

THE SPONGES—THEIR SIGNIFICANCE

From *Après Darwin*, by DR. HÉLAN JAWORSKI

Sponges foreshadow glands.—The Choanoflagellates of space are the collar cells of sponges—The evolution of certain Infusoria, in particular the Stentors, is repeated throughout the animal kingdom in the evolution of the renal tube.—The structure of the compound kidney is foreshadowed by that of the sponges.

Always aquatic, some inhabiting fresh water, but most of them the sea, living attached to rocks, stones, or bits of wood, sponges exist in infinite variety. The simplest of them look like polyps, bags attached at the base, with large orifices.

But in the sponges, this orifice is not surrounded by tentacles, and no longer plays the part of "mouth-anus", as in the polyps. Here it is exclusively an anus, an exit. Water enters continuously through a series of numerous little holes in the walls of the bag, which function like tiny sucking mouths. Then the water passes through the cavity of the sponge, the cloacal cavity, and leaves it through the anus, the excretory orifice.

That is a short description of a basic type of sponge. The majority of sponges are much more complicated. They are composed of a multitude of elements; they are really colonies, and as they grow they acquire several pockets.

The walls thicken, fold, elongate; the little mouths become veritable tubes of ever-increasing complexity which form a network of inhalatory canals. It can also happen that certain canals dilate into pockets, separating a superficial rind from the central part.

The inhalatory canaliculi, the pores, may extend into the superficial part which is bathed by sea water; or new, secondary pores may be produced. However it comes about, "water penetrates the sponge through numerous orifices of tiny dimension and irregular arrangement; it passes through canals, hollowed out of the substances of these zoophytes, which join with one another to form bigger and bigger streams, rather like the roots of a plant."

Do sponges show the rhythmical contractions and dilatations which we have observed in polyps? To be sure there are very localised movements of systole and diastole which remind us that we are not far from polyps. But instead of provoking and accelerating the flow of liquid, these contractions seem to have the contrary function of limiting, or even of stopping it. Indeed, the little inhalatory pores are narrowed by contractile muscular rings, as is each secondary cloacal orifice. The main and in certain species only cloacal orifice is a well-developed anal sphincter which regulates the inflow and out-

flow of water throughout the whole animal.

Sponges have a vague generalized sensibility, and even in the absence of differential muscular or nervous elements show contractile movements.

The wall of the body of a sponge can be split up into three layers: the outer layer, the skin, if you like; a mesial layer of jelly which contains the sponge amœbae, and skeletal needles, the spicules, which have already been noted in certain polyps; and finally, an internal layer in which are found special cells, the collar cells, with which we are also familiar.

These cells are interiorized choanoflagellates and, according to certain authors, a colony of *Codosiga*.

In fact, choanoflagellates are united in groups inside the sponges to form what have been called "vibratile baskets".

The movements of their flagella direct the current of water in the canaliculi. Spherical in calcareous sponges and tubular in others, the vibratile baskets, placed between the two systems of inhalatory and excretory canals, constitute the central part of the sponge. Primitively they were in the cloacal pocket; but as the jelly developed the walls of the pocket were pushed back, and the baskets with them; the cloaca itself is now no more than a common meeting place where the water from all the multiple cavities collects, before being ejected by the anus. The collar cells of the vibratile baskets are characteristic of sponges, as sting cells are of polyps.

We have given a general idea of the structure of sponges. It must not be forgotten that modifications can occur in the shape of the excretory canals, giving rise to lacunar cavities. The orifice of a basket opens into this system of crypts, which can in its turn subdivide. Siliceous or horny spicules may increase the degree of complication in non-calcareous sponges. One can only guess at the complexity of the waterways, and at the great variety which can occur in the shape and arrangement of sponges.

"But there is one characteristic", writes Delage, "to which attention should be drawn, since it is never lost even in the midst of these infinite complications: *the absolute separation of inhalatory and excretory routes*. Throughout these canals, which cross the sponge in all directions, and often without apparent order, there is never one which goes directly from an inhalatory canal to an excretory canal. Communication between the systems exists solely through the medium of the baskets, so that every drop of water which enters through the pores must go through the baskets in order to reach the osculum (anus)."¹

The activity of a sponge is evidently altogether interior. Its external morphology is only of secondary importance, indeed, it is negligible; the sponge must adapt itself to the objects which give it support. Individuals of the same species may vary considerably in shape and colour.

