With the compliments
S. C. Bishop.

New York State Museum Bulletin

Published by The University of the State of New York

No. 268 ALBANY, N. Y. May 1926

New York State Museum

NOTES ON THE HABITS AND DEVELOPMENT OF THE MUDPUPPY

Necturus maculosus (Rafinesque)

BY

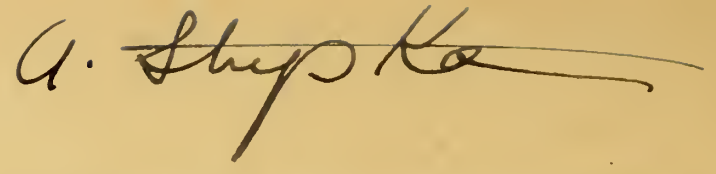
SHERMAN C. BISHOP

CONTENTS

	PAGE
Introduction	5
Distribution of Necturus	6
Habitat	6
General habits	8
Food	9
Locomotion	9
Respiration	9
Reaction to light	10
Mating habits	10
The egg-laying season	12
The nests of Necturus	14
The brooding habit	16
The egg and its envelops	17
Attachment of the eggs	17
Segmentation and gastrulation	18
Late embryonic development	18
Larval growth and development	20
Color pattern	21
Development and reduction of the larval gills	26
Yearly growth and development	27
Necturus, 1st year	27
Necturus, 2d year	28
Necturus, 3d year	29
Necturus, 4th year	30
Necturus, 5th year	30
Necturus, 6th year	31
The adults	31
Size	31
Form	32
Color	32
Sexual differences	33
Glands of the skin	34
Abnormalities	36
Bibliography	36
Explanations of plates	39

ALBANY
THE UNIVERSITY OF THE STATE OF NEW YORK
1926

M216r-F26-1000



THE UNIVERSITY OF THE STATE OF NEW YORK

Regents of the University
With years when terms expire

1934 Chester S. Lord M.A., LL.D., *Chancellor* - Brooklyn
1936 Adelbert Moot LL.D., *Vice Chancellor* - - - Buffalo
1927 Albert Vander Veer M.D., M.A., Ph.D., LL.D. Albany
1937 Charles B. Alexander M.A., LL.B., LL.D., Litt. D., - - - - - - - - - - - - - - - Tuxedo
1928 Walter Guest Kellogg B.A., LL.D., - - - Ogdensburg
1932 James Byrne B.A., LL.B., LL.D. - - - - New York
1931 Thomas J. Mangan M.A., LL.D. - - - - - Binghamton
1933 William J. Wallin M.A. - - - - - - - - Yonkers
1935 William Bondy M.A., LL.B., Ph.D., D.C.L. - New York
1930 William P. Baker B.L., Litt.D. - - - - - Syracuse
1929 Robert W. Higbie M.A. - - - - - - - - - Jamaica
1938 Roland B. Woodward B.A. - - - - - - - Rochester

President of the University and Commissioner of Education

Frank P. Graves Ph.D., Litt. D., L.H.D., LL.D.

Deputy Commissioner and Counsel

Frank B. Gilbert B.A., LL.D.

Assistant Commissioner and Director of Professional Education

Augustus S. Downing M.A., Pd.D., LH.D., LL.D.

Assistant Commissioner for Secondary Education

James Sullivan M.A., Ph.D.

Assistant Commissioner for Elementary Education

George M. Wiley M.A., Pd.D., LL.D.

Director of State Library

James I. Wyer M.L.S., Pd.D.

Director of Science and State Museum

Charles C. Adams, M.S., Ph.D., D.Sc.

Directors of Divisions

Administration, Lloyd L. Cheney B.A.
Archives and History, Alexander C. Flick M.A., Litt. D., Ph.D.
Attendance, James D. Sullivan
Examinations and Inspections, Avery W. Skinner B.A., Pd.D.
Finance, Clark W. Halliday
Law, Irwin Esmond Ph.B., LL.B.
Library Extension,
School Buildings and Grounds, Frank H. Wood M.A.
Visual Instruction, Alfred W. Abrams Ph.B.
Vocational and Extension Education, Lewis A. Wilson

New York State Museum Bulletin

Published by The University of the State of New York

No. 268 ALBANY, N. Y. May 1926

New York State Museum

NOTES ON THE HABITS AND DEVELOPMENT OF THE MUDPUPPY

Necturus maculosus (Rafinesque)

BY

SHERMAN C. BISHOP

INTRODUCTION

The mudpuppy, Necturus maculosus (Rafinesque), has been known to science for more than a hundred years. It is one of the largest salamanders, widely distributed and extremely abundant in many localities. The life history, habits and development have been investigated by a number of workers and recently considerable attention has been given to experimental work in endocrinology. A review of the literature, however, reveals a lack of exact information concerning certain phases of development and growth and habits of both the young and the sexually mature.

The material and notes on which this study is based have been accumulated chiefly during the past 3 or 4 years but the mudpuppy has been an intimate acquaintance for a much longer period. The writer has collected the species in various parts of New York and northwestern Pennsylvania and has had for study some specimens from North Carolina and Canada. Altogether several hundred specimens have been handled. The abundance of the material used in determining the rate of growth and the age of specimens is revealed to some extent in the tables of measurements given in the body of the report.

This account is not concerned with the segmentation of the egg or with gastrulation and early formation of the embryo, although some references to the literature of these phases are included for the convenience of those interested. It deals particularly with the

late embryonic stages, the posthatching period of rapid development, the growth of the species to sexual maturity and the habits of both young and adults.

The writer is greatly indebted to Paul A. Webb of Meadville, Pa., for the use of much material not otherwise available to him, for help in collecting and measuring specimens and for much information concerning habits; to Professor Barnard S. Bronson of the State College for Teachers and Hugh P. Chrisp of Albany, N. Y., who made possible, by the generous use of their automobiles, many profitable field excursions. The drawings have been prepared by W. J. Schoonmaker, assistant to the Zoologist, and E. J. Stein assisted very materially by making several photographs.

THE DISTRIBUTION OF NECTURUS

The range of Necturus maculosus as established by Stejneger and Barbour[1], is as follows: "Tributaries of the Great Lakes, the Mississippi River system, the upper Hudson River, and Lake Champlain. Rivers of North and South Carolina, Georgia and Alabama."

HABITAT

The ability the mudpuppy has to exist in waters of extremely diverse character and to compete successfully with the enormous number of animals with which it is associated, accounts in large part for its wide distribution. The Great Lakes and their tributaries harbor them by thousands. They persist in certain of the Finger Lakes in New York in spite of intensive collecting over a period of many years. Not only are they found in the clear open waters of lakes and streams where the character of the bottom prevents plant growth, but also in shallow weed-choked bays and streams and in the perennially muddy and polluted waters of creeks, rivers and canals. They are common in the Hudson and Mohawk rivers near Albany and in the turbid Mississippi; in waters ice-bound months at a time and in the tepid streams of some of the southeastern states; in shallow, rapid streams with rocky beds and in deep, slow streams with mud banks and bottoms; and in canals, reservoirs and backwaters. In the north they are most numerous and reach their best development in clear streams and lakes.

The mudpuppy is not always found in the same part of a stream or lake at all seasons of the year. There is evidence of certain

[1] Stejneger, Leonhard and Barbour, Thomas. A Check List of North American Amphibians and Reptiles. Cambridge. 1923. 2d ed. p. 1.

movements or migrations which are controlled to some extent by the breeding habits; and the sexually mature animals are able to live where it is probable the young would not long survive. In muddy streams the species is known chiefly from adults taken by fishermen, the character of the environment precluding an intimate acquaintance with the eggs and larvae. It is probable that the adult females living in such a habitat find it necessary to move into shallower tributary streams for the egg-laying period. Even in clear streams some segregation occurs and the young ones are sometimes found in numbers where the adults are absent.

Necturus is so eminently successful in the clear tributaries of the Allegheny in northwestern Pennsylvania and the adjoining counties in New York that one of these streams, Woodcock creek in Crawford county, Pennsylvania, may be described somewhat in detail to present a typical stream habitat. The creek rises in the eastern part of the county and flows westward to join French creek near Saegertown. In its lower reaches it crosses wide meadows among low hills and the course is marked by many shallow riffles (plate 1). Over considerable stretches bedrock forms a pavement which is strewn with flat stones and small boulders. These areas alternate with the gravelly riffles and deeper pools of quiet water. Any large flat stone lying on the surface or partially imbedded may serve as a hiding place for the mudpuppy. Food is abundant. Crawfish, larvae and nymphs of aquatic insects, and small fish seek the shelter of the stones which often conceal Necturus. Earthworms are carried into the streams with every rain. Small mollusks occupy the crevices between the rocks and attach themselves to the lower surface of stones.

The mudpuppies are in competition with the common creek fishes, suckers, chubs and minnows of various species, and with Cryptobranchus which is present in considerable numbers. Among its enemies must be reckoned the older individuals of its own species which have become addicted to the egg-eating habit. Cryptobranchus also takes the eggs of Necturus but probably not in great numbers. Herons and crows frequent the shallows and may be expected to take the smaller individuals when opportunity offers. Small, white, parasitic worms attach themselves to the surface of the skin of the mudpuppy and leave their marks in the shape of irregular whitish patches which persist for a considerable time. Finally the water mold, Saprolegnia, attacks both eggs and animals.

GENERAL HABITS

The mudpuppy is preeminently aquatic notwithstanding the statements of Smith[1], DeKay[2] and Holbrook[3] that occasionally it comes out on land. Aquatic animals of any kind, even fishes, will sometimes rush out of the water and pay for the venture with their lives. It is essentially nocturnal in clear streams and shallow waters of lakes, but in muddy waters and in weedy streams and bays it is more or less active throughout the day. In the muddy Clyde river the writer has taken it at all hours while fishing with hook and line. In the early spring it is particularly voracious and is often taken by hundreds. Fishermen in general regard it as poisonous, and the usual procedure in freeing a specimen is to cut away the hook, crush the head of the beast and throw it on the bank to die. Milner[4] gives the following account:

A fisherman at Evanston, Ill., a few years ago had nine hundred hooks set in the lake, and in one day took from these five hundred lizards, removing them all himself, as his men, sharing the popular notion on the lakes, believed them to be poisonous and preferred to cut away hook and all to taking hold of the slimy amphibian.

In the fall the sexually mature are found in pairs and small groups in situations that offer good nesting sites for the females. The young of the year and a few older individuals may sometimes accompany them but not in considerable numbers. While the adults are on the breeding grounds the sexually immature may often congregate in the deeper waters of larger streams. Here they hide beneath the flat stones of the bottom, and individuals of all ages from 1 to 4 or 5 years may occupy the same retreat. In late August, 1925, in one of the larger tributaries of the Allegheny, young of various ages were found in water varying in depth from 18 inches to 2 feet; but not one adult was found at this locality during 10 days of active collecting. In the shallower waters of lesser tributaries the adults were occupying every suitable retreat.

Necturus is more or less active throughout the year; early writers, however, reported them only in certain seasons. Kneeland[5] remarks:

These animals are rarely if ever seen, except during the winter; those I obtained were sucked up through the pumps for the supply of the water for the copper stamps; they are never thus caught in the summer or autumn. They change their skin at this season; . . .

---

[1] Smith, I. U. Isis. 1832. p. 1088.
[2] DeKay, J. E. Zoology of New York, pt. 3. 1842. p. 87.
[3] Holbrook, J. E. North American Herpetology, 2d ed. 1842. 5:113.
[4] Milner, J. W. Rep't U. S. Commission of Fish and Fisheries. 1874. p. 62.
[5] Kneeland, Samuel. Proc. Bost. Soc. Nat. Hist. 1857. 6:153.

The reason why they approach the shore at this season may be on account of this change in the skin and possibly for breeding purposes.

Holbrook[1] in his brief account of the habits says: "The Menobranchus maculatus is seldom taken, except in the months of April and May, which is their spawning season."

Morse[2] says: "The Mud-puppy may be found often under the ice in the coldest winters."

Food

The natural food of Necturus consists of fish, fish eggs, crawfish, aquatic insects and their larvae and worms. Hay[3] adds mollusks to the diet. In captivity earthworms and raw liver are sometimes eaten. The abundance of Necturus in lakes and streams and its habit of eating eggs marks it as an enemy of certain fishes. Milner[4] gives the following account which has been widely quoted:

Mr George Clarke, of Ecorse, Mich., had a minnow-seine fitted to the bag of a sweep-seine, and at one haul took two thousand of the "water lizards." Estimating the extent that the net passed over, he calculated the average number of lizards to each square rod to be four. He says, further, in one of the Detroit papers, "The lizards were so gorged with white-fish spawn that when they were thrown on the shore, hundreds of eggs would fly out of their mouths."

