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THE ANDERSON TREE FROG

(*Hyla andersonii* Baird)

OBSERVATIONS ON ITS HABITS AND LIFE HISTORY

BY G. KINGSLEY NOBLE AND RUTH C. NOBLE

The American Museum of Natural History

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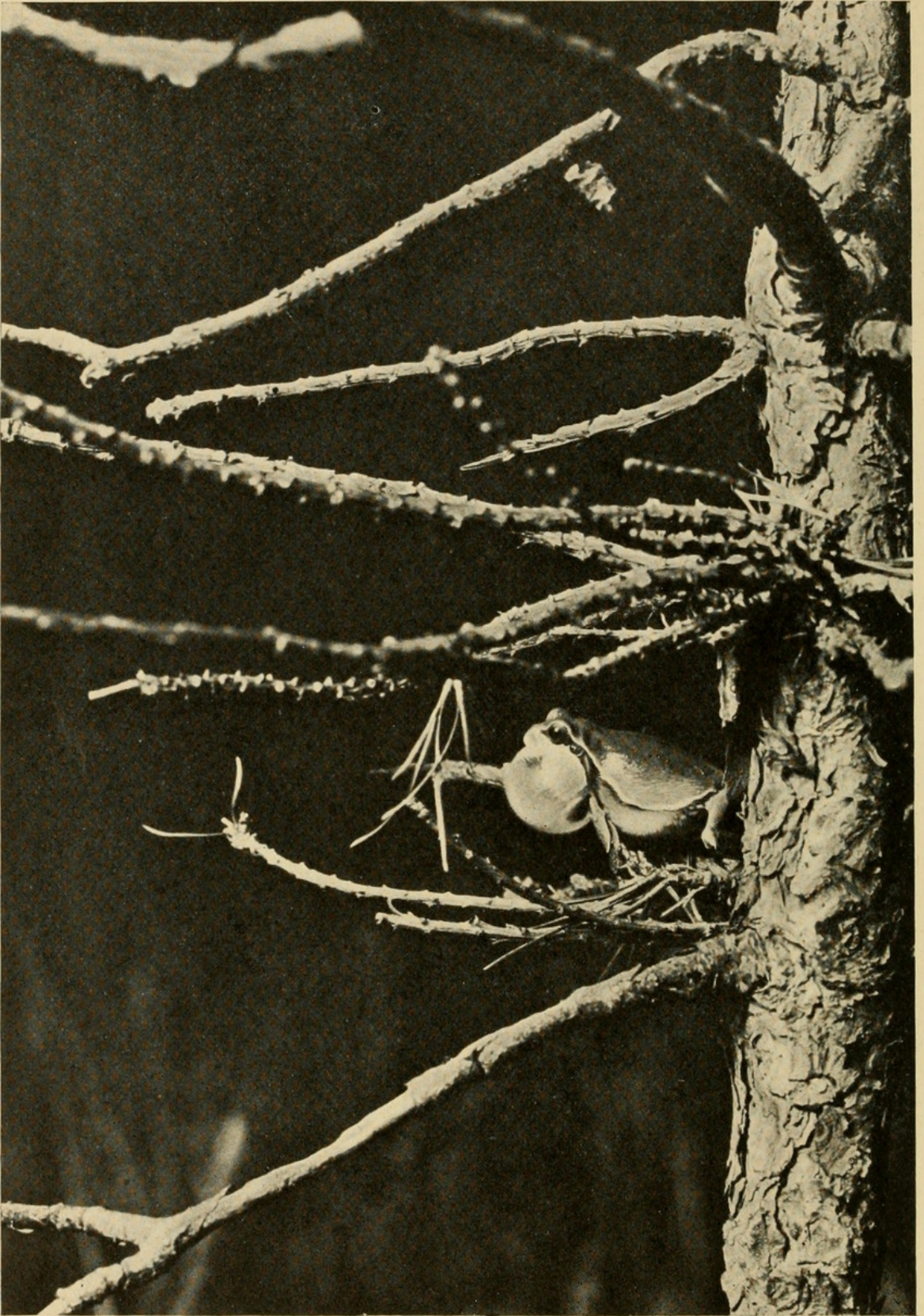


FIG. 145. THE CALL

Male *H. andersonii* calling from a pitch pine on the edge of a pine-barren bog, Lakehurst, New Jersey. *Flashlight Photograph.*

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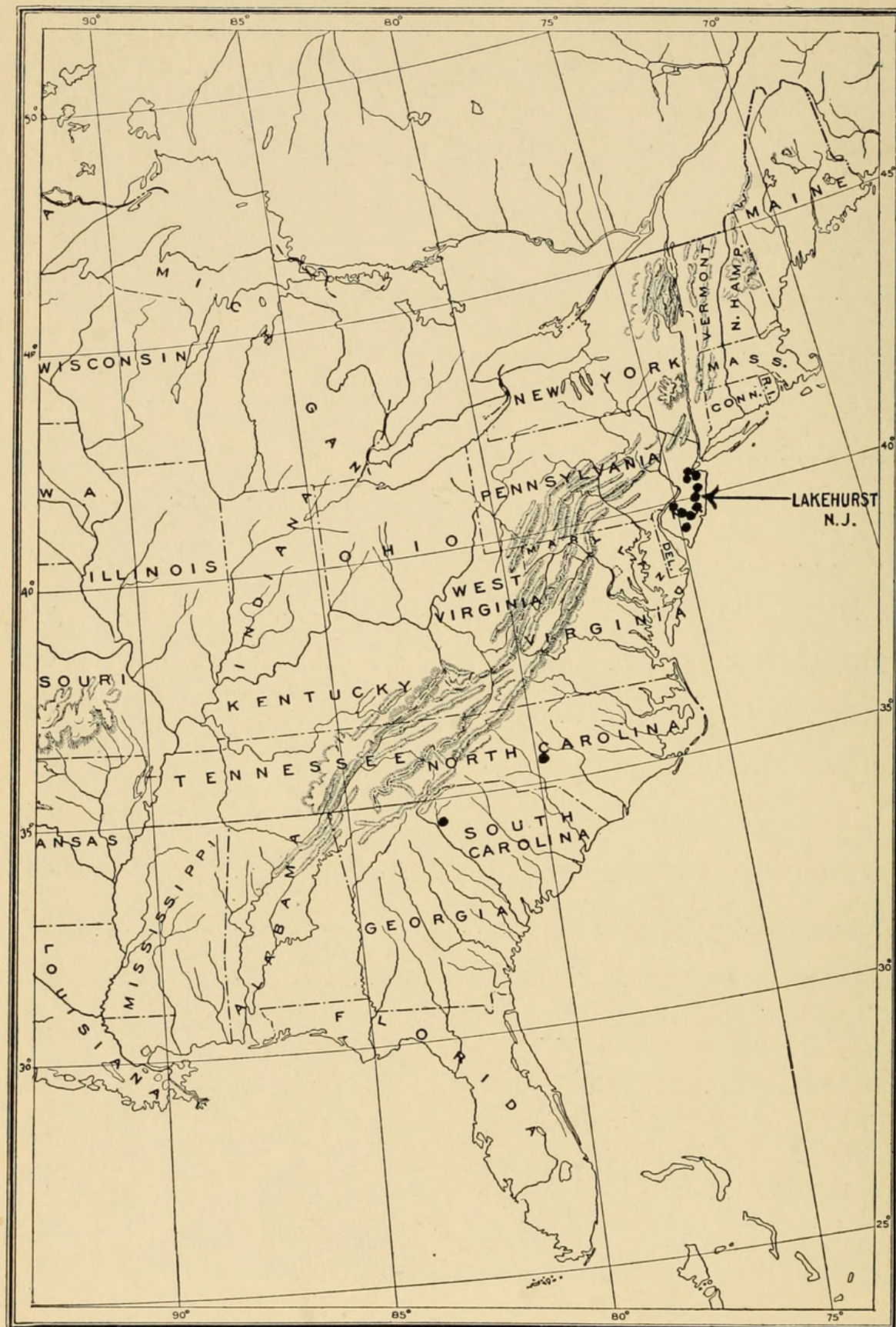


FIG. 146. DISTRIBUTION OF *HYLA ANDERSONII*
Spots indicate locality records.

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INTRODUCTION.

The Anderson Tree Frog has often been considered the most attractive of North American hylas, and yet no attempt has hitherto been made to study its life history in detail. Former observations were made as opportunity permitted and none were continued at frequent intervals throughout a season.

The following observations represent only a single season's work, but they were made with a definite plan in view. The question which we have had before us throughout the work was: what are the relationships of *H. andersonii* so far as these may be deduced from its habits and life history? Wright (1914), by comparing the life histories of certain American batrachians with those of European species, has brought forth some clear-cut evidence as to the relationships of the species he considered. In the present paper we have made no attempt to discuss morphological or embryological data which do not have a direct bearing on our main problem.

The following observations were made by the writers at intervals during May, June and July, 1922. To these observations there have been added others made by one of us on various occasions during the three preceding years. Field observations have been supplemented by studies in the laboratory. Our knowledge of the life history of the Anderson Tree Frog is still far from complete. In the hope that someone more favorably situated than ourselves will continue this work, we have made some attempt to give a complete picture of what is known concerning the life history of this delightful tree frog. Not only have most of the published accounts been

available to us, but we have been fortunate in having near at hand Messrs. W. T. Davis, J. P. Chapin, W. De W. Miller, G. S. Myers, K. P. Schmidt, C. L. Camp and others who are very familiar with the Anderson Tree Frog in the field. Many of the problems which arose we have discussed with these gentlemen. Wherever their observations have supplemented our own we have included them below with full acknowledgment. It was obvious from the first that no complete study of the life history of *H. andersonii* could be made in a few months time. Emphasis was therefore laid upon those features which might be expected to shed light upon the relationships of the species. These features we have discussed under separate headings.

HISTORICAL.

