5

Porifera[P] and Placozoa[P]
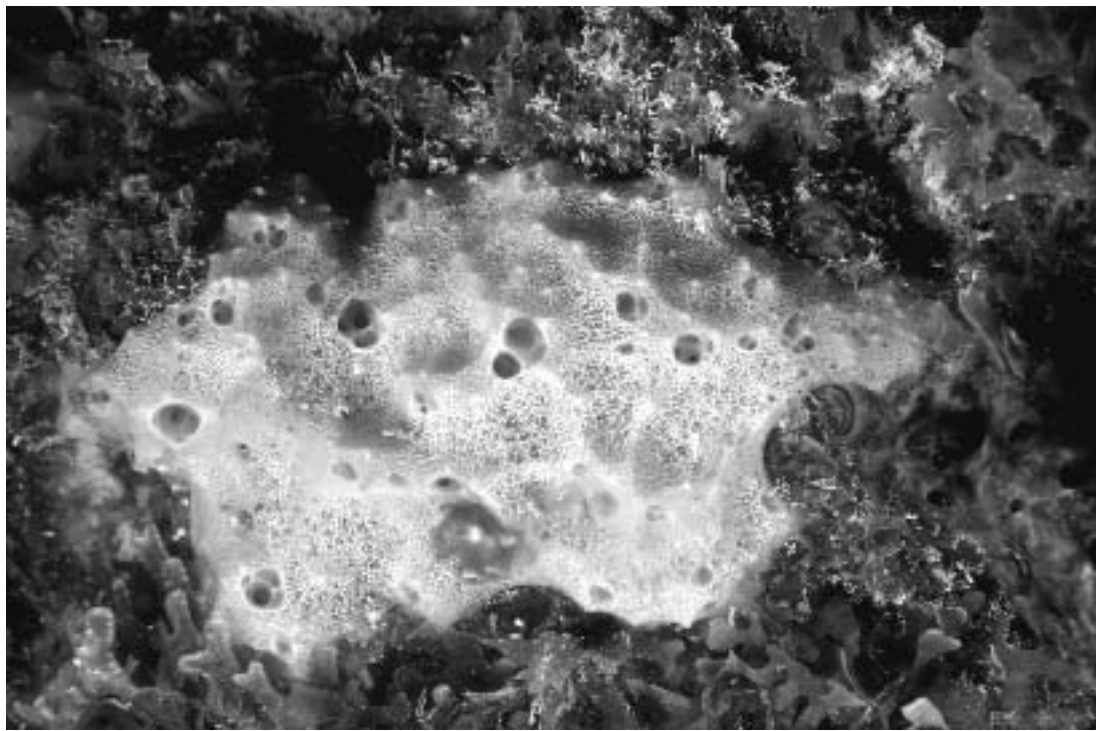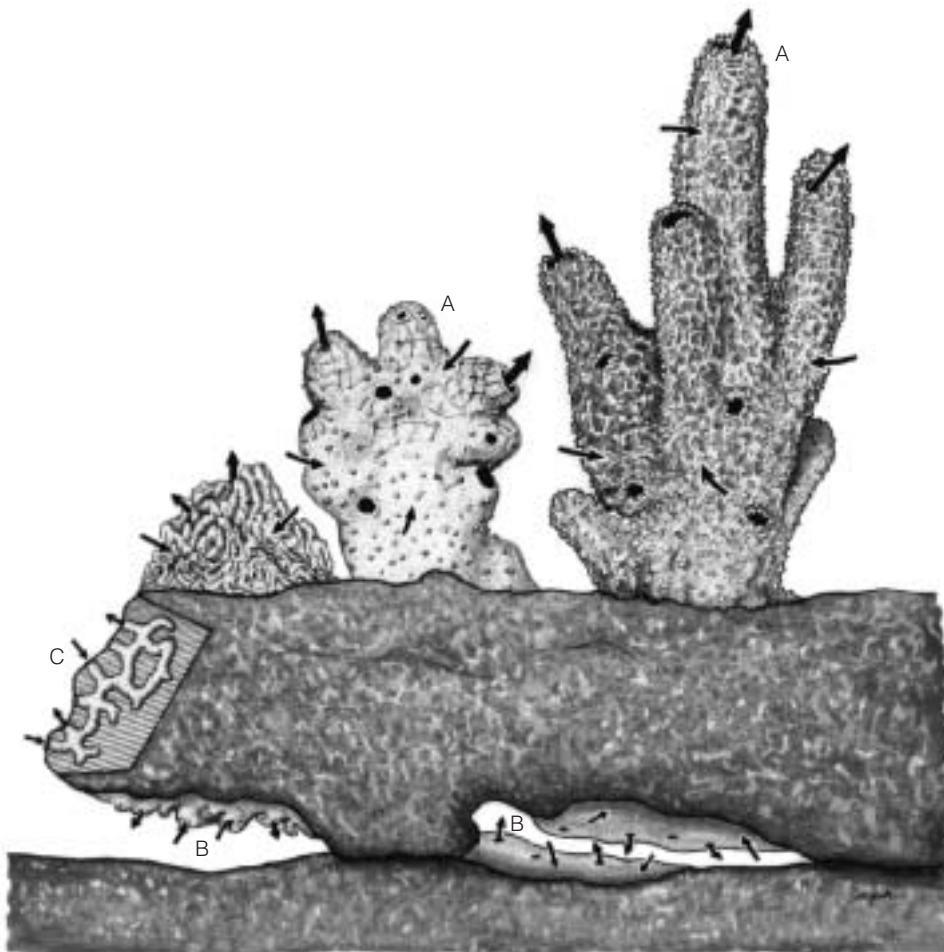
PORIFERA[P]

Sponges are a conspicuous and colorful component of many seascapes. The attached, often upright sponges are to coral reefs, sea grottoes, and floats what stalagmites and stalactites are to terrestrial limestone caves, except that sponge colors are as vivid and varied as those of van Gogh's flowers. When we look at sponges underwater in tropical seas, it seems a stretch to admit these motionless organisms with their irregular, often branched bodies to the pantheon of animals. Yet despite their superficial similarity to plants, they are indeed animals, but, like plants, they capture and concentrate dilute resources using their large surface area. Instead of relying on leaves and roots to trap light, CO_2, and water for photosynthesis, sponges have expanded their surfaces to catch the organic food particles suspended in seawater. Other, higher metazoans also evolved the ability to suspension feed, but sponges were surely the first to do so, and they continue to enjoy undiminished success. This chapter explores the functional design and diversity of these strange but engaging animals.

Sponges evolved a multicellular body uniquely specialized for **filter feeding,** the separation of suspended food particles from water by passing them through a mesh that strains out the food. The body is unique because it continuously remolds itself to fine-tune its filter-feeding system. This constant rearrangement of tissues is brought about by the ameboid movements of cells that wander throughout the sponge, adopt new positions, and change from one differentiated form to another. Such **dynamic tissues** and **totipotent cells** suggest that sponges are an intermediate form between protozoan colonies and other metazoans in which tissue and cell specializations tend to be more permanent. Because of its intermediate evolutionary status, Porifera generally is considered to be the sister taxon of the remaining Metazoa (Eumetazoa).

As the name Porifera (= pore bearers) suggests, the sponge body is exceptionally porous. Water enters through the pores and flows throughout the body in a system of flagellated canals. Food and other metabolites are removed from the water flow for use by the sponge. Adult sponges are sessile and attached organisms, although some are capable of limited movement of the body or its parts. The connective tissue is well developed and typically forms a complex and often elegant skeleton. Sponges range in size from a few millimeters to more than one meter in diameter and height (as in, for example, loggerhead sponges). The body symmetry may be radial (sphere, cone, cylinder), but asymmetry predominates. **Indeterminate growth,** enlargement without a fixed upper size limit, is common. The growth forms may be massive (thick), erect, branching, or encrusting, depending on the species and environmental conditions (Fig. 5-1). Many species are brightly colored red,


FIGURE 5-1   Porifera: growth forms of sponges and their relationship to microhabitat. **A,** Two massive sponges on top of a calcareous rock require an exposed surface, but their elevated form enables them to utilize water well above the substratum. The attachment area is a relatively small part of their total body surface. **B,** The encrusting sponges below the rock use much of their surface for attachment, but their low encrusting form enables them to exploit the limited space of crevices. **C,** The sponge on the cutaway vertical rock surface at the left actually utilizes space *in* the substratum. Arrows indicate water flow through the sponges.

purple, green, yellow, or orange, but some are brown or gray. The color results from cell pigments or endosymbionts.

Approximately 8000 species of sponge have been described. Most are marine, and they abound in seas wherever rocks, shells, submerged timbers, or corals provide firm sites of attachment. Some species, however, anchor in sand or mud. Most prefer relatively shallow water, but some taxa, including most glass sponges, live in deep water. Some 150 species have colonized fresh water.

FORM

The filter-feeding body of a sponge is built around one of three anatomical designs: asconoid, syconoid, or leuconoid. The simplest of these, the **asconoid** design, is a hollow cylinder attached by its base to the substratum (Fig. 5-2A, 5-3A). The body surface is covered by a monolayer of flat cells called the **pinacoderm** (= platter skin). The hollow interior, the **atrium** or spongocoel, is lined with a monolayer of
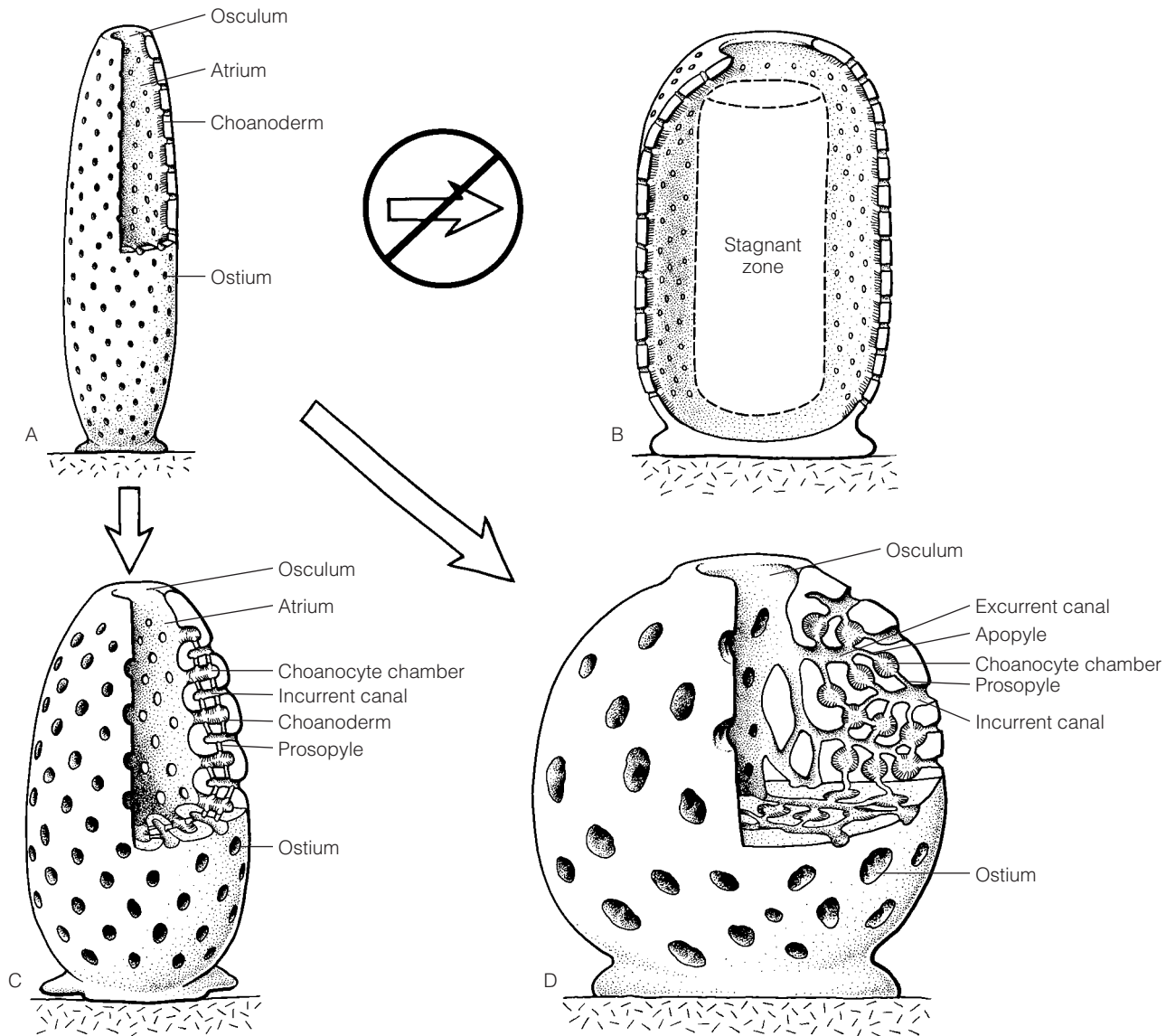
FIGURE 5-2 Porifera: relationship between body design and body size. **A,** Asconoid design, a simple cylinder approximately 1 mm in diameter, limits sponges to small body sizes. Water flow is created by the flagellated choanoderm. Because these flagella move water effectively only near the choanoderm surface, an increase in body diameter, as shown in **B,** would create a volume too large to be pumped by the flagella unless wall thickness increased or the body was redesigned. Large body size resulted from a change in *design.* **C,** The syconoid design, which results in sponges in the centimeter size range, improves the area-to-volume ratio by alternating surface inpockets with interior outpockets. **D,** In the leuconoid design, the flagellar pumps occur in thousands of spherical chambers and the water volume is restricted to minute capillary-like vessels that enter and leave the chambers. Leuconoid sponges can reach large sizes, in excess of 1 m.
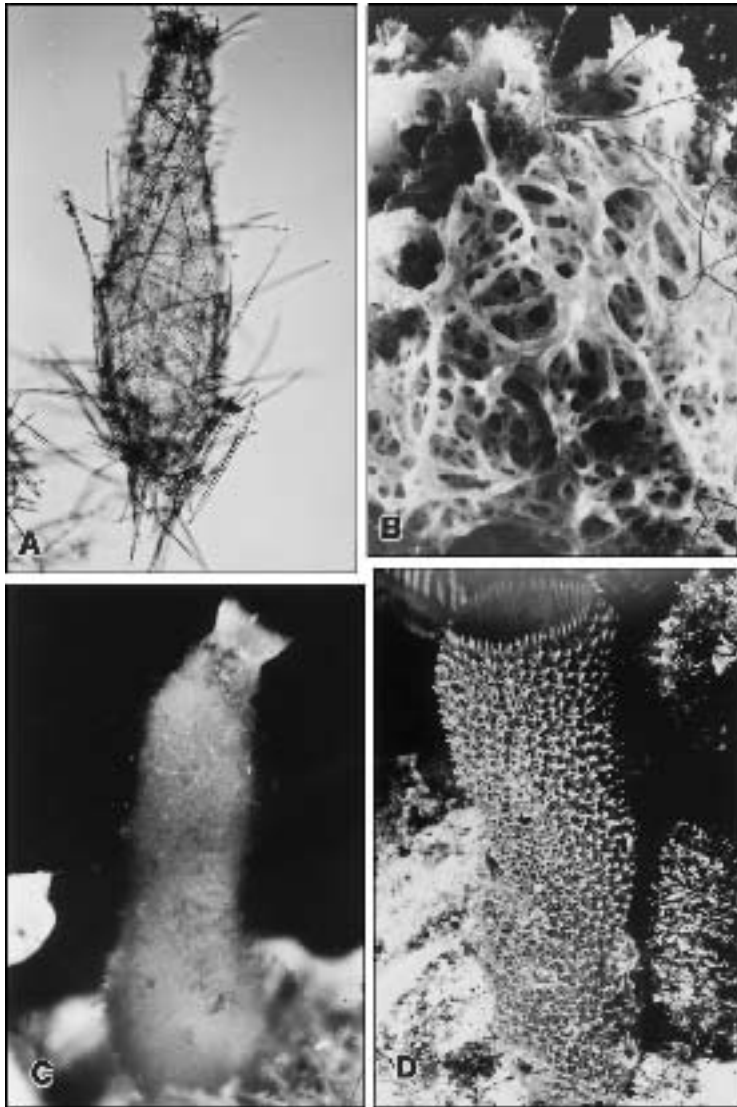
FIGURE 5-3   Porifera: living sponges of asconoid, syconoid, and leuconoid design. **A,** The asconoid calcareous sponge, *Leucosolenia* sp. (length ~1 cm); the asconoid calcareous sponge *Clathrina coriacea* (each tube in network ~1 mm in diameter); **B,** the syconoid calcareous sponge *Sycon barbadensis* (~3 cm in height); **C,** the leuconoid demosponge *Niphates digitalis* (~30 cm in height).