They are usually large, and tend to reproduce vegetatively. The inhalatory pores are found most often on the convex surface, when there is one, and the excretory openings on the concave surface.

Polyps are carnivorous, but sponges feed on debris of all kinds, on excrement, and on the millions of particles of which "plancton" is composed.

Within fresh-water sponges may be found algae which live in symbiosis with them, as they also do with the green hydra. Special varieties of algae may even inhabit special varieties of sponges.

If coloured particles, such as carmine granules for instance, are thrown into water inhabited by sponges, these granules may soon be seen to make their way towards the sponges and to penetrate them through the tiny pores. In the case of young siliceous sponges grown on glass plates, Y. Delage has observed these coloured granules rushing in crowds towards the collar cells which, in an instant, took up the colour as if they had been stained by reagents.

Furthermore, it has been observed that the amœboid cells carried particles absorbed by the collar cells throughout the organism, so that in the end the colouring agent invaded the whole sponge.

Y. Delage writes: "The choanocytes (collar cells) appear also to be organs of excretion. *Excretion is prominent amongst sponges*, for these animals rapidly defile the water which surrounds them if it is not frequently renewed. . . . The presence of an acid in the water which surrounds the sponge has been demonstrated by Loisel."²

Having said all this, we can now seek for the significance of sponges.

In order to recognize and to characterize the excretory cells of any animal, a coloured substance such as aniline or carmine, etc., is injected into the general cavity. . . . Next day the animal is killed and examined in order to see where the colouring matter has become fixed. Some cells retain and accumulate ingested substances, whilst others reject them; thus a distinction may be drawn between "eliminator kidneys" and "accumulator kidneys".

In decapod crustaceans and vertebrates those liver cells which select and retain the putrefaction products of meat combine to a certain extent this double function. Excretory globules, which make up the different kinds of kidney, are found either sparse and isolated, or grouped into systematized organs.

The colour-fixation experiment may be more directly performed: Prussian blue is poured on to the concave surface of the diaphragm, covered, as is the rest of the abdominal wall, by the thin and delicate layer of tissue called peritoneum; the liquid may be seen to disappear in vortices at certain points on the surface of the diaphragm, whence it passes into the lymphatic vessels which are contained in this thickness of the diaphragmatic membrane.

When the peritoneal globules acquire a certain status as in the echinoderms, it is even possible to find some ciliated vibratile cells which cause movement of the contents of the peritoneal cavity. The peritoneal cells are "assisted in this task by special vibratile apparatus, either fixed ("urns" and

"baskets") or mobile within the fluid of the body-cavity ("vibratory globules" of sea-urchins).

"The ciliation of the coelomic cells (of the general body-cavity) is doubtless much more widespread than has been hitherto believed. It must also be remembered that in some animals the peritoneal cells are veritable musculo-epithelial elements, constituting the muscles of the walls of the body, and that in annelids such as *Owenia* they are, according to Gilson, musculo-glandular elements, of which the glandular parts directly line the coelomic cavity. Without even insisting upon these differentiations, which are marked, the peritoneal epithelium often shows modifications which enable it to perform a nutritive function."³ "Thus can be seen the remarkable aptitude possessed by these peritoneal cells for differentiating in various ways."

Following these experiments and observations there would appear to be a relationship between the kidney, the peritoneum, the lymphatic vessels, and the vibratile baskets (perhaps even the canals) of sponges. We must study these organs to see whether the relationship is valid.

One question may be asked at once. We know that every cell secretes. But when speaking of the organism only those cells are described as secretory whose glandular function causes appreciable changes in the medium surrounding them. This relative, arbitrary, and imprecise classification arises from our present insufficient knowledge of the intimate mechanisms of secretion and excretion. The latter, often in a liquid form, may be unnoticed, and in general very little is known about the process in the lower animals.

