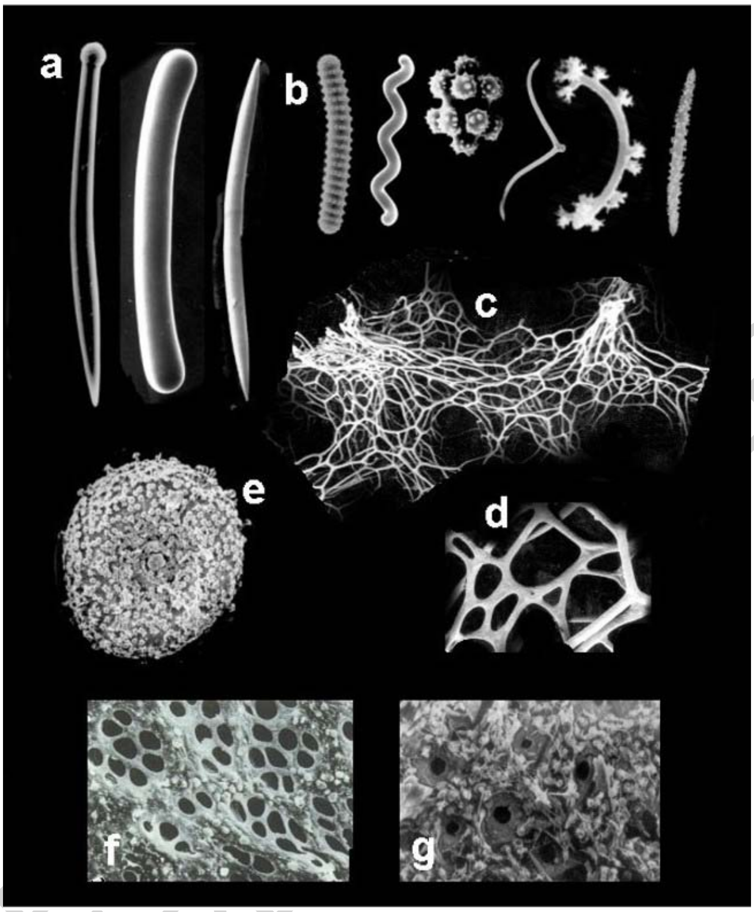

Figure 2. Anatomical details of sponge organization: a) macroscleres, b) microscleres, c– d) two different magnifications of spongin skeleton of the horny sponge Spongia officinalis, e) gemmule of a fresh water spongillid, f) surface of a demosponge showing the incurrent openings, g) internal side of a calcarean sponge with the layer of choanocytes (a) courtesy of R. Manconi; b) courtesy of B. Calcinai; c–d), courtesy of R. Pronzato; e) courtesy of R. Manconi; f) courtesy of C. Cerrano; g) courtesy of E. Gaino

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Biographical Sketches

Giorgio Bavestrello is Full Professor at the Istituto di Scienze del Mare, Ancona University, Italy, where he teaches the course of Zoology for biologists. His research topics regard the ecology and taxonomy of zoobenthonic organisms, particularly Sponges and Hydrozoans. Much of his research has been devoted to the three-dimensional architecture of the sponge aquiferous system.

Michele Sarà is Full Professor at the Dip.Te.Ris. of Genoa University, where he has taught the course of Zoology for biologists. His research topics cover the taxonomy, cell biology, and ecology of Sponges. His interests include theoretical studies about evolutionary process.