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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 82 : ARTICLE 8 NEW YORK : 1944

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Volume 82, article 8, pages 345–370, text figures 1–3,
plates 61–66, tables 1–5

Issued May 25, 1944

INTRODUCTION

In recent years there has been a renewal of interest in the "*pipiens* problem." For some time it has been apparent that the diagnostic characters used to separate *Rana pipiens* Schreber and *Rana sphenocephala* (Cope), or more recently, *Rana brachycephala* (Cope), *Rana pipiens* Schreber, and *Rana sphenocephala* (Cope) are not reliable (Trapido and Clausen, 1938; Grant, 1941; Porter, 1941). As a result there is no uniformity of opinion among herpetologists regarding the proper name for meadow frogs from many localities. For example, some would restrict *Rana sphenocephala* to Florida and Georgia and designate meadow frogs from other localities as *Rana pipiens*. Others would extend the range of *Rana sphenocephala* north to New Jersey on the Atlantic coast, to southern Illinois in the Mississippi Valley, and west into Texas. This confusion is all the more regrettable since these frogs are widely used for experimental purposes and proper identification is of the utmost importance.

There have been four principal methods[1] of treating the *pipiens* group of eastern North America.

1. Cope (1889) divided the populations into three subspecies, *Rana virescens brachycephala*, *Rana virescens virescens*, and *Rana virescens sphenocephala* (inasmuch as *virescens* is now *pipiens*, these would be *Rana pipiens brachycephala*, *Rana pipiens pipiens*, and *Rana pipiens sphenocephala*).

2. Kauffeld (1937) and Stejneger and Barbour (1939) have regarded Cope's subspecies as full species and so recognize *Rana brachycephala*, *Rana pipiens*, and *Rana sphenocephala*.

3. Dickerson (1906), Wright and Wright (1933), Stejneger and Barbour (1933), and most students have not differentiated between *pipiens* and *brachycephala* and recognize only *Rana pipiens* and *Rana sphenocephala*.

4. Still others, such as Boulenger (1920) and Kellogg (1932), have been unable to find constant differences that would enable them to divide the meadow frogs into different species or subspecies and so regard them all as *Rana pipiens*.

The characters used by Cope (1889) to distinguish *brachycephala*, *pipiens*, and *sphenocephala* may be tabulated as follows:

	brachycephala	*pipiens*	*sphenocephala*
Length of body / Length of head	3.5	3.0	2.5 (less than 3)
External vocal sacs in male	Lacking or rudimentary	Present	Present
Snout	Less acuminate	Acuminate	Most acuminate
Cross bars on tibia	Complete	Generally interrupted	Lacking
Dorsal spots	Larger, not widely yellow bordered	Smaller, not so distinctly yellow bordered	Smaller, not yellow bordered
Longitudinal band on front of femur	Absent	Present	Usually present
Anterior extension of heel	Just reaches snout	Just reaches snout	8–10 mm. beyond snout
Webbing	Most	Intermediate	Least

[1] Recently Mittleman and Gier (1942) have suggested that the meadow frogs of "Texas, Kansas, Oklahoma and possibly certain adjacent States" are distinct from other populations and propose to call them *Rana pipiens berlandieri*. Their evidence was given careful consideration, but no support for their contention could be gathered from the living and preserved material used in this report. The meadow frogs from various localities in these states are extremely diverse (pl. 64, figs. 5, 6, pl. 65, fig. 7), and there seems no reason for combining them as a natural taxonomic unit. In fact there are greater differences between species from Oklahoma and parts of Texas than between the former and specimens from southern Indiana and parts of New Jersey.

Kauffeld (1937) prefers not to rely on color differences, as characters of this nature are highly variable. The differences he finds are as follows:

	brachycephala	*pipiens*	*sphenocephala*
Snout	Long	Shorter	Very short
Length of body / Length of head	3.5–4.0	3.0–3.5	2.0–2.5
Anterior extension of heel	Does not reach tip of snout	Just reaches tip of snout	Extends beyond snout
Webbing	Full	More indented than *sphenocephala*	Indented
Dorsal folds	Lacking	Short, numerous	Short, numerous
Dorsolateral fold	Wide, flat, and extends into supraocular region	Narrow, high, and not extending into supraocular region	As in *pipiens*
White tympanic spot	Absent	Usually present	Always present

We might conclude from an examination of the diagnostic characters given by Cope and by Kauffeld that many of the variations are of the nature of north-south geographic gradients or clines (along the Atlantic coast at least, *brachycephala* is the northern form; it is replaced by *pipiens* in southern New York, and the latter by *sphenocephala* still farther to the south). Thus, as we proceed from north to south the body/head ratio becomes less, the snout more acuminate, the cross barring on the tibia less, the webbing more reduced, and the relative leg length greater.

The ranges of these three varieties are poorly defined by Cope. Typical forms of *sphenocephala* are said to occur in Georgia and Florida, but he also refers specimens from Louisiana, Indiana, and Minnesota to this subspecies. The variety *pipiens* is found "along the eastern and southern coasts from Maine to the mouth of the Rio Grande, and up the Mississippi to southern Illinois, and in the intermediate country." In addition, specimens from New Mexico, Mexico, and northern Canada are referred to this subspecies. The range of *pipiens* would, therefore, include the region where "typical" *sphenocephala* is found. The range of *brachycephala* is not definitely indicated. In the east it is listed from Illinois, Quebec, Maine, South Carolina, Massachusetts, and he remarks that it is "the only species of *Rana* found between the eastern part of the Great Plains and the Sierra Nevada Mountains."

It is clear from the above that Cope's three varieties do not replace each other geographically as is the case with most subspecies. Instead we find the range of typical *sphenocephala* included in the range of *pipiens*, and the ranges of *pipiens* and *brachycephala* coextensive over a considerable territory. Obviously Cope was not dealing with subspecies as they are understood at the present time.

Kauffeld is more definite in defining the ranges of the three forms, especially in the eastern United States. Meadow frogs that he identifies as *Rana brachycephala* are found in "southern Canada and New England except extreme southern Connecticut, New York except southeastern portion, northwestern New Jersey, northern and western Pennsylvania, west to the Pacific Coast States." *Rana pipiens* extends from "extreme southeastern New York, Long Island, southern Connecticut, New Jersey except the northwestern portion, southeastern Pennsylvania, Delaware and Maryland, south throughout the Coastal Plain and west into Texas." "*Rana sphenocephala* is a purely Austral form confined to the Austroriparian Division." Here again the range of *sphenocephala* seems to be included in the range of *pipiens*.

In contrast to Cope and Kauffeld, most workers have not recognized *brachycephala* and, in the eastern United States, call northern meadow frogs *Rana pipiens*, and those in the south *Rana sphenocephala*. The line of demarcation is apparently a personal matter, as some consider the meadow frogs from as far south as Virginia to be *pipiens* and others designate specimens from New Jersey as *sphenocephala*. The characters used to distinguish these two species are in general those that separate Cope's and Kauffeld's *pipiens* and *brachycephala* from *sphenocephala*. The principal points of difference noted by Dickerson (1906), Wright (1932), and Wright and Wright (1933) are:

	pipiens	*sphenocephala*
$\frac{\text{Body length}}{\text{Snout length}}$	6.00–6.80	5.23–6.30
$\frac{\text{Body length}}{\text{Head length}}$	2.80–3.20	2.38–2.80
$\frac{\text{Body length}}{\text{Tibia length}}$	1.73–1.94	1.55–1.82
Dorsal spots	Outlined with light	Not outlined with light
White tympanic spot	Absent	Present
Anterior extension of heel	Reaches tip of snout	Extends beyond snout
Lateral spots	Many	Few
Head shape	Less pointed	More pointed
Coloration of posterior face of femur	Light reticulum	Dark reticulum
Longitudinal bar on anterior face of femur	Absent	Present

As with most controversial species, the *pipiens* group has its lumpers, among whom have been Boulenger (1920) and Kellogg (1932). Boulenger gave careful consideration to the possibility of recognizing *brachycephala*, *pipiens*, and *sphenocephala* but, after examining specimens from many localities in North and Central America, came to the conclusion that it was impossible to distinguish among these three forms as defined by Cope (1889), or between *pipiens* and *sphenocephala* as defined by Dickerson (1906). In spite of the fact that Boulenger presented a most thorough investigation of the problem, his conclusions have been ignored.

Kellogg (1932), in his study of Mexican amphibia, was faced with the necessity of finding a proper name for the meadow frogs of that country. After a "critical examination and tabulation of many specimens" he was unable to find any constant geographical peculiarities. He states further that "unique variations in color pattern were found in almost every local series studied, and as none of these variations are exactly alike it seems necessary to disregard such peculiarities and group all the leopard frogs of North and Central America under one name." The conclusions of Kellogg have fared no better than those of Boulenger. They, too, are simply ignored.

The one possible conclusion to be gained from this literature survey is that no unanimous opinion has been reached on the "*pipiens* problem." Conflicting opinions have been advanced but never supported by an analysis of the reliability of the diagnostic characters employed. For this reason it was felt that considerable light could be thrown on the problem by a statistical treatment of the characters commonly employed to distinguish the various races or species. Therefore, a total of more than 500 meadow frogs, both living and preserved, has been studied, and the results will now be given.

To Mr. Charles Bogert I am indebted for much advice and to Mr. Thane Bierwert for the photographs in plates 62 to 65.

VARIATION IN CHARACTERS

BODY PROPORTIONS OF FRESHLY KILLED FROGS

THE MEASUREMENTS presented in this section were made on recently pithed frogs which were being used in experiments on hybridization and embryonic temperature tolerance. (Measurements of fresh and preserved frogs have not been combined, as some shrinkage may have resulted in the latter, making the two groups not strictly comparable.) A total of 206 animals from 11 localities was measured. Those from Montreal, Province of Quebec, were collected by Dr. Ronald Grant and those from Tulsa, Oklahoma, and Bloomington, Indiana, were collected by Dr. A. P. Blair. Those from Rossie, New York, and Long Island, New York, were collected by the author. Specimens from the remaining localities—northern Vermont; western Wisconsin; Mt. Ephraim, New Jersey; Ocala and Englewood, Florida; and Chalmette, Louisiana—were secured through dealers. (In these cases the exact locality where the specimens were collected was given by the dealers. To verify this material, the specimens were compared with those from the same general region in the collections of the American Museum of Natural History.)

Measurements and ratios will be given for individuals of each locality with the material grouped according to Kauffeld's species. Animals from Montreal, Vermont, Rossie, New York, and Wisconsin will thus be combined as *brachycephala;* those from Long Island, New Jersey, and Indiana as *pipiens;* and those from Florida, Louisiana, and Oklahoma as *sphenocephala*. It will be noticed that this arrangement divides the animals into northern, central, and southern groups which should demonstrate any north-south gradients (clines).

The relative leg length is thought by many to be the most reliable criterion for distinguishing the races or species of the *pipiens* complex. This is usually expressed as differences in the ratio of leg length/body length, body length/tibia length, or in the anterior extension of the heel when the leg is drawn anteriorly along the body.

VARIATION IN THE LEG/BODY RATIO

The length of the body, as here used, is the distance from the snout to the cloacal opening. The leg was measured from the cloacal opening to the tip of the longest toe. When making this measurement the leg was stretched outward at an angle of 45 degrees to the long axis of the body.

Minor variations do exist in leg/body ratio, but they do not exhibit any pronounced geographic regularity (table 1). The southern populations grouped as *sphenocephala* in general have the highest means (and hence relatively longer legs). They are fairly homogeneous in this respect, the extremes being 1.70 and 1.76. The populations grouped as *pipiens* are not so uniform. The Long Island and New Jersey individuals have the lowest means of any locality, while those from Indiana have a mean which is greater than three of the four *sphenocephala* samples. A similar lack of uniformity is apparent in the *brachycephala* samples. The Vermont mean is very low, 1.66, only those from Long Island and New Jersey being lower, while the Rossie mean is the highest observed. In general these samples show more intraspecific than interspecific differences. Thus, although the differences in the means for the three species are significant (d/σ_d being 3 or more),[1] it is clear that they are due in part to the relative proportions of the different local populations in the samples. The mean for *pipiens*, for example, would have been much greater if more Indiana and fewer New Jersey individuals had been used. Similarly, the mean for *brachycephala* would have been greater if a proportionately larger number of Rossie frogs had been measured.

