

PHYSIOLOGY OF THE FRESH WATER MEDUSA.

The structure of this remarkable animal has already been investigated and described by Professors Allman and Lankester, with the result of showing that, although constituting a new genus, it is in all respects a true Medusa. After the publication of their papers I began to work out the physiology of the new form, and the following are the results which so far I have obtained.

The natural movements of the Medusa precisely resemble those of its marine congeners. More particularly, these movements resemble those of the marine species which do not swim continuously, but indulge in frequent pauses. In water at the temperature of that in the Victoria Lily-house (85° F.) the pauses are frequent, and the rate of the rhythm irregular—suddenly quickening and suddenly slowing even during the same bout, which has the effect of giving an almost intelligent appearance to the movements. This is especially the case with young specimens. In colder water (65° to 75°) the movements are more regular and sustained; so that, guided by the analogy furnished by my experiments on the marine forms, I infer that the temperature of the natural habitat of this Medusa cannot be so high as that of the water in the Victoria Lily-house. In water at that temperature the rate of the rhythm is enormously high, sometimes rising to three pulsations per second. But by progressively cooling the water, this rate may be progressively lowered, just as in the case of the marine species; and in water at 65° the maximum rate that I have observed is eighty pulsations per minute. As the temperature at which the greatest activity is displayed by the freshwater species is a temperature so high as to be fatal to all the marine species which I have observed, the effects of cooling are of course only parallel in the two cases when the effects of a series of high temperatures in the one case are compared with those of a series of lower temperatures in the other. Similarly, while a temperature of 70° is fatal to all the species of marine Medusæ which I have examined, it is only a temperature of 100 degrees that is fatal to the freshwater species. Lastly, while the marine species will endure any degree of cold without loss of life, such is not the case with the freshwater species. Marine Medusæ, after having been frozen solid, will, when gradually thawed out, again resume their swimming movements; but this freshwater Medusa is completely destroyed by freezing. Upon being thawed out, the animal is seen to have shrunk into a tiny ball, and it never again recovers either its life or its shape.

The animal seeks the sunlight. If one end of the tank is shaded, all the Medusæ congregate at the end which remains unshaded. Moreover, during the daytime they swim about at the surface of the water; but when the sun goes down they subside, and can no longer be seen. In all these habits they resemble many of the sea-water species. They are themselves non-luminous.

I have tried on about a dozen specimens the effect of excising the margin of the nectocalyx. In the case of all the specimens thus operated upon, the result was the same, and corresponded precisely with that which I have obtained in the case of marine species. That is to say, the operation produces immediate, total, and permanent paralysis of the nectocalyx, while the severed margin continues to pulsate for two or three days. The excitability of a nectocalyx thus mutilated persists for a day or two, and then gradually dies out—thus also resembling the case of the marine naked-eyed Medusæ. More particularly, this excitability resembles that of those marine species which sometimes respond to a single stimulation with two or three successive contractions.

A point of specially physiological interest may be here noticed. In its unmutated state the freshwater Medusa exhibits the power of localizing with its manubrium a seat of stimulation situated in the bell. That is to say, when a part of the bell is nipped with the forceps, or otherwise irritated, the free end of the manubrium is moved over and applied to the part irritated. So far, the movement of localization is precisely similar to that which I have previously described as occurring in *Tiaropsis indicans* (*Phil. Trans.*, vol. clxvii.) But further than this, I find a curious difference. For while in *T. indicans* these movements of localization continue unimpaired after the margin of the

bell has been removed, and will be ineffectually attempted even after the bell is almost entirely cut away from its connections with the manubrium; in the freshwater Medusa these movements of localization cease after the extreme margin of the bell has been removed. For some reason or another the integrity of the margin here seems to be necessary for exciting the manubrium to perform its movements of localization. It is clear that this reason must either be that the margin contains the nerve-centres which preside over these localizing movements of the manubrium, or much more probably, that it contains some peripheral nervous structures which are alone capable of transmitting to the manubrium a stimulus adequate to evoke the movements of localization. In its unmutated state this Medusa is at intervals perpetually applying the extremity of its manubrium to one part or another of the margin of the bell, the part of the margin touched always bending in to meet the approaching extremity of the manubrium. In some cases it can be seen that the object of this co-ordinated movement is to allow the extremity of the manubrium—i.e., the mouth of the animal—to pick off a small particle of food that has become entangled in the marginal tentacles. It is therefore not improbable that in *all* cases this is the object of such movements, although in most cases the particle which is caught by the tentacles is too small to be seen with the naked eye. As it is thus no doubt a matter of great importance in the economy of this Medusa that its marginal tentacles should be very sensitive to contact with minute particles, so that a very slight stimulus applied to them should start the co-ordinated movements of localization, it is not surprising that the tentacular rim should present nerve-endings so far sensitive that only by their excitation can the reflex mechanism be thrown into action. But if such is the explanation in this case, it is curious that in *Tiaropsis indicans* every part of the bell should be equally capable of yielding a stimulus to a precisely similar reflex action.

