

FURTHER OBSERVATIONS ON THE BIONOMICS OF THE TADPOLES OF *RANA AFGHANA* GÜNTHER.

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In recent years considerable advance has been made (*vide* list of references) in our knowledge of the adaptive modifications undergone by the remarkable tadpoles of the section *Ranae Formosae* of the subgenus *Hylarana* of the genus *Rana*. These tadpoles possess an extensive suction disc by which they adhere very firmly to smooth rocks and boulders in the fiercest currents of the small torrential streams of south-eastern Asia. From time to time, I have made observations on the tadpoles of *Rana afghana* which are found in great abundance in suitable places in the Eastern Himalayas and in the hills of Assam. In the living condition, the animal has been studied hitherto from the dorsal surface, but during a recent visit—May-June 1934—to the Tista Valley below Darjeeling advantage was taken to study the mechanism of attachment by watching in a mirror the rôle of the different structures on the ventral surface of the animal. I have described elsewhere¹ the nature of the simple apparatus used for such a purpose. With the help of a mirror, it was possible to elucidate precisely the mode of progression and fixation of the tadpoles and to follow the course of the respiratory current with the help of carmine powder. Besides observations on these points, attention is directed to the nature of the food and to the probable feeding habits of the tadpoles.

PROGRESSION.

Crawling.—As has been indicated above, tadpoles of *Rana afghana* live on rocks in swift currents, and under these conditions they crawl about with the head always pointing upstream. A tadpole, quietly lying on the substratum, holds on to a rock both by means of its disc, including the posterior lip which forms the anterior border of the disc, and the broad anterior lip. As the tadpole begins to crawl, the animal appears to move forward with a series of short jerks, and corresponding with these movements the anterior lip seems to be relaxed and is thrust forwards in a continuous series of rapid waves. It has been assumed (5, p. 242) that during progression the anterior lip and the sucker perform the function of adhesion alternately, but recent observations have shown conclusively that the forward movement is initiated and carried on entirely by the broad anterior lip, while the sucker, which is firmly attached to the substratum throughout progression, follows in its wake with the forward movements. The sucker is pulled forward while still attached to the substratum, and in this process the vacuum inside it is not disturbed. In a normally active tadpole, under water, these

¹ Hora, S. L., Biological Notes on a Fish from Brazil in the Society's Aquarium. *Proc. Zool. Soc. London*, p. 205 (1932).

movements are too rapid to be analysed but the following device proved very helpful. A tadpole was placed in a wet dish and, by poking with a sharp point, it was made to crawl for some time. When the animal was sufficiently exhausted, the crawling movements became very slow, so that every action of the tadpole could be clearly observed and analysed.

During the forward movement, the mouth opened and closed in rapid succession in conformity with the jerking movements of the anterior lip. On account of the prominent black jaws, it was easy to observe these movements.

With the help of a pair of sharp scissors, the anterior lip was cut off, and it was observed that tadpoles treated in this way lost the power of crawling. They progressed slowly by slight jerks of the body which was detached from the substratum.

The above observations indicate that the anterior lip is the chief organ of progression, and that its power of fixation is so great that not only can it withstand the rush of water at the anterior end but can pull forward the entire body which is attached to the substratum by means of the sucker.

Occasionally tadpoles were observed to crawl backwards; but the mechanism by which this reverse movement was effected could not be elucidated. The anterior lip does seem to play some part in this process, but the reverse movement was so rare and of such a short duration that the actual mechanism could not be studied. It was noticed, however, that in the reverse movement the "steps" were somewhat longer than those in the forward movement, and that the distal part of the anterior lip trailed along at each "step."

The backward crawling movement of the tadpoles of *Rana afghana* is remarkable, especially when it is remembered that the teeth on both the lips and the spines on the tuberculated area along the posterior and lateral parts of the disc are directed backwards. All these sharp points are meant to prevent the slipping of the tadpole backward. It follows, therefore, that without the actual lifting of the organs of attachment from the substratum, any movement in the reverse direction would seem hardly possible. At all events only one of the two main organs of attachment could be disengaged with safety at a time. It seems probable that in the reverse movement the suctorial disc is disengaged first, moved backwards and fixed in a new position. The anterior lip is then disengaged and pulled backwards. By the repetitions of these movements, the tadpole is probably enabled to crawl in the backward direction.

Swimming.—Reference has already been made (5, p. 242) to the darting movement of these tadpoles. This movement is too rapid and its mechanism could not be studied with the naked eye. The body did not appear to be thrown into noticeable series of waves and the tail seemed to flap just a little. Probably the succession of muscular waves along the body was so quick that to the naked eye the body appeared to be held straight during progression.

In a dish containing water, the tadpoles were observed to swim occasionally, but the movements were very clumsy. Progression was effected by the undulating movements of the body and the head moved alternately from side to side. With an increase in the rate of progression,

the awkward slow movements of the animal became more and more graceful till in the darting movement the body appeared to be straight as mentioned above.

