THE EARLY DEVELOPMENT OF *RANA CAPITO SEVOSA*

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The geographic range of the dusky gopher frog, *Rana capito sevosa*, was recorded by Netting and Goin (1942) as limited to the Gulf Coast region between Saint Tammany Parish, Louisiana and Baldwin County, Alabama. A wider distribution of the dusky gopher frog in Mississippi and Alabama was reported recently by Neill (1957). *R. capito sevosa* apparently intergrades with the northern crawfish frog, *R. areolata circulosa*, in Mississippi, as well as with the Florida gopher frog, *R. capito capito*, in the region between Mobile Bay, Alabama and the Apalachicola drainage in Florida. Neill (*op. cit.*) proposed that the dusky gopher frog and the Florida gopher frog be listed as subspecies of *R. areolata*, namely, *R. a. sevosa* and *R. a. aesopus* respectively. He recommended also that the gopher frog from the lower Atlantic Coastal Plain (Carolinas and Georgia), described by Schwartz and Harrison (1956) as a new subspecies, *R. capito stertens*, be designated as *R. areolata capito*. The nomenclature used herein follows the more familiar terminology found in Schmidt's 1953 check list. This does not necessarily imply a rejection of Neill's revisions.

Continual efforts have been made by members of the field crews of Tulane University to accumulate data on the habits and life history of the dusky gopher frog in Louisiana. This elusive frog has been collected from several localities in Saint Tammany Parish. Adult specimens are represented in the Tulane University Vertebrate Collections from Slidell[1] (11 ♂♂, 2 ♀♀, TU 4883, 4919), Covington, (1 ♀, TU 4901), Talisheek (1 ♂, TU 4888), and Pearl River (6 ♂♂, 4 ♀♀, TU 1352, 4902, -05, -07, 5461).

Breeding aggregations of *R. capito sevosa* have been encountered in clear, woodland pools located three miles north of Pearl River, off state highway 41. Preliminary observations indicate that the peak of breeding activity is during the early part of February. *Rana pipiens* (= *R. pipiens sphenocephala*) commonly has been observed participating in the congregations. The mating call of the dusky gopher frog may be likened to the roar of an outboard motor, more continuous and hoarser than the guttural croaks of the leopard frog. The voice is stated (Goin and Netting, 1940) to be less "snore-like" than that of the Florida gopher frog, *R. capito capito*.

The dusky gopher frog reacts quickly to slight disturbances in the water, diving to, and swimming rapidly along, the bottom of the pool. Efforts to capture mated pairs have not been successful. However, egg masses and tadpoles have been collected on several occasions.

[1] The locality at Slidell, La. is the source of the type specimen of the dusky gopher frog (Carnegie Museum No. 16809), an adult male collected by Percy Viosca, Jr. on April 11, 1926 and described by Goin and Netting (1940).

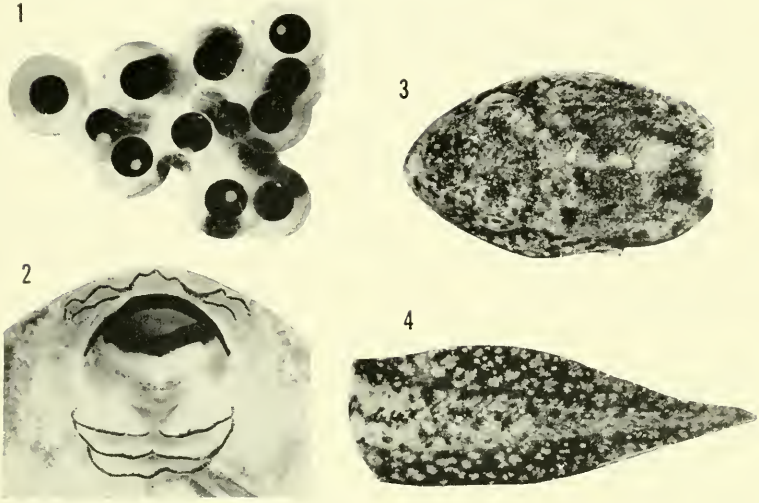
Those masses containing large-sized eggs, assumed not to be those of *R. pipiens*, were assigned with reservation to *R. capito sevosa*. Likewise, the tadpoles of the dusky gopher frog and the leopard frog could not be separated with absolute assurance. Precise identification of the eggs and tadpoles of *R. capito sevosa* awaited the opportunity when eggs could be obtained from known parents, or when larvae collected in the field could be reared through metamorphosis.

On the evening of February 9, 1955, an egg mass containing approximately 6,000 eggs was taken from a temporary pool in the pine-oak woodland at Pearl River by a Tulane University party of Liner, Tinkle, and Lubritz. The plinthlike, submerged egg mass was collected shortly after 7:00 p.m. and apparently had been recently deposited. The eggs were examined by the writer the following morning (11:00 a.m.), at which time they were in the late cleavage stage (stage 9, defined in Shumway, 1940). The eggs appeared to be larger than those of the southern leopard frog. This impression was confirmed by measurements of the vitellus diameter. The diameter of 100 eggs ranged from 1.67 to 2.18 mm, the mean being 1.84 mm and the standard deviation, 0.11. Eggs of *R. pipiens* from three localities in eastern Louisiana (Boutte, New Orleans, and Slidell) varied from 1.44 - 1.76 mm, with a mean of 1.62 mm and a standard deviation, 0.09. The difference in egg sizes in significant (the difference between the means is greater than three times the standard error of the difference).

Most of the eggs were preserved (TU 16999); approximately 400 eggs were distributed in groups of twenty into white enamel pans containing pond water. The embryos were reared in an air-conditioned laboratory, in which the temperature was maintained at 20° C ± 3°. All stages of development through and beyond metamorphosis were obtained. The transformed frogs were *R. capito sevosa*.

