

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 148

**Systematic and Biological Studies of  
the Leopard Frogs (*Rana pipiens* Complex)  
of the United States**

BY

ANN E. PACE

*Department of Biology, Queens College,  
CUNY, Flushing, N. Y.*

*(New address: James Ford Bell Museum of Natural History,  
University of Minnesota at Minneapolis)*

Ann Arbor  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
August 19, 1974

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

FRANCIS C. EVANS, EDITOR

The publications of the Museum of Zoology, University of Michigan, consist of two series—the Occasional Papers and the Miscellaneous Publications. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb.

The Occasional Papers, publication of which was begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When a sufficient number of pages has been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The Miscellaneous Publications, which include papers on field and museum techniques, monographic studies, and other contributions not within the scope of the Occasional Papers, are published separately. It is not intended that they be grouped into volumes. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Birds, Fishes, Insects, Mammals, Mollusks, and Reptiles and Amphibians is available. Address inquiries to the Director, Museum of Zoology, Ann Arbor, Michigan 48104.

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 148

**Systematic and Biological Studies of  
the Leopard Frogs (*Rana pipiens* Complex)  
of the United States**

BY

ANN E. PACE

*Department of Biology, Queens College,  
CUNY, Flushing, N. Y.*

*(New address: James Ford Bell Museum of Natural History,  
University of Minnesota at Minneapolis)*

Ann Arbor  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
August 19, 1974



## CONTENTS

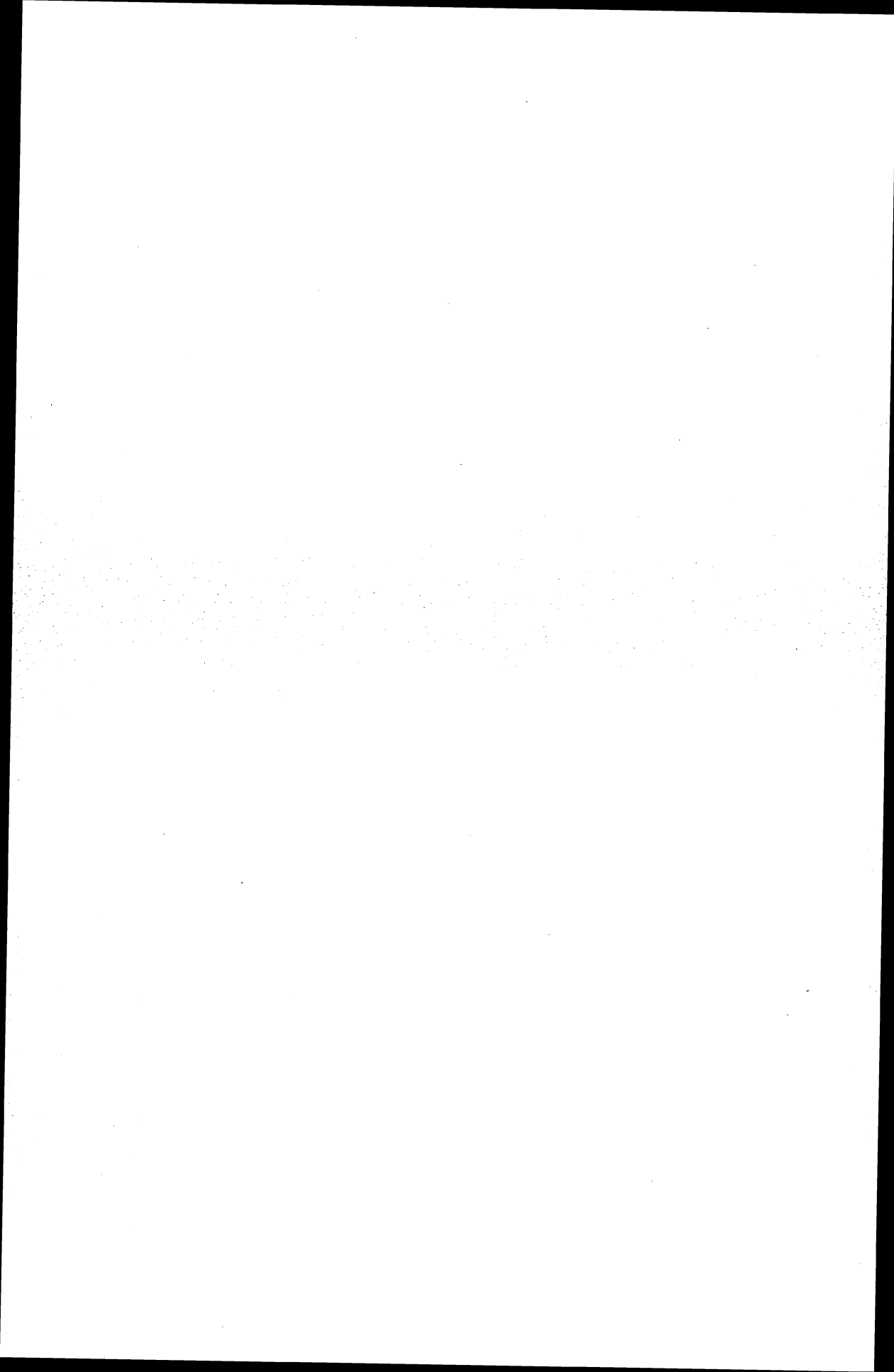
	PAGE
INTRODUCTION . . . . .	1
ACKNOWLEDGMENTS . . . . .	7
MATERIALS, METHODS, AND MISCELLANEOUS NOTES . . . . .	8
NOMENCLATURE . . . . .	11
Nomenclatural History . . . . .	11
Species Characterizations and Synonymies . . . . .	14
VOCALIZATIONS . . . . .	30
Vocal Repertoires . . . . .	30
Functions of Vocalizations . . . . .	31
Species Differences . . . . .	34
VARIATION IN SECONDARY SEX CHARACTERS . . . . .	41
Vocal Sacs . . . . .	41
Mullerian Ducts . . . . .	46
Mullerian Ducts and Vocal Sacs . . . . .	51
Tympanal Size . . . . .	51
Thumb Pads . . . . .	52
VARIATION IN CHARACTERS FOUND IN BOTH SEXES . . . . .	52
Dorsolateral Folds . . . . .	52
Tympanal Spots . . . . .	55
Dorsal Spot Patterning and Snout Spot . . . . .	58
Ventral Melanism . . . . .	61
Geographic Variation in Body Proportions . . . . .	63
Variation in other Morphological Characters . . . . .	66
VARIATION IN LEOPARD FROGS FROM THE SOUTHWEST . . . . .	66
INTERSPECIFIC DISTRIBUTIONAL RELATIONSHIPS . . . . .	70
Parapatry . . . . .	70
Probable Cases of Species Range Disjunctions . . . . .	74
Apparent Range Disjunctions Omitted from Distribution Map of <i>Rana</i> <i>pipiens</i> . . . . .	78
Distributional Relationships in the Middle West . . . . .	79
<i>R. pipiens</i> and <i>R. blairi</i> in Nebraska . . . . .	82
INTERSPECIFIC HYBRIDIZATION IN NATURE . . . . .	83
GROWTH RATES AND DEVELOPMENTAL TIME . . . . .	87
LIFE HISTORIES OF LEOPARD FROGS . . . . .	91
<i>Rana pipiens</i> . . . . .	91
<i>Rana blairi</i> . . . . .	93
Comparison of <i>R. pipiens</i> and <i>R. blairi</i> . . . . .	94
<i>Rana utricularia</i> . . . . .	95
DISRUPTIVE SELECTION AND PARAPATRY . . . . .	100
DISTRIBUTIONAL HISTORY AND RELATIONSHIPS WITHIN THE COMPLEX . . . . .	101
<i>R. pipiens</i> and <i>R. palustris</i> . . . . .	101
The Prairie Peninsula and Distributional Relationships in the Middle West . . . . .	103
<i>Rana berlandieri</i> and Florida Populations of <i>R. utricularia</i> . . . . .	104
SUMMARY AND CONCLUSIONS . . . . .	106
APPENDIX I: LOCALITIES OF SPECIMENS EXAMINED . . . . .	107
APPENDIX II: LOCALITIES OF FIELD AND CALL RECORDS . . . . .	130
APPENDIX III: CATALOGUE NUMBERS OF FROGS WITH UNUSUAL DORSOLATERAL FOLDS . . . . .	134
LITERATURE CITED . . . . .	135

## ILLUSTRATIONS

FIGURE	PAGE
1. Geographic distribution of <i>R. pipiens</i> in the United States . . . . .	17
2. <i>R. pipiens</i> ♂, (a) view of vocal sac region and (b) dorsal view . . . . .	19
3. Reproduction of plate accompanying original description of <i>R. pipiens</i> . . . . .	20
4. Geographic distribution of <i>R. utricularia</i> . . . . .	22
5. <i>R. utricularia</i> ♂ from Kansas, (a) view of vocal sac region and (b) dorsal view . . . . .	23
6. <i>R. utricularia</i> ♂ from Florida, (a) view of vocal sac region and (b) dorsal view . . . . .	24
7. Geographic distribution of <i>R. berlandieri</i> in the United States . . . . .	25
8. Reproduction of illustration accompanying original description of <i>R. berlandieri</i> . . . . .	26
9. Geographic distribution of <i>R. blairi</i> . . . . .	27
10. <i>R. blairi</i> ♂, (a) view of vocal sac region and (b) dorsal view . . . . .	28
11. Vocal response of (a) <i>R. pipiens</i> male and (b) <i>R. palustris</i> male to mating call of conspecific male . . . . .	32
12. Relationship of pulse duration to pulse rate in mating call of <i>R. utricularia</i> . . . . .	36
13. Sonagrams of mating calls of <i>R. utricularia</i> (low temperatures) . . . . .	37
14. Sonagrams of mating calls of <i>R. utricularia</i> (high temperatures) . . . . .	38
15. Sonagrams of mating calls of <i>R. utricularia</i> , <i>R. pipiens</i> , and <i>R. palustris</i> (sympatric) and <i>R. capito</i> . . . . .	39
16. Relationship of pulse rate to temperature in mating calls (a) of <i>R. utricularia</i> and (b) of <i>R. pipiens</i> , <i>R. palustris</i> , and <i>R. capito</i> . . . . .	39
17. Relationship of pulse rate to temperature in mating calls of <i>R. berlandieri</i> and <i>R. blairi</i> . . . . .	40
18. Geographic distribution of call types in the <i>R. pipiens</i> complex in the United States . . . . .	42
19. Geographic distribution of call types in Indiana and Kentucky . . . . .	43
20. Geographic distribution of vocal sac types in the United States . . . . .	44
21. Distribution of males with and without vestigial oviducts in the United States . . . . .	48
22. Distribution of Florida males with and without vestigial oviducts . . . . .	49
23. Diagrammatic representation of dorsolateral fold types . . . . .	53
24. Geographic distribution of frogs with continuous and discontinuous dorsolateral folds . . . . .	54
25. Geographic variation in tympanal spotting . . . . .	57
26. Geographic variation in snout spotting . . . . .	59
27. Relationship between snout-urostyle length and head width for <i>R. pipiens</i> , <i>R. utricularia</i> , and <i>R. blairi</i> from Missouri and Iowa . . . . .	60
28. Relationship between snout-urostyle length and head width for <i>R. pipiens</i> and <i>R. utricularia</i> from Indiana . . . . .	64
29. Relationship between snout-urostyle length and head width for <i>R. utricularia</i> males from Florida with and without Mullerian ducts . . . . .	65
30. Distribution of male leopard frogs (excluding <i>R. pipiens</i> ) with and without vestigial oviducts from southeastern Arizona . . . . .	68
31. Distribution of male leopard frogs (excluding <i>R. pipiens</i> ) with and without external vocal sacs from southeastern Arizona . . . . .	69
32. Variation in size of adult male leopard frogs (excluding <i>R. pipiens</i> ) from southeastern Arizona . . . . .	71

## ILLUSTRATIONS

33. Variation in dorsolateral folds of leopard frogs (excluding <i>R. pipiens</i> ) from southeastern Arizona . . . . .	72
34. Geographic distribution of <i>R. pipiens</i> , <i>R. utricularia</i> , and <i>R. blairi</i> in Illinois . . . . .	80
35. Geographic distribution of lactate dehydrogenase types in the United States . . . . .	85
36. Relationship between size at seven weeks and age at metamorphosis of <i>R. pipiens</i> , <i>R. utricularia</i> , and their hybrids . . . . .	89
37. Relationship between size of metamorphosed frogs and age at metamorphosis for <i>R. pipiens</i> and <i>R. utricularia</i> . . . . .	90
38. Latitudinal variation in size of mature males of <i>R. utricularia</i> from the Atlantic Coastal Plain . . . . .	96
39. North-south variation in dorsal spot patterning in <i>R. pipiens</i> and <i>R. palustris</i> in Michigan . . . . .	102
40. Geographic distribution of <i>R. palustris</i> in the United States . . . . .	103





## INTRODUCTION

Populations of leopard frogs occur over most of North and Central America from Great Slave Lake and James Bay in Canada to Panama, and across the continent from the Atlantic coast to the Sierra Nevada and Rocky Mountains in the north and to the Pacific coast in the south. Their habitats are as varied as their extensive geographic distribution suggests. They have been found in alpine ponds and streams, in desert springs, and in brackish coastal waters, as well as in temperate and tropical swamps and marshes. Leopard frogs from different regions also vary morphologically and physiologically, and for many years there was little agreement about how these various populations should be treated taxonomically. That situation changed for the most part following Moore's (1944) study of geographic variation in morphological and color characters of these frogs. He concluded that: "(1) the meadow frogs of eastern North America consist 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 populations from which they come." Moore applied the name *Rana pipiens* Schreber to all eastern leopard frogs and his conclusions were chiefly responsible for subsequent taxonomic practices and experimental interpretations concerning these frogs.

The prominence of leopard frogs in discussions of speciation theory (Brown, 1957, 1958; Blair, 1961; Ross, 1962; Mayr, 1963) is due primarily to experimental studies of physiological, genetic, and developmental variations among populations by Moore and others. In many general texts leopard frogs have served essentially as the sole example of the role that physiological adaptation to local environmental conditions is thought to play in speciation (Maynard Smith, 1966; Keeton, 1967; Baker and Allen, 1971; and most other texts that deal with speciation). In particular, leopard frogs have been cited repeatedly in the debates over the question of when different kinds of pre- and post-mating isolating mechanisms appear as populations diverge (Mayr, 1963; Moore, 1949).

Despite widespread interest in leopard frogs, the evolutionary status of their various populations was not clear until recently. Studies of mating calls (in particular, see Littlejohn and Oldham, 1968; Mecham et al., 1973) have finally verified the assertion that there are, in fact, numerous different species in the United States. This is an important advance because it affects speciation theories supported by previous conclusions about leopard frogs and because it reveals a new set of problems of general interest in speciation theory.

The prominent use of leopard frogs in biology and the complexity of the changes in our understanding of their relationships seem to make a chronological review worthwhile. Accordingly, I will here briefly trace the development of ideas about speciation in leopard frogs and the experimental work from which those ideas were derived. Then I will review the history of conclusions from more important aspects of field work.

It is appropriate to begin in 1939 with Moore's discovery that there were marked differences in embryonic temperature tolerances and developmental rates among sympatric populations of different species of North American amphibians. These differences in temperature tolerance correlated with differences in time of breeding (therefore with differences in mean water temperature at time of egg laying) and were also related in general to the geographic distributions of the species involved. For example, of the five *Rana* species Moore studied in the vicinity of New York City, *R. sylvatica*, with the lowest minimum and maximum temperature tolerance, was the first member of the genus to breed and was also the frog with the most northern distribution. *Rana catesbeiana*, with the greatest embryonic tolerance of high temperature, was the last to breed and had the least extensive northern distribution.

Moore (1942) also observed that leopard frogs have a wider geographic distribution than any single North American *Rana* species and that developmental rates and embryonic temperature tolerances are different in populations from different latitudes. Embryos from southern populations are more heat tolerant than those from northern populations and are sometimes less cold tolerant. In general the southern embryos develop more slowly at low temperatures and more quickly at high temperatures than the northern ones. The other less widely distributed species he studied did not vary geographically in these characteristics.

Moore's initial hybridization experiments with members of the *Rana pipiens* complex were performed primarily to study the influence of the sperm nucleus on rate of development. He discovered, however, that in some crosses involving leopard frogs from distantly separated localities (for example, crosses between Florida leopard frogs and Vermont leopard frogs) the hybrids were abnormal and survival was very low (Moore, 1941). Thus, in what appeared as a result of his study of morphological variation to be a single species there were differing degrees of genetic compatibility between members of some geographically distant populations.

Further cross-fertilizations involving leopard frogs from other localities indicated that the degree of abnormality in the embryos was related to latitudinal distance between parental populations and, to a much lesser extent, to longitudinal distance (Moore, 1946). Since the latitudinally distant populations were adapted to different thermal regimes while the longitudinally distant ones in general were not, Moore

concluded that the failure of hybrids to develop normally when parents were from latitudinally distant populations was probably due to some sort of physiological imbalance between genes from one parent directing "low temperature physiology" and those from another parent controlling "high temperature physiology."

Additional studies involving frogs from different elevations seemed to confirm the conclusion that adaptation to different temperature regimes was responsible for observed genetic incompatibilities. For example, Ruibal (1955) reported that high altitude, cold-adapted Mexican populations were more compatible with the Vermont cold-adapted genome than were low altitude, warm-adapted Mexican populations. Since the high altitude Mexican populations were more compatible with lowland Mexican populations than with the Vermont populations, however, the relatively greater compatibility of the highland populations with the Vermont populations was attributed to their adaptation to lower temperature rather than to closer genetic relationship with the Vermont populations.

When Moore analyzed geographic variation in leopard frogs, he considered all of the frogs from a single state as members of a single population and computed an average or "population index" for the variation shown by these frogs. A single exception was his consideration of frogs from northern New York as members of one population and those from southern New York as another. Unfortunately this procedure masked much of the significant variation, smoothed out abrupt changes whenever these did not coincide with state lines, and created the impression of a series of gradual clines in different characters running in different directions. In retrospect, Moore's conclusion may be considered somewhat surprising, for some abrupt geographical changes in morphological characters remained, as well as geographic concordance of changes in different characters, such as vocal sacs, oviducts, and tympanal spots in males. Moore remained puzzled by the lack of complete concordance between different morphological characters. Thus, most males without vestigial oviducts had external vocal sacs, but in some areas they did not. Frogs without oviducts from Nebraska, Kansas, Missouri, and some from southern Illinois, lacked external vocal sacs by Moore's criteria (not specified), yet he rejected the suggestion of Mittleman and Gier (1942) that leopard frogs of "Texas, Kansas and Oklahoma and possibly certain adjacent states" were distinct from other populations.

In spite of the genetic incompatibility he had discovered between leopard frogs from geographically distant populations and the frequent correlation between amount of morphological difference and degree of genetic incompatibility, Moore and others assumed that the distant populations are connected by chains of populations capable of interbreeding, and are therefore conspecific. Although never actually demonstrated, this assumption has been repeatedly stated as fact (e.g., Ross, 1962; Mayr, 1963; Keeton, 1967). Results from developmental

and genetic studies on leopard frogs have consequently been used as a model of the manner in which differences accumulate between conspecific populations that are varying distances apart along temperature or other environmental gradients. Since the differences associated with temperature gradients appeared to be responsible for developmental failures in hybrids, it was supposed that this model might be extended to support the argument that intersterility may commonly evolve in allopatry and be responsible for the failure of two divergent populations to amalgamate, even when premating deterrents are absent.

Despite general acceptance of Moore's view of the taxonomic status of these populations and his ideas about speciation derived from experimental studies, a number of herpetologists and natural historians, observing leopard frogs in the field, continued to remark, on the one hand, upon the similarities of frogs from some very distant areas and, on the other hand, upon the great differences between some frogs from neighboring areas. One of the earliest references to differences in calls of leopard frogs was that of Garman (1890), but the significance of such differences was not then well understood. Stejneger (1893) recognized leopard frogs from Clark County, Nevada, as being different from *R. pipiens* which he had found in Lincoln County, Nevada, about 75 miles away. Bragg (1941) had noted: "After observing the two forms in the field, I feel certain that the frog about Las Vegas, New Mexico is very similar to, if not identical with, the grass-frog of New England. . . and the leopard frog of Wisconsin and different from that of Oklahoma. . ." He distinguished this leopard frog from the common species of central Oklahoma primarily on the basis of behavior and of certain aspects of breeding biology (the former breeding only in spring or early summer, the latter breeding then and after rains in July and August as well). Bragg did not distinguish these species morphologically except to note that the former did not have a tympanal spot and that it was a short-headed or "at least not a long-headed" type.

Years of work in the field with different members of the *Rana pipiens* complex also led Wright and Wright (1949) to doubt the conclusions reached by Moore in his 1944 study of geographic variation. They viewed his data as supporting their subdivision of leopard frogs even when Moore discussed characters they did not use: "At times we have questioned Cope's use of external vocal sacs in separation of the *R. pipiens* forms. It is strange that Moore finds that 'from southern New York and south along the Atlantic coast the males possess well-developed external vocal sacs. In the Mississippi Valley males from southern Indiana, Oklahoma, Arkansas and Mississippi have well-developed external vocal sacs. . .' This reads much like our range characterization for *Rana p. sphenoccephala*" (op. cit., p. 497). The stated intent of their summary of their own and other herpetologists' observations was to provoke a more thorough study of these forms with emphasis on field work over the areas where the forms occurred.

Largely as a result of this kind of field work, evidence has accumulated that the differences between leopard frogs do not develop as gradually with geographic distance as Moore was led to believe. Based on differences in behavior of young leopard frogs in Ellis County, Oklahoma, Bragg (1949) found "consistently that some pools were occupied by one form and other pools by the second with no case of mixing of the two. . . ." Bragg compared these frogs with specimens from Oklahoma in the University of Oklahoma Museum and concluded that there were at least two forms of leopard frogs in Oklahoma, although he, unfortunately, did not state what morphological differences led him to this conclusion. In 1950 he reported differences in behavior and calls of males from Ellis County (Bragg, 1950c): "From behavior, difference in calls, and expectations on geographical grounds, these seemed to be the western leopard frog, *R. brachycephala* [= *R. pipiens*]. . . this same type of call was heard in Stephens County in one pool, though in another only *R. berlandierii* [= *R. blairi*] was calling. This is the third time, therefore, that overlapping ranges of these two forms (with neither intergradation nor interbreeding occurring) has been reported." In the same paper Bragg noted the presence of a third species, *R. sphencephala* [= *R. utricularia*], in Craig and Ottawa counties (extreme northeastern Oklahoma), based on the calls produced by males in breeding choruses: "Despite years of successful experience in collecting frogs in breeding congresses and their great concentration in a small area, the writer succeeded in securing only two specimens. At the second pool six were collected. These frogs are clearly different from those mentioned above as *R. brachycephala* and also different from the common *R. berlandierii*. The latter was present the same night in another pool near Miami [Ottawa County] and it had been previously collected at the edge of the Craig County pool."

McAlister (1962) analyzed geographic variation in male vocalizations, and in numerous morphological features, of leopard frogs from Texas and concluded that three, possibly four, major groups of populations occurred in this state and that "the major regions of morphological disjunction in Texas *R. pipiens* occur along the western border of the Texas and southern border of the Kansas biotic provinces." Although his conclusions regarding the evolutionary status of the populations in these regions of disjunction are not entirely clear, he evidently assumed initially that they were panmictic, but ultimately concluded that some sort of "reduction in gene exchange. . . is requisite for the type of polymorphism observed."

Post and Pettus (1966) described the distributions of two morphologically distinct but allopatric kinds of leopard frogs in eastern Colorado. Since that time they have reported sympatry of these two forms in several localities (Post and Pettus, 1967; Pettus and Post, 1969). In one area where the two forms had presumably been in contact over a long period, they had distinctly different breeding seasons and did not hybridize. In another locality, where breeding

ponds had been created relatively recently by human activities, there was some overlap in the breeding season and hybrids were found "in moderate [unspecified] frequencies."

Mecham (1968) described sympatry of two distinct types of leopard frogs from an area near the locality where Wright and Wright (1949) had previously observed two kinds of leopard frogs. Later the same year Littlejohn and Oldham (1968) described differences in calls of four distinct entities in the southcentral United States and illustrated their approximate distributions in that region. The distributions of these "call types" corresponded to the distributions of morphologically distinct forms previously described by McAlister from Texas and by Post and Pettus from Colorado. There was evidence of only slight hybridization, or none, between these forms in most places where they were in contact in Texas.

I began the present study in 1966 because of my interest in speciation and in the origin of adaptive isolating mechanisms. Working with animals about which a great deal of information was available with regard to geographic variation in morphological traits and physiological differences between populations, but in which nothing appeared to be known about the biological interactions among individuals from different populations in the field, seemed a challenge which could profitably be met using techniques that had been applied to other groups of confusingly similar sound-producing animals (anurans, insects).

Sounds produced by an animal primarily or solely during its breeding season can reasonably be expected to have something to do with the breeding biology of that species. Presumably such sounds serve in most cases to attract conspecific individuals of the opposite sex, though they may have other related functions as well (e.g., territoriality). If geographic differences in sounds associated with breeding exist, then analysis of these sounds along geographic transects should rather quickly give more information about the question of effective amounts of gene exchange than physiological and morphological studies of characteristics not directly associated with species interactions; whenever two very similar species live together, or in very similar environments, selection might be expected often to produce convergence rather than divergence with regard to characters such as temperature tolerance, but not in regard to vocalizations. Even when there is no gene exchange between two species, their temperature tolerances would be expected to be more similar in the parts of their ranges that overlap or are adjacent than in the more distant parts if the more distant parts of their ranges have different temperature regimes. Mating calls, on the other hand, should not be more similar unless considerable gene exchange has occurred.

My field studies of vocalizations of these frogs have shown that there are two distinct, widely distributed species in eastern North America. These two species are essentially allopatric, although I have

heard them calling together in several localities in southcentral Indiana. After discovering that call types remain distinct where these species contact one another, and that certain morphological characters correlated with each call type, I examined preserved material to determine the distributions of the morphological types and the extent to which distinguishable morphological types corresponded to distributions of call types (known from other studies) throughout the United States. The distribution of each of the four species known by their calls was then determined from museum specimens, and some additional areas of sympatry were detected.

Recognition of the existence of numerous species within the *R. pipiens* complex led Brown (1973) to conclude that it is "quite unfortunate that leopard frogs have been used so extensively in experimental research over such a long period of time" and that "with the knowledge at hand about leopard frog speciation, one could come to the reasonable conclusion that these amphibians are not the best animals to use in experimental research at the present." With the means available to identify individual specimens, of at least one sex, and maps for most of the United States that allow identification on the basis of locality in nearly all cases, this pessimistic view is no longer necessary. Indeed, the variations in breeding biology, life history, and development that exist among these closely related species of leopard frogs make the members of this group particularly valuable experimental animals.

#### ACKNOWLEDGMENTS

This paper is derived from a doctoral dissertation in Zoology at The University of Michigan. I thank the members of my doctoral committee, Dr. Richard D. Alexander, Dr. William R. Farrand, Dr. Nelson G. Hairston, and Dr. Charles F. Walker, for reading various versions of the manuscript and for their helpful criticisms of it. In particular I thank Dr. Alexander for many stimulating discussions of frogs and of speciation.

For permission to examine specimens in their care and for assistance while working at these institutions I am grateful to: Dr. Richard G. Zweifel, American Museum of Natural History; Dr. George R. Zug, United States National Museum; Dr. Philip W. Smith, Illinois Natural History Survey; Mr. Edmund V. Malnate, Academy of Natural Sciences of Philadelphia; and Dr. Stanley N. Salthe, Brooklyn College, CUNY. For permission to copy tape recordings or to use information derived from them I thank Dr. Richard G. Zweifel of the American Museum of Natural History and the staff of the Sound Library of the Cornell Laboratory of Ornithology.

Dr. Francis C. Evans made available housing and research facilities at The University of Michigan's Edwin S. George Reserve during the

spring of 1969. Dr. Christina Richards provided considerable assistance with developmental studies and the use of the Amphibian Facility at The University of Michigan during 1970. Dr. Henry K. Townes gave me helpful advice with nomenclatural procedure, although he is not responsible for my decisions. I thank Mr. Louis P. Martonyi for his fine photographs of preserved specimens.

Special thanks go to James E. Lloyd and his family who shared their home with me during most of the several weeks I spent in Gainesville, Florida, in 1967; to Guy G. Musser and Margareta Becker with whom I have stayed on numerous occasions, both during field trips and while I was working at the American Museum of Natural History; to Mary Jane West Eberhard for accompanying me in the field during the summer of 1968; and to Lorraine K. and Richard D. Alexander for their assistance with field work and for their constant encouragement during all phases of this study and preparation of the manuscript.

This study was supported in part by grants from the National Science Foundation, GB-3366, to Theodore H. Hubbell, and GB-25986, to Nelson G. Hairston, The University of Michigan, for research in Systematic and Evolutionary Biology.

#### MATERIALS, METHODS, AND MISCELLANEOUS NOTES

This work deals only with the leopard frogs of the United States. Throughout the remainder of the text, whenever all or part of this complex of sibling species is being discussed I will use the term "the *Rana pipiens* complex," "the *pipiens* complex," or simply the common name "leopard frogs," with appropriate geographic restriction. Except in citations from other works, the use of "*Rana pipiens*" alone will be restricted to a single species, the geographic distribution of which (in the United States) is shown in Figure 1. All Canadian leopard frogs are almost certainly *Rana pipiens* (Figs. 2, 3). Variation in material from Mexico and Central America suggests that several species occur there. Since few data are available on mating calls of these forms (and none correlated with specimens), only a few Mexican and Central American specimens were examined and none of these is considered here. Although material from the southwestern United States could have been ignored for the same reason, specimens from this area were examined primarily in order to trace the distribution of *R. pipiens* throughout the United States. *R. pipiens* may extend into at least the northern part of Mexico (Mecham, 1971). Mexican and southwestern leopard frogs are currently being studied by Mecham (1968, 1969, and 1971) and others (Platz and Platz, 1973).