A more important consideration for us is: are the differences in leg/body ratio among

[1] The statistical measures of variability and reliability here used are as follows: $\sigma = \sqrt{\frac{\Sigma d^2}{N}}$ for samples of 15 or more (for samples of less than 15, $N-1$ instead of N is used); $\sigma_M = \frac{\sigma}{\sqrt{N}}$; $\sigma_d = \sqrt{\frac{N_1}{N_2}\sigma_{M_1}{}^2 + \frac{N_2}{N_1}\sigma_{M_2}{}^2}$.

the three species of sufficient magnitude to be of practical use in taxonomy? In other words, will it be possible to assign an individual or small series of frogs to the correct species on the basis of this character alone? The answer to this question must be given in the negative. The differences in mean among brachycephala, pipiens, and sphenocephala are in most cases less than the standard deviation. To be useful in identifying individuals or small series the differences should be at least two and preferably three times the standard deviation. This can be better visualized by examination of the histograms in figure 1 where the frequency of the different ratios is shown by the height of the rectangles. The variation is so great that it would be impossible to separate the three species, or to assign an unknown individual to the correct group on the basis of this character alone.

TABLE 1

VARIATION IN BODY PROPORTIONS OF MEADOW FROGS. THE SAMPLES ARE GROUPED ACCORDING TO THE SPECIES AS RECOGNIZED BY KAUFFELD (1937)

		Leg/Body		Body/Tibia		Tibia/Leg		Foot/Leg	
	N	*M* σ_m	σ	*M* σ_m	σ	*M* σ_m	σ	*M* σ_m	σ
brachycephala									
Montreal, P.Q.	20	1.69 ± .01	.06	1.85 ± .01	.05	.32 ± .01	.02	.47 ± .00	.01
Vermont	13	1.66 ± .02	.05	1.83 ± .02	.07	.33 ± .00	.01	.48 ± .01	.02
Rossie, N.Y.	11	1.76 ± .02	.07	1.74 ± .02	.07	.33 ± .00	.01	.47 ± .00	.01
Wisconsin	49	1.70 ± .01	.05	1.81 ± .01	.05	.33 ± .00	.01	.47 ± .00	.01
pipiens									
Long Island, N.Y.	14	1.65 ± .01	.05	1.88 ± .01	.05	.32 ± .01	.02	.48 ± .00	.01
New Jersey	35	1.64 ± .01	.06	1.90 ± .01	.07	.32 ± .00	.01	.48 ± .00	.01
Indiana	18	1.75 ± .03	.12	1.73 ± .01	.06	.33 ± .00	.01	.46 ± .00	.01
sphenocephala									
Oklahoma	8	1.76 ± .03	.07	1.72 ± .02	.05	.32 ± .01	.02	.46 ± .00	.01
Louisiana	17	1.73 ± .02	.07	1.71 ± .02	.07	.34 ± .00	.01	.46 ± .00	.01
Ocala, Fla.	13	1.70 ± .01	.04	1.76 ± .02	.06	.33 ± .00	.01	.47 ± .00	.01
Englewood, Fla.	8	1.73 ± .03	.09	1.72 ± .03	.07	.34 ± .00	.01	.46 ± .00	.01
Combined samples:									
brachycephala	93	1.70 ± .01	.06	1.81 ± .01	.07	.33 ± .00	.01	.47 ± .00	.01
pipiens	67	1.67 ± .01	.08	1.85 ± .01	.09	.32 ± .00	.01	.47 ± .00	.01
sphenocephala	46	1.73 ± .01	.07	1.73 ± .01	.07	.33 ± .00	.01	.46 ± .00	.01

VARIATIONS IN THE BODY/TIBIA RATIO

The body was measured as described before, and the tibia by flexing the leg and taking the distance between knee and ankle joint. The ratios are given, as before, for each locality and for the three species (table 1). Much that was said for the leg/body ratio is applicable for the body/tibia ratio. Again we find the samples grouped as *sphenocephala* to be fairly consistent, and there is no significant difference among their means. The samples grouped as *pipiens* and *brachycephala* show considerable variation in the mean value of the body/tibia ratios. In the case of *pipiens* the Indiana sample has a value similar to *sphenocephala*, while the New Jersey sample has the highest observed value for its mean. Among *brachycephala* the Rossie sample falls within the range of *sphenocephala*, while the values for the other samples are consistently higher. Although the differences in means

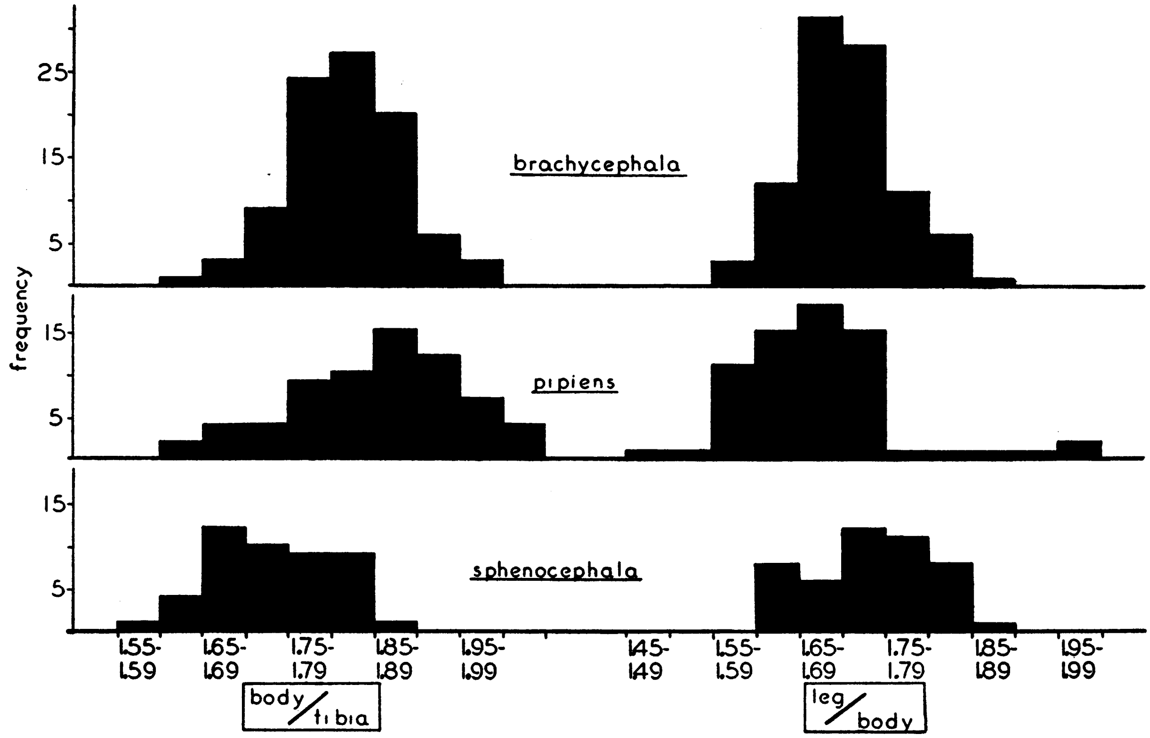


FIG. 1. Frequency polygons for body/tibia ratios (left) and for leg/body ratios (right) in freshly killed meadow frogs. The samples are grouped according to the species as recognized by Kauffeld (1937).

among the three species are significant, it must be realized that again this is due in part to the make-up of the sample. For example, the mean for the combined *pipiens* samples would have been different if more Indiana and fewer New Jersey individuals had been used.

Although each species is characterized by a different mean the considerable variation shown in the samples makes it impossible to use the body/tibia ratio to distinguish the three species. In figure 1, histograms are given for this character. The ranges for *brachycephala*, *pipiens*, and *sphenocephala* are so nearly coextensive that it would be impossible to assign individuals or small samples to the correct species on the basis of this character. Again there are more intraspecific than interspecific differences.

VARIATIONS IN TIBIA/LEG RATIO

This ratio was determined and found to be practically the same in all populations (table 1). The average for the entire sample is 0.33. Thus, because the tibia approximates a constant fraction of the entire leg length, it can be used as a measurement instead of the latter. This will be convenient when preserved material is used, since in this case leg length cannot be determined readily.

VARIATIONS IN THE FOOT/LEG RATIO

No significant difference could be detected in the foot/leg ratio (table 1) in the frogs used in this study (foot length being the distance from the heel joint to the tip of the longest toe). The mean ratio for the entire population was 0.47. The foot and tibia together form 80 per cent of the entire leg length.

Kauffeld (1937) and other authors have not measured leg length directly. Instead, they have drawn the leg anteriorly along the body and by noting how far the heel extends with reference to the snout have made a crude comparison of body length and leg length.

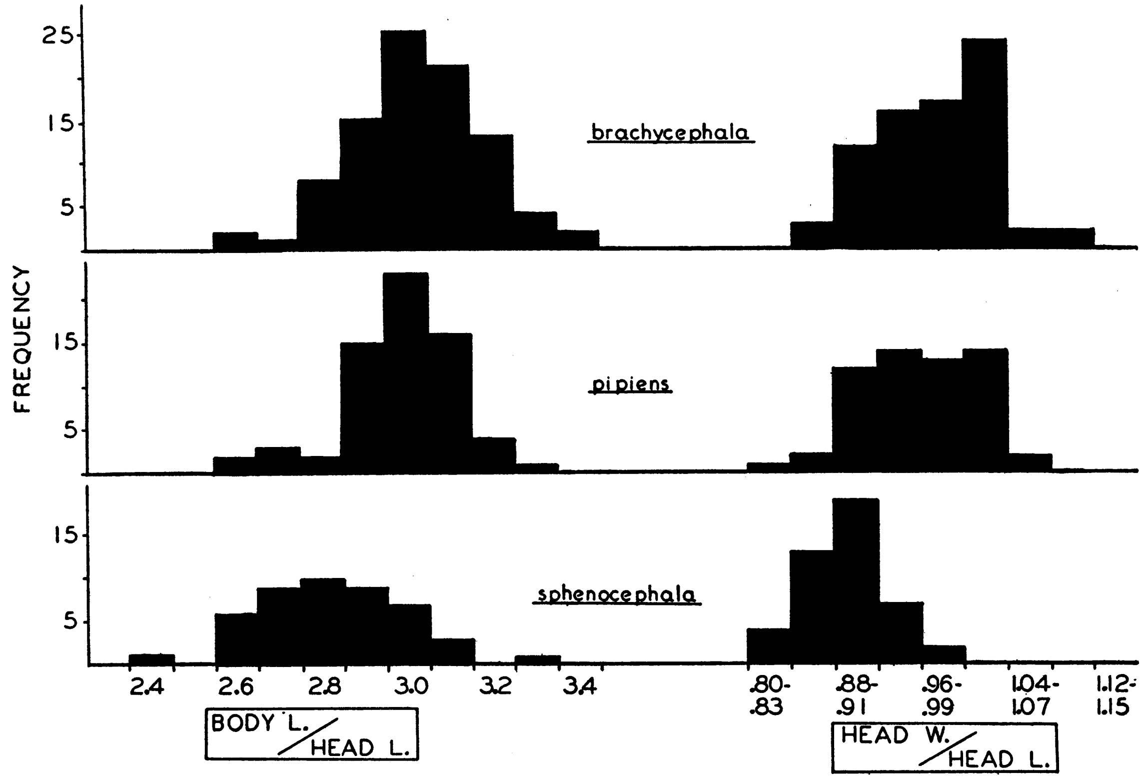


FIG. 2. Frequency polygons for body-length/head-length ratios (left) and for head-width/head-length ratios (right) in freshly killed meadow frogs. The samples are grouped according to the species as recognized by Kauffeld (1937).