The purpose of this paper is to describe the early development, heretofore unrecorded, of the dusky gopher frog. The phrase "early development" encompasses both embryonic and larval periods. An embryo is designated here as the prefeeding individual, beginning with the cleavage of the egg and continuing until the external gills are lost. Larva and tadpole are considered synonymous terms, each referring to the individual that feeds and passes through a period of metamorphosis before assuming the adult shape.[2] Following the scheme proposed by Taylor and Kollros (1946), the embryonic stages are designated by arabic numerals; the larval stages, by Roman numerals (except for practical considerations in fig. 5).

[2] The time of hatching is generally considered as the transition period from embryonic to larval development. However, since hatching occurs at different stages of development in anurans, then that which constitutes an embryo in a late-hatching species would be a tadpole in an early-hatching species. This difficulty is circumvented by the terminology employed in this paper.



Figures 1-4. *Rana capito sevosa.* 1 Late gastrula stage; 2, 3, 4 features of a tadpole at stage VI.

Embryonic Development

As previously mentioned, the embryos were in the late cleavage stage (stage 9) when examined at 11:00 a.m. of February 10. The dorsal lip of the blastopore (stage 10) was evident at 7:00 p.m. The embryos exhibited a circular blastopore (stage 12) at 10:00 a.m. the following day, at which time the photograph shown in figure 1 was taken. Two gelatinous envelopes are present; the inner one is not visible in the figure. The diameter of the outer envelope of 100 eggs averaged 4.00 mm (standard deviation: 0.24, range: 3.44 - 4.48 mm); the inner, 2.37 mm (standard deviation: 0.15, range: 2.06 - 2.75). The embryos were observed at close intervals thereafter; the data are recorded in Table 1. The age, in hours, accompanying a given stage refers to the time that had elapsed since fertilization (stage 1). It is estimated that the eggs were fertilized at 7:00 p.m. of the evening they were collected. Based on this estimate, the onset of stage 25, the last of the embryonic stages, occurred 259 hours after fertilization. Total length of twenty embryos measured at stage 25 averaged 13.30 mm (range: 12.02 - 14.46 mm).

The embryos hatch in the tail bud stage (stage 17). No active muscular movements or contractions are involved in the hatching process. The activity of cilia on the ectodermal surface apparently plays an important role. The embryo begins to rotate slowly by means of ciliary action during the closure of the neural tube (stage 15). Just prior to hatching, the embryo comes to rest with its head pressed against the vitelline membrane ("vitelline capsule", "fertilization membrane", "chorion"). The membrane bulges at its point of con-

TABLE 1.
THE EMBRYONIC DEVELOPMENT OF *Rana capito sevosa*

Age in Hours	Stage	Age of Hours	Stage
0	1[a]	110.5	19M
16.0	9	115.0	19L
22.0	10	120.0	20E
37.0	12L	133.2	20L
46.5	14E	138.0	21
61.0	16E	156.5	22
68.2	16M	169.0	22
77.7	17E	193.0	23
86.0	17L (Hatching)	216.7	23
92.5	18E	236.5	24
98.0	18L	259.0	25

[a] The stages are described in Shumway, 1940; the letters E, M, and L signify early, middle and late.

tact with the head and then ruptures. The rate of ciliary beat increases and the embryo, without bending or twitching its body, slides slowly through the aperture. The rupture of the membrane or the emergence of the embryo is not abrupt or explosive, suggesting no mechanical effects of vitelline fluid pressure. Noble (1926) claims that a group of eosinophilic cells ("frontal gland") in the head ectoderm of anuran embryos secretes a dissolving factor. This secretion may be instrumental also in softening or dissolving the jelly in the path of the emerging embryo, although other factors must be operative since the outer jelly coat appears to soften or liquify prior to the inner jelly coat. After hatching, the embryo clings to the jelly mass by means of its V-shaped mucous gland ("suckers"). Active spontaneous swimming begins at stage 23.

The mouthparts begin to differentiate in late embryonic development. Horny beaks, pigmented at the inner edges, appear in the mouth at stage 24. Marginal papillary fringes are also present in a rudimentary condition at this stage. At stage 25, the greater part of the horny beaks are pigmented, the lateral papillary fringes contain small papillae, and the first upper and three lower labial ridges are present. Labial teeth appear in late stage 25 embryos. The first upper ridge is invariably the first to possess teeth, followed shortly thereafter by the differentiation of teeth on the three lower ridges. As discussed below, labial teeth do not appear on the second upper row until larval stage II.

LARVAL DEVELOPMENT

Commencing with the larval period (stage I), the tadpoles were fed boiled spinach. When the tadpoles approached metamorphosis, they were transferred to terraria containing pond water at one end. Juvenile frogs were fed vestigial-winged fruit flies, meal worm larvae, and pieces of liver.

The larvae were preserved at intervals, and staged according to the

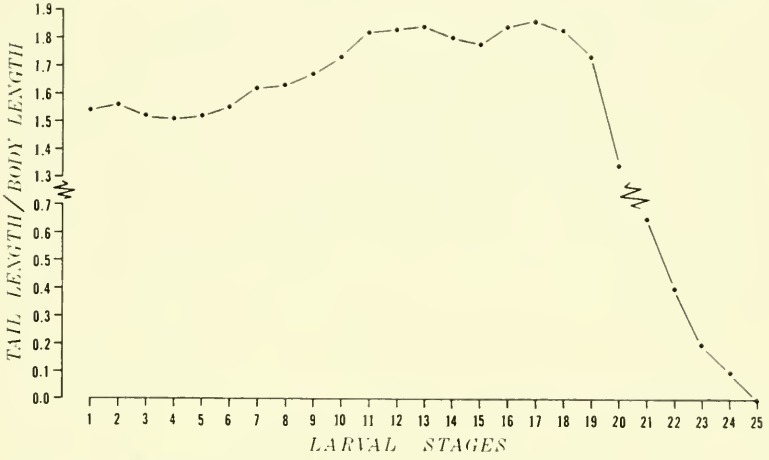


Figure 5. Mean body ratios of *R. capito sevosa* during larval development.

system of Taylor and Kollros (1946). Two measurements were taken: (1) body length, measured from the tip of the snout to the curvature of the body at the point of insertion of the tail, in line with the lateral axis; and (2) tail length, measured from the tip of the tail to the point of its insertion on the body. A third dimension, total length, was computed by adding the values of body length and tail length. Tadpoles in an early stage of development were measured to the nearest 0.01 mm with the aid of a Filar micrometer eyepiece inserted into a stereoscopic microscope; those too large to be handled satisfactorily under a microscope were measured with a dial caliper.

