Porifera

Introductory article

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Porifera, or sponges, are primitive Metazoa. They are multicellular but have no developed tissue organization, utilizing independent cellular activity to carry out all body functions. They are a successful group in ancient and recent aquatic environments with origins in pre-Cambrian times.

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Introduction

Sponges are sedentary filter-feeding invertebrates in which flagellated cells, choanocytes, organized as a single layer, pump a unidirectional water current through the body. This current enters through a system of small pores (ostia), and exits by way of larger apertures (oscules). A system of canals conducts the water current between inhalant and exhalant apertures.

The organisms are isolated from the environment by a perforated epithelium, one cell deep, made up of squamous cells (pinacocytes). Neither the bounding pinacocyte layer nor the pumping choanocyte (collar cell) layer has the stabilizing basement membrane seen in other Metazoa; all cells retain mobility. Enclosed between these two epithelial layers is the mesohyl, a region which varies greatly in extent and which corresponds to the connective tissues of higher organisms.

Sponges, where mobile cellular systems carry out all vital functions, provide many clues as to how more complex systems have evolved.

The simplicity and flexibility of sponge organization has conferred many evolutionary advantages. They are a diverse group, some being among the largest and longest-living invertebrates; they occupy all marine habitats and have colonized fresh water; they have complex sexual and asexual reproductive processes and play important roles in benthic ecosystems.

All major recent higher taxa of Porifera were present in the early to mid-Cambrian. The significant events in sponge evolution thus took place in pre-Cambrian time. Sponge design and functioning can best be understood by considering what, in evolutionary terms, was necessary for organisms first to become multicellular (**Table 1**) and then to achieve integration of the body functions in the absence of tissues or organs.

Sponge cells retain a high degree of mobility and independence but the body functions as a whole. Integrated cellular behaviour achieves effective feeding, physiological exchanges, reproduction and dispersal of reproductive products.

How is this accomplished when there is no permanent histological system and when cells change their position, structure and function?

Where all cells are mobile, a requirement for integration is that like and unlike cells can recognize on contact, then adhere to or reject each other. Adhesion may be brief, an exchange of molecular signals, or more permanent when, for example, a group of cells cooperate to secrete fibrous and mineral skeletal elements.

The recognition and adhesion processes evident in sponges require operation of complex, membrane-located molecular arrays and appropriate genetic controls of their expression. Such systems provide insights into the evolution of immune systems, integrative systems and tissue and organ systems.

Basic Design

With feeding layer (choanoderm) and an external epithelium (pinacoderm) both only a single cell deep, the great part of the sponge body is mesohyl. This layer is made up of a collagen–polysaccharide matrix through which cells migrate, and in which the mineral and fibrous skeleton is secreted. Increase in size and strength of the body which permitted the diversification of sponges resulted from increase in volume and complexity of the mesohyl.

In simple (asconoid) forms the body wall is thin and water enters through single elongate perforate cells (porocytes) which traverse the mesohyl and open to the central spongocoel, lined by the choanocytes. The water current exits through an apical osculum. Few sponges have such asconoid structure (**Figure 1a**).

Greater complexity is achieved by folding of the epithelial layers and increase in volume of the mesohyl. A system of canals is developed to conduct the water to the now subdivided choanoderm and to permit water to flow from choanocyte chambers to exhalant oscules. Where choanoderm folding and mesohyl thickening have progressed only slightly and the canal system is simple, the sponge organization is termed syconoid (**Figure 1b**). In most sponges there is subdivision of the choanoderm into chambers dispersed throughout an extensive, regionally differentiated mesohyl and canal systems are complex. Such organization is termed leuconoid (**Figure 1c**).

Table 1 Factors required to become a multicellular organism

Cell recognition systems
Cellular adhesion systems
Cellular integration systems
Elaboration of a matrix or connective tissue
Skeletal systems to permit increase in size
Feeding, reproductive and dispersal mechanism

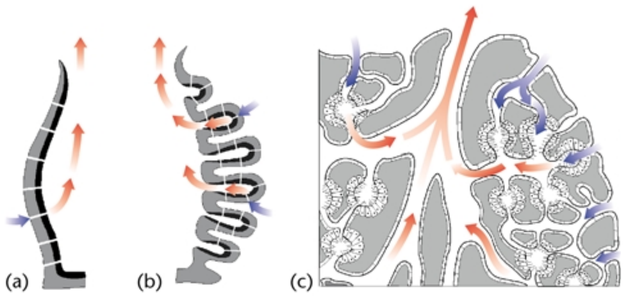

Figure 1 Organization of the sponge body: (a) half section of a simple asconoid; (b) half section of a syconoid with slightly thickened mesohyl and folded choanoderm and pinacoderm; (c) sector of a leuconoid, with subdivided choanoderm and extensive mesohyl, traversed by a complex system of canals. (After Bergquist PR (1998) Porifera. In: Anderson DT (ed.) *Invertebrate Zoology*, chap. 2, p. 13. Melbourne: Oxford University Press.)