Hyla andersonii has until comparatively recent years been considered one of the rarest of American batrachians. When Cope wrote his standard work on "The Batrachia of North America," only two specimens had ever been taken: the type specimen, described by Baird (1854) captured at Anderson, South Carolina, and a second specimen collected by Professor J. Leidy "in a cedar swamp near the town of Jackson in New Jersey, sixteen miles east of Philadelphia." Cope (1862) gave a description of this second specimen from life. This description, with a few emendations, was later repeated by him (Cope 1889) and again by Fowler (1907). A third specimen of *Hyla andersonii* was recorded the year Cope's general work appeared (Peters 1889). It was captured the previous year "on the border of a pine barren at May's Landing, N. J." Abbott (1890) who had this specimen in captivity, criticises Peters for his description of the call. A few years later Moore (1894) published a short but informing account of observations he made at Pleasant Mills, N. J. This was followed by the capture of an additional specimen at Clementon, N. J., and Stone (1901), in a note concerning the specimen, states that "the species would no doubt prove more abundant if specially sought for, the comparative remoteness of the New Jersey barrens, where most of the specimens were found, and the retiring habits of the animal both tending to make its detection difficult."

This prophecy was soon substantiated. Davis (1904, 1905 and 1907) made a series of observations at Lakehurst and Farmingdale, N. J., tending to show that the species was not rare in the New Jersey

pine-barrens. We owe to Davis our first account of the tadpole, and its metamorphosis. Fowler (1909) has given an excellent color description based on additional specimens. Of equal value is the splendid color plate given by Miss Dickerson (1906). She kept under observation one of the specimens secured by Mr. Davis and has given a good account of the species in captivity. Recently Barbour (1916) captured (July 8 at Lakehurst) "well up in a pine tree" two pairs while in embrace. These laid the same evening under abnormal conditions and no record was made of the egg-masses or eggs. More recently Miller (1916) has extended the known range of the species by finding it in several localities, "all in the sandy pine-barren 'island' north of the Pine-Barrens proper." Since 1916 the species has been studied at Lakehurst on one or more occasions by Messrs. C. L. Camp, K. P. Schmidt, R. Deckert, G. S. Myers, the writers and perhaps others. Lastly it may be pointed out that mention has been made of *H. andersonii* by various authors not listed above. Among these are Boulenger (1882), Sherwood (1898), Ditmars (1905), Stone (1906) and Deckert (1918). Further, Davis (1922) has very recently reported the occurrence of the species in North Carolina.

DISTRIBUTION.

Hyla andersonii is a tree frog of the pine-barrens. The type specimen is credited with coming from Anderson, South Carolina and the species was named by Baird after that town. But as Anderson lies neither in the pine-barrens (Livingston & Shreve 1921) nor even in the coastal plain, we suspect that the type specimen actually came from some other locality. As shown in the accompanying map, all the other locality records for *H. andersonii* lie within the pine-barrens or their outlying "islands." Although *H. andersonii* is abundant throughout most of its range, this range does not extend the entire length of the pine-barrens. The species has not been recorded south of South Carolina nor in the pine-barrens of Long Island. It is, however, widely spread throughout the New Jersey pine barrens occurring even in the pine-barren "island" just south of the Raritan River.

It should be noted, however, that the pine-barrens of New Jersey have a flora somewhat distinct from those of North Carolina. Mr. W. T. Davis who has studied both regions assures us that the facies of the country about Southern Pines, N. C., where he and



FIG. 147. THE PINE-BARRENS AT LAKEHURST, NEW JERSEY

A. Portion of the square mile of bog that was intensively studied. Four pairs of *H. andersonii* were taken while in embrace in a small pool on the left side of the road, directly behind the figure. Not one was found to breed in the deep water to the right. B. Cedar swamps bounded our area on two sides. It is from these cedars that most males call.

Dr. Chapin collected *H. andersonii* is very different from that of the New Jersey pine-barrens. The soil of both regions, however, is sandy, and much of the vegetation is the same. Until more extensive investigations can be made in the Carolinas, it is perhaps most conservative to say that *H. andersonii* is confined to the "pine-barrens."

It will be noticed that the distribution of *H. andersonii* cannot be expressed by a single term such as "Carolinian Life Zone" or "Coastal Plain." To be sure, it is to be found in these regions, but its range does not agree at all closely with either area. Many have attempted to reduce the distribution of life in North America to a few terms,—to a few zones—or to a few physiographic areas. But always objections have been brought forth in opposition to these attempts.

Confronted by such conflicting views, one is at first inclined to deny that the distribution of any one form can be explained in terms of another. The physiology of no two related animals is the same,—why should we expect that related animals would react the same to temperature? If we should pick two animals at random that have the same reaction to temperature, we might find that they reacted differently to ten additional stimuli. Further, the distribution of one species might be due to one factor, and of another species to another. There is no reason why one should expect to discuss the distribution of frogs in terms of the distribution of birds. But one may, I believe, make a distinct advance by speaking of the distribution of one frog in terms of another's range. During the breeding season batrachians congregate in distinct habitats. At other times of the year they do not wander far from these habitats. There is some reason to suppose that closely related species will have somewhat similar breeding habits. It was on the basis of this that Wright made comparisons between the affinities of certain European and American batrachians.

Hyla andersonii is a "coastal plain form." Many other species seem to be typically coastal plain forms in our area. These may be listed with their breeding habitats:

- (1) *Scaphiopus holbrookii*—Temporary pools in sandy regions.
- (2) *Acris gryllus*—Weedy, especially water-lily, ponds.
- (3) *Hyla andersonii*—Small pools in sphagnaceous bogs of pine-barrens.
- (4) *Rana virgatipes*—Larger pools of pine-barrens.

(5) *Rana pipiens*—Shallow ponds.

(6) *Bufo fowleri*—Shallow ponds.

Whether or not it is because the last two species are not particular as to the exact nature of their breeding cite, the fact remains that they have a much greater distribution in our local region than the other four species. Further, these two species often extend their range beyond the coastal plain, and probably because of this tolerance. *Scaphiopus holbrookii* has been taken in various parts of New England where the soil was sandy. *H. andersonii* and *R. virgatipes* are confined to the pine-barrens. Why *R. virgatipes* has a more extensive range to the south than *H. andersonii* it is impossible to say at this time. *Acris gryllus* is not found in the pine-barren bogs, and probably because of its preference for less acid water. When the life histories of all our American Amphibia are known, the species arranged according to their breeding cite preferences, many of the present anomalies of distribution among our Batrachia will be explained.

HABITAT.

The pine-barrens of New Jersey have been well described by various botanists (Stone 1911, Harshberger 1916, etc.). *H. andersonii* is not limited to any association within the pine-barrens. Specimens have been captured in many different kinds of bushes and trees. When pursued, *H. andersonii* invariably leaps to the ground and, with a series of short jumps, disappears among the grass and sphagnum of the bog. Specimens captured by us on the ground have been taken only in sphagnaceous areas.

Specimens of *H. andersonii* are taken most easily by running down the calling males at night, with an electric hand lamp. Such specimens have been captured on the ground, on low bushes, on the top of bushes six to eight feet in height and rarely in trees or tall bushes more than eight feet from the ground. We have captured only two specimens in the latter position, but Mr. Myers has observed a third.

BREEDING SEASON.

Previous to our work during the spring of 1922, the eggs of *H. andersonii* had only been observed twice and both under abnormal conditions. Barbour (1916) reports the capture of pairs in embrace at Lakehurst, New Jersey, on July 8. Eggs were laid in

a crowded vessel during the night. Messrs. Davis and Chapin captured a pair at Southern Pines, North Carolina, which later embraced and laid eggs the night of June 13, 1922, and also on the following night under abnormal conditions. No detailed observations were made on the egg laying process and no record made of the egg form. Previous to this, Davis had found tadpoles of *H. andersonii* in "all stages of development" at Lakehurst on July 21, 1907. From these observations it seemed probable that the breeding season of the Anderson Tree Frog at Lakehurst extended through June and part of July and may have begun earlier.

At Lakehurst, New Jersey, during 1922, the breeding season had apparently not begun by May 14. A few males were calling, but these from concealment on the ground (with a single exception, Camp), and mostly from among the sphagnum. On May 20 and 21 at exactly the same place in the bog, the breeding season was well under way. Two females were observed before embrace and taken during oviposition; a third female was taken just before oviposition. The chorus of the males was loud, approximately twenty-five to fifty calling within an area of one square mile. On June 4 and 5, approximately one hundred males were calling in this same area. One female was captured just before the embrace, and four pairs were taken in embrace. Although eggs had been found on May 20 and 21, no tadpoles could be found June 4 and 5. On June 18-19, the chorus of *H. andersonii* within the square mile of territory we were studying reached its maximum. At least two hundred and fifty males were calling within this area. Although no mated pairs were found, tadpoles of a wide range of sizes (up to appearance of hind limbs) were captured. On July 22-23, the chorus had diminished. Only about forty males were calling. Tadpoles of all sizes from shortly after the formation of the operculum up to metamorphosis were captured in this same region.

These observations make it clear that the breeding season of *H. andersonii* is not an explosive one, but is more or less protracted. Rains occurred at Lakehurst on the days preceding our observations of May 20-21, June 4-5 and June 17-18. The days, therefore, were comparable so far as humidity was concerned. (Unfortunately, no thermometers were used to determine this exactly.) Comparing this data with random observations made on previous years at Lakehurst, the breeding season of *H. andersonii* seems to be more or less dependent on the rains and may extend from the middle of May to the middle of July.

It was perhaps not surprising to find that in correlation with this protracted breeding season, the species breeds in more or less isolated pairs. As this method is not the general rule among our local Salientia, it may be of interest to make some comparisons between the breeding season of *H. andersonii* and that of other local forms. So little is known concerning the factors controlling these differences that only the most obvious will be mentioned.

I. Internal factors

1. Maturing of gonads, may be either
 - a. Uniform for all individuals of a species within an area, or
 - b. Irregular, small colonies breeding at different times.
2. Physiological cycle (correlated with the development of gonads) may be
 2. Genetic (closely related species living under similar conditions may have different breeding season), or
 - b. Acquired. It is well known that Amphibia in captivity gradually modify their breeding season, and may eventually lay at very irregular times. The life cycle characteristic of the species may have been induced by the environment, just as it has been modified by the new environment of captivity.