Thus, in *brachycephala* it is said that the heel does not extend to the snout, in *pipiens* it just reaches the snout, while in *sphenocephala* it extends beyond the snout. This measure has no advantage and some disadvantages over more direct methods of expressing relative length, so it has not been studied systematically. The measurement is really a comparison of body length with total leg minus foot length. As it has been shown that there is at best a slight difference in leg length and since the foot forms a constant fraction of the total leg length, we find in the data of table 1 no support whatsoever for Kauffeld's contention. His assumptions were tested more directly by noting the anterior extension of the heel in 10 frogs from Florida, all of which should have had the heel extending beyond the snout. Instead, in five the heel failed to reach the snout (*brachycephala* character), in four the heel just reached the tip of the snout (*pipiens* character), and in only one did the heel extend beyond the snout as should have been expected (*sphenocephala* character).

In summarizing these measurements and ratios it must be concluded that the frogs used in this study show little difference in relative leg or tibia length. Animals in the north, *brachycephala*, may have legs as long as the typical *sphenocephala* of Florida. It is difficult to understand the basis for considering these differences as so pronounced as to be useful in taxonomy. It may be significant that no one holding such an opinion has ever given measurements on a series of frogs from different localities to substantiate his viewpoint.

VARIATIONS IN BODY/HEAD-LENGTH RATIO

Differences in this ratio (body length measured as described, and head length as the distance from the tip of the snout to the posterior edge of the tympanic membrane), were used to separate *brachycephala*, *pipiens*, and *sphenocephala* by both Cope (1889) and Kauffeld (1937). Thus, according to the latter the ratio is 3.5–4.0 in *brachycephala*, 3.0–3.5 in *pipiens*, and 2.0–2.5 in *sphenocephala*. In table 2 the mean ratios for the 11 samples are given. It will be seen that the differences are not of the magnitude found by Kauffeld. The means of both the combined *pipiens* and combined *brachycephala* samples are 3.0, and for *sphenocephala* 2.8. Moreover, not one specimen was encountered with a ratio as high as 3.5–4.0 (the range for *brachycephala*), and only one individual in 203 had a ratio in the range 2.0–2.5 which, according to Kauffeld, is characteristic of *sphenocephala*. As has been the case with other ratios given there is as much variation of the means within each of the three species as between them. In figure 2, frequency polygons of the ratios are given. It will be seen that the ranges are nearly coextensive. Only two individuals from the *brachycephala* sample have a greater ratio than *pipiens* or *sphenocephala*, and only one *sphenocephala* can be distinguished from *pipiens* and *brachycephala*. It will be seen that the ratios for *sphenocephala* are grouped toward the lower part of the range. Nevertheless, it would be impossible to allocate a given individual or small series to the correct taxonomic group on the basis of this character.

Variations in the Head-Width/Head-Length Ratio

This is a measure of the narrowness of the head, a character which has been used to separate the three species. It is generally expressed in a comparative way, the head of *sphenocephala* being narrower than northern

TABLE 2

Variation in Body Proportions of Meadow Frogs. The Samples are Grouped According to the Species as Recognized by Kauffeld (1937). The Mean Body Length is Given as L in Millimeters

			Body / Head Length			Width of head / Length of head	
	N	*L*	*M* σ_m	σ	*N*	*M* σ_m	σ
brachycephala							
Montreal, P.Q.	19	76	3.1 ±0.0	0.1	17	1.00 ± .00	.01
Vermont	13	81	3.1 ±0.0	0.1	—	— —	—
Rossie, N.Y.	10	57	2.8 ±0.1	0.2	10	.95 ± .02	.06
Wisconsin	49	74	3.0 ±0.0	0.1	49	.95 ± .01	.04
pipiens							
Long Island, N.Y.	14	75	3.1 ±0.0	0.1	14	.99 ± .01	.02
New Jersey	35	73	3.0 ±0.0	0.1	27	.92 ± .01	.04
Indiana	17	70	2.9 ±0.1	0.2	17	.95 ± .01	.04
sphenocephala							
Oklahoma	8	67	2.9 ±0.1	0.2	8	.90 ± .01	.02
Louisiana	17	73	2.9 ±0.0	0.1	17	.87 ± .01	.04
Ocala, Fla.	13	72	2.7 ±0.0	0.1	13	.89 ± .01	.04
Englewood, Fla.	8	100	2.8 ±0.0	0.1	6	.91 ± .01	.03
Combined samples:							
brachycephala	91	73	3.0 ±0.0	0.2	76	.96 ± .00	.04
pipiens	66	73	3.0 ±0.0	0.1	58	.95 ± .01	.05
sphenocephala	46	77	2.8 ±0.0	0.2	44	.89 ± .01	.04

populations. (Head width was taken as the width of the head just posterior to the tympanic membrane.) The mean ratios are given in table 2. The populations show slight variations in this character. Those listed as *brachycephala* and *pipiens* have means of 0.92 or more, while in those grouped as *sphenocephala* the means are 0.91 or less. The means alone give no indication of the variation, and it will be seen from the frequency polygons of figure 2 that there is considerable overlapping. Within the range of *brachycephala* are found 98 per cent of the *pipiens* and 91 per cent of the *sphenocephala*. The *sphenocephala*, however, are grouped at the lower portion of the range. Thus, if we arbitrarily divide the frogs into those having a ratio of 0.92 or more, and those having a ratio of less than 0.92, we find the following distributions for the individual frogs:

	Less than 0.92	0.92 or more
brachycephala	20%	80%
pipiens	26	74
sphenocephala	79	21

The mean for *brachycephala* is 0.96 and for *sphenocephala* 0.89. The magnitude of this difference may be appreciated by the following examples: a frog with a head length of 25 mm. and a head width of 24 mm. would have a ratio of 0.96; another frog with a similar head length but with a head width of 22 mm. would have a ratio of 0.89. If we apply measures of reliability to these means we find the difference between *brachycephala* and *pipiens* significant ($d/\sigma_d = 5$). The difference between *brachycephala* and *pipiens* is not significant.

It has been convenient to postpone until this time a consideration of the constancy of these ratios in frogs of different body lengths. As a marjoity of the specimens used were sexually mature individuals (60–90 mm. in body length) this question cannot be adequately treated. However, the following generalizations can be made. There was no indication of any difference in relative growth of the body to the hind legs. In large and small individuals from the same locality the leg/body ratio was surprisingly constant. There was a suggestion that the head becomes wider in larger specimens as the value of the head-width/head-length ratio apparently increases slightly with increasing size. This increase is so slight as to be questionable and does not prohibit the use of this ratio for mature individuals. The body-length/head-length ratio increases noticeably with an increase in size. With an increase in average body length of 5 mm. this ratio increases approximately 0.1 of a unit (for example, from 2.9 to 3.0). It is probable, therefore, that the low body-length/head-length ratio for the Rossie sample is due more to the small size (some immature animals were included) of the frogs than to any real difference between them and the other *brachycephala* samples (table 2). The variations of this ratio with size will not modify the conclusions reached, as the combined samples of *brachycephala*, *pipiens*, and *sphenocephala* are so nearly similar in average body length (table 2, second column of figures).

BODY PROPORTIONS OF PRESERVED FROGS

A total of 302 animals from the collections of the American Museum of Natural History was measured for body length, tibia length, head width, and head length in the manner previously described. The number of animals from each state, average body length, body/tibia, body/head-length, and head-width/head-length ratios are given in table 3.

Variations in Body/Tibia Ratio

This ratio appears to be slightly less in preserved than in freshly killed specimens from the same locality (compare tables 1 and 3). This is probably due to a greater shrinkage of the body than of the tibia in preserving fluids. There is considerable minor variation, much of which is not significant, in the mean values of this ratio. However, no constant trends are discernible (table 3). The lowest means, 1.57 and 1.58, are found in Kentucky and Rhode Island in animals that are strikingly different in some other respects. Means of 1.60–1.69 are found in Florida, Mississippi, Louisiana, Illinois, Texas, Kansas, Missouri, and South Dakota. Means of 1.70–1.79 are found in Maine, Massachusetts, northern New York, New Jersey, Maryland, North Carolina, Georgia, and Arkansas; while those of 1.80 or greater are found in Quebec, Ver-

TABLE 3
VARIATION IN BODY PROPORTIONS OF PRESERVED MEADOW FROGS. THE BODY LENGTH L IS GIVEN IN MILLIMETERS

LOCALITY	N	L	Body/Tibia $M \pm \sigma_m$	Body/Tibia σ	Body/Head Length $M \pm \sigma_m$	Body/Head Length σ	Head Width/Head Length $M \pm \sigma_m$	Head Width/Head Length σ
Quebec	6	68	1.82 ± .04	.09	2.99 ± .05	.12	1.00 ± .01	.03
Maine	3	57	1.72 ± .06	.10	2.76 ± .06	.11	1.00 ± .03	.05
Vermont	20	71	1.83 ± .02	.07	3.08 ± .05	.21	1.03 ± .01	.05
Massachusetts	7	71	1.75 ± .02	.06	3.08 ± .03	.09	.98 ± .03	.07
Rhode Island	4	66	1.58 ± .04	.07	2.95 ± .04	.08	1.02 ± .03	.05
N. New York	5	73	1.77 ± .05	.10	2.92 ± .05	.10	1.03 ± .01	.03
S. New York	21	59	1.84 ± .02	.07	2.93 ± .04	.19	.92 ± .01	.06
New Jersey	36	56	1.78 ± .02	.10	2.78 ± .03	.17	.94 ± .01	.07
Maryland	4	54	1.77 ± .05	.09	2.75 ± .04	.08	.88 ± .01	.02
North Carolina	8	62	1.76 ± .05	.15	2.74 ± .05	.15	.92 ± .02	.05
Georgia	11	60	1.74 ± .03	.08	2.60 ± .02	.06	.87 ± .01	.04
Florida	86	63	1.69 ± .01	.07	2.62 ± .01	.10	.86 ± .00	.04
South Dakota	5	65	1.66 ± .03	.06	2.92 ± .10	.22	1.00 ± .04	.08
Missouri	10	55	1.60 ± .02	.06	2.78 ± .04	.12	.92 ± .02	.06
Kansas	5	68	1.68 ± .02	.04	2.99 ± .06	.14	1.03 ± .03	.07
Illinois	12	59	1.63 ± .02	.07	2.71 ± .04	.15	.90 ± .01	.05
Kentucky	3	56	1.57 ± .06	.10	2.59 ± .05	.08	.85 ± .02	.03
Arkansas	19	60	1.71 ± .01	.06	2.87 ± .03	.12	.92 ± .01	.04
Texas	11	61	1.65 ± .03	.08	2.75 ± .03	.10	.90 ± .01	.04
Louisiana	20	64	1.65 ± .03	.07	2.72 ± .03	.11	.86 ± .01	.04
Mississippi	6	69	1.68 ± .03	.07	2.78 ± .05	.13	.91 ± .01	.03