flagellated collar cells called **choanoderm** (= collar skin). Many small pores, known as **ostia** (sing., ostium) perforate the cylinder wall. A larger opening, the **osculum** (pl., oscula), is situated at the upper, free end of the body. The flagellated choanoderm creates a unidirectional water flow that enters the ostia, passes over the choanoderm en route to the atrium, and exits through the osculum. This circulatory system of choanoderm, pores, and chambers is called an **aquiferous system.**

All asconoid sponges are small and have cylindrical, or tubular, bodies, which typically do not exceed a diameter of 1 mm. Species of *Leucosolenia* may be a single tube or a cluster of tubes joined at their bases, whereas *Clathrina* species form a network of tubes (Fig. 5-3B). The asconoid design limits body size because growth in diameter produces an unfavorable area-to-volume ratio. The amount of water flow through the asconoid atrium (a volume) depends on the flagellated choanoderm (a surface). Because volume increases faster than area with growth, the body volume soon exceeds the pumping capacity of the choanoderm (Fig. 5-2B; see Chapter 4 for a general discussion of area and volume). Thus the attainment of larger body sizes in sponges required a change of design.

One such innovation, the **syconoid** design (Fig. 5-2C, 5-3C), increased surface area and reduced atrial volume by forming alternating inpockets and outpockets of the body wall. The arrangement can be visualized by interdigitating the extended fingers of your two hands and imagining that your fingers are hollow. The outpockets of the choanoderm are called **choanocyte chambers** (or radial canals). The inpockets of the pinacoderm are **incurrent canals.** Incurrent canals discharge into the choanocyte chambers via numerous small openings known as **prosopyles** (= front gates). At the outer surface of the sponge, water may enter the incurrent canals directly or first pass through a narrow ostium formed by a secondary growth of tissue. Thus, water flow in the syconoid

aquiferous system generally follows the route: ostia → incurrent canals → prosopyles → choanocyte chambers → atrium → osculum. This new design decreases the volume of the atrium and increases the area of flagellated choanoderm. As a result, syconoid sponges generally are larger than asconoid sponges. Their diameters are typically in the range of one to a few centimeters. Syconoid sponges include species in familiar genera such as *Grantia* and *Sycon* (previously called *Scypha;* Fig. 5-3B).

Sponges of **leuconoid** design achieve the largest body sizes, ranging from a few centimeters to more than one meter (Fig. 5-3D, 5-4B–E). In leuconoid sponges, the aquiferous system is a complex network of water vessels that permeate a solid, spongy body. It consists of spherical choanocyte chambers that lie at the intersection of incurrent and excurrent canals (Fig. 5-3D, 5-6). Small-diameter **excurrent canals** and often multiple oscula replace the relatively voluminous atrium and single osculum of asconoid and syconoid sponges. Water enters a leuconoid sponge via surface ostia before flowing into incurrent canals (Fig. 5-2D). From the incurrent canals, water passes through prosopyles into choanocyte chambers. Water exits each choanocyte chamber through an **apopyle** (= back gate) and then flows through the excurrent canals, which become progressively larger in diameter as they join with other excurrent canals. Large excurrent canals discharge exhaust water to the exterior via one or more oscula.

The choanocyte chambers of leuconoid sponges occur in high densities. In *Microciona prolifera,* for example, there are approximately 10,000 chambers/mm^3, each 20 to 39 µm in diameter and containing approximately 57 flagellated cells (choanocytes). The leuconoid design vastly increases the area of flagellated choanoderm while minimizing the water volume that must be moved.

Most shallow-water marine sponges and all freshwater sponges are built on the leuconoid design. Leuconoid sponges achieve large body size because water pumping is decentralized: Any growth increment produces a sufficient number of new choanocyte chambers to ventilate the new increment. Common leuconoid growth forms include crusts, mounds, branches, fingers, plates, tubes, and vases (Fig. 5-3D, 5-4B–E).

BODY WALL

The body wall is thin in asconoid sponges, thick in most leuconoid sponges, and intermediate in thickness in syconoid species, but a clear-cut distinction occurs between the glass sponges (Hexactinellida) and all others (Demospongiae and Calcarea). In demosponges and calcareous sponges (among which are most sponges), the body wall is cellular, but the glass-sponge body wall is a syncytium. A **syncytium** is a large or extensive multinucleated cytoplasm enclosed by an external membrane but not divided into cells by internal membranes.

Cellular

The bodies of demosponges and calcareous sponges (which together make up the Cellularia) are composed of cells organized into two types of tissue, epithelioid and connective (Figures 5-5, 5-6). **Epithelioid** tissue resembles epithelium (see Chapter 4), but it lacks epithelium's intercellular junc-

tions and hemidesmosomes and is not underlaid by a basal lamina (see Chapter 6). Sponge epithelioid tissues are the pinacoderm, which covers the outer surface of the body **(exopinacoderm)** and lines the incurrent and excurrent canals **(endopinacoderm),** and the flagellated choanoderm, which forms the atrial lining (asconoid design) and the lining of the choanocyte chambers (syconoid and leuconoid designs). The connective-tissue layer between the pinacoderm and the choanoderm is called the **mesohyl** (= middle wood) because it forms a bushy, fibrous network that is especially obvious in bath sponges.

The pinacoderm consists chiefly of two types of differentiated cells. By far the most common of these is the **pinacocyte** (= platter cell). Pinacocytes are flattened (squamous) cells that abut each other edge-to-edge to form a skinlike cellular pavement over the body surface and line the incurrent and excurrent canals (Fig. 5-5, 5-6). Pinacocytes generally lack flagella, except for species of *Plakina* and *Oscarella* that have a flagellated endopinacoderm lining their canals. A less common but nevertheless important pinacoderm cell is the **porocyte** (Fig. 5-5, 5-6). Porocytes form the ostia of all asconoid as well as many syconoid and leuconoid sponges. They also constitute the prosopyles and apopyles of many syconoid and leuconoid sponges, although in others the ostia are gaps between adjacent pinacocytes and the prosopyles can be simple gaps in the choanoderm. Each porocyte surrounds a pore, the diameter of which is regulated by contraction of cytoplasmic filaments. Thus, porocytes are miniature sphincter valves.

The mesohyl is the only layer of the sponge body wall that typically is not bathed with environmental water. In this sense, the mesohyl is the sole internal compartment of the body. As a connective tissue, the mesohyl is composed of a proteinaceous, gel-like matrix that contains differentiated and undifferentiated cells as well as skeletal elements (Fig. 5-5, 5-6). Among the many cells present in the mesohyl are macrophage-like **archeocytes** (= progenitor cells), which are large ameboid cells bearing a conspicuous nucleus and numerous large lysosomes. Archeocytes are totipotent and can differentiate into any other type of sponge cell. They are also phagocytic and play a role in digestion and internal transport. **Lophocytes** (= crest cells) are archeocyte-like ameboid cells that secrete collagen fibers from their trailing end as they move through the mesohyl. They produce and maintain the fine collagen fibers of the mesohyl. **Spongocytes,** which occur only in the taxon Demospongiae, resemble archeocytes, but secrete collagen that polymerizes into thick skeletal fibers known as **spongin** (see Skeleton, the next section). **Sclerocytes** (= hard cells) secrete the mineralized skeletal spicules of many sponges (see Skeleton). **Myocytes** (= muscle cells) are musclelike cells containing actin and myosin that aggregate around the oscula of some demosponges. They regulate the size of the oscular aperture and thus help to control water flow through the sponge. Finally, **oocytes** and **spermatocytes,** which will be described later in more detail, are reproductive cells that undergo gametogenesis in the mesohyl to form sperm and eggs.