II. External factors

1. Temperature
 - a. Air temperature,—affects those batrachians hibernating on land. These are, for the most part, early breeders (Wright, 1914).
 - b. Water temperature,—affects the species hibernating in the bottoms of ponds. These are chiefly late breeders.
2. Rains (often correlated with a change in temperature)—are the chief controlling factors in the breeding of Batrachia within the tropics. This has been shown experimentally by Bles (1906) but field observation has further demonstrated the fact. In temperate regions, the rains play a vital part in the life cycle of some forms (as *Scaphiopus*), but much less in the case of others.

As a result of the interaction of these external and internal factors, the various species of Batrachia within our local area are found to breed at different times. We may group them according to the time and period of their breeding season into several categories with the understanding that these categories are subject to fluctuations according to variability of both external and internal factors:

I. Explosive Breeders

1. Temperature controlled; mostly early breeders which have hibernated on land. *Bufo americanus*, *Rana pipiens* and *Rana sylvatica*.
2. Rain controlled; *Scaphiopus holbrookii*, often selecting a poor breeding cite.

II. Protracted Breeders

1. Temperature controlled; including a few early but mostly late breeders, forms which have either hibernated in the water, *Rana palustris*, *Rana clamitans*, *Rana catesbeiana* and *Rana virgatipes*, or others on land,—*Pseudacris tri-seriata* (?), *Hyla crucifer*, *Hyla versicolor*, and *Acris gryllus*.
2. Rain controlled; *Bufo fowleri*, *Hyla andersonii* may choose a poor breeding cite but more often one favorable to the welfare of the tadpoles.

The distributions made above are only approximate, and, moreover, apply chiefly to our local area. At Ithaca, New York, Wright (1914) found that temperature was the chief factor controlling the breeding season of the Salientia. Wright was able to arrange the species he considered in a series according to their first appearance and time of breeding. South of Wright's locality, even in the New York region, the rains begin to play an important part in the breeding of the Salientia. In the tropics, as we have recently seen in Santo Domingo, it is the rains—and apparently only the rains (correlated of course, with slight changes of temperature)—which initiate the breeding season.

In the case of *H. andersonii* our observations have not been of sufficient frequency to determine exactly the part played by the rains and the part by temperature in determining the breeding season. By comparing several seasons' observations, it would seem that both rain and temperature are effective, but as the season is a long one—possibly due to an irregular maturing of the gonads in the colony—it would seem that the rains may be the more important factor, although, of course, not as effective as in the case of explosive breeders such as the Spadefoot toad (*Scaphiopus*).

We may add, in passing, that not sufficient consideration has been given to the rains in initiating the laying process of Amphibia in general. The breeding season of not only some northern Salientia, as *Scaphiopus*, but even of some northern Caudata, may be controlled primarily by the rains. This has been very thoroughly demonstrated in the case of *Hynobius nebulosus* by Kunitomo (1910). It is to be hoped that more exact data of this sort will be

forthcoming for other northern species. It would be interesting to know whether the breeding season of a single species may be primarily rain or temperature controlled, according to the northernness of its breeding site.

VOICE.

One of the most characteristic features of *H. andersonii* is its distinctive voice. As in the case of all known hylids, only the male is thus provided. The call has been variously described as a "keck-keck" (Abbott), a "peep-peep" (Peters), a "quack-ack" (Moore), a "whang" (Deckert) or a "aquack-aquack-aquack" (Davis). One would gather from the literature that the Anderson Tree Frog had a variety of calls. Our common tree toad (*Hyla versicolor*) has two distinctive calls. Although Wright (1914, p. 46) states that "an individual tree-toad may give one or two voice-forms totally unlike the normal and better-known call," undoubtedly these "abnormal calls" will be found referable to what Overton (1914, p. 33) has called the "turkey root." Since Overton's paper appeared, we have watched on several occasions *Hyla versicolor* give its "turkey root." On none of these occasions was there any bobbing of the head such as Overton describes. The call, variable as to number of syllables, is given with a half inflated pouch. When *H. versicolor* calls with fully inflated pouch it gives its characteristic trill; when it calls with only half inflated pouch, a series of mournful notes arise.

H. andersonii has only one call and that is given with fully inflated pouch (Fig. 148). It is a series of ten to twenty, or even more, resonant nasal notes, usually increasing in volume. Each note is a sonorous, high nasal quănk. If one tries to shout the word quank while holding the nostrils closed, a sound is produced not unlike the note made by this frog. The call sounds somewhat different from a distance, especially when several frogs are calling at once. Then the notes tend to run together, each note having two syllables, a-quănk, a-quănk.

SEX RECOGNITION.

Although the call of *H. andersonii* is loud, often carrying nearly a mile on quiet evenings, nevertheless, little or no significance has been attributed to it, or to the voices of any frogs and toads, in the breeding season. Voice is stated not to control the direction of migration towards the breeding grounds, or the movements of in-

dividuals on the grounds (Boulenger, 1912, p. 22, Cummins, 1920, p. 325). It is generally believed that "courtship does not take place in any of the tailless batrachians. The female is seized by the first comer, ————" (Boulenger, 1898, p. 68). Some years ago it was pointed out by Courtis (1907, p. 678) and later by Miller (1909, p. 650) and by Wellman (1917, p. 107) that the breeding female toad (*Bufo*) may respond positively to the trill of the male. But Cummins (1920, p. 243, italics his) has recently shown that in the case of frog material the "*voice does not direct the movement of the frogs into the pond*" and "that 'sex recognition' . . . results from the differential behavior of the two sexes when clasped, . . ."

The following observations made during 1922, on *Hyla andersonii* would tend to show that in that species, and by inference in tree frogs in general, the voice plays a considerable rôle in bringing the two sexes *in contact*.

At Lakehurst on May 13-14, *H. andersonii* was calling only from concealment (with one exception) on the ground, chiefly among the sphagnum of the bog. On May 20-21 some were calling from the ground, but mostly from trees and bushes a few feet from the ground. On all other occasions during June and July, *H. andersonii* called chiefly from some point of vantage above the ground; only very few were seen calling from the ground.

As pointed out above, the breeding does not occur simultaneously throughout the limited region under observation. By means of the flashlamp, individual frogs were studied for several consecutive hours on the days indicated above. The following observations were made the night of May 20-21.

Case I. 11:30 P.M. A male was observed calling from edge of small and weed-grown ditch, about one and one-half to two and one-half feet across, one to ten inches deep; bottom covered with sphagnum and water weed.

Female was first observed three feet away from male, hopping in his direction. Without hesitation the female leaped on back of the male; but the latter gave a slight wriggle, which threw her off his back and he continued calling.

Female turned and leaped again on the back of the calling male. Again he threw her off with a wriggle, but this time, as she moved again toward him, he caught sight of her and quickly turned about and embraced her with the normal supra-axillary amplexus. The pair maintained their position about eight inches from the water

(Fig. 149c) until 12:30 A.M., when the female leaped with her mate into the stream, and a moment later ovulation began.

Case II. A male was observed calling at 3:00 A.M. (May 21) from the edge of the same stream about one hundred yards away from place where the above observations were made. The character of the stream was identical to that of Case I. The male was sitting on a soaking mass of sphagnum close to the water's edge. The female was first observed two feet away, making short leaps toward the male. The female approached to within six inches of the male and while he continued calling, she hopped rapidly about him twice. In making these two circuits she had to splash through about one-half inch of water. In completing the last circuit, the female approached so close to the male that the side of her body touched his side and she nudged him with her limbs as if to draw as close to him as possible. On completing his call, he turned and embraced her.

The pair in embrace hopped for about six yards along the edge of the stream and began to ovulate in the water. They were finally placed in a vessel where ovulation was completed.

The following observations were made during the night of June 4-5:

Case III. A male that was calling from a bush, and photographed twice, (Fig. 149a) seemed particularly nervous because he frequently changed his position a few inches. Suddenly, at 12:30 A. M., he left the bush without warning. He was followed with the flash-light to which he paid no attention, and although we changed the position of the light frequently, the frog hopped straight across the bog over ruts and small depressions to a small stream flowing in a sphagnum-grown ditch. There he took up a position (Fig. 149b), three inches from the water and approximately thirty feet from his first calling station, and began to call.

Half an hour later a female came hopping across the bog. She was first observed about fifteen feet from the male. She came straight toward the male which continued calling. When about four inches from him she turned slightly and hopped past him but he paid no attention to her. She then continued her journey toward a thicket where over thirty males were calling. The female began to cross through a weed-grown bog, and as it was apparent that we could not follow her, she was collected. Later we found only a few yards ahead a flooded but very shallow bog in which there were four mated pairs. It was over one hundred and fifty

yards from the point where the female was first observed to the place where she was taken. In making the journey, the female had passed no less than four calling males, but she came close only to the first.

From these data the following tentative conclusions may be reached:

1. *H. andersonii* begins calling in early May from concealment on the ground.

2. In the middle of May and throughout June and July the males call chiefly from bushes or from trees.

3. At various intervals throughout May and June (and some years, in July) when the rains have flooded the bogs and changed the ditches into small sphagnum-choked streams, the males leave their calling stations and make their way to the nearest of these small streams. This migration occurs about midnight. The males begin calling again from their new positions near the sphagnaceous streams.

4. The females are *attracted toward the male by his call*. This attraction is so great that it causes the female to leap upon the calling male.

5. After a more or less persistent courtship on the part of the female, during which she strikes the male one or more times, the male recognizes the female and embraces her.

6. It is possible that the female may, under certain circumstances, climb a tree after the calling male. At least, this seems to be the most feasible explanation for the observation made by Barbour (1916) of a pair in embrace while high in a tree.

7. The female may exercise some choice in the selecting of a mate. The call is not the only factor involved in bringing the sexes together.

Although no one has observed this method of female courtship in any species of *Rana* and only part of the phenomenon has been witnessed in *Bufo* material, we believe it will be shown to be the rule in the case of *Hyla*. On June 7 at 11:00 P.M. near Patchogue, Long Island, we observed a female *H. versicolor* swiftly approach a calling male from behind and leap directly on his back. The male broke off his call at once, turned, and embraced the female.

