OBSERVATIONS ON THE ECOLOGY AND NATURAL HISTORY OF ANURA

V. The Process of Hatching in Several Species*

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The general pattern of embryonic development exemplified by frogs and toads is well understood. Similarly, descriptions of anuran larvae and of their metamorphosis are quite common. It seems strange, therefore, that little should have been published as to what happens between the embryonic and larval phases of existence, that is, during the process of hatching; yet a search of the literature reveals little upon this subject.

The meager literature, mostly European, concerning the process of hatching of anuran larvae was reviewed by Noble (1926) who also presented histological evidence for the presence of groups of eosinophil epithelial cells in the cephalic integument of the embryos of certain species which were regarded as a "frontal gland." This gland was thought to produce a secretion which dissolves the gelatinous envelopes surrounding the embryo, thus facilitating its escape. Since, however, certain larvae hatch in a premotile condition whereas others are able to swim actively immediately after hatching, the presence of a functional frontal gland does not tell the whole story of the process of hatching. What forces are involved in driving the emerging larva into the water? Does the number of gelatinous coats or the well-known differences in their elasticity, general stickiness, or firmness in different species alter the process?—if so, in what manner?

During my studies of the last few years on the natural history and embryology of the Great Plains toad, *Bufo cognatus* Say, I have observed the process of hatching many times. The results of these observations were briefly reviewed before the academy last year, and are given in considerable detail in a forthcoming paper in the *American Naturalist.* Briefly, it was found that rotation of the embryo within its capsule was a prerequisite to hatching, that this rotation ceased just before the larva's emergence, that an opening appeared opposite the head of each larva as if a frontal gland were operative, and that this opening was much smaller than the head of the larva. The tadpole hatches, therefore, with considerable difficulty. It is forced through an opening considerably smaller than itself, very probably by hydrostatic pressure, produced during embryonic development through an accumulation of liquid within each embryonic capsule, working against the considerable elasticity of the gelatinous tube holding the animals. This results in an almost explosive emergence of the larva. The tadpole is thrown violently outward, and usually upward, for several millimeters or centimeters from the opening in the tube as the latter contracts sharply when the pressure is released.

This process was watched carefully in over one hundred cases and no significant variation from the account given above was found. It seems likely, therefore, that this is the usual and normal process of hatching in *Bufo cognatus.*

*** Contribution from the Zoological Laboratory of the University of Oklahoma, No. 214.**

Early in the spring of 1939, I secured embryos of another common toad, *Bufo woodhousii woodhousii* (Girard), in order to compare the process of hatching in this form with that in *B. cognatus*. Greatly to my surprise, it was found that in scarcely any particular are the two species the same. Rotation of the embryo appeared to be incidental to the process of hatching in *B. w. woodhousii* instead of a necessity for it. Large openings, instead of small ones, appeared in the gelatinous coats; and this occurred at least an hour before the larva's emergence, instead of less than a minute before, as in *B. cognatus*. Furthermore, these openings did *not* include corresponding openings in the capsule surrounding the embryo. Instead, the openings in the gelatinous tube allowed the hydrostatic pressure within each capsule to work the latter through the openings, so that each embryo fell from the eggstring in which it was produced, still enclosed in a bubble of fluid which then lay free in the outside water. Within the next hour or so, the membrane of this bubble (the so-called chorion) became noticeably thinner as the embryo rotated slowly and feebly within it, till finally it broke, usually near the head of the embryo. Some time later, the chorion had slowly disappeared as though dissolved, thus completing the process of hatching.

Because of the differences found in these two closely related species, hatching was then studied in several other Anura. These were *Bufo americanus americanus* (Holbrook) (the dwarf form from Cleveland County, recently described), *Rana sphenocephala* (Cope), *Hyla versicolor versicolor* (Le Conte), and *Microhyla* (*Gastrophryne*) *olivacea* (Hallowell), all from Norman, Oklahoma and its vicinity. I could find in the literature no descriptions of hatching in any of these species.

In *B. a. americanus*, the embryo becomes relatively longer than in the other two species of toads observed. Sometime before hatching, the length comes to exceed the diameter of the embryonic capsule and accordingly the tail becomes bent along the inner side of the capsular wall. Rotation of the embryo in the capsular fluid occurs but it is relatively slight as compared to that in several other species. As hatching time approaches, each embryo turns so that the head is pressed firmly against the chorion. Gradually an opening appears through the chorion and the gelatinous tube opposite the head of each embryo, the tail straightens, and the head of the animal is extended through the opening.

At this time, or just prior to it, feeble bending movements of the neck of the embryo may occur. Throughout some fraction of the next hour or so, the embryo lies thus, its head already emerged, its cilia beating feebly. From time to time the embryo twitches, flipping the head to one side or the other, and the hole through which the head protrudes becomes somewhat larger. Quite suddenly, the ciliary beat becomes stronger and the larva moves gently through the opening, to catch on the gelatinous coat by means of the secretion of the adhesive organ. The time between the first appearance of the opening and the final emergence of the larva varied between twenty minutes and about one hour in those which I observed.

