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A REVIEW OF MIDDLE NORTH AMERICAN TOADS OF THE GENUS *MICROHYLA*

By MAX K. HECHT AND BESSIE L. MATALAS

As currently understood, three nominal species of the narrow-mouthed toads, *Microhyla*, inhabit the southeastern and central portions of the United States, with ranges extending into Mexico. In "A check list of North American amphibians and reptiles," Stejneger and Barbour (1943) list *Gastrophryne areolata* (Strecker), *Gastrophryne carolinensis* (Holbrook), and *Gastrophryne olivacea* (Hallowell). The purpose of this paper is to ascertain the taxonomic status and ranges of these forms.

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Approximately 650 narrow-mouthed toads in the collections of the United States National Museum (U.S.N.M.), American Museum of Natural History (A.M.N.H.), Cornell University (C.U.), University of Michigan Museum of Zoology (U.M.M.Z.), Chicago Natural History Museum (C.N.H.M.), and the University of Rochester (U.R.) have been examined.

NOMENCLATORIAL HISTORY

In 1836 Holbrook described *Engystoma carolinensis*, from Charleston, South Carolina. *Engystoma olivaceum* was described by Hallowell from "Kansas and Nebraska" in 1856 and redescribed as a new species, *Engystoma texense*, in 1859 by Girard. Strecker (1909) described *Engystoma areolata* from a specimen in the collection of J. D. Mitchell taken in the Guadalupe River bottom, Victoria County, Texas. Wright and Wright (1933) recognized three species in the United States: *Gastrophryne areolata*, *G. carolinensis*, and *G. texensis*. In the same year Smith referred

G. texensis to the synonymy of *Gastrophryne olivacea*. Parker (1934) combined the New World genus *Gastrophryne* with the Old World *Microhyla*, although Stejneger and Barbour have preferred to retain *Gastrophryne*. Burt (1938a) attempted to show that *Microhyla areolata* (Strecker) was a synonym of *Microhyla olivacea* (Hallowell). Recently Taylor (1943) has described *Microhyla mazatlanensis* based on three specimens from Mazatlán, Sinaloa, Mexico, and this name must be considered in this survey.

DIAGNOSTIC CHARACTERS

At the beginning of the present investigation measurements were tabulated and various ratios were calculated. However, these were found to be of no diagnostic value, not only because relative proportions

change with age, but also because it is difficult to make precisely comparable measurements on specimens preserved in divers ways. Nevertheless, head width, head length, and snout to vent length are

of interest even though their diagnostic value is negative. The only characters found to be of taxonomic value were those of coloration. Burt (1938a) separates two supposed species, *M. carolinensis* and *M. olivacea*, with which he synonymized *areolata*, as follows:

"Upper surface light greenish or gray, usually without dark blotches or other markings; Texas, except extreme eastern part. *Microhyla olivacea*.

"Upper surface darker, often chocolate-colored or tan, usually blotched or other markings; extreme eastern Texas. *Microhyla carolinensis*."

Whereas these differences are useful in separating Texan specimens, an additional population west of the continental divide must also be considered. The three forms may be contrasted in tabular form as follows:

<i>carolinensis</i>	<i>olivacea</i>	<i>mazatlanensis</i>
1. Ventral surface mottled (fig. 1)	1. Ventral surface immaculate or with scattered melanophores (fig. 3)	1. Ventral surface with scattered melanophores (fig. 5)
2. Dorsum dark (brown, silvery gray) and blotched above or markings obscured by dark background, sometimes with dorsolateral stripe, indistinct or if distinct bordered by a dark margin (fig. 2)	2. Dorsum light (usually tan), not blotched, rarely with dark spots, a faint bar sometimes present on femur and tibia (fig. 4)	2. Dorsum light tan or grayish with at least some spots, a distinct bar on femur and tibia (fig. 6)

INTERGRADATION

A. BETWEEN *carolinensis* AND *olivacea*: The pattern on the ventral surface provides the simplest basis upon which a separation of the forms *carolinensis* and *olivacea* can be predicated, and it is in this character that intergradation can best be shown. In specimens of *olivacea* from the western periphery of its range, the ventral surface is immaculate. The number of melanophores appearing on the ventrum increases on specimens from localities farther east.

Populations including individuals representing both types of pigmentation occur in Victoria County, Texas, and in Latimer County, Oklahoma. Specimens from the same localities were found to have an intermediate combination of characters, ventral pigmentation being present in the form of mottling on the throat and sides of the abdomen (see figs. 7 and 8). The Victoria County series in the United States National Museum (U.S.N.M. Nos. 23133, 23744-23746, 23942, 42317-42331, 42333-42339, 42341, 51509, 78645-78659, 78662-78683, 78691-78695) includes normal *M. carolinensis*, and *M. olivacea* as well as a large series of intermediates. The following is a tabulation of the three types of individuals

from localities in Victoria County where both forms have been taken:

	<i>olivacea</i>	<i>carolinensis</i>	Intermediates
Guadalupe River bottom	0	0	7
Collette Creek	1	6	18
Victoria	4	3	16
TOTALS	5	9	41

Converted into percentages we find that 9 per cent are *olivacea*, 16 per cent are *carolinensis*, 75 per cent are intermediates. Specimens from Latimer County, Oklahoma, examined include U.M.M.Z. Nos. 73208, 73209, 77596, 77597, in which series of both *M. carolinensis* and *M. olivacea* as well as intermediates also occur. In this series there are three *olivacea*, one *carolinensis*, and six intermediates or, in terms of percentages, 30 per cent, 10 per cent, and 60 per cent, respectively. It is not known whether any selection was exercised by the collectors of these series.

There is geographic variation in the ventral pattern of *M. carolinensis* which complicates the situation. Some specimens from central and northern Florida

have a large non-pigmented area on the abdomen while on others many smaller non-pigmented areas have coalesced. In the Florida Keys this condition has reached its extreme development. In the southernmost Keys the amount of ventral pigmentation decreases. At Key West there is marked reduction in ventral mottling, so much so in fact that some specimens (29 per cent) closely resemble the western form, *olivacea* (see fig. 9). A few specimens have the normal *carolinensis* ventral pattern.