When the movements of individuals of other species of frogs have been followed throughout the night, we believe it will be clearly

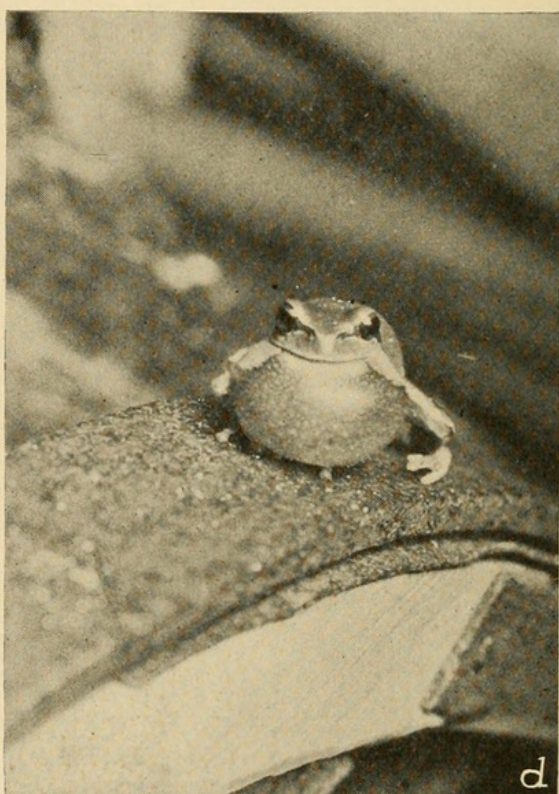
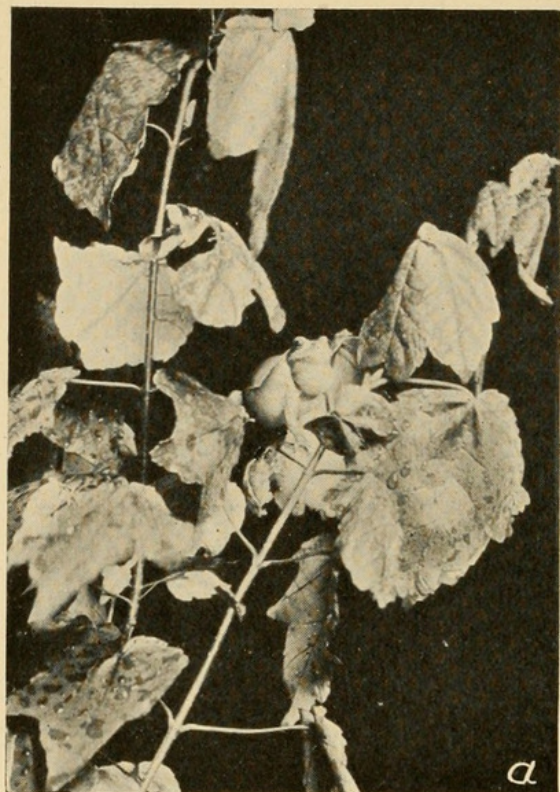


FIG. 148. FLASHLIGHT PHOTOGRAPHS ILLUSTRATING THE DIVERSITY OF THE CALLING STATIONS.

a. Beginning the call from top of a pine-barren maple; note the inflation of the body, and the rain drops on the leaves. *b.* The height of the call. *c.* Calling from the wheel of an old abandoned cart on the edge of the pine-barrens. *d.* The height of the call.



FIG. 148. FLASHLIGHT PHOTOGRAPHS ILLUSTRATING THE DIVERSITY OF THE CALLING STATIONS.

e. Beginning the call from the top of a bush about three feet high. *f.* The height of the call. *g.* The rest between calls from a blue-berry-bush. *h.* The call; note the position of the hands and feet.

demonstrated that voice plays a considerable rôle in bringing the two sexes together. The problem of sex retention is a more difficult one, and can be determined only by careful experimental work.

It will very probably be shown that voice plays a considerable rôle, not only in bringing the two sexes in contact, but also in attracting individuals together to form breeding colonies. We have found that males of *Scaphiopus holbrookii*, *Bufo americanus* and *H. andersonii* often came toward us when we imitated their call. In the case of one male *H. andersonii*, the hand-light was directed from a variety of angles and yet when we called, the frog always came toward us. We have never noticed a male *H. andersonii* jump on a calling male of the same species. It therefore seems likely that the attraction of the call is not as great in the case of the male as in that of the female. It, nevertheless, may play a considerable rôle in the ecology of a species, and to our tentative conclusions above we may now add two others.

1. The gregariousness of a species during the breeding season is a function of the attracting power of the call upon males of the same species. For example, *Scaphiopus holbrookii* is more gregarious than *Rana palustris* because it is readily attracted by the calling of the colony.

2. When several species are breeding in one marsh, the species are usually separated into colonies because of the *specific* attraction of the different calls.

SEXUAL DIMORPHISM.

With the several excellent descriptions of coloration of *H. andersonii* available, especially the color plate of Miss Dickerson (1906, color plate VII), it would be superfluous to give a new description of this form. Nevertheless, it has not hitherto been pointed out, although recognized by some (Davis, Myers), that there is a distinct sexual dimorphism in this hylid. I find the following constant differences between the two sexes. These differences are sufficiently marked to permit one to distinguish between the two sexes in the field.

1. Throat of breeding male, purplish gray; throat of breeding female pale gray or white, rarely as dark as the throat of palest male.

2. Green patch below angle of jaw broadly edged with

white in all females, without a white border in the breeding male, or with a very narrow and indistinct one.

3. Breeding females distinctly larger than males. Average head and body length (snout to vent) in the ten females taken in embrace is 40.9 mm. (extremes 44 and 38 mm.). Average head and body length of fifteen breeding males is 36.7 mm. (extremes 35 and 38 mm.).

In addition to these three characters of which the best field mark is the second, there are the two sexual differences to be expected. First, the vocal pouch of the breeding male is always more or less indicated even in quiet individuals. Secondly, the male bears on the inner and upper side of the thumb (prepollex region) a patch of minute pigmentless asperities hardly recognizable without a lens. The female bears in this same position glandular skin as smooth as the adjoining regions.

As pointed out by Dickerson (1906), the color pattern of *H. andersonii* is very constant, the change of coloration being limited to a darkening or lightening up of the tones. These changes of color are correlated with at least three factors,—(1) excitement, (2) light, and (3) humidity.

A pair in embrace are usually of a different color. If the female is ovulating and moving only short distances about the pool, the male is much the darker probably because of the sexual excitement accompanying fertilization; but if the female is moving rapidly along the edges of a bog, the male merely retaining his position on her back, the female is the darker. These facts were clearly shown in the three cases discussed above.

The effect of light and moisture on the color of these hylids may be readily demonstrated by keeping them in terraria of various degrees of humidity. Individuals in cold, wet terraria are very dark.

METHOD OF OVIPOSITION.

Amplexus in *H. andersonii* is supra-axillary. No other type or no abnormal amplexus was observed. The partly closed hand of the male is dug into the sides of the female just behind the head of the scapula, and just below the diapophyses of the anterior vertebrae. These diapophyses prevent the hand of the male from slipping dorsally, the scapula prevents it from slipping anteriorly, while the viscera of the female prevents it from sliding posteriorly.

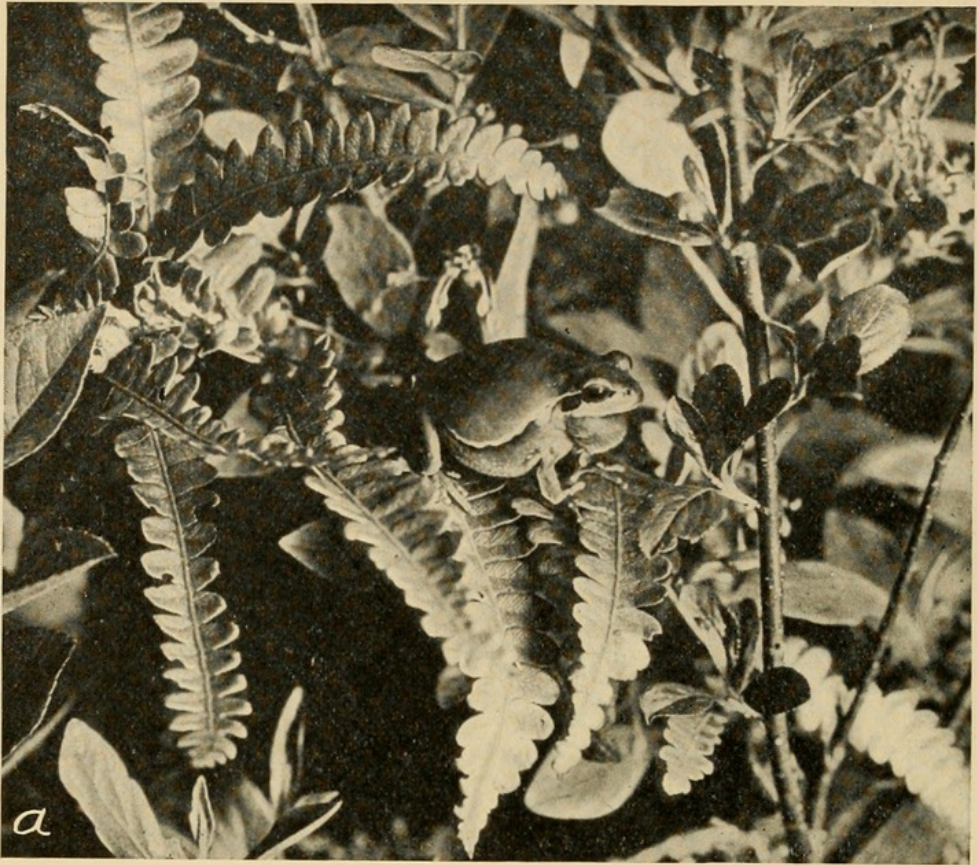


FIG. 149. FLASHLIGHT PHOTOGRAPHS OF *H. ANDERSONII* ILLUSTRATING STAGES IN THE BREEDING PROCESS.

a. Beginning the call from ferns and bushes on a bank about two and one-half feet above the level of the bog (see text, Case III). *b.* The new calling station, about 30 feet from the first, close to a small sphagnaceous stream. *a.* and *b.* same individual.



