PARALLEL EVOLUTION IN THE FISH AND TADPOLES OF MOUNTAIN TORRENTS.

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The structural modifications of the fish and of the Batrachian larvae that inhabit the small mountain torrents of the Oriental Region afford a remarkable instance of parallel evolution on a comprehensive scale. The phenomena they exhibit may indeed, be called communal convergence. One of us [1] has quite recently discussed these modifications in the fish, while the other [2] has from time to time published observations on the external features of the tadpoles. We propose in the present paper to give a short general survey of the facts and to discuss a specific instance in anatomical detail.

Speaking generally, modifications in the tadpoles of mountain torrents chiefly consist either in the formation of floats for floating away lightly on the surface of the flood, as in some species of *Megalophrys*, or in that of " suckers " for clinging to fixed objects.

These structures in the tadpoles seem to have been evolved independently of any high degree of specialization in the adult frog or toad,[3] just as the larva of an insect may be highly modified in correlation with a peculiar mode of life, while the adult remains of an unspecialized type. Identical structural resemblances in the tadpoles mean that a true genetic affinity exists, but similar structures are frequently evolved independently for the same function but along different lines, for example the oral float on the mouth of the larvae of certain species of *Megalophrys* [4] and that on the mouth of *Microhyla achatina*,[5] or the powerful oral sucker of the tadpole of *Helophryne natalensis* [6] and that of *Bufo penangensis*.[7] In the floats of the two former tadpoles there is a general similarity in form and function, but in the *Megalophrys* the internal surface of the float bears rows of peculiar horny tooth-like processes and these are replaced

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[1] Hora, *Rec. Ind. Mus.* XXIV, pp. 31-36 (1922).

[2] Annandale, *Rec. Ind. Mus.* VIII, p. 29 (1912); *ibid.* XV p. 17 (1918); *Proc. As. Soc. Bengal* (n. s.) XIII, p. clxxxvi (1917).

[3] Boulenger, *Rec. Ind. Mus.* XV, p. 65 (1918).

[4] Hora, *Journ. As. Soc. Bengal* (1922).

[5] Smith, *Journ. Nat. Hist. Soc. Siam* II, p. 37, figs. A_1–A_4 (1916).

[6] Hewitt, *Ann. Natal Mus.* II, p. 477, pl. xxxix, figs. 5, 6, 7 (1913).

[7] Flower, *Proc. Zool. Soc. London*, p. 908, pl. lx. figs. 3, 3*a* (1899).

in the *Microhyla* by soft ridges. Moreover, it is much more evident in the latter tadpole than in the former that the whole float is formed by a hypertrophy of the lower lip. Similarly in the *Helophryne* and the *Bufo* there is a structural difference, only to be observed on close examination. The sucker of the *Bufo* is formed (much in the same general way as the float of *M achatina* but correlated with an entirely different function) by a hypertrophy of the lower lip, while in the *Helophryne* both lips are equally developed.

In this respect the *Helophryne* closely resembles an unidentified larva discussed by one [1] of us from the Malabar Zone of Peninsular India. Indeed the structural analogy is so close that it does not seem too much to claim that there is also a homology, in other words that a genetic affinity exists.[2] We can claim genetic affinity only between those tadpoles in which similar structures are present with a similar function and produced by the same modifications of structures or organs common to widely different forms, but when these conditions occur to such a degree as to produce morphological identity it is not extravagant to do so.

Suckers may be produced by the evolution of a new organ, as in the species of *Rana* described later, or by hypertrophy of the lips, as in the tadpoles of the *Helophryne* and the *Bufo* discussed above. In the latter instance many different stages in the evolution of the perfect structure are known.[3] But in species like *Rana afghana* the peculiar structure seems, so far as our present knowledge goes, to have arisen strictly *de novo*. That it has really done so is of course improbable, but the earlier stages have not been discovered and have perhaps been eliminated. There is no evidence for any homology between the adhesive apparatus and that found on the ventral surface of all very young Batrachian larvae.[4]

It has been observed by one of us both in the Khasi Hills and the Nilgiris that the tadpoles abundant in the large pools of hill-streams, at spots at which the current is not rapid, belong to quite a different type from any we have mentioned, being very large and stout, with powerful tails, comparatively small mouths, no marked structural peculiarities of an obviously adaptive nature and either a very conspicuous or a very dense pigmentation. Good examples of this type are the tadpoles of *Rana alticola* [5] in Assam and of *R. malabarica* in South India. The former has a conspicuous black ocellus on the tail and possesses parotid glands which produce an abundant secretion on irritation. The latter are of a

[1] Annandale, *Rec. Ind. Mus.* XV, p. 22, pl. 1, figs. 6, 6*a* (1918).