The choanoderm consists of flagellated collar cells, or **choanocytes** (= collar cells), that generate the water flow through the sponge. Choanocytes have an apical collar of long microvilli around a single flagellum (Fig. 5-5). The collar is in
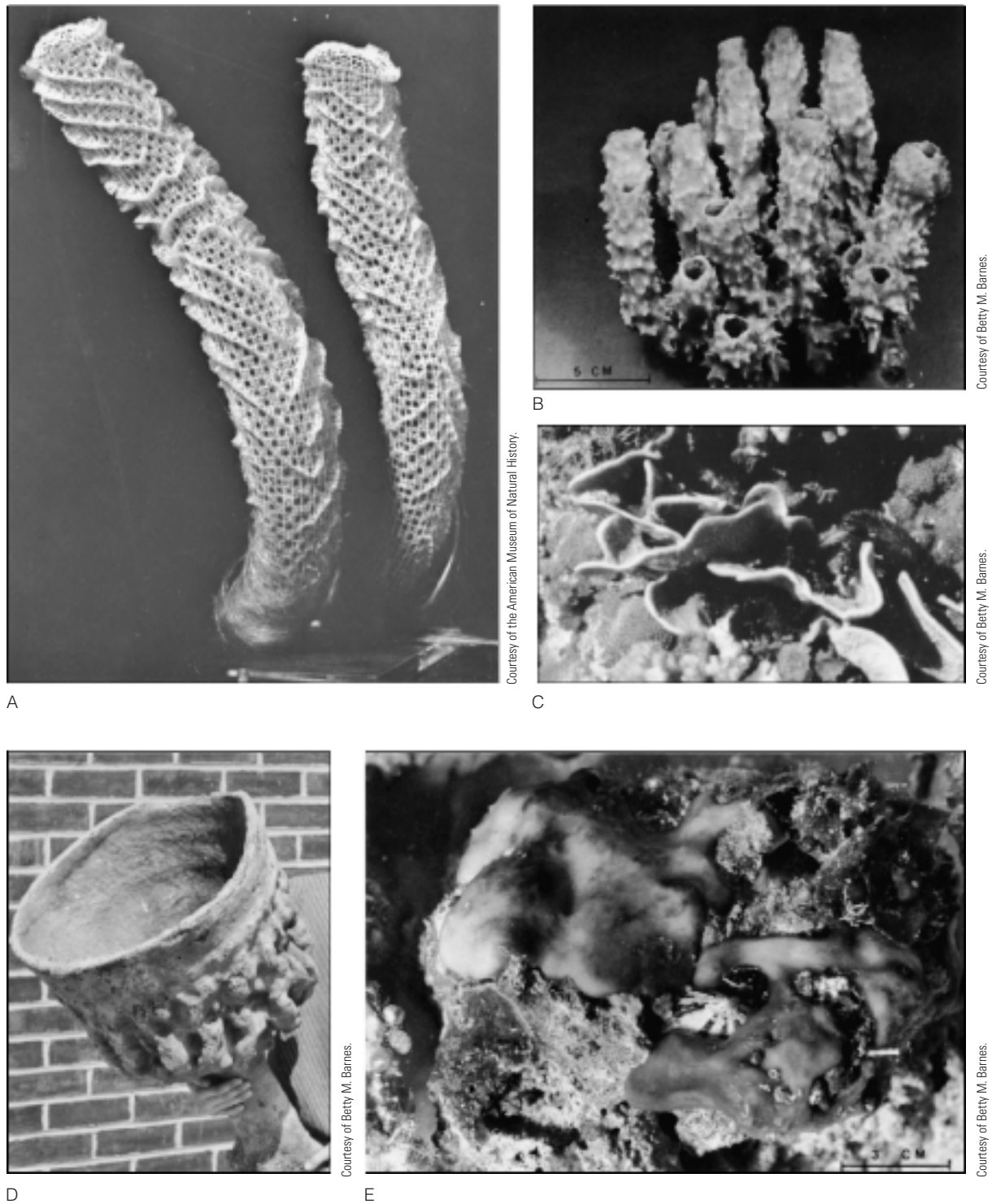
FIGURE 5-4   Porifera: living **(B, C,** and **E)** and preserved sponges **(A** and **D)**. **A,** *Euplectella aspergillum,* Venus's flower basket, a glass sponge (Hexactinellida) in which the siliceous spicules are fused to form a lattice. **B,** *Callyspongia vaginalis,* a tropical leuconoid sponge (Demospongiae) with a tubular body form. **C,** *Phyllospongia,* a leaflike sponge (Demospongiae) on a reef flat in Fiji. **D,** *Poterion,* a large goblet-shaped leuconoid sponge (Demospongiae). **E,** *Chondrilla nucula,* a common West Indian sponge (Demospongiae) with a tough, cartilaginous spongin skeleton.
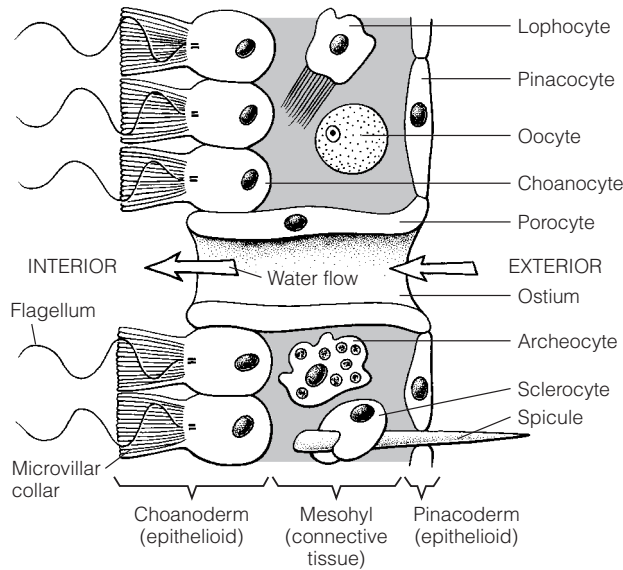
FIGURE 5-5 Porifera body wall: section through an asconoid sponge. *(Modified and redrawn from Rigby, J. K. 1987. Phylum Porifera. In Boardman, R. S., Cheetham, A. H.,and Rowell, A. J. (Eds.): Fossil Invertebrates, Blackwell Science, Cambridge, MA. pp. 116–139.)*

the form of a cylinder or an inverted cone. The basal part of the choanocyte flagellum of many species (such as *Microciona* sp. and *Grantia compressa*), if not all, bears a bilateral **vane,** as in the choanoflagellates (Fig. 4-13A).

Syncytial

The glass sponge's body wall lacks the sheetlike pinacoderm pavement that covers the body and lines the aquiferous system of cellularian sponges. Instead, the living tissue in hexactinellids is arranged in three-dimensional, cobweb-like strands called a **trabecular syncytium** or network (Fig. 5-7). The membranes that normally separate cells are absent and the cytoplasm is continuous and uninterrupted throughout the syncytium.

A cellular choanoderm also is absent; in its place is another syncytium, the **choanosyncytium.** Individual **collar bodies,** each with a collar and flagellum but lacking a nucleus, arise from the surface of the choanosyncytium. Each group of collar bodies occupies a syconoid-like pocket that is supported by the trabecular network. The many collar bodies of each pocket arise developmentally as outgrowths of a single nucleated stem cell, the choanoblast.

Each strand in the trabecular syncytium surrounds and encloses an axis of mesohyl. The mesohyl contains bundles of collagen fibers, spicules, and *cells*—sclerocytes, archeocytes, and presumably germ cells. In *Rhabdocalyptus dawsoni,* the mesohyl cells are joined to the trabecular syncytium by slender cellular extensions and are themselves partially syncytial (Fig. 5-7B), but in *Dactylocalyx pumiceus,* these cells are reported to be independent of the syncytium. Thus, the glass sponges may be constituted of a unique combination of cellular and syncytial tissues.

The gross anatomy of hexactinellids is syconoid, but the aquiferous system, because it has both incurrent and excurrent canals, resembles the leuconoid design. Water in
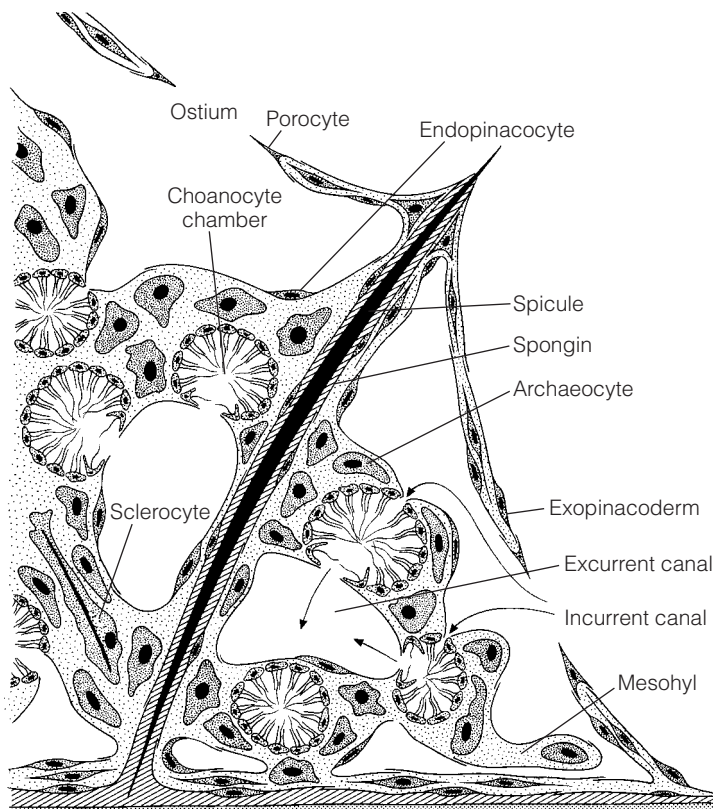
FIGURE 5-6 Porifera body wall: section through the body wall of a freshwater leuconoid sponge. *(From Ax, P. 1996. Multicellular Animals: A New Approach to the Phylogenetic Order in Nature. Springer-Verlag, Berlin, Heidelberg, NY. p. 71.)*
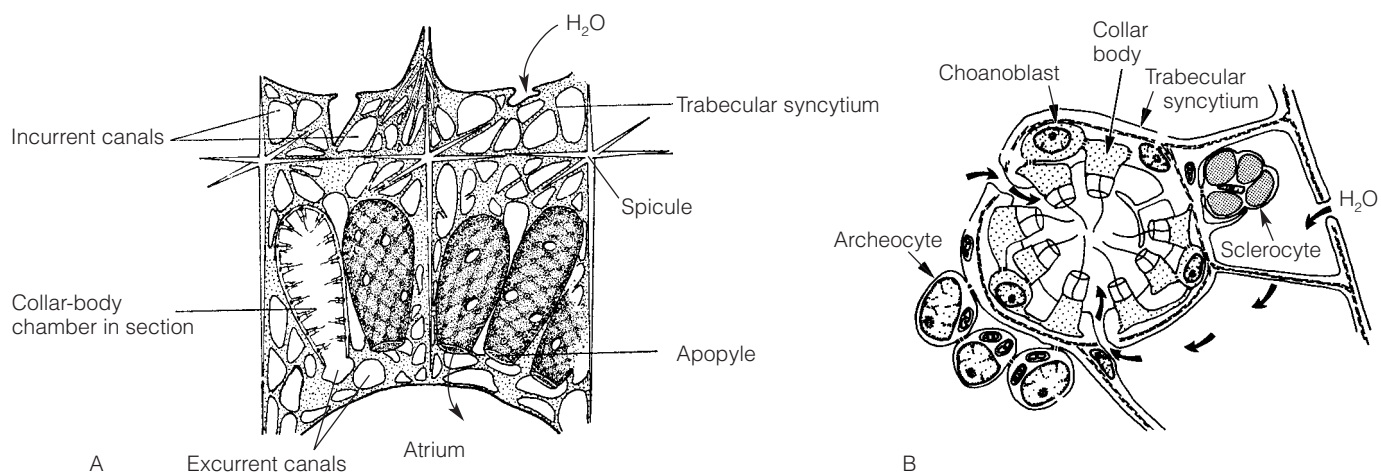
FIGURE 5-7 Porifera body wall: glass (hexactinellid) sponges. **A,** *Euplectella aspergillum* (Venus's flower basket). **B,** *Rhabdocalyptus dawsoni.* *(A, After Schulze, in Bergquist, P. R. 1978. Sponges. Hutchinson, London. pp. 59 and 26; B, From Leys, S. P. 1995. Cytoskeletal architecture and organelle transport in giant syncytia formed by fusion of Hexactinellid sponge tissues. Bio. Bull. 188:241–254)*

hexactinellids flows from: surface openings in the trabecular network → incurrent canals → collar-body chambers → excurrent canals → atrium → osculum.

WATER PUMPING

The volume of water pumped by a sponge is impressive. In general, a sponge pumps a volume of water equal to its body volume once every 5 seconds. Because water is incompressible, the volume entering must be equal to the volume exiting the sponge at any moment. The flow velocity is fastest through
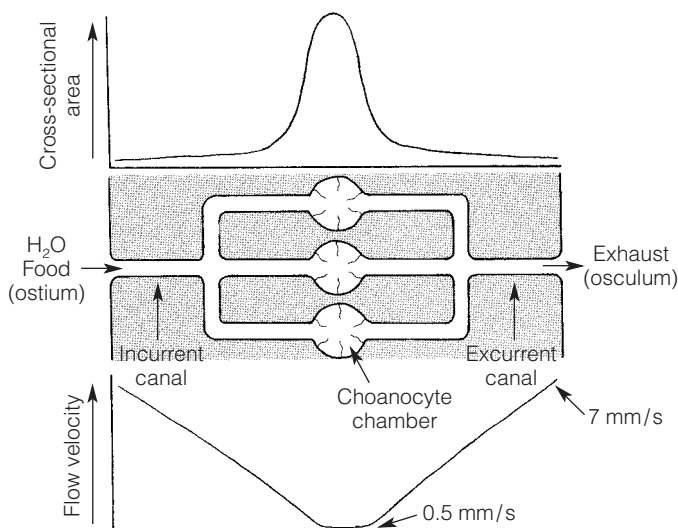
FIGURE 5-8 Porifera: water pumping and physiological exchange. The 30-times greater cross-sectional area of choanocyte chambers as compared with ostia and oscula causes the water flow velocity to slow in the chambers. The slow flow improves the effectiveness of food capture by the choanocytes. *(Based on data in Reiswig, 1975b)*

the osculum and slowest in the choanocyte chambers, because these two regions have, respectively, the smallest and the largest total cross-sectional areas in the aquiferous system (Fig. 5-8). Many sponges, however, can slow the overall flow rate or even stop it entirely to avoid the intake of silt. They do this by regulating the size of the osculum (using contractile myocytes), closing the ostia (sometimes using tubular porocytes), or adjusting the choanocyte flagellar beat (as in glass sponges, which lack myocytes and porocytes).

The water current is produced by the activity of the choanocyte flagella (Fig. 5-5). The undulatory beat of each flagellum is in a single plane. The flagellar vane, which is restricted to the collar region of the flagellum, may help to "pump" water from the collar. In at least one species *(Trochospongilla pennsylvanicus),* the beating plane of the choanocyte flagellum shifts every few seconds, eventually rotating around 360°. The choanocyte flagella and collars are oriented away from the ostia (in the asconoid design) or prosopyles (in the syconoid and leuconoid designs), and each flagellum beats from base to tip, driving water toward the excurrent canals and osculum.

The oscula of many sponges are situated on chimneys well above the main body and ostia (Fig. 5-1A). That elevated position exposes the oscula to environmental water currents faster than those that occur near the base of the sponge. The higher-velocity flow over the chimneys lowers the pressure at the oscula in relation to the ostia and induces a flow from the high-pressure to low-pressure (ostium-to-osculum) end of the system. Because most sponges are exposed to significant ambient water currents, such induced flows undoubtedly supplement flagellar pumping and conserve metabolic energy.