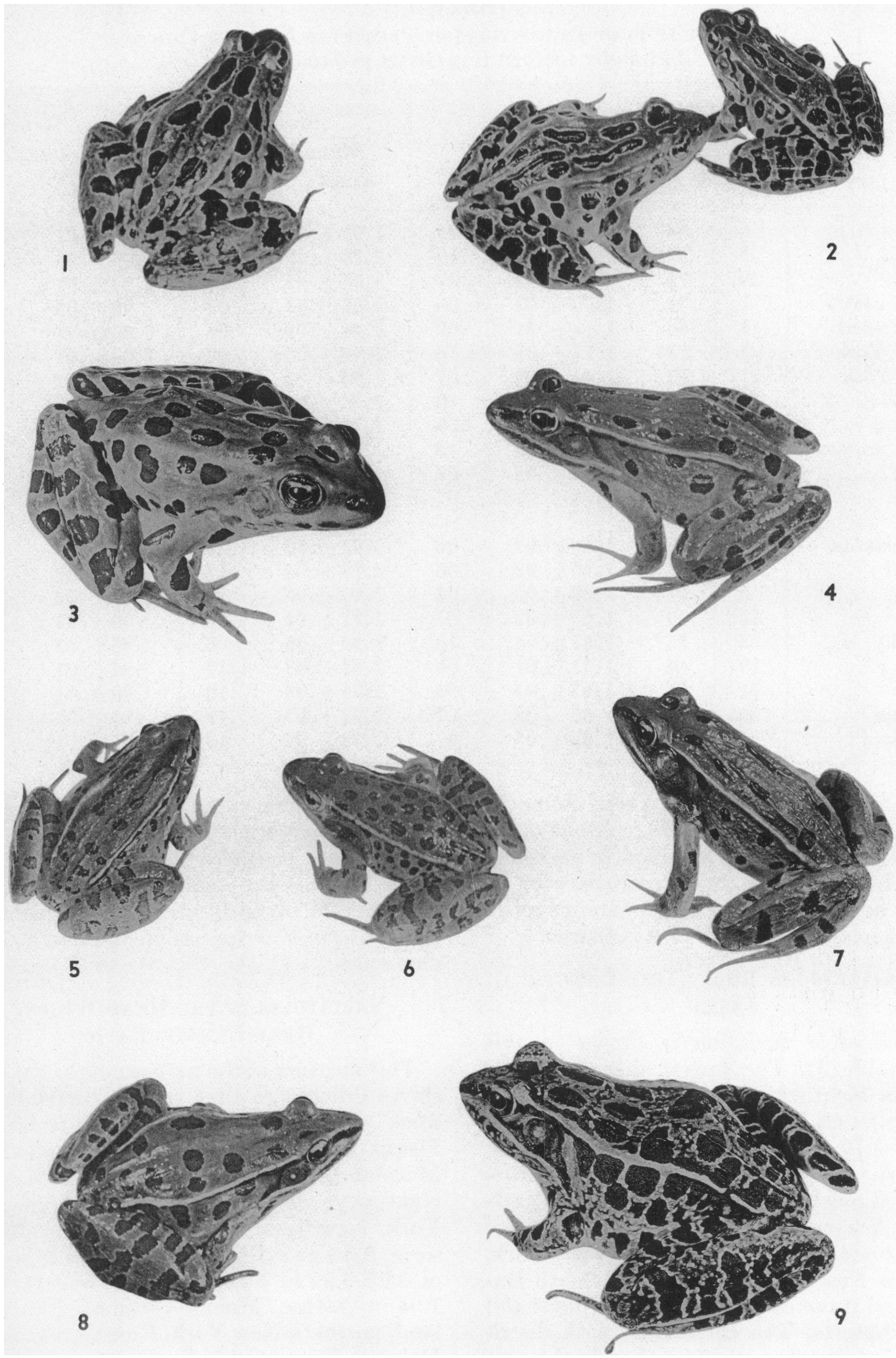
mont, and southern New York. Some of these differences in means are real, but many are not and should be ascribed to sampling errors. In no event is there any reason for dividing the meadow frogs into different species or subspecies on the basis of this character.

VARIATIONS IN BODY/HEAD-LENGTH RATIO

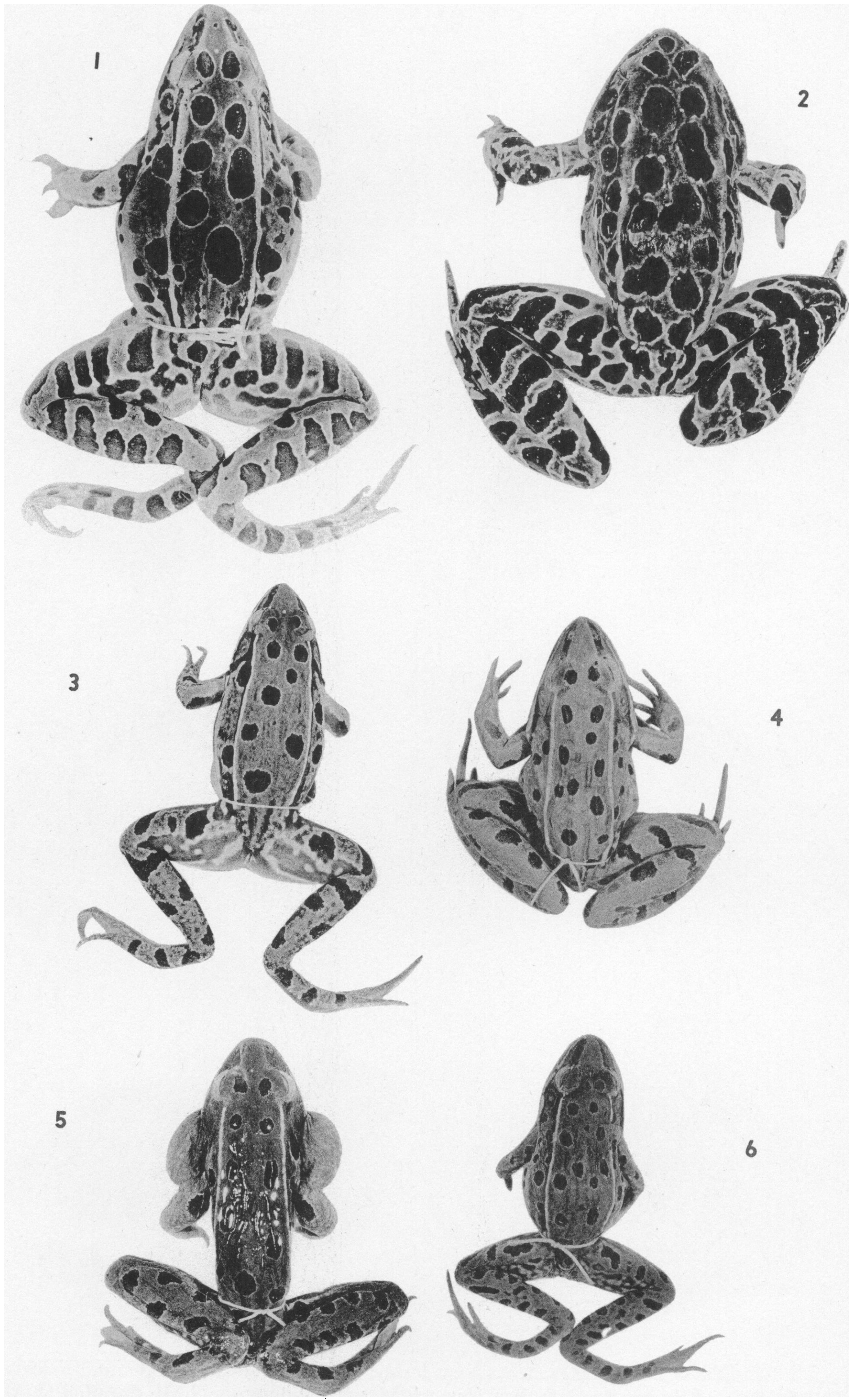
Considerable variation is shown in this ratio (table 3). The lowest mean, 2.59, is found in Kentucky. Average ratios of 2.60–2.69 are found in Florida and Georgia; those of 2.70–2.79 in Maine, New Jersey, Illinois, Missouri, Maryland, North Carolina, Mississippi, Louisiana, and Texas; those of 2.80–2.89 in Arkansas; those of 2.90–2.99 in Quebec, Rhode Island, northern New York, southern New York, Kansas, and South Dakota; and those of 3.00–3.09 in Vermont and Massachusetts. The correlation with distribution is somewhat stronger than in the case of the body/tibia ratio, as there is a tendency for northern populations to have a slightly higher and southern populations slightly lower ratios. Once again, however, it would be most difficult to divide the individuals into different races or species on the basis of this character.

VARIATIONS IN THE HEAD-WIDTH/HEAD-LENGTH RATIO

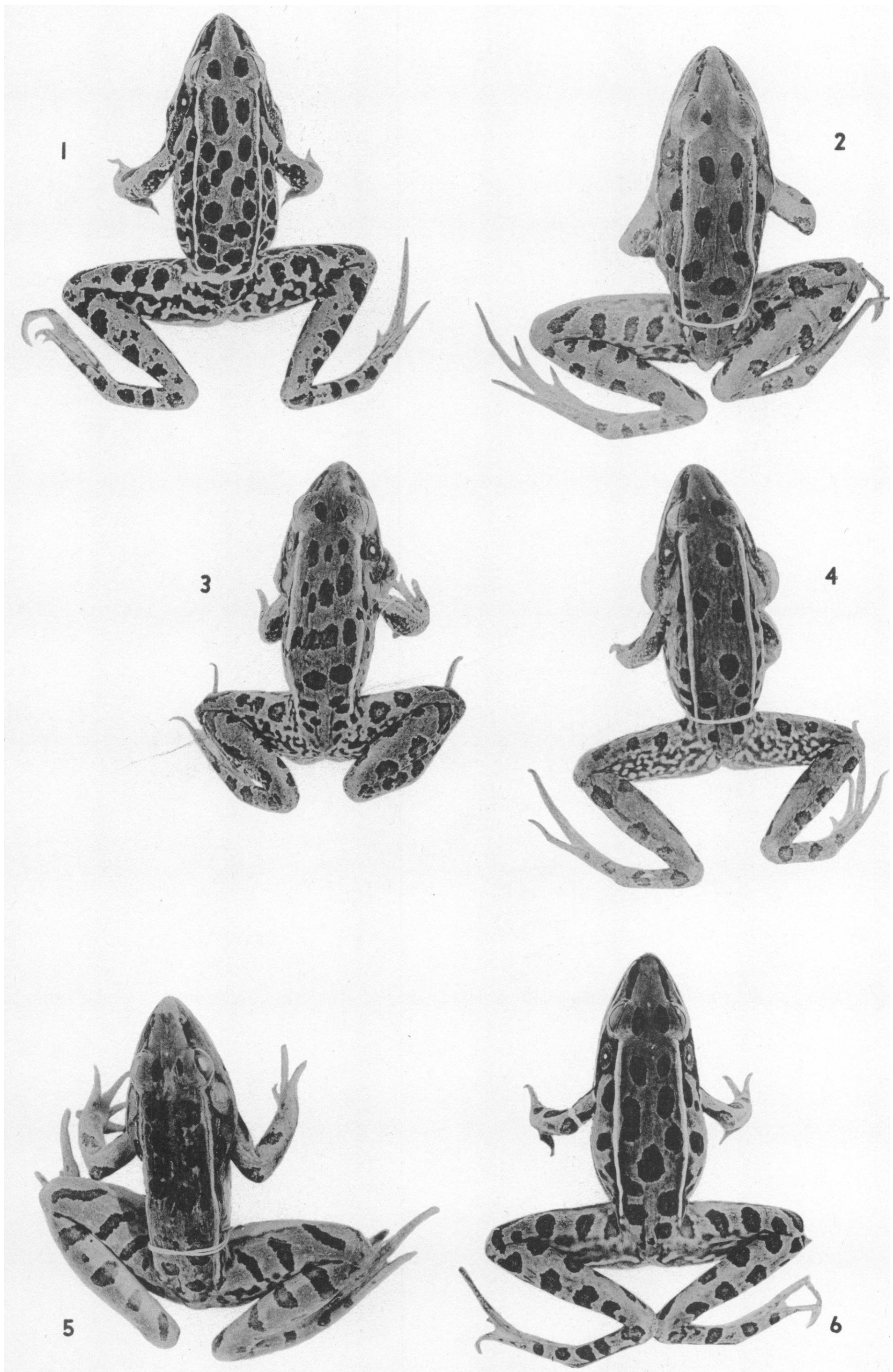
This measure of the narrowness of the head shows differences that can be correlated to some extent with distribution (table 3). Means of 0.85–0.89 are found in samples from Maryland, Georgia, Florida, Louisiana, and Kentucky; of 0.90–0.94 in southern New York, New Jersey, North Carolina, Mississippi, Arkansas, Illinois, Texas, and Missouri; of 0.95–0.99 in Massachusetts; and of 1.00–1.04 in Quebec, Maine, Vermont, Rhode Island, northern New York, Kansas, and South Dakota. There is an indication of a cline with