Examination of metamorphosing tadpoles of *carolinensis* in the Cornell University collection discloses ventral mottling on individuals in which limbs were beginning to emerge. Prior to the development of limbs, the ventral surface is immaculate. No material of comparable larval stages of *olivacea* has been available.

In *olivacea* the dorsum is unblotched in specimens from the western parts of its range. However, on the eastern edge of the range dark brown blotches appear on the tan dorsum, usually in specimens having some ventral pigmentation. The type of *Engystoma areolata* Strecker (U.S.N.M. No. 38999) has these dark blotches on the dorsum as well as definite traces of the ventral mottled pattern. The dorsal blotches are more characteristic of *carolinensis* on which they are not always evident, however, because of the darker ground color. Since the only specimens of *areolata* in collections all come from the region of intergradation, we regard the type and similar specimens as intergrades.

Throughout the range of *carolinensis*, occasional individuals are found that have two light dorsolateral stripes, but these occur more frequently in extreme southern Florida. In populations in the Florida Keys, three principal patterns are evident which may be segregated as follows: (a) the "Key West" form in which the dorsal pattern consists of two prominent, light tan, dorsolateral stripes, bordered by a distinct dark margin on a tan background, with the ventrum mottled (see fig. 11); (b) the *olivacea*-like form, virtually without a pattern so that specimens have a uniformly light tan dorsum, with the ventral coloring

usually much reduced (see figs. 9 and 10); (c) a third form includes individuals like mainland *carolinensis*, in which the dorsum may be dark and blotched or with indistinct dorsolateral stripes (without black margins) and the ventrum mottled. Most specimens from Lignum Vitae Key (U.S.N.M. Nos. 95716-95720), the northernmost of the Keys from which material has been available, have the ventral and dorsal pigmentation of mainland *carolinensis*; only one from this Key resembles the *olivacea*-like specimens. Of two individuals from Big Pine Key (U.S.N.M. Nos. 95827 and 85454) one is most nearly like "Key West" whereas the other is *olivacea*-like. One from Cudjoe Key (U.S.N.M. No. 95825) is likewise similar to *olivacea* in pattern characters. Without difficulty it is possible to assign each specimen from the Keys to one of the three forms described.

Referring to the first form as the "Key West" pattern, the second as *olivacea*-like, and to the third as *carolinensis*, we find that the three types of individuals inhabiting the Keys (arranged from north to south) may be tabulated as follows:

	<i>caro- linensis</i>	"Key West"	<i>olivacea- like</i>
Lignum Vitae	6	0	1
Big Pine	0	1	1
Cudjoe	0	0	1
Key West	3	18	8
	—	—	—
TOTALS	9	19	11

Converted to percentages, therefore, we find in the Florida Keys a heterogeneous population in which 23 per cent have mainland *carolinensis* characters and 48 per cent have the "Key West" pattern, whereas 29 per cent are *olivacea*-like.

The *olivacea*-like individuals differ not only in the dorsal pattern but in the ventral pattern as well, indicating perhaps a greater genetic difference between them and the mainland form than between the "Key West" sort and mainland *carolinensis*. However, in view of the locality data for the small samples available it is a reasonable assumption that individuals with the various patterns interbreed as indicated by intermediates. Conceivably some de-

gree of ecological isolation could exist, although this seems unlikely.

B. BETWEEN *olivacea* AND *mazatlanensis*: Taylor (1943) described *Microhyla mazatlanensis* from specimens collected at Mazatlán, Sinaloa. These same specimens he had previously called *Microhyla olivacea* (1938). From the diagnosis given, little can be found that warrants the description of a new form although the form appears to be recognizable on the basis of pattern characters. He states in part: "Related to *Microhyla olivacea* but distinctly smaller in size, the head a little narrower, the snout projecting more, a little more flattened above and rounding at the tip." Without more precise data this diagnosis is virtually without meaning. Snout to vent measurements of the type and paratypes are 22.2 mm., 23.3 mm., and 24.8 mm., respectively, and thus fall within the size range of *olivacea*. Presumably the series is composed of small adults, and it is for this reason that the head appears to be narrower and the snout longer. It has been observed that smaller specimens of both *carolinensis* and *olivacea* tend to have more acute snouts and relatively narrower heads than adults approaching full maturity and maximum size.

Perhaps the most useful data given are those in the color description: "Above nearly uniform brown with some scattered black spots tending to form a pattern medially; a broken black line begins behind the eye and continues to some distance on the side; trace of an inguinal spot, which together with a single bar or spot on

the femur, the tibia, and feet, form a continuous line when the limb is folded. Venter cream, with a very slight peppering of pigment on the chin; sides slightly mottled with lighter and darker; underside of the feet purplish brown, and the hands similarly colored, but to a lesser extent."

The black-spotted dorsum, the "peppered" ventrum (referred to in this paper as traces of mottling or the presence of scattered melanophores), and the continuous bar formed by the markings on the femur and tibia by the folded limb would seem to indicate that Taylor's *mazatlanensis* is virtually identical with the specimens from Peña Blanca Springs, Santa Cruz County, Arizona (U.M.M.Z. Nos. 75737, 75738, totaling 15 specimens), and those from Sonora 10 miles north of Pilares (U.M.M.Z. No. 78333), Guirocoba (A.M.N.H. Nos. 51244-51247), and Noria (U.M.M.Z. Nos. 72174-72177) which have these same markings (see figs. 5 and 6). The individual from Pilares, Sonora (U.M.M.Z. No. 78333), lacks a distinct bar on the femur and tibia, and the blotches on the dorsum are not prominent, although the ventral "peppering" is present. Likewise some specimens of *olivacea* (see fig. 4) have leg spots so arranged that a bar is formed on the tibia and femur as in individuals from Edinburg, Texas (C.U. Nos. 2302, 2303), Gage County, Nebraska (A.M.N.H. No. 52155), and from Musquiz, Coahuila (C.N.H.M. Nos. 403-405). In some respects these specimens are intermediate between *mazatlanensis* and *olivacea*.

SIZE AS A TAXONOMIC CHARACTER

Snout to vent measurements were made on all specimens to ascertain whether there were any size differences between the forms. As in some other microhylids, the sexes can be separated in most cases by the blackish throat that appears to be present only on mature males. Most males develop these blackish throats by the time they attain a length of 22.5 mm., so this was used arbitrarily as the minimum adult size for females.