Measurements.—The linear dimensions of the tadpoles at each stage of development are recorded in Table 2. The body dimensions are expressed in terms of ratios in figure 5. The tail length body length ratios were calculated from the data of Table 2 and plotted against stages of development. The tail is approximately 1.5 times as long as the body during the early stages (I-VI). The ratios are higher in the mid-period of larval development; the highest value is 1.84 for stage XVII. The ratios decrease rapidly during the metamorphic period (stages XVIII-XXV).

Length of larval period.—No attempt was made to ascertain precisely the extent of variation in growth rates of the tadpoles. Critical observations were made during four periods, namely, when the majority of the tadpoles reached stages V, X, XVII, XXV. At stage V, the hind limb is a small, undifferentiated bud, reaching a maximum size of one millimeter. The majority of the tadpoles entered stage V at 34 days after the onset of larval development (stage I). Thirty-two days elapsed between stage V and stage X, the latter being characterized by the presence of five interdigital indentations on the distal part of

TABLE 2.

MEASUREMENTS (IN MILLIMETERS) OF TADPOLES OF *Rana capito sevosa*

Stage	Number of Tadpoles	Total Length Mean (Range)	Body Length Mean (Range)	Tail Length Mean (Range)
I	14	17.5 (16.4 - 18.5)	6.9 (6.1 - 7.5)	10.6 (9.6 - 11.4)
II	20	20.0 (18.3 - 21.8)	7.8 (7.1 - 8.6)	12.2 (11.3 - 14.0)
III	21	26.7 (22.8 - 29.0)	10.6 (9.4 - 11.6)	16.1 (13.4 - 17.6)
IV	14	32.6 (31.6 - 34.6)	13.0 (12.4 - 13.7)	19.6 (18.4 - 20.4)
V	11	40.1 (35.1 - 43.8)	15.9 (14.3 - 17.1)	24.2 (20.7 - 27.4)
VI	11	47.6 (44.7 - 53.8)	18.3 (16.4 - 20.5)	28.3 (26.4 - 30.9)
VII	13	53.0 (49.4 - 55.9)	20.2 (18.5 - 22.4)	32.8 (30.1 - 35.8)
VIII	3[a]	58.1 (57.0 - 59.4)	22.1 (22.0 - 22.4)	36.0 (36.0 - 37.0)
IX	2	59.5 (58.5 - 60.4)	22.3 (21.7 - 22.8)	37.2 (36.6 - 37.7)
X	2	60.8 (60.2 - 61.4)	22.3 (22.0 - 22.6)	38.5 (38.2 - 38.8)
XI	4	62.2 (59.0 - 65.0)	22.1 (21.0 - 23.5)	40.1 (38.0 - 42.5)
XII	4	63.4 (62.0 - 64.5)	22.4 (21.5 - 23.5)	41.0 (40.5 - 42.0)
XIII	6	63.7 (61.5 - 66.0)	22.4 (22.0 - 23.5)	41.3 (39.5 - 42.5)
XIV	3	63.8 (62.5 - 66.5)	22.8 (22.0 - 24.0)	41.0 (40.0 - 42.5)
XV	1	63.0	22.7	40.5
XVI	3	66.2 (64.0 - 69.5)	23.3 (22.5 - 24.5)	42.8 (41.5 - 45.0)
XVII	4	71.2 (69.5 - 74.0)	24.9 (24.0 - 26.5)	46.3 (45.5 - 47.5)
XVIII	2	70.8 (68.5 - 72.0)	25.0 (24.0 - 26.0)	45.8 (44.5 - 47.0)
XIX	2	67.8 (67.0 - 68.5)	24.8 (24.0 - 25.5)	43.0 (41.5 - 44.5)
XX	5	57.5 (49.5 - 63.5)	24.5 (23.0 - 27.5)	32.9 (25.5 - 39.5)
XXI	3	43.0 (40.5 - 46.5)	26.0 (25.0 - 27.5)	17.0 (15.5 - 19.0)
XXII	2	36.3 (33.0 - 39.5)	26.0 (25.0 - 27.0)	10.3 (6.0 - 14.5)
XXIII	4	31.3 (30.0 - 33.0)	26.0 (24.5 - 27.5)	5.3 (4.0 - 7.0)
XIV	2	30.3 (27.5 - 33.0)	27.5 (25.5 - 29.5)	2.8 (2.0 - 3.5)
XV	10	28.2 (26.5 - 30.1)	28.2 (26.5 - 30.1)	———

[a] Considerable mortality among the tadpoles necessitated reducing the sample size.

the hind limb bud. The majority of the tadpoles entered stage XVII, when the foot of the hind limb is differentiated, 40 days after stage V. The first tadpole transformed (stage XXV) 35 days later, or 141 days after the onset of larval development. Thirty-one tadpoles metamorphosed within a two-week period; consequently, the length of the larval period under laboratory conditions may be placed at 141-155 days or approximately 5 months.

Mouthparts.—The mouthparts contain a full complement of teeth at stage V. Teeth differentiate on the first upper and three lower labial ridges during the last of the embryonic stages (stage 25) and increase in number up to larval stage V. Teeth first appear on the second upper labial ridge at stage II.

