THE MOLLUSCS—THEIR SIGNIFICANCE

(From Après Darwin)

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(Continued from page 172)

Amongst molluses the olfactory organs are also found in the branchial cavity. The abundance of sensitive pigmented elements in the siphons give these organs a remarkable sensitivity to light. More or less complicated olfactory buds are also found on the head. All these scattered notes are systematized and fused in the organism.

Some gastropods have a trunk which is a prolongation of the snout. So that if one were to think of two siphons stuck together like the barrels of a gun, one would see that the elephant's trunk, a prolongation of the nasal fossae into two hollow tubes, is perhaps not, as one thought when reading the preceding chapter, a purely vermidian feature, but more probably mixed.

This mixed note is again found in the nasal fossae of the adult human, containing as they do part of the primitive buccal cavity. In passing it should be noted that from the point of view of embryonic development a certain rapport, nay, a veritable parallelism, can be demonstrated between the formation, on the one hand, of the vulva and anus, and on the other of the nose and mouth.

Later we shall observe molluscan features in the mouth. For the moment it must suffice to mention another mollusc organ, the "radula" or horny tongue garnished with teeth. This tongue is a rasp or file which with a to-and-fro movement reduces food to small pieces or to pulp. The file is stretched over a muscular bulb which has been shown to possess special innervation; this allows us to suppose that molluscs also know the pleasures of taste.

The teeth on their rasp-tongues are already complex organs,

interiorized horny formations. The scales of certain cyclostome fishes, the epidermal scales of reptiles, the feathers of birds, the nails and teeth of mammals, are all homologous organs, we know. At the moment we are only interested in the molluscan features which they among others represent.

In the formation of enamel one stage recalls the hair-follicle, another corneous formation. Between all these organs which differ so much at first sight—the scales of fishes, the horns of ruminants, the teeth, etc.—there are but nuances, transitions. Histology has been able to relate them to one another, and thanks to this science we are able to pursue the fundamental note in all its variations.

So we discover that the polar emigration of molluscan features does not take place all at once. Molluscan organs are only found at the two poles in man, but on the other hand they exist over the whole surface if the body of certain fishes (Selachii) whose placoid scales are veritable cutaneous teeth. Soon these teeth become regularly interiorized, though in the lower vertebrates they are still found over the bucco-pharyngeal mucosa. The final arrangement is not yet reached in horses, and in certain ruminants which possess a dental lamina in regions where teeth will never grow. Armadillos present an atavistic note which we shall have reason to inquire into later.

Finally, scales, horns, and teeth are organs having the same nature as bone. Between ivory and bone there are transitional stages. The main difference is that in ivory the bony cell is external, whilst in bone it is interiorized. The connection between enamel and ivory is somewhat similar to that between cartilage and bone.

"The formation of enamel is not the constant or principal function of the enamel organ, whose essential role is rather to initiate dental formation, and to ensure the completion of the definitive tooth..."

"Where the epithelial covering is deficient, bone, not ivory, is formed." And we know that old teeth are very like bones. Taking into consideration the molluscan note, together with all that we already know, we can see how complex is the synthesis of functions united in bone!

But this bony tissue, of which we shall have to treat again when we come to the fishes, has led us a long way from the genital note of the molluscs.

One question may be asked here: is there a feminine sexual character about the molluscan organs at the head end of the body? With regard to olfaction, which has already been mentioned in discussing bipolarity, the connection becomes apparent "when one of the sexes emits odours, or else possesses olfactory organs capable of perceiving them. Examples of the first case are found amongst the mammalia, in the musk-deer, the Cervidae, the beaver, and others. The dimorphism of the antennae of many insects, such as May-bugs, silkworms, and butterflies, probably corresponds to the second." It suffices to think of the he-goat's smell, of the behaviour of dogs in the presence of a bitch, perhaps even of the use of heady perfumes . . .

In the same way, noises emitted by the members of one sex are another means of attraction, and it has long been noted amongst birds that song is the particular prerogative of males. . . . Thus many activities which at first seem to be far removed from the reproductive function are in fact indirectly related to it, and deserve, physiologically as well as morphologically, the designation of secondary sexual characters.

"This interpretation is reinforced by the fact many of these characters are more marked at mating time, or may, indeed, only be apparent then . . . The song of the nightingale, the croaking of frogs, the chirping of crickets, and of grasshoppers, are well-known examples."

The molluscan note of nose and ears essentially interiorizes smells and sounds, and is therefore feminine.

The antlers of deer have sexual significance also, as is shown by experimental castration. The head and horns of an ox are very different from those of a bull; they are more like those of a cow.

But the sexual character of horns is much more striking in the stag. "When the male deer is castrated early, before the frontal tubercles have grown, formation of the antlers is completely inhibited." As in this case it is the testicles which have been destroyed, bipolarism can be seen as a sexual phenomenon which shows up the fundamental hermaphroditism of all beings. The fact that horned does either have diseased or atrophied ovaries, or else are very old, supports this hypothesis. It is another example of a genital note appearing at the head end.

