FURTHER OBSERVATIONS ON THE ORAL APPARATUS OF THE TADPOLES OF THE GENUS *MEGALOPHRYS*.

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(Plate III.)

The tadpoles of *Megalophrys* with the 'funnel' mouth have received considerable attention in recent years, but the precise functions of the peculiar structure surrounding the mouth are still a matter of dispute among naturalists. In November, 1926 I made extensive observations on the tadpoles of *M. parva* Boulenger in a small stream below Dumpep, Khasi Hills, Assam. I was about to send the result of my observations to press when I noticed an article by Dr. M. A. Smith entitled, "The function of the 'Funnel' Mouth of the Tadpoles of *Megalophrys*, with a Note on *M. aceras* Boulenger." [1] As the views expressed in this publication differed materially from those in my account I decided to go through the whole literature once again and to reconsider the observations made by several authors.

My previous observations [2] on the oral apparatus of the tadpoles of *M. parva* were mainly based on the material examined in captivity during my short visits to Dumpep. The view that I then advanced regarding the function of the funnel, namely that it acts as an anchoring device, was suggested to me by the form of the funnel when the tadpole lay at the bottom and by the fact that all the specimens were then obtained by vigorously shaking water weeds with a small bag-net. During my recent visit to the same place the tadpoles were again found in great abundance among the water plants, *Eriocaulon miserum* Kaern., that grew in the course of a shallow and rapid-running current (see photograph, Plate III). The plants form a very thick growth and the tadpoles lay among the roots and the bases of stems securely sheltered from the current. Moreover, the current bends the plants in the direction of the flow and under these circumstances the tadpoles lay doubly secure in their peculiar habitat. On closer examination they were found lying in all positions among these thickets. This time a thorough search was made in other parts of the stream with the result that the tadpoles were found in sheltered positions throughout its course. A few tadpoles were collected from under stones or in crevices in relatively deep water, but they were very common in similar situations in shallow water at the sides of the stream. A few were actually picked up from under moist stones in damp places a short distance away from the current. In short the tadpoles were only found in situations where they had not to contend against the

[1] Smith, *Proc. Zool. Soc. London*, pp. 983-988, figs. 2 (1926).

[2] Hora, *Journ. As. Soc. Bengal* (n. s.) XVIII, pp. 9-15, figs. 2 (1922); *Rec. Ind. Mus.* XXV, pp. 584, 585 (1923).

rapidity of the flow, and when some of them were made to drift in a rapid current flowing over a smooth rock it was observed that they were carried helplessly along by the current and were unable to maintain themselves in any definite position. By the impact of the current they were turned round and round on their longitudinal axes till they got into deeper water, where for sometime they lay motionless and apparently stupified. Soon afterwards, however, they regained activity and sought shelter under stones or in crevices. If, however, they happened to drift into a pool with smooth rocks on all sides the tadpoles came to the surface and applied their heads constantly against the rock as if seeking shelter. Once they were successful in finding a suitable place they lay for an indefinite period in any position, chiefly horizontal, with the 'funnel' folded. The positions of certain tadpoles were carefully noted on a rock in a sheltered pool and during the two or three days they were under observation there was no evidence of any movement from their respective positions. In deep pools the tadpoles sometimes lay in the open at the bottom. It may be noted that in the course of the torrential stream the *tadpoles were not seen hanging from the surface film and feeding at the surface.* Indeed this would be in my view impossible.

In pools and puddles these tadpoles have been observed by Annandale [1], Smith [2] and Griffin [3] to spend most of their time hanging from the surface film and feeding in this position, and it was probably this attitude of the animal that suggested to the earlier authors the function of the funnel as a float. Pools which occur in the course of hill streams are subject to sudden floods and in these the conditions described above for the stream below Dumpep prevail at least for a part of the year. If observations were to be made in such places during floods, there is every likelihood that they will correspond to those described by me.

It is now generally admitted that the chief function of the 'funnel' is to enable the animal to collect its food. Both Weber and Annandale (*op. cit.*) had an idea that the 'funnel' helps the animal in feeding at the surface. Describing the function of the funnel Annandale says: "It is possible also that it assists in the capture of the minute plants and animals on which the species feeds, though I can give no direct evidence for this function. If a tadpole is watched when it is hanging from the surface film, it will be remarked that the float is constantly expanding and contracting, owing to the respiratory movements of the mouth, and that, although the movements are too gentle to overcome the friction produced by the body and tail, which hang more or less vertically downwards in the water, and so to cause the animal to progress in one direction or another, they produced distinct currents on the surface, which bring towards the mouth any minute particles which may chance to be floating in its vicinity." Smith and Griffin seem independently to have reached the same conclusions based on a similar set of observations. To the former, however, we are indebted

[1] Annandale, *Fasciculi Malayenses, Zoology,* pp. 131, 132; 275-280, 1 fig. (1903).
[2] Smith, *Journ. Nat. Hist. Soc. Siam* II, pp. 37, 38; 269, 270 (1916-17).
[3] Griffin, *Ann. Carnegie Mus.* XVII, pp. 399-401, fig. 1 (1927).