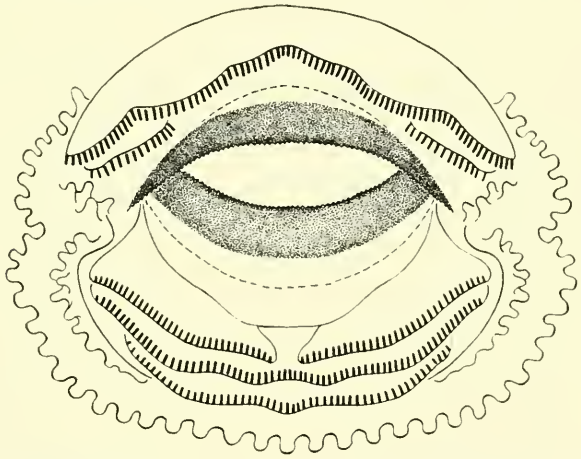


Figure 6. Mouthparts of a formalin-preserved tadpole of *R. capito sevosa* at stage XVII.

A photograph was taken of the mouthparts of a tadpole at stage VI (fig. 2). The labial tooth formula is 2 3. The first upper tooth row is divided medially; the median space is 1.0 to 2.5 times the length of either lateral segment. Each lateral segment of the second upper tooth row is equal to one fourth to one third of the first upper row.

The first lower tooth row is interrupted medially by a short space; the second and third lower rows are continuous. The first and second lower rows are equal in length. The third is 0.2 to 0.4 shorter than either the first or the second lower rows. Marginal papillae are present along the sides of the upper and lower labia and continue uninterrupted along the bottom of the lower labium. A well-defined row of submarginal papillae is present (not conspicuous in fig. 2, but shown in fig. 6). Each lateral fringe bearing the papillae is slightly emarginate.

With the emergence of the forelimbs (stage XX), the rows of

teeth disappear, the papillary fringes become resorbed, and the horny beaks are lost, the lower beak generally before the upper.

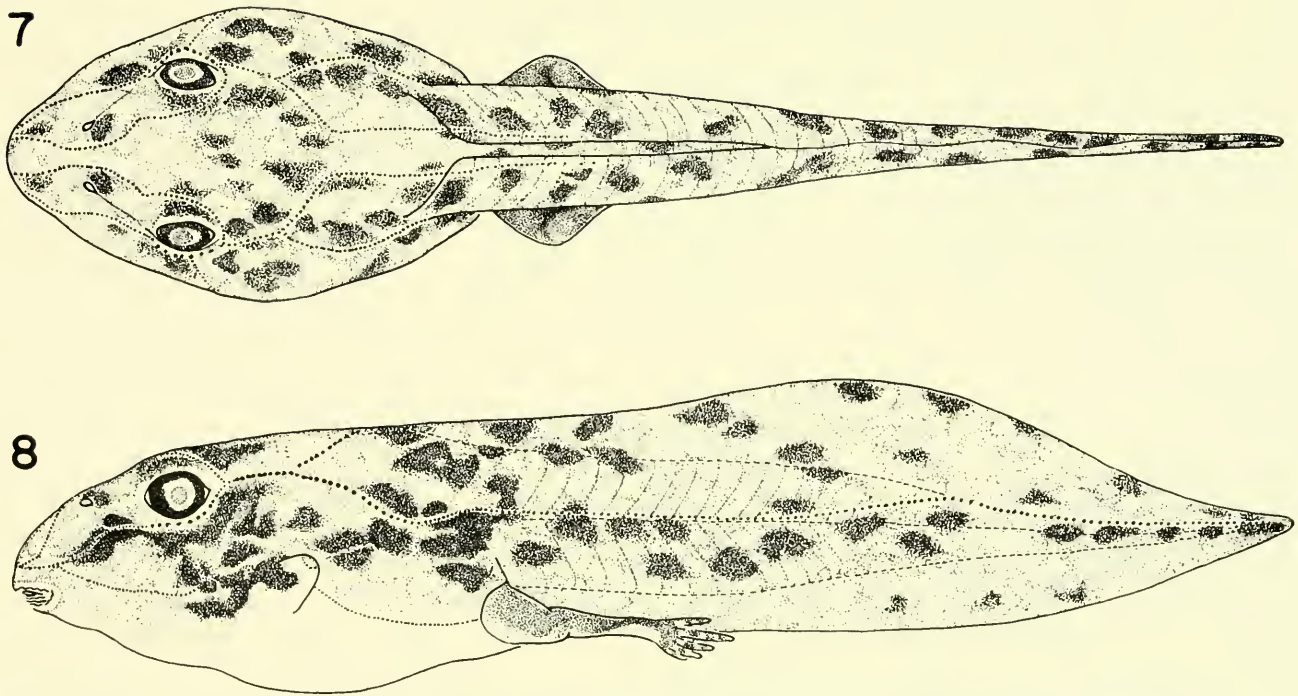
General appearance of tadpole.—A conspicuous feature of the living tadpole is its metallic yellow cast, due to the abundance of yellow chromatophores. The distribution of yellow chromatophores is shown in figures 3 and 4. The photographs were taken of a living tadpole at stage VI narcotized in M.S. 222 (Sandoz Chemical Co., N.Y.C.). The pattern is evident in tadpoles between stages IV and XVII. The yellow chromatophores are found throughout the epidermis of the head and tail, and tend to obscure the subepidermal melanophores. The distribution of subepidermal melanophores is shown in figures 7 and 8, which illustrate a formalin-preserved tadpole at stage XVII. The large clusters of melanophores on the head, tail musculature, and dorsal fin serve to characterize preserved tadpoles of the species. The belly surface is strongly pigmented, a lustrous opaque yellow. The viscera do not show through in the living tadpole, but are faintly visible in formalin-preserved specimens.

The closely spaced muciferous crypts are distinct in both living and preserved tadpoles (figs. 7 and 8). The dorsal row of pits on either side of the dorsal fin extends forward to join the main dorsolateral row of crypts. The latter courses from the tip of the tail to the back of the eye, where it bifurcates to form supraorbital and infraorbital branches, both of which extend to the tip of the snout. Beneath the eye, the infraorbital branch sends a loop ventrally, which meets the mandibular branch to the mouth region. On the ventrolateral surface of the body may be seen a row of crypts extending to the spiracle.

