

### 9-3 FILTER FEEDING AND DIGESTION IN SPONGES

Sponges, sessile and weaponless, live by drawing in an unceasing flow of water through minute pores. This flow is nutritive, it brings oxygen and it removes the waste products of metabolism, in so far as they do not diffuse direct to the outside. In the calcareous sponges (Class Calcarea) the pores are intracellular canals in specialized cells called porocytes, which are derived from the dermal epithelium. Porocytes may not be present in other sponges, but pores certainly are, and they are always small; consequently they constitute a simple but effective sorting device that



permits the passage of only the smallest particles. The course that the water follows may be very complex, but in principle it passes through the pores into the central spongocoel, and leaves this by a large opening, the osculum (Fig. 4-17, p. 89). Each individual initially possesses one such opening. As the body grows, additional oscula may form, and we then regard the sponge as a colony (Sec. 21-2), each osculum representing one individual. The definition is admittedly somewhat arbitrary; individuality is much less well defined in these organisms than it is, for example, in coelenterate colonies.

This weak individualization, like the feeble capacity for movement that we have considered earlier, is indicative of the exceptionally low level of organization at which sponges exist. Another illustration of this, the limited coordination between individual cells, is well seen in the feeding mechanism. The current of water depends upon the completely uncoordinated beating of the flagella of the choanocytes (Sec. 4-4). As we shall see later, these cells, together with wandering amoebocytes, abstract the food particles from the water and immediately ingest them, so that no structural specialization for the manipulation of the food is required. What has influenced the body form, however, is the dependence on uncoordinated flagella for the creation of the water flow. This influence is expressed in three main levels of organisation.

The simplest arrangement is the asconoid type (Fig. 9-4), consisting of a single ascon chamber (Fig. 4-17, p. 89) lined by choanocytes. The uncoordinated and circular beat of the flagella contributes nothing to directional movement of the water, but a flow from the porocytes towards the osculum is encouraged by the small size of the former and the larger size of the latter, since the water will tend to flow towards the larger opening. The flagella, however, can only establish a very small head of pressure, which is a very inefficient way of keeping a central mass of water in continuous movement. (Records for siliceous sponges show that when a tube of 1 mm bore is inserted into the osculum the level of water in the tube only rises to a height of 2-4 mm.) This hydraulic difficulty has conditioned the increasingly complex canal system of the other two levels of organisation: the syconoid and leuconoid.

The syconoid type (Fig. 9-4) results from a folding of the body wall so that the choanocytes are restricted to radially arranged canals which are essentially ascon-type chambers, the pores of which are now termed prosopyles. The radial canals discharge through internal ostia into a large excurrent chamber that opens at the osculum. This is the simpler type of syconoid structure, seen in *Sycon*. It becomes further elaborated by the development of a cortex, supported by spicules and overlying subdermal cavities. A more continuous body surface is thus formed, penetrated by dermal ostia which lead into a system of incurrent canals.



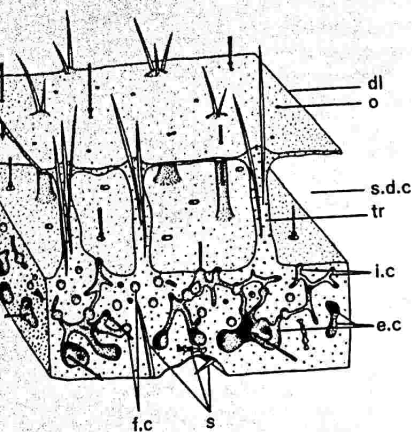


Fig. 9-5. Schema of the outer layer of the body of *Spongilla*, reconstructed from living and fixed sections. dl, pseudo-flagellated chamber; e.c, excurrent canal; f.c, flagellated chamber; i.c, incurrent canal; o, ostium; s, spicule; s.d.c, subdermal cavity; tr, trabeculum. Arrows indicate the water flow. From van Weel, 1949, *Physiologia comp. Oecol.*, 1, 110-126.

The third type (leuconoid or rhagon) is reached by further folding of the choanocyte layer, so that the choanocytes are now restricted to a large number of small flagellated chambers. The apopyles of these lead into a complex system of excurrent channels which finally open at oscula without discharging into a main spongocoel. The leuconoid type of canal system (Fig. 9-5) exists in three grades: the eurypylous, in which the apopyles open direct into the excurrent channels; the aphodal, in which a narrow duct, the aphodus, lies between the flagellated chamber and its excurrent channel; and the dipodal, in which there is also a narrow duct, the prosodus, between the incurrent canal and the flagellated chamber (Fig. 9-4).