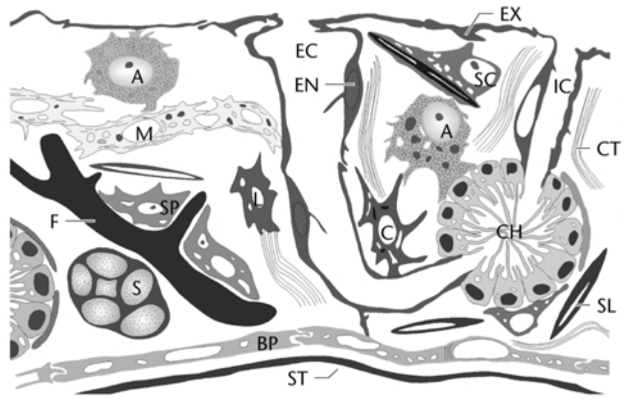

Figure 2 Stylized section of an encrusting, leuconoid sponge to illustrate the major cell types and their relationships. A, archaeocyte; BP, basopinacocytes; C, collencyte; CH, choanocyte chamber; CT, collagen tract; EC, excurrent canal; EN, endopinacocyte; EX, exopinacocyte; F, fibre; IC, incurrent canal; L, lophocyte; M, myocyte; SC, sclerocyte; S, secretory cell; SL, spicule in fibre; SP, spongocyte; ST, substrate. (After Bergquist PR (1998) Porifera. In: Anderson DT (ed.) *Invertebrate Zoology*, chap 2, p. 15. Melbourne: Oxford University Press.)

Cellular Function

Body functions carried out by tissues or organs in most animals are, in sponges, dealt with by individual cells acting independently or in small groups. Feeding involves choanoderm and pinacoderm; all other activities involve mesohyl cells (**Figure 2**).

Feeding

Sponges are predominantly particle feeders, exercising little selection. They pump a large volume of water, cycling the net body volume in 7.6 s.

The pores, the opening of the inhalant canals to the choanocyte chambers, the tentacles of the choanocyte collar and its mucous net represent a set of sieves in the path of the water current. Particles are extracted with high efficiency, with choanocytes accounting for 80% of organic carbon uptake. Surface and canal-lining pinacocytes can phagocytose particles directly.

Digestion takes place in large mesohyl cells (archaeocytes), which take up food vacuoles from choanocytes. Wastes are discharged directly through exhalant canal linings.

While particle feeding characterizes Porifera, and indeed is held to define the phylum, the recent discovery of carnivorous sponges emphasizes further the flexibility of sponge cellular systems. The carnivores are normally inhabitants of the nutrient-depleted deep sea but they have survived in shallow caves. They have no choanocytes or canals; surface pinacocytes flow over and then phagocytose small crustaceans, which become entangled in filamentous extensions of the body. Cellular resources, otherwise devoted to conducting the water current and to particle uptake, are dedicated to capture and phagocytosis.

Secretion

Sponges secrete copious amounts of mucus which often contains compounds with strong toxic effects. The most obvious secretory activity is seen in the development of the mineral spicule and fibrous spongin skeletons by 'sclerocytes' and 'spongocytes', respectively. Secretion of the fibrillar collagen mesohyl matrix is attributable to mobile, fusiform cells, 'collencytes' and 'lophocytes', and the polysaccharide matrix is laid down by heavily granular cells.

The mineral skeleton is either siliceous or calcareous, usually in the form of discrete elements, spicules which have a bewildering range of shapes, sizes and patterns of organization. The larger elements (megascleres) maintain the overall form of the sponge, while tiny spicules (microscleres) line surfaces. Fibrous collagenous skeletons occur either separately, as in bath sponges, or investing and binding siliceous spicules.

Cell recognition and rejection

The ability of sponges to accept tissue grafts of self and to reject grafts of non-self indicates that a histocompatibility system with attributes of those in higher organisms is operative. The 'immunocytes' in sponges are grey cells, heavily granular mobile cells which are responsive to an attractant released at the site of foreign tissue contact and which can remain activated for several weeks.

Totipotent cells

Sponge cells can be dissociated into cell suspensions and then, under appropriate ionic conditions, cells reassociate, or aggregate, to reconstitute individuals. Mixtures of cells of different species reconstitute separately. This process is guided by cell surface located proteoglycans and associated molecules. If dissociated cells are fractionated and fractions are then allowed to aggregate, only fractions containing archaeocytes and collencytes will reconstitute. The greatest contribution is made by the archaeocytes, which can give rise to all other cell types. They retain this ability to differentiate in diverse ways throughout life and are thus referred to as being totipotent.