In *Rana sphenocephala* the process of hatching is more simple. The capsule is relatively small and the embryo is somewhat bent within it. The embryo rotates slowly within the capsule until nearly ready to hatch, and then becomes quiet with its head pressed against the membranes. Suddenly the membranes bulge at the head of the embryo, and within the next minute or so, give way completely so that a small hole is formed. This increases somewhat in size, the rate of ciliary beat is accelerated, and the larva slides through the opening. The aperture is slightly smaller than the head of the embryo and its edges contract slightly as the larva emerges.

There is no violent contraction, however, as in *Bufo cognatus*. No muscular movements are involved in hatching, although slight twitching may occur prior to it as in the American toad.

The embryo of *Hyla versicolor versicolor* reaches a later stage of development before hatching than any of the other species so far discussed. The capsule in which the embryo develops is large and the jelly surrounding it quite soft and hyaline. Rotation of the young embryo may occur but it appears quite incidental to hatching; sometimes an embryo may lie for a long time without any rotation whatever; and when rotation does occur it is always slow and sporadic.

Long before hatching in this species, muscular movements are strong. The embryo often moves violently and suddenly within the capsule. These movements become progressively more violent and frequent as the time of hatching approaches. From ten minutes to an hour before hatching, the embryo lies with the side of the head (not the end of it as in the toads and frog studied) pressed closely against the chorion and the cilia carry the embryo slowly around the capsular wall. In this process, the chorion gradually becomes thinner, till suddenly it breaks, usually near the head, and the embryo twitches itself free by active muscular effort.

Sometimes the violent movements of the embryo break the membrane prematurely and the tail may emerge before the head. In this case, the larva eventually frees itself from the chorion by sporadic and violent swimming movements which eventually bring the head to the opening. The adhesive organ is small and apparently seldom used and the larvae are fairly strong swimmers immediately upon hatching, unlike the very young tadpoles of toads and frogs.

In *Microhyla olivacea*, muscular movements play a still more important part. The late embryo threshes about very violently and sometimes pivots on the head and spins. These movements eventually break the membranes near the head of the embryo and the larva swims quickly to freedom through the opening. As in *Hyla v. versicolor*, the adhesive organ is little used although present in a reduced form at the usual place on the head.

DISCUSSION

Several factors seem to be involved in the hatching of Anura. These are (1) a secretion (or two secretions) of a frontal gland such as described by Noble (1926), (2) the action of cilia located on the surface of the embryo, (3) hydrostatic pressure developed by the gradual accumulation of liquid within the embryonic capsule by which the chorion is forced away from the embryonic body, (4) the elasticity of the gelatinous envelopes, especially notable in the toads, and (5) the muscular efforts of the late embryo itself. Bacterial action which softens the jellies may also play a limited role, but I have seen no indication that it is an important one. There is no evidence whatever for, and much against, the suggestion made by some that the embryos of Amphibia gnaw their way to freedom, at least so far as the species reported in this study are concerned.

The differences in the details of the process as observed in the different species are due to the relative importance or unimportance of the various factors at work in the individual cases. In all of the toads, as well as the frog, studied, muscular movements are inoperative or of quite minor significance in hatching, and cilia play a correspondingly greater role in the process. However, in *Bufo cognatus* the ciliary beat serves mostly merely to keep the tip of the head placed against the chorion and to rotate the embryo within the capsule so that the secretion of the frontal gland may be effective. Actual emergence of the larva is accomplished almost wholly by hydrostatic pressure working against the elasticity of the gelatinous membranes. In *B. w. woodhousii*, hydrostatic pressure is insignificant as a factor in hatching and the embryonic secretions are more important. In *B. a. americanus*, the principal factors are the secretions and the action of cilia.

In *Hyla v. versicolor* and *Microhyla olivacea* (as well as in *Scaphiopus hammondii*, according to an as-yet-unpublished study by Dr. Minnie S. Trowbridge), ciliary action and hydrostatic pressure are relatively unimportant. Hatching in these forms is largely accomplished by the thinning of the chorion by secretions of the frontal gland until it breaks under the impact of the violent muscular movements of the embryo, such as are wholly impossible to the frogs and toads at the stage of hatching.

We may, therefore, state general conclusions as follows:

(1) Each species observed is different in some details from all of the others.

(2) These differences are due to the relative importance in each case of the five causal factors operative.

(3) In those embryos which hatch in a premotile condition (i.e. *Bufo* and *Rana*), ciliary action, hydrostatic pressure (especially prominent in *B. cognatus*), and the elasticity of the membranes are very important. In those which are motile at hatching (*Hyla*, *Microhyla*, and *Scaphiopus*) muscular movements tend in various degrees to supersede other factors.

(4) Regardless of other details, all of the species studied hatch as if the primary causal factor involved is a secretion (or two secretions) to soften the jelly and chorion, as was indicated by Noble (1926) for the several species studied by him.

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