Locomotion

Mudpuppies swim with strong lateral undulations of the body, the legs being held against the sides. In walking or crawling over the bottom the diagonally opposite legs move together.

Respiration

In poorly aerated water or in water warmer than that to which the animal is accustomed, the gills are kept in constant motion. In clear, cold, well-aerated water they are often held motionless for long periods against the sides of the neck. Under such conditions the blood supply is restricted, the bright crimson fades to a dull ruby red and the animal is quiet. When the oxygen supply of the water is low the animal at frequent intervals rises to the surface, gulps in a mouthful of air and again sinks to the bottom. Part of the air thus obtained passes out through the gill clefts and the remainder, in some instances at least, is taken into the lungs. The skin also functions in respiration and is well supplied with blood,

[1] Holbrook, J. E. North American Herpetology, 2d ed. 1842. 5:113.
[2] Morse, Max. Proc. Ohio State Acad. Sci. 1904. 4:107.
[3] Hay, O. P. 17th Ann. Rep't Ind. Dep't Geol. and Nat. Res. 1892. p. 419.
[4] Milner, J. W. Rep't U. S. Commission of Fish and Fisheries. 1874. p. 62.

particularly in the region of the tail[1]. Judging by the actions of animals under the conditions outlined above, it seems probable that the skin alone may furnish the necessary oxygen in well-aerated water, that the gills are used under ordinary stream and lake conditions and that the lungs are called into service as a last resort.

When a living specimen is exposed to the air, complete drying of the skin is prevented for a considerable time by a copious production of slime which pours out of the dermal glands and completely envelops the body. The animal gasps for breath but in the course of a few hours dies, the lungs alone being unable to furnish sufficient oxygen. In water, however, the animal may live without apparent discomfort with the gill filaments entirely lost.

Reaction to Light

Reese[2] found that all parts of the body of Necturus were sensitive to light, the head especially when the light was directed from above. When the source of the light was below the body, the tail seemed to be the most sensitive. Eycleshymer[3], experimenting with decapitated larvae, found them negatively phototropic, particularly when the light was directed on the tail. Pearse[4] also found Necturus negatively phototropic, blinded as well as normal individuals responding to stimuli.

In aquariums both larvae and adults seek the shaded areas. In a large storage tank containing several hundred individuals it was possible to drive the specimens from one end of the container to the other by the use of an ordinary hand flashlight.

MATING HABITS

Those who attempt to pry into the intimate affairs of secretive animals find the way beset with difficulties. Necturus is no exception to the rule. Dawson[5] writing in 1922 says:

At present the mating habits of Necturus are not definitely known. Strong circumstantial evidence indicates (Kingsbury '95) that fertilization is accomplished by the deposition of spermatophores and the reception of the spermatozoa which are borne upon the summits of the deposited spermatophores into the cloaca of the female. The time and exact manner of insemination are not known. . . . . Al-

---

[1] Dawson, A. B. Jour. Morph. 1920. 34:517.
[2] Reese, A. M. Biol. Bul. 1906. 11:96.
[3] Eycleshymer, A. C. Jour. Comp. Neur. and Phychol. 1908. 18:303; Anat. Anz. 1914. 46:11.
[4] Pearse, A. S. Proc. Amer. Acad. Arts and Sci. 1910. 45:168.
[5] Dawson, A. B. Jour. Morph. 1922. 36:447.

though our information on the time and manner of fertilization is still incomplete, it seems highly probable that spermatophores are produced by the male Necturus.

The dissections of both Kingsbury and Dawson prove internal fertilization and strongly indicate an autumnal mating period. Fertilization might be accomplished either by direct transfer of sperms in a venter to venter copulation or by means of spermatophores deposited in water. Dawson[1] inclines to the view that spermatophores are deposited.

In Kingsbury's important paper[2], "The Spermatheca and Methods of Fertilization in Some American Newts and Salamanders," some results of studies of Necturus are given. Spermathecae in the cloaca of females collected in fall and winter were found to contain active sperms. The habits of Necturus were little known at the time, however, and it was impossible to determine whether the sperms were acquired in an autumnal mating without ovulation or had simply been held over after ovulation in spring or fall. It is now known that ovulation occurs in the spring, and evidence is here presented to show that autumnal fertilization is the usual procedure.

In the fall of 1922 or 1923, Paul A. Webb placed a pair of mudpuppies in a large aquarium. The male manifested considerable interest in the female and behaved somewhat after the manner of the male newt, Triturus viridescens. The female received the attentions, held herself erect by supporting the body on the hind legs and tail and made no attempt to escape. The male swam and crawled around the female and frequently passed over the tail and between the legs. This performance was continued for a considerable period. An actual venter to venter copulation was not observed nor were spermatophores noticed in the aquarium. Unfortunately no record was kept of the exact date of the occurrence. These observations indicate that courtship may be a mating procedure as in Triturus and others. In the case of the newt the eggs are laid in the spring following a strenuous courtship on the part of the male. In the fall the male newt again goes through his mating antics, develops the horny excrescences on the toes and thighs and deposits spermatophores; but, so far as known, the female deposits no eggs. With Necturus the autumnal mating alone takes place. The female newt tolerates the actions of the male in the fall, the female Necturus actively participates. There is no longer the need of a spring mating

[1] Dawson, A. B. Jour. Morph. 1922. 36:447.
[2] Kingsbury, B. F. Tran. Amer. Micros. Soc. 1895. 17:261–304. pl. 1–4, figs. 1–19.

and no evidence of it. When the females are on the spawning grounds males are rarely if ever found in the immediate vicinity. The vent of the male is swollen and inflamed in the fall; it is nearly normal in the spring. Eycleshymer[1] has called attention to the segregation of the females during ovulation in the following words: "During egg-laying the males are never found with the females and where they remain is unknown." Spermatophores are doubtless formed, but whether they are deposited as in Triturus viridescens, Ambystoma maculatum and other species or taken up in contact copulation has not been determined. I have often observed, in preserved specimens, that males taken in the fall have the vent filled with a clear gelatinous mass. This is sometimes extruded and hangs at the orifice of the vent. I have not found spermatozoa within the mass, however. Kneeland[2] as early as 1857 kept Necturus through the winter and observed at times the deposition of gelatinous masses. This is suggestive of the spermatophores of Ambystoma maculatum, particularly the clear basal parts on which the sperms are deposited in whitish masses.

THE EGG-LAYING SEASON

Water temperature plays an important role in initiating ovulation in any particular region. For this reason it is impossible to make general statements concerning the egg-laying period without a study of conditions in many widely separated regions and in waters of various character.

In shallow waters of streams and lakes the season may be much earlier than in deeper bodies in the same latitude. Other conditions being equal, the season should be earlier in the southern part of the range of the animal than in northern waters.

In northwestern Pennsylvania the egg-laying season begins early in June when the water temperature near the surface of shallow streams is about 74 to 78 degrees F.[3] In the nests themselves, usually shallow cavities beneath flat rocks, the temperature is probably a few degrees lower. In 1924 the first fresh eggs of the season were found on June 5th. In 1925, June 5th again marked the beginning of ovulation and fresh eggs were found as late as June 11th. Eggs deposited June 5th began to hatch July 13th, a period of incubation of 38 days. The period of incubation is also of variable length depending on water temperature, and no hard and fast lines

[1] Eycleshymer, A. C. Amer. Nat. 1906. 40:134.
[2] Kneeland, S. Proc. Bost. Soc. Nat. Hist. 1857. 6:154.
[3] The temperatures were obtained by Paul A. Webb.

may be drawn. Conditions in a lake habitat are summarized by Eycleshymer as follows:[1]

The time of egg-laying varies in different lakes, depending upon the time when the temperature of the water reaches a certain degree. In the larger, deeper lakes with bold shores this is much later than in those possessing wide shoals. Again, in individual lakes the time is dependent upon the same conditions. The eggs are first deposited in those localities, where the water is shallow and exposed for the greater part of the day to the sun. The period of egg-laying usually covers two or three weeks.

Eycleshymer collected eggs as early as May 3d and as late as June 5th, and these extremes probably marked the beginning and closing of the early and late seasons.

Smith, reporting on conditions in Lake Monona, Wis., writes:[2]

A noticeable feature of the development as compared with other amphibians that I have studied, is the uniformity in the stage of development of embryos found in different nests in the same locality. On each of the following dates from four to seven nests were secured: June 22, 25, 29, July 5. On each date all the eggs were found so nearly in the same stage of development that only slight differences could be detected in eggs from different nests. This uniformity points to a very short spawning season—perhaps two or three days—in this locality; it would seem that all the eggs in a restricted area are laid at nearly the same time.

The writer has studied Necturus in northwestern Pennsylvania in streams tributary to the Allegheny and in general his observations on the length of the spawning season agree with those of Smith. As noted above, in 1925 the period covered 7 days. It has also been shown, however, that the water temperature was relatively high and that the streams were shallow. In deeper, colder waters there is every reason to believe the period of general deposition may start later in the season and that individuals may consume considerable time in depositing a single batch of eggs. On June 6, 1924, Paul A. Webb found a female in the process of egg-laying. Transferred from the warm waters of the stream to a tap water aquarium in the laboratory the process was resumed, but with a water temperature of from 62 to 66 degrees F. an entire day was consumed in depositing about a dozen eggs.

Eycleshymer found eggs in various stages of development in the same nest. Smith reported great uniformity in the stage of development of eggs in different nests in the same locality. The observations of both were probably accurately made. A sudden lower-

[1] Eycleshymer, A. C., Amer. Nat. 1906. 40:132.
[2] Smith, B. G. Biol. Bul. 1911. 20:193.

ing of water temperature might slow down or prevent for a short time the deposition of the eggs and account for the unequal development. There is another possibility though perhaps more remote. A single nest was found which contained 180 eggs. This number is considerably above the average and may represent the complements of two females.

Holbrook[1], who had little first-hand knowledge of Necturus, gives April and May as the spawning season and remarks that as many as 120 eggs have been counted in a single female. Eycleshymer[2] found 62 eggs in a single nest and a total of 117 eggs in three nests. Eycleshymer's figures are much below the average for the species and represent only one-third or one-half of the normal complements of full grown individuals.

THE NESTS OF NECTURUS

Smith, again reporting on conditions in Lake Monona, Wis., found nests in water from 3 to 5 feet deep and about 50 to 100 feet from shore where the bottom was strewn with loose flat stones. The larger stones frequently served as shelters for the nests. It is pointed out in this account that the water was so filled with minute algae that the bottom could not be seen and eggs were found by lifting stones to the surface. This is significant as will be shown later in the account of the brooding habit in Necturus. "The number of eggs present in a nest was determined in five cases as follows: 18, 61, 80, 84, 87. The average is 66."[3] The lower numbers certainly do not represent the full complement of a normal female. In three nests examined in Woodcock creek, Pennsylvania, the eggs numbered respectively 87, 96 and 140. The average of these is about 107. Paul Webb counted the eggs on several occasions and found that they numbered from 90 to 180 to a nest. If a female is disturbed during ovulation she may move to another spot and start over again. If she is robbed of her eggs she may continue to deposit in the same nest or move to another. I have found Cryptobranchus occupying a despoiled nest of Necturus. Embryos in nests in the immediate vicinity were in early stages of development so that the larvae could not have hatched and departed. Eycleshymer[4] found several nests in which the animals were distended with eggs and

---

[1] Holbrook, J. E. N. Amer. Herpetology, 2d ed. 1842. 5:113.
[2] Eycleshymer, A. C. Anat. Anz. 1904. 25:234.
[3] Smith, B. G. Biol. Bul. 1911. 20:191.
[4] Eycleshymer, A. C. Amer. Nat. 1906. 40:135.

inferred that the parent had devoured them because the nest had been disturbed. Smith[1] also discussed the nests of Necturus in a stream habitat but the account concerned the discovery of empty egg capsules in August. Eycleshymer[2] wrote of nests of Necturus in a lake habitat as follows:

The objects beneath which the eggs are most frequently found are clean logs or boards which lie partially imbedded in the sand. The writer has also found them beneath pieces of tin, canvas, and even an old hat.

The depth of the water in which these nests are found is variable. The writer has found nests covered by only 4 inches of water, again a nest was found beneath a board at a depth of 10 feet, but these are unusual conditions. The majority of nests are found at a depth of from 2 to 4 feet. The nests are often found in close proximity to one another; and it is not at all exceptional to find several nests on a single board frequently not more than a foot apart. In one instance ten nests were taken from a single board not more than ten feet long.