In order to ascertain the validity of this

means of determining the sex, 55 specimens (including 25 *olivacea* and 30 *carolinensis*) were dissected. Ten per cent of those without black throats were males of adult size, although every dark-throated individual (26 of the total) was a male.

Wright and Wright (1942) state that males of *carolinensis* range in size from 20 to 30 mm., females from 22 to 36 mm. For *olivacea* they give the following figures: males, 20 to 28 mm.; females, 19 to 29.5 mm. It would appear from these figures

that *carolinensis* females are much larger than individuals of *olivacea* of the same sex, suggesting that this might be another difference between the two forms. *Microhyla mazatlanensis* is diagnosed by Taylor as being "distinctly smaller" than *Microhyla olivacea*. However, when the means of snout to vent measurements of specimens allocated by us to the three forms (as well as the figures Taylor gives) are compared they show that this is not so.

Snout to vent measurements (in mm.) of

	275 <i>carolinensis</i>	105 <i>olivacea</i>	27 <i>mazatlanensis</i>
Males	26.0 (22.5-33.5)	27.1 (22.5-33.0)	26.0 (22.5-28.0)
Females	27.5 (22.5-36.5)	28.1 (22.5-38.0)	27.7 (22.5-30.0)

adults exceeding 22.5 mm. permit comparisons in tabular form, with sexes segregated only on throat color characters. The differences between the means (extremes in parentheses) are negligible, although size differences between the sexes are evident. Specimens without dark throats comprise roughly 50 per cent of each sample.

From these figures it is concluded that size is of no importance as a taxonomic character.

DISTRIBUTIONS

Microhyla c. carolinensis is primarily an inhabitant of the Austroriparian biotic province of the southeastern United States as defined by Dice (1943), although it ranges northward into the Carolinian and Illinoian provinces. The eastern narrow-mouthed toad occurs from Cove Point, Calvert County, Maryland (A.M.N.H. Nos. 43999, 44000, 45290, 45291), along the coastal plain south to Florida. In Virginia, North Carolina, South Carolina, Georgia, and Alabama this frog occurs from the Piedmont to the coast with some records in the latter three states for the mountains. It has been taken in five scattered counties in Tennessee (Sullivan, McMinn, Hamilton, Henry, and Shelby), and in Kentucky from Warren County (Barbour, 1941) as well as from Mammoth Cave National Park, Edmonson County (U.S.N.M. Nos. 118379, 118380). Dickerson (1906) records *carolinensis* from southern Illinois, but no specimens are available to substantiate the statement. Cagle (1941) states that *carolinensis* is not known from Illinois but "may be expected in the extreme southern part" of the state. Hurter's specimens from St. Louis County, Missouri (U.S.N.M. Nos. 57700, 57701), are north of the latitude in which southern Illinois lies, but on the western side of the Mississippi River. It seems not improbable therefore that this frog occurs in southern Illinois. *M. c. carolinensis* is also

generally distributed in Mississippi, Louisiana, and eastern Arkansas, but in Missouri is known only from St. Louis, Butler, and Barry counties. In Texas, it is known from Lamar, Liberty, Bowie, Shelby, Harris, Galveston, and Victoria counties. Interbreeding with *olivacea* is assumed to occur in Victoria County, Texas, and Latimer County, Oklahoma, as indicated by the presence of intermediates.

The second race, *M. c. olivacea*, occurs within no fewer than five biotic provinces as defined by Dice (*supra cit.*); it is generally distributed in eastern and central Kansas and Oklahoma (except for the Panhandle) and in central and southern Texas, with one record as far west as Jeff Davis County (Wright and Wright, 1942). It is also known from Gage County, Nebraska (Loomis, 1945), and from Jackson, Cass, and Platte counties, Missouri (Anderson, 1941). In Mexico it has been taken at the following localities: Musquiz (C.N.H.M. Nos. 402-405, 28699-28704, 28759) and Torreon (Taylor, 1940) in Coahuila; Progreso, Rio Santa Maria, Chihuahua (U.S. N.M. No. 105161, a badly mutilated specimen which appears to be *olivacea*); Conejos in Durango (Taylor, 1940).

The third race, *Microhyla c. mazatlanensis*, probably is generally distributed in the foothills of northwestern Mexico (Sinaloa and Sonora) barely ranging into southern Arizona; roughly its range may

be said to occupy the eastern portion of the Sonoran and the northern portion of the Sinaloan biotic provinces as mapped by Dice (*supra cit.*). If our belief concerning the identity of the type is correct, *mazatlanensis* is known from the following localities: Mazatlán, Sinaloa (type locality); 10

miles north of Pílares, 5 miles north of Noria, and from Guirocoba in Sonora; and Peña Blanca Springs, in Santa Cruz County, Arizona. Except for the type and paratypes all the other specimens reported have been examined.

DISCUSSION

The data presented above indicate that populations with pattern characters ranging from those of typical *carolinensis* to those of typical *olivacea* occur in southern United States and northeastern Mexico with a third population, *mazatlanensis*, on the other side of the continental divide. The transition between *olivacea* and *carolinensis* presumably occurs along a line from Victoria County, Texas, to Latimer County, Oklahoma, where intermediates (including the type of *Engystoma areolata*) are found. Farther west, there is no evidence of any dichotomy in characters between *olivacea* and *mazatlanensis*. Rather, the differences between the two populations are mean differences, with no abrupt transition. The single specimen from Pílares in northeastern Sonora has characters of both *mazatlanensis* and *olivacea*, and presumably a series of annectent populations ranges across the continental divide. This is possible since a number of amphibians and reptiles range across the divide in this region, according to Bogert and Oliver (1945). It may be noted that the areas of intergradation between *carolinensis* and *olivacea* are in the same general region in which subspecies of mammals, reptiles, and other amphibians also intergrade.

The narrow intergradation area indicates either that *carolinensis* and *olivacea* are approaching complete isolation or that previously existing isolating mechanisms

have broken down. Pattern differences between these two forms, despite a lack of other morphological differences, indicate some degree of isolation. Whether the two populations can be called incipient species or whether the differences arose during previous isolations is a matter for speculation. Comparative life history studies dealing with populations in the critical areas in the range of this species may reveal other differences between the two forms and throw more light on the problem.