A total of 4246 preserved leopard frogs (including 1136 males) was examined from the following collections: American Museum of Natural History (AMNH) (848 total, including 276 males); United



States National Museum (USNM) (1163 total, including 272 males); Academy of Natural Sciences at Philadelphia (ANSP) (140 total, including 28 males); Illinois State Natural History Survey (INHS) (255 total, including 112 males); and The University of Michigan Museum of Zoology (UMMZ) (1825 total, including 433 males). An additional 15 males collected in the Florida panhandle by D. Bruce Means and others were also examined. These males are in the private collection of Stanley N. Salthe, Brooklyn College, and were preserved as frozen specimens. Catalogue numbers and localities of all specimens examined are arranged by species in Appendix I.

Snout-urostyle measurements were made using dial calipers on most frogs examined, regardless of sex or age. Data were also taken on most specimens concerning the condition of the dorsolateral folds, the nature of pigmentation on the tympanum, and the distribution and number of spots on the dorsum. Initially many other measurements were also made, such as tibial length, length of longest toe, head width, head length, tympanal size, and eye size. Some of these measurements, especially tympanal size and eye size, were impossible to make precisely. While there was much geographic variation in the sizes of some of these body parts relative to the snout-urostyle length there were no discrete changes in these ratios. Since I was primarily interested in finding ways in which different populations, distinguished by their call types, could be differentiated in preserved material, measuring was discontinued when it was determined that the changes in ratios were not discrete. Because significant differences were found in secondary sex characters of males of different call types, special attention was given to preserved adult males.

Male leopard frogs in breeding condition can always be distinguished from females by two features of their external morphology. Mature males have conspicuously enlarged thumb pads which females lack. They also have paired lateral vocal sacs that are absent in females. Even when external vocal sacs are absent the skin overlying the internal vocal sacs is usually stretched in adult males, and it is therefore possible to determine whether or not a given specimen is an adult male even without looking at the thumb. All frogs with conspicuously enlarged thumb pads or with any external evidence of internal vocal sacs were judged to be males of, or approaching, breeding age and were dissected to determine whether or not they possessed Mullerian ducts.

The data on geographic distribution of call types of the eastern species were collected between 1966 and 1970. Preliminary observations of leopard frog breeding behavior and calling were made in the vicinity of Ann Arbor, Michigan, during 1966. During 1968, again in the Ann Arbor area, most efforts were directed at trying to learn how calls affect the behavior of males and females during the breeding season. In 1969, on the E. S. George Reserve of The University of Michigan, in Livingston County, Michigan, an attempt was made to study the movements of males and interactions of males in one

population during the breeding season. Possibly due to unusual weather conditions there was, however, very little calling of leopard frogs in southeastern Michigan (at least in Livingston and Washtenaw Counties). There may also have been less breeding during this year than usual. No egg masses of *R. pipiens* were found on the E. S. George Reserve by me or by DeBenedictis (1970). I found only one spent female and no gravid females. Some information on functions of vocalizations in *R. pipiens* was collected in the vicinity of Ann Arbor, Michigan, during 1972.

Two extensive field trips were made during 1967. The first was begun on 10 February in Sarasota County, Florida, and ended 23 April in Putnam County, New York. Most of this work involved driving along secondary roads at night listening for leopard frogs. Frogs were tape-recorded when heard and attempts were made to collect specimens. Sometimes an area was traversed during the day and notes were made of locations of marshes, ponds, flooded pastures, etc. where calling leopard frogs would be likely to be encountered. The same area was then traversed at night with stops being made at these places. This approach was generally less successful than had been anticipated. Farm ponds seldom had leopard frogs in them. In some areas these were the only bodies of water, excluding rivers, canals, and streams, that were conspicuous during the day. At night leopard frogs could sometimes be heard from areas at some distance from the road which, during the day, gave no sign of being leopard frog breeding habitat. The most successful way of detecting calling leopard frogs proved to be to drive slowly along secondary roads at night listening for the calls of louder-voiced anurans, especially *Hyla crucifer* and species of *Pseudacris*. Leopard frogs are frequently not audible when the car engine is running, except in large choruses or when very close to the road, but where they are calling there are nearly always spring peepers (*H. crucifer*) and chorus frogs (*Pseudacris*) as well (although these frogs also call from areas where leopard frogs do not). During the summer of 1967 I spent three weeks in Florida, again tracing distributions of leopard frogs by listening and by tape recording calls.

In the summer of 1968 I returned to Florida. This time I remained in the vicinity of Gainesville approximately six weeks, collecting information on the communicative significance of different calls. Difficulty in securing gravid females restricted this part of the investigation to interactions between and among males.

During the spring of 1970 I made a brief trip to Indiana and Kentucky (3-14 April). On this trip I traced the zone of contact between *R. pipiens* and *R. utricularia*, using the same approach described previously: listening while driving along secondary state highways and other country roads and stopping to listen for calling leopard frogs. Frogs located were usually tape-recorded and specimens were collected if this could be done without too great an expenditure of time or effort. The primary aim was to trace the distribution of call

types in a locality of the central United States west of the Appalachians where I suspected that the two eastern call types contacted one another, and to discover the nature of the contact. Specimens collected on this field trip were subsequently used in studies of development.

Nearly all tape recordings were made with a Uher 4000 Report-L tape-recorder at seven and one-half inches per second. A few were made in 1972 with a Nagra tape recorder at 15 inches per second. Some recordings were made with the aid of a 26-inch parabolic reflector with a six-inch focal distance. All recordings were analyzed with a Kay Electric Company Vibralyzer, Vibralyzer (Model 7030A), or Sonograph (Model 7029A). Because recorded specimens were frequently not captured, body temperatures had to be estimated from measurements of air and water temperatures and of relative humidity. The body temperature of a calling male *R. pipiens* is probably very close to the water temperature, since these frogs usually call while nearly submerged at the surface of the water. In *Rana utricularia*, however, males sometimes call while sitting completely out of the water and estimation of their body temperature is more difficult, especially if the calling site of the male is not known. Since relative humidity was always very high, evaporative cooling of frogs calling out of the water was probably not significant. Where air and water temperatures differed by more than a few degrees, the effective body temperature of calling *R. utricularia* was arbitrarily estimated by adjusting the water temperature toward the air temperature by one-third of the difference between them. This particular adjustment was chosen because it seemed to eliminate most of the variation which existed when pulse rates of calls were plotted against either air temperature or water temperature alone.

## NOMENCLATURE

### NOMENCLATRURAL HISTORY

The nomenclatural and taxonomic confusion surrounding members of the *Rana pipiens* complex has existed for hundreds of years. Mark Catesby (1742) was the first European naturalist to describe one of these frogs. Although he named it *Rana aquatica* this pre-Linnaean name was only rarely used. *Rana halecina*, often attributed to Pehr Kalm (1761), was commonly used for leopard frogs until about 100 years ago. Derived from the Latin word *haleco* (herring), this name was actually not used until the 12th edition of *Systema Naturae* and was evidently formalized by Linnaeus (1766) from the Swedish word *silhopptassor* (herring-hopper) which Kalm said the Swedish immigrants in New Jersey used for this frog. Linnaeus published *Rana halecina* in synonymy of another species (*Leptodactylus* [*Rana*] *ocellata*). Daudin (1802) was the first to use the name in a way which would make it available. Daudin, however, clearly states that

*R. halecina* as he uses it refers to the same frog described by Schreber (1782) under the name *R. pipiens*. *R. halecina* is therefore a junior synonym of *R. pipiens*.

Another name, also derived from Kalm's writings (see Garman, 1888, for a thorough review), has occasionally been used for leopard frogs. In his account of his travels in North America, Kalm gave some information about the appearance and biology of leopard frogs. His description of the color and form of the frog began with the words "*Rana virescens plantis tetradactylis. . .*" *Rana virescens* was not used as a binomial by Kalm and when first used as a binomial (Cope, 1889) it was used for a species that had already been given a name (*R. utricularia*) (Harlan, 1826).

Schreber's (1782) description of *R. pipiens* was based on a frog sent to him from New York by Dr. Johann David Schoepf, a doctor with the Royal Brandenburg Troops in America during the Revolutionary War. Schreber believed that this frog, which he pictured in a colored illustration (reproduced in black and white in Fig. 3), represented the same species Catesby and Kalm had described previously (Catesby's description was also accompanied by a colored plate). Schreber's intention was to give a more accurate description of the frog and to provide a proper name for it. The name he chose was based on Kalm's description of a call he had heard and which he thought belonged to the green, spotted frog he collected. Kalm described the call as a bird-like "piiit," and so Schreber named the frog "*Der Pip Frosch*," *Rana pipiens*. The frog Schreber described and illustrated probably came from Manhattan Island, unless it was actually collected by someone other than Dr. Schoepf and was only sent to Schreber by Schoepf. Even though *R. pipiens* is not now known to occur on Manhattan, the frog in Schreber's illustration, with its large, dark, distinctly areolated dorsal spots and unspotted tympanum, is most probably a northern leopard frog—and not the same species Kalm and Catesby had seen after all. The name *Rana pipiens* is doubly inappropriate for this frog since the call Kalm described undoubtedly belonged not to the southern leopard frog he observed, but to the small spring peeper, *Hyla crucifer*, which he did not describe and which he apparently only heard but did not see.

In 1826 Richard Harlan described a new species of leopard frog. He named it *Rana utricularius* (using the Latin word *utricularius* meaning player-on-the-bag-pipes) because of the large balloon-like external vocal sacs by which he distinguished it from *Rana halecina*. Although he described it as being from Pennsylvania and New Jersey and said that *R. halecina* is from more southern coastal areas, there are two possible explanations for this. The first is that the frog illustrated in general herpetology works of the day (e.g., Shaw, 1802) was the northern leopard frog, while the one discussed in those same works was often the southern one. A second possibility is that Harlan distinguished males from the vicinity of Philadelphia and New Jersey, some

of which do have unusually large external vocal sacs, from males from further south, though in both of these regions male leopard frogs have vocal sacs that are clearly external, in contrast to those of *Rana pipiens*.

Later Cope (1889) placed Harlan's name in the synonymy of *Rana virescens*, stating that Harlan's and Kalm's names applied to the same species. Since Cope (1889) was actually the first to use *R. virescens* as a binomial, the availability of this name dates from his publication rather than from Kalm's (1761), and Harlan's name therefore has priority. Cope was responsible for several names which have occasionally been used for certain leopard frogs. In 1889 he described and illustrated these forms. *Rana virescens sphenocephala* was merely a new name supplied by Cope for a frog from Florida which had been named *Rana oxyrhynchus* by Hallowell in 1856. The name *Rana oxyrhynchus* had already been used (Smith, 1849; but attributed by Smith to Sundervall [=Sundevall]) for an African frog. The Florida frog was characterized by a very long, pointed snout and most of the frogs determined as this form by Cope were from southern localities. Another name introduced by Cope, *brachycephala*, referred to the relatively broad head of frogs from mostly northern localities. *Rana virescens austriicola*, introduced by Cope in 1889 to refer to common Mexican leopard frogs lacking external vocal vesicles, was never widely used. No type was designated by Cope for this subspecies.

Baird (1859) described and illustrated an unusual leopard frog from southern Texas which he called *R. berlandieri*. This frog was large and had what appeared from the drawing to be eversible external vocal sacs (Fig. 8).

The name *Rana onca*, credited by Yarrow (1875) to Cope, was given to a single specimen collected in Utah (probably the very southern part around the vicinity of St. George, based on the itinerary of the 1872 expedition (Yarrow, 1875) and on the distribution of *R. pipiens* in the state as known from my study). Although the type of *R. onca* is a female and has none of the secondary sex characteristics which I have used in separating members of the *R. pipiens* complex, it is so similar in general appearance to the specimens in the type series of *R. fisheri*, described by Stejneger from Vegas Valley, Nevada, in 1893, that I have followed Tanner (1931) in treating *fisheri* as a synonym of *onca*. These frogs are quite distinct from the leopard frog collected near Overton, Nevada (between the Vegas Valley and St. George), and illustrated in Wright and Wright (1949: 477, 508) as *R. onca*, as well as from *R. pipiens*, which is known from Lincoln County in southern Nevada (Fig. 1). (See description of *R. onca* in following section for details.)

Although there are some other valid names which may refer to members of the *R. pipiens* complex occurring in Mexico and Central America, it seems unlikely that any of these names applies to any of the remaining undescribed species within the United States. Aside from this possibility, I have given here a summary of all names which could

potentially be applied to populations of leopard frogs occurring within the United States.

#### SPECIES CHARACTERIZATIONS AND SYNONYMIES

For each species in the following section I have first given a formal synonymy. This is followed by a list of scientific and common names which have been used for members of that species by authors whose works are of particular significance in the development of our understanding of this species group. Several of these authors correctly distinguished that species from at least one other member of the species complex. The brief descriptions of the ranges, mating calls, and distinguishing morphological features of each species are intended as an introduction to the species and as a frame of reference for the more detailed discussions of vocalizations, morphological variation, geographical distribution, and related aspects of the biology of these species which follow. The range maps and most of the illustrations of the frogs appear in this section. The other figures referred to in this section appear later in the place where they are discussed in more detail. A key to adult males in the *Rana pipiens* complex from the United States (north of the dashed line in Fig. 1) is presented in Table 1, and Table 2 summarizes the morphological characteristics of these frogs.

TABLE 1

#### KEY TO ADULT MALES IN THE *RANA PAPIENS* COMPLEX FROM THE UNITED STATES (NORTH OF THE DASHED LINE IN FIG. 1)

1.	Skin at angle of jaw overlying internal vocal sac not differentiated in texture or color from surrounding skin (may be somewhat stretched) (Fig. 2a); no distinct white spots on centers of tympana; dorsolateral folds continuous and not displaced (Fig. 23a), usually wide and low, but discernible to the point where the leg joins the body; dorsal spots usually ringed with light coloration . . . . .	<i>Rana pipiens</i> (Figs. 2 and 3)
1'.	Skin at angle of jaw overlying internal vocal sac differentiated from surrounding skin in some way (e.g., texture or pigmentation); tympanal spots, dorsolateral folds, and dorsal spots variable . . . . .	2
2(1')	Mullerian ducts absent, or specimen from Florida . . . . .	3
2'.	Mullerian ducts present and specimen from Texas . . . . .	<i>Rana berlandieri</i> (Fig. 8)
3(2).	External vocal sacs large, spherical, apparently thin-skinned, lying loose at angle of jaw when not inflated (Fig. 5a) or from Florida (Fig. 6a); dorsolateral folds usually continuous and not displaced (Fig. 23a) . . . . .	<i>Rana utricularia</i> (Figs. 5 and 6)
3'.	External vocal sacs small, usually visible only because skin at angle of jaw is conspicuous when internal vocal sac is not inflated owing to texturings of the skin below the labial stripe (Fig. 10a); dorsolateral folds usually discontinuous and displaced medially (Fig. 23d, rarely 23e) . . . . .	<i>Rana blairi</i> (Fig. 10)

TABLE 2  
MORPHOLOGICAL CHARACTERISTICS OF UNITED STATES MEMBERS  
OF THE *RANA PIPIENS* COMPLEX

Form	Dorsolateral Folds	Tympanal Spot	Snout Spot	Vocal Sacs	Mullerian Ducts
<i>Rana pipiens</i>	continuous, not displaced; broad, not distinctly raised	nearly always absent	usually present	not external	usually present
<i>R. utricularia</i>	continuous, not displaced; usually narrow and distinct	usually present	usually absent	nearly spherical balloon like	absent except in Florida
<i>R. berlandieri</i>	discontinuous and displaced	usually absent	usually absent	external, usually eversible	present
<i>R. blairi</i>	discontinuous and displaced; usually narrow and distinctly raised	usually present	usually present	external, small textured below labial stripe	absent
<i>R. onca</i>	indistinct; often short but may be continuous or discontinuous	usually absent	absent on <i>onca</i> type present some <i>fisheri</i>	textured, external but very small	probably present
unnamed, no call data <sup>1</sup>	discontinuous and displaced, may be indistinct	usually absent	often present	pea-sized, external	absent
unnamed, no call data <sup>1</sup>	discontinuous and displaced, posterior part often a series of dots	light center not usually distinct spot	usually absent	apparently absent	absent
unnamed, no call data <sup>1</sup>	indistinct, but usually discontinuous and displaced	absent	usually absent	tiny, may be eversible	present

<sup>1</sup>For localities of unnamed forms, see Figs. 30-33 and Appendix I; these three forms represent tentative arrangements of specimens based on morphological attributes and may not be specifically distinct from one another.

*Rana pipiens* Schreber

- Rana pipiens* Schreber, 1782, Der Naturforscher, 18: 185, pl. 4. "New York," restricted to White Plains, New York, by K. P. Schmidt (1953) for unknown reasons; neotype here designated ♂ from Fall Creek, Etna, Thompkins County, New York; University of Michigan Museum of Zoology, cat. no. 71365. (There is no evidence that the frog on which Schreber based his description came from White Plains. According to his journal, Johann D. Schoepf (1911), who sent the specimen to Schreber from "New York," was never in White Plains, at least not during or prior to 1782.)
- Rana halecina* Daudin, 1802, Hist. Nat. Rainettes, 41. No type designated.
- Rana virescens brachycephala* Cope, 1889, Bull. U. S. Natn. Mus., 34: 403-406. "Yellowstone River," Montana; United States National Museum, cat. no. 3363 (the female of this series is the one for which measurements are given and has previously been treated as the type (Cochran, 1961)).
- Rana burnsi* Weed, 1922, Proc. biol. Soc. Wash., 35: 108. New London, Kandiyohi County, Minnesota; Chicago Natural History Museum, cat. no. 3065.
- Rana kandyohi* Weed, 1922, Proc. biol. Soc. Wash., 35: 109. New London, Kandiyohi County, Minnesota; Chicago Natural History Museum, cat. no. 3066.
- Rana noblei* Schmidt, 1925, Amer. Mus. Novit., 175: 1. "Yunnanfu, Yunnan, China," in error; American Museum of Natural History, cat. no. 5285. (I here follow Schmidt (1953) in regarding this name as a synonym of *Rana pipiens*. The specimen is a female without dorsal spots. Schmidt says the locality is in error, but does not state how he knows or what the correct locality is.)

Historically important names used for this species include: *Rana brachycephala*, Kauffeld (1937); *R. pipiens*, Trapido and Clausen (1938); *R. p. brachycephala*, Mittleman and Gier (1942); *R. p. pipiens*, *R. p. brachycephala*, Wright and Wright (1949); *R. p. pipiens*, Bragg (prior to 1948); *R. brachycephala*, Bragg (1948 and later); CF complex, Post and Pettus (1966); northern call type, Littlejohn and Oldham (1968); northern form, Mecham (1968); *R. pipiens*, Mecham (1971); northern form, Platz and Platz (1973).

*Range* (Figs. 1 and 18)—This is probably the most widely ranging member of the species complex. It is the only leopard frog known in Canada. In the United States it is found in New England, in New York and Pennsylvania, in most of Ohio and northern Kentucky, in northern and central Indiana, in northern Illinois, in Iowa and west to and through the Rocky Mountains. In the Far West it is found in the Snake



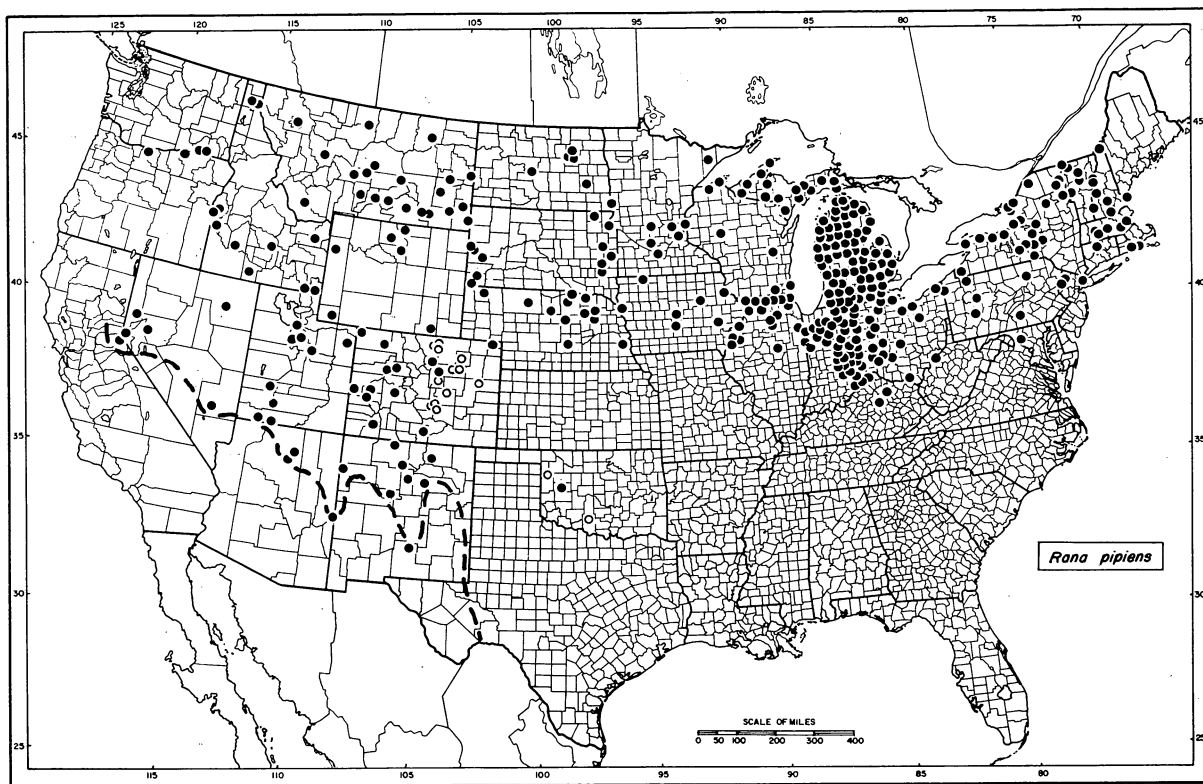


Fig. 1. Geographic distribution of *Rana pipiens* in the United States. Solid dots represent specimens examined (see Appendix I for list of localities). Open circles represent literature records considered reliable (Post and Pettus, 1966; Bragg, 1950c). In the vicinity of the dashed line in the southwestern United States and southward the keys (Tables 1,3) cannot be used with confidence since the evolutionary status of different populations of leopard frogs in this region is uncertain.

River Valley, the Columbia River Valley, and in Lake Tahoe and other areas of California and Nevada. It is also found at higher elevations at least as far south as Alpine, Arizona, and may occur in at least the northern part of Mexico as well (Mecham, 1971).

*Mating Call* (Figs. 11 and 15)—The mating call of this species is a long trill lasting more than one second (usually at least two seconds, but may be five or more). At 50° F. the pulse rate is ten per second (Fig. 16b). The pulses are relatively short, lasting only about 1/8 the interval between them.

*Distinguishing Morphological Features*—The male usually has Mullerian ducts. Adult males have well developed internal vocal sacs but no external vocal sacs. The skin overlying the vocal sacs may be very stretched, especially during the breeding season, but this skin is not differentiated in any way from the surrounding skin (Fig. 2a). In both juveniles and adults of both sexes the dorsolateral folds are characteristically not broken or deflected (Figs. 2b and 23a). They are usually broad and low and do not contrast strongly with the ground color. The tympanum may be uniformly colored, but usually there is an irregular blotch of lighter pigment on the center; there is not a distinct light spot on the center of the tympanum (Fig. 25). Usually a high proportion of the back is covered with dark pigment, in relatively few dorsal spots (Figs. 2b and 3). The dorsal spots are usually much darker than the ground color and distinctly areolated. A snout spot is present in well over 50% of the specimens (Fig. 26).

*Rana utricularia* Harlan

*Rana utricularius* Harlan, 1826, Am. J. Sci. Arts, 10: 53-65. Pennsylvania and New Jersey, (restricted to vicinity of Philadelphia by Schmidt (1935)); no type designated, neotype here designated ♂ with very large external vocal sacs from Philadelphia, Pennsylvania; Academy of Natural Sciences of Philadelphia, cat. no. 2803.

*Rana oxyrhynchus* Hallowell (not of Smith, 1849), 1856, Proc. Acad. nat. Sci. Philad., 8(1857): 141-143. "a sulphur spring near the St. John's River, about three hundred miles from Key West;" no type located in the collection of the Academy of Natural Sciences of Philadelphia.

*Rana virescens sphenoccephala* Cope, 1889, Bull. U. S. Natn. Mus., 34: 399-401. New name for *R. oxyrhynchus* Hallowell, preoccupied by *R. oxyrhynchus* Smith, an African frog; neotype here designated ♂ with vestigial oviducts from Enterprise, Volusia County, Florida; University of Michigan Museum of Zoology, cat. no. 56130.

*Rana virescens virescens* Cope, 1889, Bull. U. S. Natn. Mus., 34: 401-403. No type designated.

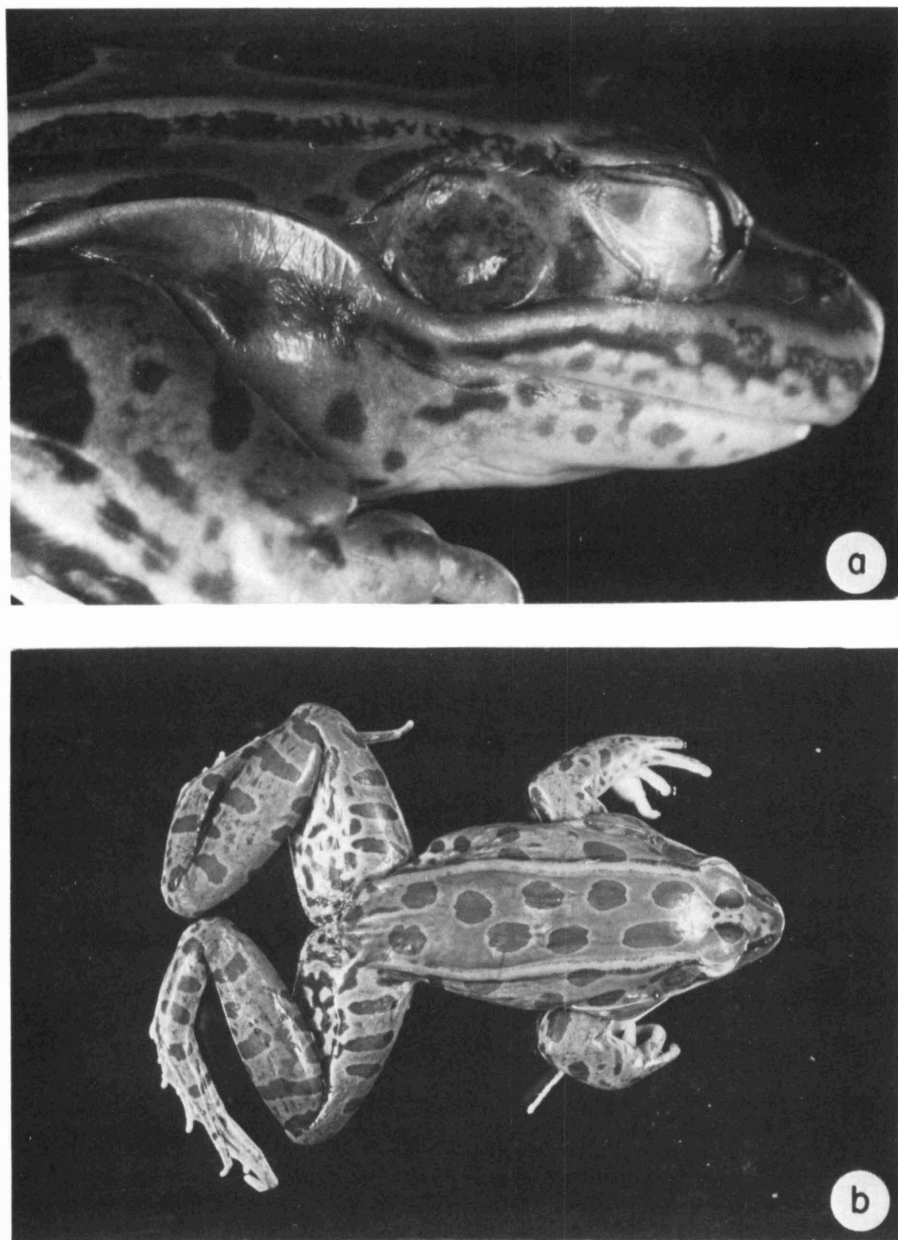


Fig. 2. *Rana pipiens* male (UMMZ 103358) from 1 mi N of Columbia, Fayette County, Indiana: (a) shows the stretching of the skin overlying the internal vocal sacs that sometimes occurs in this species and in *R. palustris* [note lack of differentiation of this skin from the surrounding skin]; (b) shows typical condition of dorsolateral folds and dorsal spots (ringed with light) in *R. pipiens*.