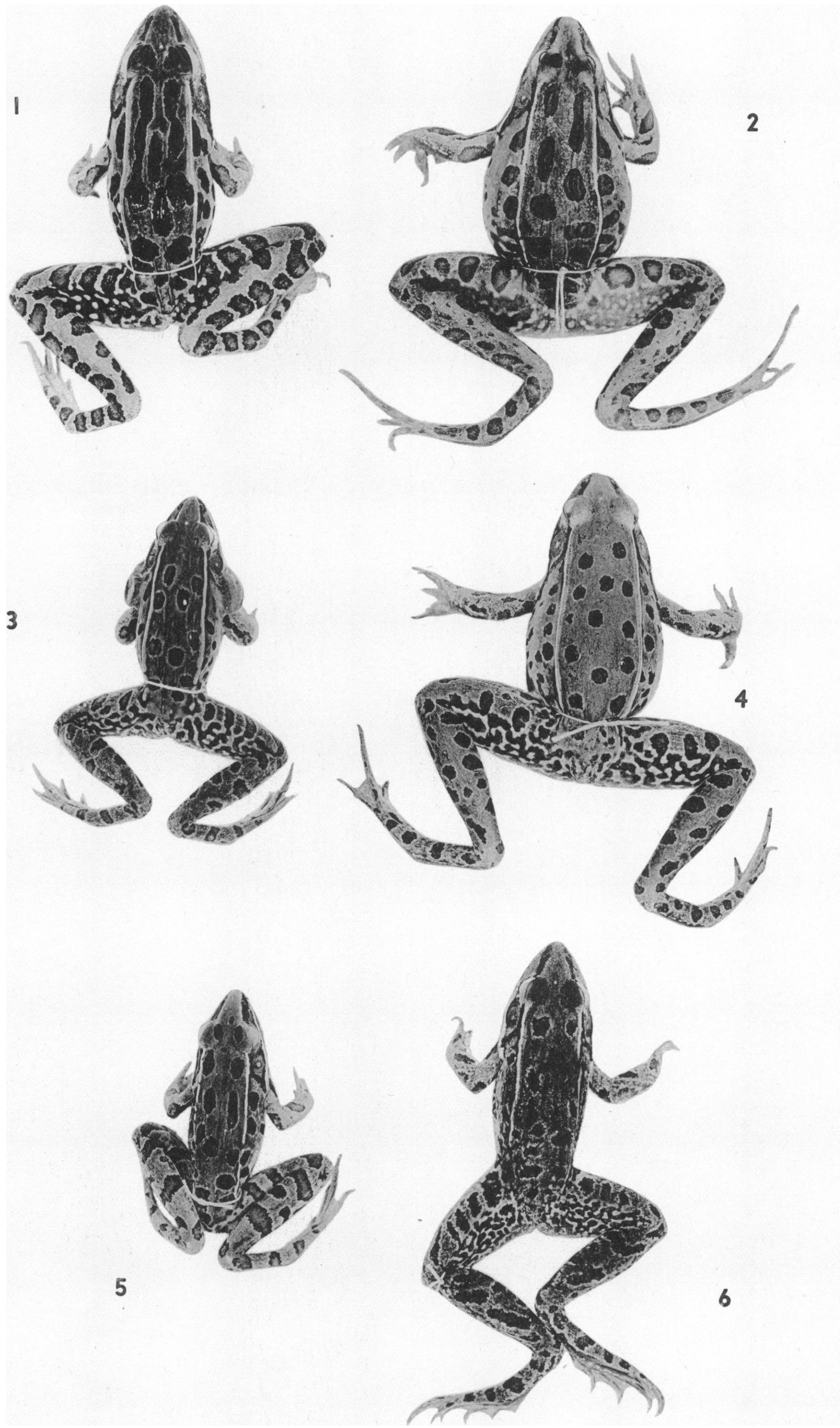
Photographs of living *Rana pipiens* from: 1, western Wisconsin; 2, Montreal, Quebec; 3, Alburg, Vermont; 4, Mt. Ephraim, New Jersey; 5, 6, Bloomington, Indiana; 7, Mt. Ephraim, New Jersey; 8, Chalmette, Louisiana; 9, Englewood, Florida.



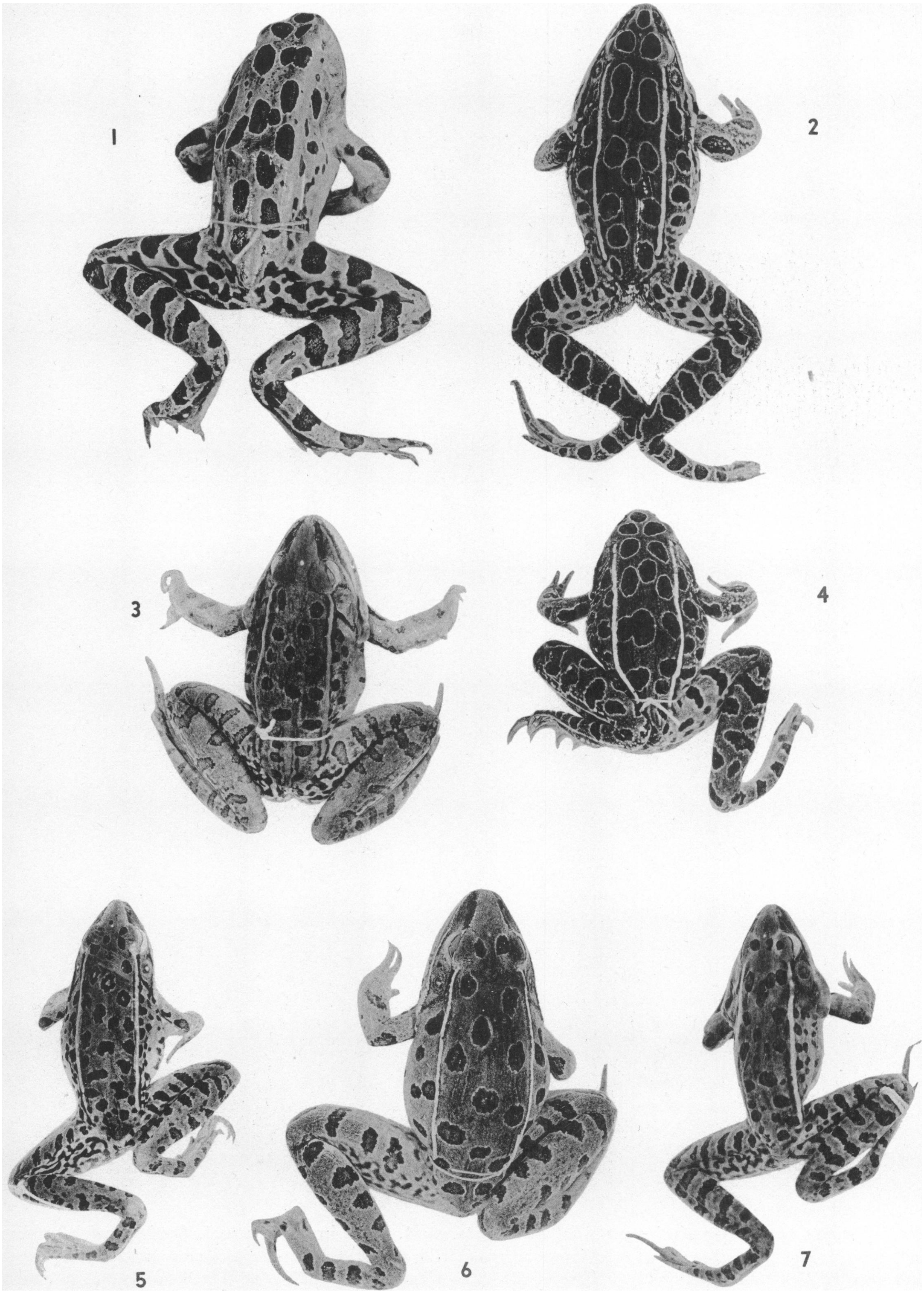
Photographs of *Rana pipiens* from Massachusetts, New York, and New Jersey: 1, Cuttyhunk, Massachusetts (A.M.N.H. No. 3385); 2, Rossie, New York (A.M.N.H. No. 51042); 3, Elmhurst, Long Island, New York (A.M.N.H. No. 14522); 4, Staten Island, New York (A.M.N.H. No. 23030); 5, Leonia, New Jersey (A.M.N.H. No. 35503); 6, Garfield, New Jersey (A.M.N.H. No. 35512).



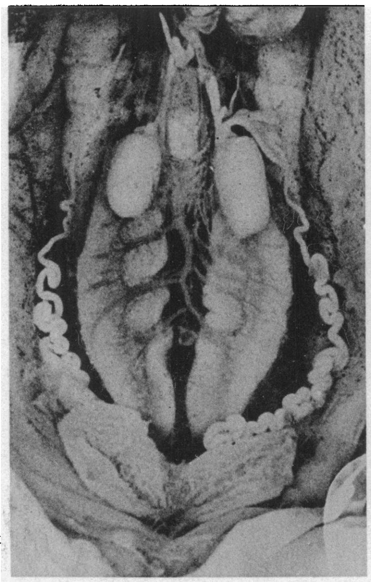
Photographs of *Rana pipiens* from New Jersey, North Carolina, Georgia, and Florida: 1, Lakehurst, New Jersey (A.M.N.H. No. 16954); 2, Wilmington, North Carolina (A.M. N.H. No. 21348); 3, Ashburn, Georgia (A.M.N.H. No. 34390); 4, Jacksonville, Florida (A.M.N.H. No. 11499); 5, Ozona, Florida (A.M.N.H. No. 106); 6, Tampa, Florida (A.M.N.H. No. 49896).



Photographs of *Rana pipiens* from Florida, Mississippi, Louisiana, and Texas: 1, Okeechobee County, Florida (A.M.N.H. No. 44197); 2, Canaveral, Florida (A.M.N.H. No. 6480); 3, Biloxi, Mississippi (A.M.N.H. No. 40264); 4, Louisiana (A.M.N.H. No. 18719); 5, Lake Caddo, Texas (A.M.N.H. No. 12892); 6, Belton, Texas (A.M.N.H. No. 32603).



Photographs of *Rana pipiens* from Minnesota, South Dakota, Nebraska, Missouri, Illinois, Kentucky, and Oklahoma: 1, Fort Snelling (St. Paul), Minnesota (A.M.N.H. No. 876); 2, Bristow, Nebraska (A.M.N.H. No. 32814); 3, Stone County, Missouri (A.M.N.H. No. 40317); 4, Pine Ridge, South Dakota (A.M.N.H. No. 32463); 5, La Center, Kentucky (A.M.N.H. No. 32290); 6, Anna, Illinois (A.M.N.H. No. 32249); 7, Tulsa, Oklahoma (A.M.N.H. No. 51048).



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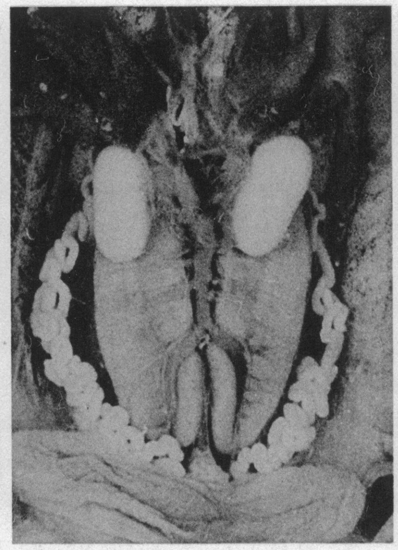

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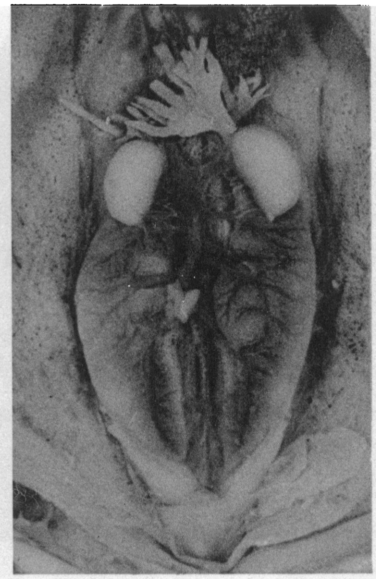