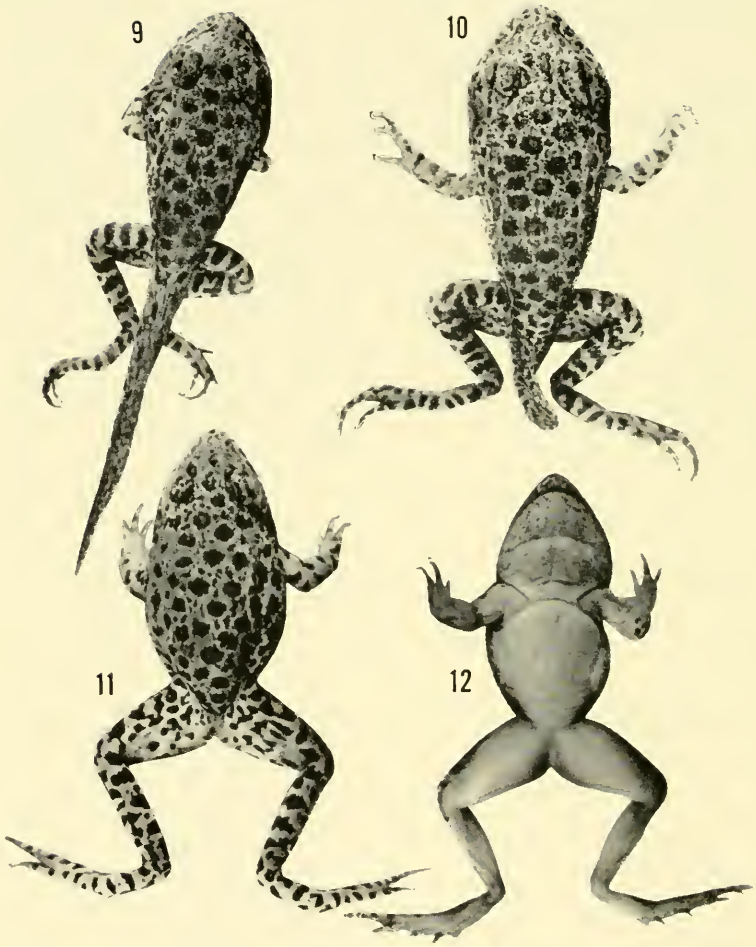
The spiracle is a circular aperture at the end of a short spiracular tube located on the left ventrolateral surface midway between the tip of the snout and the cloaca. The cloaca is dextral, opening on a level with the edge of the ventral fin. The dorsal fin is highly arched, rising above the level of the head and reaching its highest point midway between the tail tip and the insertion of the tail on the body. The tip of the tail is a blunt point.

The eyes are above the lateral axis and nearer the lateral outline in dorsal view than the mid-dorsal line. The eyes are not visible when the tadpole is viewed from the ventral surface.

Transformation.—The pattern of dorsal spots appears when one or both forelimbs protrude (fig. 9). The spots are dark green against a pale green background; in formalin-preserved specimens, the spots and ground color are dark brown and light brown respectively. The spots are irregular in shape and are not light-margined. The dorsolateral folds are delimited as slightly raised surfaces. The legs are conspicuously marked with bands that are equal to or greater than the width of the interspaces. The ventral surface has a white lustre in life and is unspotted.



Figures 7-8. **7** Dorsal and **8** lateral view of a formalin-preserved tadpole of *R. capito sevosa* at stage XVII.



Figures 9-12. Stages in the metamorphosis of *R. capito serosa*. **9** stage XX; **10** stage XXIII; **11, 12** stage XXV.

During the period (stages XXI-XXV) that the tail is resorbed (fig. 10), the dorsolateral folds thicken and brown spots appear on the throat surface. At the end of metamorphosis (stage XXV, figs. 11 and 12), small dark green spots are present in the interspaces between the larger spots on the dorsum and the throat region contains scattered brown pigment spots. Unlike the adult, the dorsolateral folds are not conspicuously elevated, the dorsal skin is smooth, the head is subtriangular, the belly and the undersurface of the thighs are unspotted, and the tympana and post-tympanic folds are undifferentiated. The body length (snout to vent) of ten frogs preserved at transformation

averaged 28.2 mm (range: 26.5 - 30.1 mm); the tibia (tibiofibula) length, 12.5 mm (range: 11.3 - 13.2 mm).