FIG. 149. FLASHLIGHT PHOTOGRAPHS OF *H. ANDERSONII* ILLUSTRATING STAGES IN THE BREEDING PROCESS.

c. The embrace. After the female had flung herself twice upon the calling male, he finally turned and embraced her (see text, Case 1). A male *Bufo fowleri* is calling close at hand (left of picture). Oviposition did not take place until an hour later. d. The beginning of oviposition; note the position of the male and the sphagnum projecting above the water.

Oviposition takes place always in the water and only in small basins, or slow-moving streams on the pine-barrens, never, however, in stagnant water. All eggs, tadpoles and pairs in embrace were found in puddles and streams lined with sphagnum. The water of the pine-barrens is always more or less coppery, even after hard rains. The color is due to tannin derived from the roots of the bog plants. This tannin makes the water slightly aseptic. Eggs will develop in other kinds of water. We have found that several lots developed normally in tap water. We were not, however, successful in raising the tadpoles in tap water. Dilutions of bog and tap water proved more satisfactory. From our observations it would seem that the bog water is essential to the normal development of the tadpole.

The details of oviposition were studied in four pairs, two in the field and two in the laboratory. Mirrors were used to determine the exact course of the egg. The process of egg-laying was found to be the same in both captive and wild specimens.

In Cases I and II, discussed above, oviposition began almost immediately after the female leaped from land into the deeper water of the streamlet. The characteristic attitude in the water is shown in the photograph of another pair (Fig. 149d).

The egg-laying process seems to be initiated by the female. She bows her back suddenly, at the same time protruding the cloaca. A bunch of eggs appears in the orifice of the cloaca and as the female bows her back, either these eggs or the cloaca of the female touches the male between the legs. Immediately the male wriggles. It is assumed that the male emits the spermatozoa at this moment, but these are invisible. In the fully bent position (Fig. 150) the cloaca of the female is anterior to that of the male. As soon as this position is reached, the female straightens her body, suddenly ejecting the eggs. The eggs may have received a wash of sperm as they were protruding from the cloaca. It is more likely, however, that they strike the spermatozoa as they are shot from the cloaca. It will be observed that this method of fertilization is unlike that of the spring peeper, *H. crucifer*. Here the egg (rarely 2 eggs) is held in the orifice of the cloaca not only during the upturning of the cloaca, which, as in *H. andersonii*, seems to function in stimulating the male, but also during the return movement and subsequent forward movement of the whole posterior

region of the female. Hence, the egg of *H. crucifer* is apparently fertilized while held in the cloacal orifice of the female, while it may or may not be fertilized at this time in the case of *H. andersonii*. The ovipositions of *H. andersonii* and *H. crucifer* may be compared as follows:

<i>H. crucifer</i>	<i>H. andersonii</i>
(1) Cloaca upturned, and egg or its capsule (rarely two eggs) appears in orifice of cloaca.	(1) Back bowed greatly, and cloaca upturned; part of a bunch of eggs (7 to 14) appear in orifice of cloaca.
(2) Cloaca of female usually touches posterior ventral surface of male's body in upward movement.	(2) Same.
(3) Emission of spermatozoa apparently takes place as cloaca touches or passes near ventral surface of male.	(3) Same.
(4) Back straightened and cloaca of female brought forward beneath body where the egg (or eggs) is shot out against some object to which it adheres.	(4) Back straightened and eggs are shot out against body of male to which they do not adhere, but glance off to the bottom of the pond.

The remainder of the egg-laying process of *H. andersonii* cannot be compared in detail with that of *H. crucifer*. At the moment the eggs are extruded, the hind limbs of the female are convulsively straightened, forcing the pair forward in the water. The female makes one or two nervous half strokes which continue the headway of the first stroke. In one to three seconds they have again come to rest, the female again bows her back and the process is repeated. After two to ten (possibly more) layings, the pair come to rest and oviposition may not continue until half an hour later. The exact length of these "rests" between sexual periods were not determined in the field. In the laboratory this "rest" was extremely variable.

The most remarkable feature of this egg-laying is the course taken by the eggs (Fig. 150). The female bows her back very much as in the case of the ovipositing *H. versicolor*, and even makes

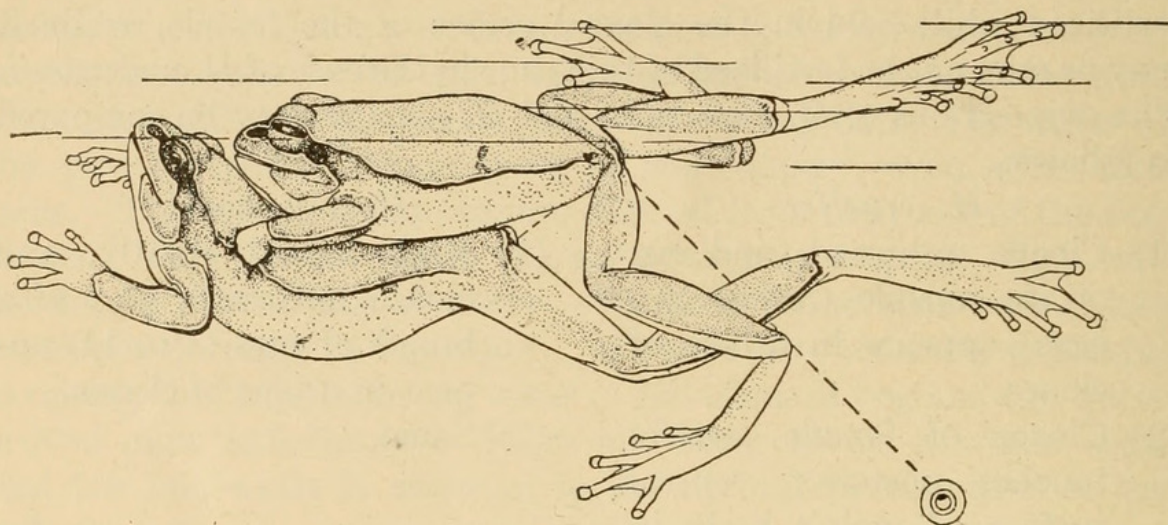


FIG. 150. THE OVIPOSITION OF *HYLA ANDERSONII*

This bombardment of the male with eggs seems to be a specialization derived from the method of oviposition found in *H. versicolor*, where the female lifts her cloaca above the water. In this diagram, only one egg has been represented (instead of nine), and the legs of the male have been abnormally extended in order to show better the course of the eggs.

some attempt to raise the cloaca above the water, as in that species, but the eggs never (or very rarely) reach the surface of the water. On being shot from the cloaca they strike the male on his ventral surface immediately below his cloaca and are carromed off to the bottom of the pool. Of the many times we watched this bombardment of eggs both in the two pairs studied in the field, and the laboratory specimens, only twice—and then in laboratory specimens—did we see the eggs miss the posterior part of the male's ventral surface. In these cases the eggs missed the male entirely and fell considerably to the rear of the pair.

This phenomenon of egg bombardment is of special interest from a phylogenetic point of view. The eggs of most species of *Hyla* float. In the case of *H. versicolor*, it would seem that the air bubbles entangled in the jelly when the female raised her cloaca above water, caused the eggs to float. In other forms it would seem more likely that it was some phenomenon of surface tension (Harrison 1922) holding the eggs near the surface where they were laid. Now in *H. andersonii*, the eggs cannot reach the surface for a very definite mechanical reason,—namely, the male is in the way. Nevertheless, the female goes through all the movements as if intending to

lay the eggs on the surface of the water. It would thus seem that in *H. andersonii*, its habit of laying bottom eggs has been derived from the more characteristic surface egg habit.

The eggs of *H. andersonii*, although shot from the cloaca in bunches of from seven to fourteen (average, nine), do not adhere to one another. They fall to the bottom of the pool where they usually adhere to sphagnum or debris. Here they swell rapidly and frequently lose their attachment to the sphagnum. At Lakehurst, many eggs (in late cleavages) were found lying free on the bottom of the sphagnaceous streams.

In nature, *H. andersonii* was estimated to lay eight hundred to one thousand eggs. None of our laboratory animals laid more than eight hundred eggs.

THE EGG AND ITS CAPSULES.

The eggs of *H. andersonii* may be readily distinguished from all other eggs found in the pine-barrens by the following characters: The eggs are—

1. Single, not adhering to one another, usually scattered among the water weed.

2. Attached to sphagnum (rarely debris), or free and rest on bottom.

3. Found on bottom of small, non-stagnant pools, or in slow-moving streams of the pine-barrens.

4. With dark cap of the animal pole extending only over one-third of the surface of the egg. (Early cleavage stage.)

Before cleavage the cap on the animal pole is usually dark brown, the other two-thirds of the egg, creamy-white. As the cleavage continues, new pigment is formed. At the end of cleavage, before any gastrulation has begun, about two-thirds the surface of the egg is pigmented (Fig. 151). Harrison (1922) has noticed a similar phenomenon of pigment increase during segmentation in some of the Australian hylas he studied. In making a comparison of the eggs of *H. andersonii* with the eggs of other frogs, care should be taken to use only eggs very recently laid, not those which have gone beyond the 32 cell stage.

As gastrulation continues, the egg becomes much lighter in color. The late gastrula is pale brown, often with streaks of a darker tone.