Life Histories

Diverse sexual and asexual reproductive processes occur in sponges; but because they are not localized in tissues or organs, sexual processes are difficult to observe.

Sexual reproduction

Sperm develop from choanocytes, eggs from archaeocytes. When fertilization is internal, eggs and developing embryos are dispersed throughout the mesohyl. Once formation of a ciliated larva is complete it breaks free through canal walls and has a short free life (2 h to 21 days) before settlement and growth. Such development, where larvae are incubated, is termed viviparous and the larvae formed are either solid, well-differentiated structures (parenchymellae) or hollow undifferentiated blastulae. When eggs and sperm are extruded, often into mucous strings where fertilization occurs, and larvae develop outside the adult body, the process is termed oviparous.

Asexual reproduction

Asexual reproduction in sponges provides a mechanism for dispersal while maintaining attachment space, and for surviving extreme conditions.

The formation of gemmules, regression bodies with vitelline-loaded archaeocytes encapsulated within a spongin coat, characterizes fresh-water sponges. On hatching, all adult cells derive from the archaeocytes, an excellent illustration of their totipotency. Less-structured gemmules occur in some shallow-water marine sponges.

Formation of buds which subsequently detach is a common asexual process. Some are elevated on spicule stalks along which cells flow to form the bud; others are simply rounded pieces of surface tissue which are detached by wave action. Surface buds lack any internal organization, but despite this simplicity they are capable of intricate behaviour and precise substrate selection during the attachment period.

Habitats and Diversity

Sponges have colonized all aquatic habitats. Those with a calcium carbonate skeleton are limited, by factors controlling calcium secretion, to shallower waters; those with fibrous and siliceous skeletons occur from intertidal to abyssal depths.

In some habitats sponges are the dominant macrobenthic organisms, contributing up to 80% of the biomass. Consequently, their activities impact greatly upon marine ecological processes at macro- and microlevels.

Interactions with substrate

Some of the largest and longest living sponges (up to 300 years) occur in the southern polar regions. Under the ice shelf, communities have been studied directly and the age of individuals determined. In these still waters the siliceous spicules shed over long periods form a mobile mat several metres deep. Sponges are attached to the base rock below the mat, but conditions are rendered unsuitable for settlement of other organisms, particularly their echinoderm predators. Macrosponges in such habitats structure their immediate environment.

In all oceans, from tropics to polar regions, boring sponges occur and excavate calcareous substrates. In temperate waters they most commonly bore galleries in mollusc shells and coralline algae. However, in coral reef environments, bioerosion by the many species belonging to the genus *Cliona* removes 6–7 kg of calcium carbonate from the coral substrate in 100 days. This, depending upon the density of the sponge population, equates to removal of a coral layer 0.1 mm to 1.0 m deep per year. The pronounced subtidal notch seen on some reefs is the result of boring sponge activity over geological time. Boring sponges have a major role in structuring reef environments and in contributing to reef sediments.

Trophic ecology

In most coral reef environments 'macrosponges' make significant contributions to trophic exchanges. In some regions, many species contain symbiotic Cyanobacteria and Eubacteria. These sponges become net primary producers and contribute up to three times more oxygen to the sea water than they consume in respiration. Their importance to the reef ecosystem increases with distance from land as waters become less productive. There are interesting regional variations in the contribution sponges make to tropic exchanges; for example, along the Great Barrier Reef of Australia it is significant, in the Caribbean relatively minor.

Diversity

It is more difficult to estimate the number of species of recent sponges than it is to estimate numbers for higher invertebrate taxa. Since sponges do not have defined body regions, symmetry or appendages, deriving a robust, natural classification of the group has been and remains a problem. As a result, recognition and description of new species is a highly specialist task. Best estimates at present are that there are around 9000 described species and an equal number remaining to be described. Particular microhabitats, such as vertical rock and cave walls and galleries in rock and coral boulders, have barely been investigated to date, even in shallow seas.

Fossil History and Phylogeny

All major groups presently included within the Porifera were present and diversified in the lower Cambrian. Families and genera that survived until the late Mesozoic largely exist today. The discovery of living representatives of once dominant Palaeozoic and Mesozoic reef builders, the Stromatoporoidea and Sphinctozoa, has greatly assisted interpretation of the relationships of those fossil groups, now recognized as sponges.

Classification of recent Porifera recognizes three classes, diagnosed largely by the chemical composition and construction of the mineral skeleton. The Calcarea have massive or discrete calcareous spicular skeletons; the Hexactinellida have siliceous spicule skeletons, including some with three growth axes (hexactinal); and Demospongiae, the largest, most diverse modern group have siliceous and collagen, fibrous skeletons, either in combination or separately. Massive calcareous skeletons also occur in some demosponges, but the crystalline structure is aragonitic rather than calcitic as in Calcarea. Relationships within these long-separate classes are reflected in the subclass arrangements.

Further Reading

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