The small populations that exist in the Florida Keys would be described as a new subspecies by some workers. But there is no evidence of isolation or more than partial differentiation; only mean differences can now be detected. However, individual specimens of the population inhabiting the Keys are as distinct from *carolinensis* as *mazatlanensis* is from *olivacea*, but the situation for the population as a whole is anomalous. Scarcely a fourth of individuals from the Keys are like mainland *carolinensis*, 29 per cent are *olivacea*-like, and 48 per cent have the "Key West" pattern. Because interbreeding among the three types of individuals may be inferred on the basis of samples, pending better evidence to the contrary, we conclude that the populations on the Keys are not worth taxonomic recognition.

SUMMARY AND CONCLUSIONS

1. *Microhyla carolinensis* (Holbrook), *Microhyla olivacea* (Hallowell), and *Microhyla mazatlanensis* Taylor apparently interbreed where their ranges adjoin and therefore should be ranked as subspecies.

2. *Microhyla areolata* (Strecker) is not a straight synonym of *Microhyla olivacea* but represents an intermediate population between *carolinensis* and *olivacea*. There-

fore, it should be included under the synonymy of both forms.

3. What appears to be a poorly differentiated local population inhabiting the Florida Keys is composed of 29 per cent *olivacea*-like individuals, 48 per cent "Key West," and 23 per cent normal *carolinensis*. Because intermediates exist and because interbreeding presumably occurs between individuals of the three pattern phases, these heterogeneous populations in the Keys are referred to *M. c. carolinensis*. It is conceivable that each of the three pattern phases manifests a different habitat preference, but the locality data available for the specimens examined are not sufficiently precise to determine this. Or isolating mechanisms that existed in the past may have broken down; it is not impossible that the overseas highway, which now connects the islands comprising the Keys, has permitted dispersals where previous geographical isolation existed. Further in-

vestigations in the Keys will be necessary to prove or disprove such assumptions.

KEY TO THE SUBSPECIES OF *Microhyla carolinensis*

1. Ventrums mottled.
 - A. Dorsum dark; dorsolateral stripe sometimes present, indistinct, or, if distinct, bordered by a dark margin
..... *carolinensis*
2. Ventrums immaculate or with scattered melanophores.
 - A. A blotch or spots on the femur and tibia which form a bar or continuous line when the limb is folded; dorsum with dark spots.
..... *mazatlanensis*
 - AA. Spots rarely present on the femur and tibia; if present usually not forming a distinct bar when the limb is folded; dorsum tan and generally without markings. . . *olivacea*¹

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¹ Some of the specimens from the Florida Keys will fall in this part of the key.

² This bibliography includes references cited as well as the sources of literature records included on the spot map.

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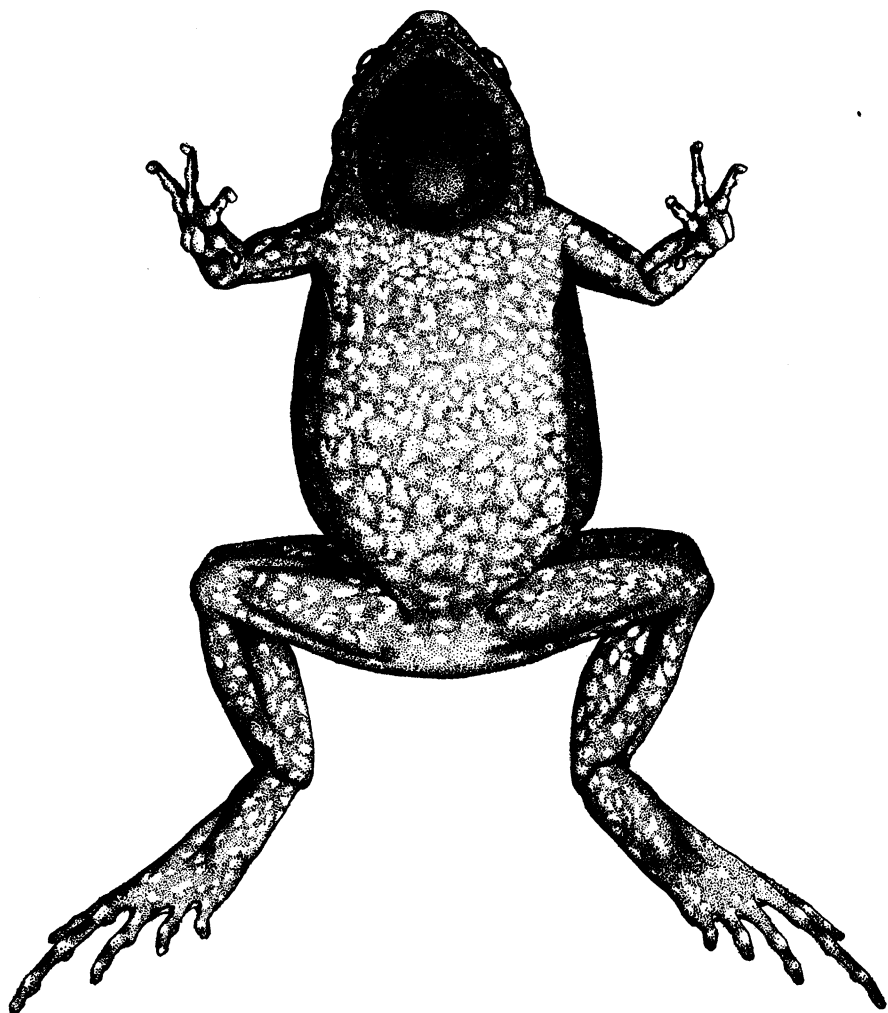


Fig. 1. Ventral view of mainland *Microhyla c. carolinensis*, C.U. No. 4733, from Jefferson County, Louisiana (male, $\times 3$).