In pursuance of this point I tried the experiment of cutting off portions of the margin, and stimulating the bell above the portions of the margin which I had removed. I found that in this case the manubrium did not remain passive as it did when the whole margin of the bell was removed; but that it made ineffectual efforts to find the offending body, and in doing so always touched some part of the margin which was still unmutated. I can only explain this fact by supposing that the stimulus supplied to the mutilated part is spread over the bell, and falsely referred by the manubrium to some part of the sensitive—i.e., unmutated—margin.

But to complete this account of the localising movements it is necessary to state one additional fact which, for the sake of clearness, I have hitherto omitted. If any one of the four radial tubes is irritated, the manubrium will correctly localise the seat of irritation, whether or not the margin of the bell has been previously removed. This greater case, so to speak, of localising stimuli in the course of the radial tubes rather than anywhere else in the umbrella except the margin, corresponds with what I found to be the case in *T. indicans*, and probably has a direct reference to the distribution of the principal nerve-trunks.

On the whole, therefore, contrasting this case of localization with the closely parallel case presented by *T. indicans*, I should say that the two chiefly differ in the freshwater Medusa, even when unmutated, not being able to localise so promptly or so certainly: and in the localisation being only performed with reference to the margin and radial tubes, instead of with reference to the whole excitable surface of the animal.

All marine Medusæ are very intolerant of fresh water, and therefore as the fresh water species most presumably have had marine ancestors,¹ it seemed an interesting question to determine how far this species would prove tolerant of sea water. For the sake of comparison I shall first briefly describe the effects of fresh water upon the marine species.² If a naked-eyed Medusa which is swimming actively in sea water is suddenly transferred to fresh water, it will instantaneously collapse, become motionless, and sink to the

¹ Looking to the enormous number of marine species of Medusæ, it is much more probable that the freshwater species were derived from them, than that they were derived from freshwater ancestry.

² For full account, see *Phil. Trans.*, vol. clxvii., pp. 744-745.

bottom of the containing vessel. There it will remain motionless until it dies; but if it be again transferred to sea water it will recover, provided that its exposure to the fresh water has not been of too long duration. I have never known a naked-eyed Medusa survive an exposure of fifteen minutes: but they may survive an exposure of ten, and generally survive an exposure of five. But although they thus continue to live for an indefinite time, their vigor is conspicuously and permanently impaired. While in the fresh water irritability persists for a short time after spontaneity has ceased, and the manubrium and tentacles are strongly retracted.

Turning now to the case of the freshwater species, when first it is dropped into sea water at 85° there is no change in its movements for about fifteen seconds, although the tentacles may be retracted. But then, or a few seconds later, there generally occurs a series of two or three tonic spasms separated from one another by an interval of a few seconds. During the next half minute the ordinary contractions become progressively weaker, until they fade away into mere twitching convulsions, which affect different parts of the bell irregularly. After about a minute from the time of the first immersion all movement ceases, the bell remaining passive in partial systole. There is now no vestige of irritability. If transferred to fresh water after five minutes exposure, there immediately supervenes a strong and persistent tonic spasm, resembling rigor mortis, and the animal remains motionless for about twenty minutes. Slight twitching contractions then begin to display themselves, which, however, do not affect the whole bell, but occur partially. The tonic spasm continues progressively to increase in severity, and gives the outline of the margin a very irregular form; the twitching contractions become weaker and less frequent, till at last they altogether die away. Irritability, however, still continues for a time—a nip with the forceps being followed by a bout of rhythmical contractions. Death occurs in several hours in strong and irregular systole.

If the exposure to sea water has only lasted two minutes, a similar series of phenomena are presented, except that the spontaneous twitching movements supervene in much less time than twenty minutes. But an exposure of even one minute may determine a fatal result a few hours after the Medusa has been restored to fresh water.

Contact with sea water causes an opalescence and essential disintegration of the tissues, which precisely resemble the effects of fresh water upon the marine Medusæ. When immersed in sea water this Medusa floats upon the surface, owing to its smaller specific gravity.