for the experimental demonstration of the method of feeding of these animals in quiet waters at the surface. I have, however, never observed the animal feeding at the surface under natural conditions, but a study of the plankton-gathering devices [1] of certain animals living in ecological association with these tadpoles and feeding on a similar type of food suggested to me that the oral apparatus was a feeding mechanism. In swift streams there is always a quantity of plankton food, which is gathered from the rapid current in different ways. This is accomplished in a *Simulium* larva by means of a pair of fans placed besides its mouth, in certain caddis-worms which live in tubes by means of nets of silk that strain organisms out of water, and in certain may-fly and caddis-fly larvæ, which stick firmly to current-swept boulders, by spreading out their bristle-fringed feet widely " to gather in any organism that may be adrift in the passing water " (Needham & Lloyd, p. 364). The oral apparatus of the *Megalophrys* tadpole is not only capable of gathering plankton, while the animal quietly lies at the bottom, but is capable of performing the same function while the tadpole is suspended from the surface film or is floating in mid-water. It may, however, be remarked that the tadpole of *Megalophrys* is not a passive creature like the other plankton-gathering animals referred to above, for it sets up a strong current [2] which is both respiratory and assimilatory. When open at the surface the oral apparatus with its " teeth " breaking the surface film would serve to prevent large particles from entering the mouth while at the same time permitting the entry of small particles. The ' funnel ' in its folded condition under water serves the same function and possibly serves to prevent the escape of small particles in flowing water. Devices for this last purpose are common among several aquatic insects.[3] In the bubbling waters of the shallow and swift-flowing streams I believe the plankton food is uniformly distributed throughout the different levels of the current. The *Megalophrys* tadpoles harbouring in sheltered places under such circumstances are thus enabled to suck in the necessary amount of food from the passing current. In a pool, pond or lake on the other hand " Plancton organisms tend to be uniformly distributed in a horizontal direction " (Needham & Lloyd, p. 306), and it is known that, " A number of filamentous blue-green algae, such as Anabaena and a few flagellates, accumulate on the surface during periods of calm, hot weather (Needham & Lloyd, p. 296). In the behavior of the *Megalophrys* tadpole at different times of the year we meet with a very close correlation between its position in water and the presence of food at a particular level. In a swift current, though the food is equally plentiful at the surface, the tadpole is unable to make use of it on account of the physical conditions described above.

The next point that deserves consideration is the form of the ' funnel ' at the surface and below it. Here I would like to draw attention to the beautiful tail-coronet of a *Stratiomys* larva (Miall, p. 190) which

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[1] Needham & Lloyd, *Life in Inland Waters*, p. 364 (New York: 1916).
[2] Boschma, *Bijdr. Dierkunde Amsterdam* (Max Weber Feest-nummer) XXII, pp. 9-12, 1 fig. (1922).
[3] Miall, *Aquatic Insects*, p. 385 (London: 1903).

behaves, in its relation to the surface film, in the same way as does the 'funnel' of the *Megalophrys* tadpole. Both expand at the surface only and remain folded up under water; in both advantage is taken of the surface film to save the muscular energy which would otherwise have to be expended in swimming to counteract the tendency to sink. In the case of the *Megalophrys* tadpole the unfolding of the 'funnel' is due to a muscular action on the part of the animal, the contraction of the muscles "will cause the basal part of the funnel to become rigid and therefore to unfold itself, while the free extremity is probably flaccid under all conditions, being forced to straighten itself by external pressure as the tadpole rises to the surface" (Annandale, p. 278). In the *Stratiomys* larva probably something of the same nature happens when the tail-coronet is unfolded at the surface.[1]

It is obvious, therefore, that a certain amount of muscular energy is expended in the act of unfolding the 'funnel' and in its continuous expansion. In normal times, I believe, the animal spends most of its time under water and is thus saved from spending this energy. Moreover, if the 'funnel' were to be expanded under water much more muscular energy would be required, for at the surface the physical properties of the surface film would materially help in the unfolding of the funnel and in its continued suspension. We have seen that there is a flaccid portion all round the margin of the 'funnel' that is not supplied with muscles. Under water only the basal portion of the 'funnel' can, therefore, be expanded and in this position the marginal flaccid portion will flap with the eddies of the current and will, therefore, be a source of distinct disadvantage to the animal. The muscles are situated only in the ventral wall of the 'funnel' and for the size of the structure are by no means strong. So the unfolding of the 'funnel' requires some extra help which is afforded by the surface film and this probably accounts for the fact that the animal is never seen with the 'funnel' expanded under water.

Dr. Malcolm A. Smith has found these tadpoles feeding "in the shallowest puddles, among thick vegetation" and he remarks about their natural posture as follows: "Here amongst water-weed they spent most of their time, with the body resting upon a brick and parallel with the surface of the water, and in this situation they were to be seen constantly feeding" (Smith, p. 985, 1926). We have seen above that in pools the plankton food is horizontally distributed and it is always more plentiful near the edges. In shallow water where the tadpole can rest with its body touching the bottom the muscular pull needed for the continuous expansion of the 'funnel' will be considerably reduced, for there will then be no pulling at the surface caused by the weight of the tadpole. These are the two main factors which determine the distribution of the tadpoles near the edge of a puddle. In a flowing stream the tadpoles were found in larger numbers along the shore, and probably in this case also the food conditions govern their distribution.