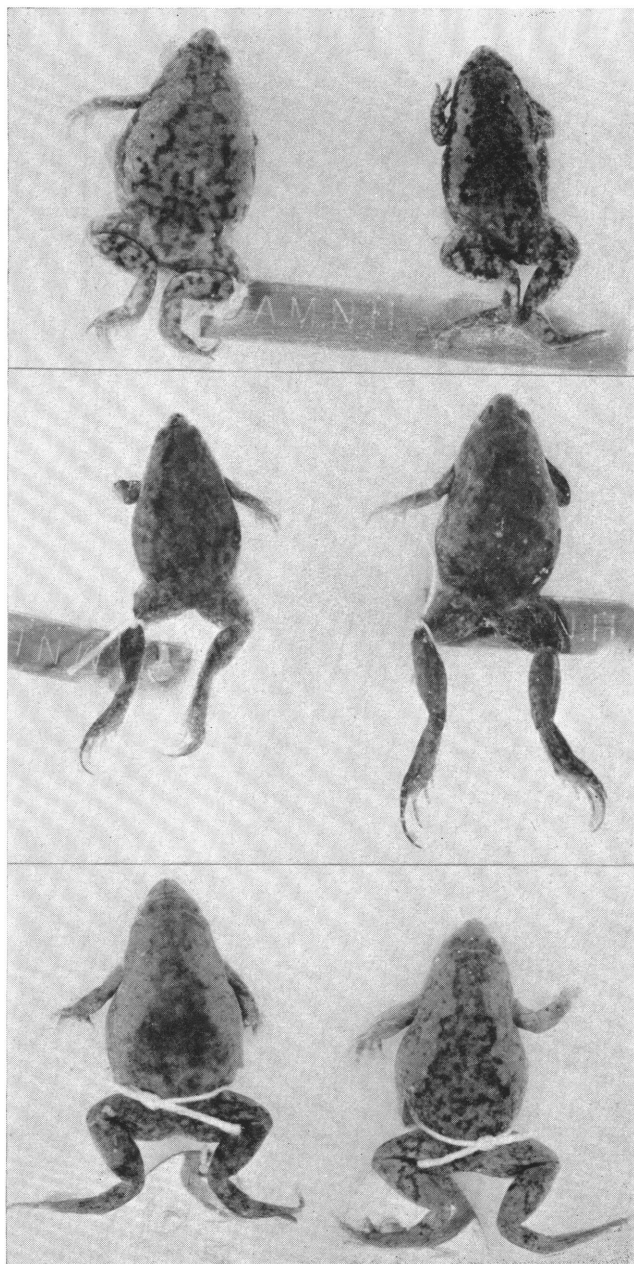


Fig. 2. Dorsal view of mainland *Microhyla c. carolinensis* (slightly enlarged). Upper row, A.M.N.H. No. 51978, from Maxton, Robeson County, North Carolina; middle row, A.M.N.H. Nos. 52001, 52002, from Highlands County, Florida; lower row, A.M.N.H. Nos. 932, 933, from Stevenson, Jackson County, Alabama.

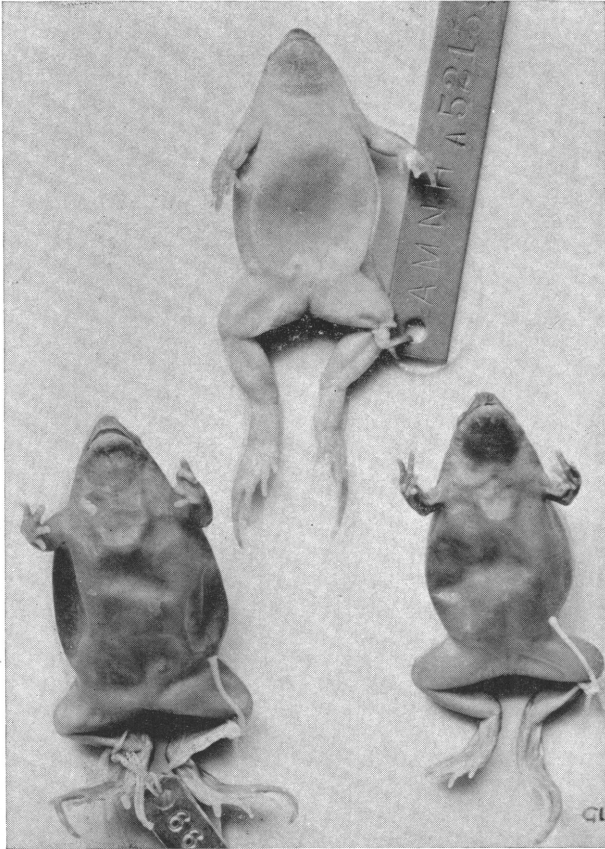


Fig. 3. Ventral view of *Microhyla c. olivacea* (slightly enlarged). Upper row, A.M.N.H. No. 52155 from 2 miles southwest of Barnston, Gage County, Nebraska; lower row, U.M.M.Z. No. 66866, from Bourbon County, Kansas.