If the glandular function be considered from the point of view of the materials withdrawn from the organism, we would have to conclude that the kidney cell eats excreta. That is also precisely what the sponge does. If on the other hand we think of the products of secretion, and of the intensity and rapidity with which they are added, it becomes evident that the sponge, by its active excretion, quickly fouls the water in which it lives.

The glandular cell often secretes a special kind of mucus. And sponges in general are noted for the thick mucous quality of the secretions. When a sponge is lifted out of the water this mucus flows from it like foetid white of egg. Mucus can be considered as a primordial product of secretion.

Secretion being a property of all living things, no particular structure can be exclusively associated with it, but nonetheless glands have a characteristic appearance which is better defined the more perfect they become.

"On the other hand, Reichel and Ranvier, in a comparative study of the glands of the buccal cavity in vertebrates, have established an important fact; namely, that glandular organs having a certain anatomical name do not have the same histological character in all species; the sub-maxillary gland of one species is neither histologically similar nor functionally equivalent to that of another."⁴

In spite of this a great analogy of structure can be observed between sponges and glands.

This correspondence is already apparent in the process of formation. Prenant writes: "As soon as the gland acquires a certain volume, the anatomical or functional units are grouped into *glandular lobules* which in their turn form larger masses, the glandular lobes."⁵

We know that this is also the case with the sponge, which is formed as a result of the union of similar elements. The total mass is often divided into large lobes.

But, leaving aside these over-simple analogies (which is not to say that they are false for all that) let us look at the sponge from a completely different point of view.

The characteristic organ of sponges which, for some authors, separates them altogether from higher animals, is the collar cell. Alone it forms the body of choanoflagellates, but in this case possesses pulsatile vesicles. As these same vesicles have been observed, if only exceptionally, in the collar cells of sponges, there can be said to be no essential difference between the choanoflagellates of space and the collar cells of sponges. The latter can be considered as interiorized Protozoa, choanoflagellates.

Now, what does the group of choanoflagellates show? We shall find there *Monosiga*, a collar cell identical with that of the sponge, but solitary; *Codosiga*, equally similar, but grouped in colonies like florets on a long peduncle. *Hirnidium* has collar cells grouped in colonies of ten, side by side. In *Salpingoeca*, the same collar cell has a capsule shaped like an urn. In the genus *Phalansterium* the collar, which hitherto has been mobile and retractile, has become narrow; it looks like a tube similar to those of the other forms in their maximum state of retraction. So, in *Phalansterium*, the collar is so small that some authors deny its existence.

This exiguity of the collar is a very important fact for us.

In passing it should be noted that the colonies of this same *Phalansterium* are created by gelatinous tubes secreted by the individuals, which become joined together. Finally, in *Protospongia*, the cells, one after another, provide themselves with a collar and a whip as soon as they reach the periphery of the colony, *and lose the same collar and whip when they become interiorized* once more in the colonial jelly.

These gradual transformations, these exact phenomena, enable us to grasp the tendency of the collars to diminish, even to disappear, as soon as they become *interiorized* into the colonial jelly, whilst the "collar cell" tends to take on an amœboid appearance. *It would therefore be an error to seek for typical collar cells within organisms.* Here, the collar disappears, though not always so completely as in *Protospongia*.

As we know, the complexity of organisms necessitates a rapid fusion which does not permit exact observation of the stages between a normal primitive cell, and the same cell when it has become modified, interiorized, and henceforth constitutional.

Nonetheless, we shall find collar cells in higher organisms.

Already in the sponges "these cells are very tightly packed, to the extent that the edges of the collars become polygonal through reciprocal pressure."⁶ Further, in many sponges the gradual transition can be studied from collar cells which occupy the base of the cavities or baskets, to monociliated cells which line the exhalatory canals. The choanocytes are related to the "Solenocytes" or "cornet cells" of the renal tubes of certain worms (Polychæta). The renal tubes of the Hirudinae (leeches) already resemble urinary glands:

It is well-known that between flagellated cells and cells with small and numerous cilia there are intermediate forms. In the vibratile basket the typical whip cells, in which the base of the whip is surrounded by a collar, have another whip which, inside the cell, is embedded in the mass of protoplasm. Thus, the collar is found again in the cornet cells of the renal tubes of certain polychæte worms, and the second whip in the kidney cells, the seminal cells, and others.