In northwestern Pennsylvania the writer has found nests in water varying in depth from a few inches to 2 feet. The "nests" themselves are shallow excavations beneath large flat stones partially imbedded in the stream bottom. Occasionally the stones lie almost on the surface but when imbedded there is usually a down stream entrance. They are commonly found near the rifts but not in the fastest water. The males are never found with the females on the spawning grounds. While the females are in the shallows with their eggs, the males occupy the deeper pools of quiet water. At least this is the situation in streams in northwestern Pennsylvania.

Necturus exercises less care in the selection of a retreat than Cryptobranchus but in some instances there was evidence that a considerable amount of material had been removed from the nest. In the writer's experience with Cryptobranchus it has been found that the male selects the nest site and prepares it for the female. With Necturus the female alone is found on the spawning grounds and is probably responsible for the selection of the site and its preparation.

The lower surface of the stone or board which forms the covering of the nest is the surface to which the eggs are attached. The eggs may be scattered over an area 12 inches or more in diameter or crowded together in a space only 6 or 8 inches square. The eggs are deposited one at a time and are attached by a circular, disk-like

[1] Smith, B. G. Biol. Bul. 1911. 20:193–94.
[2] Eycleshymer, A. C. Amer. Nat. 1906. 40:133–34.

expansion of the outer envelop, some 5 or 6 mm in diameter. There is a slight constriction below the attachment disk when the eggs hang in natural position buoyed up by the water but this lengthens to a slender stalk when the support to which the eggs are attached is lifted above the surface (plate 2).

THE BROODING HABIT

Smith[1] in part 1 of his paper on the embryology of Cryptobranchus remarks (p. 88): "The brooding habit seems to be lacking in Necturus." Again, in part 2 of the same report (p. 552) Smith says: "The absence of a brooding habit in Necturus is noteworthy." As pointed out in an earlier paragraph, Smith's studies of the nests of Necturus were carried on in Lake Monona, Wisconsin, where, "The presence of minute algae, etc., in the water made it so opaque that it was impossible to see the bottom; the eggs were obtained by wading in the water, feeling about with the feet for a large flat stone, then bringing it to the surface." Smith found only the empty egg capsules in a stream habitat in northwestern Pennsylvania and these were discovered in August, perhaps a month after the young had hatched. In a note on "The Breeding Habits of Salamanders and Their Bearing on Phylogeny," Dunn[2] writes, "Necturus lays non-pigmented eggs with large vitellus which are abandoned in the water."

In the writer's studies of Necturus a considerable number of nests have been found and in every instance the eggs were guarded by a female. These nests were in the clear, shallow streams of Crawford county, Pennsylvania, where it was possible to capture and examine the guardian parent. The females were found in nests with eggs in all stages of development and in nests in which the young were escaping from the egg capsules. The brooding habit is so well established that the female often makes little effort to escape when the sheltering rock or board is removed from the nest. With Cryptobranchus the male guards the nest and is usually found either among the eggs or under them. The female Necturus simply occupies the shallow retreat and is not in contact with the eggs except as her back may brush them as they hang from the support. She is not a particularly good guardian, however, for in one nest containing a large spent female a small Cryptobranchus 8½ inches long was found. Eggs had been deposited in the nest as indicated by the rings of jelly marking places of attachment on the under side

[1] Smith, B. G. Jour. Morph. 1912. 23:88.
[2] Dunn, E. R. Copeia, no. 115. 1923. p. 27.

of the stone. In the business of stealing eggs Necturus itself is not guiltless. The writer has several times found them in the nests of Cryptobranchus where the guardian male was so busy with enemies of his own sex and species that he had little time to devote to the smaller invaders.

THE EGG AND ITS ENVELOPS

Surrounding the egg or embryo is a thin, tough and elastic membrane enclosing a jelly-like substance which may be slightly milky. A second thin layer, clear and transparent, incloses the first. The outer layer is much thicker, of jelly-like consistency and extremely elastic. The egg itself has a diameter of 5 to 6 mm, the inner envelop about 7 mm, the next outer layer about 8 mm. The short diameter of the outer envelop is about 11 mm and the long or vertical diameter (as the egg hangs in natural position) about 14 mm. Smith[1] gives details of the structure of the egg capsule in the following terms:

There are three layers to the gelatinous envelop: (*a*) a comparatively thin but very dense inner layer, consisting of several lamellae; (*b*) a thicker median layer of moderate density, consisting of many lamellae; and (*c*) a very thick outer layer of homogeneous material, much less dense than either of the preceding. This outer layer is produced to form a stalk by which the capsule is attached to some solid support.

The writer has not observed the lamellae composing the two inner envelops. They are not at all evident in some early embryo material preserved in formalin, and the middle envelop as shown in Smith's figure (1912 p. 80, fig. 4) is much thicker and denser than in my specimens. Freshly laid eggs are yellow, the color usually light but varying in intensity in different lots.

ATTACHMENT OF THE EGGS

Concerning the deposition of the eggs Eycleshymer remarks:[2] "In just what manner the female deposits the eggs is . . . problematic. . . . In some way the female brings her body in such a position that the eggs are deposited on the sheltering object." Just how this was accomplished in one instance is shown in the figure here presented (plate 3). The female mentioned in an earlier paragraph, discovered in the act of laying her eggs, was transported to the laboratory where the process was continued. A large flat

[1] Smith, B. G. Jour. Morph. 1912. 23:79.
[2] Eycleshymer, A. C. Amer. Nat. 1906. 40:134.

stone supported on smaller stones provided a suitable "nest." The female turned herself upside down and supported her body with the toes of the front feet resting against the edge of the stone. This position she maintained for hours and deposited about a dozen eggs in the course of a day. The position assumed by this female is exactly that which might be expected in view of the disposition of the eggs; and it is no doubt the position taken by Eurycea bislineata, Pseudotriton ruber, Gyrinophilus danielsi and others which attach the eggs to the lower surface of a support in water.

SEGMENTATION AND GASTRULATION

The early cleavage stages in the egg of Necturus are discussed by Eycleshymer[1] in his paper on, "Bilateral Symmetry in the Egg of Necturus." In an earlier paper[2] the same writer gave an account of a series of puncture experiments on Necturus eggs and discussed briefly the early formation of the embryo. A few late embryo stages and an early larva are figured by Keibel[3]. Smith[4] gives drawings and photographs of the eggs and figures to show the late history of the blastophore and late cleavage stages.

LATE EMBRYONIC DEVELOPMENT

In 1925 the egg-laying season of Necturus in Woodcock creek, Crawford county, Pennsylvania, began on June 5th and continued without interruption through June 11th when the last fresh eggs were noticed. On June 21st a considerable number of embryos were transferred to the laboratory of Paul A. Webb for the study of late stages. On this date and thereafter at intervals of a few days specimens were preserved in formalin. About two hundred embryos were preserved on each of the dates given below:

	Incubated	*Period before hatching*
June 21st	16 days	22 days
June 25th	20 days	18 days
July 3d	28 days	10 days
July 13th	38 days	Hatching

Nests left undisturbed in the streams were also watched and on July 13th while hatching was well under way, several thousand

[1] Eycleshymer, A. C. Anat. Anz. 1904. 25:230.
[2] Eycleshymer, A. C. Anat. Anz. 1902. 21:341.
[3] Keibel, Franz. Die Kultur der Gegenwart, sec. 3, div. 4, v. 2, pt. 2. 1913. p. 346.
[4] Smith, B. G. Jour. Morph. 1912. 23:80, fig. 4, pl. 2, figs. 55–56; p. 480, figs. 107–08, pl. 10, figs. 268–79.

young were collected and transferred to open, shallow containers in the laboratory. These collections have furnished abundant materials for the study of late embryo and early larval development; and the results obtained have been checked against fresh material secured in the field.

June 21, 1925, 16 Days Old, 22 Days Before Hatching

The average length of the embryos at this stage is 14.8 mm. Eycleshymer[1], who watched the development of embryos through the hatching period, recorded the first indication of pigment in embryos 11 to 12 mm long. In specimens of that size the pigment appeared as small black dots well imbedded in the semitransparent connective tissue. In the specimens here considered there is a slight but definite development of chromatophores at the surface, enough pigment being present to give a light tinge of color to the dorsal surface of the head and trunk. The chromatophores are most abundant on the head and gradually thin out towards the tail (plate 4, figure 1). The position of the eyes is indicated by a slight development of tissue.

The buds of the gills are elongate, set in an oblique row and in some instances provided with one or two short branches. The buds of the fore legs are low rounded protuberances; those of the hind legs are not as well developed but perfectly evident in most specimens. They appear as rounded humps at the base of the tail. There is distinct evidence of metameric development on either side of the mid-line of the back. The yolk hangs as a deep broad keel so that the depth of the body is equal to about one-third of the length. The tail where it extends beyond the trunk comprises about one-fifth of the total length.

June 25, 1925, 20 Days Old, 18 Days Before Hatching

The average length of the embryo at this stage is 16.9 mm. The depth is 4.6 mm. The chromatophores are much more numerous at the surface and are distributed not only over the head and trunk but extend laterally over the upper surface of the yolk, distally almost to the tip of the tail and on the sides of the head to the base of the gills. In some specimens the eyes are not only indicated by development of tissue but by a slight concentration of pigment. The gills are longer and slimmer and provided with two or three short filaments. The buds of the fore legs have elongated considerably

[1] Eycleshymer, A. C. Anat. Anz. 1914. 46:7.

and are directed backward and upward. The buds of the hind legs show little advance. There is a marked growth of the tail and tail keels and the back is more strongly arched than in the earlier stage. Tissue concentrated in the region of the vent indicates rapid development of the posterior end of the intestinal canal. The tail now comprises almost one-fourth of the total length but the bulk of the body is still in the yolk (plate 4, figure 2).

July 3, 1925, 28 Days Old, 10 Days Before Hatching

Specimens at this age average 19.2 mm with the tail 5.7 mm. The pigmentation is more intense and extends over the upper sides of the yolk and to the extremity of the tail. On the head the pigment extends well over the snout and slightly below the lower margin of the eyes. In this stage there is no evidence of segregation of pigment to form the bands which are so conspicuous in older individuals. The eyes are so developed that the iris and pupil may be distinguished. The superficial chromatophores, which marked the position of the eyes in the stage preceding this, have for the most part disappeared and the iris is colored by more deeply imbedded pigment. The gills bear short filaments in two rows. On the under side of the head there is a transverse groove which starts below the eyes, follows the contour of the snout and marks the position of the developing mouth. A slight but definite swelling in the throat region is followed by a second transverse groove, the gular fold. The nostrils are evident just below the eyes on the ventral surface of the head. There is little advance in development of leg buds. In some individuals, however, the buds of the fore legs are more elongate and slightly constricted at the middle. The yolk mass is still large but not as prominent because of the lengthening of head and tail (plate 4, figure 3).

LARVAL GROWTH AND DEVELOPMENT

July 13, 1925, Larvae at Hatching, Length of Incubation Period, 38 Days

Plate 5, figure 1

The average length of twenty larvae picked at random from a lot collected in the field and preserved on the day of hatching is 22.5 mm. This does not accord with the measurements of Smith[1] who obtained an average length of 18 mm. The discrepancy may possibly be explained: If the eggs are removed from the place of attach-

[1] Smith, B. G. Biol. Bul. 1911. 20:195.

ment, the envelops are more or less ruptured and permit, in many cases, the premature escape of the embryo. We have guarded against this possible source of error by collecting the larvae in the field at the time of hatching.

The measurements tabulated below indicate a variation in length of 4 mm in the different individuals.

21.0 mm	22.0 mm	22.5 mm	23.0 mm
21.5	22.0	22.5	23.5
21.5	22.0	22.5	24.0
21.5	22.0	23.0	24.0
21.5	22.0	23.0	25.0

The extremes of 21 and 25 mm probably mark the limits of variation in length at hatching.

The lot from which the measured specimens were taken furnished some two hundred additional individuals having a length of 22 mm.

At hatching the gills are provided with two rows of filaments, the terminal ones considerably elongated and flattened. The toes of the front feet are evident as four short, pointed branches. The toes of the hind feet are scarcely differentiated but the hind legs themselves show some advancement in their greater length. The eyes are well pigmented and apparently functional at hatching. The mouth, lips, nostrils and gular fold are well formed. The yolk is still conspicuous and colors the sides and ventral region between the fore and hind legs. The tail shows marked development and comprises about four-elevenths of the total length. The dorsal keel proper originates at a point above the insertion of the hind legs and is continuous with a slightly raised ridge which runs along the mid-dorsal line of the back to a point above the fore legs.