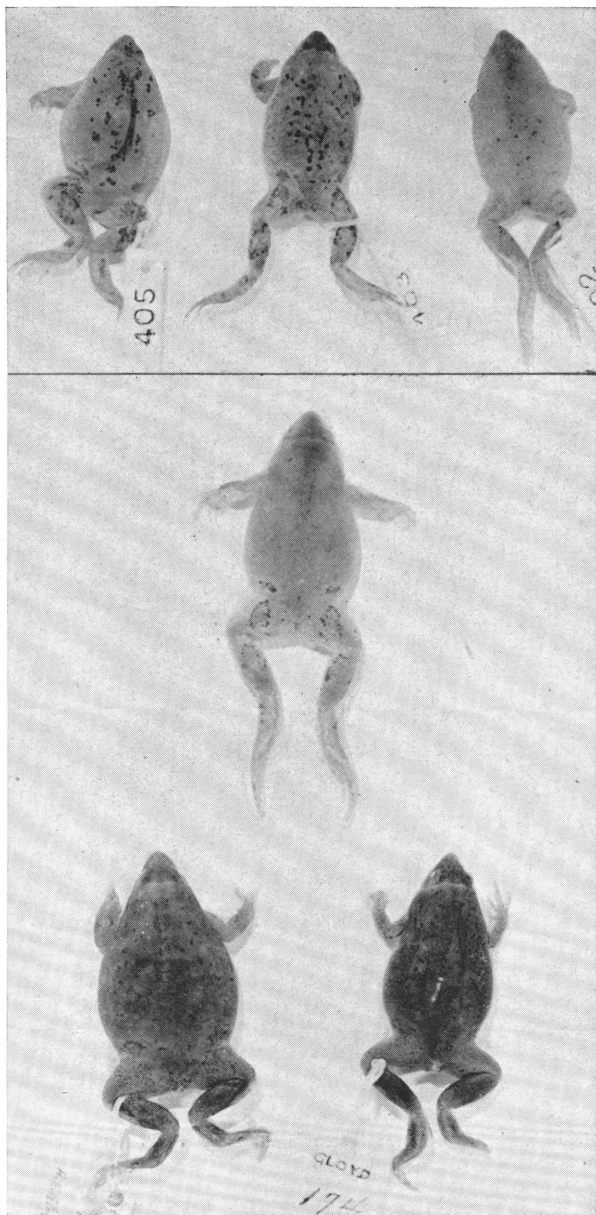


Fig. 4 Dorsal view of *Microhyla c. olivacea* (slightly reduced) showing the variation in the development of the leg bar. Upper row, C.N.H.M. Nos. 402, 403, 405, from Musquiz, Coahuila, Mexico; middle row, A.M.N.H. No. 52155 from 2 miles southwest of Barnston, Gage County Nebraska; lower row, U.M.M.Z. No. 66866, from Bourbon County, Kansas.

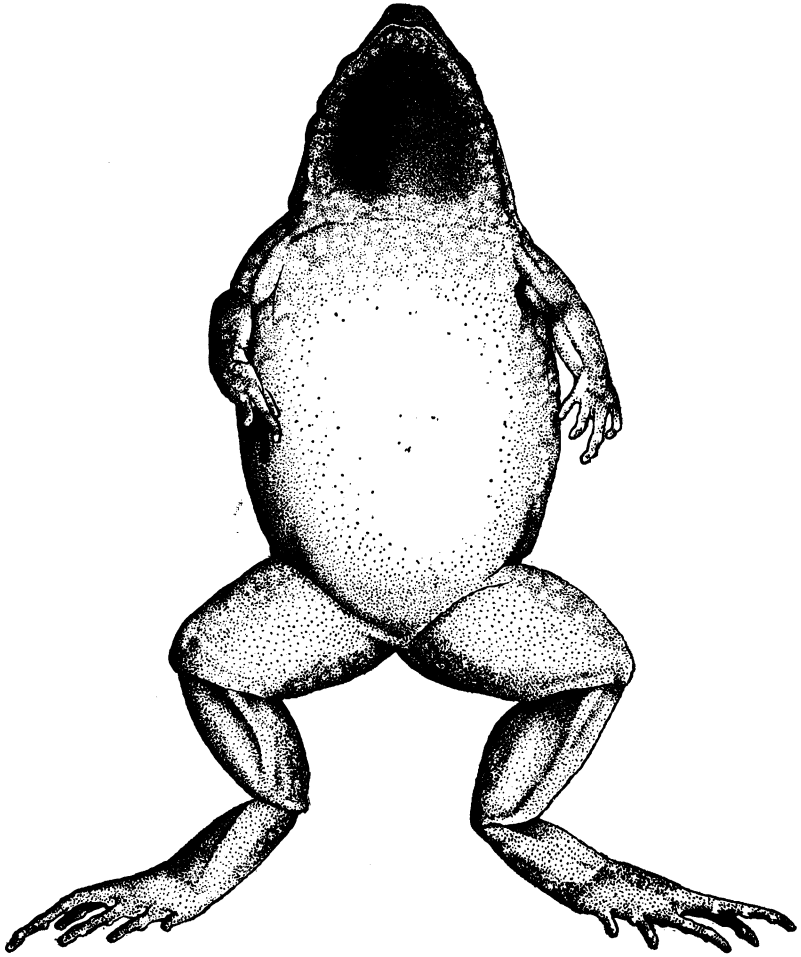


Fig. 5. Ventral view of *Microhyla c. mazatlanensis*, A.M.N.H. No. 51245, from Guirocoba, Sonora, Mexico (male, $\times 3$).



Fig. 6. Dorsal view of *Microhyla c. mazatlanensis*, U.M.M.Z. No. 72176, from Noria, Sonora Mexico (male, $\times 3$).

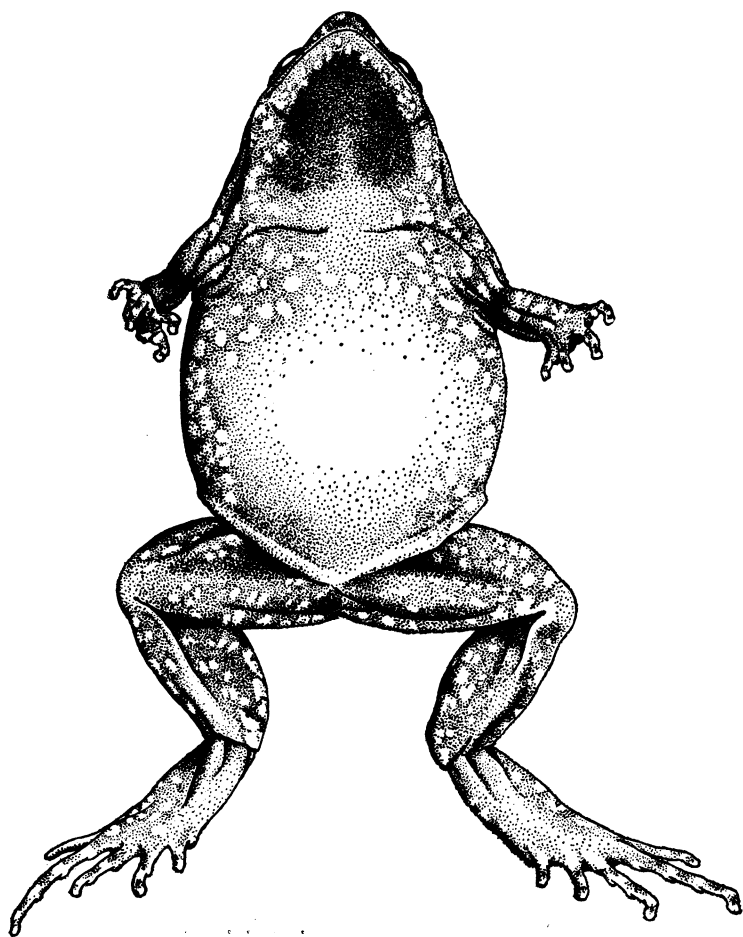


Fig. 7. Ventral view of *Microhyla carolinensis-olivacea* intergrade, U.S.N.M. No. 42338, from Victoria County, Texas (male, $\times 3$).