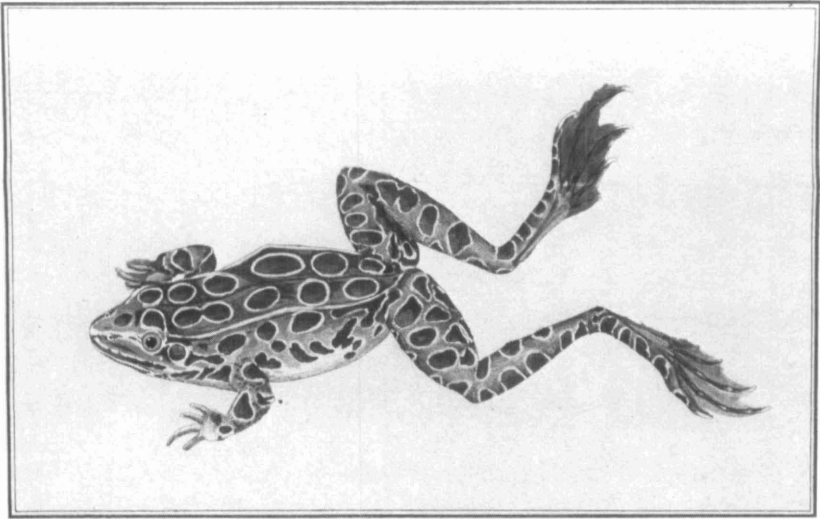


Fig. 3. Black and white copy of the colored illustration accompanying Schreber's (1782) description of *Rana pipiens*. In the original the ground color is green, the spots brown, the rings around the spots and the dorsolateral folds yellow. The tympanum is uniformly brown.

Historically important names used for this species include: *Rana pipiens* (part), *R. sphenoccephala* (part), Kauffeld (1937); *R. p. sphenoccephala* (part), Wright and Wright (1949); *R. sphenoccephala*, Bragg (1948 and later); eastern call type, Littlejohn and Oldham (1968).

In spite of the fact that Cope's name, *sphenoccephala*, has been applied to southern leopard frogs by various authors during the past 65 or 70 years, *Rana utricularia* Harlan, though used less often, is the more appropriate name for several reasons. First, as I have explained previously, Harlan's name is the oldest available name for this species.

Although some objections may be raised to using such an old name, doing so will eliminate any necessity for introducing a new name. The leopard frogs of the Florida peninsula differ from the rest of the Coastal Plain (and Mississippi River Valley) leopard frogs in a number of striking ways which parallel the morphological differences existing between species of the *Rana pipiens* complex from other parts of the country (see pp. 104-106). The name *sphenoccephala* applies to the Florida subspecies; *utricularia* to the more northern one.

Although *sphenocephala* has sometimes been used for this species, it has also been applied to frogs that are actually members of different species. Because different leopard frog species generally have ranges that are nearly mutually exclusive, and because the ranges of most of these species in the United States are now fairly well-known (as a result of the present study), the locality is frequently all that is needed to determine what species is being discussed. Occasionally such determination is impossible unless a sufficient morphological description of the animal is given. The name *sphenocephala* was used in some cases (e.g., Dickerson, 1906) to refer to any specimen with a distinct light spot on the center of the tympanum (common in both this species and in *R. blairi*, see Figs. 10 and 25), or to any specimen with a relatively narrow head and pointed snout. Cope (1889), for example, designated as *Rana virescens sphenocephala* a specimen from Fort Snelling, Minnesota. *R. utricularia* is a descriptive name for this species (see p. 12) and except when Schmidt synonymized *Rana utricularia* with *Rana pipiens* in his 1953 checklist, and when Gunther (1900) used the name for Mexican leopard frogs possessing external vocal sacs, *Rana utricularia* has consistently been applied (e.g., Harlan, 1826; H. Garman, 1892) to the southeastern leopard frog in which males have large external vocal sacs (Fig. 5a), and distinguished from the northern leopard frog (*Rana pipiens*) in which the males lack external vocal sacs (Fig. 2a).

*Range* (Figs. 4 and 18)—Found throughout most of the Atlantic Coastal Plain from southern New York and northern New Jersey and through the Gulf Coastal Plain to somewhere between Corpus Christi and Victoria, Texas. It is found in southern Missouri, southern Illinois, southwestern Indiana, most of Kentucky, and extreme southern Ohio. It is found in southeastern Kansas and eastern Oklahoma and is the only leopard frog known from Tennessee, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Florida, South Carolina, North Carolina, Virginia, and Delaware.

*Mating Call* (Figs. 13, 14, and 15)—The presumed mating call of this species is a series of 4-11 pulses which is usually repeated several times. Each series generally lasts less than one second. The pulses are relatively long, lasting about 1/7 the interval between them (Fig. 12). At 60° F the pulse rate is approximately ten per second and at 50° F it is about five per second (Fig. 16a). Pulses of calls from the north-central states appear to be somewhat longer than those from other parts of the species' range, but this may be a temperature effect.

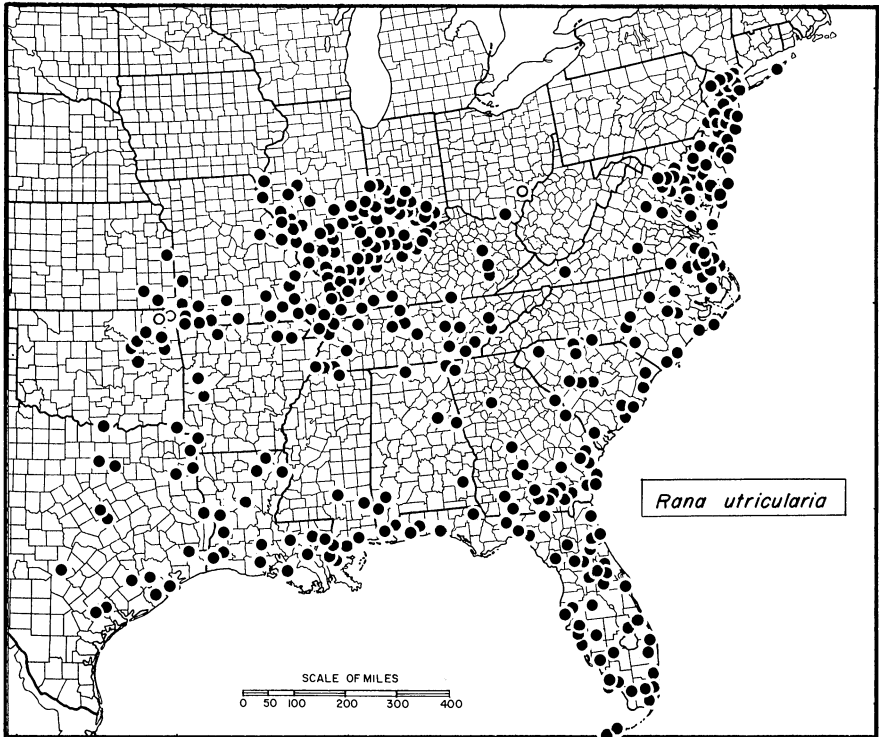


Fig. 4. Geographic distribution of *Rana utricularia*. Solid dots represent specimens examined by me (Appendix I); open circles represent reliable literature records from near the periphery of the species' range (Bragg, 1950c; Zenisek, 1963).

*Distinguishing Morphological Features of R. utricularia utricularia*—Males of this form are without oviducts. They have well developed internal vocal sacs and very large sac-like external vocal sacs which are usually darkly pigmented, possibly more darkly pigmented during than outside the breeding season (Fig. 5a). Dorsolateral folds are usually narrower than in *R. pipiens* and often conspicuously raised and lighter than the ground color. Distinct white tympanal spots are often present (Fig. 25). Even when they are not present the center of the tympanum is usually uniformly light (Fig. 5a) and does not appear blotchy as in *R. pipiens*. Dorsolateral folds are usually continuous and neither displaced nor deflected medially (Figs. 5b and 23a). Snout spots are usually absent (Fig. 26). Dorsal spots are not usually areolated and, while darker than the ground color, the contrast is not as great as in *R. pipiens* (Fig. 5b).

*Distinguishing Morphological Features of R. u. sphenoccephala*—The males of this Florida form usually have Mullerian ducts (Fig. 22) and in some cases have textured external vocal sacs. In some (Fig. 6a) the vocal sacs fold inward when not inflated. Dorsolateral folds are

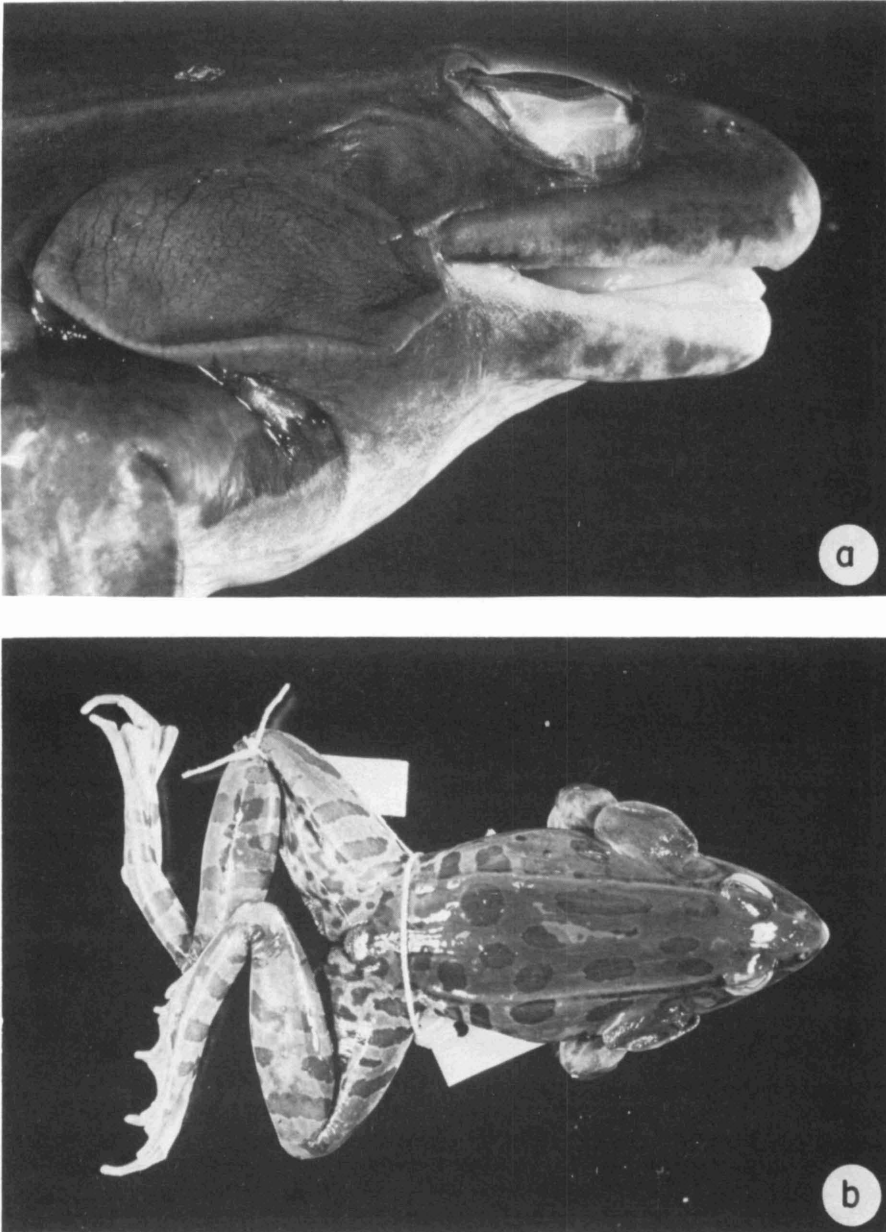


Fig. 5. *Rana utricularia* male (UMMZ 66884) from Miami County, Kansas, showing (a) typical balloon-like external vocal sacs and (b) continuous dorso-lateral folds and dorsal spots not distinctly ringed with light.

continuous and not displaced (Figs. 6b and 23a) and in this they are like *R. u. utricularia*. The tympana usually have white spots on their centers (Figs. 6b and 25). Snouts are nearly always unspotted (Figs. 6b and 26). Adults are of larger average size than those from the rest of the

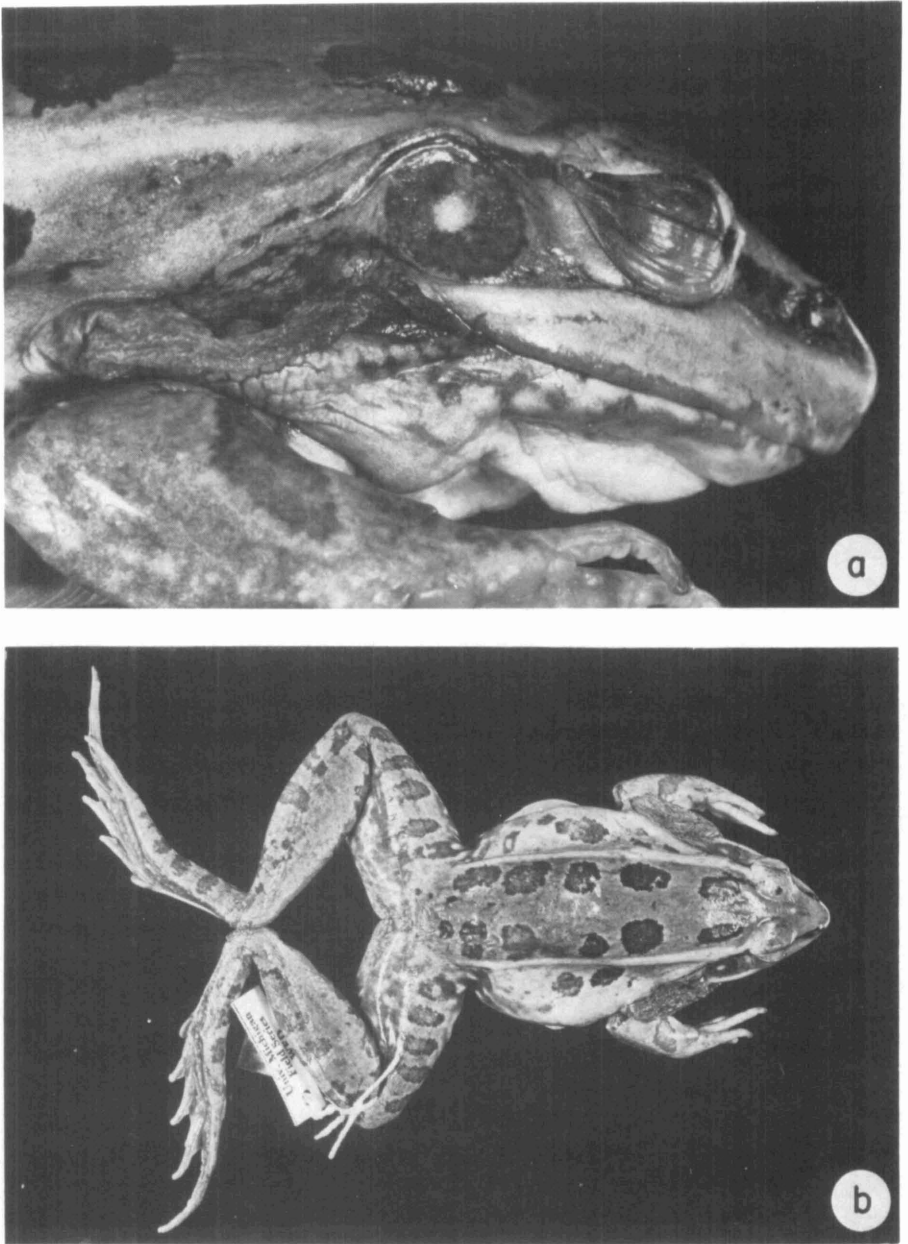


Fig. 6. *Rana utricularia* male (UMMZ 108400) from 1.6 mi W of Hollywood, Broward County, Florida: (a) shows the vocal sac with thicker ventral surface which causes the sac to fold inward somewhat when not inflated; (b) is a dorsal view of the same frog. This male has well-developed vestigial oviducts.

coastal plain (Figs. 29 and 38) (although some individuals are very small; see also Neill, 1958). Juveniles and adults of both sexes are often very dark dorsally and ventrally (Duellman and Schwartz, 1958) and have larger dorsal spots than *u. utricularia* from more northern



localities. The neotype here designated is represented in Figure 22 by the solid dot closest to the star indicating the type locality as described by Hallowell (1856).

*Rana berlandieri* Baird

*Rana berlandieri* Baird, 1859, U. S. Mex. Bound. Surv., II: 27-28, pl. 36, figs. 7-10. "Southern Texas generally;" no type designated by author. Lectotype here designated the ♂ with eversible vocal sacs collected by Van Vliet in Brownsville, Texas (United States National Museum, cat. no. 131513). This specimen has been regarded as a cotype (Cochran, 1961) and is the one figured (see Fig. 8) by Baird (1859).

Historically important names used for this species include: *Rana pipiens berlandieri* (part), *R. p. sphenoccephala* (part), Wright and Wright (1949); southern call type, Littlejohn and Oldham (1968).

*Range* (Figs. 7 and 18)—In the United States this species is known only from southern Texas. It is known from as far north as Johnson County, in central Texas, and San Patricio County, along the Gulf Coast. It may also occur west of the Pecos River (known from Ward County, Texas, whose western border lies along the Pecos River).

*Mating Call*—The presumed mating call of this species, illustrated by an oscillogram in Littlejohn and Oldham (1968), is a many-pulsed trill lasting about 2/3 second at a projected rate of about 26 pulses per second at 70° F (Fig. 17). The pulses are relatively short, in contrast to those of *R. utricularia*, but longer than those of *R. pipiens*.

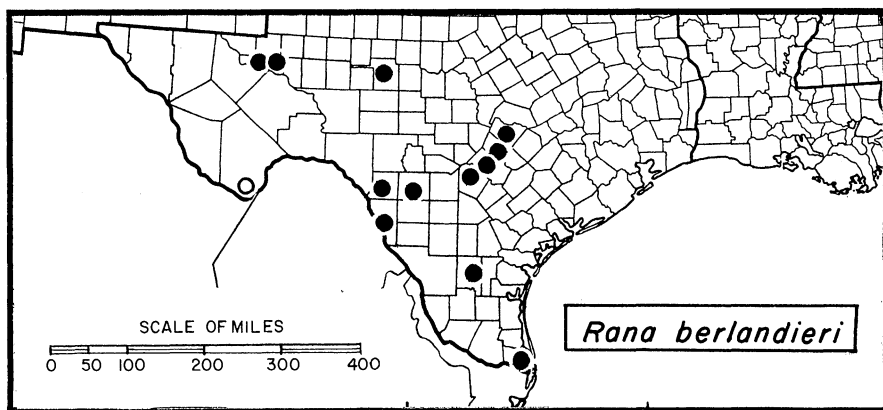


Fig. 7. Geographic distribution of *Rana berlandieri* in Texas. Solid dots represent specimens positively identified; open circle represents specimens tentatively identified as this species. (Localities are listed in Appendix I).

*Distinguishing Morphological Features*—Males with external vocal sacs which are nearly (to completely) eversible (Fig. 8). Males have Mullerian ducts. Tympanum usually without distinct white spot (Fig. 25) and tip of snout usually without a spot (Fig. 26). Dorsolateral folds are usually discontinuous with the discontinuous portion displaced medially (Fig. 23d). The skin is often warty. Dusky pigmentation on ventral surfaces is fairly common as in *R. u. sphenoccephala*.

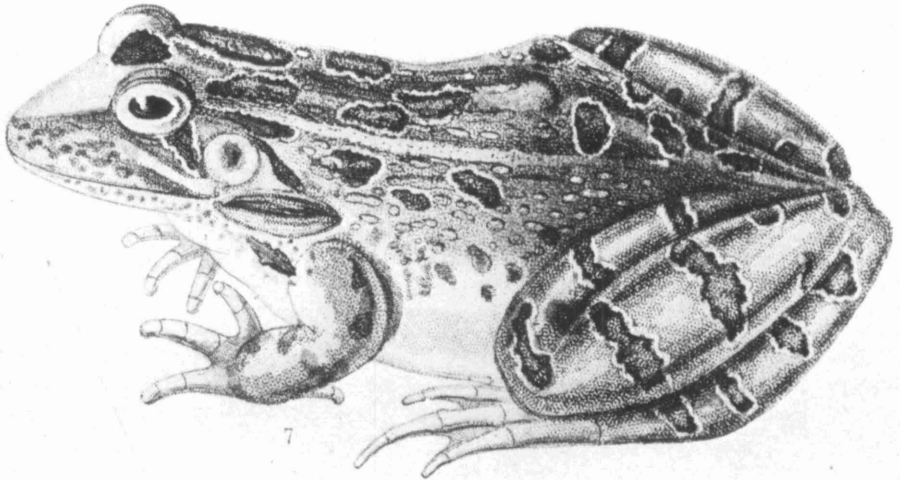


Fig. 8. Copy of illustration accompanying Baird's (1859) description of *Rana berlandieri*. It corresponds to a male specimen in the United States National Museum (catalogue number 131513) which I have designated lectotype. This illustration shows the essentially eversible vocal sacs characteristic of the species.

*Rana blairi* Mecham, Littlejohn, Oldham, Brown, and Brown

*Rana blairi* Mecham, Littlejohn, Oldham, Brown, and Brown, 1973, Occ. Pap. Mus. Texas Tech. Univ., 18: 1-11. "1.6 km. W New Deal, Lubbock Co., Texas;" University of Michigan Museum of Zoology, cat. no. 131690.

Historically important names used for this species include: *Rana pipiens berlandieri*, Mittleman and Gier (1942); *R. p. brachycephala* (part), *R. p. sphenoccephala* (part), *R. p. pipiens* (part), Wright and Wright (1949); *R. sphenoccephala*, *R. pipiens*, Bragg (prior to 1948); *R. berlandieri*, *R. berlandieri*, Bragg (1948 and later); DF complex, Post and Pettus (1966); western call type, Littlejohn and Oldham (1968); Plains Leopard Frog, Mecham (1971).

*Range* (Figs. 9 and 34)—Found in the central plains and prairie regions of the United States, from eastern Colorado, northeastern New Mexico, northern Texas, Oklahoma (except the southeastern third of

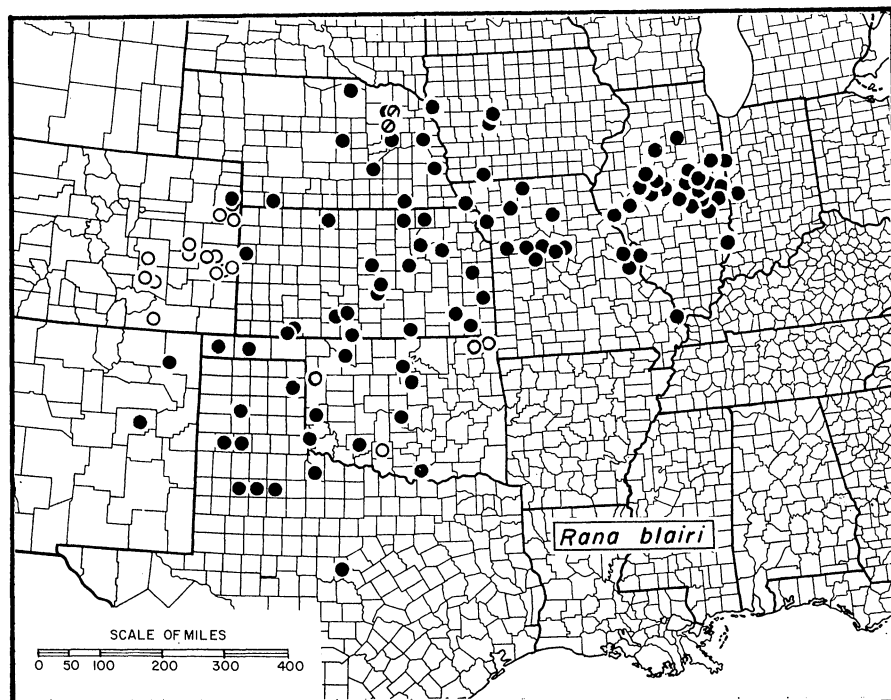


Fig. 9. Geographic distribution of *Rana blairi*. Solid dots represent specimens examined by me (Appendix I); open circles represent literature records (in addition to those indicated on the maps of mating call distribution, Figs. 18 and 34) which I consider reliable for reasons stated in the text (Post and Pettus, 1966; Bragg, 1950c). The two circles in Nebraska with lines through them represent two possible hybrids between this species and *R. pipiens*.

the state), most of Kansas, part of Nebraska and Iowa, and in northern Missouri, central Illinois, and in scattered localities further east (western Indiana) and south (southern Illinois).

*Mating Call*—The presumed mating call of this species consists of only a few pulses (about three to five) given at a projected rate of about five to six per second at 72° F (for illustrations see Littlejohn and Oldham, 1968; Mecham, 1971; Mecham et al., 1973; see also Fig. 17).

*Distinguishing Morphological Features* (Fig. 10)—The external vocal sacs of the male are small and apparent when not inflated primarily because the skin just posterior to the angle of the jaw beneath the labial stripe is conspicuously textured with fine longitudinal striations. These texturings are present only on this patch of skin and not on the surrounding skin, although the surrounding skin may have different texturings on it. Mullerian ducts are absent. Dorsolateral folds are usually discontinuous and displaced at the posterior near the point where the leg joins the body (Fig. 23d). Tympanum usually with a distinct white spot on the center. Tip of snout usually with a small

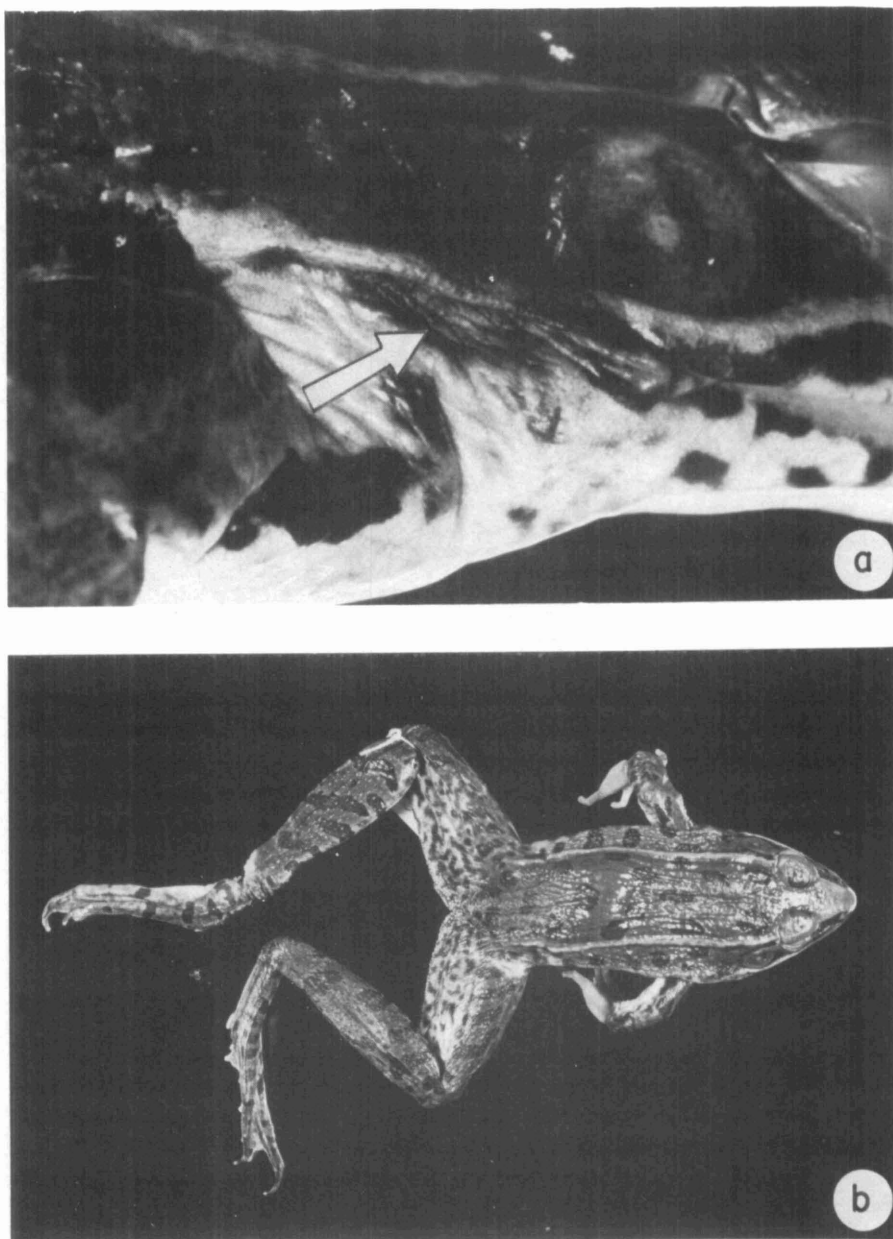


Fig. 10. *Rana blairi* male (UMMZ 86387) from Franklin County, Kansas, showing (a) typical striated skin of the external vocal sac below the labial stripe (arrow) and (b) discontinuous displaced dorsolateral folds (as in Fig. 23d).

spot. Dorsolateral folds are usually distinctly lighter in color than the ground and are narrow and more conspicuously raised than in *R. pipiens*. Dorsal spots are not generally ringed with light and the margins of the spots may be edged with darker pigment. The ground color is a

tawny gray. The skin is usually at least somewhat warty, especially on thighs and groin.

*Rana onca* Cope

*Rana onca* Cope, 1875 (1883), In: Yarrow, Rep. Coll. Bat. Rep., Chapter IV of Vol. 5 of G. M. Wheeler, Rep. geog. geol. Explor. Sur. west of 100th meridian: 528-529, pl. 25, figs. 1-3. "Utah;" United States National Museum, cat. no. 25331.