Color Pattern

A very narrow light line follows the sharp edge of the dorsal ridge. A strongly pigmented median dorsal band originates on the snout a little in front of the eyes and continues along the back and on the tail where it fades out towards the tip. On the head it maintains a width about equal to the distance between the eyes but just behind the gills it narrows abruptly. The dark dorsal band is bordered on each side by a somewhat narrower yellow band which in this stage is free from dark pigment. These light bands originate opposite the base of the third gills and continue along the upper part of the sides and the basal third of the tail where they are usually lost in the general pigmentation of the upper tail fin. On the head the dark median area is bordered on either side by a short light bar which originates in front of the gills and passes to

the upper margin of the eye. In some individuals it narrows above the eye and continues to the snout.

Below the lateral light bands are the conspicuous dark stripes of the sides, extending from the gills to the tip of the tail. They are continued on the head in bands that curve downward in front of the gills, pass through the eyes and run together on the snout. Below the dark bands the pigment gradually fades out as it spreads over the yolk distended abdomen, the upper surface of the limbs and the gill branches. In some individuals there are a number of small, rounded light spots quite regularly spaced throughout the length of the lateral dark band.

Besides those preserved at the time of collection, July 13th, a considerable number were placed in formalin solution on each of the following dates:

	No. of days after eggs were laid	*No. of days after hatching*
July 16th	41	3
July 18th	43	5
July 21st	46	8
July 23d	48	10
July 27th	52	14
Aug. 3d	59	21
Aug. 7th	63	25
Aug. 20th	76	38
Aug. 23d	79	41
Aug. 27th	83	45
Aug. 30th	86	48

July 16, 1925, 41 Days Old, 3 Days After Hatching

The measurements of twenty-five specimens preserved three days after hatching are tabulated below:

24.0 mm	24.0 mm	25.0 mm	25.0 mm	25.5 mm
24.0	24.5	25.0	25.0	25.5
24.0	25.0	25.0	25.0	26.0
24.0	25.0	25.0	25.0	26.0
24.0	25.0	25.0	25.0	26.5

The average is 24.9 mm with extremes of 24 and 26.5 mm, a variation of 2.5 mm. There is a noticeable advance in development of the gills and toes, a slight reduction of the yolk and a considerable increase in the intensity of the pigmentation (plate 5, figure 2). The lateral light bands of the body stand out in strong contrast against the dark longitudinal bands and are now almost continuous with the light bars of the head which pass above the eyes. On the tail the light bands are still confined to the basal third. The ventral keel of the tail remains unpigmented but a few scattered chromatophores fleck the sides of the abdomen. The change in the gills is brought about through the lengthening and flattening of the fila-

ments, the terminal pair in particular being longer than the others, somewhat constricted at the base and pointed distally.

July 18, 1925, 43 Days Old, 5 Days After Hatching

Measurements of twenty specimens are given:

25.0 mm	25.5 mm	26.0 mm	26.0 mm
25.0	25.5	26.0	26.0
25.0	26.0	26.0	26.5
25.5	26.0	26.0	26.5
25.5	26.0	26.0	27.0

The average length is 25.8 mm with the range from 25 to 27 mm. On this date it was possible to select from the general collection about two hundred individuals each 25 mm long.

During this period of 2 days the slight increase in length of gill filaments and the more intense pigmentation are about the only features worthy of note.

July 21, 1925, 46 Days Old, 8 Days After Hatching

Twenty specimens give the following measurements:

25.0 mm	26.0 mm	26.5 mm	27.0 mm
25.0	26.0	27.0	27.0
25.0	26.0	27.0	27.0
25.5	26.0	27.0	27.0
26.0	26.5	27.0	27.0

Here again the variation is from 25 to 27 mm, but the average of 26.3 mm shows a gain in length of .5 mm in the three-day period.

July 23, 1925, 48 Days Old, 10 Days After Hatching

Measurements of a considerable number of individuals on this date show scarcely a gain in length but the gills at this time are provided with filaments which are longer, slimmer and more flattened. The toes of the hind feet show as separate members, the fourth shortest. The dark longitudinal bands are very dark in life and stand out in strong contrast against the lateral light lines. The latter are continuous on the trunk and head and extend in some instances one-half the length of the tail (plate 6, figure 1).

July 27, 1925, 52 Days Old, 14 Days After Hatching

Two weeks after hatching, twenty larvae measured:

26.5 mm	27.0 mm	27.0 mm	27.5 mm
26.5	27.0	27.5	28.0
26.5	27.0	27.5	28.0
26.5	27.0	27.5	28.0
27.0	27.0	27.5	28.0

The average is 27.2 mm, with extremes of 26.5 and 28 mm, a gain of 4.7 mm in 2 weeks.

August 3, 1925, 59 Days Old, 21 Days After Hatching

The twenty larvae measured:

27.0 mm	27.5 mm	28.0 mm	28.0 mm
27.0	27.5	28.0	28.5
27.0	28.0	28.0	28.5
27.0	28.0	28.0	29.0
27.0	28.0	28.0	29.0

The average is 27.8 mm, with variation from 27 to 29 mm. Another lot of fifteen individuals hatched July 15–18th and measured 21 days later, averaged only 26.6 mm. It is evident that there is some variation not only among individuals hatched from the same batch of eggs but between different lots or series of specimens.

The larval color pattern is almost completely established at this age and the following description from life will indicate, to some degree, the character of its development. Under the microscope the median dorsal band is grayish brown and extends from a point just back of the nostrils to the tail, where it involves only the dorsal fin. To the unaided eye the color appears very dark, almost black. The dorsal band is bordered on either side by the narrower light line, yellowish white, with irregular edges. These light lines originate above the nostrils, pass just above the eyes and continue along the sides of the body and on the tail, one-third or one-half its length. The light lines are usually interrupted or broken just above the gills. Below the light lines the dark bands of the sides pass along the sides of the snout, through the eyes and continue to the tip of the tail. The color is grayish brown, like the dorsal stripe, but darker. The sides below the dark lateral bands are distinctly greenish gray, flecked with yellow in small, rounded spots. The color of the lower sides fades into the distinctly yellow belly.

The sides of the head below the eyes are yellowish flecked with gray; the throat is dirty white except where colored by the heart, and the lips are slightly pigmented. The ventral tail fin is light gray. The gills are beautifully developed, two rows of flattened filaments to each branch and all of a delicate pink color. The fore legs are provided with four well-formed toes; the hind legs are held out at a right angle to the body but have the toes only slightly developed. The yolk occupies the abdominal region but there is little distention of the wall.

August 7, 1925, 63 Days Old, 25 Days After Hatching

The average length at this age is 29.5 mm. The extremes are 29 and 30 mm for the series measured (plate 6, figure 2).

At about this age the larval development of the gill filaments reaches its highest point. Thereafter there is a gradual shortening of the filaments and they take on a more regular arrangement. The full development of the larval gills is discussed under a separate head in a later paragraph.

August 20, 1925, 76 Days Old, 38 Days after Hatching

By August 20th an average length of 33 mm had been attained. The lateral light stripes are continuous over the gills and extend on the tail almost to the tip. Both dorsal and lateral dark stripes have, in some instances, a few small, round yellow spots. Below the lateral bands the sides of the abdomen are strongly spotted. The extreme upper margin of the dorsal tail fin is largely free from pigment and a few chromatophores speck the ventral fin. The toes of all feet are well formed. There is a marked shortening in the gill filaments.

August 23, 1925, 79 Days Old, 41 Days After Hatching

For a considerable period after August 20th specimens were preserved at intervals during which an average increase in length of 1 mm had been attained. On August 23d the length was 34 mm. The following description from life will indicate the changes in the color pattern: The median dorsal band is sharply defined and dark but there is an increase in the number of small, rounded spots which are free from pigment. This band extends to the tip of the tail and colors the dorsal fin except at the extreme upper margin. The lateral light bands coalesce on the snout in front and continue along the body to the tip of the tail where they are more or less broken by intrusions of pigment from the mid-dorsal band. The lateral dark bands meet on the snout, continue through the eyes and along the trunk to the tip of the tail. These bands are greenish gray and darker than the dorsal stripe. The sides below the lateral bands are mottled with yellowish white spots. The belly, particularly the posterior half, is still colored by the yolk. The chin has a considerable number of chromatophores present and a few are scattered over the belly. The legs and feet are strong and well pigmented above.

August 27, 1925, 83 Days Old, 45 Days After Hatching

On this date some two hundred individuals were selected which had an average length of 35 mm. There are no striking changes in the color pattern.

August 30, 1925, 86 Days Old, 48 Days After Hatching

Length 36 mm. The yolk mass is confined to the posterior half of the abdomen and is much reduced. The gill filaments also show marked reduction.

The increase in length of larvae during the eight day period following hatching is greater than that attained during the next 17 days. Thereafter the growth is slower, coincident perhaps with the reduction of the yolk.

DEVELOPMENT AND REDUCTION OF THE LARVAL GILLS

Plate 11, figures 1–6

A series of drawings has been prepared to illustrate some of the changes that take place in the development of the larval gills. Figure 1 represents the gills at the time of hatching. The filaments are short, pointed, almost straight and disposed in two rows. The terminal pair are broader than the others and considerably flattened. A few chromatophores are present at the base. Development is rapid and the condition in a larva 3 days after hatching is shown in figure 2. The gills are larger and the filaments longer and quite slender. The condition 10 days after hatching is shown in figure 3. There is a notable increase in the size and length of the filaments. The terminal filaments consist of a pair of broad, blunt pointed, flattened plates and the others show some advance. The gills reach their highest development about 25 days after hatching and thereafter there is a gradual shortening of the filaments (figure 4). Figure 5 shows the condition 38 days after hatching. The filaments have been reduced and present a comb-like appearance but the gill itself is stouter and wider in proportion to its length than in preceding stages. During the next 10 days there is little change in the appearance except in the increased pigmentation (figure 6).

The rapid growth of the filaments and their subsequent reduction are phases of development through which the larvae of true salamanders pass during growth and transformation. The facts are significant and should receive some attention when relationships of Necturus are considered. If the length of the gills is compared to the length of the head it will be found that the maximum size is attained at about 3 weeks and again at sexual maturity. During the intervening years the growth is exceedingly slow.

YEARLY GROWTH AND DEVELOPMENT

With the material at hand, it is possible for the first time to give definite measurements to show the annual growth of Necturus maculosus to sexual maturity. The data tabulated below give the results of measurements of specimens taken at one locality on French creek, Crawford county, Pennsylvania, between August 20 and 30, 1925. For the past three years eggs of Necturus at this locality have hatched between July 13th and July 25th. The measurements therefore represent a little more than the annual increments of growth, that is, specimens regarded as a year old are actually about 13 months old.

Necturus, First Year

Plate 7, figure 1

49.0 mm	52.5 mm	55.5 mm	60.0 mm
50.5	52.5	56.5	60.0
51.0	53.0	57.0	60.0
51.0	53.0	57.5	60.0
51.0	54.0	57.5	60.5
51.0	54.0	58.0	60.5
51.5	54.0	58.5	63.0
51.5	54.5	59.0	63.0
52.0	55.0	59.0	63.0
52.5	55.0	59.5	63.0
52.5	55.5	59.5	64.0

The average length of these forty-four specimens is 56.1 mm. Thirty-nine of the lot varied in length only 11.5 mm, or from 49 mm to 60.5 mm. The specimens falling within these limits may safely be regarded as yearlings. The five remaining specimens are 63 and 64 mm in length. Judged by length only, these five specimens might be regarded either as well advanced yearlings or stunted two-year-old specimens. In general, however, the two-year-old specimens are decidedly more robust and as these specimens are slender, they are probably individuals hatched early in the season and fortunate in their food supply. The extreme variation in length in specimens one year old is 15 mm.

At the age of one year the larval pattern is still well developed but the median dorsal band instead of being dark gray or almost black is definitely yellowish brown. In the majority of specimens the dorsal band ends abruptly at the origin of the dorsal tail keel; in others it continues to color the fin to the extremity of the tail. The lateral light bands are a deep dull yellow. They are prominent on the head back of the eyes and in some instances extend to the nostrils in front. They persist along the trunk and in many specimens unite at the anterior end of the dorsal tail fin and continue to the tip. Where this occurs the dorsal fin is lacking in dark pigment (plate 9, figures 1 and 3). This distribution of pigment is not

uncommon in specimens recently hatched and is also found in those 2, 3 and 4 years old. It is pertinent here to call attention to the figures given by Smith[1] to show the tails of larval Necturi from northwestern Pennsylvania and Detroit river. Writing of the color pattern in a larva from Pennsylvania he says:

This specimen differs from the western larvae in that the dorsolateral stripes unite in the median line at the base of the tail, to be continued as a single stripe along the dorsal edge of the tail. Since this peculiarity is present in all the fourteen larvae that I have examined from the eastern habitat, it would appear to be a constant difference between the eastern and western forms.