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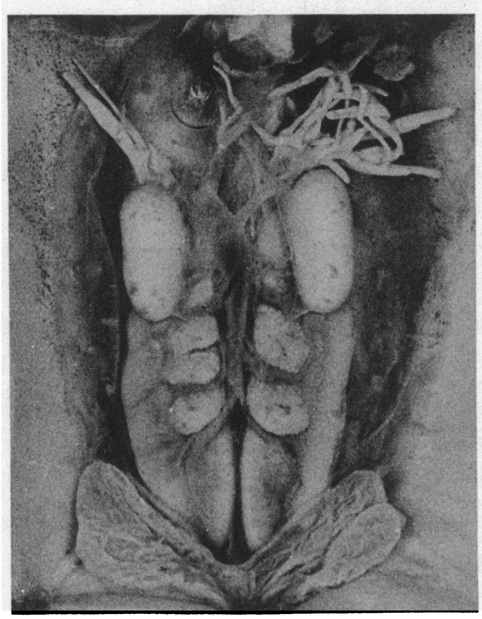

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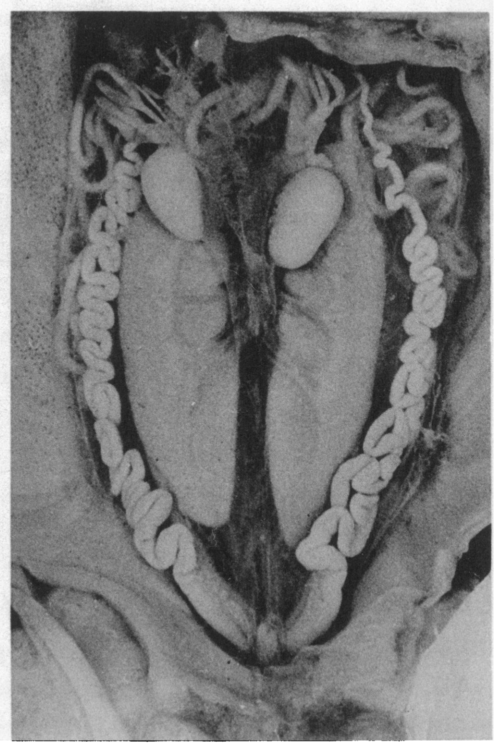

5

Ventral views of urino-genital system in *Rana pipiens:* 1, male from Montreal, Quebec, with oviduct; 2, male from Oshkosh, Wisconsin, with oviduct; 3, male from Tulsa, Oklahoma, showing absence of oviduct; 4, male from Mt. Ephraim, New Jersey, showing absence of oviduct; 5, male from Englewood, Florida, with oviduct. Several large nematode worms are visible, especially dorsal and lateral to the testes.

northern animals having wide heads and more southern animals having progressively narrower heads.

SUMMARY OF VARIATION IN BODY PROPORTIONS

A study of body proportions in more than 500 meadow frogs from eastern North America has revealed the following.

The leg/body means were found to be fairly constant (table 1, fig. 1). Somewhat greater differences were noticed in the means of body/tibia ratios (tables 1 and 3, fig. 1), but the considerable overlapping of the ratios makes any separation of the populations into groups impossible.

Samples grouped as *sphenocephala* have slightly longer heads (i.e., lower body/head-length ratios) than those grouped as *pipiens* and *brachycephala* (table 2, fig. 2). Again, however, the great individual variability makes this ratio useless in separating meadow frogs into the three species recognized by Kauffeld (1937).

The greatest differences were found in head shape, southern populations having narrower heads (low head-width/head-length ratios) than more northern populations (tables 2 and 3). Even here individual variability results in considerable overlapping of the ratios (fig. 2), making this ratio questionable as an important taxonomic character.

A consideration of the degree of the differences and of their low correlation with distribution leads to the conclusion that none of these ratios, or any combination of them, serves as an adequate basis for separating the meadow frogs of eastern North America into either species or subspecies.

VARIATION IN PIGMENTATION

The greatest variability occurs in pigmentation. So extensive and irregular are these differences that some students (Kauffeld, 1937) have thought it best not to employ characters of this nature to separate the species or races, but to rely entirely on differences of body proportion. The specimens shown in plates 61 to 65 will give an indication of some of the types encountered. In those cases where large samples from a single locality were available, it was found that the individuals were of the same general pattern, although considerable minor individual variation does exist. In addition it is usually possible to distinguish samples from different localities by means of pigment pattern. The differences between two localities may be extremely slight, or they may be well marked. In a series of animals from St. Albans, Vermont, the average number of dorsal spots is 9.6 ± 0.8 ($\sigma = 2.5$) and the extremes are 6 and 13. Another series from Shoreham Center, Vermont, 80 miles away, have an average spot number of 17.8 ± 1.6 ($\sigma = 3.5$) and extremes of 14 and 22. The differences between animals from two localities in New Jersey only 50 miles apart is very striking. Those from Lakehurst have many dorsal and lateral spots, a white center in the tympanic membrane, a light dorsolateral fold, usually a light reticulum on the posterior face of the femur, and are generally light in color. In contrast those from the Great Swamp region have few dorsal and lateral spots, lack a white tympanic spot, have a dark dorsolateral fold, have a dark reticulum on the posterior face of the femur, and are generally darker in color. These differences are so pronounced that every specimen in the samples can be correctly assigned to one population or the other on the basis of these characters. These two cases of differences between local populations in Vermont and New Jersey are not unique; it usually is possible to distinguish local populations by means of their pigment pattern.

The pigment characters studied were those found useful by Cope (1889), Wright and Wright (1933), and Dickerson (1906). Every specimen was examined for the presence or absence of complete cross bars on the right tibia, the number of these bars if present, the presence or absence of a longitudinal bar on the anterior face of the femur, the presence or absence of a white tympanic spot, whether the reticulum on the rear of the femur was light or dark, the number of dorsal spots, the number of lateral spots on the right side, and whether these lateral spots tended to form a reticulum or not. In the results, which are given in table 4, the specimens are grouped by states as a matter of convenience. However, in all probability every state has many local

TABLE 4

VARIATION IN PIGMENTATION CHARACTERS IN MEADOW FROGS

Locality	Number of Specimens	With Tibia Bars (%)	No. of Tibia Bars	Without Femur Bar (%)	Without Tympanic Spot (%)	With Light Reticulum (%)	Number of Dorsal Spots $M \pm \sigma_m$	Number of Dorsal Spots σ	Number of Lateral Spots $M \pm \sigma_m$	Number of Lateral Spots σ	Without Lateral Reticulum (%)	Population Index
ATLANTIC COAST												
Quebec	19	63	2.0	100	89	100	11.6±0.6	2.5	14.5±0.7	3.1	100	90
Maine	3	100	1.3	100	67	100	13.3±0.9	1.5	13.7±1.5	2.5	100	93
Vermont	24	71	1.4	79	50	100	12.4±0.8	4.0	15.6±0.8	3.7	100	80
N. New York	15	87	2.3	93	40	100	12.9±0.6	2.3	15.7±0.8	3.1	100	84
Massachusetts	7	29	2.5	100	57	100	11.4±1.1	3.0	16.3±3.4	8.8	100	77
Rhode Island	4	50	2.0	75	75	100	11.0±1.9	3.7	15.7±1.9	3.8	100	80
S. New York	33	33	1.2	30	54	3	13.1±0.6	3.4	9.1±0.7	3.5	71	38
New Jersey	45	9	1.0	49	44	36	13.8±0.5	3.3	10.0±0.8	4.6	78	43
Maryland	5	60	1.0	80	0	100	16.6±1.3	2.8	9.3±1.5	2.5	60	60
North Carolina	7	29	1.0	57	29	72	11.1±0.7	1.8	10.8±2.1	5.3	86	55
South Carolina	3	0	—	100	0	67	14.7±2.2	3.8	11.0±2.0	2.8	67	47
Georgia	11	27	1.3	36	18	9	13.5±1.3	4.3	10.6±1.2	3.5	82	35
Florida	149	44	1.3	39	7	16	14.1±0.3	3.4	10.5±0.5	2.8	27	27
CENTRAL REGION												
Ontario	4	100	3.5	100	100	100	15.8±1.1	2.2	17.8±1.0	1.9	100	100
Michigan	2	100	2.0	100	0	50	12.5±2.6	3.6	23.0±1.0	1.4	100	70
Wisconsin	7	71	1.8	100	57	100	14.6±1.3	3.4	12.3±1.7	4.3	100	86
Minnesota	15	80	2.4	100	20	100	14.6±0.8	3.0	13.3±0.8	3.0	100	80
South Dakota	15	80	1.5	100	20	100	16.1±0.7	2.9	13.7±1.1	4.2	100	80
Nebraska	29	76	2.0	97	17	100	15.0±0.7	3.6	11.8±0.8	4.1	100	78
Indiana	20	75	1.7	55	0	90	16.9±1.2	5.5	16.6±1.5	6.6	96	63
Kentucky	3	67	1.0	100	33	100	24.0±5.1	8.6	21.6±4.8	8.1	100	80
Illinois	11	73	1.8	82	0	100	19.5±1.4	4.7	13.8±1.2	3.9	100	71
Missouri	25	84	2.0	60	16	96	17.9±1.0	4.8	13.2±0.9	4.2	88	69
Kansas	5	80	1.5	100	20	100	17.8±2.5	5.5	14.8±2.3	5.1	100	80
Arkansas	21	62	1.3	86	29	95	19.6±0.9	4.1	14.0±0.9	4.1	100	74
Oklahoma	9	78	1.7	78	14	100	22.2±1.7	5.1	17.0±1.8	5.4	100	74
Mississippi	6	17	1.0	50	33	100	12.2±1.3	3.1	10.5±0.6	1.4	100	60
Louisiana	34	64	1.4	48	0	67	12.9±0.7	4.3	10.1±0.6	3.3	85	53
Texas	27	56	1.7	67	22	78	15.7±0.7	3.7	12.7±0.9	4.7	100	65

populations, each exhibiting significant differences. With the exception of the average number of dorsal spots, the lateral spots, and of tibia bars, the data refer to the percentage of the sample possessing or lacking a given character. The characters are defined in such a way that the higher the percentage the more the sample resembles the *pipiens* of Dickerson (1906), and of Wright and Wright (1933), or the *brachycephala* of Cope (1889) and Kauffeld (1937). Thus, if a sample were 100 per cent in all percentage characters it would be a "typical" *pipiens* (or *brachycephala*); if it were 0 per cent in all it would be a "typical" *sphenocephala*.

Tibia Bars

According to Cope (1889) complete tibia bars are characteristic of *brachycephala*. They are interrupted in *pipiens* and absent in *sphenocephala*. Every sample contained specimens with and without cross bars on the tibia except in those from Maine, South Carolinal Ontario, and Michigan. In these exceptiona, cases the number of individuals was very small, and a larger sample would probably have shown this uniqueness to be due to sampling errors. In general a greater percentage of the specimens from New England, Canada, the Mississippi Valley, and the eastern Plains region have tibia cross bars than those from the Middle Atlantic and southeastern states (pls. 61–65). Furthermore, the number of bars (average of those with bars only) is greater in the former localities than in the latter.

Femur Bar

Cope (1889) finds the femur bar absent in *brachycephala*, present in *pipiens*, and usually present in *sphenocephala*. Dickerson (1906) finds it present in *sphenocephala* and absent from *pipiens*. In 11 samples (some very small) no individuals were encountered with a longitudinal bar on the anterior face of the femur. Samples from New England, Canada, the Mississippi Valley (except Louisiana), and the eastern Plains region have a higher percentage of individuals without the femur bar than those from the Middle Atlantic, southeastern, and Gulf states.

Tympanic Spot

Kauffeld (1937) finds the tympanic spot to be absent in *brachycephala*, usually present in *pipiens*, and always present in *sphenocephala*. Dickerson (1906) states that a sharply defined tympanic spot is found in *sphenocephala* but not in *pipiens*. Some difficulty was encountered in classifying the preserved specimens with respect to the presence or absence of a tympanic spot (even in a living animal the distinctness of the spot varies considerably, depending on the degree of expansion or contraction of the surrounding pigment cells). The spot itself varies from an irregular blotch of white (pl. 61, figs. 4, 9, pl. 65, fig. 2) to a sharply defined circular area in the center of the tympanic membrane (pl. 61, figs. 5, 8, pl. 63, figs. 1, 3, 6). Those with sharply defined circular spots are not restricted to the southern states (pl. 61, fig. 5, Indiana; pl. 63, fig. 1, New Jersey; and pl. 65, fig. 5, Kentucky), and animals from this region may lack the spot entirely (pl. 63, fig. 5, Florida). Thus a sharply defined white tympanic spot is not a constant feature of southern populations, as Kauffeld and others have suggested. Samples from New England and Quebec show more animals without a white area than those from other parts of the country (table 4).