*Rana fisheri* Stejneger, 1893, North Am. Fauna, No. 7:227-228, pl. 3, figs. 5a-5c. "Vegas Valley, Nevada;" United States National Museum, cat. no. 18957.

Historically important names used for this species include: *Rana onca* (part), *R. fisheri*, Wright and Wright (1949).

*Range*—The type specimen is from Utah. This female frog was probably collected in the vicinity of St. George, Utah, since the other localities mentioned in the 1872 itinerary (Yarrow, 1875) are well within the range of *R. pipiens* in Utah (Fig. 1). As mentioned in the preceding discussion of nomenclatural history and further explained below, I have considered the frogs in the type series of *R. fisheri* as *R. onca*, thus extending the range of *R. onca* into southern Nevada.

*Mating Call*—No information.

*Distinguishing Morphological Features*—As Tanner (1931) has noted, the original illustration of the type specimen of *R. onca* (reproduced by Wright and Wright, 1949) looks very much like the specimen. Although *R. onca* is treated as a member of the *R. pipiens* complex by most authors (e.g., Wright and Wright, 1949), its very indistinct dorsolateral folds and sexual dimorphism in tympanal size (tympana of males relatively larger than those of females) suggest the possibility that it is more closely related to some other species group. At any rate, it can readily be distinguished from the four preceding members of the *R. pipiens* complex by these two features. The indistinctness of the dorsal spots of these frogs is also unusual for leopard frogs and more suggestive of the coloration of *R. pretiosa*. Wright and Wright's (1949) photographs of a frog from Overton, Nevada, which they called *R. onca*, clearly show the frog's distinctive dorsolateral folds (as in Fig. 23e) and white-spotted tympana. These indicate very strongly that it represents a third species, distinct from both *R. onca* and *R. pipiens*. Males of *R. onca* (based on specimens in the type series of *R. fisheri*) apparently lack external vocal sacs, but at least some have vestigial oviducts.

## VOCALIZATIONS

## VOCAL REPERTOIRES

Although many early natural historians attempted verbal descriptions of leopard frog calls, and some even tried to describe differences between the calls of frogs from different populations (e.g., H. Garman, 1890; Wright and Wright, 1949; Bragg, 1950c), these descriptions were never sufficiently precise to permit adequate comparisons with sounds heard in the field. One reason is the inherent difficulty of describing non-verbal sounds, a difficulty that has largely disappeared with the recent development of electronic equipment for recording and analyzing sounds. There is, however, another difficulty that is probably more important.

Leopard frogs, unlike many other anurans, produce numerous different vocalizations which are frequently heard simultaneously from a single chorus. The chorusing of a large group of sexually active leopard frogs of one species is thus a confusion of rather hoarse rattling sounds. Some of these are quite distinctive and different from any of those made by other kinds of leopard frogs, but other sounds are not so distinctive, and comparisons between populations are not simple even with the aid of sound-analyzing equipment. This is demonstrated by the fact that McAlister (1962) apparently did not realize that two distinct call types occurred in Travis County, Texas, although he presented data derived from spectrographic analysis of recordings indicating this fact.

Numerous recent authors (e.g., R. S. Schmidt, 1966; Littlejohn and Oldham, 1968) have referred to the most distinctive and conspicuous vocalization in a leopard frog's repertoire as its "mating call," and Littlejohn and Oldham described differences in the structure of presumed mating calls of leopard frogs from numerous populations in the central part of the United States. The fact that these are the most distinctive vocalizations makes them most likely to be the ones involved in species discrimination and mate attraction. Furthermore, at least in *R. pipiens*, this call is the one given most frequently by lone males in the field, as would be expected of a mate-attracting call. I have therefore continued to refer to these vocalizations as mating calls, although direct experimental proof that these calls attract sexually active conspecific females is still lacking in spite of attempts to demonstrate it.

In anurans with simple vocal repertoires the mating call is produced over and over again and other vocalizations are rarely, if ever, heard. When other sounds are produced the context is usually clear (for example, release calling by one male when clasped by another). The difficulty encountered in attracting female *R. pipiens* to a loudspeaker continuously playing the long trilled mating call may be related to the fact that males in a chorus normally produce several different sounds, all of which may be important in actual mate selection by a female.

The three kinds of sounds heard most often in a *Rana pipiens* chorus are illustrated in Figure 11a. The first part of the sequence labeled "stimulus" is the long, many-pulsed trill (A) I have referred to above as the mating call of this species. The second part of this sequence and the three similar sounds in the "response" sequence (short trills with a faster pulse rate than the presumed mating call) are a second category of sounds (B). The remaining three groups of pulses in the response sequence constitute the third category of sounds (C). In some parts of the following discussion I refer to these three kinds of sounds, respectively, by the letters A, B, and C, as indicated above. The entire sequence illustrated in Figure 11a would be represented: A-B-B-C-B-C-B-C. These three kinds of sounds are also made by *Rana palustris* in similar sequences and under similar circumstances as shown in Figure 11b.

#### FUNCTIONS OF VOCALIZATIONS

Observations and field experiments in the spring of 1972 on the vocalizations of a small colony of *R. pipiens* in Washtenaw County, Michigan, yielded the following results and hypotheses:

The usual calling sequence is A-B(-B) or A-B(-B)-C(-C-C-C-C). A somewhat isolated male tends to produce a greater proportion of A's than B's and very few or no C's, and does not begin call sequences with B's or C's. A male in the middle of a dense chorus increases the proportions of B's and C's in call sequences and sometimes begins sequences with B's and C's. When a male is stimulated by playbacks of A sounds, either when he is not otherwise calling steadily or when the A sound is deliberately placed between his call sequences, he usually responds by joining the playback with his own A sound, and then terminates his call, usually with one B (or two) and several C's. (In earlier experiments (Fig. 11) a single tape recorder was used for playback and recording of responses and the initial joining of A sounds was not detected.) During one interval of 550 seconds 35 A sounds were played to a somewhat isolated male (i.e., a male in a pond with only a few, distant, barely-audible other males). Six of these A sounds also included a B sound, but the responses of the frog discussed here were given before the B sound on the tape was played, so these will be ignored for present purposes. Twenty-two times the frog joined the A sound with his own A (delay: 1.6-4.3 seconds). Eleven times he responded by giving one to four C's (delay: 1.6-3.1 seconds). Twice the frog made no sounds and once it was not clear whether or not a response was given. In the case of A sounds being joined by A's the interval from the last sound made by the frog to the beginning of his A sound varied from 2.1 to 44.3 seconds and in the case of the C responses the intervals ranged from 3.7 to 14.7 seconds. All of these C sounds, which appeared to be given in response to hearing an A sound, were preceded by an A-B(-B) or A sound on the part of the frog. On

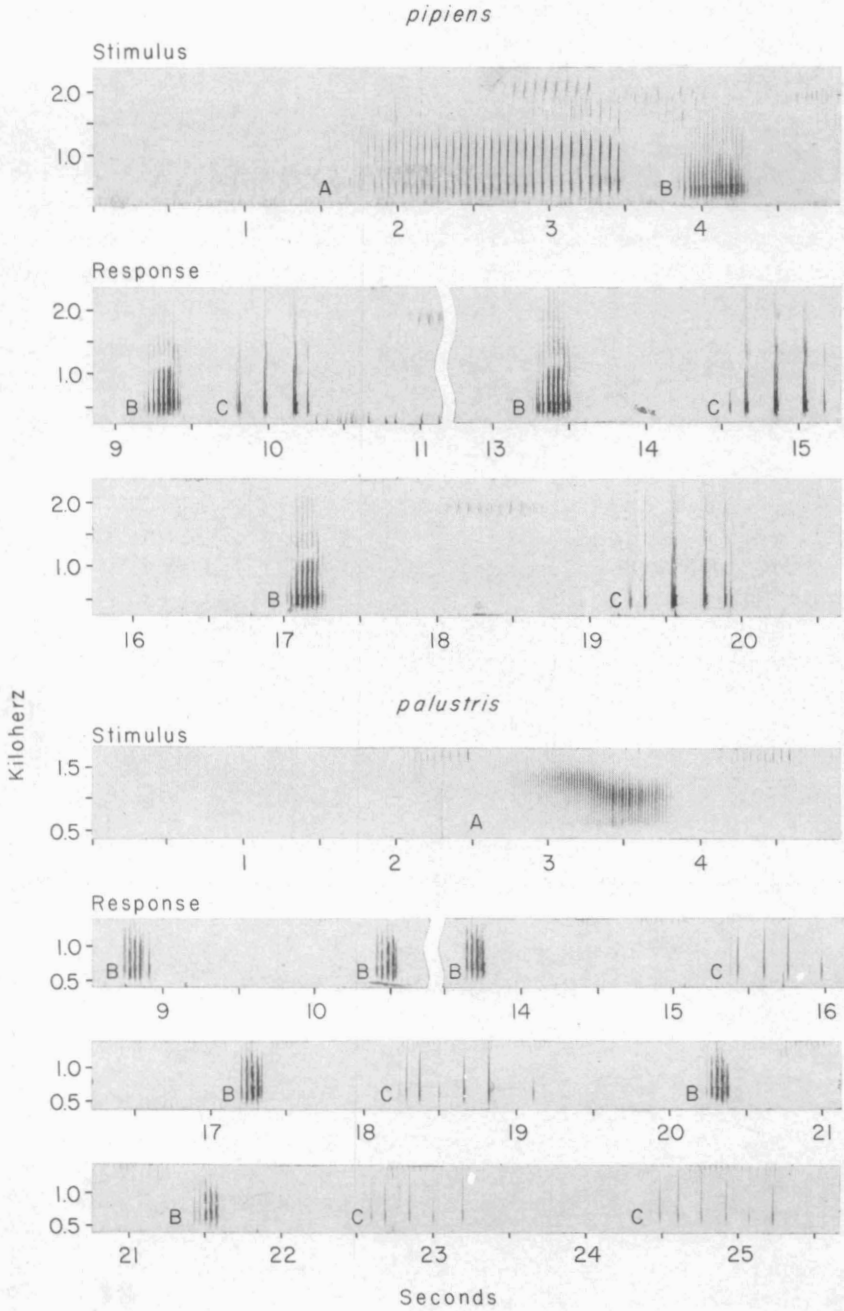


Fig. 11. (a) Response of male *R. pipiens* (above) to playback of recording of its own mating call ("stimulus"). (b) Response of *R. palustris* male (below) to playback of its mating call. In both species the actual time delay between end of the playback sequence and the beginning of the "response" sequence is estimated in part. The recording of the response was made on the same tape recorder as the playback and three seconds were added to the actual time delay recorded as



three occasions during this period when the frog gave an A-B(-B)-C-C-C(-C) sequence without playback of an A sound between the B and C segments the intervals between the end of his B sound and the beginning of the C segment ranged from 3.5 to 13.3 seconds. This suggests the possibility that the frog was stimulated by the first A to produce the A-B-C sequence and that the second A, which apparently stimulated the C segment, merely elicited a response which the first had made likely. The production of C sounds is probably related to the number of A sounds heard during any period of time. At any rate the playing of A sounds to this male increased the numbers of calls produced, the proportions of different sounds made, and the timing of their production.

A C-C-C sequence was played 37 times during a 420-second interval to this same frog. He gave six A sounds, which were of shorter than normal duration, and possibly one short B. Thus C sounds inhibited calling, changed the relative proportions of A's and B's produced, and eliminated C's.

Effects of playing B's to calling males are not as clear. Evidently B's inhibit calling, though less than C's. During a 180-second interval during which B's were played at varying intensities to the same male discussed above (occasionally with the end of an A sound preceding it) the male produced four short A's and two long A's which were followed by a B. The two long A's appeared to be stimulated by low intensity B's. The other two low intensity B's did not stimulate calling. B's played at about the same intensity as A's and C's discussed above, and B's played at a higher intensity were more inhibitory. Of 18 of these sounds played only one was followed by an A with short enough delay to make it likely that it was stimulated by the B. This was a short A, like those produced when C's are played. The other three A sounds, which were also short, were produced with a long delay after the B sound.

These results, together with other observations, suggest the following hypotheses:

1. The long, slow, trilled call (A) is a long-range female attractant which probably attracts both males and females to choruses (mating call).
2. The short, rapid, repeated trills (B) are close-range direction-finders by which males inside a chorus increase the likelihood of approaching females coming to them rather than to other males in the chorus.
3. The short terminal sounds (C) have an aggressive or spacing function between males.

an estimate of the amount of time required to switch the recorder from playback to record. The possibility that an A sound was produced during this interval or during the playback cannot be eliminated in either case. All recordings were made in the same pond at Ann Arbor, Washtenaw County, Michigan, on 19 May 1966. The air temperature was 52° F and the water temperature was 64° F.

Certain comparisons are suggested with published discussions of some insect sounds. Thus, many species of meadow grasshoppers (Orthoptera: Tettigoniidae: Conocephalinae) alternate two distinct sounds in long-continued calling, one of which (postulated as a male-male aggressive or spacing sound) is often produced exclusively in dense aggregations; the other (postulated as a female-attractant) is sometimes the only sound produced by isolated males at night (Alexander, 1960, 1968a). Similar calls are known in some cicadas; in both cicadas and meadow grasshoppers stimulation by one sound causes production of the other (Alexander and Moore, 1958, 1962). In some cicadas, males in aggregations produce one call (female- and male-attracting) until a female is seen, then change to a second call (courtship), then to a third call just before mounting (Alexander, 1968a). Pair formation within groups is probably largely independent of the long-range attractant, and dependent on the short-range (courtship) sound. In *R. pipiens*, the short-range sound (B) differs in being produced after a long-range call even without stimulation from an approaching female. The number of these short-range sounds produced by a male increases when he hears more long-range sounds.

If, as seems likely, at least some of these vocalizations are involved in establishing and maintaining territories, it is possible that a female is able to select the dominant male (or the male in the best breeding site) in a group of acoustically interacting male frogs. In this sense, a chorus of leopard frogs may resemble more closely the leks of birds like prairie chickens than it does the choruses of anurans with simple vocal repertoires. Supporting this hypothesis is the fact that most egg masses are usually found in an area much smaller than that occupied by calling males (Wright and Wright, 1949; Merrell, 1968; DeBenedictis, 1970; present study). Merrell (1968) estimated effective population size in *R. pipiens* by multiplying the number of egg masses by two, even though most of these egg masses were found in one small segment of the area occupied by calling males. Because his observations indicate a strong probability that only a few males were involved in fertilizing these eggs, he may have made a rather large error. If females are capable of selecting the dominant male in a chorus they may also be unlikely to be attracted to a lone male. A large chorus may be indicative of a successful breeding site, especially if adults are likely to return to the pond from which they hatched.

#### SPECIES DIFFERENCES

The mating call of *R. pipiens* may resemble the primitive type of leopard frog mating call since in a number of ways it is more similar to the mating calls of its more distant relatives than it is to the calls of other species of leopard frogs. The mating calls of *R. pipiens*, and of *R. capito* and *R. palustris* (Fig. 15) and *R. areolata* are long, low-pitched trills composed of 20 or more short pulses. In *R. pipiens* the trill may

TABLE 3

KEY TO PRESUMED MATING CALLS OF LEOPARD FROGS IN THE UNITED STATES (NORTH OF THE DASHED LINE IN FIG. 1)<sup>1</sup>

1.	Call lasting more than one second (usually at least three); pulse rate about 20 per second . . . . .	<i>Rana pipiens</i> (Figs. 11, 15, and 16b)
1'.	Call usually lasting less than one second . . . . .	2
2(1')	Call consisting of only two to six pulses delivered at a projected rate of about three per second . . . . .	<i>Rana blairi</i> (Fig. 17)
2'.	Call consisting of four or more pulses delivered at a projected rate of greater than six per second . . . . .	3
3(2')	Pulse rate (projected) usually less than 13 per second . . . . .	<i>Rana utricularia</i> (Figs. 12, 13, 14, 15, and 16a)
3'.	Pulse rate (projected) usually greater than 15 per second . . . . .	<i>Rana berlandieri</i> (Fig. 17)

<sup>1</sup> Ambient temperature about 60° F.

have as many as 50 pulses, is at least one second long, and may last as long as five seconds, depending in part on the temperature. Mating calls of other leopard frogs that have been described (see Mecham et al., 1973 for summary) are shorter, rarely more than one second in duration, and usually if not always with fewer than 20 pulses. The mating call of *R. utricularia*, for example, is a short group of relatively long pulses (usually 4 to 11 in number) (Fig. 12) and is nearly always briefer than one second (Figs. 13 and 14). Table 3 provides a key to the known mating calls of the *Rana pipiens* complex.

The differences between mating calls of *Rana pipiens* and *R. utricularia* are particularly striking and can most easily be seen by comparing them with the mating calls of *R. palustris* and *R. capito* (Fig. 15). The illustrated calls of *R. pipiens*, *R. utricularia*, and *R. palustris* were recorded on the same night in a mixed-species chorus in southeastern Indiana and are therefore directly comparable. The illustrated call of *R. capito* was recorded near Gainesville, Florida. The calls of *R. capito* and *R. pipiens* were about twice the length of the segment illustrated. Mecham (1971) shows similar long trilled calls of *R. montezumae*, *R. dunni*, and *R. megapoda* (Mexican relatives of the *R. pipiens* complex).

Of the three species of spotted frogs with long, many-pulsed calls that I have recorded (*R. pipiens*, *R. palustris*, *R. capito*) *R. pipiens* and *R. palustris* can readily be distinguished on the basis of differences in the pulse rates of their mating calls (Fig. 16b). The call of *R. pipiens* has the slower pulse rate; that of *R. palustris* is about two and one-half times that of *R. pipiens* at the same temperature. The pulse rate of *R. capito*'s mating call is intermediate, but probably very close to that of *R. pipiens*.

The similarity in pulse rates of the mating calls of *R. pipiens* and *R. capito* may be explained by the fact that they are not sympatric in



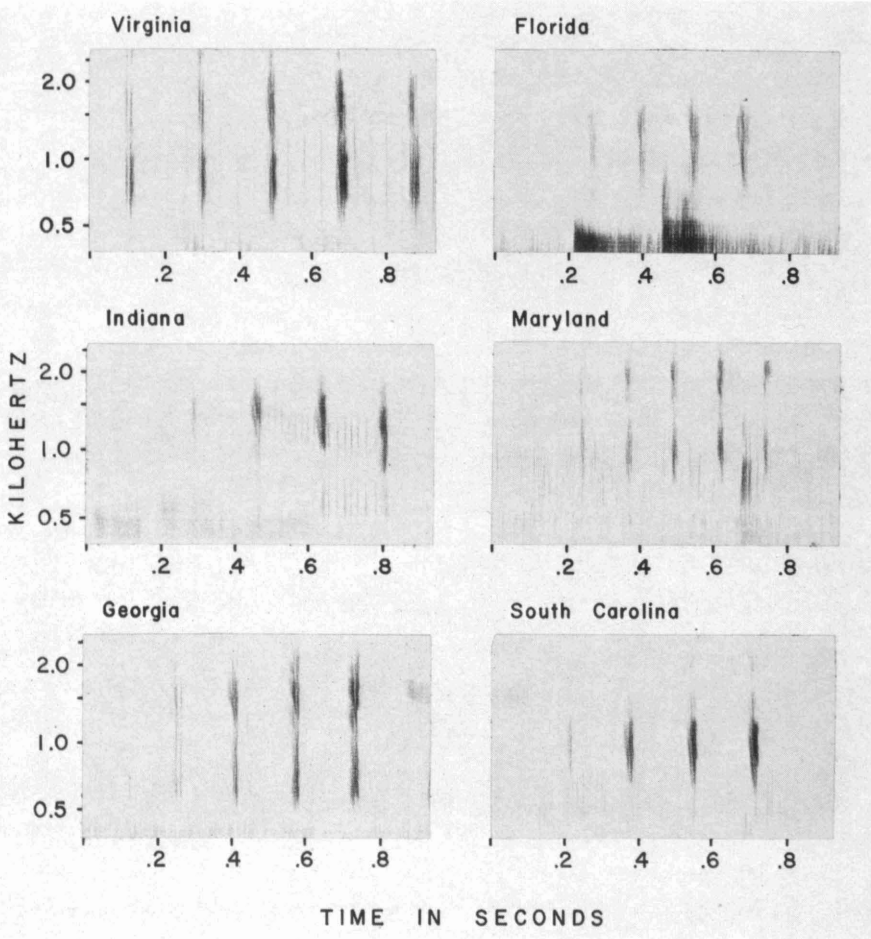


Fig. 13. Audiospectrograms of calls of *R. utricularia* recorded at low temperatures. Locality and temperature data: Virginia: Lancaster Co. (air 46°F; water 50°F). Florida: Collier Co. (effective temperature about 56°F). Indiana: Ripley Co. (air 47°F; water 55°F). Maryland: Saint Mary's Co. (air 61°F; water about 55°F). Georgia: Hart Co. (air 53°F; water about 56°F). South Carolina: York Co. (air 50°F; water 68°F).

they can usually be distinguished whether the temperature is known or not.

The similarity of the presumed mating call of *R. utricularia* (Figs. 13, 14, 15) to the C call of *R. pipiens* (Fig. 11a), together with the hypothesis of function of the C call in *R. pipiens* and the absence of a long, trilled call similar to A in *R. utricularia*, suggest the possibility that the female-attracting call of *R. utricularia* is derived from a call which originally functioned primarily in male-male interactions. If this is true, it could be related to the prolonged breeding season of *utricularia* and the fact that males call irregularly and unpredictably (though they can be stimulated to call in numerous ways, for example by playing tape-recordings of calls) and breed during all months of the

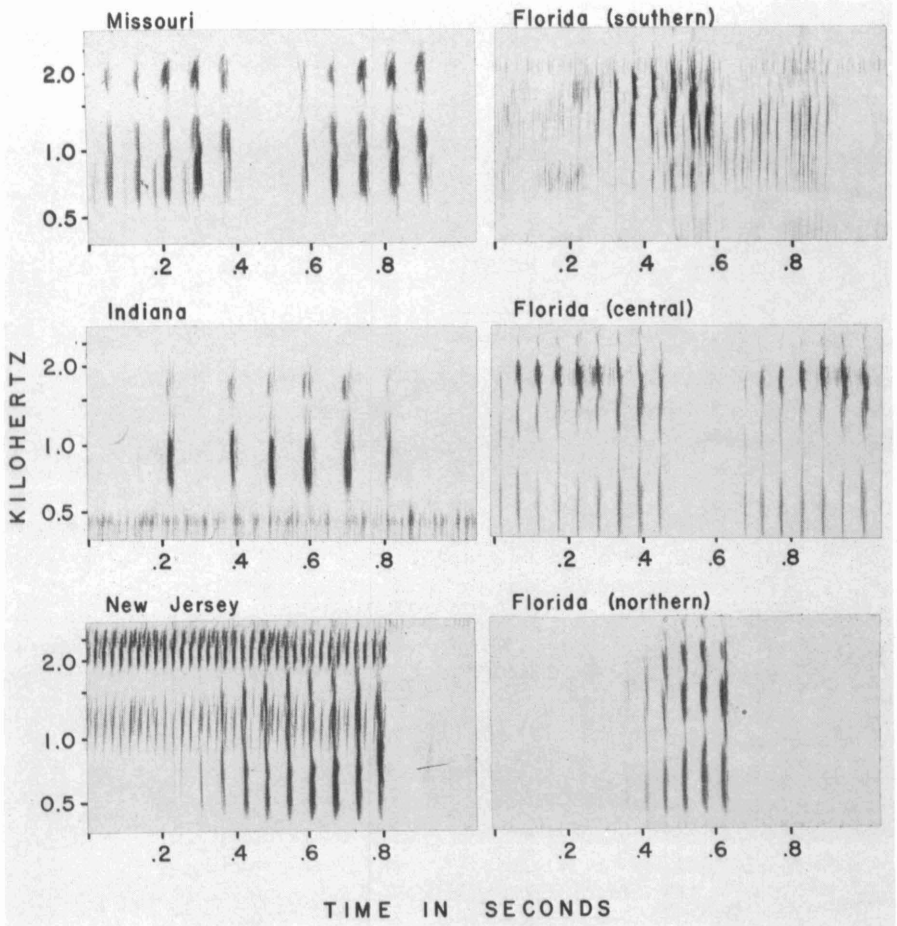


Fig. 14. Audiospectrograms of calls of *R. utricularia* recorded at high temperatures. Locality and temperature data: Missouri: Barry-Lawrence Cos. (air 70°F; water 70°F). Southern Florida: Dade Co. (air 72°F; water 72°F). Indiana: Monroe Co. (air 68°F; water about 65°F). Central Florida: Polk Co. (air 63°F; water 70°F). New Jersey: Cape May Co. (water about 73°F). Northern Florida: Levy Co. (air 63°F; water 70°F).

year in some parts of the range. Males of this species may maintain territories more or less throughout the year, and females may have come to respond to this (previously only territorial) call of the male in the way females of *R. pipiens* probably respond to the A call (or the combination of A, B, and C calls) of the males of that species.

Differences between mating calls of species in the *R. pipiens* complex have previously been summarized by Littlejohn and Oldham (1968) with additional information on some of these species in Mecham (1971), Brown and Brown (1972), and Mecham et al. (1973). I have presented graphs showing the relationship between pulse rate and temperature for two of these species (*R. blairi* and *R. berlandieri*) utilizing their data (Fig. 17). For *R. utricularia* I have indicated the relationship between pulse rate and pulse duration (Fig. 12) and

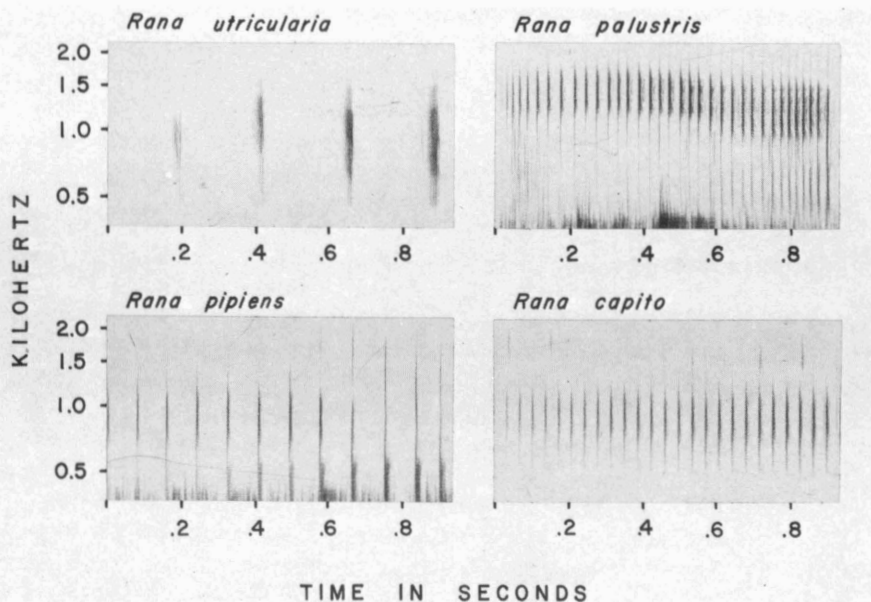


Fig. 15. Audiospectrograms of calls of *R. utricularia*, *R. pipiens*, and *R. palustris* from 2 miles east of Napoleon, Ripley County, Indiana (air 48° F; water 53° F) and of *Rana capito* from Alachua County, Florida (air and water about 63° F).

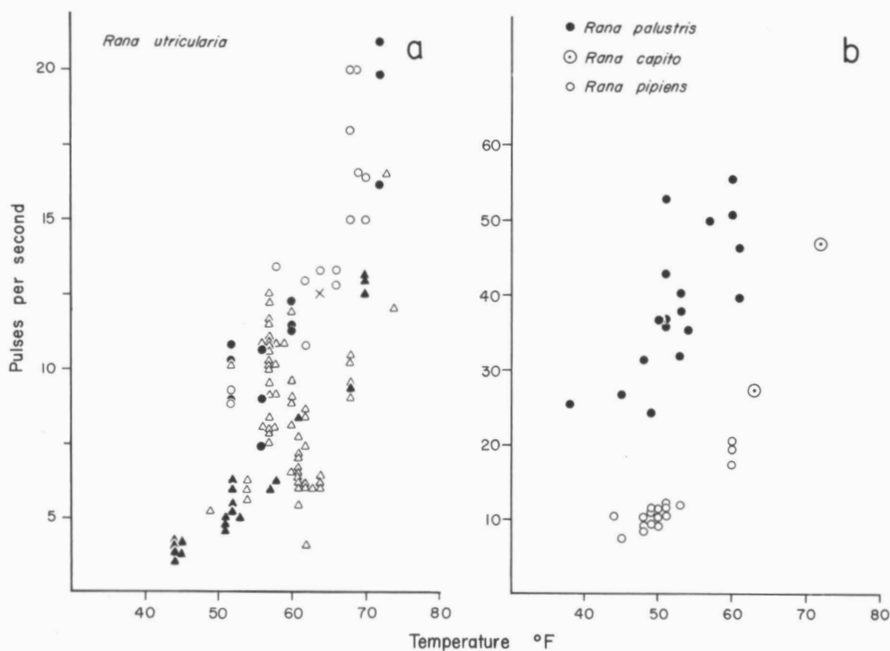


Fig. 16. (a) Relationship between pulse rate and temperature for mating calls of *Rana utricularia* from southern Florida (solid circles), northern Florida (open circles), Atlantic Coastal Plain (open triangles), and inland central United States (Missouri and Indiana) (solid triangles). The single "X" is from Texas (Littlejohn and Oldham, 1968). (b) Relationship between pulse rate of mating calls and temperature for *R. palustris*, *R. pipiens*, and *R. capito*.