In diluted sea water (50 per cent) the preliminary tonic spasms do not occur, but all the other phases are the same, though extended through a longer period. In sea water still more diluted (1 in 4 or 6) there is a gradual loss of spontaneity, till all movement ceases, shortly after which irritability also disappears; manubrium and tentacles expanded. After an hour's continued exposure intense rigor mortis slowly and progressively develops itself, so that at last the bell has shrivelled almost to nothing. An exposure of a few minutes to this strength places the animal past recovery when restored to fresh water. In still weaker mixtures (1 in 8, or 1 in ten) spontaneity persists for a long time; but the animal gradually becomes less and less energetic, till at last it will only move in a bout of feeble pulsations when irritated. In still weaker solutions (1 in 12, or 1 in 15) spontaneity continues for hours, and in solutions of from 1 in 15 to 1 in 18 the Medusa will swim about for days.

It will be seen from this account that the freshwater Medusa is even more intolerant of sea water than are the marine species of freshwater. Moreover the freshwater Medusa is beyond all comparison more intolerant of sea water than are the marine species of brine. For I have previously found that the marine species will survive many hours' immersion in a saturated solution of salt. While in such a solution they are motionless, with manubrium and tentacles relaxed, so resembling the freshwater Medusa shortly after being immersed in a mixture of 1 part sea water to 5 of fresh; but there is the great difference that while this small amount of salt is very quickly fatal to the fresh-water

species, the large addition of salt exerts no permanently deleterious influence on the marine species.

We have thus altogether a curious set of cross relations. It would appear that a much less profound physiological change would be required to transmute a sea-water jelly-fish into a jelly-fish adapted to inhabit brine, than would be required to enable it to inhabit fresh water. Yet the latter is the direction in which the modification has taken place, and taken place so completely that sea water is now more poisonous to the modified species than is fresh water to the unmodified. There can be no doubt that the modification was gradual—probably brought about by the ancestors of the freshwater Medusa penetrating higher and higher through the brackish waters of estuaries into the fresh water of rivers—and it would I think be hard to point to a more remarkable case of profound physiological modification in adaptation to changed conditions of life. If an animal so exceedingly intolerant of fresh water as is a marine jelly-fish may yet have all its tissues changed so as to adapt them to thrive in fresh water, and even die after an exposure of one minute to their ancestral element, assuredly we can see no reason why any animal in earth or sea or anywhere else may not in time become fitted to change its element.

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A NEW GENUS OF RHINOCERONTIDÆ.

While the genus *Aphelops* must be regarded as the direct ancestor of the recent rhinoceroses with canine and incisor teeth, now confined to Asia and the Islands, the ancestral genus of the African forms and their extinct congeners, which are without the teeth named, is less known. It can now be shown that the missing genus inhabited North America, and that, like *Aphelops*, it is hornless. It may be named and characterized as follows: *Peraceras*, Cope; superior dentition; I. o; C. o; P-m. 4; M. 3; nasal bones weak, hornless.

This genus is established on a new basis recently discovered by Mr. R. H. Hazard, in the Loup Fork formation of Nebraska, which may be called *Peraceras superciliosus*. It is founded on a nearly perfect skull, which lacks the lower jaw. Its size is about that of the Indian rhinoceros. It is narrowed anteriorly, but is very wide between the orbits. Posterior to these it contracts rapidly, and rises to a rather elevated occiput. Sagittal crest narrow; a prominent angle above each orbit. The premaxillary bone is narrow and weak. The nasal notch extends to above the middle of the third superior premolar. The occiput is rectangular in outline, with truncate summit. Its surface above is concave, divided by a strong median crest; lower down a vertical groove intersects its lateral border. The crests of the molar teeth are rather simple, and the posterior notch is soon isolated on attrition. Wear also isolates an external median fossa of the second premolar. Length of skull from end of premaxillary bone to condyles, M. 700; length of alveolar border of premaxillary, .025; length of molar series, .315; length of three true molars, .160; width of crown of second true molar at base, .075; superciliary width, .255.

This species is nearest to the *Peraceras malacorhinus*, a species which I formerly referred to *Aphelops*, but which I have little doubt belongs to the present genus. It differs from *P. superciliosus* as follows: In the latter species the front is wider, and is plane or concave, not convex; the superior edge of the maxillary is not wide and incurved, and has not the oblique ridges; the infraorbital foramen consequently has a more lateral opening. The narial notch does not extend so far posteriorly by the one and a half molar teeth. The occiput is wider, is divided by a median crest not found in *P. malacorhinus*, and has the vertical lateral grooves much shorter. The acute supraorbital angle is not seen in the *P. malacorhinus*.

The rhinoceroses of the Loup Fork formation whose generic position can now be ascertained, are the following: *Peraceras malacorhinus*; *P. superciliosus*; *Aphelops meridi-anus*; *A. Negalodus*; *A. fossiger*.—*Am. Naturalist*.