[2] No frog of the family Cystignathidae is known from the Oriental Region, but the Batrachia of the hills of the Malabar Zone are still imperfectly studied and the adult of this tadpole is a burrowing form and, therefore, liable to escape notice. The Ethiopian affinities of the fauna of the Malabar Zone are well recognised by Zoogeographers.

[3] Annandale, *Rec. Ind. Mus.* VIII, p. 19 (1912).

[4] Boulenger, *Rec. Ind. Mus.* XX, pp. 100, 168 (1920).

[5] Thiele, *Zeitsch. wiss. Zool.* XLVI, p. 75, pl. x, fig. 6 (1888).

dense and uniform black colour. Similar conditions are found as regards structure in the fishes of large pools of hill-streams, which are usually species with strong swimming-powers but not highly specialized, belonging to such genera as *Barbus* and *Barilius*.

The general analogy between the structure and form of these less specialized members of the fauna of hill-streams becomes in many instances particular as between fish and tadpoles when the more specialized members, living in more peculiar conditions, are critically examined. We know of no exact parallel between the oral floats of the larvae of *Megalophrys parva* and its allies and any similar structure in a mountain fish, but when we come to the production of adhesive organs many specific parallels occur. Between the enlarged lips and ventral mouth of several fish of the genera *Glyptothorax* and *Glyptosternum* and of tadpoles like those of *Bufo penangensis* there is a close analogy, and just as we find the oral suckers in different stages of evolution in different species of tadpoles, so also do we find them in different fish of the suborder Siluroidea. In the larvae, for example, of *Rana assamensis* and its close allies the lips, though ventral and enlarged, are not greatly enlarged and the organ produced is not conspicuous. Almost every stage between this condition and that of *Bufo penangensis* has been observed. Similarly in such species as *Glyptosternum andersoni* and *G. feae* the lips are comparatively small, while in other species of the same genus (e.g. *G. labiatum* and *G. blythi*) they are much more highly developed. In both groups the evolution can be correlated with life in waters of stronger and stronger current.

It is, however, in the ventral suckers of certain tadpoles of the section Ranae Formosae[1] of the subgenus *Hylorana* on the one hand and similar structures in fish of the genera *Garra* (or *Discognathus*) of the family Cyprinidae and *Glyptothorax* of the family Sisoridae on the other that the closest analogy is to be sought, especially, so far as the fish are concerned, in the former genus.

We have thought it worth while not only to give a brief general account of the convergence that occurs between these fish and tadpoles but also to consider the minute structure of the adhesive disc of such Ranid tadpoles as *Rana afghana* (Günther) [=*R. latopalmata*, Blgr.] and *R. livida* (Blyth) and to compare it in detail with that observed in the fishes of the genus *Garra*, in which the modifications are of a similar nature and occupy a similar position on the ventral surface just behind the mouth.

The disc of *Rana afghana*[2] is a well-marked structure; it is almost as broad as the body and a little more than half its length. The disc is provided with a free border except at the anterior end, where the border is replaced by the posterior lip. The comparatively thin central portion of the disc in preserved

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[1] Boulenger, *Rec. Ind. Mus.* XX, pp. 123, 130 (1920).
[2] Annandale, *Rec. Ind. Mus.* VIII, pl. iv, fig. 3*a*.

specimens is as a rule depressed in the form of a saucer. Through the skin of this region are visible three large prominences, which on dissection are found to be the extremeties of two muscles and a tendon. They represent (i) a strong tendon (*t*) attached internally to the middle of the disc: it proceeds upwards for a short distance and then divides into two portions, which are both attached to the vertebral column: and (ii) two pairs of muscles composed of striated fibres which have similar attachments at both ends but are quite distinct from the tendon. By keeping the free border closely in touch with a fixed object and then raising the central portion of the disc by contracting the muscles, the animal can convert the whole structure into an efficient organ of adhesion by creating a partial vacuum between it and the fixed object. The function of the elastic tendon is to counteract too strong contraction, which might tear the delicate surrounding tissues.

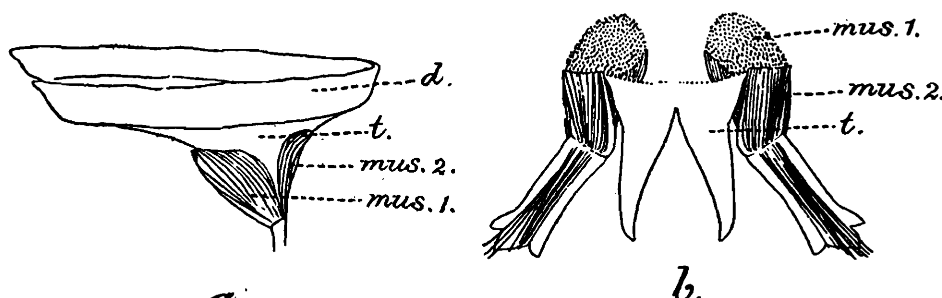

FIG. 1.—Disc and its musculature in *Rana afghana*.
a. Slightly oblique lateral view of disc with its muscles and tendon.
b. Anterior view of muscles and tendon after removal of disc.
d.=disc; *t*.=tendon; *mus*. 1., and *mus*. 2.=muscles of disc.
(cf. *Rec. Ind. Mus.* XXIV, p. 47, fig. 9b.)