Finally, castration modifies not only hirsutism, but also the voice drawing attention to the molluscan significance contained in the bivalve larynx.

The digestive tube is, as we have seen, a formation of polyp origin, whilst the bivalved mouth derives from the molluses; so it is natural, in studying embryonic development, to consider the mouth as a superimposed formation. Amongst fishes the two maxillae may even constitute an isolated formation. The digestive apparatus of fishes is a tube closed at either end, and at the moment of hatching it is not yet open. Then a vast buccal cavity develops, separated from the intestine by a valvular ring. Here, polyp and molluse characteristics are found in the pure state, and separately; their fusion is secondary.

The larva of the lamprey has a spiral mouth. Other fish (Petromyzon) have a maxillary ring, with horny teeth and two stylets; but, amongst some of them (Elasmobranchii) this maxillary ring is double, separated from the skull and divided into two mobile halves, like the valves of molluscs. The superior labial ring represents half of the maxillary ring joined to the palate. Amongst selachians and rays there is no attachment to the skull; the two jaws joined together look like valves of molluscs, with teeth. Thus the maxillary formation is very complicated; and the molluscan note, as we shall see again, is by no means exclusive. It is none the less dominant in the enormous mouth of Eurypharynx, a curious fish whose whole body consists of two large valves terminated by a tail. The combfish swims by opening and closing its valves alternately. This is not an isolated case of locomotion among creatures equipped with valves; it is a demonstration of locomotion produced by mastication. Here first principles repeat themselves again, all function originates as movement.

So, far from being surprised, we should find it quite natural

that some fishes incubate their eggs in the mouth of the male. This might seem strange to one who had not followed our course of study.

We shall see later what has happened to the sting-capsules of cephalopods. Let us recall for a moment that the heart of a mollusc encircles its rectum, whilst in a fish it must be sought in the throat; this phenomenon corresponds to rotatory transposition, which must not be confused with bipolar emigration. The latter is a sexual phenomenon, whilst the former is evolutionary. Bipolar emigration is in the first instance doubling, followed by displacement; rotatory transposition is simply displacement.

The spiral coiling of molluscs is not a new phenomenon; far from it. We first remarked it in the protozoa. Let us recall Spirostomum, shaped like a worm and twisted like a screw, Metopus, a permanent spiral found again in Spirochona, etc. . .

In plants the leaves are inserted spirally, and flowers such as orchids are sometimes intensely whorled. Spiral coiling often reappears in animal plants, but it is most marked in the siphonophorse, where it is accompanied by condensation phenomena. Interiorized in the echinoderms, whose digestive tube describes spiral turns, coiling is not unknown in the group of worms where, for instance, it is interiorized in the genital organs and in the tightly-coiled digestive tube of siphunculids. It even becomes exteriorized in Trichinella spiralis (hence the name), and in spirorbs, amongst others of the tubicolar annelids. But in the molluscs this coiling is enormously accentuated; it is most apparent in the gastropods. The spiral coiling of the visceral mass often follows that of the shell.

This coiling is accompanied $b\bar{y}$ a torsion which can attain and even exceed 180°.

Whilst the molluscs show this exaggeration of coiling, there is to be seen in them also a sort of uncoiling, such that one movement seems to correct the other, and one might expect that basically things would remain much the same. This would be a grave error, for in reality the contrary movement merely corrects excessive coiling; fundamental modifications have been taking place, which culminate at just this point. Molluscs

accentuate a movement which did not start with them, and which, as we shall see, is found again after them . . . ! It must be clearly understood that, in molluses, the coiling which seems to disappear is in reality interiorized and condensed.

The coiling of a mollusc's shell has the same character as the external metamerism of worms; exteriorization, the apotheosis of an ancient primeval urge from the very beginnings of life, here appears in all its fulness in order to become interiorized, to melt away and disappear from all superficial examination. This is easy to verify because coiling is accompanied by modifications of bilateral symmetry; one side of the body subsides, organs atrophy or disappear. Opistobranchs have a bilateral symmetry which seems almost normal, and coiling is little accentuated; nevertheless they have only one gill, one kidney, one cardiac chamber, and this spite of the fact that the natural history of this animal demonstrates an uncoiling which must thus be no more than a stage of interiorization.

Fissurella vaginula, such as Siphonararia, seem externally to have returned to normal; but interiorly asymmetry is shown by the lateral position of the anus and the disposition of the viscera.

In the lamellibranchs, bilateral symmetry remains disturbed; it has given way to dissymmetry which is reduced in cephalopods, but reappears very clearly in the development of Amphioxus, a fact too well known to need stressing.

Spiral coiling is still often evident amongst certain tunicates; it is found again in those flat fishes where one eye, without ceasing to function, migrates around the head, or else buries itself to reappear flush with the other.