SKELETON

Whatever their growth form, most sponges live in moving water and support themselves with a well-developed skeleton. The skeleton is chiefly a mesohylar endoskeleton, but an
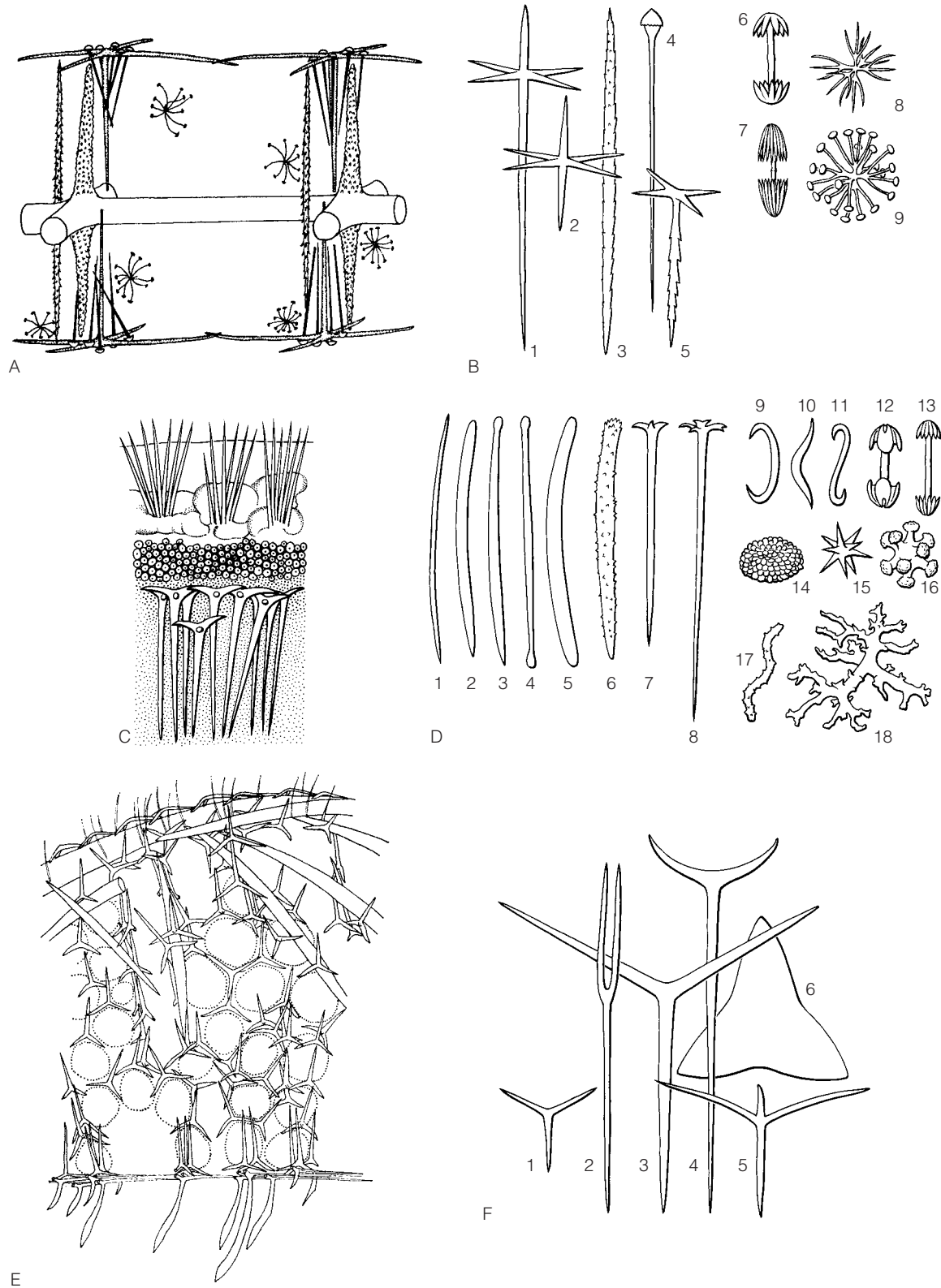
FIGURE 5-9   Porifera: spicular skeletons and spicules. **A,** Body-wall skeleton of *Farrea sollasii* (Hexactinellida). **B,** Hexactinellid megascleres and microscleres. Megascleres: 1–5, microscleres: 6–9. **C,** Body-wall skeleton of *Geodia* (Demospongiae). **D,** Demosponge megascleres and microscleres. Megascleres: 1–8, microscleres: 9–18. **E,** Body-wall skeleton of the leuconoid sponge *Afroceras ensata* (Calcarea). **F,** Selection of calcarean spicules. *(A and E, From Bergquist, P. R. 1978. Sponges. Hutchinson, London. 268 pp.; C, Modified and redrawn from Bergquist, 1978)*

exoskeleton also may occur regionally or over the entire body. The stiffness or rigidity of the skeleton varies widely among species and growth forms. Among soft encrusting forms, such as *Oscarella* and *Halisarca,* the sole skeleton is the gelatinous mesohyl supported only by fine collagen fibers. More commonly, the mesohylar matrix is supplemented with mineral **spicules,** spongin, or both. Although spicules occur principally in the mesohyl, they can project freely through the surface pinacoderm, thus affording the sponge some protection (Fig. 5-3A,C). Such projecting spicules commonly guard the oscula and sometimes the ostia.

Spicules stiffen the mesohyl to varying degrees depending on their density, arrangement, and the extent to which they fuse or interlock. In the extreme, a spicular skeleton can be a rigid, brittle, three-dimensional lattice or framework, as in the glass sponge *Euplectella aspergillum* (Fig. 5-4A, 5-9A) or the calcareous sponge *Minchinella* sp. The relict sphinctozoan sponge, *Vaceletia crypta,* has a chambered calcareous *exo*skeleton. The calcifying demosponges ("sclerosponges") secrete a massive basal exoskeleton of $CaCO_3$ on which the body rests. These sclerosponges also secrete siliceous spicules in the mesohyl (Fig. 5-10).

Some sponges lack spicules, but secrete organic spongin (Fig. 5-11A,B). Such sponges, for example the bath sponges *(Spongia, Hippospongia),* are often compressible, elastic, and "spongy." A high density of spongin produces a skeleton that is firm, tough, and rubbery, as in the tropical chicken-liver sponge, *Chondrilla nucula* (Fig. 5-4E).

Spongin and spicules occur together in most species of sponges. In some species of *Haliclona,* spongin welds together the tips of spicules to form a skeletal network (Fig. 5-11C). In other parts of the skeleton, spicules are embedded into the spongin fibers themselves (Fig. 5-11D). Sometimes,

Ostium
Excurrent canal
Osculum
Pinacoderm
Incurrent canal
Mesohyl
Choanocyte chamber
Basal pinacoderm
Spicules
$CaCO_3$
Substrate
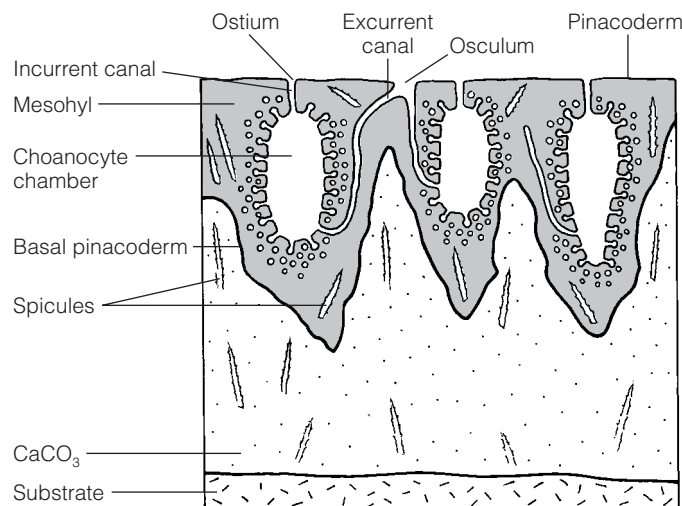
FIGURE 5-10   Porifera: body wall and skeleton of a calcifying sclerosponge (Demospongiae: Ceratoporellidae). The calcareous exoskeleton is secreted by the basal exopinacoderm and contains embedded siliceous spicules. Siliceous spicules also occur in the mesohyl of the living tissue. *(Modified and redrawn after Hutchinson from Bergquist, P. R. 1978. Sponges. Hutchinson, London. 268 pp.)*

foreign material, such as sand grains, is incorporated into the skeleton as a substitute for the spicules, as happens in the tropical ethereal-blue sponge *Dysidea etheria* and other species (Fig. 5-11E). In *Dysidea janiae,* the sponge produces no spicular skeleton of its own, but instead uses the calcareous skeleton of its symbiotic red alga *(Jania).* The result of these and other combinations of spicules and spongin is a wide variety of skeletal properties, from soft and spongy to hard and brittle.

Spicules are siliceous (SiO_2) or calcareous $(CaCO_3)$ elements whose composition, size, and shape are used at all levels in the classification of sponges (Fig. 5-9). As a result, an extensive nomenclature describes the forms and sizes of spicules. At the most general level, spicules are separated into two size classes, large **megascleres** and small **microscleres.** Megascleres typically form the principal skeletal framework, whereas the considerably smaller microscleres may support the pinacodermal lining of the canal system or, in high density, toughen the body wall (Fig. 5-9A,C,E). Megasclere names are based on the spicule's number of axes or number of rays or points. The suffix *-axon* refers to the number of axes; *-actine* indicates the number of points. A monaxon spicule, for example, has one axis and is shaped like a needle or rod, although it may be straight or curved, with pointed, knobbed, or hooked ends (Fig. 5-9D1-6). Triaxons have either three rays (triactines; Fig. 5-9F) or six (hexactines; Fig. 5-9B).

Spicules are secreted extracellularly by sclerocytes in calcareous sponges, intracellularly in sclerocytes in demosponges, and intrasyncytially in glass sponges. From one to several sclerocytes typically secrete a single spicule in the calcareous sponges. A three-rayed spicule, for example, originates between three sclerocytes derived from a single stem cell (scleroblast; Fig. 5-11G). Each member of the trio then divides and one ray of the spicule is secreted between each pair of daughter cells. The three rays fuse at their bases. Each of the three pairs of sclerocytes now moves outward along a ray, one cell lengthening its end while the other cell thickens its base (Fig. 5-11G). The secretion of a siliceous monaxon spicule is initiated around an organic filament in an intracellular vesicle (Fig. 5-11F). As the spicule crystallizes and grows, the cell first elongates and then divides into two cells, each of which adds additional silica to a growing tip of the spicule.