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[1] Dr. F. Brocher has very ably discussed the phenomenon of the surface film and its importance in understanding the biology of aquatic organisms. (*Ann. Biol. Lacustre* IV, pp. 89-138, 44 figs. 1909-11).

The fact that the tadpole is capable of maintaining itself at any depth requires further consideration. There is no doubt that the oral-apparatus helps to make the anterior end buoyant as has been shown by experiments described in one of my former papers (Hora, pp. 584, 585 : 1923), but the finer adjustments that are needed by the animal to suspend itself at a particular level are, in my opinion, performed by the developing lungs. I have already shown[1] the nature of these structures, but it may be well to repeat the main facts. In young individuals the lungs are represented by two thin-walled sacs which are distended with bubbles of air. As growth progresses these sacs are considerably reduced in dimension, their walls become gradually thickened and they assume more and more the form of the regular lungs of the adult. I have observed tadpoles giving out bubbles of air both under water and when hanging from the surface. Dr. H. M. Smith (p. 987, 1926) says that, " All of the brevicipitid larvae that I am aquainted with, however, —*Kaloula pulchra* excepted—have the power of remaining suspended at any depth they like in the water." I hope it will be possible to demonstrate at no distant date that the developing lungs of these tadpoles have also been modified in the same way as those of the ' funnel ' mouthed tadpoles of *Megalophrys*, for without a hydrostatic organ it is not possible to imagine how their suspension is regulated.

It has been pointed out already that these tadpoles live in hill-streams which are liable either to break up into a series of pools and puddles that may dry up altogether, or to become rapid torrents generated by a single shower. It is under such varying conditions that the oral apparatus and the hydrostatic lungs of the *Megalophrys* tadpoles seem to have been evolved. The ' funnel ', besides enabling the animal to feed at all times and under all conditions, makes the anterior end buoyant which is a distinct advantage when the animal happens to be carried away by a flood. The anterior part of the body is saved from being carried against rocks. The ' funnel ' also enables the animal to hang from the surface film and to have free access to the atmospheric air required for the hydrostatic lungs. The lungs on the other hand make the whole animal buoyant, so that it spins round in a swift current without damaging any part of its body against a rock and, moreover, they act as well-regulated hydrostatic organs enabling the animal to maintain itself at any depth. In tadpoles living in drying-up pools with a decreasing quantity of oxygen in solution for respiration, the free air in the lungs would help to oxygenate the blood but this requires further elucidation as the facts at our disposal do not warrant any conclusions.

In the preceding pages I have attempted to show the diversity of ways in which organs like the ' funnel ' and lungs of *Megalophrys* tadpoles perform their functions under diverse conditions, and it is evident that there is a close correlation between the mode of life of the tadpole and the environmental conditions that prevail at different times of the year. On this point Dr. H. M. Smith says that, " It seems highly improbable, however, that so highly specialized a structure can have been evolved for more than one particular purpose ; and any others

[1] Hora, *Rec. Ind. Mus.* XXV, p. 585 (1923).

it may at times perform are merely incidental ones." Moreover, he remarks: "There is certainly a very close connection between the unfolding of the funnel and hanging by it from the surface of the water, while the fact that the creature has never been seen below the surface of the water with its lips unfolded suggests that the function of the funnel is connected with the surface of the water and with that only." It is, however, well known that highly specialized structures are sometimes capable of performing different functions under different conditions. When an animal becomes so highly specialized that it cannot respond to a change in the environment it is doomed to destruction. Only those organisms can survive under these conditions whose structures are sufficiently plastic to enable them to exist under changing conditions. I would, however, like to give here a few common examples to refute Dr. Smith's statement. It is admitted that the wing of a bird is a highly specialized structure and it is also known that some of the diving birds are good fliers. Those who have watched these birds feeding under water know with what ease and perfection the wings are used as paddles for swimming. One has only to watch a cormorant being fed in glass tanks full of water at the London Zoological Gardens. Take the case of the climbing perch (*Anabas testudineus*) of India and further east. The ventral fins are used in the normal way under water, but are differently used when it begins to climb a tree. "In one of the Loaches (*Misgurnus fossilis*) air is swallowed and passed along the alimentary canal until it is finally voided at the anus."[1] "In the adult *Ceratodus* an organ occurs which is equally lung and air-bladder."[2] Though in the beginning a structure may serve a particular purpose, in the course of its evolution it may take on other functions so as to keep the organism in direct adaptation to its environmental conditions. A highly specialized organ in its structure sometimes shows the various uses to which it may have been applied at different times in the course of its evolution and sometimes it so happens that a structure functions in a totally different way from that for which it may have been originally evolved.

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[1] Bridge, *Cambridge Nat. Hist. Fishes* VII, p. 292 (1904).
[2] Kerr, *Text-book of Embryology* II, p. 168 (1919).

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