The egg is surrounded by the vitelline membrane and by the

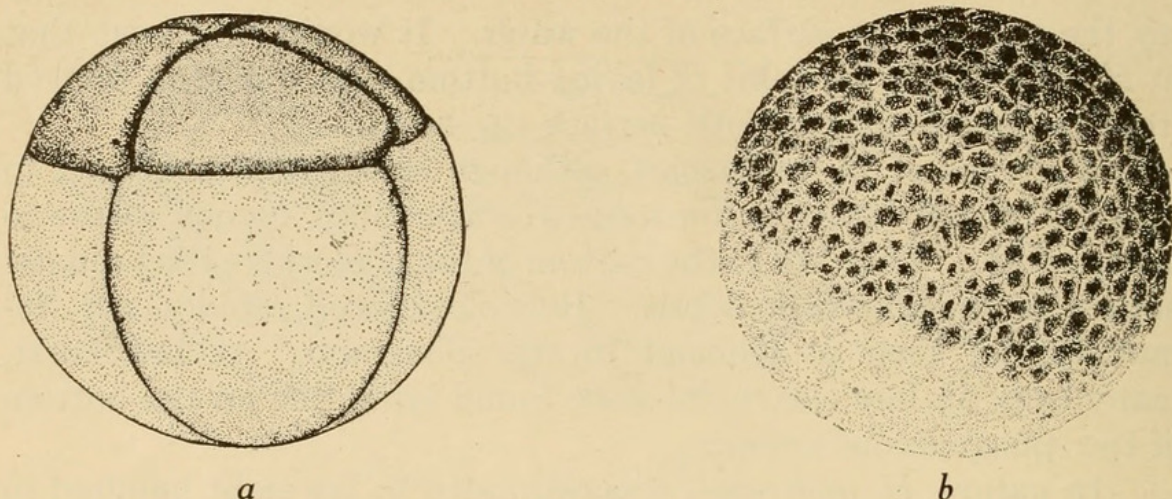


FIG. 151. PIGMENTATION OF THE EGG OF *H. ANDERSONII*

a. Eight cell stage viewed from side of the gray crescent. *b.* Late cleavage stage, to show the increase of pigmentation.

two gelatinous membranes of the usual type. The gelatinous capsules vary enormously according to their age, and treatment. The following measurements are taken from a series preserved in formalin. They agree well in size with some living specimens.

Diameter of Ovum—1.2–1.4 mm.

“ “ Inner Capsule—1.9–2.0 mm.

“ “ Outer Capsule—3.5–4.0 mm.

The vitelline membrane may be best demonstrated just after maturation when the animal pole is slightly flattened leaving a space between membrane and ovum.

In passing, a word may be said in regard to egg membranes in general. The eggs of most batrachians possess two gelatinous capsules in addition to the vitelline membrane. European pelobatids are stated by Boulenger (1898) to possess only the inner capsule, while Wright (1914, p. 16) allows us to infer that some American Salientia may lack the same. We should like to emphasize that the outer egg capsule of all batrachians is subject to great modification, even within a species. Thus, our pelobatid *Scaphiopus holbrookii* has two layers of “jelly” about the eggs. At oviposition, the outer layer is extremely adhesive. As development continues, this outer capsule swells rapidly, losing its adhesive quality, and changing its appearance.¹ We do not believe that the presence or

¹ The eggs of *S. holbrookii* are not twisted around the grasses in the spiral manner indicated by Deckert (in Overton 1914); on the contrary, they are laid on the upper side of grass stems which have been flattened down by the female. As the outer gelatinous membrane swells, the egg-masses take on the appearance of being arranged in a spiral, having much the same form as the egg-masses of European pelobatids.

absence of the outer capsule in all batrachian eggs can be determined without investigating the structure of these membranes at the moment of oviposition.

We have had no difficulty in distinguishing two gelatinous capsules in the living eggs of *H. crucifer*, although Wright (1914) figures only one capsule.

DEVELOPMENT OF THE EGG.

The egg of *H. andersonii*, in spite of its reduced pigmentation, shows some indication of a "gray crescent." At least one side of the fertilized egg is paler than the other. The pale region is in no sense a crescent, but is an area probably homologous to the gray crescent of *Rana*. The first cleavage plane tends to cut the mid-point of this "crescent" at right angles. However, some irregularities occur. The second cleavage plane is as usual meridional, but in most eggs it cuts the first cleavage plane not at its mid-point, but nearer the "crescent" side. As a result, the two cells containing the crescent material are usually smaller than the opposite pair. The third cleavage is latitudinal. It cuts the egg at right angles to its axis and at such a point that on the "crescent" side the third cleavage furrow sharply demarcates the pigmented from unpigmented region. Later cleavages are usually irregular. This is probably due to the fact that the second cleavage plane does not cut the egg systematically, but leaves less material on the "crescent" side than on the other. It would be interesting to know the conditions in other species of *Hyla*.

With the little comparative material available to us it does not seem advisable to discuss the later stages in any detail. The changes of pigmentation which accompany the development within the egg have been mentioned above. The late gastrula shows some dorsal flexure as in *Bufo* and *Rana*. No marked differences between the gastrulation in these groups were noted.

Eggs laid in the laboratory hatched in four days. This is probably a much shorter period than would occur in nature. Although the period of development within the egg may be greatly modified by temperature, not all eggs placed under identical conditions develop in the same time. Wright (1914, p. 19) found that the eggs of the species he considered all developed in about the same time under laboratory conditions,—namely, in four or five days. But Boulenger (1898) has found a marked difference in the

developmental period of two such allied genera as *Alytes* and *Discoglossus*. We have found that the eggs of *Scaphiopus* hatched within thirty-six hours, while the eggs of most species of *Rana* require five days under the same conditions.

Lastly, a word may be said in regard to laboratory conditions. If a breeding pair is placed in a very small container, the chances that all the eggs will be fertilized and develop are very much better than if they are in a large jar. We experienced none of the difficulties with our material that Wright (1914) mentions.

THE ADHESIVE ORGANS AND THEIR DEVELOPMENT.

Very few have studied the adhesive organs of batrachian larvae. Although the form of these organs differs in the various species and may be utilized as a character diagnostic of the species, these organs have been described in only a few hylids. It is, therefore, perhaps not surprising that we should find that the adhesive organs of *H. andersonii* bridge, during their ontogeny, the gap supposed to exist between the bufonid and hylid types.

Thiele (1888, pl. 10) found that the adhesive organs of *H. arborea* arose as two swellings, one on either side of the midline in a way very similar to the ontogeny of these organs in *Rana agilis*. Thiele pointed out that the more primitive method of development was that of *Pelobates* and *Bufo*, where the organs arise by modification from a crescentic furrow. It is, therefore, of considerable interest that we should find some indication of this crescentic type of development in *H. andersonii*.

In the early embryo of *H. andersonii* there appears a crescentic swelling on the ventral surface of the head (Fig. 152). This becomes slightly more pigmented than the surrounding region, but never invaginates to form a furrow as in European species of *Bufo*. As development continues, the two horns of the crescent increase in size and gradually differentiate into the definitive adhesive organs, while the posterior part of the crescent (Fig. 152) becomes less and less distinct.

By the time the tadpole is ready to hatch, the adhesive organs have assumed a position lateral to the mouth. It will be noticed from fig. 152 that these organs, when fully formed, are not as far anterior as the adhesive organs of *H. arborea*. In *H. crucifer* we find that the adhesive organs have a similar position lateral and posterior to the mouth.

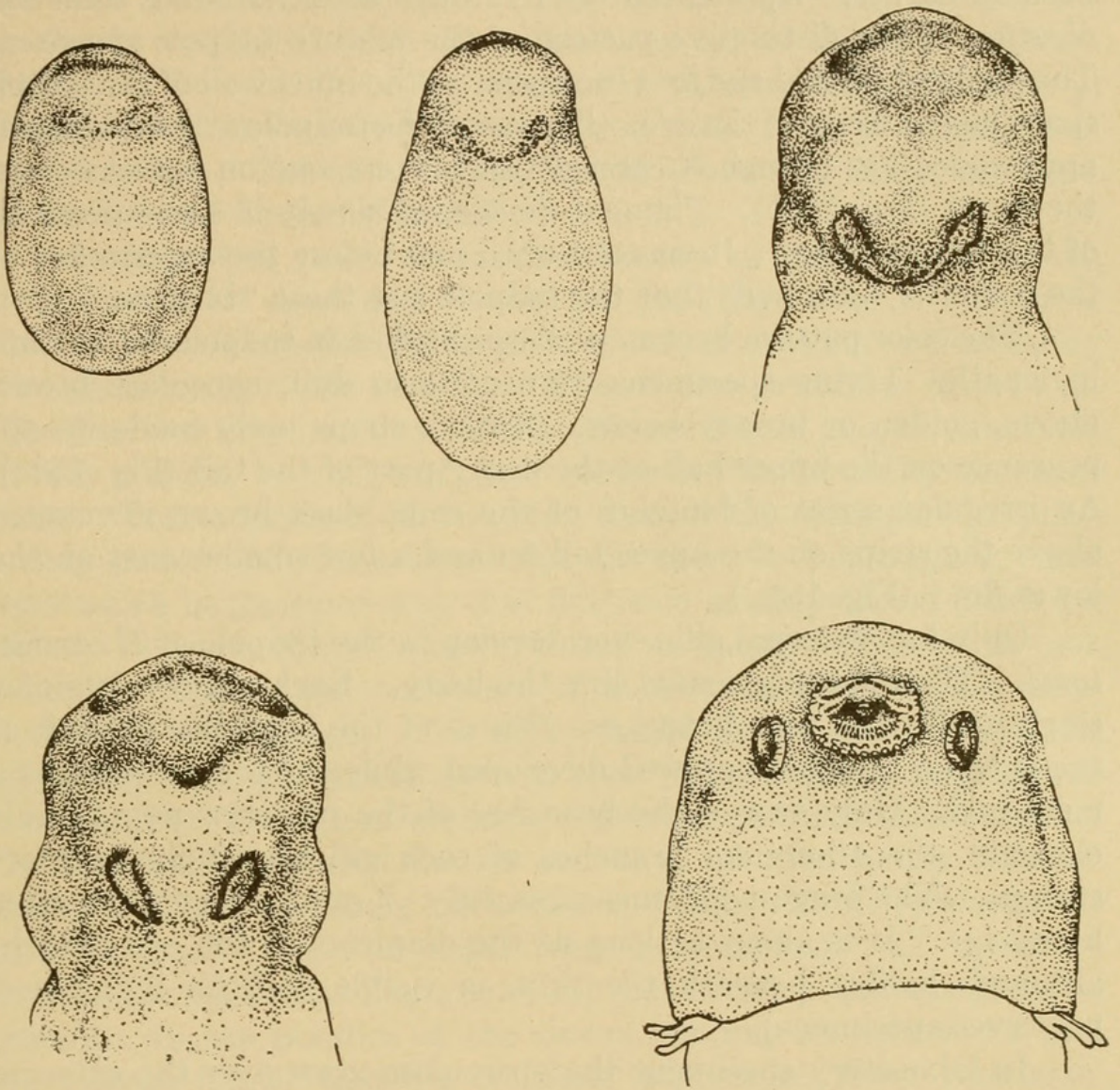


FIG. 152. DEVELOPMENT OF THE ADHESIVE ORGANS.