It is unnecessary to continue this review since spiral coiling is found quite distinctly throughout the whole Biological Tree and in man.

An adult man seems to be exclusively dominated by bilateral symmetry. But compared with the upper pole, where the face looks forward, in the lower pole the cheeks of the buttocks are turned backwards, so that in reality the spiral half-turn described by our body has been obliterated in the trunk, and appears only at the two ends.

The arms fold forwards, and the legs backwards, in opposite directions; this opposition is due to a local coiling motion which occurs in the third month of embryonic life.

In the organs themselves, coiling takes place. Let us recall for example the spiral coiling of the abdominal visceral mass, where the liver is relegated to the right side. The movements of the heart itself show that in contracting it turns a little on its axis; in the same way the "optic nerve chiasma", the crossing-over the cerebral peduncles, the "decussation of the pyramids", a crossing-over which leads to the right half of the body being controlled by the left cerebral hemisphere, and vice-versa, these are the results of coiling. This crossing over of the nervous system is already present in certain molluscs (Chisastoneura). In man, therefore, coiling and asymmetry are the signature of a fundamental hermaphroditism.

In the next book, where embryonic development will be studied, we shall have the opportunity of reconsidering these capital questions which are of such great interest. The ventral aspect of vertebrates corresponds in effect to the dorsal aspect of worms, and we can see now that a vertebrate is not a reversed worm, but a spirally coiled worm whose coiling, whether interiorized or condensed, has not been useless, and has not completely disappeared, no more than metamerism itself.

But, what is the reason for this coiling?

Since the feminine genital character has been discovered in molluscs, it is in the sphere of reproduction that the explanation of the curious phenomenon must be sought. If feminine sexuality and spiral coiling are not the exclusive property of these creatures, it is none the less true that it is here that they reach their highest development.

Conjugation is not purely a matter of pure sexual alimentation. Even in many cases of complete conjugation, a small part of the nucleus is expelled; and this phenomenon is greatly amplified in sexual maturation. Such maturation has in fact considerable importance. As Y. Delage tells us, "in fertilization it plays the same role as the charge does to a rifle shot".

Now, the phenomena of maturation are not the same in the two sexes. The male germinal cell, having been much reduced at first, then swells a little and divides into two secondary "spermatocytes"; each of these in its turn divides into two "spermatids", fractions of cells which are transformed into spermatozoa. To sum up, the male germinal cell gives rise to four spermatozoa.

After a period of multiplication and quantitative reduction the female germinal cell grows to a size much greater than the male cell; moreover it accumulates reserves of nutritive substance.

Then begins the maturation division which, if not essentially different from that of the male cell, yet shows one distinctive peculiarity.

The division of the female genital cell is unequal. The female cell also divides into two daughter cells, but one is a dwarf and is abortive. Then the normal daughter cell divides into two grand-daughter cells, one of which again is a dwarf, and abortive. To sum up, the primary female cell gives rise to a single large ovule and to two atrophic cells whose fate it is to disappear.

Thus female maturation results in sterilization, in atrophy of half, or even of three-quarters of the primary female element.

Is not this phenomenon found in the mollusc, with the disappearance of half of the body? One could say that the atrophy is caused by coiling, but after all, the mollusc coils up because half of its body diminishes.

Such an explanation of spiral coiling is at first surprising. But it seems quite natural when one recalls that "the whole is but the integration of the parts".

The ovary itself shows this coiling carried to its extreme, for it is in fact a gland turned backwards, a reversed gland. Furthermore, detailed study of the phenomena of karyokinesis shows a rotative transposition of the "chromatin spindle" . . .

More could be said on the subject of these phenomena of "maturation mitoses", but it would involve entering into too much technical detail. Sufficient to recall, a propos of the reduction of nutritive protoplasm in the spermatozoon, and of the reduction of active protoplasm in the ovule, the remark of Professor Delage, which can be applied to worms and molluses. "This is what the first cannot feed itself, and the second divide."

In truth, worms are parasites, and molluscs have lost all, metamerism and segmentation.

The total significance of these two great groups can be synthesized with regard to reproduction in general.

"With regard to the phenomena of fecundation it can be seen that where two individuals are similar to one another except for their sex, one cell of the organism, capable of reproduction and destined for this purpose, is first rendered incapable of fulfilling it by being deprived of some of those things necessary for the purpose, which it originally possessed."

In the male, these are the nutritive substances, in the female, the power of movement.

"Thus two incomplete cells become complementary to one another, each one having kept in itself that which is lacking in the other."

Similarly, with worms and molluscs, that which is lacking in one group must be sought in the other. The large, heavy, squat, immobile molluscs or organisms reduced to head and belly. Long, thin, lively worms are their complete opposites. The union of these two would form a whole. Impossible in the world outside, is not this the perfect union realized when mating takes place at the summit of the Biological Tree? . . .

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