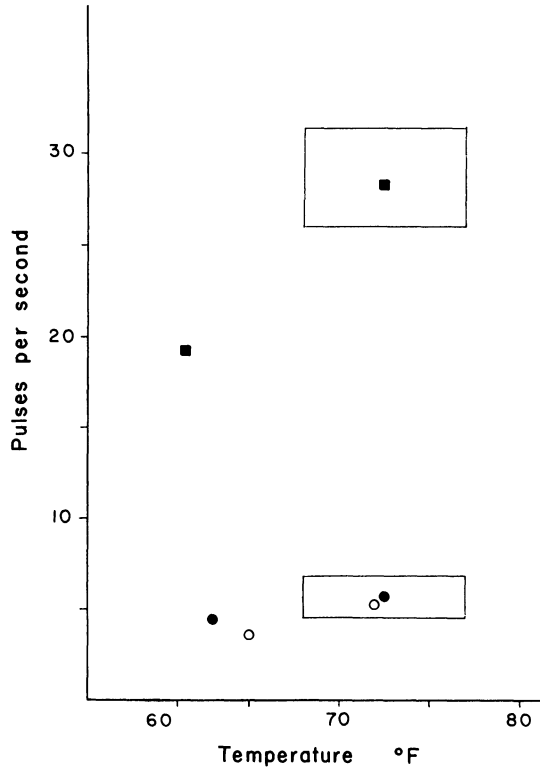


Fig. 17. Relationship between pulse rate and temperature for mating calls of *Rana berlandieri* (squares) and *R. blairi* (solid and open circles). The rectangles enclose the range of variation of pulse rate and temperature reported by Littlejohn and Oldham (1968) for seven *R. berlandieri* and seven *R. blairi*. Within each rectangle the solid symbol represents the mean pulse rate plotted against the midpoint of the temperature range for that sample. The solid symbols outside the rectangles are data (Littlejohn and Oldham, 1968) for single individuals. Open circles represent mean pulse rates and mean temperatures reported by Brown and Brown (1972) for two samples involving seven *R. blairi*.

between pulse rate and temperature (Fig. 16a) for calls from different geographic regions based on my own and other recordings. There appears to be some geographic variation in call characteristics of *R. utricularia* which should be examined more closely. Frogs from the central part of the United States (Indiana and Missouri) have somewhat lower pulse rates at a given temperature (Fig. 16a) and relatively longer pulse durations (Fig. 12) than those from elsewhere in the range of this species. The significance of this apparent variation is not known at this time.

The geographic distributions of *R. pipiens*, *R. utricularia*, *R. blairi*, and *R. berlandieri* were determined from my own tape recordings and those available from other sources (Appendix II). These distributions, based on differences in mating calls, are shown in Figures 18, 19, and 34. My data (see especially Fig. 19) supported the conclusion of



Littlejohn and Oldham (1968) that populations of frogs with one type of mating call were largely allopatric to those with other types but were sympatric in a narrow zone where their ranges were in contact and did not hybridize effectively in these areas (with one possible exception). I had previously noticed differences in the appearance of coastal plain leopard frogs and those from Michigan, which have distinctive calls, and while doing field work in south-central Indiana I soon discovered that I could readily distinguish males of the northern call type (*R. pipiens*) from those of the southeastern call type (*R. utricularia*) on morphological grounds alone. Subsequently I carefully examined specimens from tape-recorded populations, or from areas near recording localities indicated in Figures 18 and 19, in an attempt to discover whether there were consistent morphological differences among the populations with distinct mating calls. Although numerous morphological characters had been mentioned previously in the literature, the only character found that was unique for each species (call type), was the structure of the external vocal sacs of males. Variations in this aspect of morphology have not previously been described in leopard frogs. They are discussed in detail in the following section and variations in other aspects of morphology and coloration are considered in light of distribution patterns revealed by analysis of mating calls and vocal sac structure.

## VARIATION IN SECONDARY SEX CHARACTERS

### VOCAL SACS

Adult males of most species of frogs have vocal sacs that are thought to function as resonators or radiators of sounds produced by these animals. Anuran vocal sacs have generally been classified according to where they are located in the animal and whether they are paired or single. In addition they have often been distinguished on the basis of the condition of the skin overlying the area where the vocal sacs expand when inflated. If this skin is different from that which surrounds it, the frog is said to have external vocal sacs. Male frogs in which the skin overlying the vocal sacs is not different from the surrounding skin have often been said to have internal vocal sacs, but this is not a distinct category from external vocal sacs since internal vocal sacs, derived principally from mylo-hyoid muscle, are present in both cases (Liu, 1935).

All male leopard frogs have paired vocal sacs located laterally, behind, and below the angles of the jaw. Although the functional significance of variations in the external structure of vocal sacs is not known, several of the species in the *Rana pipiens* complex that I have examined have distinctive external vocal sacs. The geographic distribution of these vocal sac types in most cases corresponds precisely with the distribution of call types in leopard frogs (cf. Figs. 18 and 20)

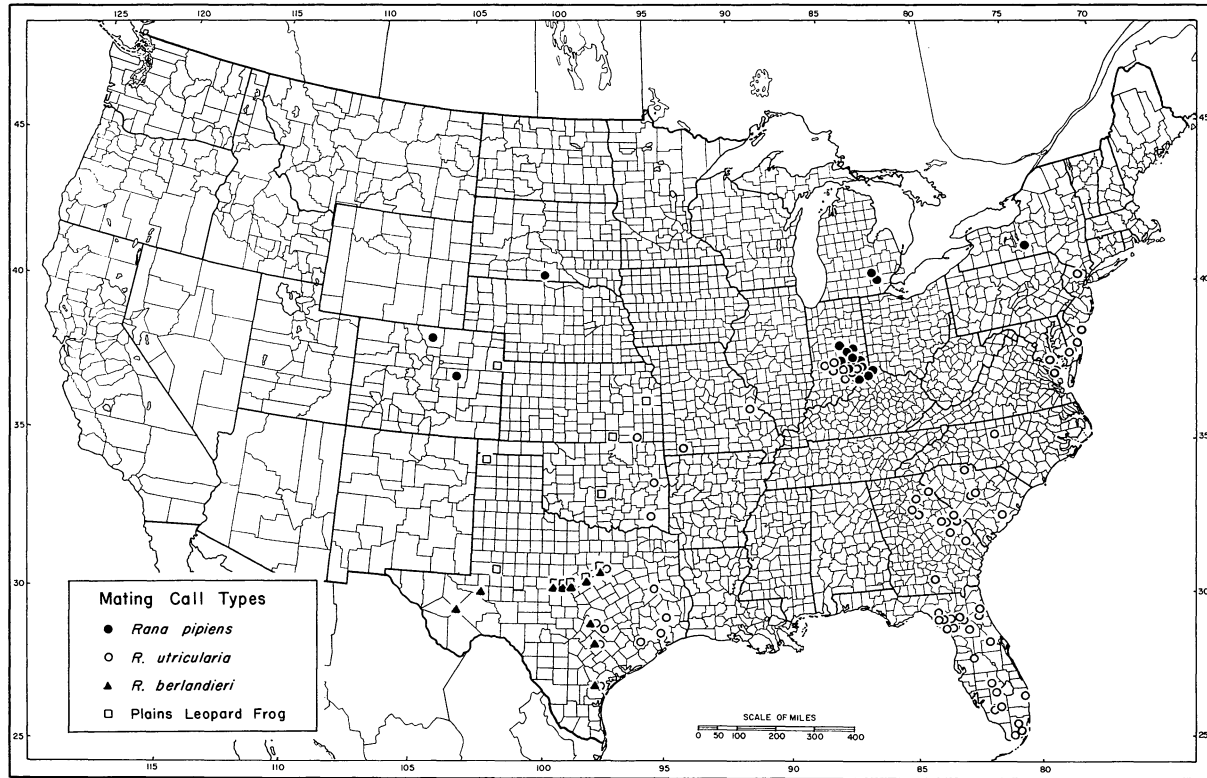


Fig. 18. Geographic distribution of four species in the *Rana pipiens* complex from the United States based on field listening records and analyses of tape recordings of mating calls. Symbols represent one to several localities for each species. Data are from three different sources (localities are listed in Appendix II). The first is my records (listening records and tape recordings). Additional data are from tape recordings supplied by the Cornell Laboratory of Ornithology, the University of Michigan Museum of Zoology, and the American Museum of Natural History, and from previously published records (Littlejohn and Oldham, 1968). The latter records have been replotted where possible from actual localities mentioned in the text and footnotes of this paper. Only in cases where specific localities were not mentioned and where points on their distribution map clearly represent additional records were records transferred from their map to mine. (See Fig. 34 for additional call data, from Illinois.)

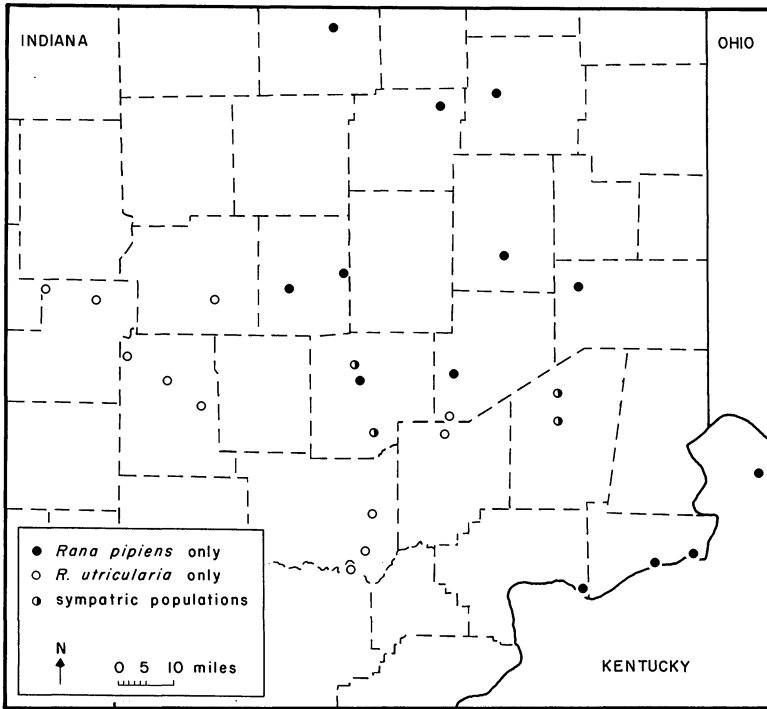


Fig. 19. Geographic distribution of *Rana pipiens* and *R. utricularia* in Indiana and Kentucky based on field records of mating calls. Solid dots represent populations with only *R. pipiens*; open circles represent localities where only *R. utricularia* was heard; half-colored circles represent localities where both species were heard.

where known and species determination of preserved material was based primarily on the external appearance of vocal sacs in males.

*Rana pipiens* males do not have external vocal sacs. The internal vocal sacs are well-developed and in some cases, especially in males collected during the breeding season, the skin overlying the vocal sacs appears to be stretched. This is presumably the result of frequent inflation of the internal vocal sacs during calling. The skin overlying the vocal sacs is not, however, differentiated in any other way from the surrounding skin (Fig. 2a).

Each of the other members of the *R. pipiens* complex identified by a distinctive call type has external vocal sacs—that is, some modification of the skin overlying the internal vocal sacs. At least among those members of the complex that have been identified by distinctive calls the kind of modification is characteristic of the species.

In *Rana utricularia* the external vocal sacs are large and almost spherical in shape when inflated. They appear to be thin-skinned and are usually pigmented differently from the surrounding skin (Fig. 5a). Although the appearance of external vocal sacs of males of this species is similar throughout most of its range, there is some geographic variation in size and in Florida there is considerable variation in vocal

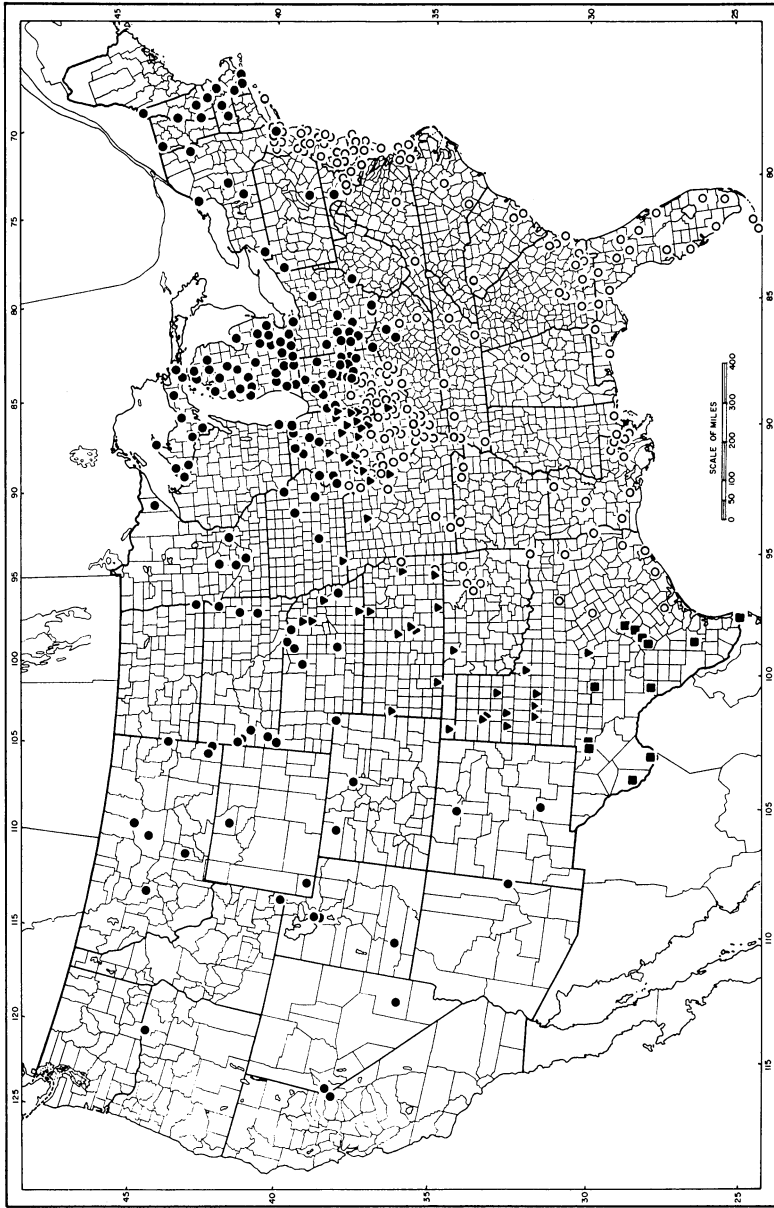


Fig. 20. Geographic distribution of different kinds of external vocal sacs in some leopard frogs from the United States. Solid dots represent male frogs without external vocal sacs (Fig. 2a); open circles represent frogs with balloon-like external vocal sacs (Fig. 5a); inverted solid triangles represent males with striated textures on the patch of skin overlying the internal vocal sac below the labial stripe (Fig. 10a); solid squares represent males with eversible (or nearly eversible) vocal sacs (Fig. 8). Omitted from this map are frogs from the southwestern United States (California, Nevada, Arizona, New Mexico, and extreme west Texas) from the area south of the dashed line in Fig. 1 that lack external vocal sacs (but which, based on other morphological criteria, are not the same species indicated here by solid dots), or that have other types of external vocal sacs than those mentioned above. Also omitted are those males from the coastal plain with slight modifications of the balloon-like external vocal sacs mentioned in the text (and

sac structure. A total of 105 presumably adult males was examined from this state. Sixty-seven of these had vocal sacs indistinguishable from those of "typical" males from the rest of the species' range. The other 38 had external vocal sacs that were slightly different. In some the entire vocal sac appeared to be thicker-skinned with a textured surface. In others the skin on the ventral surface of the vocal sac was apparently thicker or stiffer than that on the dorsal surface. This difference caused the sac to fold when not inflated and lie in a groove continuing back from the angle of the jaw (Fig. 6a). In some cases the skin folded in completely, making the sac nearly eversible. Although these modifications of the vocal sacs were more common in frogs from southern Florida than northern Florida they were not restricted to southern Florida and, in fact, were seen in occasional specimens (10 of 112 total) from Louisiana, Georgia, South Carolina, and New Jersey. Although more of the frogs from Florida with smooth balloon-like external vocal sacs were without Mullerian ducts (see next section, p. 47) than with (37 without, 30 with) and more of the ones with textured or in-folding vocal sacs were with ducts than without (23 with, 15 without), the condition of the vocal sacs is not a reliable indicator of whether the frog has Mullerian ducts or not.

In *R. berlandieri* the vocal sacs are fairly well-developed pouches at the angles of the jaw. The skin which forms these sacs is textured and the sacs nearly eversible, tucking or folding into a groove or pouch when not inflated. Baird's (1859) illustration accompanying the original description of this species (see Fig. 8) illustrates this vocal sac condition very clearly. The vocal sacs of some *R. utricularia* males from Florida resemble somewhat those of *R. berlandieri* (Fig. 6a).

The vocal sacs of *R. blairi* are small, inconspicuous structures. Unlike their condition in *R. utricularia* and *R. berlandieri* the patches of skin overlying the internal vocal sacs in this species usually do not form sac-like structures unless the underlying internal vocal sacs are inflated. Frogs of this sort were described by Moore (1944) as being without external vocal sacs. Moore does not explain his criteria for deciding whether to consider vocal sacs as external or not, however, and I have considered the vocal sacs of this species to be external because the small area of skin overlying the internal vocal sacs, though generally not conspicuously expanded in preserved material, is textured with longitudinal striations and usually pigmented more darkly than the smoother, or differently-textured, skin that surrounds it (Fig. 10a).

As part of his study of the three (or four) species of leopard frogs occurring in Texas, McAlister (1962) estimated the volume of right vocal sacs of 28 freshly pithed adult male leopard frogs from Central and East Texas. He found that the range of variation in relative pouch volume (that is, volume of the internal vocal sac) within counties approximated that between the several counties and concluded therefore that there was no difference in vocal pouch construction (at least as revealed by measurements of the volume of the internal vocal sac).

Since he lumped his samples by county and does not name the counties it is difficult to determine how many species might have been included in each of his samples. McAlister also examined a series of male frogs from 58 Texas counties and grouped them according to whether they had external or internal vocal sacs. Samples from four of the counties were classified as having internal vocal sacs [only]. One of these counties—Hidalgo—lies within the range of *R. berlandieri*. The other three counties—Archer, Dawson, and Howard—fall within the range of *R. blairi*. The remaining 54 counties were not named. He did not mention any differences in external appearance of vocal sacs.

The frogs that are generally considered to be the closest relatives of the *R. pipiens* complex show a similar sort of variation in modifications of the skin overlying the internal vocal sacs. In *R. palustris*, as in *R. pipiens*, there are no external vocal sacs although in this species the undifferentiated skin overlying the internal vocal sacs is also stretched in some cases.

*R. a. areolata* and *R. a. circulosa* have balloon-like external vocal sacs somewhat like those of *R. utricularia*. According to Gloyd (1928): "The vocal sacs of the males are lateral and relatively much larger than those of *R. pipiens* [probably *R. utricularia*]. When singing they are distended until they resemble miniature balloons, each one almost as large as the head itself." The external vocal sacs of *R. sevosa* and *R. capito* are similar to, but smaller than, those of *R. areolata*. According to Deckert (1920), when *R. capito* calls "the vocal vesicles over the arms are distended into hemispheres about the size of large hazel nuts."

The evolutionary status of the populations of leopard frogs in the southwestern United States is still unclear. Although the existence of three distinct call types in Arizona has been reported (Platz and Platz, 1973), the data on these calls and their distributions have not been published. *R. pipiens*, which does not have external vocal sacs, occurs there, primarily at high elevations. There are other leopard frogs from this area, strikingly different from *R. pipiens* in coloration and general appearance, but which also appear not to have external vocal sacs (Fig. 31). Still other males do have external vocal sacs and these are variable in structure. Morphological variation in these leopard frogs will be considered in a separate section after I have dealt with interspecific morphological variation in the four species for which distributional data based on call information are available.

#### MULLERIAN DUCTS

Mullerian ducts of male frogs are homologous to the oviducts of females and are sometimes referred to as vestigial or, less commonly, rudimentary oviducts. Moore (1944) was the first to note that while the ducts are well developed in many male leopard frogs those from some localities do not have them, and that the males from a given locality are generally consistent in possessing or lacking these structures. He also

observed that in some parts of the country males without external vocal sacs usually had vestigial oviducts and that males with external vocal sacs usually did not have them. The fact that this correspondence between a male's vocal sacs and his oviducts did not hold for leopard frogs from all parts of the country was one of the things that led Moore to conclude that the recognition of subspecies or species in this group was not warranted.

The geographic distribution of male leopard frogs with and without vestigial oviducts is shown in Figures 21 and 22. A comparison of this distribution with the distribution of *Rana pipiens* (Figs. 1 and 18) shows that most of these males do have vestigial oviducts. When the snout-urostyle lengths of 278 *R. pipiens* males with Mullerian ducts were compared with those of 40 males of the same species lacking Mullerian ducts on both sides, it was found that the mean snout-urostyle length of males with ducts (63.5 mm) was significantly greater than the mean snout-urostyle length of males without these ducts (59.7 mm) ( $p < 0.001$ ), although the range in size of males with ducts (46.7-80.5 mm) is greater and completely overlaps that of the males without ducts (50.0-72.3 mm). Fourteen males were dissected that had an oviduct on one side but not on the other. The mean snout-urostyle length of these males (62.3 mm) was intermediate between the other two groups and not significantly different from either one. All 332 of the males examined had thumb pads sufficiently enlarged and darkened that their sex could be determined without dissecting them. However, they may not all have been mature. Since there is no striking pattern to the geographic distribution of the oviductless *R. pipiens* males, this evidence indicates that the Mullerian ducts may become better developed as the animal grows or that there is some other relationship between the development of vestigial oviducts and the size attained.

As far as is known, males of *R. blairi* never develop Mullerian ducts. Post and Pettus (1966) noted that, in Colorado, males of their "DF complex" (which corresponds to *R. blairi*) lack oviducts. Littlejohn and Oldham (1968) observed that their "western call type" (*R. blairi*) lacks oviducts, and that the "absence of vestigial oviducts seems absolute." I examined 79 males from Illinois, Indiana, Iowa, Kansas, Missouri, Oklahoma, Nebraska, New Mexico, and Texas that I judged to be of this species on the basis of the structure of their vocal sacs. All were without Mullerian ducts (Fig. 21). Two frogs from Nebraska which resemble *R. blairi* but possess oviducts may represent hybrids between this species and *R. pipiens*.

Males of *Rana utricularia* also usually fail to develop Mullerian ducts regardless of their size (Figs. 4 and 21). Only in peninsular Florida do these males develop Mullerian ducts, and males with ducts are more common there than those without them. Numerous authors have pointed out differences between leopard frogs from southern Florida and from northern Florida and the rest of the southeastern coastal plain. Springer (1938) and Neill (1958) commented on the

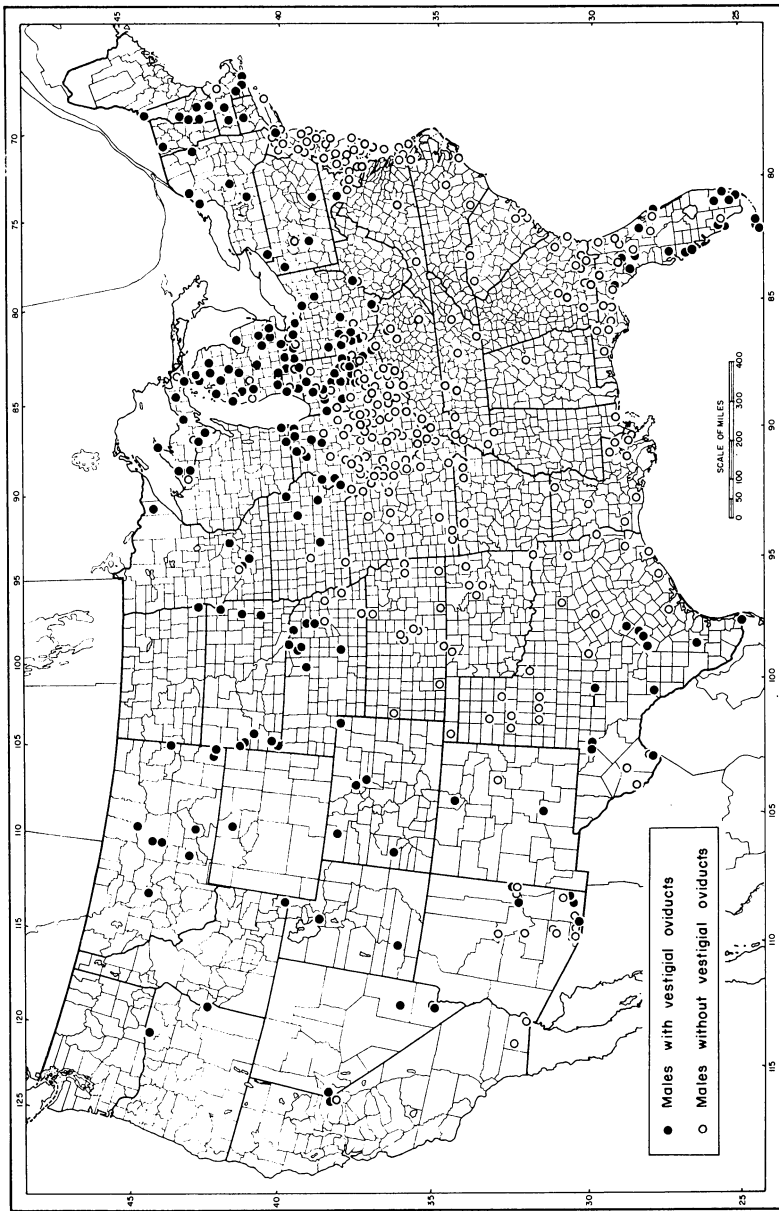


Fig. 21. Geographic distribution of leopard frog males in the United States with (solid dots) and without (open circles) vestigial oviducts. Each symbol represents from one to twenty frogs.



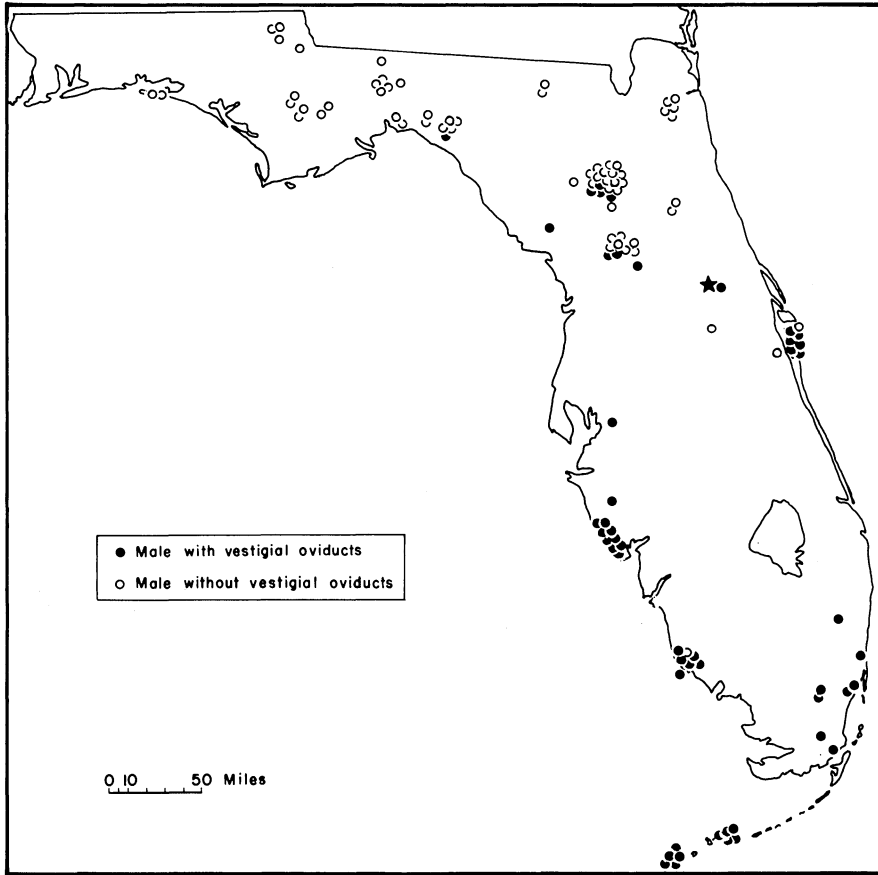


Fig. 22. Geographic distribution of leopard frogs in Florida with (solid dots) and without (open circles) vestigial oviducts. Each symbol represents one male. The star indicates the type locality of *Rana virescens sphenoccephala* Cope.

unusually large size of some southern Florida leopard frogs. Neill (1958) and Duellman and Schwartz (1958) described some of the differences in coloration of these frogs, and Moore (1944) pointed out that they characteristically have vestigial oviducts. Moore (1942) also showed that embryonic temperature tolerances and developmental rates are different for these south Florida leopard frogs.

The distribution of males in Florida with and without Mullerian ducts is shown in Figure 22. Each circle represents one male. When the snout-urostyle lengths of these males were compared it was found that the males with ducts were significantly larger ( $\bar{x} = 68.3$  mm) than those without them ( $\bar{x} = 54.8$  mm) ( $p < 0.001$ ). The only male from south of  $28^{\circ}$  North latitude that did not have Mullerian ducts, and was judged by the development of its external vocal sacs to be of breeding age, was from southeast of Naples in Collier County. It was 53.3 mm in snout-urostyle length and one of the smaller, but presumably adult,

males from this area. Five others from Collier County (all with oviducts) were 51.6-81.8 mm in snout-urostyle length.