All but the last stage occur within the egg capsules. The frontal organ (extreme anterior end) is conspicuous in all but the last stage.

It will be noticed from fig. 152. that the frontal organ in *H. andersonii* is very distinct. This would indicate that it must have considerable functional significance.

DEVELOPMENT OF THE TADPOLE.

Eggs raised in the laboratory in shallow watch glasses hatched four days after oviposition. The recently hatched tadpoles varied somewhat in size, an average specimen measuring 4.5 mm. in total length. The color of these tadpoles was pale yellow finely stippled or suffused with brown. As the tadpoles grew older the pigment

became darker. Approximately five days after hatching some indication of the distinctive pattern of the mature tadpole appeared. The pigment of the head first increased on the inner wall of the lymph space just anterior to the eye. This gave the tadpole a "pathological appearance" as though it carried two blisters, one on either side of the snout (Fig. 153b). Pigment developed slowly in the outer wall of this lymph space. It was not until just before the appearance of the posterior limb buds that the tadpole lost these "blisters."

The color pattern became well established in tadpoles of 11 mm. in length. Living specimens were uniform dull, chocolate brown above, golden or bronzy below. A dark stripe early made its appearance on the upper half of the fleshy part of the tail (Fig. 153c). An irregular series of blotches of the same dark brown developed above the stripe on the upper tail fin and a few smaller ones on the lower fin. (Fig. 153c.)

Only two external gills ever develop in the tadpole of *H. andersonii*. These are pigmented like the body. Each gill consists of a single stalk with four branches. Three of the branches of each of the anterior gills become well developed while the fourth remains a mere bud. Only two of the branches of the posterior pair of gills elongate, the other two branches of each gill remaining as short stumps. The longest gill measures only .7 mm. (three days after hatching). It is about as long as the diameter of the eye (which, although hidden beneath the skin, is visible in both living and preserved specimens).

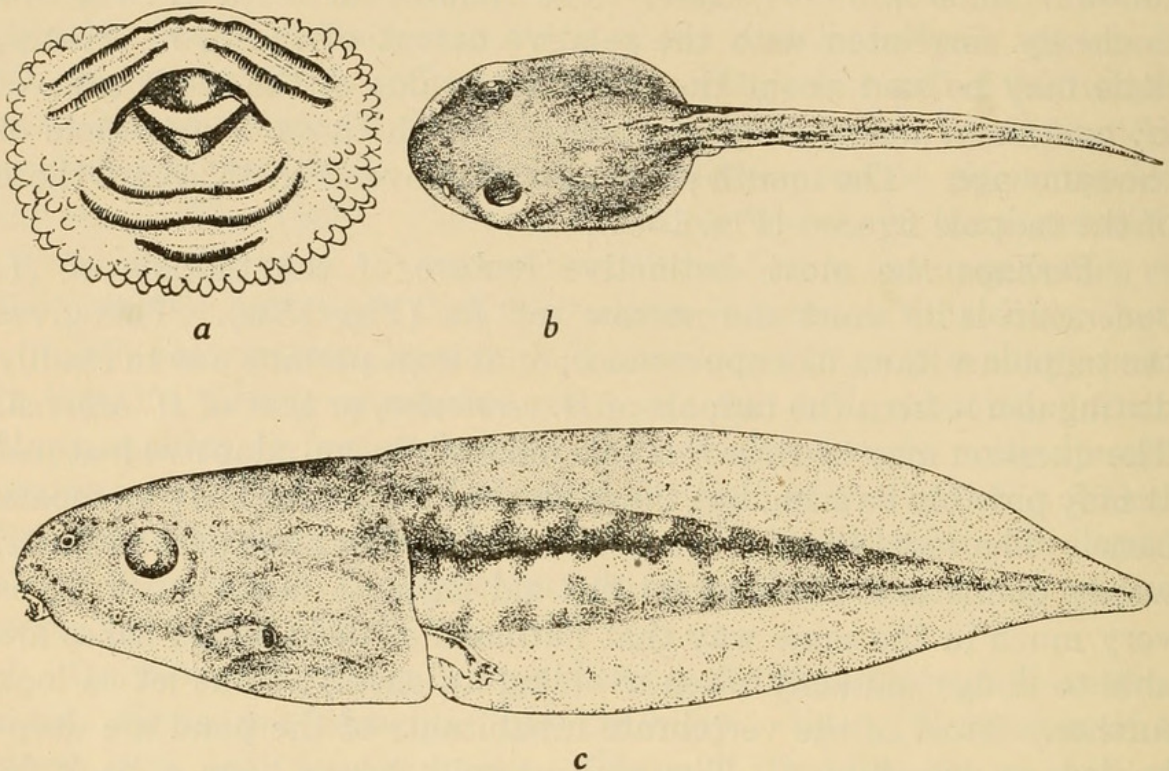
In laboratory specimens the operculum grew over the external gills six days after hatching. The tadpoles at this age averaged 8 mm. in total length. The pale coloration of the early tadpole had darkened, and some indication of the dark tail streak had appeared. Although the mandibles were well formed and pigmented, no horny teeth had yet developed. The vent at this stage had just begun its asymmetrical growth which soon resulted in its characteristic dextral twist.

The horny teeth began to develop immediately. As the tadpole matured, the teeth increased in number. This may be seen in our series of preserved specimens. In a tadpole of 11.5 mm. total length, the number of teeth in each row, reading the rows from above down, is as follows: 38/10 + 10//31/24/5. In one of 17 mm., the formula is: 52/21 + 21//47/45/21. In a mature tadpole of 32.5 mm. total length and having the limb buds well developed, the formula is as

follows: 96/36 + 35//67/82/40. The number of teeth in each row is closely correlated with the relative extent of the row. Hence, little may be said about the diagnostic value of the teeth rows of *H. andersonii* unless they be compared with those of a tadpole of the same age. The mouth parts figured above (Fig. 153a) are those of the tadpole figured (Fig. 153c).

Perhaps the most distinctive feature of the tadpole of *H. andersonii* is its short and narrow tail fin (Fig. 153c). This gives the tadpole a *Rana*-like appearance, or at least permits one to readily distinguish it from the tadpole of *H. versicolor*, or that of *H. arborea*. The question may be raised: is this reduced fin an adaptive feature? It may possibly be such, but the evidence at this time is by no means clear. The tadpoles of *H. versicolor* live for the most part in quiet, weedy ponds and these broad fins aid them to make quick turns very much in the same way that flattened or deep-finned fishes are able to dodge suddenly when avoiding an enemy. But let us look further. Most of the vertebrate inhabitants of the pond are deep-bodied or deep-finned. The ambystomid larvae have a back fin which undoubtedly serves them in their jerky dashes. A glance at a neighboring brook and we have a different picture. Here most of the forms have reduced the fin and have adopted better "stream lines." This is especially noticeable in the larvae of *Desmognathus* and *Eurycea*. The rule holds true for practically all mountain brook salamanders as *Rhyacotriton* in this country and many exotic genera. In the puddles of the slower streams we sometimes find the narrow-finned tadpoles of *Rana pipiens* or *Rana clamitans*. The comparison, however, between brook salamanders and brook tadpoles may not be drawn too closely. Frequently narrow-finned tadpoles occur in the ponds. It is interesting, however, that the tadpole of *H. andersonii* dwells primarily in the slow streams of the pine-barrens, and as if in adaptation to the current, it has given up its broad "pond life fin" for the sake of a more efficient one. We say "given up," for it seems probable from what has appeared above, that the species was evolved from a type having much the habits of *H. versicolor*. Whether or not we have pushed too far this comparison of brook salamanders and brook tadpoles, the fact remains that *H. andersonii* with its short fin has much more the habits of a *Rana* or a *Bufo* tadpole than it has the characteristic *Hyla* mannerisms (see below).

Metamorphosis first occurred at Lakehurst in the area under

FIG. 153. TADPOLES OF *HYLA ANDERSONII*.

a. The mouth parts of mature tadpole. *b.* Early tadpole, showing the conspicuous lymph sacs on either side of the snout. *c.* Mature tadpole, showing the characteristic pattern.

observation on July 23. None of the laboratory animals reached metamorphosis, probably because of our limited supply of bog water. Metamorphosis usually followed the day after the right fore-limb appeared. The left fore-limb appeared usually a day before the right limb. The spiracle became greatly widened to permit the passage of the left limb through it. The usual phenomena of metamorphosis occurred. The head widened, the mouth changed its shape and the body decreased in size. The head and body length (excluding the tail) of five tadpoles, having only the posterior limbs present, averages 13.1 mm., the head and body length of five others, having all four limbs present and the head already changed in form, averages 12.1 mm. Metamorphosing tadpoles became slightly greener in coloration but did not assume the full color of the adult while in the water.

DESCRIPTION OF A MATURE TADPOLE.

A tadpole is said to be mature at the time of the appearance of the hind limbs. In some forms this does not correspond to the full

development of larval characteristics. In *H. andersonii* the larval color pattern may or may not be complete at this stage. For this reason, we have utilized slightly older specimens in drawing up the following description. As is customary in the describing of adult batrachians, the detailed description is based upon a single typical specimen, the diagnosis upon several specimens.

Diagnostic Characters Spiracle sinistral, anus dextral, eyes visible from the ventral surface, upper fin crest not extending beyond the vertical of the spiracle, distance from spiracle to base of hind limb contained about 1.3 times in its distance from the snout; labial teeth $2/3$. Uniform brown above, yellowish on the tail, a conspicuous irregular stripe of dark brown extending the length of the tail. Greatest length of tadpole, 35 mm.

Detailed Description Length of body contained 2.6 times in the tail length; width of body 1.7 times in its own length; nostril nearer the eye than the tip (midpoint) of snout; eye dorso-lateral, visible in part from the ventral surface, nearer the snout than the spiracle; distance between nostrils contained 1.66 times in the interorbital width, exactly equal to the width of the mouth; spiracle sinistral, its distance from the base of the hind legs 1.29 times in its distance from the snout; anus dextral; depth of the muscular portion of the tail at its base contained 2.5 times in the greatest depth of the tail.