RESPIRATION.

In the tadpoles of *Rana afghana* the respiratory current enters through the nostrils though these structures are not in any way specially modified for this function. Reference may here be made to the nostrils of *Ascaplus truei* which according to Noble (8, p. 65, fig. 8), are specially modified for respiration in swift currents. In the tadpoles of *R. afghana*, the floor of the buccal cavity was noticed to rise and fall, and the passage of the respiratory current, which flows in from the nostrils, could also be inferred from the movements of the surface of the head in this region. When a cloud of carmine powder was floated over the head of the tadpole, it was sucked in through the nostrils but immediately "coughed" out through the mouth. The animal moved to another place at the same time. In tadpoles that had become languid through exertion the colouring matter was allowed to pass over the gills and was ultimately ejected through the spiracle. When clouds of carmine were floated along the lower margins of the head, no particle was taken in showing thereby that no current flowed below the head. When the anterior lip was damaged, the carmine powder was noticed to enter below the head but no definite current could be traced.

The tadpoles are capable of suspending respiration for short periods as is usual in the case of hill-stream fishes (3, p. 591).

The tadpoles frequently push their heads out of water by crawling along the sides of the dish in which they are kept, but they can stay in this position only for a short period. A tadpole kept in a wet dish desiccated and died within about an hour or so, showing thereby that the animal is not fully adapted for aerial respiration. When the head was out of water, the floor of the mouth showed no movement but a regular rise and fall of the area round the nostrils was observed.

It may be noted that the lungs of these tadpoles are small and thick-walled (3, p. 584; 6, p. 382) and are apparently non-functional. In these circumstances aerial respiration can take place to a limited extent only through the skin of the animal.

FIXATION.

Sucker is the chief organ of fixation, but if its margin is in any way injured or damaged its efficiency is greatly impaired. The rows of backwardly directed teeth on the posterior lip and of spines on the tuberculated area prevent the sucker from slipping backwards in strong currents. It has been indicated above that in the natural habitat, the sucker is kept in action for almost the whole of the time, even during progression. The broad anterior lip, with its several rows of backwardly directed teeth, is also a powerful organ of adhesion. It may be pointed out here that the lips in conjunction with the mouth do not form a vacuum sucker. Normally the respiratory current does not flow in through the mouth and the

lips lie closely adpressed to the substratum, but there is no mechanism in this area that can produce a vacuum. The efficacy of adhesion in this region depends upon the strength of the anchoring devices, and on "seizing" which takes place when two surfaces are brought together in close contact. It has further to be noted that in the absence of a respiratory current flowing in through the mouth there is no area of low pressure in the region of the mouth, as is usually the case in a number of hill-stream fishes.

In the absence of any direct observations, it was presumed by me (5, p. 243) that the folds of the lips at the corners of the mouth form respiratory channels. In the case of *Rana afghana* tadpoles the respiratory current does not enter through the mouth (*vide supra*, p. 323), but it was observed that these folds serve a very important function during progression. When the anterior lip is thrust forward, the anterior jaw and the associated structures are also carried forwards along with it. At this time the folds open out so that the posterior lip which forms the anterior border of the sucker is not disturbed from its position. By this simple device, the action of the sucker is not impaired in any way. In the case of the tadpoles of *Ascaphus truei*, Noble has observed that "folds in sucker arranged to permit opening of the mouth (for locomotion) without seriously detracting from the suctorial nature of the apparatus" (8, p. 68). The lips of this animal do not form a sucker, but it seems probable that during progression the anterior lip moves in the same way as described above in the case of the tadpole of *R. afghana*, while the posterior lip is pulled forwards when still attached to the substratum. The folds of the lips permit the thrusting forward of the anterior lip without detracting from the adhesive properties of the posterior lip. It seems probable that wherever folds exist at the corners of the mouth in hill-stream tadpoles, they subserve the function as detailed above.

NATURE OF FOOD AND MODE OF FEEDING.

The alimentary canal of the tadpoles of *Rana afghana* consists of a long tube of almost uniform diameter throughout and possesses 3 or 4 coils. It is about five to six times as long as the distance between the tip of the snout and the anal opening. In its entire length, it is full of brownish, pulpy substance which, when examined under a binocular microscope, seems to consist of fine particles of sand and slime. No green filamentous algae were found inside the gut. It is probable, therefore, that the tadpoles feed on the slimy matter that is found encrusting apparently smooth rocks and stones even in very swift currents. The particles of sand no doubt get entangled in the slime as they drift down with the current. As is usual with the tadpoles of frogs, the slimy matter is probably rasped off the rocks with the help of the powerful jaws. No direct observations could, however, be made on the actual mode of feeding, but it seems probable that the anterior V-shaped jaw scrapes the food material and the broad posterior jaw prevents it from being washed away by the current. In any case it seems certain that in the tadpoles of *Rana afghana* the respiratory current does not serve as the food current of the animal.

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