As pointed out above, when the dorsal band ends at the base of the tail, the keel above is without dark pigment and takes its color from the united lateral light bands; when the dorsal band continues to the tip, the dorsal keel is dark (plate 9, figures 2 and 4). Age, size of specimen or locality seem to have nothing to do with this variation in pigment arrangement.

The dark lateral bands in year old specimens continue as in younger larvae, from the snout through the eyes to the tip of the tail. The lower sides may be definitely spotted or almost uniform in color. This series is marked by great uniformity in the light ventral color. In the majority of specimens the margins of the lips are dusky and there are intrusions of pigment on the sides of the head below the eyes. A few specimens have chromatophores scattered over the entire venter. The gills and their filaments are very short when compared with those of larvae 3 to 6 weeks old. In the latter the gills may be over half as long as the head; in the year old specimens, less than one-third.

Necturus, Second Year

Plate 7, figure 2; plate 9, figures 3 and 4

Specimens to establish the limits of size of two-year-old Necturi were secured with difficulty. In 10 days' collecting only seventeen specimens were discovered but it is believed that with this series the average size can be determined with considerable accuracy. The measurements follow:

70.0 mm	81.0 mm	90.0 mm
70.0	83.5	92.0
74.0	84.0	92.0
78.0	85.0	92.0
80.0	85.0	95.0
81.0	86.0	

As might be expected, the variation in size is greater than in the series of one-year-old specimens. The individuals which the writer

[1] Smith, B. G. Biol. Bul. 1911. 20:197, figs. 4–5.

has regarded as falling within the two-year-old limit vary from 70 to 95 mm. The average length is 83.4 mm. The shortest member of this group is only 4 mm longer than the longest one-year-old specimen but length has not been the only factor considered in determining age. Differences in body proportions are strikingly evident when the series of both ages are placed side by side.

In seven specimens the median dorsal band persists as a rather narrow stripe, distinct and bordered by dull yellow. In the other specimens this band is wider, dull yellow mottled with dark brown, the dark predominating. The yellow bands bordering the median stripe are dulled by scattered chromatophores of darker pigment and this is particularly true on the head. In a few instances they remain well marked from the snout to the tip of the tail. The dark lateral bands are constant in all specimens of the series and in four individuals they are continued on the tail to color the dorsal fin. In three specimens rounded dark spots are scattered over the dorsum. The venter in the majority of the specimens is very lightly pigmented and in no instances are there rounded dark spots present. The gills and filaments continue to be proportionally shorter than in larvae 3 to 6 weeks old.

Necturus, Third Year

Plate 7, figure 3

97.0 mm	107.0 mm	111.0 mm	116.5 mm	126.0 mm
97.0	108.5	114.0	118.0	128.0
101.0	109.0	114.0	120.0	128.0
103.0	109.5	115.0	120.0	
105.0	110.0	115.0	124.0	
105.0	110.0	116.5	125.0	

In this series of twenty-seven specimens the average length is 113 mm. The extremes of 97 and 128 mm show a variation in length of 31 mm. The average gain in length over members of the two-year-old class is 29.6 mm.

The median dorsal band persists as a narrow uninterrupted stripe in only five specimens. These are among the smallest of the series and range from 97 to 110 mm in length. In a single specimen 124 mm long the dorsum is entirely dark, its color impinging on the lateral dark areas without a separating light stripe. In the balance of the specimens the dorsal area is dusky brown with a broken and irregular median band indistinctly developed. The longitudinal light stripes which in young larvae are disposed more on the sides of the trunk, gradually assume a dorsal position. This is due to the change in shape of the body rather than to any definite shift in pigment. The head in the majority of the specimens is a dull yellowish brown although in a few specimens in which the dorsal band is distinct,

the median area of the head is dark. The dark lateral bands still persist although somewhat broken and mottled. They are usually distinct on the sides of the head and pass through the eyes. The lower sides are strongly spotted. In four specimens the venter is white; in two, gray spotted with black; in the others, rather uniformly, lightly pigmented.

Necturus, Fourth Year

Plate 7, figure 4

130.0 mm	140.0 mm	144.0 mm	149.0 mm	161.0 mm
130.0	140.0	145.0	152.0	161.5
131.0	140.0	146.0	157.0	164.0
135.0	142.0	147.0	159.0	164.0
137.0	142.0	147.0	160.0	165.0
139.0	143.0	148.0	160.0	165.0
				167.0

The range in length is from 130 to 167 mm in the series studied and the variation is 37 mm. The average length of the thirty-one specimens is 148.7 mm. This is an average gain in length of 35.7 mm in 1 year.

In the four-year-old specimens the color above is usually chocolate brown with a few scattered, rounded, bluish black spots. In one specimen 145 mm long the dark lateral band persists along the trunk and there is an indication of the dark dorsal stripe. In four, remnants of the light stripe remain but are very dull in color and broken. The dark sides are mottled with bluish black spots and irregular areas free from dark pigment. The dark lateral bands are most in evidence on the tail and on the sides of the head. The majority of the specimens have attained a color pattern essentially like that of the sexually mature. In this series three have white or very light bellies; fourteen are uniform dusky grayish brown and the balance have a few rounded dark spots on a dusky ground. The gills are still comparatively short.

Necturus, Fifth Year

Plate 7, figure 5

169.0 mm	175.0 mm	183.0 mm	192.0 mm	202.0 mm
169.0	176.0	184.0	192.0	203.0
170.0	176.0	185.0	195.0	203.0
170.0	176.0	186.0	195.0	205.0
170.0	177.0	186.0	196.0	206.0
170.0	178.0	186.0	196.0	208.0
170.0	178.0	186.0	196.0	210.0
171.0	178.0	188.0	198.0	210.0
171.0	179.0	188.5	198.0	210.0
172.0	179.0	190.0	200.0	210.0
174.0	180.0	190.0	200.0	
174.0	180.0	190.0	200.0	
174.0	181.0	190.0	201.0	
175.0	182.0	190.0	202.0	

The sixty-six specimens in this series have an average length of 187 mm. They vary from 169 to 210 mm or 41 mm. The average gain in length over specimens 4 years old is 38.3 mm.

In individuals of this size the variation in color is essentially that of the sexually mature, except that very rarely the dark lateral stripe of the side is retained. In one specimen 182 mm long the band is conspicuous on the head and tail and quite well preserved on the sides of the trunk.

In determining the age of specimens which have a length over 200 mm, consideration must be given to the general conformation for many specimens of this length are probably in their sixth year.

Necturus, Sixth Year

Plate 7, figure 6

While it is altogether probable that many individuals only 200 mm long are in their sixth year, a study of the considerable series of specimens from Pennsylvania indicates that where water conditions are good and food is abundant, a minimum length of about 230 mm may be attained. The measurements given in this report are based on collections made in one locality where there is every indication that the species is successful. Numbers alone do not give an accurate measure of the success of a species for an area may be overpopulated with consequent increase in competition, reduction of available food and retarded growth. A species may be regarded as successful where it maintains itself in full vigor, copes with its enemies and does not exhaust its food supply. An interesting comparative study of development might be made if it were possible to secure a sufficient number of specimens from more barren waters.

Individuals may reach sexual maturity at a length of 200 mm. Since mating takes place in the fall and ovulation in the spring following, the males in any series of the same age must mature the sexual elements several months before the female. Some dissections of females taken in the fall and winter show that the eggs have attained a diameter of about 3 mm. The mature egg is about 6 mm in diameter.

THE ADULTS

Size

Plate 8

Several hundred specimens from various parts of Pennsylvania and New York have been available for study. In addition a few individuals from North Carolina and Canada have been examined. The largest specimen in the entire series measured 432 mm (17

inches) in length and it is probable that this size is rarely exceeded. The writer believes with Eycleshymer[1] that there is little foundation for the statements of authors, (Jordan,[2] Hay,[3] Pratt,[4] *et al.*), that the species attains a length of 24 inches or more. In fact the average length is nearer 12 inches although specimens 15 inches long are not uncommon.

In a male 302 mm long the body proportions are as follows: head length, 51 mm, measured from end of snout to the base of the first (dorsal) gills; the width at the widest point, 38 mm; tail from posterior end of vent, 34 mm; tail shorter than normal and the tip seems to have been regenerated; width of the trunk, 38 mm; legs short and of equal length, 35 mm; the third toe of each foot longest. In a female 325 mm long the corresponding measurements are: head length, 54 mm; width, 38 mm; tail, 100 mm. In any considerable series the females average a little larger than the males.

Form

The body is stout, somewhat depressed and with a distinct median dorsal groove. The head is broad and flat behind the eyes and gradually narrows to the truncated snout. Labial and gular folds are well developed. The costal furrows number fifteen if axial and inguinal are counted. In proportion to its size, the eyes are extremely small. The gills are about one-third as long as the head or, if filaments are included, about one-half as long. The filaments are very slender, flattened and brushlike in appearance. The blood supply to the filaments is under control and when the flow is restricted the filaments lose their bright red color and shrink almost half their length. The mouth is large and extends on the sides of the head to a point just behind the eyes. The nostrils are on the front of the snout near the lateral angles. The tail is broad and strongly compressed and widest a little beyond the middle of its length.

Color

While there is considerable variation in the color of adult specimens, greater uniformity is found than in Cryptobranchus which is so often associated with Necturus where the ranges overlap. Variation in Necturus is expressed not only in the general ground color but in the arrangement, number and conspicuousness of the dark

[1] Eycleshymer, A. C. Amer. Nat. 1906. 40:123.
[2] Jordan, D. S. A Manual of the Vertebrate Animals, 10th ed., 1910. p. 175.
[3] Hay, O. P. 17th Rep't State Geol. Ind. 1892. p. 419.
[4] Pratt, H. S. A Manual of Land and Fresh Water Vertebrate Animals of the U. S. 1923. p. 147.

spots. The color of a large majority of specimens is a deep rust brown—small flecks over blue-black. Where the brown is absent the black pigment strikes through to form rounded spots one-eighth to one-fourth of an inch in diameter. The spots may be almost or quite absent in a few specimens or developed only on one side of the body. A few individuals in any collection of considerable size will have the back marked with a double series of regularly disposed spots. These specimens are likely to have a lateral series which is reminiscent of the lateral stripe of the young. The upper surfaces of the legs are usually spotted, rust brown over blue-black. Often there is a reddish or orange tinge of color about the margins of the tail, particularly noticeable in the smaller specimens. In some individuals the only remnant of the dark lateral stripe is found in the dark bar which passes through the eye. This may be short and indistinct or well developed. In other specimens the sides of the tail also retain a dark central area. The venter in adults is usually rather uniformly pigmented but lighter than the back. A considerable number have the belly marked with a light median stripe, broad in some and reduced to a narrow line in others. A few have dark spots on a dull ground.

Sexual Differences

The sexes are, in general, alike in form and color. There are, however, some slight differences in body proportions. Measurements of a considerable number of individuals indicate that the head of the male is on the average a little longer than that of the female. In a pair, each 275 mm long, the head of the male is 48 mm long while that of the female is 45 mm. The male of another pair of equal length (280 mm) has a head length of 51 mm while that of the female is only 49 mm. A male 285 mm long has a head length of 52 mm which exactly equals that of a female 312 mm long. Head measurements are of doubtful value, however, in the determination of sex when preserved specimens are used and are unnecessary when it is possible to examine the vent.

The vent in the male is a longitudinal slit, obliquely wrinkled at the margin, bounded posteriorly by a transverse crescentic groove and provided with a pair of nipplelike papillae, one on each side just in front of the groove. The male vent is larger than that of the female and in the breeding season is surrounded by a swollen and inflamed ridge. This ridge marks externally the limits of the large cloacal gland lying below the surface. The vent is capable of being everted and in such a condition presents to the surface many

fine tubules and the two strongly diverted papillae. The slightest abrasion while the vent is swollen and inflamed causes it to bleed freely. In the female the vent is a simple slit, smooth externally and usually surrounded by a narrow light-colored area.

It is quite possible to distinguish the sex in four-year-old individuals. The vent in a male 142 mm long has the characteristic crescentic groove and the paired papillae are evident as short backward directed lobes.

