MATING HABITS AND LIFE HISTORY OF AMPHIUMA TRIDACTYLUM CUVIER AND EFFECT OF PITUITARY INJECTIONS[1]

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INTRODUCTION

In view of the fact that so little is known of the mating habits of *Amphiuma tridactylum,* an attempt was made at the Reelfoot Lake Biological Station during the months of June, July, and August to study in detail something of their life history. Wolf (1929), Rugh (1934, 1935), and others have succeeded in inducing sexual reactions and ovulation in frogs by means of anuran anterior pituitary injections. The author felt that by using their methods on *Amphiuma tridactylum* she might induce sexual reactions, with possible attendant ovulation, and so observe more fully the more important phases of mating and ovulation and, at the same time, corroborate the work of the authors cited. The scarcity of the literature on the life history of these forms has lead the author to attempt to add new observations. She wishes to express her appreciation to M. V. Parker for the collection of the specimens used in this study.

DESCRIPTION OF AMPHIUMA TRIDACTYLUM CUVIER

Amphiuma, known colloquially as lamprey or lamp-eel, congo-eel, or congo snake, is the largest of the American salamanders. It is a semi-larval type belonging to the suborder Salamandroidea of the order Caudata (or Urodela). Many texts have erroneously grouped *Amphiuma* in the same family as *Cryptobranchus* because both have certain similar larval features, but they actually have arisen from very different stocks and have no close relationship (Noble, 1931). Ryder (1879) and Cope (1889) united into a single species *Amphiuma means* and *A. tridactylum* because they found no characteristics peculiar to any set of individuals. Noble and other modern herpetologists however, continue to list two separate species both found in the southeast as far west as Louisiana and Missouri. The author believes all *Amphiuma* taken from the Memphis and Reelfoot Lake regions are *A. tridactylum* and has so called them.

Amphiuma in general form is very much like the fresh water eel (Fig. 1). The body is elongate, cylindrical, and slightly depressed, the tail including approximately one-fifth of the entire length. The older the animal, the shorter is the tail in proportion to the body.

[1]Contributions from Reelfoot Lake Biological Station No. 12. The study here reported on was made possible by a grant from the Reelfoot Lake Biological Station of the Tennessee Academy of Science, to whom the author wishes to express her appreciation.

There is no obvious neck, but the body gradually narrows anteriorly ending in a rounded tip and a flattened projecting muzzle. The cornea of the lidless eyes is continuous with the skin and the nostrils are like pin holes. To quote from Cope:

> The lips are large and full; those of the upper jaw overhanging and concealing those of the lower except at the end of the muzzle. The lower lips commence on each side of the symphysis and are decurved over the integument of the ramus, from which they are separated by a deep longitudinal groove.
>
> In the premaxillo-maxillary series there are thirty-one teeth. The series terminates below a point posterior to the eye, and a little in front of the rictus oris. The vomerine series form an angle with the apex forwards. Their posterior end is nearly, but not quite, so far posterior as the extremity of the maxillary row. All the teeth are compressed, and their anterior edge is abruptly recurved towards the apex, so that the apex looks partly posteriorly. The posterior nares have a valvular opening, which looks backwards and outwards a little in advance to the extremity of the vomerine series, and nearer to them than the maxillaries. The tongue is represented by a muscular mass which occupies the floor of the mouth. It is only free laterally, being separated by a deep groove from the mandibular ramus. This groove is vertically divided by a membranous lamina for its entire length.

The color of *Amphiuma* is "a dark slaty brown above and a slaty color below." The skin is entirely smooth and slimy from mucous. Cope has made a detailed study of the location of the mucous pores. They are numerous and in rows in the head, but there are no distinct rows on the body. "The number of lateral dermal grooves is about sixty. . . . The segmental grooves are only distinct on the sides; on the belly they are indistinct and on the dorsal region they are entirely wanting.

"The branchial fissure . . . is bordered anteriorly and posteriorly by a narrow free membranous lamina. A short distance behind this is located the anterior limb." It is approximately one-half an inch long terminating in one, two, or three toes. The posterior limbs are about one-half again as long and are located slightly anterior to the vent or cloaca. The toes on these limbs vary also from one to three. The vent is a longitudinal slit with internal face densely pappillose (Fig. 1, *B*).