Femur Reticulum

Considerable variation exists in the pigmentation of the posterior face of the femur, but it is possible to distinguish two main types. The ground color (continuous phase) may be light and the spots and streaks (dispersed phase) dark. This is called a light reticulum (pl. 62, figs. 1, 2) and is thought to be characteristic of *pipiens* (Wright, 1932). Or the ground color may be dark and the spots light. This is called a dark reticulum (pl. 64, figs. 1, 2) and is said to be characteristic of *sphenocephala*. The variation on these two types seems endless. A light reticulum may be white, or it may be nearly as dark as the spots. The spots in a light reticulum may be so large as to occupy nearly the entire surface, or they may be so small as to be nearly absent. A dark reticulum may be so extensive as to cover nearly the entire surface, or it may be restricted to narrow lines between large light spots. Samples from New England, Canada, the Mississippi Valley, and eastern Plains region are either exclusively or predominantly of the light reticulum type. Samples from southern New York and New Jersey and from Georgia and Florida are predominantly of the dark reticulum type. The small samples from the intermediate states, Maryland, North Carolina, and South Carolina, have a larger proportion of forms with a light reticulum (table 4).

Dorsal Spots

In any one locality the number of dorsal spots shows tremendous individual variation. The samples from New England and Quebec average fewer dorsal spots than those from most other localities, the means ranging from 11.0 to 13.3 (table 4). With the exception of a small sample from North Carolina, the average number in samples along the Atlantic coast south of New England varies from 13.1 to 16.6. In the central region samples from Michigan (two specimens), Mississippi, and Louisiana have few spots. The remaining samples from the Mississippi Valley and eastern Plains region are the most heavily spotted animals encountered, the averages ranging from 14.6–24.0.

Lateral Spots

Considerable variation is also encountered in lateral spot number (the number of spots on the right side only was counted). In some specimens no count could be made, as the spots tended to form a reticulum. Samples from New England and Quebec have many lateral spots, the averages varying from 13.7 to 16.3 (table 4). South of New England the animals average fewer lateral spots, the extremes being 9.1 and 11.0. In the central region no very definite trends are apparent.

Relative Spot Number

When a comparison is made of the mean number of dorsal and lateral spots (table 4), it is found that in samples from New England, Quebec, Ontario, and Michigan there are more lateral than dorsal spots. In all other samples the reverse is true; the mean number of dorsal spots is greater than the mean number of lateral spots.

Lateral Reticulum

As mentioned above, in some localities the lateral spots tend to "fuse" and so form a reticulum. In New England, Quebec, and throughout the Mississippi Valley and eastern Plains region (except for a few individuals from the Indiana, Missouri, and Louisiana samples) the lateral spots do not form a reticulum (table 4). On the Atlantic coast south of New England there is a distinct tendency for the lateral spots to form a reticulum. In Florida, for example, this occurs in 73 per cent of the individuals.

Population Index

The percentage data in table 4 are arranged to show the per cent of the population having the character of the northern *pipiens* of Dickerson (1906) and Wright and Wright (1933), or *brachycephala* of Cope (1889) and Kauffeld (1937). The greater the value the more the sample resembles these northern forms. For purposes of comparison a "population index" can be determined by finding the average of these percentages. Such a population index is given in table 4. It was obtained by adding the percentages of individuals with tibia bars, without femur bars, without a tympanic spot, with a light reticulum, without a lateral reticulum, and dividing by five. If the population index were 100, the sample might be thought of as a typical *pipiens* (or *brachycephala*) and if the index were 0, a typical *sphenocephala*. It should be emphasized that no special significance is attached to this population index. It refers only to some of the pigmentation differences and is merely a convenient way of indicating trends shown by the data. On the Atlantic coast the highest values are found in Quebec and Maine and the lowest in Georgia and Florida. The trend is not regular in the intermediate localities. A marked drop occurs as we pass from New England to southern New York and New Jersey. South of these localities the value rises slightly and then drops again. In the central region a similar gradient is present, but it is not so steep as on the Atlantic coast and apparently decreases in a more regular manner.

VARIATION IN SECONDARY SEX CHARACTERS

Vestigial Oviducts

As is well known, the male of *Rana pipiens* has fairly well developed oviducts (see Christensen, 1930). Their function, if any, is unknown, and they never reach the degree of development of the homologous structure in the female. During the course of cross fertilization experiments in which meadow frogs from different localities were used it was noticed that males from some localities did not possess oviducts. Consequently an examination was made of previous experimental material as well as specimens from the collection of the American Museum of Natural History to determine the distribution of populations possessing oviducts in the male. Except for several interesting specimens, the males from a given locality are consistent in possessing or lacking this structure. Many hundreds of males from Vermont have been examined, and none has lacked oviducts (however, one specimen was observed with this organ absent from one side). In figure 3 the distribution of populations with and without oviducts in the males is shown. Males from southern New York and south to northern Florida lack oviducts. In the one specimen available from Maine oviducts were absent. The same is true for males from Louisiana, Mississippi, eastern Texas, and in the Mississippi Valley north to southern Indiana, Illinois, and Missouri (pl. 66, figs. 3, 4). The males possess oviducts in New England (except for the one Maine specimen), Quebec, Ontario, and west through Wisconsin, Iowa (according to Christensen), and South Dakota (pl. 66, figs. 1, 2). In the Rocky Mountain region only a few individuals were available for study. Some of these possessed oviducts and others lacked them. The males from central and southern Florida possess well-developed oviducts (pl. 66, fig. 5). In northern Florida the population is mixed. Of 14 males from Gainesville oviducts were lacking in 11 and were present in three. Two males in a total of eight from the Ocala region possess oviducts.

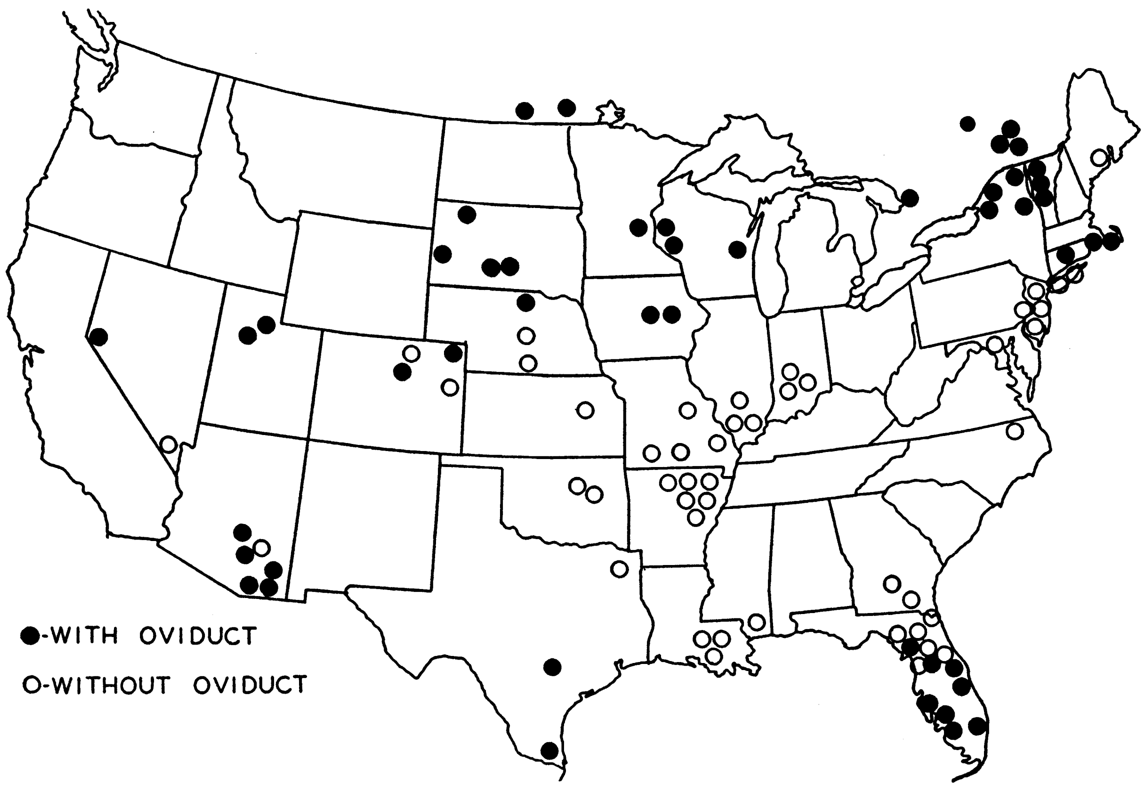

FIG. 3. Geographic distribution of male meadow frogs with and without oviducts. The circles indicate from one to four males lacking an oviduct, and each dot represents one to four males with an oviduct (except for the very large samples from Vermont, Long Island, and New Jersey where several dots or circles represent dozens or hundreds of individuals). Data for Iowa and Connecticut from Christensen (1930).

External Vocal Sacs

Cope (1889) found the external vocal sacs to be well developed in males of his varieties *pipiens* and *sphenocephala* but not in *brachycephala*. The reliability of this character has been questioned, but apparently only by those who have confused internal with external vocal sacs. Males from eastern Canada, New England, and northern New York possess well-developed internal vocal sacs, but the external vocal sacs are absent or poorly developed. From southern New York and south along the Atlantic coast the males possess well-developed external vocal sacs (pl. 61, figs. 6, 7, pl. 62, fig. 5, pl. 64, fig. 3, pl. 65, fig. 7). In general those males on the Atlantic coast lacking oviducts possess well-developed external vocal sacs. This correlation does not hold in all localities. The single male from Maine that lacked oviducts also lacked external vocal sacs. The males of southern Florida which possess oviducts usually have well-developed external vocal sacs. In the Mississippi Valley males from southern Indiana, Oklahoma, Arkansas, Louisiana, and Mississippi have well-developed external vocal sacs (these have no oviducts). Males from southern Illinois that lack oviducts may or may not have external vocal sacs. Males from Wisconsin, Minnesota, South Dakota, Nebraska, Kansas, and Missouri do not have external vocal sacs regardless of whether or not they have oviducts. Individuals from Texas may or may not have well-developed external vocal sacs. Here again there is no correlation with presence or absence of oviducts.

Two additional male secondary sex characters, namely, the size of the forearm and the size of the thumb, seem to vary in degree of development in different parts of the country. They have not been systematically investigated.

EMBRYOLOGICAL DIFFERENCES

The variation encountered in meadow frogs is not restricted to adults. Striking and consistent differences characterize the embryonic stages of animals from different parts of the country. The rate of development, embryonic temperature tolerance, temperature coefficient for development, and egg size are all subject to variation. Characters of this nature have previously been found to differ in many species of frogs, toads, and salamanders, and they represent important adaptations to environmental temperature differences (Moore, 1939, 1942a, 1942b).

Eggs of individuals from Quebec, Vermont, Long Island, New Jersey, Wisconsin, Indiana, Louisiana, northern Florida, and southern Florida have been studied (Moore, 1941, 1943, and unpublished observations). Although it does not seem necessary to give in detail either the experimental methods or complete data, the general conclusions contribute to any discussion of variation in meadow frogs.

Individuals from Quebec, Vermont, Wisconsin, Long Island, Indiana, and New Jersey exhibit no significant differences among themselves in either rate of development or embryonic temperature tolerance. However, the material from Louisiana and Florida is different. Eggs from Louisiana and Florida are more resistant at high temperatures. The upper limit of temperature tolerance in northern localities is 28–29° C., and in Louisiana and northern Florida it is 32–33° C. Eggs from southern Florida appear slightly more resistant, being able to develop at 34° C. Eggs from the northern localities and Louisiana are able to develop at 6° C., but those from both northern and southern Florida are killed at this temperature. The rate of development of eggs from Louisiana, northern Florida, and southern Florida not only differs from that of eggs from the more northern states but also among each of these localities. In general, eggs from the northern localities develop more rapidly at temperatures below 18° C. and less rapidly at higher temperatures than eggs from the southern localities. Thus, at 24° C. eggs from Louisiana develop 6 per cent more rapidly than those from New Jersey, and eggs from northern Florida develop 12 per cent faster. Eggs from southern Florida appear to develop slightly more rapidly than those from northern Florida at this temperature.