Glands of the Skin

That mudpuppies are "slimy" to the touch is evident to anyone who has handled living specimens. A thin layer of slime or mucous is at all times present on the surface of the skin and probably serves the mudpuppy in the protection it gives against Saprolegnia; for Necturus as well as fish are subject to attack by these destructive organisms[1].

A recent paper by Dawson[2] includes an account of the dermal glands of Necturus. Two distinct types are recognized: (1) those which produce mucous, and (2) those filled with a dense granular secretion. Occasionally mixed glands are found. The glands of Necturus are not aggregated in special areas and little specialization has taken place except in the cloaca. The mucous glands are generally distributed over the surface of the body except on the soles of the feet and in the gular fold and are more abundant on the ventral surface than the granular glands. The latter are largest and most abundant on the dorsal surface of the body and in areas along the dorsal and ventral edges of the tail. The product of the mucous glands is a clear, slimy fluid which is poured out over the surface of the skin when the animal is slightly irritated. Granular secretion is discharged under strong stimulation.

Dawson[3] also gives an interesting account of the pigmentation and changes in coloration. Some of his findings, briefly summarized, are as follows: Pigment may be present in ordinary epidermal cells. Special pigment-bearing cells of the epidermis, apparently of two types (pyramidal and highly branched) may be contraction and expansion phases of one kind of cell. The epidermal chromatophores are not derived from those of the dermis and specialized pigment cells may perhaps be produced by metamorphosis of ordinary epidermal cells. Melanophores and xanthophores were found in the

[1] Morse, Max. Proc. Ohio State Acad. Sci. 1904. 4:107.
[2] Dawson, A. B. Jour. Morph. 1920. 34:526.
[3] Dawson, A. B. Jour. Morph. 1920. 34:487–589, pls. 1–6, 36 figs.

dermis, the former usually arranged in two layers, the latter with the melanophores of the outer layer. Changes in coloration are brought about by expansion and contraction of the dermal melanophores. The melanophores are expanded in bright light and contracted in darkness and at low temperatures. Melanophores appear to be of fixed form, within which pigment granules migrate in "contraction" and "expansion."

Individual specimens may have a ground color that differs markedly from the average. But when a considerable number of specimens are confined in a tank and subject to definite control of light, the ground color is remarkably uniform. As before mentioned, in bright light the chromatophores are expanded and the general color is dark. In the dark the chromatophores contract and the color may vary from light to dark tan. A single large specimen from Cayuga Lake, N. Y., exhibited albinistic tendencies. The color in life was a uniform dull yellow without darker markings. The writer has not found all black specimens but a single larva in a series reared from the egg was so dark that the lateral stripes were scarcely distinguishable.

Garnier[1] described specimens from the Maitland river which were characterized in part by their smaller size, uniform black color, sooty abdomen and white gular fold. For this variety the name "Latastei" was proposed. But the name has gone into the synonymy of Necturus maculosus and the specimens have been regarded simply as aberrantly colored individuals. The writer has examined one from Pointe au Baril, Georgian Bay, collected in the summer of 1925 by Leonard Giovannoli of Lexington, Ky. This specimen is small, 92 mm long, dark bluish-brown above and marked with two faint lines of small light dashes which run from a point back of the eyes to the base of the tail. The belly is light. There is a striking resemblance in color to specimens of Necturus punctatus of the same size. The Pointe au Baril specimen would be conspicuous in any series of Necturus maculosus and it is significant that it was collected in the general region which supplied Garnier's specimens.

It is to be expected, perhaps, that near the periphery of the range of a widely distributed species, individuals will show more than the usual variation from normal. In this connection attention may be directed to the recently described dwarf form of N. maculosus which is found in North Carolina[2].

---

[1] Garnier, J. G. Proc. Can. Inst. 1888. 3d ser. 5:218.
[2] Brimley, C. S. Jour. Elisha Mitchell Sci. Soc. 1924. 40:166.

Abnormalities

In the entire series of several thousand young larvae only three abnormal individuals were found. Two of these were "spiral tailed monsters," adopting the term applied by Smith to similarly distorted individuals of Cryptobranchus. The third specimen was of unusual color, the light bands being obscured by uniform distribution of dark pigment.

The figures (plate 10) show the character of the abnormal specimens better than any written description. In size they compared favorably with normal larvae of the same age, being equally endowed with yolk. In open competition they would not long survive. Their bodies being permanently twisted they were obliged to swim in circles and as often as not upside down. They responded to stimuli as promptly as the normal individuals but the movements were without definite direction. In moving from one part of the container to another, the path formed a series of closely overlapping spirals.

BIBLIOGRAPHY

The following list gives the complete titles of the papers referred to in the text of the report and to a considerable number of other papers which have a general interest. No attempt has been made to give a complete bibliography of the species.

Baird, S. F. Revision of the North American Tailed-Batrachia, with Descriptions of New Genera and Species. Jour. Acad. Nat. Sci. Phila., n. s., 1850. 1:281–94

Brimley, C. S. The Water Dogs (Necturus) of North Carolina. Jour. Elisha Mitchell Sci. Soc. 1924. 40:166–68

Claypole, E. J. The Blood of Necturus and Cryptobranchus. Proc. Amer. Micros. Soc. 1894. 15:39–76, pls. 1–6

Cope, E. D. On the structure and Distribution of the Genera of the Arciferous Anura. Jour. Acad. Nat. Sci. Phila. 2d ser. 1866. 6:67–112

———— —— The Batrachia of North America. Bul. U. S. Nat. Mus. 34. 1889. p. 23–27, pls. 1–4, text figs.

Dawson, A. B. The Integument of Necturus maculosus. Jour. Morph. 1920. 34:487–589, pls. 1–6, 37 figs.

———— —— The Cloaca and Cloacal Glands of the Male Necturus. Jour. Morph. 1922. 36:447–65. pls. 1–3

DeKay, J. E. Zoology of New York, pt 3. 1842. p. 87

Dunn, E. R. The Breeding Habits of Salamanders and Their Bearing on Phylogeny, Copeia, No. 115. 1923. p. 25

Eycleshymer, A. C. The Formation of the Embryo of Necturus, with Remarks on the Theory of Concrescence. Anat. Anz. 1902. 21:341–53, figs. 1–31

———— —— Bilateral Symmetry in the Egg of Necturus. Anat. Anz. 1904. 25:230–40, figs. 1–47

———— —— The Development of Chromatophores in Necturus. Amer. Jour. Anat. 1906. 5:307–13, figs. 1–7

———— —— The Habits of Necturus. Amer. Nat. 1906. 40:123–36

———— —— The Growth and Regeneration of the Gills in the Young Necturus. Biol. Bul. 1906. 10:171–75

——— —— The Reaction to Light of the Decapitated Young Necturus. Jour. Comp. Neurology and Psychol. 1908. 18:303–08

——— —— Some Observations on the Decapitated Young Necturus. Anat. Anz. 1914. 46:1–13, figs. 1–5

Gage, S. H. Notes on the Epithelium Lining the Mouth of Necturus and Menopoma. Proc. Amer. Soc. Micros. 1885. p. 126–27

Gamble, D. L. The Morphology of the Ribs and Transverse Processes in Necturus maculatus. Jour. Morph. 1922. 36:537–66, figs. 1–31

Garnier, J. G. On a New Species of Menobranchus. Proc. Can. Inst. 1888. 3d ser. 5:218–19

Gray, J. E. On the Genus Necturus or Menobranchus, with an Account of its Skull and Teeth. Proc. Zool. Soc. London. 1857. 25:61–64, 3 figs.

Harlan, Richard. Observations on the Genus Salamandra, and the Establishment of the Genera Menopoma and Menobranchus. Med. and Phys. Researches. 1835. p. 164–76, pl. 1

Hay, O. P. The Batrachians and Reptiles of the State of Indiana, 17th Ann. Rep't Ind. Dep't Geol. and Nat. Resources, 1892, p. 419

Holbrook, J. E. North American Herpetology, 2d ed. 1842. 5:113

Huxley, T. H. On the Structure of the Skull and of the Heart of Menobranchus lateralis. Proc. Zool. Soc. London. 1874. p. 186–204, pls. 29–32

Jordan, D. S. A Manual of the Vertebrate Animals, 10th ed. 1910. p. 175

Keibel, Franz. Die Entwicklungsgeschichte der Wirbeltiere. Die Kultur der Gegenwart. Sec. 3, div. 4, v. 2, pt 2. 1913. p. 346

Kingsbury, B. F. The Histological Structure of the Enteron of Necturus maculatus. Proc. Amer. Micros. Soc. 1894. 16:19–64, pls. 1–8

——— —— On the Brain of Necturus maculatus. Jour. Comp. Neur. 1895. 5:139–205, pls. 9–11

——— —— The Spermatheca and Methods of Fertilization on Some American Newts and Salamanders. Tran. Amer. Micros. Soc. 1895. 17:261–304, pls. 1–4

——— —— The Rank of Necturus Among Tailed Batrachia. Biol. Bul. 1905. 8:67–74

——— —— **& Reed, H. D.** The Columella Auris in Amphibia. Jour. Morph. 1909. 20:549–628, pls. 1–10, 21 text figs.

Kneeland, Samuel. On a Supposed New Species of Siredon from Lake Superior. Proc. Bost. Soc. Nat. Hist. 1857. 6:152–54

Miller, W. S. The Lung, Vascular System and Brain of Necturus maculatus. Bul. Univ. Wis. Sci. Ser. 2. 1900. p. 199–246

Milner, J. W. Report on the Fisheries of the Great Lakes. Rep't U. S. Comm. Fish and Fisheries. 1874. p. 62

Mitchill, S. L. The Proteus of the North-American Lakes. Amer. Jour. Sci. 1822. 4:181–83. An early descriptive account of Necturus

——— —— Observations on Several Reptiles of North America Which Seem to Belong to the Family of Proteus. Amer. Jour. Sci. Arts. 1824. 7:63–69, pl. 2, figs. 1–3

Moodie, R. L. The Ancestry of the Caudate Amphibia. Amer. Nat. 1908. 42:361–73, figs. 1–10

Morse, Max. Batrachians and Reptiles of Ohio. Proc. Ohio State Acad. Sci. 1904. 4:107

Pearse, A. S. The Reactions of Amphibians to Light. Proc. Amer. Acad. Arts and Sci. 1910. 45:161–208, figs. 1–7

Pratt, H. S. A Manual of the Land and Fresh Water Vertebrate Animals of the United States. Phila. 1923. p. 147

Reed, H. D. Systematic Relations of the Urodela as Interpreted by a Study of the Sound-Transmitting Organs. Sci., n. s. 1909. 29:715

Reese, A. M. Observations on the Reactions of Cryptobranchus and Necturus to Light and Heat. Biol. Bul. 1906. 11:93–99

Say, Thomas, in James, Edwin. Account of an Expedition from Pittsburgh to the Rocky Mountains. 1823. 1:5–7

Sayle, M. H. The Reaction of Necturus to Stimuli Received Through the Skin. Jour. Anim. Behavior. 1916. 6:81–102, fig. 1

Smith, B. G. The Nests and Larvae of Necturus. Biol. Bul. 1911. 20: 191–200, figs. 1–7

Smith, B. G. The Embryology of Cryptobranchus allegheniensis, Including Comparisons with Some Other Vertebrates. Jour. Morph. 1912. 23:61–157, pls. 1–2, figs. 1–56

Smith, I. U. Zerlegung des Proteus of the Lakes (Menobranchus), Isis. 1832. p. 1088

Stejneger, Leonhard & Barbour, Thomas. A Check List of North American Amphibians and Reptiles, 2d ed. 1923. Cambridge

Warren, John. The Development of the Paraphysis and the Pineal Region in Necturus maculatus. Amer. Jour. Anat. 1905. 5:1–27, figs. 1–23

Whipple, I. L. The Ypsiloid Apparatus of Urodeles. Biol. Bul. 1906. 10: 255–97, figs. 1–10

Wilder, B. G. Menobranchus Edible. Amer. Nat. 1874. 8:438

Wilder, H. H. The Skeletal System of Necturus maculatus Raf. Mem. Bost. Soc. Nat. Hist. 1903. 5:387–439, pls. 62–67, figs. 1–22

EXPLANATIONS OF PLATES

Plate 1

39

Woodcock Creek near Saegertown, Pennsylvania. Typical stream habitat of Necturus maculosus (Rafinesque). Photographed June 23, 1924, by S. C. Bishop.