Most sponges (perhaps 98%) conform to the leuconoid plan, which must almost certainly have arisen independently along many different lines. Presumably, therefore, it must have outstanding advantages, and it is not difficult to see what these are. The leuconoid canal systems have an effect somewhat like that of the branching vessels of a blood system, for the water, after entering through the dermal ostia, moves increasingly slowly as it passes into an increasing number of canals of diminishing diameter. Movement within the flagellated chambers is thus slow enough to permit respiratory gaseous exchange and the filtering of food (see below). At the same time, movement of water out of the chambers is encouraged by the collars of the choanocytes being close to, and directed towards, the apopyles. These tend to be larger than the prosopyles, which further favours this pattern of movement.

When the water leaves the chambers it begins to move faster as it flows through channels of increasing size, and it is finally expelled from the oscula with considerable force, since the diameters of these openings are generally smaller than those of the excurrent channels. The acceleration of the excurrent stream helps to ensure the efficient discharge of the water from the body, with the minimum contamination of the incurrent stream. The latter condition, which is an essential element in the successful operation of a ciliary feeding mechanism, depends also on movement of the surrounding water. This explains why sponges cannot easily flourish in the

absence of currents. It is further ensured in sponges by the form of the body, which often contributes to the efficient separation of the incurrent and excurrent streams.

Bidder, in his analysis of this aspect of sponge organization, called the angle between the intake and outflow currents the angle of supply. Between the two currents there is established a re-entrant vortex, the diameter of which he called the diameter of supply. This must be large enough to provide a good chance that surrounding currents or drift will carry away the outgoing water. In non-stalked sponges (Fig. 9-6A) the angle of supply is  $90^\circ$ . The presence of a stalk increases the angle, and thereby reduces the risk of contamination of the intake current. This means that the osculum can be opened out, since the water need not be ejected with as great a force; thus evolves the type of sponge body represented by Neptune's Cup (Fig. 9-6B). If the cup is set on one side, the angle of supply becomes  $180^\circ$ . Oscular velocity is no longer an important consideration, and so the body can open out into a flattened

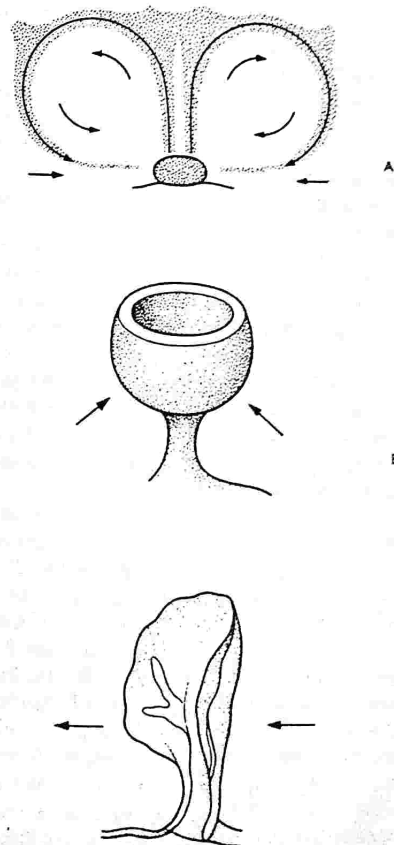


Fig. 9-6. Relationship of the form of sponges to their feeding currents. A, the bath sponge (*Euspongia*), a sessile form in which the angle between the inflow and outflow currents is  $90^\circ$ . B, Neptune's Cup, in which a stalk increases the angle of supply, so that there is less risk of mixing the two currents; the osculum therefore opens out. C, *Phakellia*, in which the body is a flattened fan, with one inflow face and one outflow face. Adapted from Bidder, 1923, *Q. Jl microsc. Sci.*, 67, 293-323.



form (Fig. 9-6C); this has the advantage of permitting a maximum flow of water through the body, and hence affords an improved opportunity of securing food.

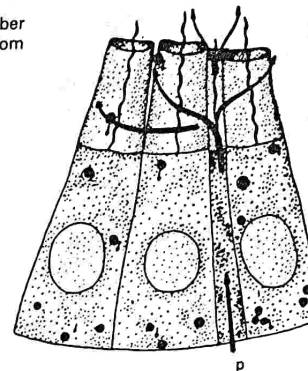
The achievements of sponges are thus not to be underestimated. They are animals with the minimum of cell differentiation, and with so little coordination that they can almost be regarded as colonies of cells. Nevertheless, by the evolution of their form along lines that can be interpreted in simple hydraulic terms, an effective feeding mechanism is undoubtedly attained. However, the elaboration of a complex hydraulic system is not a necessary condition of this achievement. As we have earlier noted, some of the deep-sea hexactinellid sponges rely upon a body is shaped as a flat or curved net, with water entering on one side and leaving on the other. In this simplicity of structure they are exploiting, with a minimal expenditure of energy, the steady currents of the abyss. Setting their lattice-like structure across the direction of flow, and filtering particles that are brought to them, they are, in Bidder's words, 'a moment of active metabolism between the unknown future and the exhausted past'.