Four other males from southern Florida were dissected because they had enlarged thumb pads. They were not included in the distribution map or in the analysis of size differences of oviduct-possessing and oviductless males because the lack of development of external vocal sacs indicated that they were probably immature. Three of the males (from Monroe and Dade counties) were 40.5-43.5 mm in snout-urostyle length. These males had neither internal nor external vocal sacs. The fourth male, from Collier County, was 51.7 mm long. It had Mullerian ducts and small internal vocal sacs though the external vocal sacs were not developed. The fact that of these four males (from an area where Mullerian ducts are usually found in adult males) the only one with Mullerian ducts is also the only one that has begun vocal sac development, lends support to the conclusion from the examination of sizes of *R. pipiens* males with and without Mullerian ducts that where they occur they may become more well-developed in older males. Further support for this idea comes from an examination of two small series of males from the region where males with and without Mullerian ducts are both common. Five males from Taylor County were dissected. The four which did not have Mullerian ducts were smaller than the one which did (54.3-55.8 mm compared with 57.1 mm snout-urostyle). Of a series of seven males from Brevard County the six with Mullerian ducts were larger (72.1-83.2 mm snout-urostyle) than the one without Mullerian ducts (61.1 mm snout-urostyle).

In *R. berlandieri* Mullerian ducts are usually, possibly always, present in adult males. This is the "southern call type" of Littlejohn and Oldham (1968) (see Fig. 21). These authors state that apparently all adult males of this call type have vestigial oviducts. I examined 27 leopard frog males from within the probable range of *R. berlandieri* in Texas that had vestigial oviducts. Five additional males did not have oviducts. Two Brewster County males had the discontinuous and displaced dorsolateral folds that are generally characteristic of *R. berlandieri* (Littlejohn and Oldham, 1968). One of these males, from Big Bend National Park, was one of a series of five specimens the rest of which had Mullerian ducts (three on both sides, one on only one side). The other specimen was from Paisano. Three males from Shafter, Presidio County, had continuous dorsolateral folds which were much shorter than usual. In this respect they resemble some of the leopard frogs from Arizona. None of the males examined by McAlister (1962) from Brewster and Presidio counties had oviducts. In contrast, he observed that males from the Stockton Plateau "occasionally possess oviducts." All the leopard frogs he examined from the plateau had displaced dorsolateral folds, while "one-fifth to one-quarter of the specimens in the Big Bend region had complete folds." Although no data are available on mating calls of frogs from this region, this morphological evidence suggests that at least some of the leopard frogs from the West Pecos region of Texas are distinct from *R. berlandieri*.

Brown (1958) discussed the distribution of oviduct-possessing and oviductless male leopard frogs as an example of a trait (presumably advantageous) originating in the center of a species' range and spreading from there toward the periphery. He supposed that the advantage of the oviductless condition might lie in developmental conservation. This view must be modified since the groups "at the periphery" that have vestigial oviducts are (except for the Florida populations of *R. utricularia*) reproductively isolated from those groups lacking oviducts. Furthermore, the oviductless populations in the central areas are reproductively isolated from some of the oviductless populations nearer the periphery. Some sort of developmental correlate of this trait, however, is suggested by the smaller average size of species lacking oviducts compared with ones possessing them and the fact that within species which show variation in this character the males with oviducts are of larger average size than males without them.

#### MULLERIAN DUCTS AND VOCAL SACS

Moore (1944) observed that in some parts of the United States males without external vocal sacs usually have oviducts and that males with external vocal sacs usually do not have oviducts. The confusion resulting from apparent lack of correspondence between type of vocal sac and presence or absence of oviducts in males from some other parts of the country was due to failure to discriminate among the various different modifications of the skin overlying the internal vocal sacs. When each of the several kinds of external vocal sacs is considered separately a very close correspondence is found. Males with one type of vocal sac are usually consistent in either possessing or lacking Mullerian ducts.

Moore (1944) says that males "from southern Illinois that lack oviducts may or may not have external vocal sacs." In Indiana the same is true, though males without oviducts usually have external vocal sacs. In Indiana and Illinois all males with external vocal sacs lacked oviducts. *Rana pipiens* males (which lack external vocal sacs) usually have oviducts, although some do not. *R. blairi* occurs in prairie habitats in central Illinois and west-central Indiana. These males were described by Moore as being without external vocal sacs. Immature *R. utricularia* males do not have external vocal sacs and, except in Florida, they do not have oviducts. It is possible that the males described by Moore from southern Illinois that lacked both external vocal sacs and oviducts were immature *R. utricularia*, but they were probably *R. blairi*.

#### TYMPANAL SIZE

There is some evidence of sexual dimorphism in tympanal size in southwestern frogs which have been considered to be members of the *R. pipiens* complex. The photographs of leopard frogs from Lakeside, Arizona, in Wright and Wright's (1949) discussion of the *R. pipiens*

complex show two kinds of leopard frogs from this area (in addition to the single individual of *R. pipiens*): those with large tympana (probably males) and those with small tympana (probably females). Wright and Wright also note (1949: 19) sexual dimorphism in tympanal size of *R. fisheri* and have photographs of a male and female that they identified as this species showing the larger tympanum of the male. The existence of sexual dimorphism in tympanal size in these frogs together with the evident differences in body shape (they are very broad-headed compared with other members of the *pipiens* complex) and the indistinctness of the dorsolateral folds suggest that they may be members of a different group, perhaps more closely allied to *R. tarahumarae* or *R. pretiosa* than to *R. pipiens*.

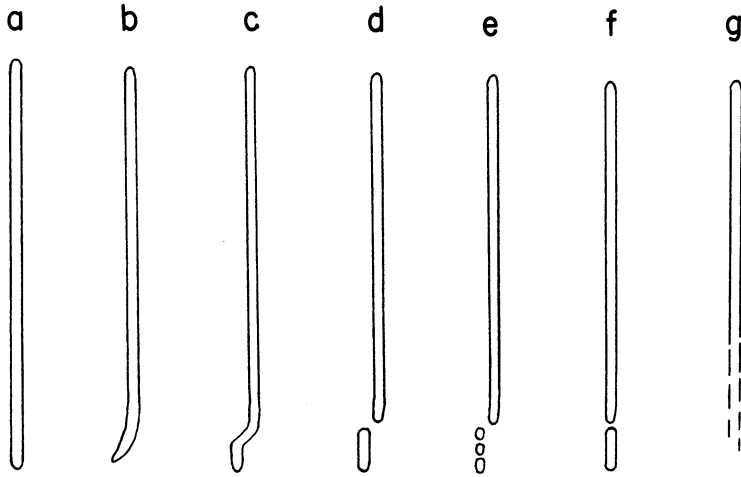
#### THUMB PADS

Populations apparently differ in the relative size of thumb pads of males, as has been noted previously (e.g., Moore, 1944). Such variation is particularly conspicuous in the southwestern United States where some small males have unusually large thumb pads. Although thumb pads were not measured on any frogs, I noticed unusually large thumb pads on eight of 31 males from Arizona (excluding *R. pipiens*). One of these males had vestigial oviducts; the other seven did not. No relationship between oviduct condition and thumb pad condition was evident in these males. The information available to me was not sufficient to determine whether there was any relationship between size of thumb pads and breeding condition in any of these frogs.

### VARIATION IN CHARACTERS FOUND IN BOTH SEXES

#### DORSOLATERAL FOLDS

Several authors (McAlister, 1962; Post and Pettus, 1966; Mecham, 1968; Littlejohn and Oldham, 1968) have recently commented on the occurrence of two types of dorsolateral folds in leopard frogs. The first type of fold (Fig. 23a) is continuous, extending in an unbroken straight line from just behind the eye to the area where the leg joins the body. The second type is discontinuous, being broken in about the posterior quarter of the body, and has the segment of the fold posterior to the break displaced medially. The displaced segment may itself be continuous (Fig. 23d) or a discontinuous series of dots (Fig. 23e). These are the most commonly observed types of dorsolateral folds in members of the *Rana pipiens* complex from the United States. As Figure 24 indicates, the geographic replacement of one of these types by the other is generally quite sharp. Only rarely are individuals of one type found within the range of the other. The regions where this replacement occurs correspond to the regions of replacement of one



### Types of Dorsolateral Folds

Fig. 23. Types of dorsolateral folds in leopard frogs. These are diagrammatic representations of right dorsolateral folds showing the major variations found in leopard frogs. Figure 23a is the "continuous, not displaced" type characteristic of *R. pipiens* and *R. utricularia*. Figure 23d is the "discontinuous, displaced" type characteristic of *R. blairi* and *R. berlandieri*. Figure 23g is characteristic of some leopard frogs from the southwestern United States (including the types of *R. onca* and *R. fisheri*). Figure 23e is characteristic of some other southwestern leopard frogs.

call type or vocal sac type by another, and (in some cases) of frogs with and without vestigial oviducts.

Several kinds of dorsolateral folds exist which seem to be intermediate to the two just described. In some frogs the posterior segment of the fold is deflected (Fig. 23b) or displaced (Fig. 23c) medially although it remains continuous with the anterior portion. Less frequently the posterior part is separated from the anterior part, but is not displaced from it (Fig. 23f). Although right and left dorsolateral folds are usually alike, all possible combinations have been observed.

Because frogs with these "intermediate" types or combinations of types of dorsolateral folds are found in scattered localities throughout the United States and are not markedly more prevalent in the areas of contact between the two more common forms it is unlikely that the apparent intermediacy is due entirely to hybridization between the two latter forms (see Appendix III).

In the southwestern United States leopard frogs with very indistinct dorsolateral folds are quite common. Although these folds are apparently continuous in some frogs and discontinuous in others, it is often impossible to place them in either category because, as in *R. clamitans*, the folds disappear entirely in the posterior half of the body.

There are some qualitative differences in the appearance of the dorsolateral folds, in addition to the ones already described, which

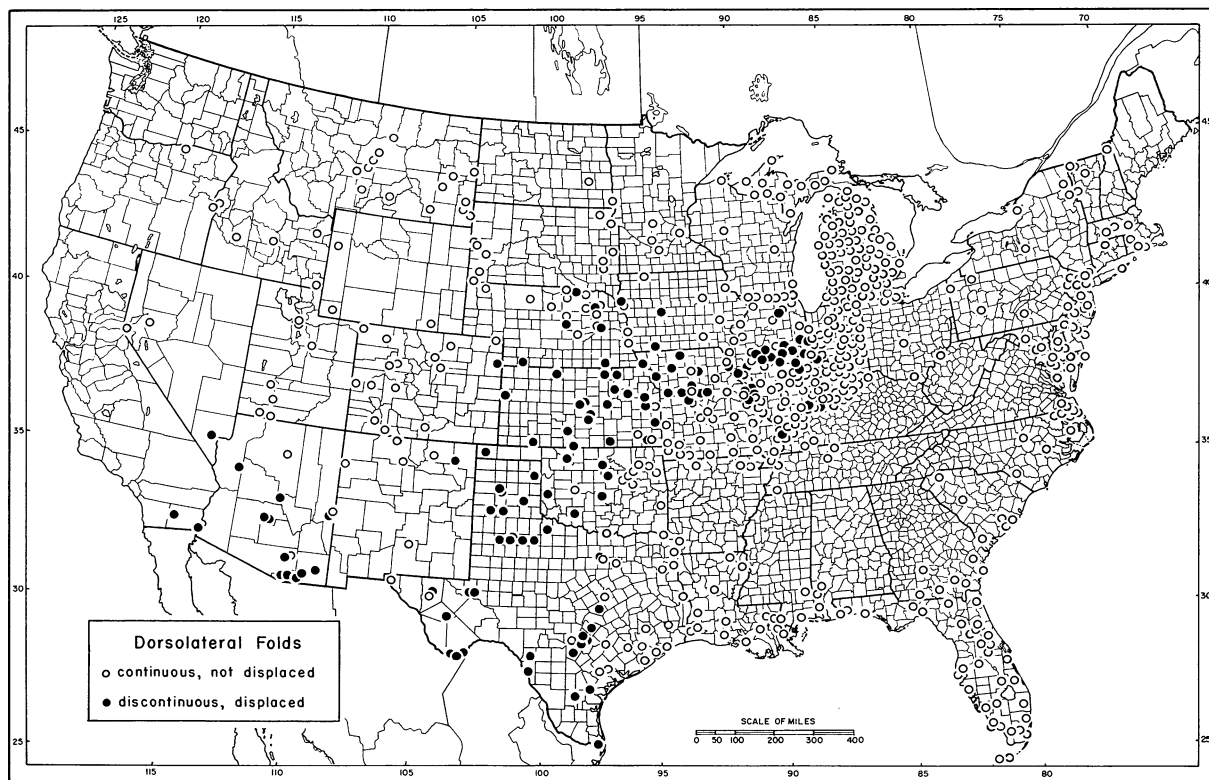


Fig. 24. Geographic distribution of leopard frogs with both dorsolateral folds continuous and not displaced (Fig. 23a) (open circles), or with both dorsolateral folds discontinuous and displaced (Figs. 23d and 23e) (solid dots). Each symbol represents from one to more than twenty frogs. A single frog from New Jersey had discontinuous, displaced dorsolateral folds on both sides. See also Figure 33 and Appendix III.

should be mentioned here. In *Rana pipiens* the dorsolateral folds are very broad and low and vary from being conspicuously to only slightly lighter in color than the background. In *R. blairi* they are usually quite conspicuous, being much lighter than the ground color, narrower than in *R. pipiens*, and more distinctly raised. In *R. utricularia* the dorsolateral folds are sometimes distinctly light and raised as in *R. blairi* and sometimes relatively low and broad as in *R. pipiens*. These differences, while distinctive, are sufficiently variable, at least in preserved material, that they cannot be used to separate one species from another.

#### TYMPANAL SPOTS

The presence or absence of a distinct white spot on the center of the tympanum has frequently been used as a taxonomic character in leopard frogs. Some authors have considered this to be the most distinctive difference between kinds of leopard frogs. Dickerson (1906), for example, gave the name *R. sphenoccephala* to any leopard frog with such white spots and the name *R. pipiens* to any leopard frog which did not have them. Wright and Wright (1949) characterized *R. p. sphenoccephala* as "like the meadow frog *R. p. pipiens*, but usually with a clear-cut, distinct white spot in the middle of the eardrum." Most authors have recognized that frogs with these spots were more common in some geographic regions than others whether or not they considered it to be a taxonomically important character.

Moore (1944) had some difficulty in classifying preserved specimens with respect to presence or absence of tympanal spots because of variations in the distinctness of the light area on the tympanum when present. He concluded that frogs with "sharply defined circular spots" were not restricted to the southern states, being present also in Indiana, New Jersey, and Kentucky; and that some frogs from the southern region may lack the spot entirely. I encountered a similar difficulty in my attempts to classify preserved specimens. In some frogs the white center is a very distinct spot while in others the center of the tympanum is lighter than the margin but the change in apparent amount of pigmentation is more gradual. In other frogs the center of the tympanum may have a distinctly lighter but very irregular blotchy area on it. In others the tympanum may be uniformly colored or, in fact, the center of the tympanum may be darker than the margin. Although I collected detailed data on the pigmentation patterns of right and left tympana, for the present analysis I have considered only two categories: (1) distinct white spot present on the center of the tympanum and (2) distinct white spot not present on the center of the tympanum. In the latter group I have included all frogs which have tympana with light centers, but no distinct spots, as well as the other categories (e.g., uniformly colored tympana, blotchy centers, etc.). The tympanal spot was considered to be "present" if it was present on

either tympanum, though the left and right tympana were usually similarly colored.

In Figure 25 the percentage of frogs with distinct white tympanal spots is given above the line and sample size below it. These proportions are given for each state except for those states in which samples include specimens of more than one species. In the latter cases species boundaries have been drawn using call data and distributions of vocal sac types and oviduct condition in male specimens. Where supplementary information could be derived from knowledge of dorsolateral fold condition in juveniles and females this was also used. Populations from an area were thus grouped according to other attributes of individuals in them. It is evident that in *R. pipiens* individuals with tympanal spots are extremely rare. One of 42 frogs from Iowa identified as *R. pipiens* had a distinct spot and one of 15 from South Dakota had such a spot. The frog from Iowa was a small juvenile (31.1 mm snout-urostyle) with only one light spot (the right tympanum had a hole in it). The frog from South Dakota was a male with Mullerian ducts, continuous dorsolateral folds, and without external vocal sacs. Possibly the presence of white tympanal spots in these two frogs (of 494 *R. pipiens* whose tympana were examined) is indicative of some introgression with *R. blairi* in Iowa and Nebraska.

Tympanal spots are present in most *R. utricularia*, being most common in members of this species from Florida. Ninety-one per cent of the 341 frogs I examined from Florida had tympanal spots. This is close to the 89% reported by Bresler (1964) for the 88 Florida leopard frogs he examined. Because the other four regions from which Bresler examined frogs are now known to have more than one species of leopard frog, his data from these regions are difficult to interpret. Only in Oklahoma, Kansas, Missouri, Arkansas, and Indiana do the proportions of these frogs with tympanal spots fall below 50%. It is not likely that this decrease in proportion of frogs with tympanal spots in the Mississippi River Valley is due to introgression with *R. pipiens* on the one hand or with *R. blairi* on the other hand since the proportions of frogs with tympanal spots are about the same in Indiana where *R. utricularia* is in contact with *R. pipiens*, and in Kansas and Oklahoma where *R. utricularia* is in contact with *R. blairi*. Only 23% of the *R. utricularia* from Arkansas had distinct tympanal spots.

*Rana blairi* also usually has distinct white tympanal spots. In *R. berlandieri* white tympanal spots are rare. They are also rare in leopard frogs from the southwestern United States, except in the non-*R. pipiens* males from Arizona that lack external vocal sacs. Eight of these latter frogs were examined and five had distinct white tympanal spots, resembling in this regard the frog identified by Wright and Wright (1949) as *R. onca*. The type of *R. onca* does not have distinct white



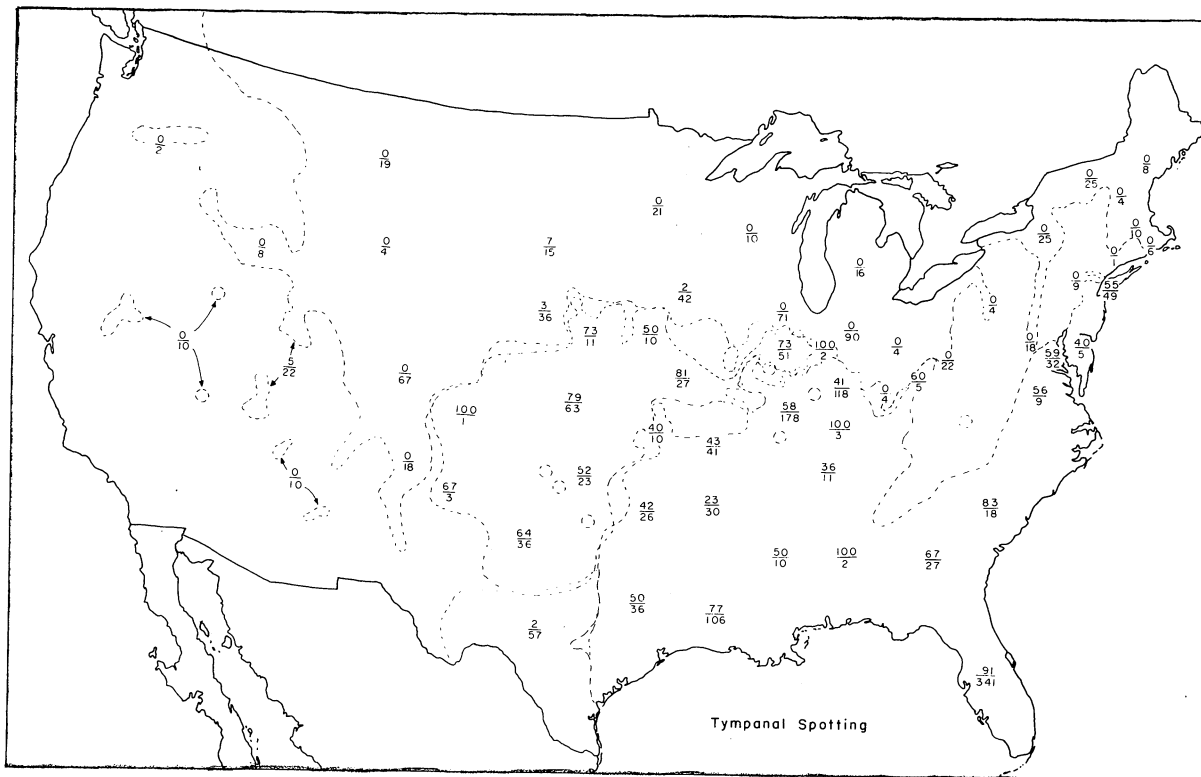


Fig. 25. Frequency of tympanal spotting in four species of leopard frogs. Species boundaries are derived from Figures 1, 4, 7, 9, and 34. The number above the line indicates the percentage of frogs (of that species for the state in which the fraction is located) possessing a distinct white spot on at least one tympanum. The number below the line is the sample size.

spots on the tympana. It is unlikely that these spots were lost due to fading, since the illustration of the type in the original description does not have white tympanal spots either.

#### DORSAL SPOT PATTERNING AND SNOUT SPOT

Although the presence or absence of a spot on the tip of the snout has never been used as a taxonomic character in leopard frogs, some authors have commented on the fact that this spot was commonly absent from snouts of southern leopard frogs and usually present on the snouts of northern leopard frogs. Smith (1961), for example, notes that among other characters "*R. p. sphenoccephala*" differs from "*R. p. pipiens*" in Illinois in lacking a dark snout spot. Although Moore (1944) considered geographic variation in the total numbers of dorsal spots, he did not make any distinctions with regard to their distribution on the dorsum, relative size, or coloration. Bresler (1964) analyzed differences in pigmentation characteristics of eyelids of leopard frogs from Ontario, Mexico, Utah, Illinois, and Florida, but did not discuss the presence or absence of spots on the snout.

The data on variation in proportions of animals with snout spots were handled like the data on tympanal spots. That is, the proportions were determined for each state except where more than one type of leopard frog occurred (based on call, vocal sac data, etc.). The same boundaries were used for lumping groups of these frogs as in tympanal spot data. The percentage of frogs from each sample possessing a snout spot is indicated by the number above the line in Figure 26. The sample size is indicated by the number below the line. For present purposes a frog was considered as having a spot on the snout if there was any dark pigment present on the snout. Occasionally this resulted in the inclusion of animals with only tiny specks of pigment, possibly less than a millimeter in diameter, as "having a spot."

The trend toward increasing prevalence of snout spots in leopard frogs as a group is not strictly related to latitude. Coastal plain populations of *R. utricularia*, for example, have a lower proportion of animals with snout spots than the Mississippi and Ohio River valley specimens regardless of latitude, although the northernmost samples from the coastal plain (New Jersey and New York) have the highest proportion of frogs with snout spots for coastal plain populations. On the other hand, much higher proportions of *R. blairi* have snout spots than *R. utricularia*, regardless of latitude. At least 75% of the *R. blairi* examined from any state had snout spots. Grouping samples of this species from all states, 145 of 162 specimens (89.5%) had snout spots.

In *Rana pipiens* the proportion of frogs with snout spots was quite variable. The overall proportion for New England, including Maine and New York, was 44% (37 of 84). Vermont was the only state in the United States, however, with a sample size greater than ten in which at least 50% of the frogs did not have snout spots. Maine, Massachusetts, and North Dakota, with sample sizes of four, ten, and four respectively,

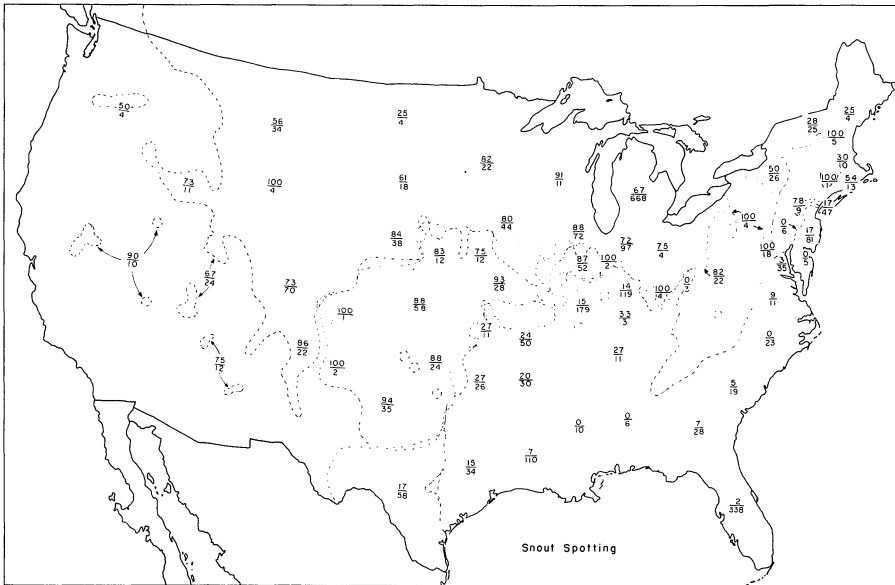


Fig. 26. Frequency of snout spotting in four species of leopard frogs. Species boundaries are derived from Figures 1, 4, 7, 9, and 34. The number above the line indicates the percentage of frogs (of that species for the state in which the fraction is located) possessing at least one spot on the tip of the snout. The sample size is indicated by the number below the line.

were the only other states with fewer than 50% of the *R. pipiens* without snout spots. In Michigan, where the sample size was considerably larger (668), 67% of the frogs examined had snout spots.

Like *R. utricularia* from the coastal plain, a very large proportion of the *R. berlandieri* had snout spots. *R. utricularia* is the only leopard frog which shows significant intraspecific variation in proportions of animals with snout spots and this is generally but not strictly related to latitude, with the most northern populations having the greatest frequency of snout spotting.

Schaaf and Smith (1970) recently noted a similar trend in *R. palustris* with regard to greater prevalence of snout spots in northern populations. Most populations of this species above the coastal plain boundary had "75% or more occurrence of a snout spot." The lowest values (25% or fewer) were reached in populations of the "Gulf Coastal Plain of Texas, Louisiana, and Arkansas, and northward in the Yazoo Basin and Mississippi River Valley to extreme southern Illinois." They suggested that the presence or absence of a dark snout spot was related to the heat budget of the frog. A large dark spot on the exposed upper surface of the snout, it was reasoned, "would enable the frog to gain radiant heat from the sun while its body was submerged in cold water [when the frog was floating at the water's surface]." They noted parallel examples from other frogs (including members of the *R. pipiens*

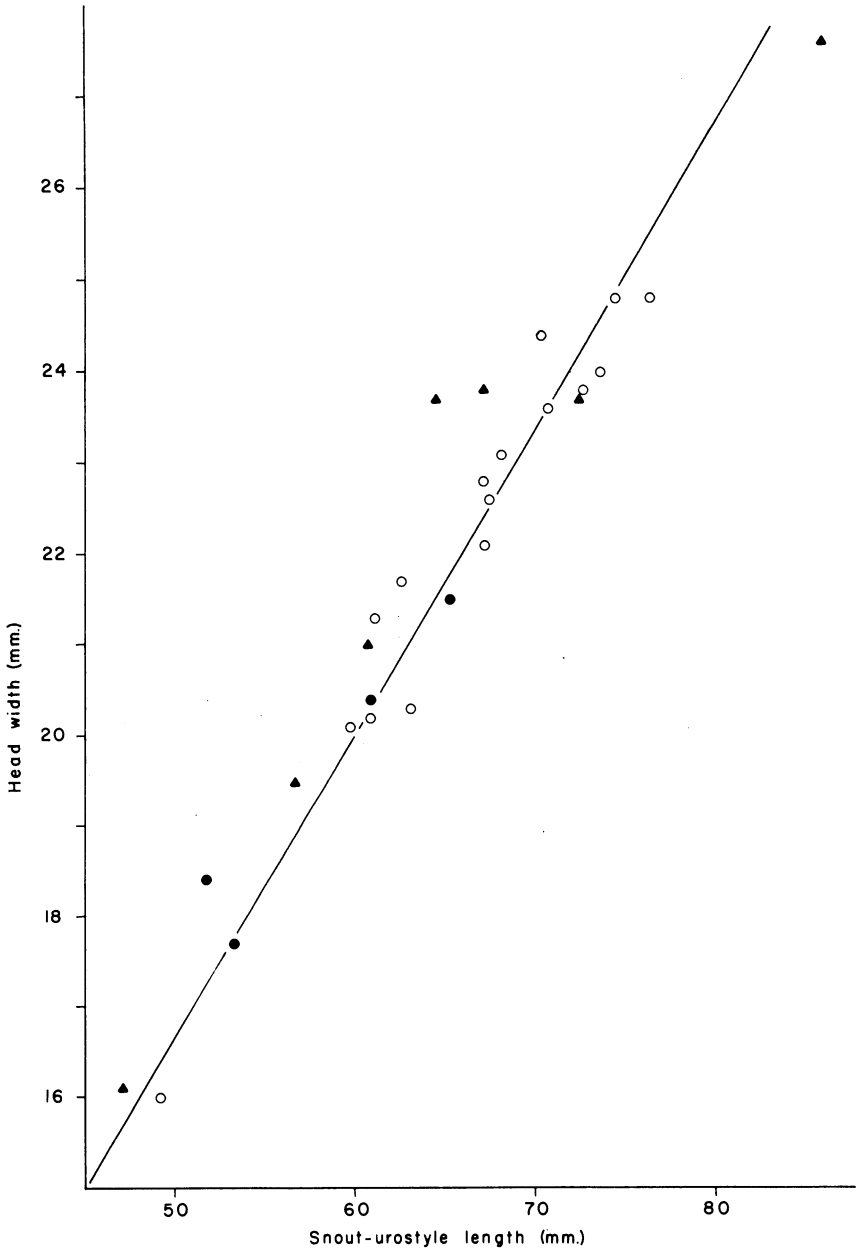


Fig. 27. Relationship between head width and snout-urostyle length for adult males of three species of leopard frog from Missouri and Iowa. Open circles indicate *R. pipiens*; solid triangles *R. blairi*; and solid dots *R. utricularia*. Symbols falling on the solid line represent frogs with snout-urostyle lengths equal to three times the head width, symbols falling below the line represent frogs with snout-urostyle lengths greater than three times the head width, and symbols falling above the line represent frogs with snout-urostyle lengths less than three times the head width.

complex) in which northern forms have more darkly pigmented dorsal surfaces.