More numerous than whip cells are the ciliated cells. Within organs the cilia resemble the bristles of a brush, and do not seem to move. The relation between these two types of formation is recognized today. "Brush-like borders are ciliate surfaces which have lost their vibratile power."

Moreover, in the differentiation of ciliated cells themselves, similar transformations can be observed. "It is also probable that in organs whose epithelium is made up of a mixture of ciliated cells and glandular non-ciliated cells, for instance in the oviduct and the epididymis of mammals, the two cellular forms are but *successive states of the same element*, which is first furnished with vibratile cilia, and then loses these cilia and elaborates secretory material. Moreover, this cycle has been well established, if not for organs bearing vibratile cilia, at least for those which have brush-like cells; the ciliated cells are but transitorily differentiated elements, and not immutably fixed cellular forms."⁷

To recapitulate, parallelism is evident in the two cases. The *collar*, already much diminished in Phalansterium, *can be guessed at in the brush cell of the kidney*. This is a valuable hint, since the ciliated form cannot therefore be considered as an essential form.

The ciliated form can be found mixed up with the glandular form, *and the brush cell is but the adaptative form which certain ciliated cells take up within glandular organs*. It has further been observed that collar cells lose their whip when interiorized into the jelly, not only in Protospongia, but in the sponge itself, where the jelly is full of amœboid cells without whip or cilia, primordial elements which go everywhere, and from which the sensory cells will also later be formed. These, in developing by a relative exteriorization, will acquire whips.

Deeply interiorized in the gland, the collar cells will not, save in certain worms, be able to develop into anything except brush cells.

This relationship of form is so exact that we shall see it realized again in cells destined to be exteriorized, such as spermatozoa. "The tail of the

spermatozoon represents an expansion of the central corpuscle or corpuscles; so that here these keep their function of kinetic centres, which belongs to ciliated cells in general." Only, in the case of the tail of a spermatozoon, the whip is of too complicated a structure to be dismissed as a simple fibrillary process. Be that as it may, in the spermatozoa of the guinea pig and other animals such as the rat, there is at the base of the whip a transitory cuff which brings to mind the collar of choanocytes. This curious fact not only now seems quite natural, but may even be said to show its true significance through this atavistic note.

After such considerations, we must look for the significance of the kidney.

This organ is found in its simplest form in worms, where it consists of a tube which ends in a funnel, lined with vibratile cilia. The movement of these cilia causes liquid to enter the tube, and drive it out again to the exterior through an orifice.

The first complication which occurs is that the middle part of this kidney becomes more or less folded and provided with glandular cells which withdraw the products of excretion from the body cavity, and reject them into the lumen of the tube. These organs, called "segmental tubes" which are found in each segment of the body, join and become elaborated to form the kidneys of higher animals. In certain Amphibia they are very obvious in the segment nearest to the head, and they persist throughout life in fishes (Ganoides and Teleosts).

Furthermore, little branches of the aorta, folded into skeins, project into the general body-cavity, and pour into it an excretory fluid.

At first the relationship between the renal tube and the vascular skein called a "glomerulus" seems remote, and the liquid which filters through the latter falls into the interior cavity and flows out of it mixed with that from the said tube, as for instance in Tritons.

But little by little the connection becomes closer. At the extremity of the tube, near the ampulla, a vase-shaped bud is formed which encloses the little vascular skein, whose liquid filtrate is thus discharged directly into the tube.

So, permanently in the Amphibians, the tube has a ciliated funnel which withdraws liquid from the general cavity, and an ampulla which, surrounding the glomerulus, receives the liquid filtered by this arterial skein. Thus the funnel does double work. Finally, as it becomes useless in the higher animals, it closes up and disappears.