Plate 1

Plate 2

A "nest" of eggs of Necturus maculosus (Rafinesque). The stone with eggs attached, removed from the water and tipped on its edge. Photographed June 23, 1924, by S. C. Bishop. About one-half natural size.

Plate 2

Plate 3

Necturus maculosus (Rafinesque)

A female in the position assumed during the egg-laying process. Drawn by Walter J. Schoonmaker.

Plate 3

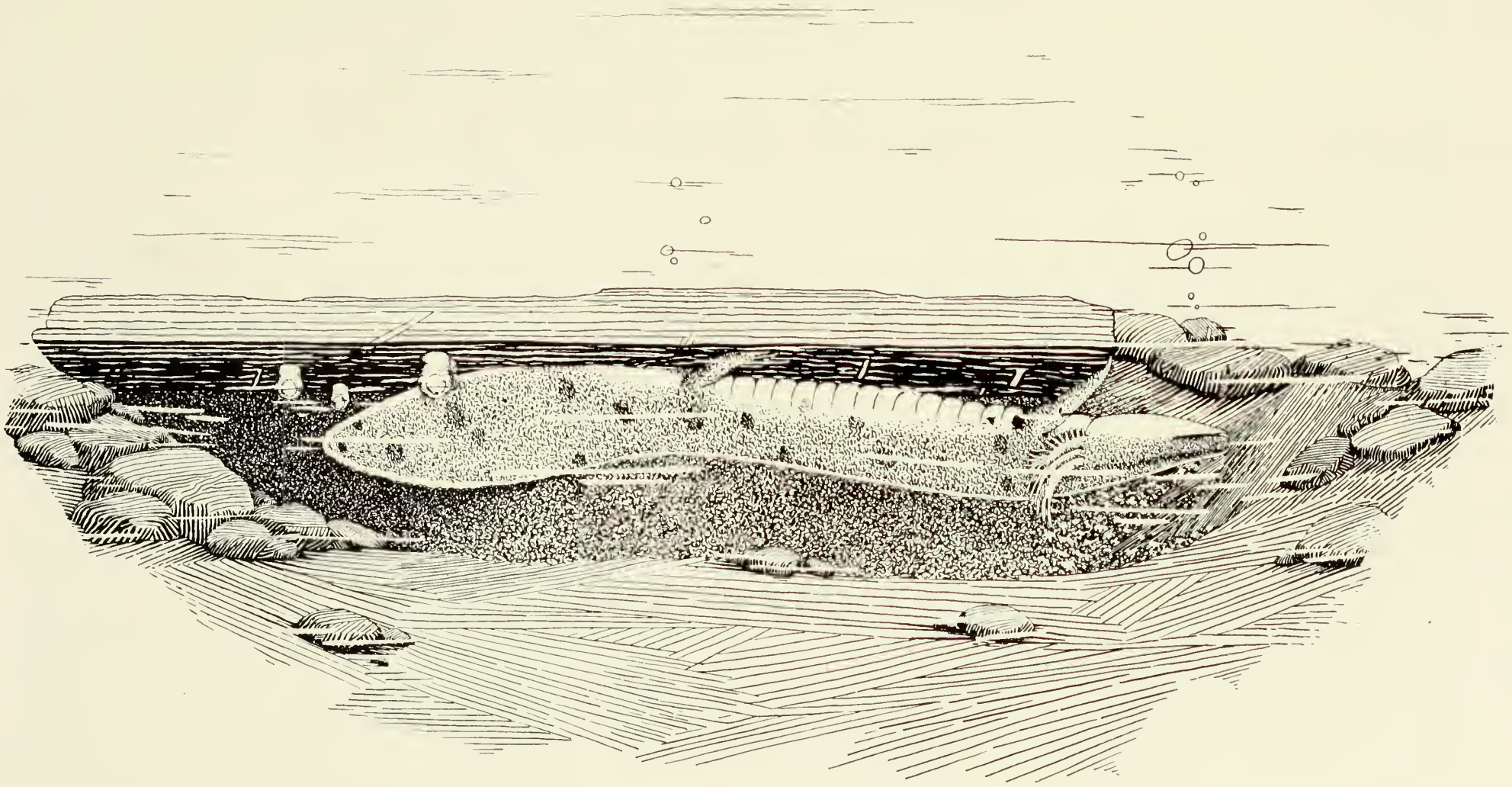


Plate 4

Necturus maculosus (Rafinesque)

Figure 1 Embryos 16 days old, June 21, 1925. Formalin specimens, twice enlarged.

Figure 2 Embryos 20 days old, June 25, 1925. Formalin specimens, twice enlarged.

Figure 3 Embryos 28 days old, July 3, 1925. Formalin specimens, twice enlarged. Photographed by E. J. Stein.

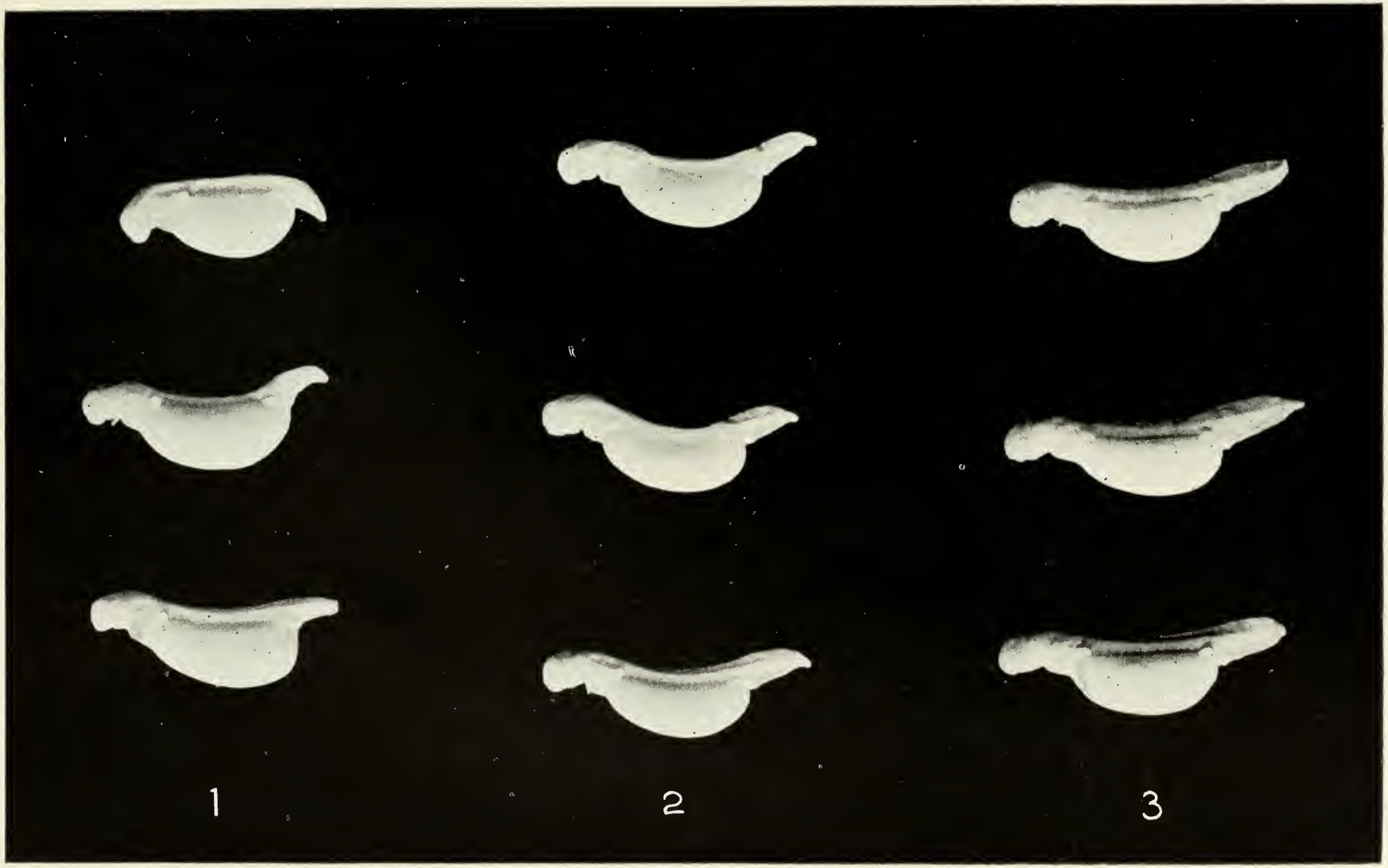

1
2
3

Plate 5

Necturus maculosus (Rafinesque)

Figure 1 Larvae at hatching, July 13, 1925. Formalin specimens, twice enlarged.

Figure 2 Larvae 3 days after hatching, July 16, 1925. Formalin specimens, twice enlarged. Photographed by E. J. Stein.

Plate 5

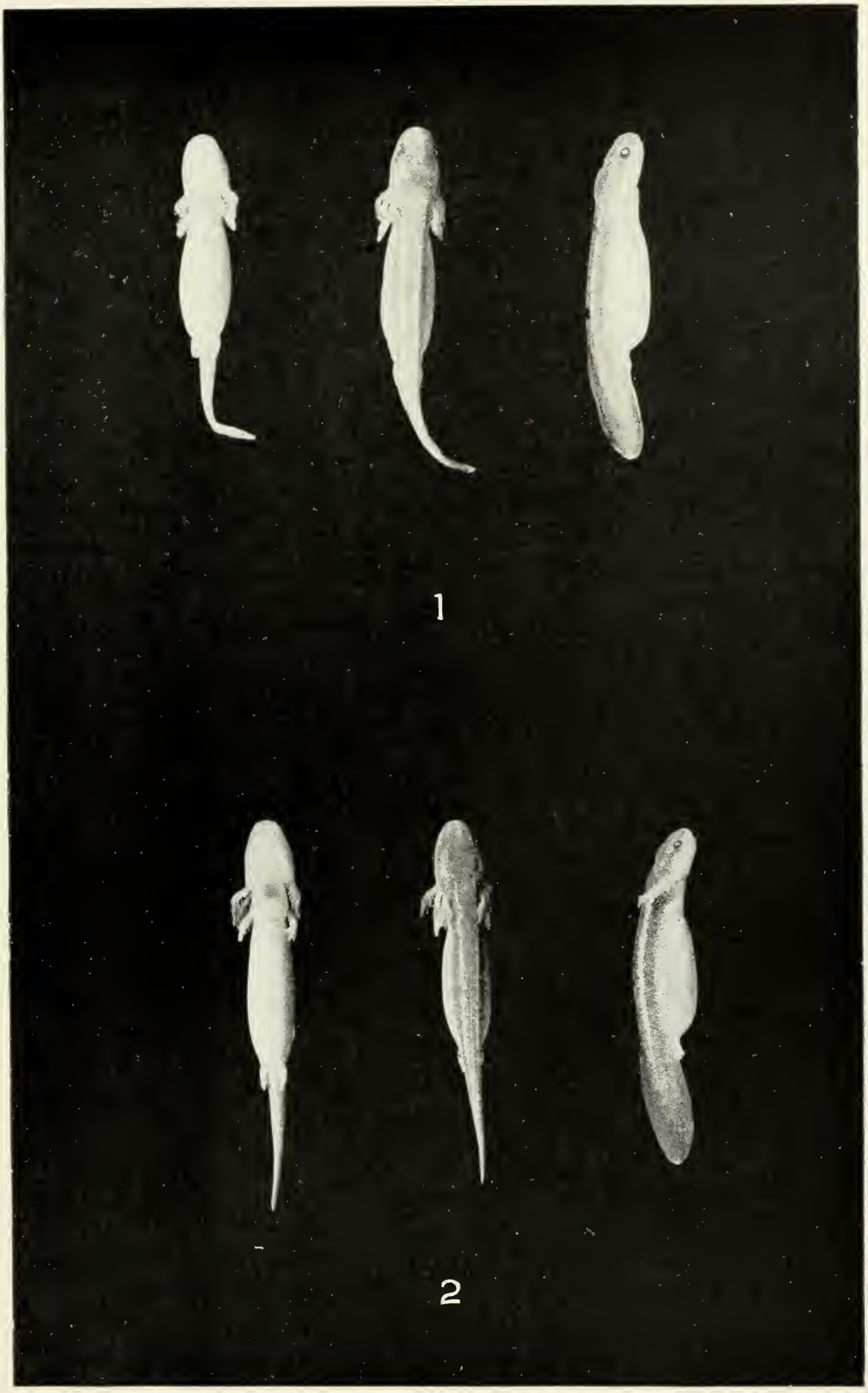


Plate 6

Necturus maculosus (Rafinesque)

Figure 1 Larvae 10 days after hatching, July 23, 1925. Formalin specimens, twice enlarged.