Of nine *Amphiuma* taken from Reelfoot Lake all but one had three digits on all limbs. The exception displayed only one digit on a single posterior limb, all others bearing the usual three. Two other specimens taken from the environs of Memphis were also tridactylate. Two females were of a dark brown cast above and light underneath. They average 28½ inches in length when caught and were much smaller in girth than the males. The smaller female was obviously still growing, although she was apparently mature sexually. When taken all males were nearly black with a light gray belly, but as the summer progressed, those to whom nothing was done of an experimental nature lost some of the black pigment; their backs assuming a dark gray or brownish cast. Average length was 32 inches at the beginning of the season. There are no external primary and secondary sexual characteristics apparent. The only way to determine

sex is to examine the cloaca. This is a slit approximately 1.9 cm. in length, with thin lips continuous anteriorly, but broken into three inconspicuous nodes on each side in the posterior region. The inside of the female cloaca is entirely dark, with the walls soft and somewhat folded in appearance. The inside of the male cloaca, on the

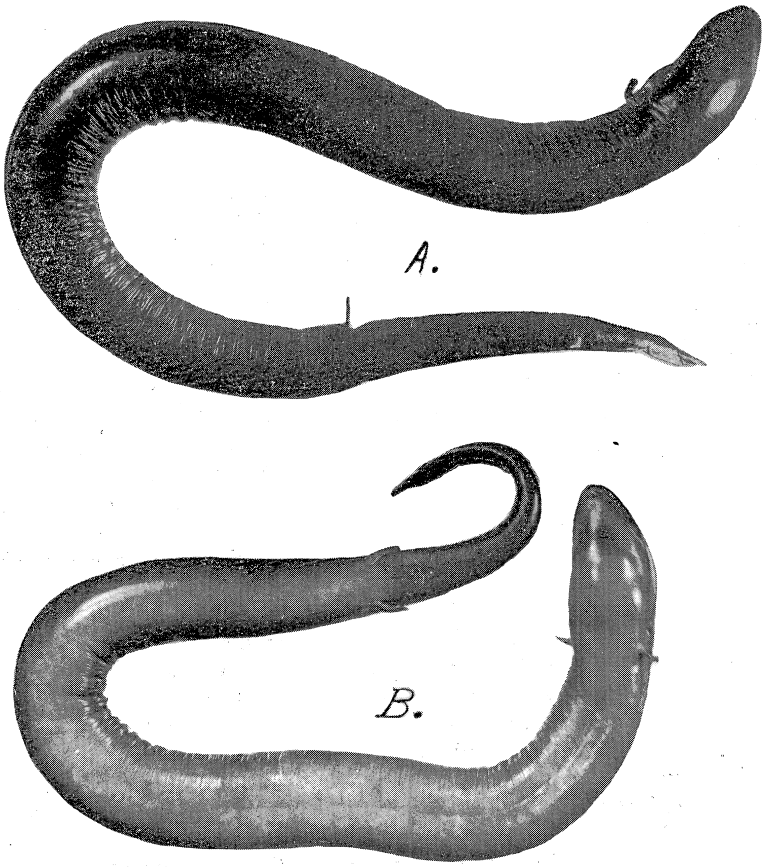

Fig. 1. Amphiuma tridactylum Cuvier. *A,* Dorsal view showing lateral dermal grooves, the flattened muzzle used in burrowing, the inconspicuous eyes and the branchial fissure just anterior to the fore limb which bears the usual three digits. *B,* Ventral view showing the projection of the upper jaw and overhanging lip which serves as an aid in burrowing. The thin-lipped cloaca is shown just posterior to the hind limbs.

other hand, displays a varying amount of white. It is usually white in the posterior end and has a small rather deep pocket in the dorsal roof. On the lateral walls may be seen the cloacal glands, oval, slightly rough patches having a white background with dotted lines of pigment. The pigmented dots appear to be much more numerous at the

base and along the sides of these oval patches. On spreading open the cloaca these lines may be seen to continue anteriorly along the roof of the cloaca, to curve medianly but terminate before meeting (Fig. 2, *C*).