The structure of the disc is precisely similar in the tadpole of *Rana livida* to that in *R. afghana.*

The mechanism of the disc is the same as that already described for the analogous structure in *Garra* [1]; except that in the fish the central portion of the disc is raised by the elevation of the urohyal, without direct muscular action in the disc itself, which is decidedly callous as a whole.

The free borders are quite smooth in the tadpoles, but in a section of the tissue under a high power (fig. 2) it is observed that the outer cells are produced into minute processes which are greatly flattened near the base and are somewhat pointed towards the end. These are covered by a chitinized cuticle. Each of the spine-like outgrowths (*s*) is provided with a nucleus at the base. The rest of the epidermis (*ep. d.*) consists of a large number of nuclei irregularly scattered in a homogenous mass of cytoplasm. Below the epidermis is a loose connective tissue in which nuclei are present at irregular intervals. This tissue (*c. t.*) is formed of a series of minute fibres, which in the outer region run paralled to the epidermis, while internally they

[1] Hora, *Rec. Ind. Mus.* XXIV, p. 47 (1922.)

run at right angles to it. In all essentials the structure described above is similar to that of the free borders of the disc of *Garra.* The spine-like outgrowths help to make the surface rough in such a way that better grip must be obtained.

The minute structure of the disc is thus much less complicated than that of the adult *Garra* or *Glyptothorax.*[1] The spine-like outgrowths on the organs of adhesion are strictly analogous in the fish and the tadpoles, but they occupy a different position and the structure of the underlying parts is completely different.

One of the most interesting features of these instances of parallel evolution lies in the fact that whereas in the larvae of the Ranae Formosae we only know, so to speak, the finished product of evolution in the highly perfected organ of adhesion, in the

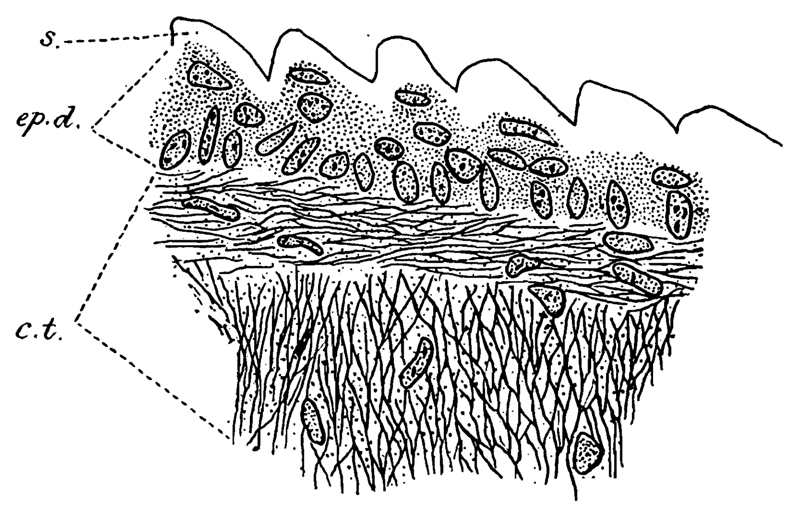

FIG. 2.—Transverse section through free border of disc of *Rana afghana.* (Highly magnified and slightly diagrammatic).
s.=spine ; *ep. d.*=epidermis ; *c. t.*=connective tissue.
(cf. *Rec. Ind. Mus.* XXIV, p. 50, fig. 13.)

genus *Garra* we have before us almost every possible stage alike in postembryonic development, in individual variability and in specific differentiation. One[2] of us has so recently given the facts that it is unnecessary even to recapitulate them here. The evolution of the mental disc of *Garra* is in this respect parallel to that of oral suckers in various tadpoles of the Himalayan streams. We have thus evidence that these particular structures have come into existence, not through mutation and not by any Mendelian segregation of characters, but through a gradual accumulation of small changes. The close correlation, especially in *Garra*, between these changes and differences in the flow of water in which species and even individuals live is at any rate suggestive. Whether we are witnessing the survival of the fittest in the Darwinian sense or must accept a frankly Lamarckian explanation only experiment can prove.

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[1] *Cf.* Hora, *op. cit.*, figs. 12, 13, p. 50; also figs. 15, 17, 18, 19 on pages 53, 55, 57.
[2] *Id.*, *ibid.*, XXII, pp. 639-643, text-fig. 1 (1921).