LOCOMOTION AND DYNAMIC TISSUES

Although sponges are basically sessile animals, some species have a limited capacity for locomotion. Both freshwater *(Ephydatia)* and marine *(Chondrilla, Hymeniacidon, Tethya)* species can move over a substratum at rates of 1 to 4 mm/day (Fig. 5-12A). The movement apparently results from the collective ameboid movements of pinacodermal and other cells. Other sponge movements include whole-body contraction *(Clathrina coriacea)* and, in many species, constriction of oscula by myocytes. These movements probably arrest or limit flow through the aquiferous system in response to an
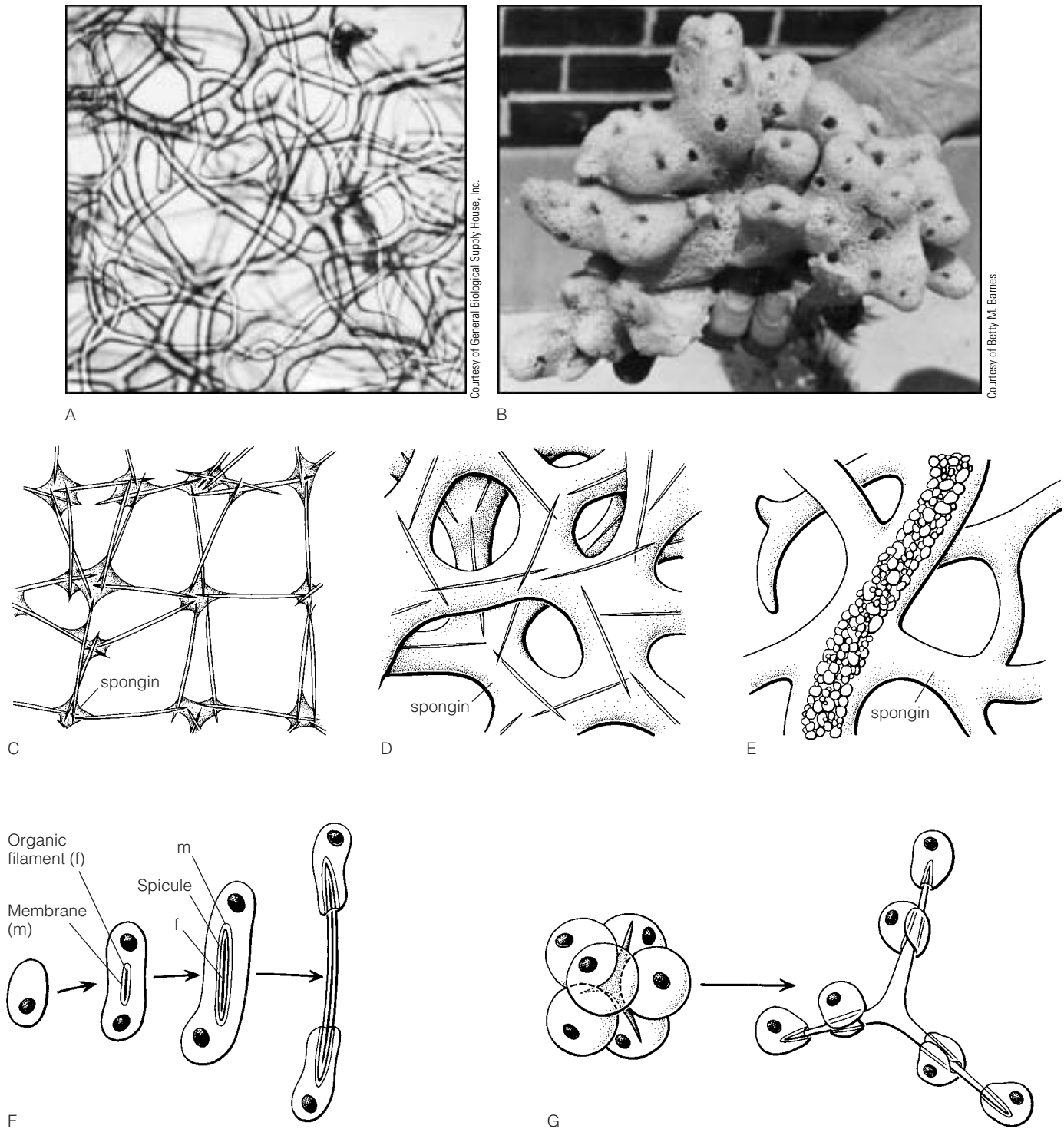
FIGURE 5-11 Porifera: spongin skeleton, spongin-composite skeletons, and spicule secretion. **A,** Photomicrograph of spongin fibers (they appear translucent). **B,** Spongin skeleton of a commercial bath sponge, *Spongia officianalis,* from the Mediterranean. The large openings are oscula. **C,** Siliceous spicules (oxeas) glued together at their tips with spongin to form a network in *Haliclona rosea.* **D,** Spongin fibers with embedded siliceous spicules (oxeas) form a reinforced network in *Endectyon.* **E,** Spongin network of *Hippospongia communis* stiffened by the incorporation of foreign material, especially sand grains, into the spongin fibers. **F,** Secretion by sclerocytes of a siliceous monaxon (oxea). **G,** Secretion by sclerocytes of a calcareous triaxon. *(C, Modified and redrawn from Hartman, W. D. 1958. Natural history of the marine sponges of southern New England. Bull. Peabody Mus. Nat. Hist. Yale Univ. 12:1–155. D and E, Redrawn from Kaestner, A.1980. Lehrbuch der Speziellen Zoologie 1(1): Wirbellosen Tiere. Gustav Fischer Verlag, Stuttgart. 318 pp.)*
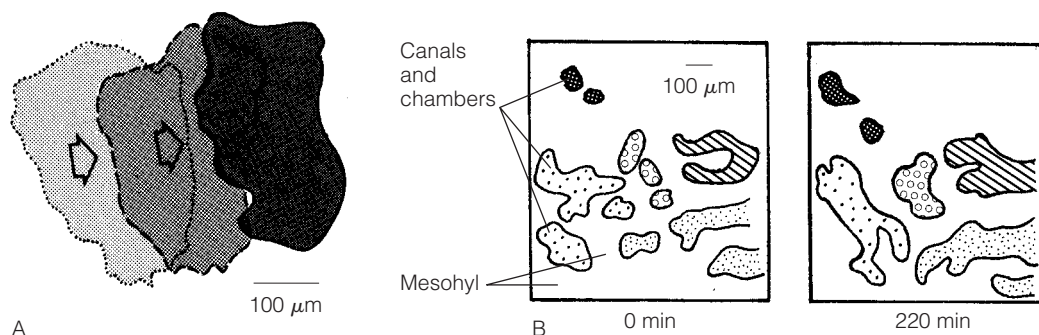
FIGURE 5-12   Porifera: locomotion and tissue dynamics of the freshwater sponge *Ephydatia fluviatilis.*
A, Locomotion of an isolated sheet of exopinacocytes. **B,** Dynamic remodeling of the aquiferous system. Each
of the shaded areas outlines canals and choanocyte chambers of a living sponge, as seen under a microscope.
Between time 0 and approximately 4 hours later, canal fusion and reshaping are evident. *(Modified and redrawn
from Bond, C. 1992. Continuous cell movements rearrange anatomical structures in intact sponges. J. Exp. Zool. 263:284–302.)*

environmental challenge, such as a sudden increase in water-borne silt.

A hallmark of sponges is the dynamism of their tissues. Mesohyl cells, all of which are ameboid, are more or less in constant motion. Similarly, endopinacocytes and choanocytes can move about to remodel the aquiferous system (Fig. 5-12B). This remodeling, which involves the addition or fusion of flagellated chambers and the merging and branching of canals, may "fine-tune" the system to optimize water flow as the sponge grows or as it encounters changes in environmental water currents. The absence of intercellular junctions, basal lamina, and hemidesmosomes in sponge tissues allows these independent and frequent cell movements.

PHYSIOLOGICAL COMPARTMENTALIZATION

The physiological importance of water flow through the aquiferous system of a sponge cannot be overstated. This single system accomplishes the tasks of gas exchange, food acquisition, waste disposal, and the release of sperm and larvae. The functions associated with, for example, the mammalian trachea and lungs, alimentary canal, circulatory vessels, kidneys, and gonoducts are, in sponges, combined in this one multifunctional system. Such a low level of physiological compartmentalization in sponges has two implications. First, because there is little segregation of function, integrating systems, such as the nervous or endocrine systems, are not well developed or necessary. In fact, sponges lack nervous tissue (discussed later in this chapter). Second, because of functional overlapping in tissues and cells, the efficiency of any individual function is likely to be low in comparison to the efficiency in animals such as ourselves, which have a specialized compartment for each function. This minimal efficiency manifests itself as a low level of activity. Few animals are less mobile or more plantlike than sponges.

We should not think that, because of their low level of compartmentalization and integration, sponges are somehow at a disadvantage. On the contrary, their low level of organization allows them to adaptively remold their bodies, to regenerate readily after damage, and to clone themselves.

NUTRITION

Sponges filter food particles from water flowing through their bodies. Generally, the filtered particles range in size from 50 μm to 1 μm or less. This range includes unicellular plankton, such as dinoflagellates and bacteria, viruses, small organic debris, and perhaps even dissolved organic material. In tropical seas, where sponges are abundant, the smallest fractions of food are approximately seven times more available than the larger size classes. All sponge cells can ingest particles by phagocytosis.

The food-trapping filters are the incurrent canals, which progressively decrease in diameter as they penetrate inward, and choanocytes (Fig. 5-13). Food and other particles are filtered as they lodge in different parts of the system, depending on their diameter. The largest particles, exceeding about 50 μm in diameter, are too large to enter an ostium and can be phagocytosed by cells of the exopinacoderm. Particles in the size range of 5 to 50 μm lodge in an incurrent canal and may be phagocytosed by endopinacocytes or by archeocytes that have entered the canal (either between pinacocytes or through porocytes in the canal lining). The smallest, bacteria-size particles enter the choanocyte chambers and are removed by phagocytosis or pinocytosis on the choanocyte surface. The choanocyte collar of microvilli, and its extracellular matrix, may be the mesh that traps the finest material.

Both choanocytes and archeocytes engulf and digest particles in vesicles, but the choanocyte often transfers particles to the archeocyte for digestion. The archeocytes probably also store nutrients such as glycogen or lipids.

Carnivorous species occur in the demosponge family Cladorhizidae. These sponges trap crustaceans and other small animals on sticky cellular threads that extend out from the surface of the sponge. Once an animal is trapped, the threads shorten, drawing the prey onto the body surface,
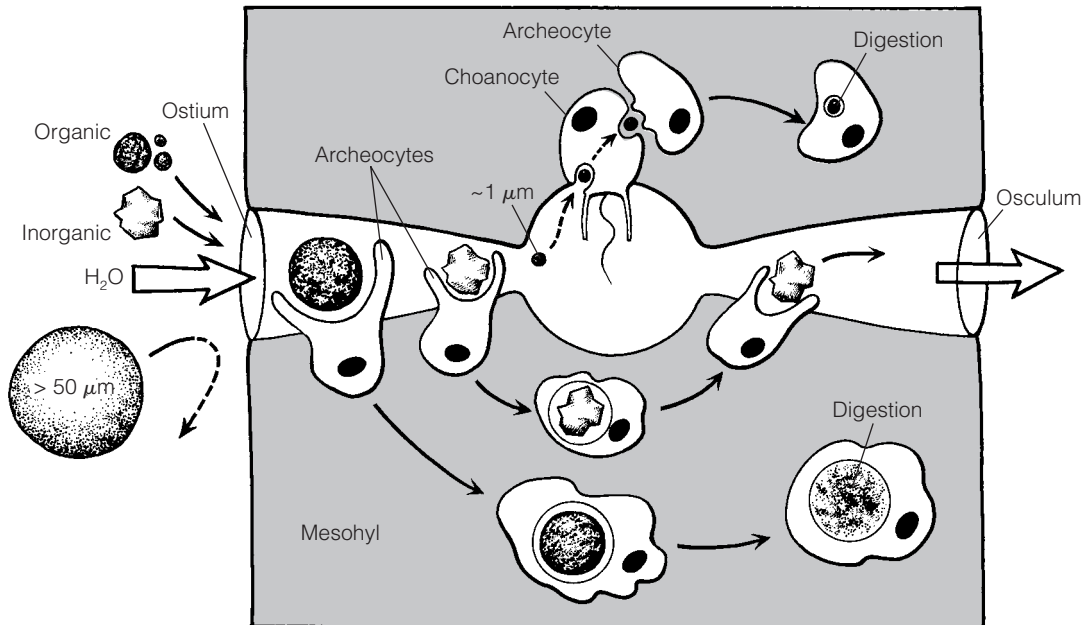
FIGURE 5-13 Porifera: diagrammatic summary of filter feeding, digestion, and egestion. See text for explanation.

which slowly overgrows the prey and consumes it, presumably with archeocytes. These strange sponges lack choanocytes and an aquiferous system.

The two sources of particulate wastes in sponges are indigestible products of intracellular digestion and inorganic mineral particles that enter the sponge in the water stream. Mineral particles must be removed from the incurrent canals, which they would otherwise block and inactivate. An inorganic particle that lodges in an incurrent canal is phagocytosed by an archeocyte, which transports it to the downstream side of the canal system and then exocytoses it into an excurrent canal (Fig. 5-13). In those species that incorporate foreign material into their skeletons, the archeocyte may transport the intercepted particle to a site of skeleton secretion.

Many sponges, both marine and freshwater, harbor photosynthetic endosymbionts in their tissues and derive a nutritional benefit from the photosynthate. Freshwater sponges typically harbor green algae (zoochlorellae) in archeocytes and other cells. Marine sponges—both calcareous and demosponges—may host dinoflagellates (zooxanthellae) or, more commonly, Cyanobacteria. One species, *Mycale laxissima* in Belize, incorporates both green and red algae in the spongin fibers of its skeleton. The cyanobacterial symbionts of some sponges, including *Verongia,* may constitute up to one-third of the sponge's biomass. Such sponges live in shallow, well-lit habitats and may have symbiotic bacteria restricted to the outer layers of the body. Excess photosynthate in the form of glycerol and a phosphorylated compound are utilized by the sponge. Some sponges studied on Australia's Great Barrier Reef obtain from 48 to 80% of their energy requirements from their Cyanobacteria. Sponges frequently contain intra- and extracellular bacteria in addition to the Cyanobacteria and other symbionts. The significance of such bacteria, however, is unknown.

INTERNAL TRANSPORT, GAS EXCHANGE, AND EXCRETION

Because the aquiferous system ventilates the entire body to within 1 mm of all cells, simple diffusion accounts for the transport of gases and metabolic wastes (largely ammonia) between the body and environmental water in the aquiferous system. Nutrients, too, probably diffuse from the widespread sites of intracellular digestion, although archeocytes, by ameboid movement, deliver nutrients to developing gametes and tissues throughout the body. At least one species of *Aplysina* (also known as *Verongia*) has specialized internal fibers that serve as tracks for the movement of nutrient-laden archeocytes.

Internal transport of food in glass sponges is intrasyncytial. Once ingested by the collar bodies, food-containing vesicles are transported by dynein motor molecules on bundles of microtubules that extend throughout the syncytium of the sponge. This mode of transport is identical to vesicular transport in radiolarian and foram pseudopodia (Chapter 3), as well as in the nerve-cell axons of higher animals.

The near absence of intercellular junctions in pinacoderm and choanoderm suggests that these layers constitute a poor regulatory barrier between the mesohyl and water of the external environment. Physiologically speaking, sponges are said to be "leaky" animals. Accordingly, the composition of their interstitial fluid (the fluid between cells) is likely to be similar

to that of the environmental water, even among freshwater species. Most cells of freshwater sponges contain contractile vacuoles, but those vacuoles are osmoregulating for individual cells and not for the sponge body as a whole.

INTEGRATION

Sponges lack nerve cells and nervous tissue, though some are capable of limited impulse conduction. In most cases, this conduction is a slow "epithelial" spread of electrical activity over a few millimeters that results in a local myocyte contraction in response to a local stimulus. Such impulse conduction is slow because specialized intercellular junctions (gap junctions), which promote epithelial conduction, are absent. Thus, the membranes between cells tend to isolate rather than conduct the wave of depolarization. An exception to this generalization, however, occurs in the syncytial tissues of glass sponges. In *Rhabdocalyptus dawsoni,* electrical impulses (action potentials) are propagated rapidly along the syncytial strands from a point of stimulation to all parts of the sponge. This activity arrests flagellar beating and shuts down water pumping by the sponge.