Observations

In relating observations on a live *Amphiuma,* Hay (1888) noted a "shrill sound something like a whistle or the peeping of a young chicken." A sound of out-rushing air from the branchial fissures was noted several times during this investigation; it usually accompanied some change in the environment or some feeling of discomfort. This may be the "whistle" to which Hay referred. Once when an *Amphiuma* escaped during the night and crawled behind a bookcase it was located by this noise; again as one was tossed from its basin of water onto the muck in its cage it made this noise while still in the

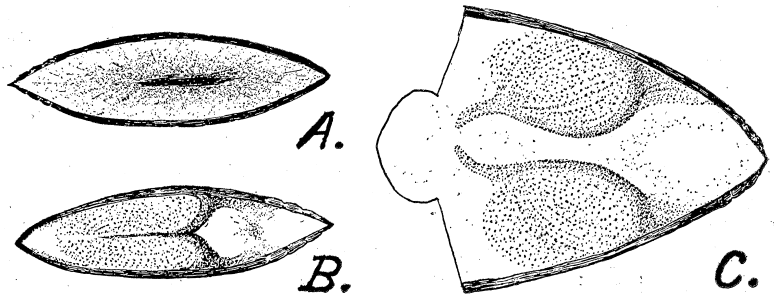

Fig. 2. The cloacal openings spread to show the differences in sexes. *A,* Female: dark with walls soft and somewhat folded in appearance. *B,* Male: white in posterior and with small pocket in the roof; cloacal glands are seen as densely pappillose oval patches on the lateral walls. *C,* Male cloaca with the anterior end cut to show the cloacal glands with dotted lines of pigment.

air. Still again when Amphiuma were first moved from aquaria to a new cage containing the muck this noise was noted as they pushed their way through the mud and seemed to seek for water.

Hargitt (1892) based his observations on a half dozen *Amphiuma means* placed in an aquarium with some fresh water clams.

> At first they were quite sluggish and seemed not at all disposed to be "at home" in their new surroundings. This was especially true of the adult. I found an empty clam shell one morning. . . . No sooner did a clam show signs of declining vitality by unusual gaping of the shell than it would be seized by one, often indeed by two, of the Amphibians, and there was seldom any release until the shell had been relieved of its occupant. The struggle which ensued when two of them would seize a single clam was exciting and amusing in the extreme. Such tugging, writhing, and twisting into perplexing coils one seldom sees, especially among members of this class.
>
> They were subsequently fed upon fresh meat from other sources, . . . but did not seem to thrive upon it, finally refusing to take it. They would

> take earthworms, but showed no disposition to take insect food. The young proved to be exceedingly voracious and . . . showed remarkable growth. The adult became more and more sluggish. . . . It moreover became quite ugly of disposition, and would bite savagely at anything within reach, even maiming itself.

When Hargitt's *Amphiuma* had been left a few days without food he "found that one of the more thrifty had turned cannibal and had half swallowed one of his less vigorous fellows." These attacks on each other occurred repeatedly when there was a shortage of fresh food. There was no evidence that they touch vegetation.

During the past summer observations were made constantly on eight adult *Amphiuma,* one of which was small and evidently still growing. Three or four more were under observation for brief periods only. For the first three weeks of June they were kept in aquaria in about three inches of water. During this time they refused all food offered, including liver, crayfish, worms, insects, and snail eggs. In the stomach contents of one newly caught was two small crayfish. Later the *Amphiuma* were removed to a cage containing muck and a large sink filled with water so that they might choose their environment. Here they ate crayfish readily in water. They usually fed at night, preferring crayfish under two inches, but would tackle much larger ones if the small size was not forthcoming. They also ate the few clams found at Reelfoot Lake, waiting until they opened partially as Hargitt has already described. About the middle of July crayfish became exceedingly scarce, but the *Amphiuma* refused all substitutes. After several weeks some of them consented to eat ten gram chunks of liver. The smallest animal proved to be the most voracious eater. During this lean period one adult became exceedingly irritable. Hay gives a brief but graphic picture of such a nasty disposition: "On irritating this Amphiuma by pushing her with a stick she would snap at it viciously and on further irritation would seize it in her jaws, and springing from the floor in the form of a spiral, would turn rapidly round and round, thus twisting the stick from one's hand. Any enemy thus attacked would certainly find his interest in the affair fully aroused." The present author's interest was indeed "fully aroused" when one attacked her forefinger in such a manner. The wound was deep, painful, and bled profusely, but it healed rapidly and without infection, thus disproving the belief of the residents at Walnut Log that the bite of the *Amphiuma* is deadly. The same *Amphiuma* later turned cannibal as did those of Hargitt's and was killed. *Amphiuma* form the favorite food of the stinging or mud-snake (*Farancia abacura*) (Meade, 1934). Two fights between *A. tridactylum* and *Farancia* were witnessed this summer near the biological station. Unfortunately witnesses terminated the encounters before it could be determined which was the victor.