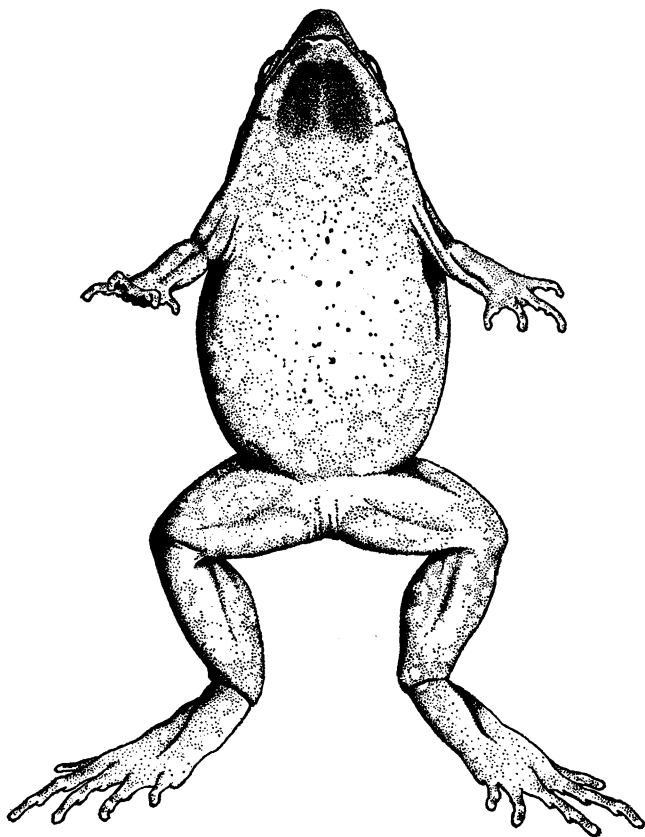


Fig. 8. Ventral view of *Microhyla carolinensis-olivacea* intergrade, U.S.N.M. No. 42325, from Victoria County, Texas (male, $\times 3$).

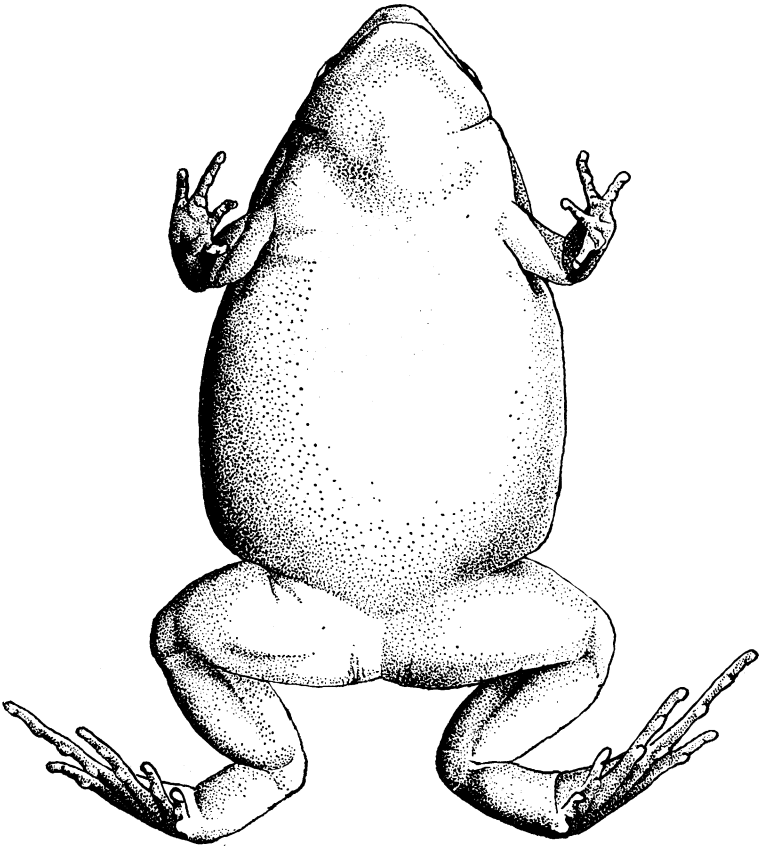


Fig. 9. Ventral view of *olivacea*-like *Microhyla c. carolinensis*, U.S.N.M. No. 83472, from Key West, Florida (female, $\times 3$).

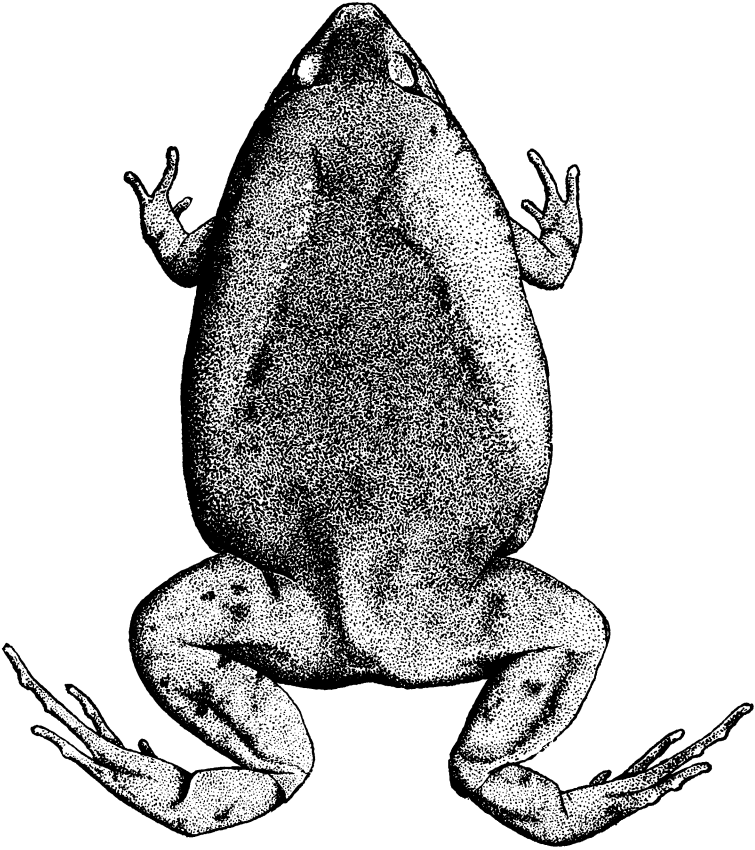


Fig. 10. Dorsal view of *olivacea*-like *Microhyla c. carolinensis*, U.S.N.M. No. 83472, from Key West, Florida (female, $\times 3$).