Individuals from the north have larger eggs than those from the south. The average diameter of uncleaved eggs from the northern states is 1.8 mm.; from Louisiana, 1.6 mm.; from northern Florida, 1.4 mm.; and from southern Florida, 1.3 mm.

Considerable differences exist in pigmentation of larvae from various localities, but as yet variation of this nature has not been studied systematically.

CROSS-FERTILIZATION EXPERIMENTS

A number of crosses have been made between individuals of different local populations (Moore, 1941, 1943). When eggs of Vermont females are fertilized with sperm of New Jersey (see also Porter, 1941) or Oklahoma males, early development is perfectly normal, and the tadpoles transform as young with intermediate pigmentation characteristics. If sperm of males from Louisiana is used, a slight retardation in rate of development is noticed in the early stages; otherwise development appears quite normal. Somewhat greater deviations from normal development result when Vermont eggs are fertilized with north Florida sperm. Not only is there a retardation in rate of development, but gill circulation may be slightly abnormal and the head enlarged. These morphological abnormalities are more pronounced when sperm of males from southern Florida is used. The retardation in rate of development in this case is greater, the head may be markedly enlarged, the heart may fail to beat, and gill circulation may be irregular or lacking. In some cases these abnormalities have led to the death of all embryos in a given experiment. In other experiments the embryonic mortality in this cross has been no greater than in the controls, with the tadpoles transforming as normal young.

When eggs of New Jersey females are used, the results are slightly different. Those fertilized with Vermont sperm develop perfectly normally. If males from Louisiana or northern Florida are used there is a slight retardation in rate, and the embryos may have minor gill abnormalities.

Louisiana eggs fertilized with sperm of Vermont males are slightly retarded in developmental rate. They develop normally when fertilized with sperm of south Florida males.

When crosses are made with north Florida eggs, and sperm from Louisiana or south Florida males, development is normal. If, instead, sperm of New Jersey or Vermont males is used, development is retarded and, with the latter, abnormalities of the head may be present. In extreme cases the head is very small, the suckers and nasal pits are fused, the stomodaeum may not form, with the result that no mouth appears. The type of abnormality is very different from that observed in the reciprocal cross.

Although experiments have been performed on relatively few local populations, it appears from the results so far obtained that the normality of development in crosses is correlated with the distance between the populations. In crosses between New Jersey and Vermont, or Florida and Louisiana, the embryos develop perfectly normally. In crosses between New Jersey and northern Florida, or Vermont and Louisiana frogs, the embryos are normal except for a slight retardation in rate of development that seems to result in no lasting deleterious effect. When crosses are made between animals from the most distant localities, Vermont and Florida, the embryos may show pronounced morphological abnormalities.

DISCUSSION AND CONCLUSIONS

IN THIS STUDY of variation in meadow frogs a total of 20 characters has been investigated. This number is by no means commensurate with the variation encountered. Many additional characters were not studied because they appeared to show little correlation with geographic distribution. The two most important conclusions derived from this investigation are: (1) the meadow frogs of eastern North America consist of a number of allopatric populations belonging to a single species; and (2) the characters thought diagnostic of different species or subspecies of meadow frogs are those of extreme individuals rather than an average for the population from which they come.

A study of the photographs of living and preserved frogs will show that, although considerable variation does occur, the variations are those of a single species (pls. 61–65). In any one local population the individuals form a fairly homogeneous group; at least in the material examined there was no indication of two different forms occupying the same region. The fact that most taxonomists recognize two or more species of meadow frogs would appear to be contrary to the conclusion here expressed that the eastern North American populations belong to a single species. However, this disagreement is largely academic, since it depends on the use of the term "species." As far as eastern American frogs are concerned, it has been customary not to use trinomials and to regard species and subspecies in the same light. As everyone is agreed that *Rana sphenocephala* is a "southern *Rana pipiens*" it is merely in keeping with current taxonomic trends to regard these allopatric populations as forming a single polytypic species (Mayr, 1942). The question now arises, Is the variation among local populations extensive and regular enough to warrant the recognition of subspecies? An answer to this question should come from a study of the differences among populations from different geographic regions.

It is nearly impossible clearly to appraise the variation shown by *Rana pipiens* from the numerical data in tables 1 to 4. By means of a "population formula," however, it is possible to gain a better conception of the differences among the various populations. Thus, if we label those populations in which 50 per cent or more of the individuals possess tibia bars, B, and those in which less than 50 per cent of the individuals possess tibia bars, b, we can group the data in a more comprehensible, though less accurate, form. If this is done for the various characters investigated we can express the variation of the local populations in terms of a population formula, such as ABcDEfghI—, and so on. By treating percentile data as a dichotomous character considerable significant variation is masked, but if the limitations and sources of error are constantly kept in mind this method does become a useful means of grouping data.

With each character the percentage, type, or ratio characteristic of the New England populations (*brachycephala* of Kauffeld) is designated by a capital letter, and that of the southeastern populations (*sphenocephala*) by a small letter. Thus a "typical" northern population would have a formula ABCDEF—, and a "typical" southern population a formula abcdef—. In table 5 the symbols with their meanings and the population formulas for the material which forms the basis of this study are given.

The populations from Canada, New England, northern New York, Michigan, and Wisconsin have identical, or very similar, formulas. (This similarity is to some extent artificial, as these northern populations were taken as a standard and the criteria so adjusted as to include their characteristics. If some other populations were taken as a standard those from New England, northern New York, Michigan, and Wisconsin might not have appeared as homogeneous.) The formulas for the other states are unique except for Minnesota and South Dakota, Illinois and Oklahoma, and Missouri and Kansas, these pairs of states having the same formulas (Minnesota and Texas also have the same formulas, but if data on head-width/head-length ratio for Minnesota were available it would probably be of the A type and so would be different from Texas). On the Atlantic coast there is a pronounced change in population formula as we pass from New England to southern New York and New Jersey. In the Mississippi Valley there is no such abrupt change in going from north to south. The usefulness of the population formulas here given is limited by the small number of specimens in some cases, and by

TABLE 5

POPULATION FORMULAS FOR MEADOW FROGS OF EASTERN NORTH AMERICA

Quebec	A	B	C	D	E	F	G	H	I	J	K	L
Maine	A	B	C	D	E	F	g	H	I	J	k	L
Vermont	A	B	C	D	E	F	G	H	I	J	K	L
N. New York	A	B	C	D	e	F	G	H	I	J	K	L
Massachusetts	A	b	C	D	E	F	G	H	I	J	K	L
Rhode Island	A	B	C	D	E	F	G	H	I	J	K	L
S. New York	A	b	c	d	E	f	g	h	i	J	k	l
New Jersey	A	b	c	d	e	f	g	h	i	J	k	l
Maryland	a	B	c	D	e	F	g	h	i	J	k	l
North Carolina	A	b	c	D	e	F	G	h	i	J	k	l
South Carolina	—	b	—	D	e	F	g	h	i	J	—	—
Georgia	a	b	c	d	e	f	g	h	i	J	k	l
Florida	a	b	c	d	e	f	g	h	i	j	K	l
Ontario	—	B	C	D	E	F	G	H	I	J	K	—
Michigan	—	B	C	D	e	F	G	H	I	J	—	—
Wisconsin	A	B	C	D	E	F	g	H	i	J	K	L
Minnesota	—	B	C	D	e	F	g	H	i	J	K	L
South Dakota	A	B	C	D	e	F	g	H	i	J	K	L
Nebraska	—	B	C	D	e	F	g	h	i	J	k	L
Indiana	A	B	C	D	e	F	g	H	i	J	k	l
Kentucky	a	B	c	D	e	F	g	H	i	J	—	—
Illinois	a	B	C	D	e	F	g	H	i	J	k	l
Missouri	A	B	C	D	e	F	g	H	i	J	k	L
Kansas	A	B	C	D	e	F	g	H	i	J	k	L
Arkansas	A	B	c	D	e	F	g	H	i	J	k	l
Oklahoma	a	B	C	D	e	F	g	H	i	J	k	l
Mississippi	a	b	c	D	e	F	G	h	i	J	k	l
Louisiana	a	B	C	d	e	F	G	h	i	J	k	l
Texas	a	B	C	D	e	F	g	H	i	J	K	L

DEFINITION OF SYMBOLS

A, Head width/head length 0.92 or greater
B, 50% or more with tibia bars
C, Average number of tibia bars (when present) 1.4 or greater
D, 50% or more without femur bar
E, 50% or more without tympanic spot
F, 50% or more with light reticulum
G, Number of dorsal spots less than 13
H, Number of lateral spots 12 or more
I, More lateral than dorsal spots
J, 50% or more without lateral reticulum
K, 50% or more of males with oviducts
L, 50% or more of males with no, or poorly developed, external vocal sacs

a, Head width/head length less than 0.92
b, Less than 50% with tibia bars
c, Average number of tibia bars (when present) less than 1.4
d, Less than 50% without femur bar
e, Less than 50% without tympanic spot
f, Less than 50% with light reticulum
g, Number of dorsal spots 13 or more
h, Number of lateral spots less than 12
i, Lateral spot number equal to, or less than, dorsal spot number
j, Less than 50% without lateral reticulum
k, Less than 50% of males with oviducts
l, Less than 50% of males with no, or poorly developed, external vocal sacs

virtue of the fact that the material is grouped by states and not by local populations. In the two states, New Jersey and Florida, from which there is most abundant material the different local pouplations have different population formulas.

The question now arises, Should the populations of *Rana pipiens* of eastern North America be divided into two subspecies, *Rana pipiens pipiens* and *Rana pipiens sphenocephala*, or even into three, *Rana pipiens brachycephala*, *Rana pipiens pipiens*, and *Rana pipiens sphenocephala?* Unfortunately there can be no satisfactory answer to this question so long as there is no generally accepted and easily applied criteria for recognizing subspecies. Students of geographic variation well realize that every local population of a given species is probably different from every other local population. Sometimes these differences are slight and other times striking. A subspecies may be thought of as a group of allopatric populations that are similar in many or most respects and different enough from other groups of allopatric populations, so that most individuals can be correctly assigned to the proper group. If we attempt to apply such a criterion to *Rana pipiens*, we must conclude that the recognition of subspecies is not warranted. The characters thought most useful in separating the usually recognized forms, namely, differences in body proportions, are for the most part invalid. A careful study of figures 1 and 2 together with tables 1, 2, and 3 will reveal that, although slight differences do exist in the mean ratio for every character studied, these differences, even when significant, are not large enough to afford a useful means of distinguishing any subspecies of *Rana pipiens* in eastern North America. Likewise in this case it seems unwarranted to recognize any subspecies on the basis of pigmentation or embryological characters. This conclusion, that *sphenocephala* and *brachycephala* are not valid, is reached in full realization that others with a different understanding of the nature of a subspecies would be quite willing to recognize three or even more subspecies on the basis of the data given in this paper. However, it is my opinion that subspecies should include relatively homogeneous local populations and, when employed in this sense, have an objective reality. When, in defining subspecies, we disregard many variations that show no regularity with distribution and emphasize a few that are regular, this category becomes artificial. Such an artificial category, which may be of some convenience in pigeonholing specimens, would seem to have little place in a natural or genetic system of classification.

CONCLUSIONS

A study has been made of the taxonomic characters customarily employed in separating *Rana pipiens* Schreber, *Rana sphenocephala* (Cope), and *Rana brachycephala* (Cope). These diagnostic characters were found invalid when samples from many localities were studied. It does not appear possible to recognize three species or subspecies of meadow frogs on the basis of differences in body proportions or pigmentation. Therefore, the meadow frogs of eastern North America should be known as *Rana pipiens* Schreber. *Rana sphenocephala* (Cope) and *Rana brachycephala* (Cope) should be reduced to synonyms of *Rana pipiens* Schreber.

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