## BIOACTIVE METABOLITES AND BIOLOGICAL ASSOCIATIONS

Many sponges produce metabolites that may prevent settlement of other organisms on their surfaces or deter grazing predators. Nine out of 16 Antarctic sponges and 27 of 36 Caribbean species were found to be toxic to fish. The fish toxins, however, did not necessarily discourage nonfish grazers, and some fish, such as angelfishes, filefishes, and the moorish idol, are specialized spongivores. Turtles, especially

the Hawksbill turtle, commonly feed on sponges and up to 95% of their feces may consist of siliceous spicules. A taxon of sea slugs (dorid nudibranchs) specializes on sponge species in a manner similar to certain caterpillars on their host plants. Some sponges use metabolites to compete for space with other organisms. For example, the Caribbean chicken-liver sponge *(Chondrilla nucula)* releases compounds that kill adjacent stony corals, allowing the sponge to overgrow their skeletons. Some species have distinctive odors, such as the garlic sponge, *Lissodendoryx isodictyalis.* A few, such as the Caribbean fire sponge, *Tedania ignis,* cause a severe rash when handled. Various sponge biochemicals are being investigated to determine their potential medical and commercial benefits.

Many sponges harbor endosymbionts that occupy space in the aquiferous system and take advantage of the water flow and protection afforded by their host. Some large leuconoid sponges are veritable apartment houses for shrimps, amphipods, and brittle stars. One investigator collected over 16,000 snapping shrimps from within the water canals of one large loggerhead sponge. Certain worms (spionid polychaetes) infest, eat, and thereby adopt the color of their sponge host. Decorator crabs attach sponges, algae, and other sessile organisms to their backs to form a microcommunity. The community grows on this mobile substratum, providing the crab with an effective camouflage. Certain other crabs (Dromiidae) cut out a cap of sponge and affix it to their back, or attach a sponge fragment that then grows, covers, and camouflages the crab.
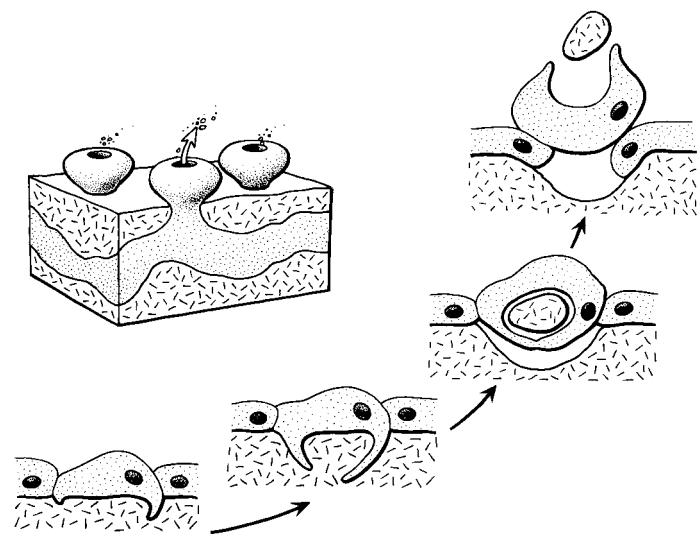
BIOEROSION

Species of the demosponge family Clionidae play an important role in the breakdown of calcareous shell and coralline rock in the sea (Fig. 5-14). *Cliona celata,* for example, bores
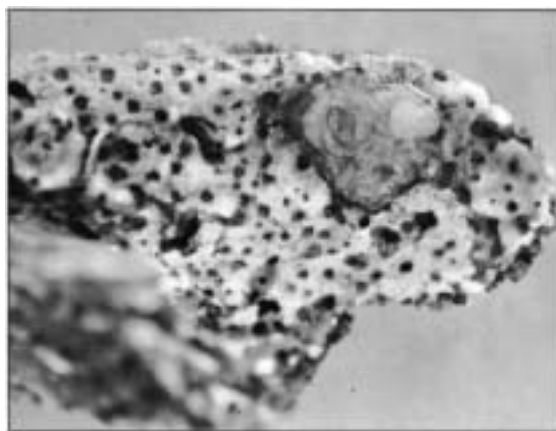
From Rützler, K., and Rieger, G. 1993. Sponge burrowing: Fine structure of *Cliona lampa* penetrating calcareous substrate. Mar. Biol.21:144–162.

A

B

FIGURE 5-14   Porifera: bioerosion by boring demosponges (Clionidae). **A,** Remains of a clamshell that has been riddled by *Cliona lampa.* **B,** The shell-boring sequence: etching cell penetrates shell by chemical dissolution; shell chip is cut away from shell; chip is released into the aquiferous system; chip is discarded in exhalant water flow.   *(B, Modified and redrawn after Hatch from Pomponi, S. A. 1980. Cytological mechanisms of calcium carbonate excavation by boring sponges. Int. Rev. Cytol. 65:301–319.)*

into mollusc shells and creates a network of subsurface tunnels. At regular intervals, a papilla of sponge tissue erupts through a hole in the surface of the shell (Fig. 5-14B). Some papillae bear ostia, others oscula. Shells washed ashore at this stage appear to be peppered with birdshot (Fig. 5-14A). Eventually, the sponge overgrows the entire shell and finally destroys it completely. Specialized archeocytes called **etching cells** are responsible for eroding the shell. Each etching cell chemically cuts away a small chip of shell. The freed chip is released into the aquiferous system and eventually discharged at the surface through an osculum. Divers regularly see these sponges "spit" particles. Because it affords the sponge physical protection from grazing predation, boring into shell or rock may enhance the survival of juvenile and adult sponges.
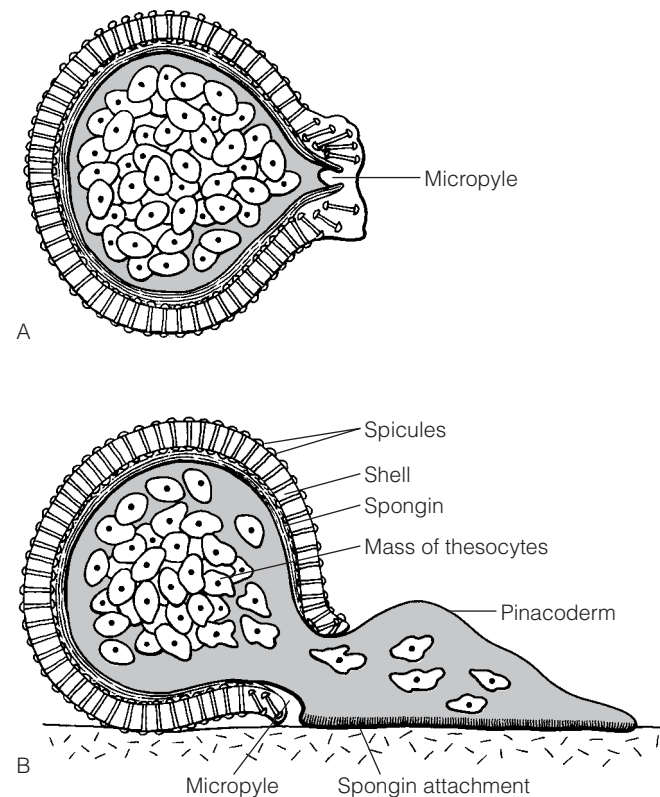
REPRODUCTION

Clonal Reproduction

Sponges reproduce clonally (asexually) by fragmentation, budding, and by the formation of overwintering propagules called **gemmules.** Fragmentation primarily results from current or wave damage, and perhaps from damage done by grazing carnivores. The dislodged fragments rely on their remodeling capacity for regeneration. The fragment soon attaches to the substratum and reorganizes itself into a functional sponge. An extreme form of fragmentation—dissociation of a sponge into individual cells or clumps of cells—can be accomplished in the laboratory by squeezing a piece of sponge through finely woven cloth. This experiment was first conducted by the zoologist H. V. Wilson early in the 20th century. Since that time, it has been repeated frequently to demonstrate species recognition at the cellular level, to model morphogenesis, and to study the mechanisms by which cells recognize and adhere to each other.

Budding is uncommon but does occur in a few sponges. In *Clathrina,* for example, the free ends of the asconoid tubes are said to swell into buds, break free, and then attach and grow into another sponge. Some species of *Tethya* produce stalked buds. Species of *Oscarella* and *Aplysilla* are reported to produce papillae that self-amputate and grow into new sponges.

Many freshwater sponges and a few marine species produce hundreds to thousands of sporelike gemmules, typically in the fall of the year (Fig. 5-15A). The autumn gemmules of freshwater species may enter **diapause,** a state of near metabolic arrest, and then require a period of very cold temperature before they are activated, germinate, and differentiate into a new sponge, usually in the spring. While the gemmule is in diapause, it is resistant to environmental extremes of temperature, salinity, and desiccation. A standard practice of sponge biologists, in fact, is to keep a humidified jar of gemmules in a refrigerator. When sponges are needed for observation or experimentation, the gemmules are germinated by "seeding" some into a container of pond water.

Gemmules are produced in the mesohyl of a dying sponge around a cluster of nutrient-laden archeocytes. Spongocytes secrete a spongin shell around the cellular mass. The shell may also contain spicules secreted by sclerocytes. The shell completely encloses the cell mass except at one pole where an opening, the **micropyle,** remains. The completed gemmule consists of a shell and its enclosed archeocytes, each of which

FIGURE 5-15   Porifera clonal reproduction: gemmules. **A,** A vertical section through a full-grown gemmule. **B,** Hatching of a gemmule.   *(A, After Evans from Hyman, L. H. 1940. The Invertebrates. Vol.1. Protozoa through Ctenophora. McGraw-Hill Book Co., New York. 726 pp.; B, Modified and redrawn from Fell, P. E. 1997. Poriferans, the sponges. In Gilbert, S. F., and Raunio, A. M. (Eds.): Embryology: Constructing the Organism. Sinauer, Sunderland, MA. pp. 39–54.)*

soon becomes spherical, resembles an embryonic cell, and then is called a **thesocyte** (Fig. 5-15A).

During the spring gemmule "hatch," the peripheral thesocytes differentiate into a pinacoderm that balloons out, like a bubblegum bubble, through the micropyle (Fig. 5-15B). This pinacoderm bubble makes contact with and attaches to the substratum. Next, the deeper thesocytes issue from the micropyle into the bubble and establish, after differentiation, the interior of the juvenile sponge. An interesting variation on this theme, which challenges the notion of individuality, is that thesocytes from gemmules of the same or different parentage (but of the same species) can intermingle during germination to form one "individual" sponge.

Sexual Reproduction and Development

Sponges, with few exceptions, are hermaphrodites. At the appropriate time, sperm are spawned from one sponge and transported by water currents to another, in which fertilization occurs internally. A few species (such as *Cliona*) are oviparous and release zygotes into the water, where they complete their development. Most sponges are viviparous, retaining the zygotes in the parent's body and releasing larvae (sometimes called larviparity). Embryos and larvae are lecithotrophic.

Sponges are said to lack genital organs (gonads), and germ cells occur in either simple clusters (sperm) or individually
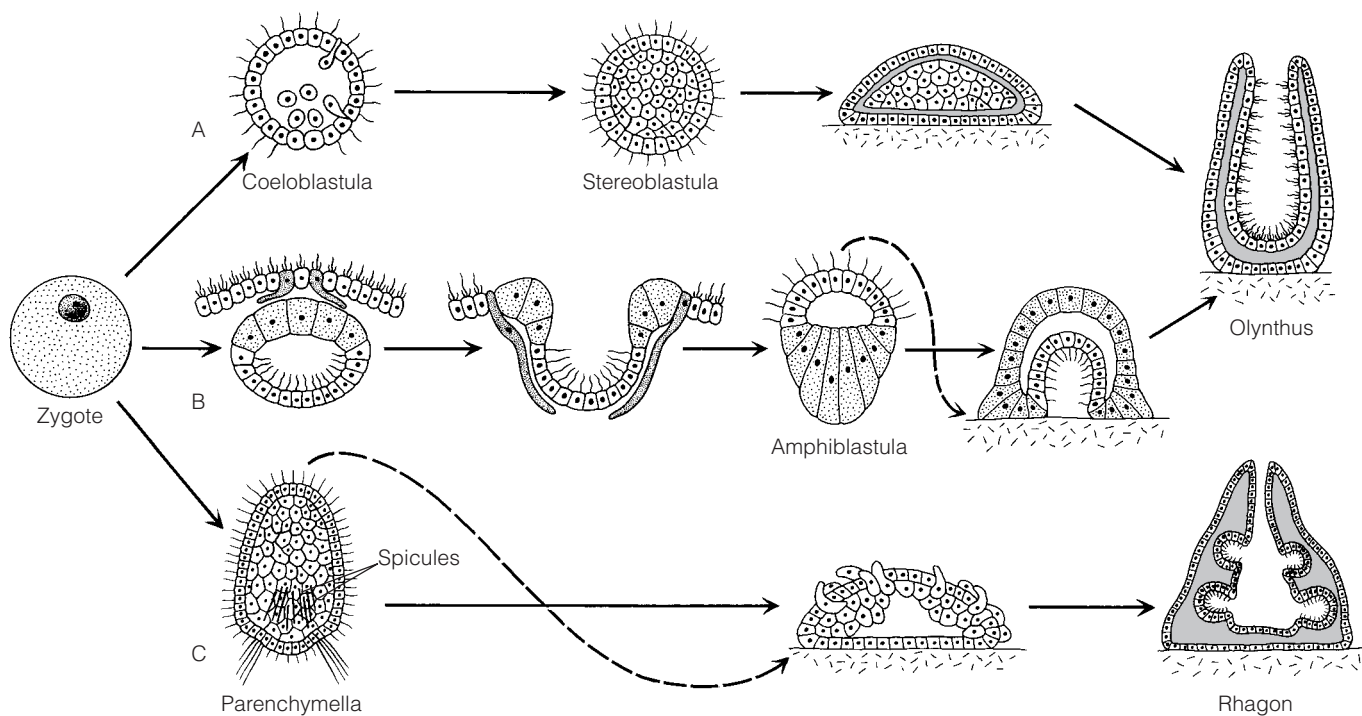
FIGURE 5-16   Porifera sexual reproduction: larval development and metamorphosis. In **A**, *Clathrina* (Calcarea: Calcinia), a hollow blastula develops in the mesohyl and is released into the water. After release, cellular ingression converts the coeloblastula into a stereoblastula, the settling stage. In **B**, *Sycon* (Calcarea: Calcaronea), the egg is derived from a choanocyte that loses its flagellum and sinks into the mesohyl below the choanoderm. After fertilization, the egg (zygote) divides to form an internally flagellated sphere that resembles a choanocyte chamber. Upon release from the sponge, the sphere inverts to position its flagella on the surface of the larva. During metamorphosis, the external flagellated cells, after losing their flagella, return to the interior of the body and differentiate into choanocytes. The metamorphosed juvenile of a calcareous sponge is called an olynthus. In **C**, *Haliclona* (Demospongiae), a differentiated parenchymella is released from the sponge into the plankton. After settlement, it undergoes a complex metamorphosis to form a juvenile, or rhagon (see text).