At first, the well-developed glomerulus filtered liquid which fell into the general body-cavity. This liquid was then taken up by the ciliary movements of the funnel. At that time the renal tube possessed a real individuality; it was still a relatively independent organ.

At first sight these evolutionary peculiarities might be thought to lead us away from the sponges, and even from the choanoflagellates, but they

bring us nearer to the Ciliata, their neighbours.

Amongst worms, and even in the large intestine of man we find a ciliated Infusorium, *Balantidium Coli*, which has a triangular furrow. In another Infusorium (*Bursaria*), this furrow becomes an enormous pit, and the animal may or may not have many pulsatile bladders. Next we find a trumpet-shaped creature which is usually fixed. The hairs and fine membranes of its mouth produce constant vortical movements of the fresh water in which it lives, in exactly the same way as the ciliated ampulla of the renal tube causes vortical movements of the liquid in the animal's body-cavity; this creature, this Infusorium, is the Stentor. Let us observe it.

Our attention is caught by a singularly remarkable phenomenon. This is the successive renewal of the ampulla. In the words of Y. Delage: "This phenomenon, incorrectly described as regeneration, consists in that, upon an individual whose peristoma (ciliated ampulla) is entirely normal, *a new peristoma can be seen to form*, just as if division were about to take place. But such division does not occur, and, through a process of unequal growth, the new peristoma, at first straight and vertical, *gradually takes the place and shape of the old one, whilst the latter recedes and atrophies before its usurper*. It could well be that this phenomenon, whose purpose now escapes us, derives from a division which became reduced to one of the processes concerned in it."

This fact shows that Stentor, in the course of its natural life, undergoes exactly the process *repeated by the renal tube as it evolves within organisms*; that is to say that beside the first ampulla a second develops which will in this case surround the glomerulus, whilst in both cases the first ampulla disappears.

The question of division is no more than an attempt at explanation, since the purpose of this phenomenon is only apparent in the outside world.

Amongst other Infusoria (*Folliculina*) the trumpet develops into two lateral wings; the animal is enclosed in a capsule. In *Fabrea* the anus is below; excretory granules are found in the excrement. One Infusorium, *Spirostomum*, is straight, but the animal has already learnt the habit of twisting itself round like a screw. *Metopus* shows all kinds of deviation of its furrow. Finally, a parasitic Infusorium (*Spirochona*) is found on the Crustacea, and another (*Licnophora*) on medusae, echinoderms, worms and certain molluscs. These parasites are basically folded Stentors, whose curve is continued internally. Amongst Infusoria of a neighbouring group, the *Vorticellae*, this torsion is restricted to the peduncles. In the same way the primitive renal tubule, at first almost straight, becomes in the course of its evolution more and more folded, until we reach the "convoluted tubule" of composite kidneys, wherein is attained the definitive configuration of this organ.

Once again it must be stressed that the elements of internal organs do not correspond exclusively to this or that natural form, but rather to several at once. Interiorized forms, it has already been understood, repeat in a fused

and condensed manner the themes which exteriorly are found scattered, separate and solitary. The renal tubule does not correspond alone to Stentor, Spirochoma or Codosiga, but to all of these forms at once.

This synthesis and repetition within the organism becomes even more complicated by the homogeneity of the whole, and the inter-relationships of the vascular, sanguine and nervous systems.

In the epithelium of the convoluted renal tubule and the succeeding parts we find brush cells with a whip which floats within the lumen of the urinary tubule, recalling the collar cell of sponges.

Now, by the time we reach the fishes, the ends of these tubes communicate with a collecting canal which runs the whole length of the body receiving liquid from the segmental tubes. In the tree, the collecting canal alone persists. Through this are formed kidneys of the second order, made up of tubes which present in their turn secondary and tertiary canals. These secondary kidneys only function for a short time during the embryonic life of birds and mammals. To what can they correspond, if not the development of the Sponge? Indeed, we see that most of them establish themselves by the system of excretory collecting canals, an elaboration which we have already noticed.