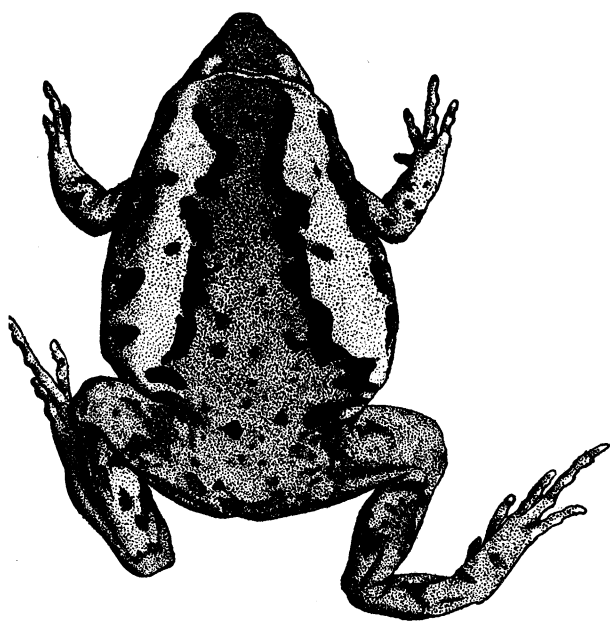


Fig. 11. Dorsal view of individual with "Key West" pattern referred to *Microhyla c. carolinensis*, U.S.N.M. No. 85447, from Key West, Florida (female, $\times 3$).

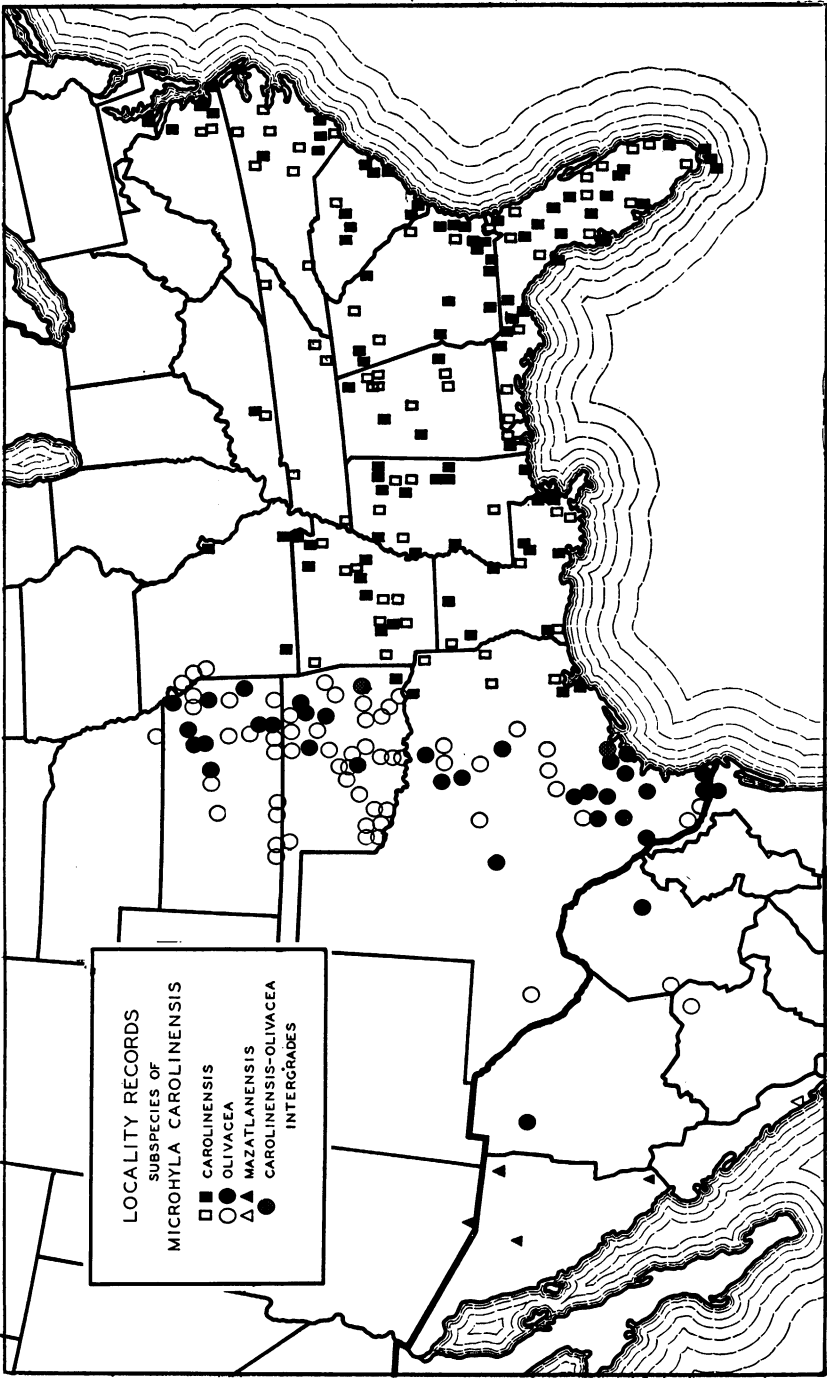


Fig. 12. Map of middle North America showing the distribution of the subspecies of *Microhyla carolinensis*. Solid symbols represent localities for material examined; hollow symbols represent literature reports