(eggs) throughout the mesohyl. Sperm arise from choanocytes or entire choanocyte chambers that sink into the mesohyl and become enclosed in a thin cellular wall to form a **spermatic cyst.** Eggs arise from archeocytes or dedifferentiated choanocytes (in some calcareous sponges). Each egg generally accumulates its yolk by phagocytosis of adjacent nurse cells. The egg and nurse cells together may be enclosed in a **follicle** of ensheathing cells.* Because the aquiferous system supplies all parts of the body equally, the germ cells also are widely distributed throughout the mesohyl of the body, but always within diffusion distance of a canal or chamber.

During spawning, sperm rupture the wall of the spermatic cyst, enter the excurrent canals (or atrium), and are released from the oscula. Certain tropical species, known to scuba divers as smoking sponges, suddenly spew sperm in milky clouds from their oscula. Such sudden sperm release may be typical for most sponges.

When the spawned sperm drift into contact with another sponge, they are swept into its aquiferous system by the incurrent water flow. Once in the aquiferous system, sperm are transported to the choanoderm or choanocyte chamber and are phagocytosed, but not digested, by a choanocyte. The choanocyte then loses its flagellum and collar, becomes ameboid, and transports the sperm head (nucleus) to the egg. The transformed ameboid choanocyte is called a **carrier cell.** After the carrier cell reaches an egg in the nearby mesohyl, it either transfers the sperm nucleus to the egg or the carrier cell and sperm nucleus together are phagocytosed by the egg. In either case, fertilization occurs internally in the "ovary" of the sponge.

The sperm of most sponges lack an acrosome, the structure responsible for penetrating the egg-cell membrane during fertilization in most other animals. An acrosome probably is unnecessary because the sperm nucleus enters the egg by phagocytosis. Acrosomal sperm do occur in *Oscarella lobularis,* suggesting that it has a conventional means of egg fertilization, but the reproductive details of this species are unknown.

The zygote cleaves holoblastically into equal-size blastomeres. The pattern of cells that results from cleavage, however, varies among species of sponges. The larvae that develop from embryos are also diverse and are described under the names coeloblastula, amphiblastula, parenchymella, and trichimella larvae.

A **coeloblastula larva** is produced by calcareous sponges, such as species of *Clathrina* (Calcinea; Fig. 5-16A). This larva is

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* By definition, an organ is composed of two or more tissues. If these cyst or follicle cells are shown to have a different tissue origin than the germ cells, then the spermatic cyst and egg follicle would be organs (gonads).

a hollow sphere composed of a single layer of flagellated cells. While in the plankton, some of the surface cells lose their flagella, become ameboid, and enter the blastocoel, eventually obliterating it. This converts a hollow coeloblastula into a solid stereoblastula.

An **amphiblastula larva** occurs in other calcareous sponges, for example, *Grantia, Sycon,* and *Leucosolenia* (Calcaronea, Fig. 5-16B). An amphiblastula larva develops as a hollow ball composed of two types of cells, anterior flagellated cells and posterior nonflagellated granular cells. Initially, within the mesohyl of the parent, the flagella are directed into the blastocoel, but a break soon develops in the granule-cell surface of the larva and it turns itself inside-out (inverts) through that opening. After inversion, the flagella project outward from the surface of the larva, enabling it to swim. It is released from the parent at that stage. Inversion is correlated with eggs that arise from choanocytes: After fertilization, the cells divide as if to form new choanocyte chambers, with the flagella directed toward the interior of the chamber. The demosponge genera *Oscarella* and *Plakina* also produce amphiblastula larvae, but these form secondarily, after passing through a parenchymella stage.

A **parenchymella larva** is characteristic of most demosponges (Fig. 5-16C). In this case, the embryo develops directly into a solid mass of cells, forming a stereoblastula. The outer layer is composed of widespread flagellated cells interspersed with occasional vesicle-containing cells that lack flagella. The larval interior houses many types of differentiated cells—sclerocytes, collencytes, pinacocytes, even choanocyte chambers—and archeocytes. To a certain degree, then, parenchymella larvae are prefabricated juveniles specialized for swimming.

Trichimella larvae typify the glass sponges. These are stereoblastulae that bear a band of flagellated cells around the equator of the larval body. The interior is occupied by yolk-bearing cells, sclerocytes (spicules), other cells, and choanocyte chambers.

All sponge larvae are lecithotrophic and therefore relatively short-lived. Typically, they are released at dawn in response to a light cue. After a period of a few hours to a few days, the larvae settle and creep over the bottom in search of a suitable site for attachment. Once a site is found, the larva metamorphoses into a juvenile sponge, which differs somewhat for each of the larval types (Fig. 5-16). Because the metamorphosis involves a rearrangement of cells into more or less definite layers, it is frequently compared with gastrulation in other metazoans, but the ingression of cells that results in the so-called stereoblastulae of many sponges might also be regarded as a form of gastrulation (see Chapter 4).

Immediately prior to metamorphosis, the cells of the coeloblastula, now a stereoblastula, dedifferentiate into a mass of totipotent cells (Fig. 5-16A). Once attached, this mass spreads over the substratum, the surface cells become pinacoderm, and the deeper cells differentiate into other typical sponge cells. Gaps that form between the interior cells merge together to form the atrium as the interior cells undergo rearrangement.

The amphiblastula larva settles and attaches on its flagellated end (Fig. 5-17B). Those flagellated cells, now attached to the substratum, lose their flagella, migrate internally, and form the sponge interior. The granular cells become the pinacoderm. When the juvenile sponge becomes functional,

begins to feed, and is a miniature asconoid in design, it is called an **olynthus** (Fig. 5-16B).

Metamorphosis of parenchymella larvae differs among species. In general, following larval attachment, the interior cells differentiate and rearrange themselves to build most, if not all, of the sponge body. The question is, What, if any, contribution to the juvenile body is made by the larval flagellated cells? In one species, *Mycale contarenii,* the flagellated cells contribute to the formation of choanocytes, as might be expected (Fig. 5-16C). But in other species (such as some freshwater sponges and *Microciona prolifera*), the flagellated cells are phagocytosed by archeocytes and do not contribute directly to the juvenile body. In any case, the metamorphosed juvenile sponge often initially has an asconoid or syconoid design, but with thick walls, before transforming into a leuconoid sponge. This early juvenile stage is called a **rhagon** (Fig. 5-16C).

Sponges in temperate zones may live for from 1 to a few years, but some tropical species and perhaps many in the deep sea can be long-lived, up to 200 or more years. Some sponges do not reproduce sexually until they are several years old, whereas others begin to reproduce when they are only 2 or 3 weeks old. Some of the calcified demosponges grow very slowly, at a rate of only 0.2 mm/year. If that growth rate is constant, these reef sponges, which can reach 1 m in size, may be 5000 years old.

DIVERSITY OF PORIFERA

Symplasma[sP] (Hexactinellida)

Glass sponges; have syncytial tissues; spicules are siliceous triaxonal hexactines that form intracellularly (sclerocytes are cellular, not syncytial). Many species have elongate bundle ("root") of monaxons that anchor the sponge in mud bottoms; trichimella larva resembles modified parenchymella. Marine; approximately 400 extant species. *Euplectella, Dactylocalyx, Hyalonema, Monoraphis, Rhabdocalyptus.*

Cellularia[sP]

Porifera with cellular tissues.

DEMOSPONGIAE[C]

Cellularia of leuconoid design; 80 to 90% of all described species. Skeleton of siliceous spicules, spongin, spicules and spongin, or mesohyl only; fused calcareous basal exoskeleton in some relict species. Megascleres: monaxons, triaxons, tetraxons; all spicules secreted intracellularly; mesohyl well developed; choanocytes typically smaller than pinacocytes and archeocytes. Marine and fresh water. (Currently, there is lack of consensus over the classification of subtaxa of Demospongiae.)

Homoscleromorpha[sC]: Demospongiae lacking distinction between mega- and microscleres. Spicule types not localized in body; siliceous spicules are di-, tri-, and tetractines; spongin mostly absent. Larviparous with coeloblastula larva. *Octavella* and *Oscarella* have only mesohylar skeleton, lack spongin and spicules. *Plakina* (syconoid).

Tetractinomorpha[sC]: Demospongiae with tetraxons, asterose microscleres, and mostly without spongin. Oviparous.

Acanthochaetes, Ceratoporella, Merlia, all "sclerosponges" with a basal calcareous exoskeleton as well as siliceous spicules; *Chondrilla nucula* (chicken-liver sponge of West Indies); *Cliona* spp. (boring sponges); *Geodia; Suberites ficus* (fig sponge); *Tethya actinia* (tangerine sponge); *Tetilla.*

Ceractinomorpha[sC]: Demospongiae with distinct mega- and microscleres, if microscleres are present; spongin is often well developed and several taxa ("keratosa") have spongin only; spicule types localized to specific tissues or regions. Larviparous with parenchymella larva. *Aplysilla longispina* (sulfur sponge); *Asbestopluma* (Cladorhizidae), carnivorous sponges; *Callyspongia vaginalis* (tube sponge); *Dysidea etherea* (ethereal blue sponge); *Ephydatia fluviatilis, Spongilla lacustris, Trochospongilla pennsylvanicus,* freshwater sponges; *Halichondria bowerbanki* (bread sponge); *Haliclona; Halisarca* lacks spicular and spongin skeleton; *Hymeniacidon heliophila* (sun sponge); *Hippospongia, Spongia* (bath sponges); *Niphates digitalis* (vase sponge); *Lissodendoryx isodictyalis* (garlic sponge); *Microciona prolifera* (red-beard sponge); *Mycale; Ophlitaspongia; Neofibularia nolitangere* (touch-me-not sponge); *Spheciospongia vesparia* (loggerhead sponge); *Tedania ignis* (fire sponge); *Vaceletia crypta,* a relict sphinctozoan with a chambered calcareous exoskeleton; and *Verongia* (also called *Aplysina*).

CALCAREA[C]

Cellularia including species of asconoid, syconoid, and leuconoid design; spicules are calcite, mostly unfused triaxons, tetraxons and monaxons; each spicule formed extracellularly by more than one sclerocyte. Mesohyl is thin; choanocytes relatively large, same size as pinacocytes and archeocytes. Larva a hollow blastula. Marine; 500 extant species.

Calcinea[sC]: Calcarea with a choanocytic flagellum not in close association with the nucleus; nucleus in base of cell; triaxons have equiangular rays of equal length. Coeloblastula larva. *Clathrina* (asconoid) forms tubular network; *Murrayona* has a reticulate rigid skeleton of fused calcareous bodies (sclerodermites).

Calcaronea[sC]: Calcarea with a choanocyte flagellum close to the nucleus; nucleus is apical in cell; triaxons are inequiangular, one ray longer than other two. Amphiblastula larva. *Grantia; Leucandra* (leuconoid); *Leucosolenia* (asconoid), single tubes or tube cluster from a stolon, among algae; *Minchinella,* rigid skeleton of fused spicules and cement; *Petrobiona,* skeleton is a solid calcareous mass; *Sycon* or *Scypha* (syconoid), cylindrical to nearly spherical body, common under rocks.