Like the four-toed salamander (Blanchard, 1934), the female *Amphiuma* remains with her eggs. The return of the mother to her nest

after having been frightened away has been witnessed (Noble, 1931). Hay relates his experience in finding an *Amphiuma* nest as follows:

> At the close of August, 1887, I spent a few days in Little Rock, Arkansas, in the employ of Dr. Branner, of the Arkansas Geological Survey. On September 1 I visited a cypress swamp for the purpose of collecting some reptiles. During the severe summer drought this swamp had been almost completely dried up and there was little chance to get anything except by turning over pieces of fallen timber. Beneath a log of considerable size I found to my surprise a large animal coiled up, which by its glistening skin I immediately saw could not be a snake; but having never before seen a living Amphiuma, it took me some time to realize that I had before me one of these animals. After making due preparation to prevent its escape I gave the animal a push with a stout stick, and then, no attempt at retreat being made, I lifted it out of the slight depression in which it was lying and let it straighten itself out. Meanwhile I had observed lying in the midst of the coils a mass of moist looking matter, nearly as large as one's fist. Picking this up, I discovered it to be a mass of eggs. This was put into a jar of alcohol and immediately the young within the egg could be seen writhing about, thus showing that they were in an advanced stage of development.
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> The eggs of the Amphiuma are the most remarkable that I know of as occurring among the Amphibians. The young, which now constitute the whole contents of the eggs are surrounded by a transparent capsule about as thick as writing paper, and these capsules are connected by a slender cord of the same substance. It is as if the gelatinous mass surrounding the eggs of a toad should become condensed into a solid covering and a connective cord. How many strings there are of these eggs I cannot determine with certainty, on account of their being inextricably intertwined; but since there are four ends visible, there are probably two strings, one for each oviduct. For the same reason I have not been able to count the eggs. A careful estimate makes at fewest 150 of them.
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> The eggs in their present state are nearly globular and average about 9 mm. in diameter. Their distance apart on the string varies from 5 to 12 mm.; fourteen of them were counted on a piece of string 9 inches long. At this rate the whole mass would form a string about 8 feet long. The connecting cord varies from 1.5 mm. to one-half that diameter. The eggs greatly resemble a string of beads.
>
> The young are coiled within the capsules in a spiral form. On removing them and straightening them they measure about 45 mm. in length. The color is dusky above, with indications of a darker dorsal stripe, and on each side a similar dark band. Below the color is pale. The body is proportionally stouter than in the adult and the head broader. The fore and hind feet have each three toes.
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> The young possess conspicuous gills; and since they are evidently near the period of hatching, it is but fair to suppose that they would continue to retain these gills for some time after extrusion. The gills are three in number on each side, and are simply pinnate in form. The median gill is longest, measuring some 9 mm. in length. From the main axis there arises about ten delicate twigs. The other gills are somewhat shorter, and give origin to about eight lateral twigs each. In all these filaments may be seen the blood vessels filled with the large blood corpuscles for which Amphiuma is noted. Three gill-slits are open of which the two posterior become closed in the adult. The eyes appear to have better advantage than later in life.

No nests were found this summer, but one resident claims to have found in August of 1935 an *Amphiuma* curled up with her eggs under a large log near the water's edge. Another said he had found a bunch

of eggs under one end of a log while the *Amphiuma* was at the other. This latter find was during "cotton picking time" which would be in September or early October in this locality.