Interestingly, the geographic trend with regard to snout spotting shown by *R. utricularia* closely parallels that in *R. palustris*. For example, in the Atlantic coastal plain low proportions of *R. palustris* with snout spots were found in eastern North Carolina, South Carolina, and the Del-Mar-Va peninsula (Delaware, Maryland, and Virginia) while the other states had higher proportions. In *R. utricularia*, Delaware, North Carolina, Maryland, and South Carolina (in order of increasing prevalence of snout spotting) had the lowest proportions of animals with snout spots. As in *R. palustris*, the values for New Jersey, New York, and Virginia were higher. In the central part of the United States the picture is somewhat similar with higher values for *R. utricularia* from Kansas, Oklahoma, Missouri, Arkansas, Illinois, Tennessee, and Kentucky and lower values for Texas, Louisiana, Mississippi, and Indiana.

Schaaf and Smith (1970) also noted the prevalence of transverse fusion of dorsal spots in *R. palustris* from Texas. Such transverse fusion of dorsal spots has been observed in occasional specimens of *R. berlandieri* from Texas and in other leopard frogs from Central America.

#### VENTRAL MELANISM

In their analysis of ventral melanism in *Rana berlandieri*, Sanders and Smith (1971) remarked that while it is common in this species it is rare or absent in other leopard frogs in the United States. They separated North American leopard frogs into two groups on the basis of this feature and suggested that the leopard frogs "of the United States should be referred to as *Rana pipiens* with its subspecies and those of Mexico as *Rana berlandieri* with its subspecies."

Although Sanders and Smith state that, as far as they know, ventral pigmentation similar to that of *Rana berlandieri* occurs rarely among *Rana pipiens* in other parts of the United States and "nowhere to the extent that it does in the Mexican populations of leopard frogs," Duellman and Schwartz (1958) found that in specimens from Marco Island (Collier County, Florida) the "belly is a dirty white and mottled with dark brown or black in the throat region." In several series of specimens from Big Pine Key, Little Torch Key, and Key West (Monroe County, Florida) the "ventral color is a grayish to brownish cream, the throat and flanks often being heavily mottled with dark gray or black." I have seen many specimens from other localities in Florida (Alachua, Collier, Dade, Hendry, Hillsboro, Monroe, Putnam, Taylor, Volusia, and Walton counties) which have dark pigment on the ventral surfaces. The extent of melanism varies from entirely dark to just some dusky coloration at the back of the throat (across the anterior pectoral

region). As Sanders and Smith (1971) and others (e.g., Schaaf and Smith, 1970) have noted, this dark pigmentation may frequently be overlooked because the melanophores often contract when the frogs are killed and fixed.

Although Florida is the only area where ventral melanism was found to be fairly common in numerous populations of what Sanders and Smith referred to as "*Rana pipiens* and its subspecies," I have observed at least some dark coloration on venters of specimens from each of the other two species in this group (excluding the southwestern United States) from various localities in the United States.

Ventral melanism is very rare in *R. pipiens*. In the few specimens (from Woodbury County, Iowa) in which any such coloration was noted, it was restricted to the sides of the throat and to the back of the throat as in the kandiyohi mutant. These specimens are from localities where *R. pipiens* is sympatric with *R. blairi* and may reflect alleles which have been incorporated into *R. pipiens* populations as a result of hybridization with that species. Knowledge that the burnsi and kandiyohi mutant forms of *Rana pipiens* "occasionally... have some spotting on the throat of pectoral areas" (Sanders and Smith, 1971), however, suggests that genes responsible for ventral melanism in *R. pipiens* may be of independent origin.

Ventral melanism was observed in specimens of *R. blairi* from Nebraska, Missouri, Kansas, and Iowa. There is considerable individual variation in amount and distribution of dark pigment on the venter. In some frogs it is evenly or blotchily distributed on the lower lip only, on others the pectoral area is dark as well, while in others the entire throat is more or less uniformly covered with grey to dark blotches.

Ventral melanism is evidently uncommon in most populations of *R. utricularia* except those mentioned above from southern Florida. My statements regarding lack of ventral melanism in a group of frogs, however, are not as positive as those regarding its presence since in most cases special mention was made of light venters on frogs only when I happened to notice a frog or group of frogs with dark pigment on the venters.

In addition to the frogs mentioned above several specimens from Arizona had dark pigment on their venters. Duellman (1955) reported leopard frogs from Santa Cruz and Cochise counties in Arizona which had venters that were "brownish or grayish, darker under the thighs and throat than on the belly." He also noted that juveniles and small adults are not so dark and have a more distinct dorsal pattern. The geographic variation in size of adults, correlated with other characters like condition of dorsolateral folds, vocal sacs, and vestigial oviducts, however, suggests that his small adults may have been another species. These frogs from Arizona with dark venters would probably be put into the group of *R. berlandieri* and its "subspecies" by Sanders and Smith, but the other leopard frogs from the United States that I have mentioned above probably would not.

The work of Schaaf and Smith (1970) on geographic variation in *R. palustris* suggests that ventral melanism might be selected for in local populations living in certain habitats (for example, black-water swamps of the Atlantic coastal plain) while being selected against in other habitats within a single species' range.

Whether any of the above mentioned frogs (*R. pipiens*, etc.) exhibit facultative melanism of the sort noted by Sanders and Smith for *R. berlandieri*, in which melanophores expand when the frog is kept in the dark for a period of time, is not known. None of these specimens were examined for the presence of tiny specks representing contracted melanophores.

#### GEOGRAPHIC VARIATION IN BODY PROPORTIONS

In his description of *Rana virescens brachycephala* (= *R. pipiens*) Cope (1889) indicated that it was a more broad-headed form than *R. v. virescens* (= *R. utricularia*). Since that time most authors who have compared northern and southern populations of leopard frogs have commented that southern ones usually have narrower, more pointed heads and relatively longer legs than northern ones.

In his analysis of geographic variation Moore (1944) compared certain body proportions (body/tibia length; tibia/leg length; foot/leg length; body/head length; and head width/head length ratios) for 11 "populations" of leopard frogs. Seven of these samples contained only one species. The remaining four may have contained two (and one may even have contained three) species. His data show that some widely separated populations are significantly different in some body proportions. Other populations (or other ratios for the same populations), however, are not. Moore attached considerable importance to these observations and concluded that: "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 a adequate basis for separating the meadow frogs of eastern North America into either species or subspecies."

I measured several body parts of *R. blairi*, *R. pipiens*, and *R. utricularia* from Iowa, Missouri, Indiana, and Florida. For the Indiana frogs snout-urostyle length, head length, and head width were measured. Head length was measured from the tip of the snout to the posterior margin of the tympanum, along mid-line of the body, and head width was measured at the posterior margin of the tympanum. For the other states right tibial length was measured as well. Although measurements were made on adult males and females and on immatures I have presented data only for adult males and only for the snout-urostyle length/head width ratio. Figure 27 shows the relationship between these lengths for all three species from Iowa and Missouri and Figure 28 shows the relationship for *R. pipiens* and *R. utricularia* from Indiana. In Figure 29 I have shown the same information for *R.*

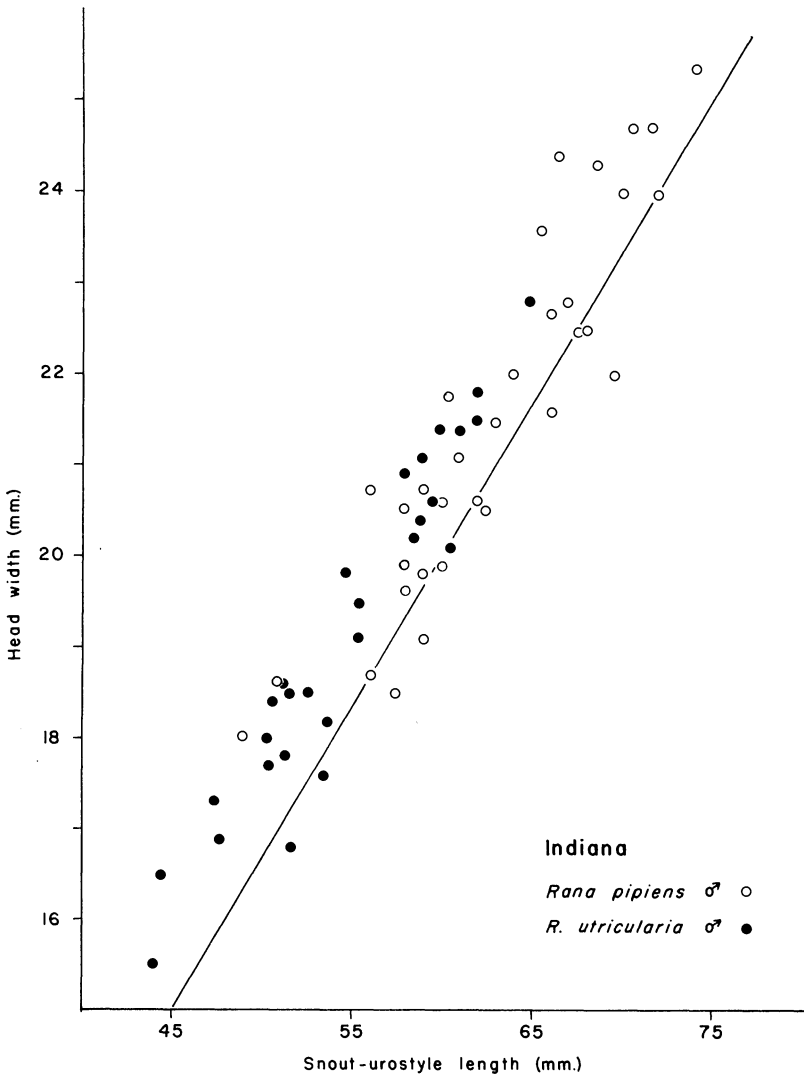


Fig. 28. Relationship between head width and snout-urostyle length in adult male *R. pipiens* and *R. utricularia* from Indiana. Open circles indicate *R. pipiens*; solid circles indicate *R. utricularia*. Points falling on the solid line indicate specimens with snout-urostyle lengths equal to three times the head width.

*utricularia* males from Florida with and without vestigial oviducts. Points falling precisely on the lines in these figures represent frogs with snout-urostyle lengths exactly equal to three times the head width. Although comparisons of proportions of points falling on or below the line for these groups suggest that regression lines might be different among them, it is clear that such information cannot be used in separating species. These results emphasize Moore's conclusions regarding body proportions of leopard frogs and I have presented them to



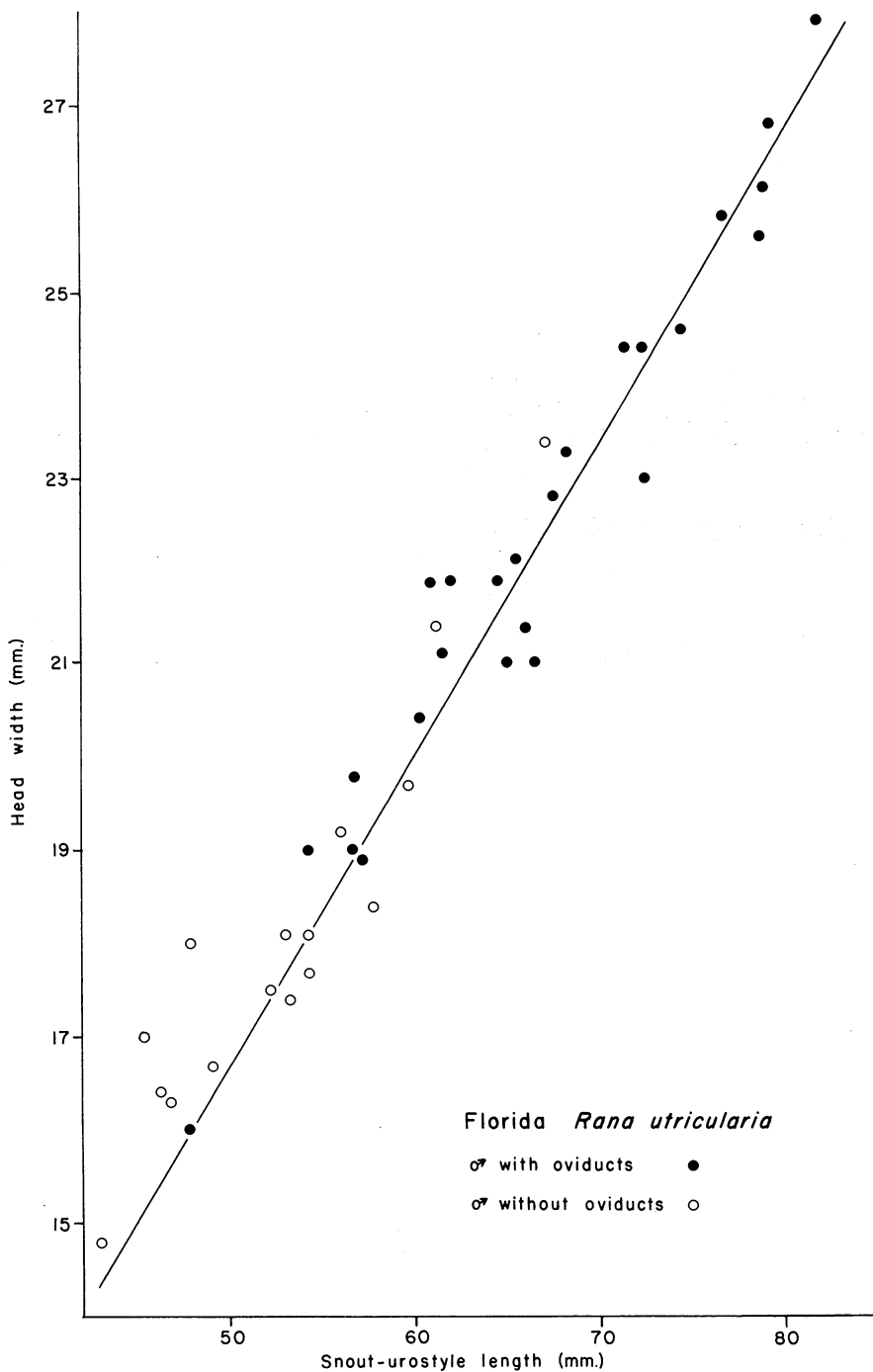


Fig. 29. Relationship between head width and snout-urostyle length for adult male *R. utricularia* from Florida. Solid circles indicate males with oviducts; open circles males without oviducts. Symbols falling on the solid line represent frogs with snout-urostyle lengths equal to three times the head width.

show that changes in body proportions from north to south are probably gradual and, at any rate, not clearly related to the fact that distinct species are involved.

#### VARIATION IN OTHER MORPHOLOGICAL CHARACTERS

There is additional interspecific variation in wartiness of the skin and apparently in bladder size, bladders of *R. blairi* being more "muscular" and unusually large compared with *R. utricularia* from the same state. These two facts are probably related to the differences in habitat of *R. blairi*, differences which are reflected in distinct aspects of development, life history, and behavior of adults and young of this species (some of which I have summarized later, pp. 93-95).

#### VARIATION IN LEOPARD FROGS FROM THE SOUTHWEST

The general aridity of the southwestern United States in Recent times presents special problems in trying to resolve relationships of populations of any aquatic or semi-aquatic animals in this region. Since leopard frogs in the desert are probably restricted to places with more or less permanent water, they have presumably been fractioned sometime since late Pleistocene into many isolated populations among which there is little opportunity for gene exchange. There is practically no information presently available about the calls of leopard frogs from the Southwest and what little there is is not correlated with specimens. Consequently the morphological data which I have accumulated about these frogs are more difficult to evaluate than in cases where such call data are available. In spite of such problems these morphological data, considered in the light of published information about these frogs, indicate that there are probably at least three kinds of leopard frogs in the Southwest in addition to *R. pipiens* and *R. berlandieri* (see Table 2).

The first report of different forms of leopard frogs occurring in nearby areas in the Southwest was that of Stejneger (1893) who reported *R. pipiens* and a new species, *R. fisheri* (= *R. onca*), from southern Nevada. Wright and Wright (1949) later reported two very different-looking kinds of leopard frogs from Lakeside, in eastern Arizona. Based on their photographs it is clear that one of these frogs was *R. pipiens*, the same species found throughout the Rocky Mountains and the northern part of the United States. The other is evidently a distinct, probably unnamed, species. Mecham (1968) presented information on differences in coloration and morphology of frogs from several nearby localities; he concluded from these data that there were two forms, acting like distinct species, and referred to one of them as the "northern" form and the other as the "southern" form. From the photographs and other information presented by Mecham it is evident

that his northern form, like one of the species illustrated by Wright and Wright, is *R. pipiens*.

In the most recent study of southwestern leopard frogs Platz and Platz (1973) presented evidence, primarily of differences in the electrophoretic mobility of hemoglobins, relating to the three largely allopatric groups of populations in southeastern Arizona. Although mating calls were not described, each form distinguishable by its hemoglobin evidently had a distinct call which could "be readily differentiated by ear alone" by the authors. Thus each form almost certainly represents a distinct species. Certain features of morphology and coloration of these frogs were also described briefly. The "northern" form of Platz and Platz, corresponding to the "northern" form of Mecham, is *R. pipiens* and will not be discussed further here. Although the data for calls were not presented, a comparison of distributions of the "lowland" and "southern" forms of Platz and Platz with my data on morphological variation in leopard frogs (excluding *R. pipiens*) from the same regions contributes some additional information on morphological attributes of these forms and indicates the persistence of some significant geographic variation.

Males of the lowland form do not have oviducts (Fig. 30). Of the six males with southern type coloration examined by Mecham, only one had oviducts. Because this male's body proportions fell within the limits shown by *R. pipiens*, Mecham suspected that it was a hybrid between *R. pipiens* and the southern form. Platz and Platz (op. cit.) note that males of the southern form may or may not have oviducts. Although they do not specify whether males with oviducts occur in both allopatric and sympatric populations (with regard to *R. pipiens*) my observations suggest this is so. Some males with southern type coloration from Cochise County in extreme southeastern Arizona have oviducts, but the nearest localities from which I have seen *R. pipiens* males are about 95 miles from Cochise County (Appendix I), suggesting that at least some southern-type males with oviducts are not of hybrid origin.

Although Platz and Platz did not mention variation in vocal sacs of males, comparison of geographic distributions of their lowland and southern forms with those of males with and without external vocal sacs indicates that males of the lowland form do not have external vocal sacs (Fig. 31). The only males from Arizona with external vocal sacs come from within the range of the southern form. A few males apparently without external vocal sacs were also seen from this area. These may represent young males of the southern species.

So few specimens with external vocal sacs were seen from the Southwest that it is difficult to determine the full extent and significance of variation in these structures. I will briefly describe some of these variations, however, because differences in the structure of external vocal sacs have been so useful in distinguishing other members

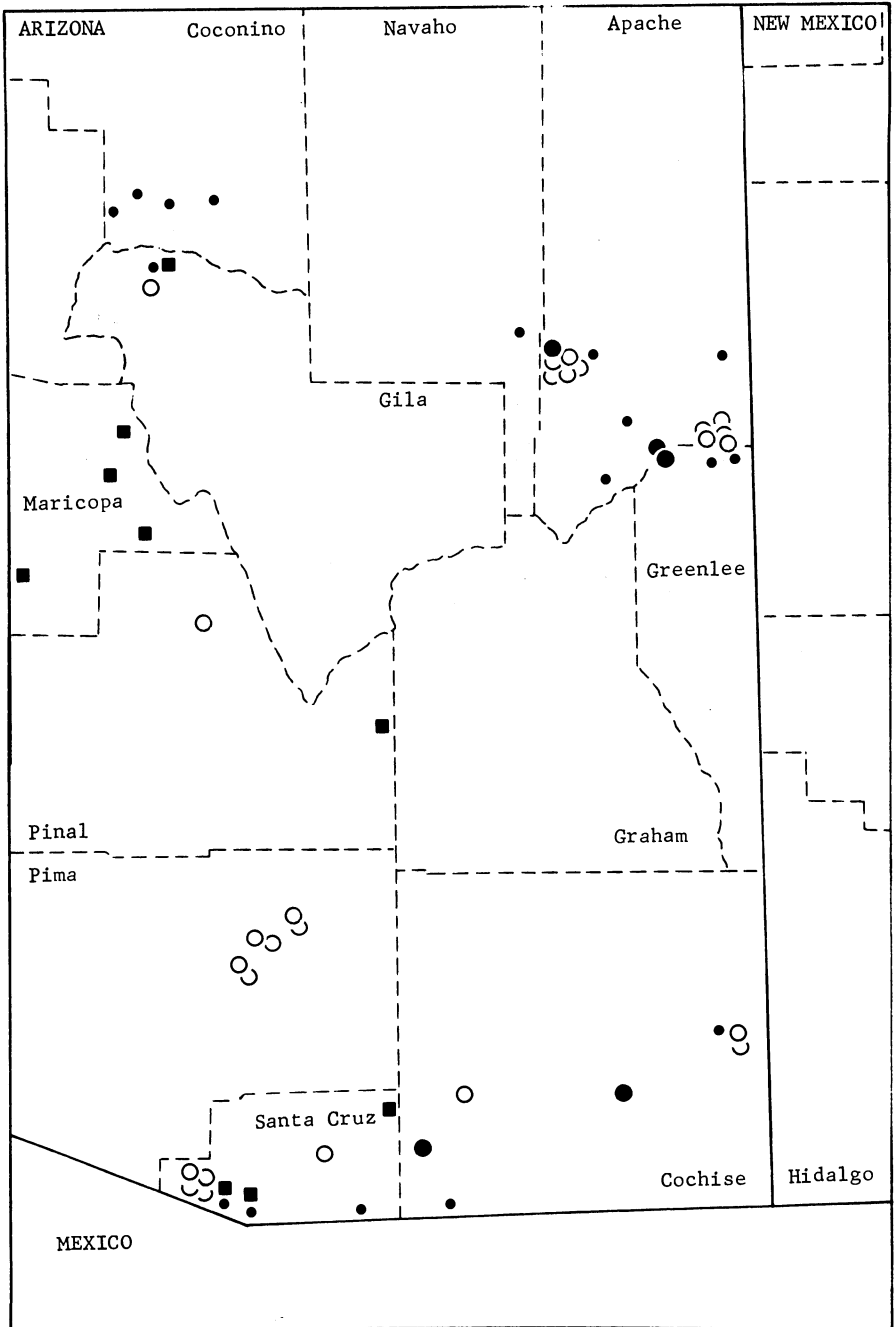


Fig. 30. Vestigial oviducts of male leopard frogs (excluding *R. pipiens*) from southeastern Arizona. Open circles indicate males lacking oviducts; large dots indicate males with oviducts. These data include information for leopard frogs reported by Meham (1968). Other symbols indicate localities for two forms distinguishable from one another and from a third form (= *R. pipiens*) on the basis of differential electrophoretic mobility of their hemoglobins (Platz and Platz, 1973): small dots indicate localities where the "southern" form was collected; squares indicate localities where the "lowland" form was collected.

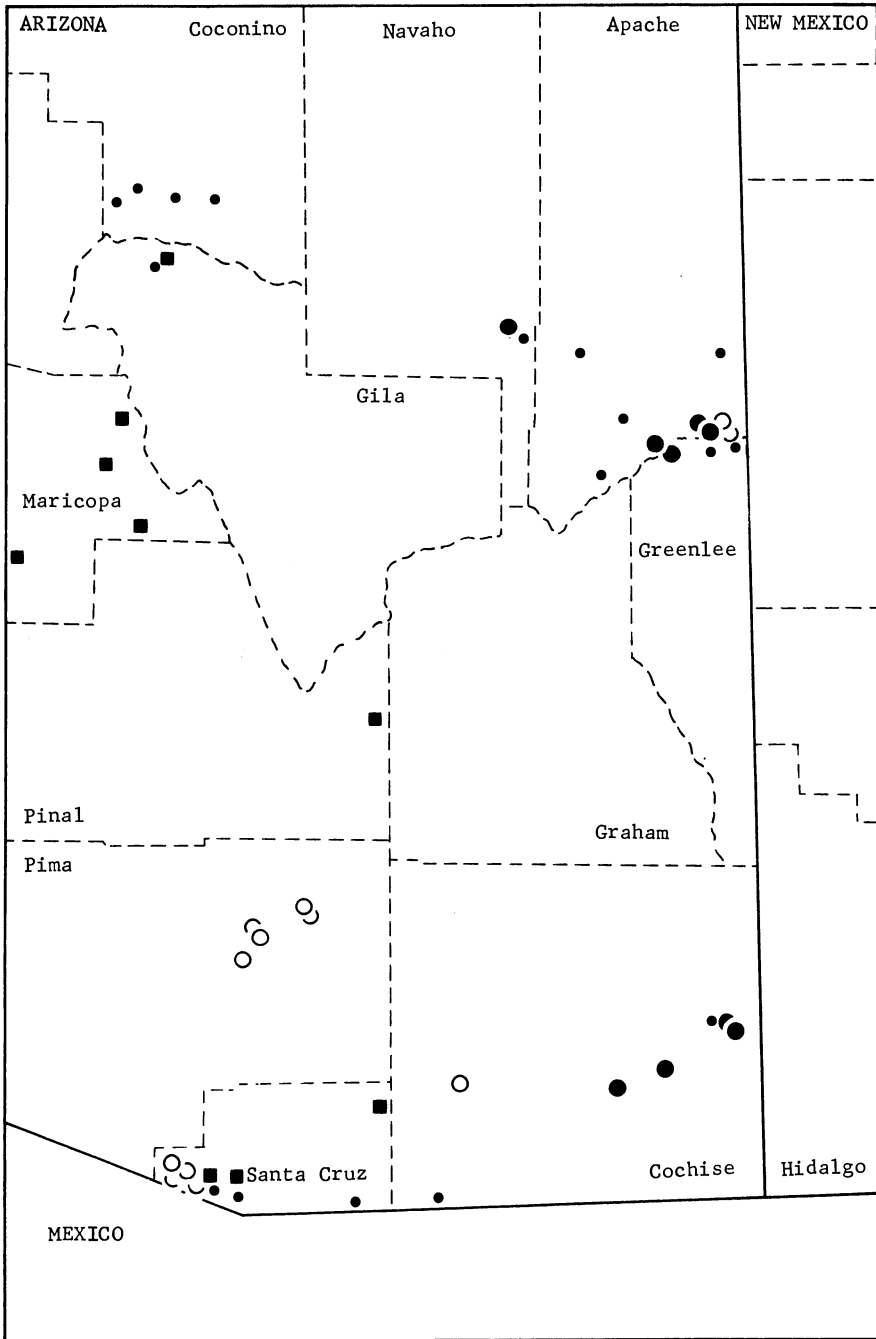


Fig. 31. Vocal sacs of male leopard frogs (excluding *R. pipiens*) from southeastern Arizona. Open circles indicate adult males in which there was no evidence of external vocal sacs; large dots indicate males with external vocal sacs. Some variation in the structure of external vocal sacs not indicated here is discussed in the text. Small dots indicate localities where the "southern" form was collected by Platz and Platz (1973); squares indicate localities where the "lowland" form was collected.

of the *R. pipiens* complex. In some of the frogs the vocal sacs were very distinctly spherical, about the size and shape of a large pea. In other frogs, although the vocal sacs were definitely external they were relatively smaller with grooves or striations on them and were tucked or folded in. In several others, though the skin overlying the vocal sacs was distinctly differentiated from the surrounding skin, there was little or no expansion of this skin into a sac.

Males of the lowland form are evidently much smaller than southern males (Figs. 31, 32). Males of the lowland form in general are less than 60 mm in snout-urostyle length while those from within the range of the southern form are generally greater than 60 mm in snout-urostyle length. This distinctive difference in size of adult males is interesting in terms of my discussion of life history variation in leopard frogs (pp. 91-100). The smaller species evidently has two breeding seasons per year (with individuals breeding during both seasons?) while the larger species has only one breeding season per year (Platz and Platz, 1973).

Variation in appearance of dorsolateral folds of these frogs is considerable (Fig. 33). A number from within the range of the lowland form have dorsolateral folds that are discontinuous and displaced, like those characteristic of *R. blairi* and *R. berlandieri*. The displaced portion is itself a discontinuous sequence of dots (Fig. 23e), however, a relatively rare condition in the latter two species. Frogs from within the range of the southern form, on the other hand, had dorsolateral folds that were very indistinct. In some cases they were discontinuous and displaced, but in other cases they were so indistinct that it was impossible to determine. Some of the southeastern Arizona leopard frogs had dorsolateral folds that were continuous, but shorter than usual, as if the displaced portion of a discontinuous dorsolateral fold had been deleted.