Figure 2 Larvae 25 days after hatching, August 7, 1925. Formalin specimens, twice enlarged. Photographed by E. J. Stein.

Plate 6

Plate 7

Necturus maculosus (Rafinesque)

Mudpuppies 1 to 6 years old. Living specimens, natural size, photographed under water. The lateral light bands so distinctive of the larvae are usually almost entirely lost during the third year. The dark bands of the sides often persist in older specimens. The living specimens available for photographing did not, in every instance, represent the average length of the species for the year. Thus the figure of the four-year-old specimen represents an individual of the maximum size for the age. Figures 1 and 2 photographed by E. J. Stein; others in the series by S. C. Bishop.

1


1
2
3
4
5
6

Plate 8

Necturus maculosus (Rafinesque)

A mature specimen of moderate size photographed in Woodcock creek. The white scars on the surface of the skin mark the places of attachment of small, flat, parasitic worms. About twenty exposures were made before the camera caught the gills fully expanded. Photographed June 23, 1924, by S. C. Bishop. Slightly less than natural size.

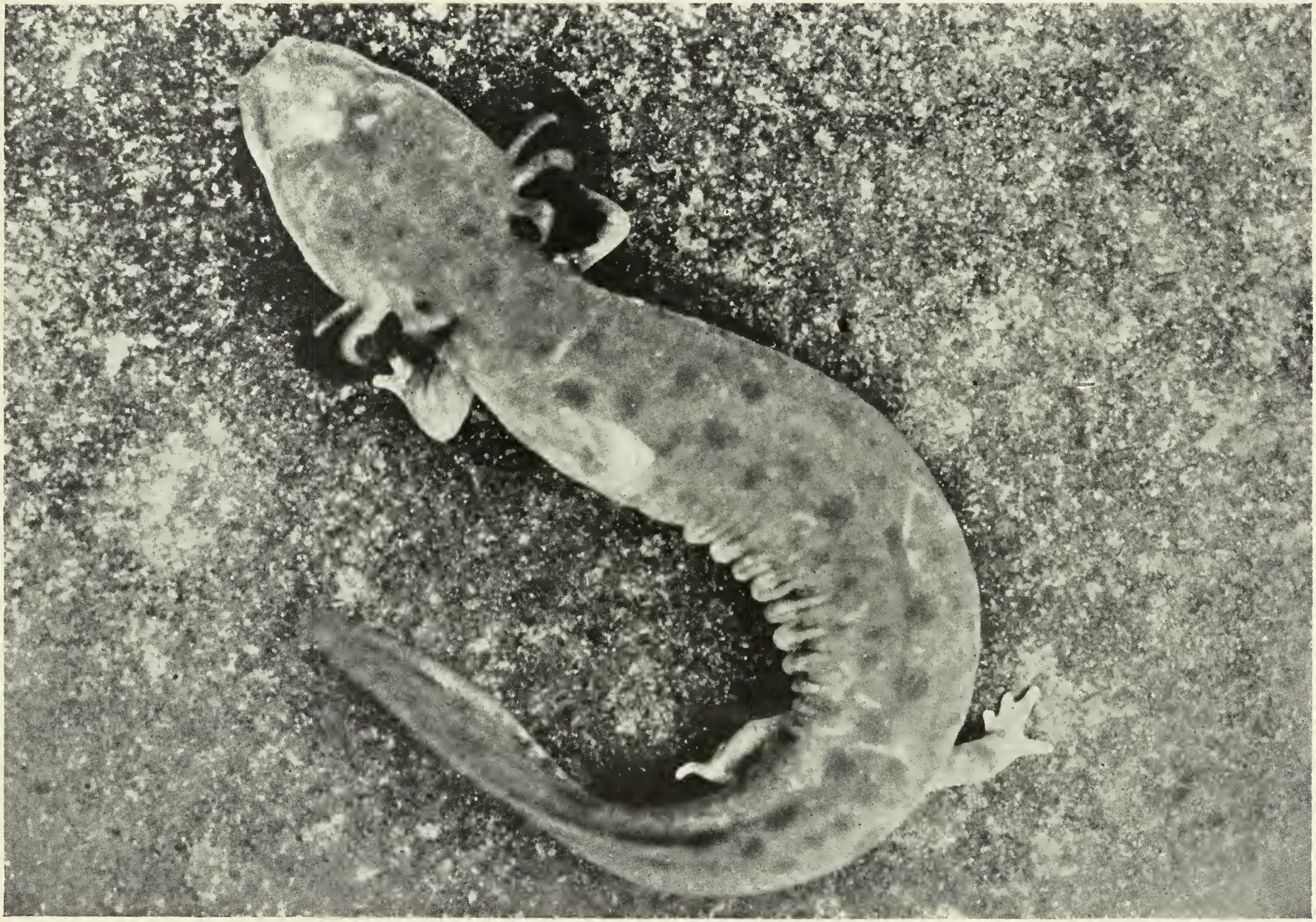


Plate 9

Necturus maculosus (Rafinesque)

Figure 1 Tail of a one-year-old specimen enlarged to show the color pattern. The dark dorsal band stops at the base of the tail and the dorsal keel takes its color from the united light bands.

Figure 2 In this specimen the dark dorsal band continues to the tip of the tail.

Figure 3 A two-year-old specimen about natural size. Dorsal keel without dark pigment.

Figure 4 The dark dorsal band continued to the tip of the tail. Formalin specimens.

Plate 9

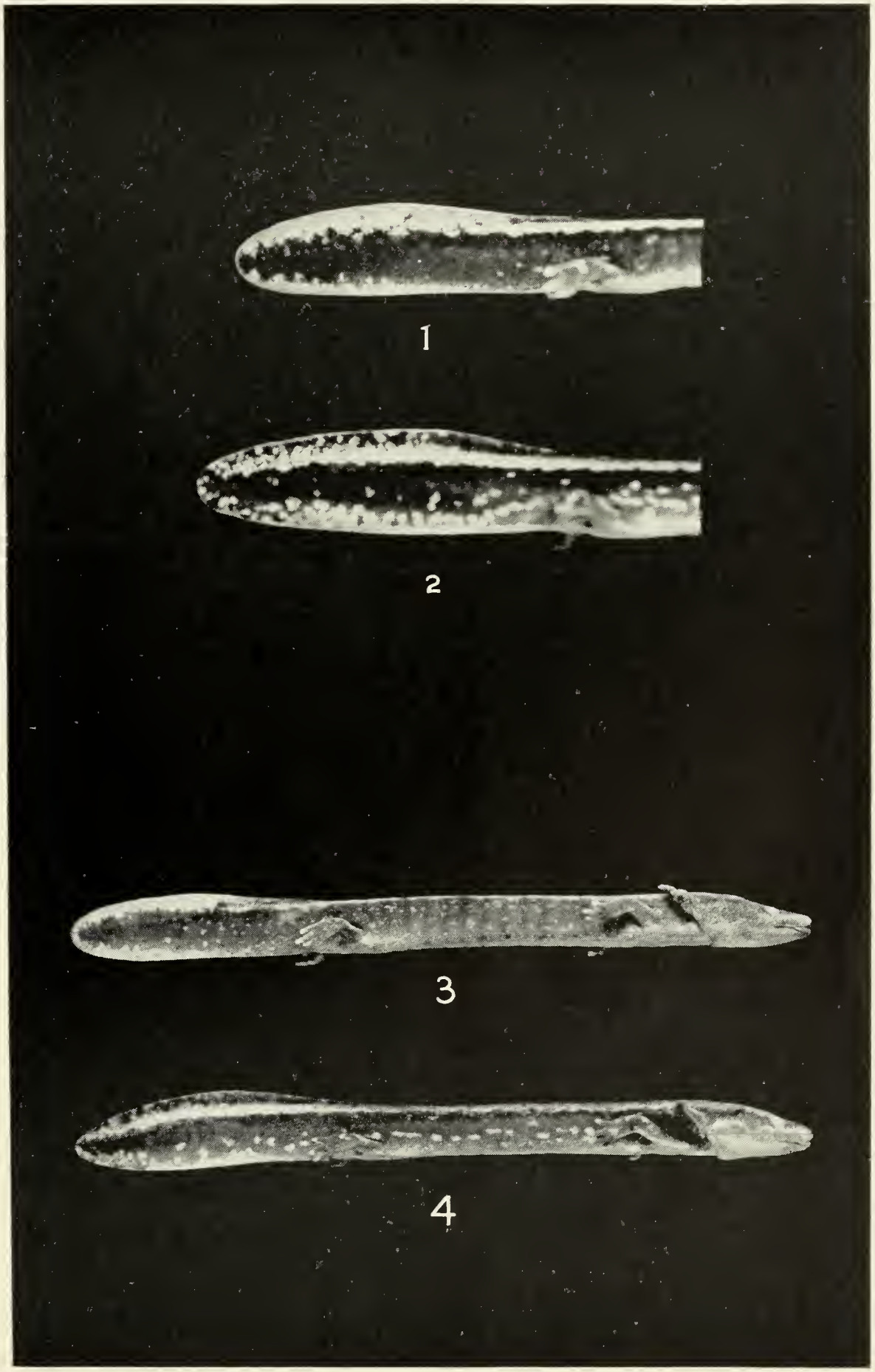


Plate 10

Necturus maculosus (Rafinesque)

Abnormal larvae. The body is spirally twisted and forces the larva to swim in circles. Photographed from life by S. C. Bishop and enlarged about 3 times.

Plate 10

Plate 11

The Development and Reduction of the Larval Gills

Figure 1 The gills at hatching, July 13, 1925. The filaments are short, pointed and regularly disposed.

Figure 2 The gills 3 days after hatching, July 16, 1925. The filaments show considerable development. Curiously enough every other one has about doubled in length.

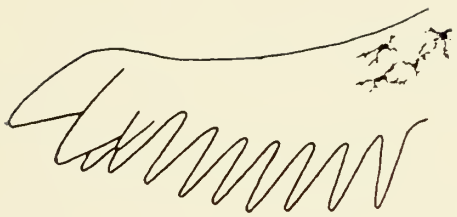
Figure 3 Ten days after hatching, July 23, 1925. Marked increase in size and length of the terminal filaments is shown and some indication of the increase in chromatophores.

Figure 4 Twenty-five days after hatching, August 7, 1925. The larval gills at the height of their development.

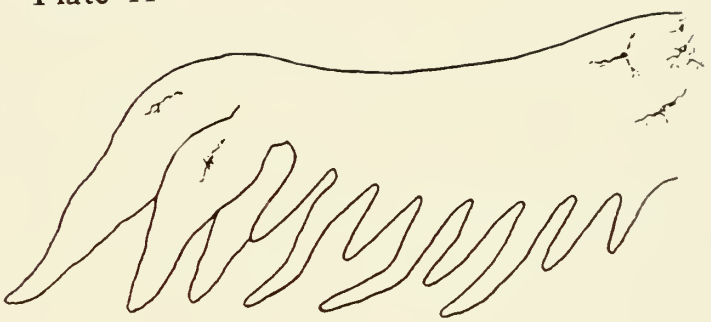
Figure 5 Thirty-eight days after hatching, August 20, 1925. The filaments have again shortened and taken on a comblike appearance.

Figure 6 Forty-eight days after hatching, August 30, 1925. Pigmentation greatly increased. The gill itself is heavier and thicker in proportion to the length of the filaments. Drawn by Walter J. Schoonmaker.

Plate II



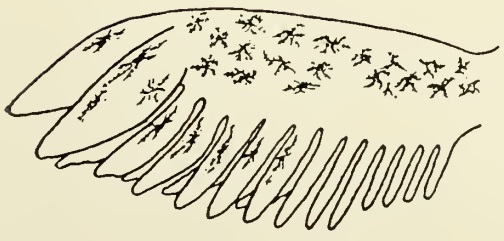
1



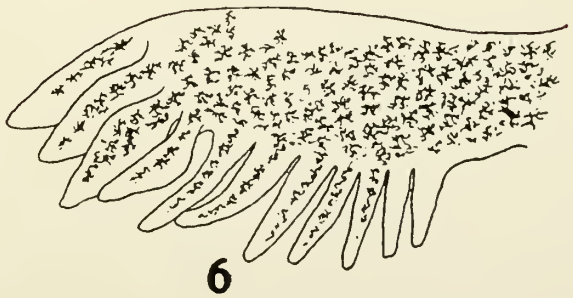
2

3

4



5



6