After a transitional form (*Stelletta*) we find a very simple sponge (*Disyringa dissimilis*) shaped like a sphere containing collar cells. Exteriorly, this sphere is prolonged into two poles by two tubes. The inhalatory one is flexible and pierced by pores through which water enters, whilst the exhalatory one contains four smaller tubes. But perhaps the oddest thing is that the end of one of these tubes is dilated into an ampulla in which spicules simulate cilia. . . .

Another sponge (*Tribachium*) has only one tube. Here, the sphere appears to represent the vibratile ampullae, or better still, the capsule surrounding the glomerulus, whilst the cloacal tube signifies the collecting canal whose end, in both cases, is encircled by a muscular ring. To recapitulate, these sponge forms correspond in miniature to kidneys of the second order. As we have said, these secondary kidneys soon disappear, at any rate for the most part, in the Biological Tree. At the beginning of the second month, in the human embryo, the definite composite kidney has begun to develop.

This definitive kidney is made up of assembly of equal parts; it is a formation of a high order of complexity, derived as much from the stages through which it passes as from its origin which is in a sense double, like that of the heart.

In fact, it derives partly from the collecting canal which we have just described, and partly from the jelly which surrounds it; to put it another way, the kidney arises from two distinct origins, which become fused. It is true that the composite kidney is a formation which we shall seek in vain exteriorized in space. But is it something quite new, a unique and isolated note? Not at all.

In fact the human kidney is formed from several lobes; the lobe is sub-

divided into lobules, and the lobule is made up of a series of tubes. . .

These tubes begin at the level of a glomerulus, become convoluted and form loops, and eventually debouch into the renal pelvis which corresponds exactly to the cloacal cavity of a sponge.

The exits are guarded by muscular rings, just like the little anuses of a sponge.

"The little mouths which ordinarily open at the very surface of the sponge", says Edmond Perrier, "are however situated at the bottom of cup-shaped depressions in *Aplysia serophobia*, *Spongelia avara*; they are transported to the tops of tubes or of special thin-walled papillae in *Plakina*, *Caminus vulcani*, *Oscurella lobularis*, etc. . . . or of thick-walled papillae in *Weberella* and *Polymastia*; they are closed by a membranous ring shaped more or less like a convex iris in *Isops*, etc. . . ." ¹⁰

Each of these species contributes a note, all are united in the kidney.

The tubes do not debouch separately; they join up with more and more neighbouring tubes so as to form collecting canals, to the extent that, if the renal lobe contains 56,000 tubes, these will connect with the cloacal cavity through not more than 15 or 20 orifices.

Now if one considers that the capsule of the glomerulus which was originally an ampulla, corresponds to the inhalatory pores of the sponge; if one considers further that the glomeruli are found principally in the cortical region of the kidney, and that the tubules converge towards the pelvis, the cloacal cavity, one can see that this arrangement is no novelty either. We find it very clearly in *Tethia*, a little sponge which looks like an orange and which possesses a rind full of cavities into which the pores debouch.

The inhalatory canals leave these cavities and describe a very convoluted or winding tube; only the exhalatory canals are found here, in the spaces left by the inhalatory canals. From an eccentric focus the spicules radiate in spokes like those of a fan, and the whole aspect is so striking that it is impossible not to recognise, in *Tethia*, the embodiment of certain notes of the global structure of the kidney. This is even more remarkable when one considers that these features of *Tethia* reappear very late; in the bear, the renal lobules are still independent. . . .

To sum up, the renal lobes are very complicated, but the fundamental features of the sponge may be found in them. Fluid circulates in one direction only, the inhalatory channels are separated from the exhalatory ones, and the latter join one another like the roots of a tree.

The urinary tubes which make up the lobule correspond to the simple tubes of worms, the starting-point for our study of the kidney.

These simple tubes are found in space in the ciliated Infusoria whose evolutionary peculiarities are repeated inside organisms higher up the Biological Tree.

Finally, from the point of view of physiology, the kidney is not a simple filter; the filtration process takes place exclusively at the level of the glome-

ulus, which is itself a pure vascular note, deriving from the polyps. The kidney, especially in the cells of the convoluted tubules, eats and accumulates substances destined to be thrown out, just as the sponge lives on garbage.

(To be continued)

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