PALEONTOLOGY AND PHYLOGENY OF PORIFERA

The fossil record of the three major taxa of extant sponges—Hexactinellida, Demospongiae, and Calcarea—is rooted in the Cambrian or Ordovician periods. Two extinct taxa of
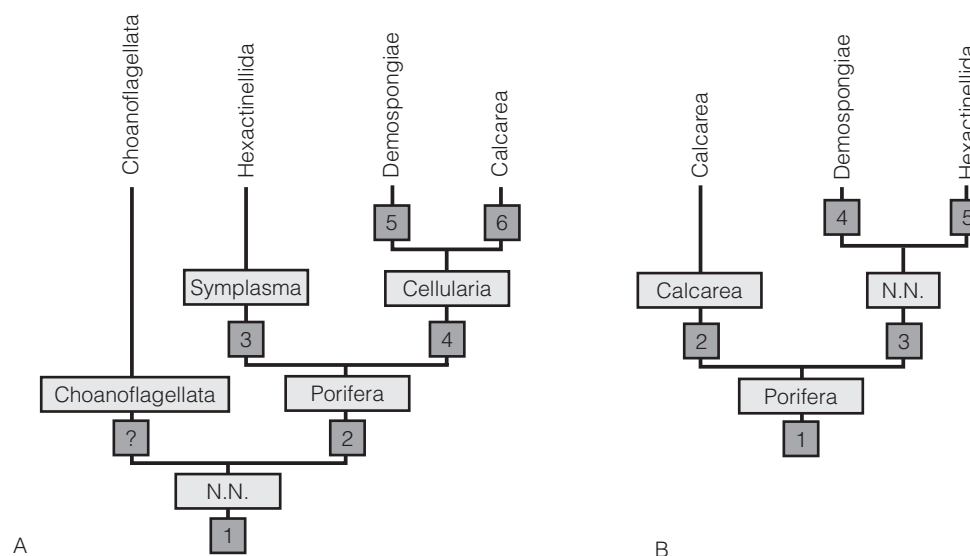
FIGURE 5-17 Porifera: competing phylogenies. **A,** Phylogeny adopted in this book. **1, N.N.:** Small choanocytes with flagellar vane; microtubular flagellar root; intracellular secretion of siliceous spicules; archeocytes. **2, Porifera:** Sessile adult; pinacoderm, mesohyl, and internal aquiferous system; dynamic tissue remodeling; archeocytes; sclerocytes; siliceous spicules secreted intracellularly around organic axial filament; stereoblastula larva. **3, Symplasma (Hexactinellida):** Syncytial trabecular network, choanosyncytium; siliceous hexactines; secondary silicification. **4, Cellularia:** Cellular tissues (possible plesiomorphy); porocytes; extracellular calcification. **5, Demospongiae:** Siliceous tetraxons; spongocytes and spongin. **6, Calcarea:** Large choanocytes; calcareous spicules; loss of siliceous spicules; coeloblastula larva. **B,** A traditional phylogeny. **1, Porifera:** As in **A,** above, plus porocytes in pinacoderm; contractile cells; blastula larva. **2, Calcarea:** Calcareous spicules secreted extracellularly by sclerocytes. **3, N.N.:** Siliceous spicules secreted by sclerocytes intracellularly around organic axial filament; parenchymella larva. **4, Demospongiae:** Spongocytes; tetraxon spicules. **5, Hexactinellida:** Syncytial pinacoderm, choanoderm; loss of porocytes. *(B, Redrawn after Böger from Ax, P. 1996. Multicellular Animals. Vol. 1. A New Approach to the Phylogenetic Order in Nature. Springer, Berlin. 225 pp.)*

PHYLOGENETIC HIERARCHY OF PORIFERA

Porifera
    Symplasma (Hexactinellida)
    Cellularia
        Demospongiae
        Calcarea

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organisms often considered to be sponges are Archaeocyatha (Cambrian) and Stromatoporata (Ordovician to Cretaceous). The archeocyathan body consisted of a double-walled, porous, calcareous skeleton in the form of an inverted hollow cone with radially arranged septa. Stromatoporates resembled present-day calcifying demosponges (sclerosponges) in that they had a massive basal calcareous skeleton with internal tubes, but unlike sclerosponges, they lacked siliceous spicules. Another taxon, Sphinctozoa (primarily Ordovician to Triassic), had a porous calcareous skeleton that was annulated like a string of pearls. The extant relict sphinctozoan *Vaceletia crypta* indicates that the skeleton was external to the soft tissue. Similarities in its soft tissues with those of demosponges suggest that *Vaceletia,* and perhaps some other sphinctozoans, should be classified in Demospongiae.

Archaeocyathans, sphinctozoans, stromatoporates, and demosponges were important reef builders in Cambrian and Mesozoic seas. Some sponge biologists, accordingly, have suggested that an evolutionary trend in sponges has been a reduction of the massive reef-building skeleton (Fig. 5-10) in favor of a spicular skeleton. The slow growth rate of extant sponges with massive skeletons, as compared with stony corals, may be a reason for the decline of reef-building sponges. On the other hand, the choanoflagellates, which share a common ancestor with sponges (Fig. 5-17), produce a siliceous spicular skeleton.

Sponge classification is controversial, even at the highest levels. Most of the recent phylogenetic discussions have included the sclerosponges (formerly Sclerospongiae) in Demospongiae, and that change is adopted here. Another recent suggestion is the establishment of two subtaxa, Symplasma (Hexactinellida) and Cellularia, which formally recognize the distinction between hexactinellid syncytial organization and the cellular bodies of Calcarea and Demospongiae. Current systematic discussions center on the phylogenetic relationships of the three extant taxa (Fig. 5-17), the position of the sclerosponge species, and the systematic relationships among Archaeocyatha, Stromatoporata, and Sphinctozoa.

PLACOZOA[P]

In 1883, a minute metazoan superficially resembling a large ameba (Fig. 5-18) was discovered in an Austrian seawater aquarium and named *Trichoplax adhaerens.* It has since been collected in the sea in various parts of the world and cultured numerous times.

The flattened body, which reaches 2 to 3 mm in diameter but only 25 μm in thickness, is enclosed in a layer of cells, one cell thick, that resembles an epithelium, particularly because typical intercellular junctions join the adjacent cells (Fig. 5-18B). The epithelioid layer, however, lacks a basal lamina, which is a typical epithelial characteristic (see Chapter 6). The cells on the upper surface of the body differ from those on the lower surface. The upper cells are flat and monociliated, and each usually contains a large, spherical lipid droplet. The lower surface is a creepsole composed of gland and monociliated cells with microvilli. Because these cells are tall and slender, the individual cilia are close together, producing a densely ciliated surface for locomotion. Between the upper and lower cell layers is a connective tissue of watery extracellular matrix and a syncytial network, the **fiber syncytium,** the fourth type of "cell" in the placozoan body. The multiple nuclei of the fiber syncytium are separated from each other by intracellular septa, which are not membranes. Such septa are common in the syncytial network of hexactinellid sponges and in fungi. The fiber syncytium, which is thought to be contractile, contains actin (and presumably myosin) and microtubules.

Trichoplax resembles a large macroscopic ameba in form and locomotion (Fig. 5-18A). The animals change shape more or less constantly as they glide slowly over the substratum. Apart from having differentiated upper and lower surfaces, *Trichoplax* is not polarized. As a result, it can move in any direction without turning. Sometimes it moves in two directions simultaneously and may pull itself apart in the process.

Trichoplax feeds on algae and other material on the substratum. It digests its food extracellularly and extracorporeally (outside of its body) between its ventral surface and the substratum or it can arch upward to produce a pocket in which food is digested. The lower cell layer absorbs the products of digestion.

The predominant mode of reproduction is clonal by fragmentation, as mentioned earlier, and by budding. The buds, which are more or less spherical bodies, appear to emerge from the upper surface of the body, but they contain cells from the upper and lower surfaces as well as connective tissue. The flagellated buds are released from the surface and swim away. Sexual reproduction has not been observed with certainty. Eggs have been described in laboratory individuals whose bodies were swollen, spherical, and detached from the substratum. Apparently, the eggs arise from cells of the ventral surface that dedifferentiate and ingress into the connective-tissue space. Definite sperm have not been observed. If eggs are confirmed and sperm discovered, then the number of specialized cells in placozoans rises to six. The DNA content of *Trichoplax* is smaller than that determined for any other animal.

The taxon Placozoa was created for *Trichoplax adhaerens,* which, like sponges, is probably an early evolutionary line among Metazoa (although the fiber syncytium and extracorporeal digestion are reminiscent of fungi). Placozoans, being composed of only four types of cells, are indeed simple metazoans. Their small, flat bodies enable them to rely on simple diffusion for transport, thus avoiding the complexity associated with a circulatory system. In some respects, placo-
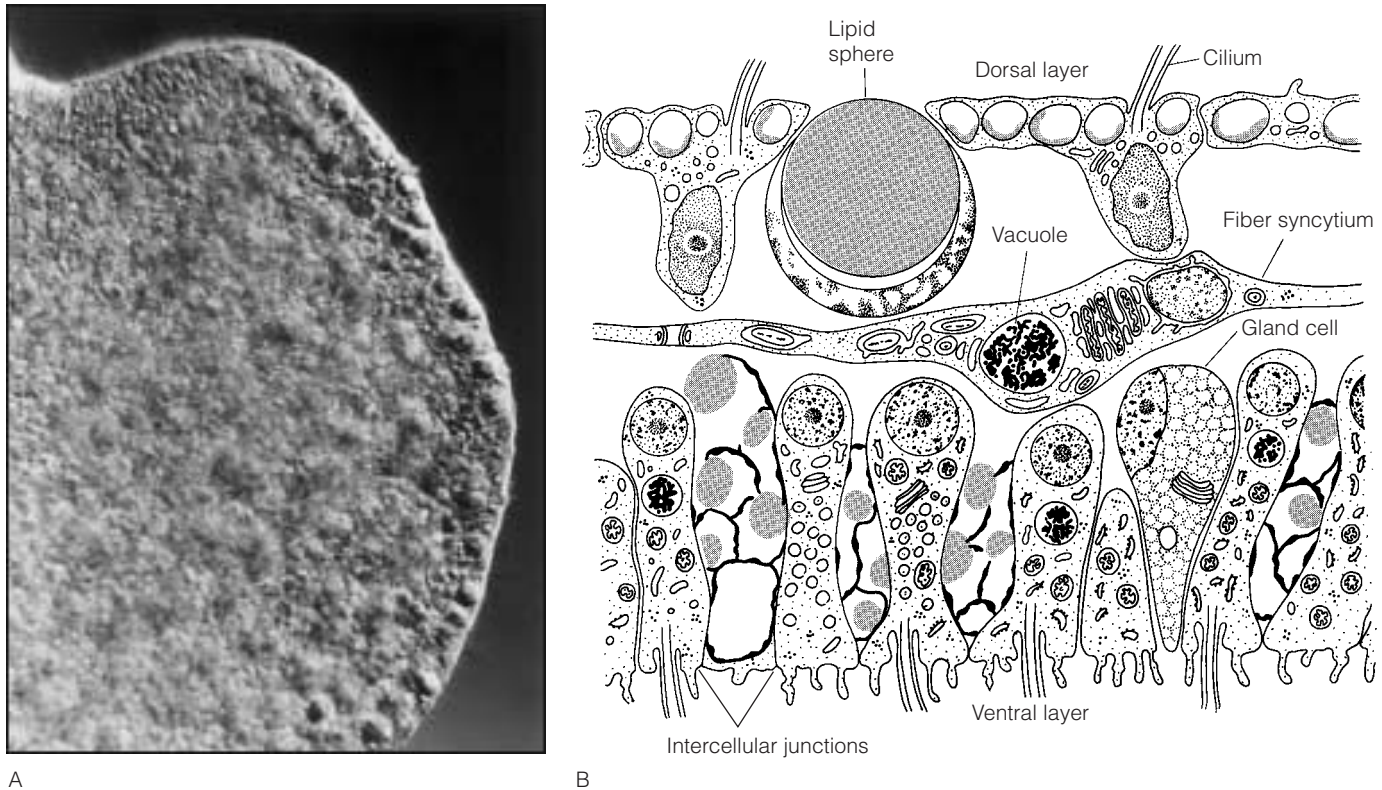
FIGURE 5-18   Placozoa. **A,** Part of a living *Trichoplax adhaerens* in dorsal view. **B,** Diagrammatic vertical section through *Trichoplax* showing part of the upper (dorsal) and lower (ventral) cell layers and the middle fiber syncytium. *(B, After Grell, K. G. 1981. Trichoplax adhaerens and the origins of Metazoa. International congress on the origin of the large phyla of metazoans. Accademia Nazionale dei Lincei. Atti dei Convegni Lincei. 49:113)*

zoans are intermediate between sponges and the remaining metazoans. They resemble the hypothetical protometazoan (Fig. 4-12D) that has adopted a benthic crawling existence and has differentiated its upper and lower surfaces accordingly. The monociliated cells resemble collar cells in which the collars have been reduced to low microvilli, perhaps correlated with locomotion over a substratum and the abandonment of filter feeding. The outer epithelioid layer is one step closer than that of sponges to a true epithelium, which appears fully formed in Cnidaria (Chapter 7). The lower cell layer is reminiscent of the digestive epithelium of the guts of other animals.

There remains the problem of a lack of anterior-posterior polarity in placozoans. If such polarity occurred in the protometazoan, then placozoans, at least the adults, must have abandoned it. Perhaps there is some merit to this idea, because anterior-posterior polarity is expressed only in the larval stages of sponges; larvae have not yet been observed in placozoans. A phylogenetic tree depicting the possible relationships of sponges, placozoans, and the remaining metazoans is shown in Figure 5-19. Finally, 18S RNA gene-sequence data also suggest that placozoans are intermediate between sponges and cnidarians.
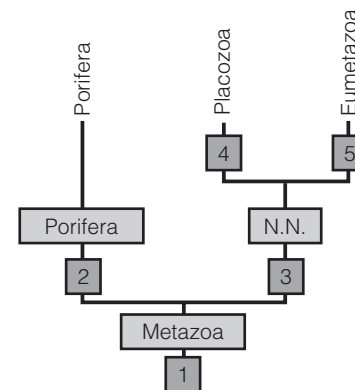
FIGURE 5-19   Phylogeny of lower Metazoa. **1, Metazoa:** Anterior-posterior body polarity, monociliated collar cells, connective tissue, epithelioid tissue in which adjacent cells are in mutual contact. **2, Porifera:** Filter feeders with an aquiferous system. **3, N.N.:** Monociliated cells with short microvilli or with microvilli absent, epithelioid tissue in which adjacent polarized cells are joined by an intercellular junction (belt desmosome), extracorporeal digestion. **4, Placozoa:** Highly flattened body, fiber-syncytium, questionable loss of anterior-posterior polarity. **5, Eumetazoa:** True epithelium composed of a sheet of polarized cells, interjoined by junctional complexes, that rests on a collagenous basal lamina; internal digestive epithelium.

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www.ucmp.berkeley.edu/phyla/placozoa/placozoa.html (Images and description of *Trichoplax.*)