The low level of coordination in the Porifera is further shown in the digestive processes that follow the filtering of their food material. It would appear, from the few species that have been studied, that the choanocytes are responsible not only for maintaining the food current, but also for the initial ingestion of the particles. In the Calcarea, where these cells are particularly large, the food adheres to the outer surfaces of the collars. The delicate processes of which these are composed (Sec. 4-4) act as a filter for trapping food particles, which are then passed down the collar surface, presumably by protoplasmic streaming, to be taken up into food vacuoles at its base.

Within these vacuoles a good deal of digestion may take place, very much as in heterotrophic flagellates, but some at least of the material is transferred to wandering amoebocytes in the mesenchyme that separates the flagellated cells from the dermal epithelium. These amoebocytes complete the digestive process, the indigestible residue being discarded from them and eventually removed from the sponge body in the outgoing stream of water. These same cells also store reserve material, and thus, in consequence of their movement through the organism, provide the equivalent of a combined storage and transport system. Amoebocytes therefore play a central part in the life of these animals; as we shall see, they contribute also in an important way to the reproductive processes.

In the other groups of sponges, the choanocytes (Fig. 9-7) are smaller, and they seem to be concerned more with ingestion than with digestion, for food material is transferred more immediately from them to the wandering cells. This happens, for example, in the fresh-water sponge, *Spongilla*, where the amoebocytes both digest the food and also pass it on to other cells which may complete the breakdown. It is said, however, that they never pass material into the choanocytes, which implies that these cells must have their own self-sufficient digestive mechanism. Nevertheless, and appropriately enough for such a cell republic, even ingestion is not exclusively a property of the choanocytes. This can be well shown by feeding sponges with suspensions of carbon or carmine, or (much better) with dead bacteria that have been labelled with fluorescent antibody, so that their fate can be traced by ultraviolet microscopy. In fresh-water sponges the prosopyles are 5  $\mu\text{m}$  in diameter, while the spaces between the adjacent microvilli of the collars are of the order of 0.1  $\mu\text{m}$ . Thus,

Fig. 9-7. Scheme of water flow in the flagellated chamber of *Spongilla*. p, prosopyle, lying between choanocytes. From van Weel, 1949. *op. cit.*



the flagellated chambers are well adapted for filtering individual bacteria, which fall within this range. Larger particles, however, such as clusters of bacteria, can still be captured. They can be phagocytosed by the dermal cells if they are too large to enter the ostia, or by amoebocytes and other cells if they are trapped in the incurrent spaces.

Whether or not sponges can make use of soluble organic material is uncertain although the possibility cannot be excluded. A complicating factor in studies of the nutrition of these animals is the presence within the mesenchyme of many species of a rich flora of bacteria and unicellular algae. The physiological significance of the bacteria is not clear, but the algae are thought to be symbionts (Sec. 23-2).

#### 9-4 FEEDING AND DIGESTION IN COELENTERATES

Coelelenterates, with a level of cellular differentiation that is so much more advanced than that of sponges, show a correspondingly greater complexity in their feeding and digestive mechanisms. They are all specialized for a carnivorous diet, capturing their food by a highly discriminatory sensory and motor system. Tentacles play a prominent part in this, used in conjunction with various combinations of mucus secretion, ciliary movement and the action of cnidoblast cells.

Cnidoblasts, so characteristic of coelenterates, secrete within their cell bodies the structures called nematocysts (Fig. 9-8), which consist of a pear-shaped capsule containing an inverted tube attached to one pole of the capsule wall. On appropriate stimulation the tube is extruded by inversion, through a mechanism not fully understood, to form a thread that fulfils a function determined by its form. The range of form (no less than 17 different types have been described) is illustrated by the four types found in *Hydra* (Fig. 9-8). One of these is the desmoneme or volvent, which has a coiled thread, with minute bristles, that winds round any surface projections of the prey. Another type is the penetrant or stenotele (it seems profligate to carry precision to the point of describing this as a stenotelic rhopaloidic heteronemic stomatopore nematocyst, although such is indeed its designation in one system of classification). This has a basal enlargement called the butt, on which are situated