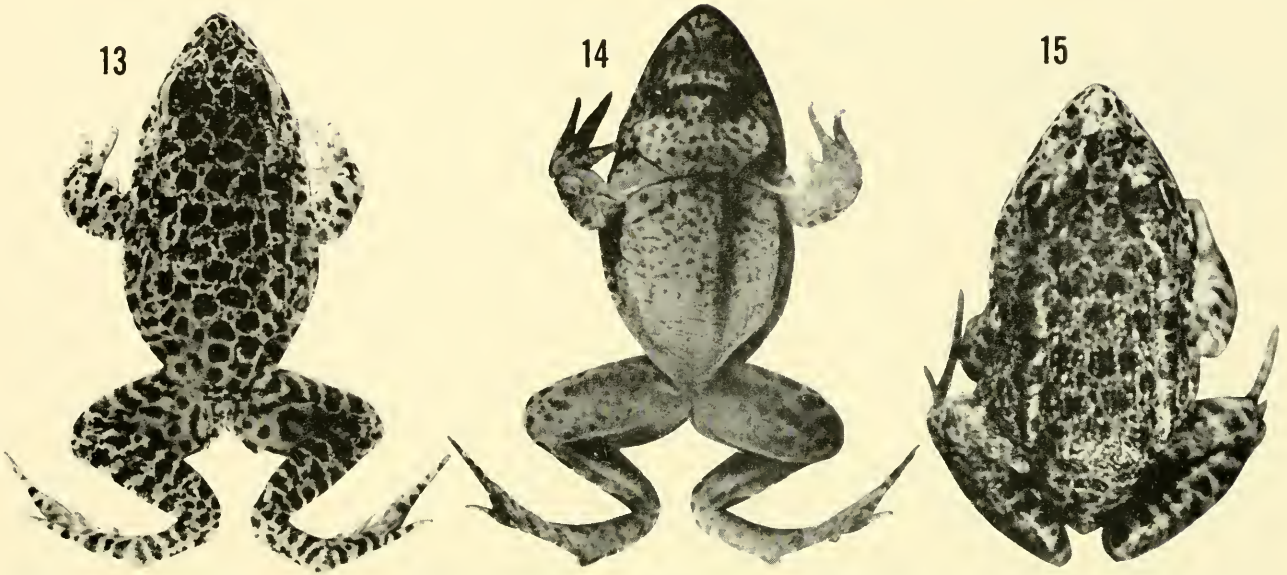
Postmetamorphosis

External changes.—Twenty-one frogs were reared beyond metamorphosis. One was reared for a period of one month after transformation, two for 2.5 months (± 3 days), one for 3.5 months, four for 7.2 months (± 5 days), and five for 9.7 months (± 4 days). Eight others died and underwent post-mortem changes before they could be preserved, rendering them useless for analyses. The five frogs preserved at 9.7 months averaged: in body length, 49.1 mm (range: 48.2 - 50.4 mm); in tibia length, 21.1 (range: 20.5 - 22.4 mm).

The most conspicuous changes in postmetamorphic growth were the formation of wartlike elevations on the dorsal skin, the thickening of the dorsolateral folds, and the appearance of brown spots on the venter and inner surfaces of the thighs. Figures 13 and 14 show a 7.2-month old dusky gopher frog. The overall appearance of the frog is brown-green; the ground color dorsally is brown-green containing dark-green spots. Characteristics of the adult are evident: a narrow, triangular head, a broad body, a warty dorsum, a heavily spotted venter, irregularly shaped, unbordered spots, and dark hindlimb bands that are wider than the interspaces. The dorsolateral folds are conspicuously elevated in the 9.7-month old frog (fig. 15).

Analysis of growth.—Measurements were taken of the body lengths and tibia lengths of the ten recently metamorphosed frogs, the thirteen postmetamorphic frogs, and the twenty-five adults contained in the Tulane University Veterbrate Collections (mentioned in the introduction). The adults possess relatively longer legs, as indicated by the significantly lower value of the mean ratio between body length and tibia length (B.L. T.L. = 2.16, range: 2.04 - 2.24) of the adults as compared to that of the recently metamorphosed frogs (B.L. T.L. = 2.26, range: 2.15 - 2.39). The ratios do not vary significantly in the laboratory-raised frogs at the various periods of growth.

The relation between body length and tibia length may be translated into a mathematical expression that reveals more precisely the rate of change of the two body components. If the tibia length is designated as y, and the body length as x, the relation between them may be expressed by the formula for heterogonic growth, $y = b \cdot x^k$ (or $\log y = k \log x + \log b$), in which b and k are constants, with k representing the coefficient of heterogony. The magnitude of k indicates the amount of discrepancy between the growth processes of the two body parts. In figure 16, the logarithms of the tibia lengths of the laboratory-raised frogs are plotted against the logarithms of the body lengths, and the resulting straight line reveals k as the tangent of its angle of incidence. The calculated value of k is 1.013. The relation between the two body components in the laboratory-



Figures 13-15. Postmetamorphic stages of *R. capito serosa*. **13, 14** 7.2-month old frog; **15** 9.7-month old frog.

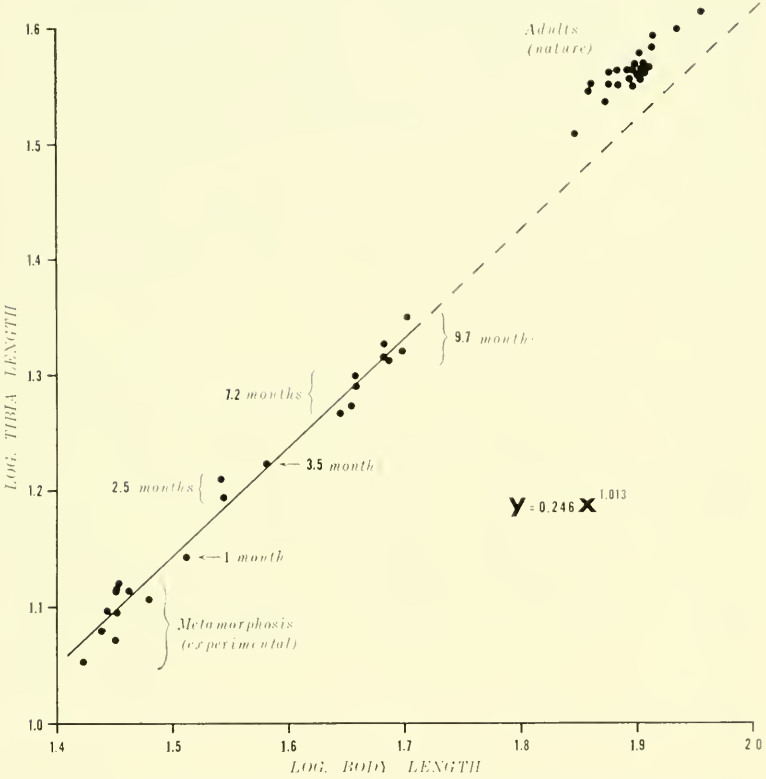


Figure 16. Log-log plot of tibia length (Y) and body length (X) of laboratory-raised *R. capito sevosa* (metamorphosis to 9.7 months) and of adults of natural populations.

raised frogs is essentially isogonic; as the body increases the tibia increases slightly more rapidly. When the values for the two body components of the adults are plotted on the same log-log graph (fig. 16), a striking fact is revealed. The values do not fit on the straight line, but fall above it. Assuming that the heterogonic formula expresses accurately the growth relations of the two body components during early growth, then either a sharp change in rate occurs as the frog approaches adulthood, or environmental factors in nature have disturbed the growth relations.