Upper labium with two series of teeth, a boundary row of teeth and an inner or lateral row on each side (Fig. 153a); the median space between these two lateral rows only a third the length of one of the lateral rows; three continuous rows of teeth on the lower labium, the second or median longest, the outer or boundary row slightly more than half as long as the median one; a complete circlet of papillae around the mouth, broken only for a short space along the upper median margin; a clump of papillae at either corner of the mouth, medial to the boundary papillae.

General color (formalin preservation) of the body, chocolate brown above, translucent below; tail yellowish; an irregular streak of dark brown running the length of the fleshy part of the tail just dorsal to the median line; lower border of the fleshy part of the tail irregularly spotted with a slightly paler brown; tail fin both above and below streaked or finely spotted with brown; the streaks sometimes forming irregular stellate figures but never a network.

In life the color pattern was the same, the brown and yellow tones of about the same intensity. The belly was very different.

It was golden, iridescent or whitish, according to the direction of the light. The throat was yellowish. The iris was golden, vermiculated with black; the black pupil was large and round. Some indication of internal structure visible, especially the nasal passage and two of the posterior cranial nerves. Lateral line system feebly indicated.

Measurements

Total Length.....	31.0 mm.
Greatest length of head and body	12.5 “
Greatest length of tail.....	18.5 “
Greatest depth of tail	7.5 “

HABITS OF THE TADPOLE.

Larvae raised in the aquarium and those studied in the field had similar habits. The larvae of *H. andersonii* are not active swimmers. At Lakehurst, these tadpoles seek out the shallows whether or not these be weed-grown. In such favored places, great numbers of tadpoles were found resting motionless just below the surface with dorsal crest touching the surface film. When approached they dived quickly into the nearest masses of sphagnum. Tadpoles of *H. andersonii* exhibited similar resting and diving behavior in the laboratory. No other tadpoles with which we are familiar make such erratic plunges into concealment.

Laboratory specimens ate some fish food (dried shrimp) and some of the water weed in their aquaria. They invariably skeletonized within a day any of their companions that died.

FOOD HABITS.

The food habits of *H. andersonii* are in no way specialized. This is to be expected since it has been shown elsewhere (Noble, in press) that the food habits of most tree frogs do not radically differ from those of frogs living near the water's edge. Frogs and toads seize anything of small size moving in their vicinity.

The stomachs of ten males which were captured during June while calling from bushes or low trees contained the following food: 5 grasshoppers (two species); 2 beetles, 3 ants (2 species), 1 dipterous insect, 2 dipterous pupae (tabaniid?), and some unidentifiable insect remains. None of the specimens taken in embrace contained

food in their stomachs, but only a few pairs were killed immediately after oviposition.

RELATIONSHIPS.

H. andersonii has been generally considered a close relative of the European Tree Frog. Long ago Cope (1889) said of *H. andersonii*, "in proportions and general appearance similar to *Hyla arborea* of Europe." Since then everyone who has had the occasion to consider the relationships of *H. andersonii* has agreed that the resemblance was very close. More recently, Barbour (1914, p. 239) has expressed the opinion that *Hyla pulchrilineata* of Santo Domingo was allied to *Hyla arborea*. We have recently had the occasion to study *H. pulchrilineata* in the field, and could find very little resemblance between these two species in either color, structural characters, voice, vocal-pouch, breeding habits, or in any other than generic characters. In a paper now in preparation, we have concluded that the two species are only distantly related.

As pointed out above, the object of the present paper is to describe those features of the habits and life history of *H. andersonii* which might shed light on its relationships. As no one has previously attempted to ally *H. andersonii* to any other species than *H. arborea*, it is important that we should first consider the resemblances and then the differences between the two species. Our information in regard to *H. arborea* is taken chiefly from Boulenger (1898).

Resemblances between *H. andersonii* and *H. arborea*.

1. General color and proportions.
2. Small size.
3. Many structural features,—as smooth skin, position of vomerine teeth, form of nuptial asperities, form of vocal pouch, etc.

Differences between *H. andersonii* and *H. arborea*.

1. Color pattern differs in many details of which the most noteworthy are as follows: the lumbar and the dorsal spots frequently found in *H. arborea* are never present in *H. andersonii*; the ground tone of *H. arborea* is subject to variation of color, of *H. andersonii*, to only a change of intensity; the details of coloration of thighs, throat and often the appendages differ remarkably in the two species.

2. Contracted pupil of *H. arborea* diamond-shaped; not so in *H. andersonii*.

3. Fingers slightly webbed in *H. arborea*; free in *H. andersonii*.

4. A strong odor of "raw peas" from *H. andersonii* after handling; no such odor from *H. arborea*.

5. A marked sexual dimorphism in *H. andersonii*; not so in the other species. In *H. andersonii*, as pointed out above, there is a difference between the sexes in the size, in the color on the sides of the throat, and in the ground tone of the throat. These differences do not appear in the several specimens of *H. arborea* before us. A breeding pair taken at Blois, France, measures 42 mm., total length in both sexes. A female of *H. arborea* from Germany measures 41 mm., while four non-breeding males from Germany measure 40.5, 40.5, 36.5 and 35 mm. respectively. Thus, there might be a slight difference in size between the sexes of *H. arborea*, but this difference is not constant. There seems to be no sexual dimorphism in *H. arborea* other than some indication of breeding asperities in the male, and sometimes a difference in size between the sexes.

6. The call of the two species is radically different. The following notes have been kindly given us by Dr. J. P. Chapin.

"In company with Dr. R. E. B. McKenny, at Blois, on the River Loire, France, during April, 1918, I found eight or ten individuals of *Hyla arborea* assembled just after dusk in a temporary pond in an open grassy field. Their notes, by which we were attracted, bore no resemblance to the voice of *Hyla andersonii*, with which I was very familiar; on the contrary, they produced a confused, hoarse, croaking chorus, which reminded me far more of the voices of common European toads. There was nothing of the curious nasal resonance of the "quank" of *andersonii*. The behavior of the individual frogs, too, was very different. They were all in the water while calling, not perched in bushes, as is usual with *andersonii*; and from the number of them in one or two small pools, I might describe them as far more sociable. In view of the striking external resemblance between *andersonii* and *arborea*, I was greatly impressed by the dissimilarity of their voices and actions."

7. The habitat of the two species differs greatly,—*H. andersonii* being confined to the pine-barrens, while *H. arborea* has a wide distribution in many types of country throughout Europe.

8. The breeding cites of *H. andersonii* are always shallow sphagnaceous streams or puddles on the pine-barrens, while

H. arborea selects "deep pools or ponds of clear water, more or less richly endowed with vegetation," (Boulenger, 1898, p. 258). Thus, *H. arborea* agrees with *H. versicolor* in the selecting of a breeding cite and differs remarkably from *H. andersonii*. Deep ponds are available to *H. andersonii* but it selects only the small pools.

9. Eggs of *H. arborea* are deposited "in several lumps, . . . attached to weeds below the surface of the water" (Boulenger, 1898, p. 259) Many more eggs are laid at one time by *H. arborea* than by *H. andersonii*, and these are adherent in the former species, not in the latter. From the form of the egg-masses, their attachment to weeds, and the number of eggs, it is apparent that the method of oviposition in *H. arborea* must be very unlike that of *H. andersonii*.

10. The external gills of *H. arborea* are "unbranched or bifid"; in *H. andersonii* there are only two pairs of gills, the posterior pair having two well developed branches, the anterior pair, three such branches.

11. The adhesive organs arise separately in *H. arborea*; in *H. andersonii* they develop from a crescent somewhat as in *Bufo*. The final position of the adhesive organs is more anterior in the former than in the latter species.

12. The mature tadpole of *H. andersonii* differs radically from that of *H. arborea* in the extent of its fin crest, and in its coloration both above and below. It also differs in having its eyes more dorsal and in having somewhat different proportions.

13. The mature tadpole of *H. andersonii* differs from that of *H. arborea* in its habits. It is a slow-moving form, accustomed to bask in the sun with dorsal fin in contact with the surface film. The description of the tadpoles of *H. arborea* given by Boulenger reminds us very much of *Scaphiopus* tadpoles for they are found "swimming about like fish in every direction."

14. Activity of the adults of the two species differ. *H. andersonii* does not stick well to smooth surfaces; when it climbs it frequently grips the branch with opposed fingers (Fig. 148h) and the feet wrap around the support. The movements of *H. arborea* agree well with the majority of hylas.

The above differences are far too numerous to be disregarded, for some of these differences are of considerable consequence. The resemblances between *H. arborea* and *H. andersonii* do not outweigh the differences. We have examined specimens of *H. regilla* which seem as nearly like *H. andersonii* as do some specimens of *H. arborea*. The resemblance in color pattern may be due to convergence, for Boulenger looks upon the spotted pattern as the more primitive and ancestral to the unspotted type, at least in the *H. arborea* group of forms. Further, Boulenger (1898, p. 252) considers that *Hyla immaculata*, described by Boettger, from China as a race of *arborea* "cannot be united with *H. arborea* . . . as it lacks the web between the fingers." *H. andersonii*, too, lacks the web between the fingers, and the question is immediately raised whether it might not be closely allied to *H. immaculata*.

It may be further pointed out that both botanically and herpetologically there are as good *a priori* grounds for seeking the ancestral stock of a form, at present restricted to eastern United States, not in western Europe, but in eastern Asia. *Cryptobranchus* and *Leiolopisma* are two striking examples of American forms having close allies in China. To this list we may now add *H. andersonii*.

CONCLUSIONS.

1. *H. andersonii* is not closely related to *H. arborea* nor to *H. pulchilineata*.
2. *H. andersonii* has been derived from a group of hylas which laid surface eggs, its method of oviposition being a modification of their method.
3. *H. andersonii* exhibits a primitive method of adhesive organ formation.
4. Voice plays an important rôle in the mating of *H. andersonii* and probably in other American tree frogs.
5. *H. andersonii*, by its coloration (including sexual dimorphism), method of oviposition, distinctive tadpole, and restricted habitat, occupies an isolated position among American species of *Hyla*.
6. The relationships of *Hyla andersonii* are to be sought in Chinese forms and probably in *H. immaculata* (Boettger).

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