Eight *Amphiuma,* two females and six males, were under observation for several weeks during the summer. Their cage was made to simulate as nearly as possible their natural habitat. On a three by six foot table a cage approximately 18 inches high was constructed. In one end was sunk an 18 x 24 inch basin, the remainder was covered with sheet tin and on this was spread muck from the bayou varying in thickness from three to six inches. In one end was placed large flat stones, along one side a log and a large piece of bark near the other. Plants found along the edge of the bayou were transplanted around the rim of the basin. Within a few days the *Amphiuma* seemed to feel quite at home. They were apparently unalarmed at being handled and ate crayfish readily.

The methods and technique of Rugh (1934) were followed as closely as existing circumstances and materials allowed. Injections of suspensions of pituitary gland in water or 10 per cent alcohol were made through a large needle into the peritoneal cavity. Pituitaries of sexually immature *Rana catesbiana,* averaging 4 inches in length, and anterior lobes of catfish (locally called bullheads) averaging 15 inches were used. Alcohol suspensions were made of one female or two male frog anterior lobes to 1 cc. of 10 per cent alcohol, and one catfish anterior lobe to 2 cc. of 10 per cent alcohol. One injection of antuitrin-S and one *Amphiuma* anterior lobe were also administered intraperitoneally. A summary of the injections given to the *Amphiuma* during the course of the experiments is given in Table 1.

Injections of pituitary seemed to have no marked effect on normal courtship reactions in either males or females. During eleven days (June 28 to July 8 inclusive) an increased interest in burrowing in the muck was manifest. The *Amphiuma* burrowed long pathways during the night wanderings and came out of water occasionally during the daytime. The following six days (July 9 to 14) five *Amphiuma* —three uninjected males, M5, M8 and M6, and both females—showed a marked preference for land. There was no difference in the actions noted between F1, the injected female, and F2 which was left untouched; one chose a burrow under a large flat rock, the other a place along the side of a log. The same male was usually found with the same female; occasionally one female would be found in the same burrow with two males (Fig. 3). There seemed to be no rubbing motions nor other obvious courtship procedure and no definite positions assumed by male and female in their burrows. On the third day of this land phase smears showed sperm present in both female cloacas but none in any of the males; the cloacal glands of the three males that came out on land were swollen and the sides and roof of the cloacas were very vascular. The other three males, M3, M4 (both injected), and M7 (untouched), did not show cloacas with swollen glands until four days later. These three remained in water entirely and at no

time were they observed in a burrow with a female. This seeming suppression of sexual activity could hardly be due to the reaction from the anterior pituitary injections because an untouched *Amphiuma* behaved similarly to the two injected ones. The interest in land of the five previously mentioned diminished rapidly and within two days all had taken to the water again and showed no further interest during the ensuing summer and fall months. A cloacal smear of one of the

TABLE 1

Summary of pituitary injections in Amphiuma

Time of Making Injections	Total Amount and Kind of Material Injected
F1:*	
Jun. 21—Jul. 5†	Six male plus seven female Rana catesbiana whole pituitary
Jul. 18—Jul. 25	Four female Rana catesbiana anterior lobes
July 27	One half catfish plus one half Rana catesbiana anterior lobes
Jul. 30—Aug. 4	Two and one half catfish anterior lobes
M3:*	
Jun. 26—Jul. 7	Five male plus twelve female Rana catesbiana whole pituitaries
Jul. 25.—Aug. 4	Four and one half catfish anterior lobes
Aug. 14	One and one half cubic centimeters antuitrin-S
Aug. 16	One male Amphiuma anterior pituitary lobe
M4:	
Jul. 5—Jul. 7	Six male plus one female Rana catesbiana whole pituitaries
Jul. 17—Aug. 4	Twenty-two male Rana catesbiana anterior lobes
M5:	
Jul. 5—Jul. 7	Water was injected as a control‡
Jul. 17—Aug. 4	Ten per cent alcohol was injected for a control
M6:	
Jul. 23—Aug. 4	Three catfish anterior lobes

*The F stands for female and M for male. The numbers after these letters are the numbers of the individual animals used in the experiment; thus F1 stands for a female animal—the one numbered one in the experiment— and M3 stands for another single animal—a male—numbered three.

†The injections were evenly spaced over the time of injection and were usually made daily. Where used, the whole pituitary was macerated in water. Where the anterior lobe was used it was macerated in ten percent alcohol.

‡Three animals: F2, M7, and M8 had no injections whatever.

females showed quantities of sperm six weeks after the first smear, but by November 15 none were apparent.