Comparisons

The early development of *R. capito sevosa* is strikingly similar to that of the Florida gopher frog, *R. capito capito*, as described by Wright (1929, 1932). The early stages of the dusky gopher frog resemble in certain aspects those of the crawfish frog (*R. areolata*)

and the leopard frog (*R. pipiens*). The discussion below is an attempt to bring forth the similarities and differences in the eggs, tadpoles, and transformed stages of the gopher, crawfish and leopard frogs. The author is familiar with the early stages of development of only the dusky gopher frog and the leopard frog. Consequently, the reliability of the comparisons reflects to a large extent the adequacy of the descriptions in the literature.

Eggs.—The eggs of *R. capito sevosa* are smaller than those of *R. capito capito*, *R. areolata circulosa*, and *R. areolata areolata*. The number of eggs per mass, as well as the size of the eggs, distinguish the dusky gopher from the leopard frog of Louisiana. Other comparative data are given in Table 3.

In a cluster, the eggs of the dusky gopher frog appear to be larger in diameter than actual measurements reveal. Bragg (1953) reports the same phenomenon for eggs of crawfish frogs, and infers that the jelly surrounding the eggs has a particularly effective lens action.

Mouthparts.—The larval mouthparts of the dusky and Florida gopher frogs are characterized by a wide median space in the second upper labial row of teeth. Wright (1929) states for larvae of *R. capito capito:* " . . . median space between the second upper labial row 1.0 - 2.0 times the length of either lateral part of this row; third lower row 0.33 - 0.66 shorter than the first or second rows . . . ". The median space in the larval mouthparts of *R. capito sevosa* is 1.0 to 2.5 times either lateral segment of the second upper row, and the third lower row is 0.2 to 0.4 shorter than the first or second lower rows. The differences in the relative length of the third lower labial row may be significant.

The second upper tooth row is interrupted in the midline by a narrow space in tadpoles of both northern and southern crawfish frogs. The illustration by Smith, Nixon and Smith (1948) of the mouth disc of larvae of *R. areolata circulosa* from central Illinois shows a median space that is less than one half of the length of either lateral row. Bragg (1953) reports a similar condition in tadpoles of *R. areolata areolata* from Oklahoma.

Wright (1914, 1929, 1932) states that the median space in the second upper tooth row is 0.5 to 1.0 times either lateral segment in tadpoles of southern leopard frogs, whereas it is 1.0 to 1.5 times either lateral part in larvae of northern leopard frogs. Wright's descriptions of "northern" and "southern" leopard frogs are based on tadpoles from the vicinity of Ithaca, New York, and Okefinokee swamp, Georgia, respectively. The description of larval mouthparts of *R. pipiens* from eastern Wisconsin (Volpe, 1955) fits Wright's account of northern *R. pipiens*. However, the mouthparts of tadpoles of leopard frogs from eastern Louisiana (Boutte, New Orleans, and Slidell) differ considerably from those of larvae of leopard frogs from Georgia. The median space in the larval mouthparts of leopard frogs from eastern Louisiana is 1.0 to 2.0 times either lateral segment

TABLE 3.
COMPARISONS OF EGGS OF GOPHER, CRAWFISH AND LEOPARD FROGS
(Measurements in Millimeters)

Taxon	Locality	Vitellus	Inner Membrane	Outer Membrane	Egg Complement	Authority
		Mean Diameter (Range in Parenthesis)				
R. areolata circulosa	Eastern Kansas	— (2.46 - 2.50)	— (3.15 -)	— (4.5 - 5.0)	7,000	Smith (1934)
	Central Illinois	2.05 (1.91 - 2.18)	2.53 (2.3 - 3.1)	4.03 (3.9 - 4.3)	3,192 - 6,807	Smith, Nixon and Smith (1947, 1948)
	Eastern Oklahoma	2.2 (1.8 - 3.8)	3.2 (2.9 - 3.2)	4.3 (4.0 - 4.5)	7,000	Bragg (1953)
R. areolata areolata	Eastern Oklahoma: Sample 1	2.1 (1.7 - 2.4)	2.8 (1.00 - 3.3)	4.0 (3.3 - 5.0)	3,000 - 4,500	Bragg (1953)
	Sample 2	2.1 (1.0 - 2.2)	2.8 (2.5 - 3.0)	4.1 (4.0 - 4.1)	—	
R. capito capito	Okefinokee Swamp, Georgia	2.0 (1.8 - 2.4)	3.9 (3.1 - 4.4)	5.3 (4.4 - 6.0)	5,000	Wright (1932)
R. capito sevosa	Pearl River, Louisiana	1.84 (1.67 - 2.18)	2.37 (2.06 - 2.75)	4.00 (3.44 - 4.48)	6,000	Present Report
R. pipiens (=*R. pipiens pipiens*)	Ithaca, New York	1.7 (1.6 - 2.0)	2.4 (2.3 - 3.0)	5.1 (4.2 - 6.0)	3,500 - 4,500	Wright (1914)
R. pipiens (=*R. pipiens pipiens*)	Wisconsin	1.73 (1.60 - 1.95)	2.45 (2.10 - 2.72)	4.15 (3.24 - 4.95)	—	Volpe (1954)
R. pipiens (=*R. pipiens sphenocephala*)	Okefinokee Swamp, Georgia	1.6 (1.4 - 1.8)	2.6 (2.4 - 3.0)	3.8 (3.4 - 4.0)	1,054 - 1,500	Wright (1932)
	Eastern Louisiana	1.62 (1.44 - 1.76)	2.30 (2.06 - 2.46)	3.66 (3.18 - 4.04)	2,000	Volpe (unpublished)

of the second upper labial row, a condition similar to that in tadpoles of the dusky gopher frog. The relative length of the third lower row of teeth constitutes the best criterion for distinguishing the larval mouthparts of the dusky gopher frog and the leopard frog of eastern Louisiana. The third lower row in the latter larvae is generally half as long (range: 0.3 - 0.7) as the first or second lower tooth rows. Smith (1934) reports that the third lower row is approximately one half of the length of the second lower row in tadpoles of the leopard frog from Kansas.