Noble and Richards (1930) were able to induce ovulation out of season in the salamanders, *Eurycea bislineata* and *Desmognathus fuscus auriculatus,* with homoplastic implants. It is possible that some positive results might have been obtained in the work on *Amphiuma* during the summer had enough material been available for homoplastic

injections. Since this was not the case, however, and since Adams (1930, 1931) was able to induce ovulation by frog and toad pituitary grafts in the urodele, *Triturus viridescens,* it was decided to use young *Rana catesbiana* pituitary of which there was an unlimited supply.

Both F1 and F2 failed to lay eggs. That this failure on the part of F1 is connected in any way with pituitary injections is questionable. F2 was relatively small, she escaped several weeks later before an autopsy was performed; failure on her part was possibly due to immaturity. However, it seems more logical to assume that the eggs were resorbed because the environment was not conducive to egg-laying although every effort was made to simulate a natural breeding ground. Resorption in Axolotl has been shown possible. Buyse and Burns (1931) mention a case in which a limited number of eggs were

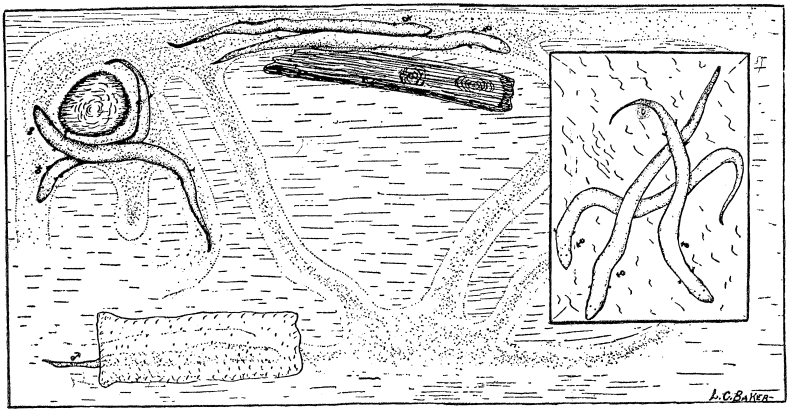

Fig. 3. Sketch showing the eight Amphiuma in burrows and water during "courtship week." The same three males always remained in the water. One female chose a place in a burrow behind a log, the other a burrow under a large stone in the corner of the cage (stone removed thereafter). The same male was usually found with the same female. Sometimes the odd male was seen in a burrow with a pair but usually he retreated to a place under a large piece of bark as shown

laid as a result of a first series of injections and after later injections, besides fresh eggs, some clumps of resorbing ova were found which were evidently left in the uterus from previous injections. Catfish have been found to resorb their eggs simply because rocks were not placed in the aquarium under which they might spawn (Breder, 1935).

The *Amphiuma* did not have a winter supply of food stored in the body as in the case of frogs used by Rugh, but injections were given at a time when they were eating crayfish readily. *Amphiuma* M3 was fed large amounts of liver previous to antuitrin-S and *Amphiuma* pituitary injections, yet spermatophores were not produced. This negative response is contrary to the findings of Ogilvie (1933) who did

succeed with Axolotls by injections of .2 cc. antuitrin-S twice daily under the skin for 4 to 6 days.

The possibility of immaturity of donors in cases of frog pituitary injections causing failure is unlikely because Stein (1935) found that young chick pituitary implants, if sufficient numbers are made, will cause ovulation out of season in *Triturus viridescens*. Rugh (1934) states that "recent observations on the frog suggest that the pituitary of immature female frogs is at least as potent as that of mature female frogs and may be more potent in relation to induced ovulation out of season."

Some idiosyncracy of Amphiuman physiology might be said to explain their negative response to heteroplastic implants and the investigations of others tends to add strength to this suggestion. Wills, Riley and Stubbs (1933) succeeded in inducing ovulation in the toad (*Bufo americanus*) by implantation of four garpike hypophyses daily

TABLE 2

Some growth relations of injected and non-injected Amphiuma

Sex and Number of Specimen	June 7	July 16	August 16	November 15
	cm.	cm.	cm.	cm.
F1*	75.0	82.6	89.0	88.3
M3	83.8	94.0	96.6	96.6
M4		81.3	86.4	83.5
M5		80.1	82.0	83.0
M6		90.3	87.0	
F2	70.0	77.5	76.3	
M7	81.3	85.2	85.2	
M8		78.8	84.5	84.7

*For the details of the experimental treatment of these animals, see Table 1

for two to six days but failure to obtain ovulation in the toad using rat hypophysis implants may be due, as he suggests, to specificity between the two groups or to a destruction of the hormone of implanted gonads by host as a result of incompatibility of tissues and subsequent reactions. Sachs (1930) failed to produce metamorphosis in *Proteus, Siren,* and *Amphiuma* by feeding and injection experiments with thyroid and thyroid extracts—even though this is easily accomplished in *R. catesbiana* and *Eurycea bislineata* (Noble, 1931). Adams (1931) was successful in inducing ovulation in frogs with toad pituitary, but not in toads with frog pituitary. She suggests lack of sensitivity or neutralization of these hormones by body fluids or secretions in toads, in the latter case, rather than "zoological specificity." Creaser and Garbman (1936) were unable to cause ovulation in *R. pipiens* with implants of fish pituitary or injections of beef anterior lobe, sheep pituitary, pregnant mares serum and human pregnancy urine. They conclude that "it appears that there is an interspecific variation in the

gonadotrophic hormone—," and suggest that "—if the mechanism of non-action or inactivation of gonadotrophic substances is understood, it will offer further information as to the nature of these hormones." Kuyper, Pheiffer, and Wills (1933) failed to induce ovulation in toads with hebin (the maturity hormone of pregnancy urine) and concludes that this hebin does not contain the active maturity principle of anterior lobe of the hypophysis of toads.

There is also the possibility of not having administered enough fish and frog pituitary to induce the sexual reactions in *Amphiuma* although M4 received twenty-two bull-frog pituitaries in nineteen days. Wills (1933) *et al.* used a much larger number of garpike pituitaries to secure results in a much smaller animal.

Faulty technique which might have prevented the pituitary from being injected into the peritoneum through struggles of the animal could not have been responsible for negative results because the effects of the pituitary was shown by the darkening of the abdomens of F1 and M3 in which cases the posterior pituitary was injected along with the anterior portion. Klatt (1933) found that implantation of intermediate and posterior lobes of pituitary produce melanophore reaction in *Triton* larvae. Blout (1932) also concluded that extra pituitary tissue brings about an increase in pigmentation in the urodele embryo due to melanophore expansion and the accumulation of chromatophoric pigment. In addition the growth rate of injected *Amphiuma* was accelerated. From June 7 to August 16 all *Amphiuma* were kept under approximately the same conditions and the average increase in size of the injected specimens was 5.24 cm. more than the average increase in the uninjected specimens. From August 16 to November 15, during which time no pituitary injections were made, there occurred a slight decrease in size of the formerly injected *Amphiuma* and no appreciable growth in the uninjected ones. Since the number of experimental animals used was insufficient to warrant any definite conclusions in regard to influence on growth rate of pituitary injections, these experiments must be continued on a much larger number of animals.

Summary

1. *Amphiuma tridactylum* from Reelfoot Lake is described and compared with the descriptions given by other investigators. Reelfoot Lake specimens largely agree with the descriptions given in the literature.

2. Specimens in captivity were observed to give a sort of whistle when in distress or introduced into a new environment. This is apparently caused by an outrush of air from the branchial fissure, since they have no voice.

3. Specimens in captivity ate clams, crayfish and meat.

4. Eggs are laid in August under logs on land. They are in the form of a rosary. The female remains with the eggs.

5. In the laboratory, there seemed to be a "courtship week" in early July, during which time Amphiuma left the water, burrowed in the muck and mated in these burrows. After this period, they returned to the water and apparently lost all interest in land.

6. Anterior pituitary injections were made in the laboratory in attempts to induce sexual reactions or ovulation, but with negative results. Before any definite conclusions can be drawn, experiments must be conducted on a larger number of animals and with other types of pituitary material.

7. The color change of the abdomen after injections is probably due to injection of some of the posterior lobe of the pituitary along with the anterior lobe. This change in color is due to melanphore expansion.

8. Specimens injected with anterior pituitary lobe showed accelerated growth. This may be due to the pituitary injection.

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