General appearance of tadpole.—The distinctive features of the tadpoles of the dusky gopher frog are: (1) the yellow lustre, an effect created by numerous yellow chromatophores, (2) the large clusters of melanophores on the head, tail musculature, and dorsal fin, (3) the conspicuous pattern of muciferous crypts, and (4) the high arc of the dorsal fin. As far as can be determined from Wrights' description (1929, 1932), these features are found also in larvae of *R. capito capito.*

The dorsal fin is highly arched in the tadpole of *R. areolata areolata,* whereas in *R. areolata circulosa,* it is "more evenly rounded from one end to the other" (Bragg, 1953). The tail fins of northern and southern crawfish frogs are not as heavily mottled with black pigment, as judged by Bragg's illustrations (*op. cit.*).

Melanophores are present in the tail fins of larvae of leopard frogs, but they are not typically grouped in large clusters. The "spots" or aggregations of melanophores are more pronounced in southern than in northern leopard frogs. Wright (1932) describes the tail fins of the latter as "marked with scattered fine spots and pencilings"; those of the former as "usually with quite prominent dark spots".

Larval dimensions.—Data on absolute body dimensions of tadpoles must be interpreted with caution, since tadpoles vary in size at different developmental stages and under different environmental conditions. Knowledge of the potential range of sizes that may be realized by tadpoles of a particular species is lacking. Most investigators, however, present data on the largest tadpole in their sample, with the view, I presume, that the largest tadpole represents the maximum size that can be achieved by the larvae of a particular species. This approach may be valid only if the samples are large and are taken from various populations throughout the geographic range of the species. The following maximum sizes have been reported for the larvae of the species under consideration: *R. capito capito,* 84 mm (Wright, 1929, 1932), *R. pipiens pipiens,* 84 mm (Wright, 1914), *R. pipiens sphenocephala,* 74 mm (Wright, 1929, 1932), *R. areolata circulosa,* 65 and 76 mm (Smith, Nixon, and Smith, 1948, and Bragg, 1953, respectively), and *R. areolata areolata,* 63 mm (Bragg, 1953). The largest size achieved by a tadpole of the dusky gopher frog under the growth conditions described herein was 74 mm. The significance of these values is questionable; one

certainly would be hesitant to consider a given value as characteristic of a particular species.

Transformation.—The newly metamorphosed dusky gopher frog lacks the warty dorsum, conspicuously elevated dorsolateral folds, and the heavily mottled venter of the adult. At this stage the dusky gopher frog simulates the appearance of the Florida gopher frog but may be distinguished from it by its broad leg bands and associated narrow interspaces (*cf.*, fig. 9 or 10 with Wright's plate XXXV, 1932). It may be further distinguished from a recently metamorphosed crawfish frog by the absence of light margins around the dorsal spots. There is no difficulty in differentiating recently transformed gopher frogs and leopard frogs. Among other distinguishing features, the dorsal spots of the latter are generally larger, fewer in number, and more regularly shaped.

The following ranges of body lengths (snout to vent) of newly metamorphosed frogs have been reported: *R. pipiens pipiens*, 18-31 mm (Wright, 1914), *R. pipiens sphenocephala*, 18-33 mm (Wright, 1932), *R. capito capito*, 27-35 mm (Wright, 1932), and *R. areolata circulosa*, 22.2 - 24.2 mm (Smith and List, 1955). The last mentioned authors record a snout-to-vent length of 31 mm for one transformed dusky gopher frog collected in Jackson County, Mississippi. The dusky gopher frogs reared in the present study averaged 28.2 mm at transformation (range: 26.5 - 30.1).

Summary

1. Embryos of the dusky gopher frog, *Rana capito sevosa*, collected at Pearl River, Saint Tammany Parish, Louisiana, were reared through metamorphosis in the laboratory.

2. The dimensions of the egg and its two gelatinous coats are: mean diameter of vitellus, 1.84 mm (range: 1.67 - 2.18); mean diameter of inner envelope, 2.37 mm (range: 2.06 - 2.75); mean diameter of outer envelope, 4.00 mm (range: 3.44 - 4.48).

3. The embryos hatch at stage 17, just prior to the onset of muscular activity, approximately 3.5 days after fertilization. The operculum covers the gills (stage 25), marking the end of the embryonic period, approximately 7 days later. The embryos at stage 25 averaged, in total length, 13.3 mm.

4. The duration of the larval period (stages I-XXV, defined in Taylor and Kollros, 1946) was approximately 5 months. The mouthparts contain a full complement of teeth at stage V. The mouthparts are characterized by a wide median space in the second upper tooth row (1.0 to 2.5 times the length of either lateral segment) and a third lower tooth row that is 0.2 to 0.4 shorter than either the first or second lower rows. Conspicuous features of the tadpole are its metallic yellow lustre, the large clusters of melanophores on the head, tail musculature, and dorsal fin, the pattern of well-defined muciferous

crypts, and the high arc of the dorsal fin. The largest size (snout-to-tail tip length) attained by the tadpoles was 74 mm.

5. Metamorphosed frogs averaged 28.2 mm in snout-to-vent length. The leg bands are equal to or greater than the width of the interspaces and the irregular spots on the back are not light-margined. However, the transformed frogs lack the warty dorsum, elevated dorsolateral folds, and mottled venter that are characteristic of the adult. Frogs reared for a period of approximately 10 months after metamorphosis resemble the adult.

6. The body length tibia length ratios are significantly lower in young laboratory-raised frogs than in adults from natural populations. Either the growth rates of the two body components change as the frog approaches adulthood, or the growth relations are different in frogs developing in nature than in the laboratory.

7. The early stages of development of the dusky gopher frog are compared with those of the Florida gopher frog, northern and southern crawfish frogs, and northern and southern leopard frogs. The early development of *R. capito sevosa* is strikingly similar to that of *R. capito capito*.

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Abstract

The eggs, tadpoles, and recently metamorphosed forms of the dusky gopher frog, *Rana capito sevosa*, from Saint Tammany Parish, Louisiana have been described. The near-identity of the early stages of development of the dusky gopher frog to the Florida gopher frog, *Rana capito capito*, attests to their close affinity.