The few male specimens seen from southern California, southern Nevada, and west Texas (not *R. pipiens* and probably not *R. berlandieri*) are nearly all without oviducts. A single specimen from southern Nevada does, however, have oviducts. Some west Texas males not only lacked oviducts but had external vocal sacs sufficiently different from those of typical *R. berlandieri* to suggest they may be members of a different species.

## INTERSPECIFIC DISTRIBUTIONAL RELATIONSHIPS

### PARAPATRY

The most striking feature of the distributional relationships of members of the *Rana pipiens* complex in the United States is their essentially contiguous geographic ranges (Figs. 1 and 9; 4 and 9), with populations at the periphery of a species' range being in general

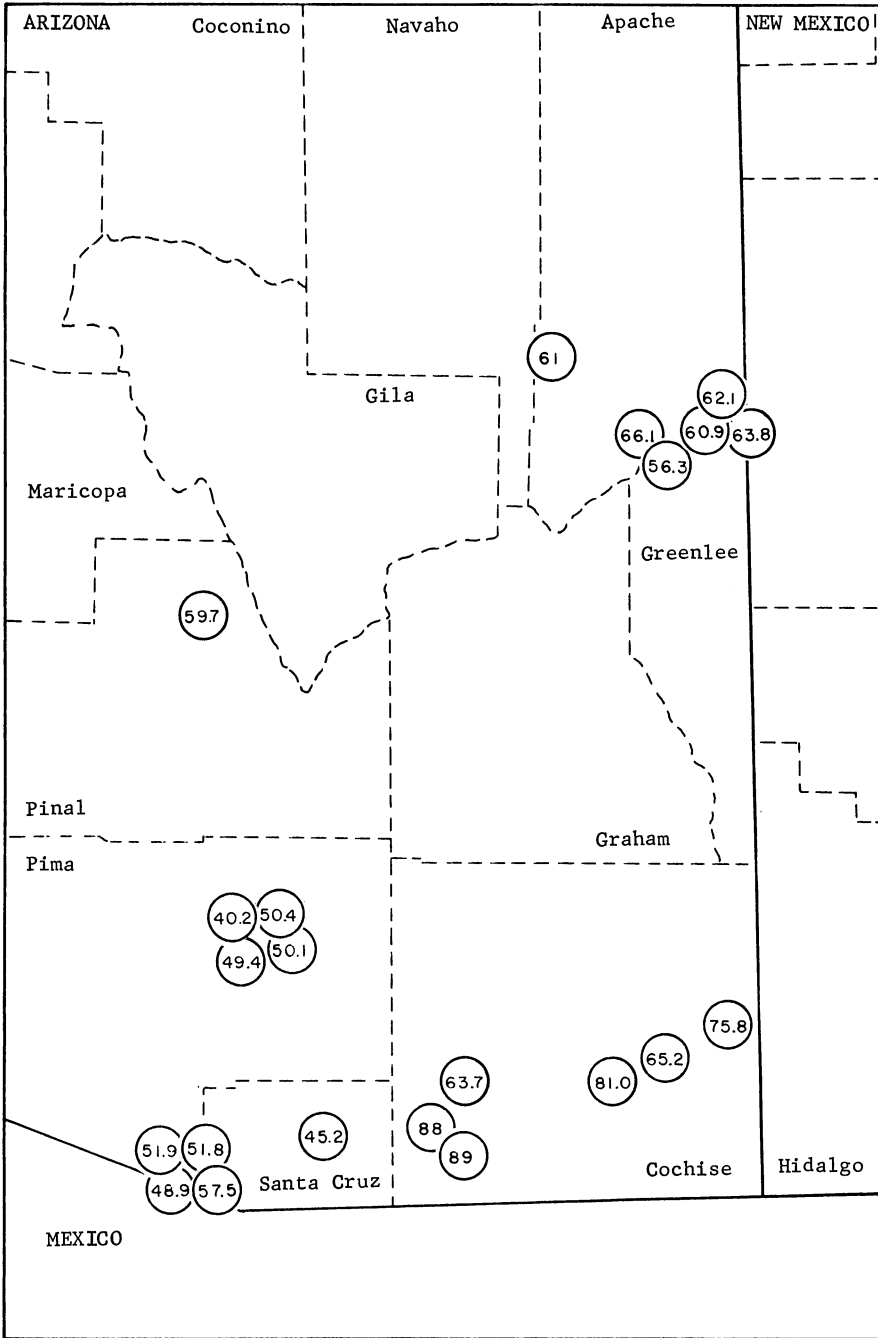


Fig. 32. Snout-urostyle lengths (mm) of 22 adult male leopard frogs (excluding *R. pipiens*) from southeastern Arizona. These measurements include snout-urostyle lengths reported for males by Wright and Wright (1949) and Mecham (1968). All other measurements are from museum specimens (localities listed in Appendix I).

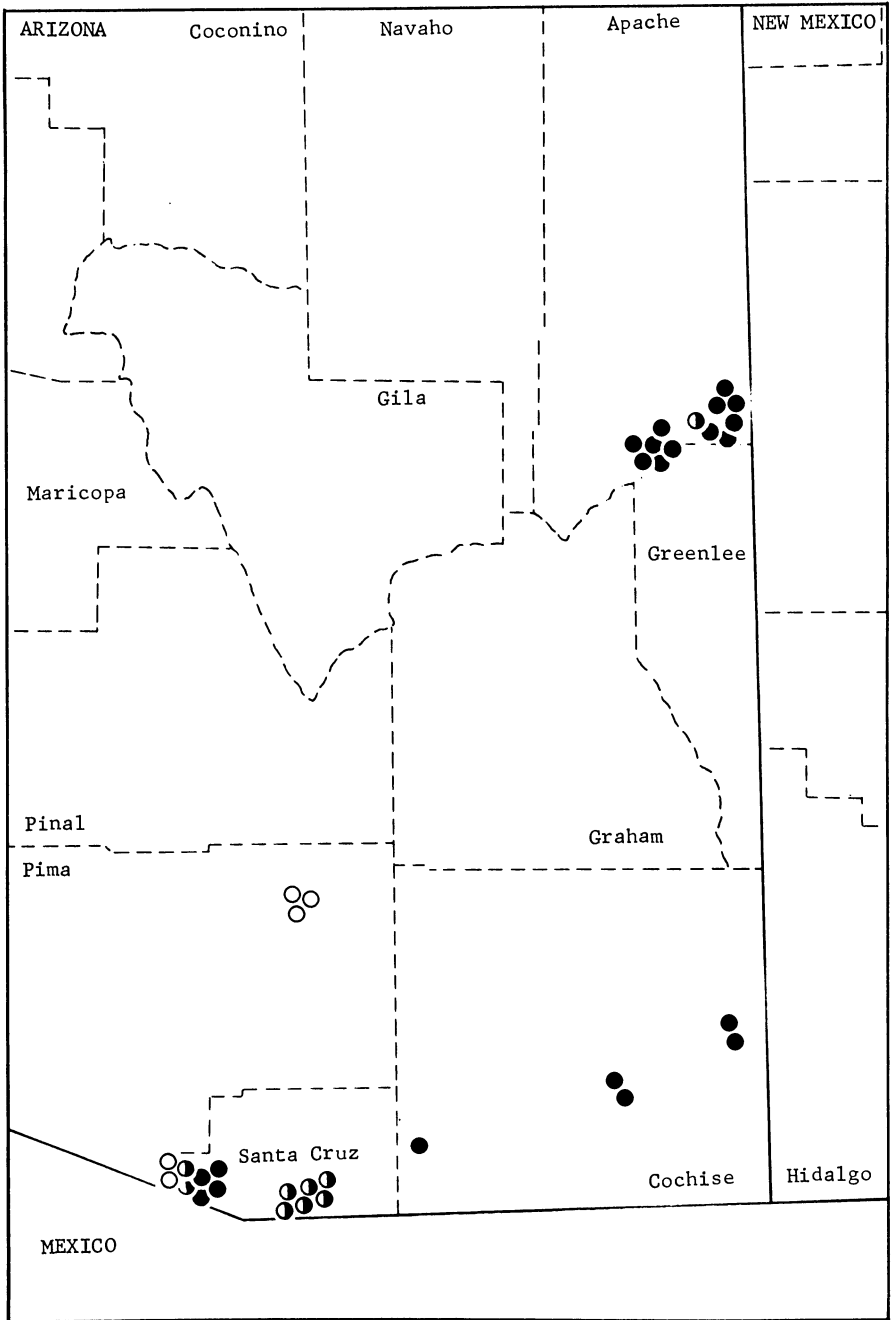


Fig. 33. Dorsolateral folds of leopard frogs (excluding *R. pipiens*) from southeastern Arizona. Included are data for all ages and both sexes. Open circles indicate specimens having discontinuous, displaced dorsolateral folds in which the displaced part is a sequence of dots (Fig. 23e); solid dots indicate specimens with indistinct dorsolateral folds which are either discontinuous and displaced or so indistinct that I could not tell. Half-colored circles indicate frogs with continuous dorsolateral folds that were unusually short (and either distinct or indistinct).



sympatric with populations of another member of the species complex. Areas of contact between the following pairs of leopard frog species have been investigated in the field: *Rana utricularia* and *R. berlandieri* (Littlejohn and Oldham, 1968); *R. utricularia* and *R. blairi* (Bragg, 1950c; Littlejohn and Oldham, 1968; Brown and Brown, 1972); *R. pipiens* and *R. blairi* (Bragg, 1950c; Post and Pettus, 1967; Pettus and Post, 1969; Brown and Brown, 1972); *R. berlandieri* and *R. blairi* (Littlejohn and Oldham, 1968; Platz, 1972); *R. pipiens* and other members of the *R. pipiens* complex (Mecham, 1968; Platz and Platz, 1973); and *R. pipiens* and *R. utricularia* (present study). In all of the above cases where the actual extent of geographic overlap was determined it was found to be very small relative to the rest of the species' ranges, fewer than 15 miles in most cases. Evidence from specimens further supports the conclusion that contiguous, narrowly overlapping ranges are characteristic of species in the *Rana pipiens* complex. Although I have discovered some exceptions based on data from museum specimens, these are relatively few in number and will be considered in detail later (pp. 74-78).

Although the term "parapatry" has been used to refer to contiguous ranges of different taxa, the term has not been used consistently by all authors and the debate about which kinds of distributional relationships ought to be referred to as parapatric has resulted in some confusion. Key (1968) has stated that parapatry is a special case of sympatry in which overlap along lines of contact between two forms is narrow or sporadic. He apparently feels that species cannot in general possess strictly contiguous ranges, but that the term might be used to describe the "case where special circumstances [direct competition] greatly restrict the zone of overlap" between two species. Smith (1969), who apparently introduced the term parapatry, stated that "parapatry never exists between two species: their geographic relationships must be either sympatric or dichopatric [= allopatric?] . . ." In spite of such conflicting opinions in the literature regarding application of this term, I have used it to refer to the predominant interspecific distributional relationships among members of the *R. pipiens* complex for several reasons.

Most important is the fact that these essentially contiguous ranges, with narrow sympatry at the periphery, mean that the limits of distribution of one member of any species pair are more clearly related to the presence of the other species than to any other feature of the physical or biotic environment, suggesting that significant, special interspecific interactions are involved in the biology of these species. Why these distributional relationships should be so nearly universal in the *R. pipiens* complex is a problem of major interest which may hold the key to understanding the history of speciation in this group. Failure to discriminate the special type and extent of sympatry involved among the members of this species complex would obscure this very important feature of their distributional and biological relationships. A special

term is therefore useful because it focusses attention on an important phenomenon and also because it makes discussions of that phenomenon less cumbersome. Some authors (e.g., Littlejohn, 1969) have apparently used the term "contact sympatry" to refer to this sort of geographic distribution of related species. I have used the term "parapatry" to suggest extensive contiguity of species' ranges, as among members of the *R. pipiens* complex, while restricting "contact sympatry" to situations where contact is known to be sporadic or in which the species' ranges or the nature of interactions among species are not well known. As a practical criterion one might use parapatry to describe contiguous, narrowly overlapping distributions in which the overlap is so narrow that maps of two different scales are required to show adequately both the overlap and the total ranges of the forms.

Parapatry between species has been reported in numerous other groups of animals. In many cases the two species involved appear to be cognate (that is, most recently diverged) species; but in others the parapatry involves species pairs that are not thought to be closely related. One such case of special interest here is that reported by Dumas (1964) for *Rana pipiens* and the western spotted frog, *Rana pretiosa*, in the Pacific Northwest. According to Dumas these two species differ slightly in their tolerances of extremes of temperature and relative humidity. Larval competition experiments led Dumas to conclude that the essentially allopatric ranges of these species were "delimited primarily by interspecific competition with *pipiens* replacing *pretiosa* owing mainly to differential tadpole mortality in ponds occupied by both species." Relative differences in mortality are even greater than Dumas' figures indicate.

The history of interactions of these two species is not well understood, but the results of Dumas' study suggest several kinds of studies involving species pairs within the *R. pipiens* complex that might yield important information for ecological theory. For example, how stable is the location of zones of contact between species? If shifts occur, how are they related to climatic and other events? Are *R. pipiens* tadpoles competitively superior to those of *R. utricularia* only within the present range of *R. pipiens*, or is the failure of these two species to overlap broadly due to some other kinds of interspecific interactions?

#### PROBABLE CASES OF SPECIES RANGE DISJUNCTIONS

Although parapatric ranges are the rule among members of this species complex, my examinations of specimens revealed a number of disjunct populations involving several species. These populations are relatively few in number and notable on that account. They are discussed separately below according to the geographic regions where they were found.

*Appalachian Mountains and Piedmont Plateau*—The western Virginia record of *R. utricularia* (Wythe County) is based on a single

male specimen. Literature records of this species from the southern Appalachian Mountains are rare. Necker (1934) reported the occurrence of leopard frogs in Cades Cove in the Smoky Mountains. King (1939) reported leopard frogs from two additional localities in the Smoky Mountains but noted that they seemed to be northern leopard frogs (*R. pipiens*) rather than southern ones. Pickens (1927) reported southern leopard frogs from Greenville, South Carolina. He wrote: "Puzzling intergradations occur with *R. pipiens* and I have found a male with the *sphenocephala* [= *utricularia*] markings mated with a female of *pipiens*. The occurrence of the southern form here at about 1000 feet is an altitudinal record." He also noted that lack of records of *R. palustris* seemed "strange in view of the locality." Whether the frogs Pickens, Necker, and King reported as *R. pipiens* do indeed represent this species or whether they represent instead southern *R. palustris* with reduced dark dorsal pigmentation (Schaaf and Smith, 1970) is not certain, but I suspect for several reasons they represent *R. palustris*. Three males of *R. utricularia* collected by Pickens at Greenville (USNM 71765-71767) are the only leopard frogs represented in that collection from Greenville. Another frog (USNM 72374) was originally catalogued as *R. pipiens*, but the dorsal pigmentation pattern indicates that this specimen is a *R. palustris*. The only other leopard frog I have seen from this locality is also *R. utricularia* (UMMZ 98886). In 1967 I spent approximately three weeks (from mid-March to early April) in this general area (mountains of North and South Carolina and Virginia) searching for *R. pipiens*. I was unable to find either species of leopard frog though *R. palustris* was fairly common.

Hutchinson (1956) reported *Rana pipiens pipiens* from Giles County, Virginia. In view of the close proximity of the confirmed locality for *R. utricularia* in Wythe County—fewer than 45 miles away—and the distance of any known or suspected locality for *R. pipiens*—known from Franklin Furnace, Scioto County, Ohio, and suspected no closer than Wayne County, West Virginia (Green, 1949), greater than 100 miles—this record, if not based on a misidentified specimen of *R. palustris*, probably represents *R. utricularia*.

Confirmed records of *R. pipiens* from Lily Pons, Frederick County, Maryland, probably represent a population disjunct from the main body of the species range. Most of these specimens were collected by J. Gillespie and J. D. Hardy and are from the same locality in which northern type hemoglobin was reported by Gillespie and Crenshaw (1966). Some of these may represent specimens used in these hemoglobin analyses. Except for one specimen (USNM 141003) collected in 1950, all specimens from here were taken between 1965 and 1967. The size of this population evidently fluctuates widely (Hardy, pers. comm., 1972). Perhaps the occurrence of this species in the Lily Pons locality is the result of activities of the Three Springs Fisheries whose many open ponds increase the number of potential breeding sites for species like *R. pipiens* and *R. palustris* which usually

breed in ponds, marshes, or other places with slow-flowing water and emergent vegetation.

Another Appalachian Mountain record for *R. pipiens* which may represent a disjunct population is that from Carlisle, Cumberland County, Pennsylvania. Although there are several literature records of *R. pipiens* from the Appalachian Mountains of Pennsylvania and West Virginia they are very scattered and this species is apparently rare. I saw 22 *R. pipiens* from Wood County, West Virginia. This species has also been reported from Cabell, Hardy, Marshall, Mason, Preston, Putnam, Ritchie, and Wayne counties in West Virginia and is apparently restricted to the vicinity of large river valleys while *R. palustris* occurs at higher elevations (Green, 1941, 1949; Green and Dowler, 1966), although the two species are sympatric at various localities (Green, 1941). Literature records of leopard frogs exist for Lebanon County (Heilman, 1951; Surface, 1913) and Dauphin County (Surface, 1913) in central Pennsylvania. *R. pipiens* was also reported by Surface (1913) from two northeastern counties (Bradford and Luzerne) and from four western counties (Allegheny, Indiana, Washington, and Westmoreland). Although Netting (1933a) reports that *R. pipiens* is "state wide in distribution with records for 30 [of Pennsylvania's 67] counties . . .," he does not list these and remarks in another paper (1933b) that *R. palustris* "seems to prefer cooler water than . . . [*R. pipiens*] . . . and consequently it is far more common in the mountainous regions of Pennsylvania and West Virginia." All of the above literature records for *R. pipiens* probably are *R. pipiens* in the strict sense.

I have seen *R. pipiens* from the following western Pennsylvania counties: Crawford; Indiana; Jefferson; and Warren. I have also seen specimens from northeastern Pennsylvania (Sullivan County) in addition to the possible isolates mentioned above from Carlisle, Cumberland County. I have listed these localities to illustrate how scattered the occurrence of this species is in the Appalachian Mountains of Pennsylvania and West Virginia. The rarity of leopard frogs in these mountainous regions apparently is in some way related to the widespread occurrence of *R. palustris* in these regions, and is not due to lack of collecting.

Hudson (1956) reported the occurrence of southern leopard frogs in southeastern Pennsylvania. He concluded, as a result of extensive collecting throughout eastern Pennsylvania, that "*sphenocephala* [= *utricularia*] occurs only in isolated localities now undergoing modifications due to industrial expansion." I have seen specimens of *R. utricularia* from Bucks and Philadelphia counties in southeastern Pennsylvania. Some of these specimens were collected about 150 years ago. It is unclear whether Hudson meant that the occurrence of leopard frogs in these localities was due to or threatened by industrial expansion.

*Western Oklahoma*—*Rana blairi* is the most widely distributed species in Oklahoma although it is replaced by *R. utricularia* in the eastern part of the state (Figs. 4 and 9). Bragg (1950c) reported sympatry of these two species in the extreme northeastern part of the state. He also reported the occurrence of *R. brachycephala* [= *R. pipiens*] in the western part of the state. The specimen indicated on the distribution map of *R. pipiens* for this state (Fig. 1) is a female from six miles east of Hydro near the border of Caddo and Custer counties. This frog has the broad and low, continuous and not displaced dorsolateral folds characteristic of *R. pipiens*. It also has large areolated spots on the dorsum (11 total, including three on the head). Although no male was available from this locality, this female specimen confirms Bragg's reports of the occurrence of this species in western Oklahoma. In 1949 he reported its occurrence in Ellis County (on the basis of behavior of juveniles) and in Beaver and Major counties (presumably on the basis of specimens in the University of Oklahoma Museum). His 1950 report of the species from Kiowa and Stephens counties was based on differences in mating call and behavior of adult males of this species (compared with the common species of central Oklahoma, *R. blairi*): "The call was a continuous clucking sound given at the water surface. . . no evidence of one individual chasing others (a common occurrence in excited congresses of *Rana berlandierii* [= *R. blairi*]) . . ." was observed in over an hour's watching. "Also early in May this same type of call was heard in Stephens County in one pool, though in another only *R. berlandierii* was calling." This was the third time that overlap of these two species had been reported (the earliest being that of Ortenburger and Freeman, 1930).

The populations of *R. pipiens* closest to these in western Oklahoma are in Colorado and New Mexico. These western Oklahoma records may represent relictual populations indicative of prior (perhaps pluvial) widespread occurrence of this species in the central United States.

*Southwestern United States*—The scattered records of *R. pipiens* from the southwestern United States (Arizona, New Mexico, and southern Nevada) may represent populations which are no longer connected with the main body of *R. pipiens* populations (in Colorado, Utah, and northern Nevada). The southern records of *R. pipiens* in the western United States occur primarily at higher elevations and indicate that *R. pipiens* was previously (presumably during pluvial times) more widely distributed at lower elevations in this area.

Mecham (1971) reported a leopard frog from northern Mexico with a mating call of 35.5 pulses per second at a temperature of 24°C (75°F). This appears to be within limits of ordinary *R. pipiens* mating calls (from northern and eastern United States) (Fig. 16b). Narrow band width sonagrams used by Mecham make estimation of pulse

durations difficult, although they appear to be somewhat longer, relative to the interval between pulses, than in recordings of *R. pipiens* from Indiana and Michigan.

*Southern Ohio*—Zenisek (1963) reported scattered populations of the southern leopard frog (identification as *R. utricularia* confirmed on the basis of black and white photographs in his unpublished doctoral dissertation) in southern Ohio. He suggested that these were relict populations which were out of contact with other populations of these frogs. Until the distributional relationships of *R. pipiens* and *R. utricularia* in southern Ohio and northeastern Kentucky are more thoroughly understood, it is difficult to determine the extent to which the populations he mentioned are actually isolated. Similarities in the distribution of *R. utricularia* and *Scaphiopus holbrookii* in the eastern United States are particularly striking and suggest that similar ecological factors may be important in determining limits of distribution of both species (cf. Wright and Wright, 1949: 124, map 7; and Fig. 4). *S. holbrookii* occurs in southern Ohio and also in the vicinity of Wytheville, Virginia, but, like *R. utricularia*, it does not occur in the intervening area.

*Southern Illinois and Southwestern Indiana*—Several groups of distributional records for *R. blairi* in southern Illinois and in adjacent parts of Indiana and Missouri represent possible disjuncts from the groups of populations found in central Illinois (Fig. 34). There is a possibility that the central Illinois populations are themselves not connected with the main body of the species range (in Kansas, Oklahoma, Nebraska, northern Texas, eastern Colorado, and northern Missouri). *Rana utricularia* is found north of the vicinity of St. Louis, Missouri (where both species occur). The two records for *R. utricularia* for this region are represented by 12 specimens from Hancock and Adams counties. There are no records of *R. blairi* from these counties. The Adams County specimens, collected at various times, are all from Quincy. The Hancock County specimens, collected in 1954, are from Carthage. I have not seen enough specimens from central and northern Missouri to determine the extent to which the distribution of *R. utricularia* (or of its habitat) acts as a barrier between populations of *R. blairi* from Illinois and Missouri.

A small, newly metamorphosed leopard frog from Warrick County in southwestern Indiana has discontinuous, displaced dorsolateral folds on both sides and may, like the specimens from Wabash County, Illinois, represent a population of *R. blairi* which is otherwise surrounded by *R. utricularia*.

APPARENT RANGE DISJUNCTIONS OMITTED FROM  
DISTRIBUTION MAP OF *RANA PIPIENS*

Specimens in two series reportedly from Miami, Florida: These frogs (AMNH 38292 and 37452-37456 plus one untagged specimen)

are considered to be erroneous records. They may represent mislabeled specimens which were collected elsewhere or they may represent specimens that were discarded after experimental or classroom use and were then collected. The long series of specimens includes 8 untagged specimens of the sort typical of peninsular Florida *R. utricularia* (large and darkly pigmented dorsally and ventrally).

A large male from Imboden (Lawrence-Randolph counties), Arkansas: This male (AMNH 44245) appears to be a typical *R. pipiens*. It has Mullerian ducts and lacks external vocal sacs although the skin overlying the internal vocal sacs is stretched. This frog is much larger than any of the typical *R. utricularia* males examined from Arkansas (this male's snout-urostyle length was greater than 76 mm, while snout-urostyle lengths of 23 *R. utricularia* males ranged from 47.3 mm to 66.1 mm). Without further information this record is considered to represent an error similar to that noted above: a specimen displaced by human activity or simply a mislabeled specimen.

#### DISTRIBUTIONAL RELATIONSHIPS IN THE MIDDLE WEST

The distributional relationships of *R. blairi*, *R. pipiens*, and *R. utricularia* in the central part of the United States warrant more detailed description. *Rana utricularia* occurs alone throughout most of southern Illinois and Missouri (Figs. 4 and 34), and *R. blairi* occurs alone in most of central Illinois and in the northern parts of Missouri (Figs. 9 and 34). These two species, at least in Illinois, occupy parapatric ranges, and the only known areas of sympatry in this state, excepting isolated populations of *R. blairi* mentioned above, fall along a line where the ranges of the two species meet. They are sympatric in several localities in the central part of Illinois. These species are also sympatric in several localities in the Mississippi River Valley from a point about 50 miles north of St. Louis to a point near where the Ohio and Mississippi rivers converge. Sympatry between the two species may be more extensive in this area than in any other area where their ranges are in contact.

The Illinois populations of *R. blairi* (including the Mississippi River Valley populations just mentioned) may be isolated from the northern Missouri populations of the species. There is an area approximately 40 miles wide, between the Illinois and Mississippi rivers, from which I have seen no specimens. If *R. utricularia* occurs alone in this area, connecting the populations of this species from Quincy and Carthage, near the Mississippi River, with the populations from the vicinity of Beardstown and Havana, on the eastern side of the Illinois River, the east-central populations of *R. blairi* would be separated from the populations from Pike and Morgan counties and from the Mississippi River Valley populations.

On the other hand the Quincy and Carthage populations may be separated from the more southern populations of *R. utricularia*. This would be the case if the intervening area was occupied solely by *R.*

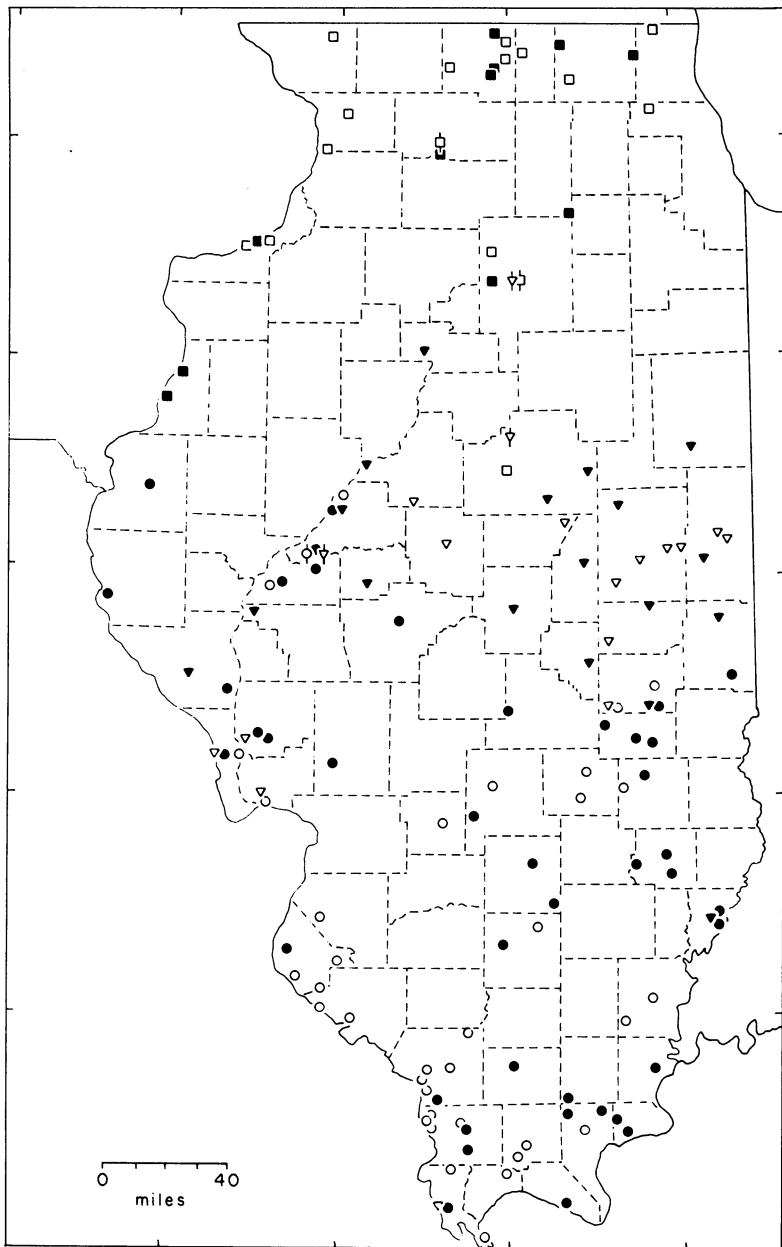


Fig. 34. Geographic distribution of three species of leopard frog in Illinois based on specimens and call records. Squares indicate *R. pipiens*; inverted triangles indicate *R. blairi*; and circles indicate *R. utricularia*. Solid symbols indicate records based on adult males; open symbols indicate records based on female specimens and juveniles; and tailed symbols indicate call records (Brown and Brown, 1972).



*blairi*. *R. blairi* was probably much more widely distributed in the Middle West during earlier postglacial times. The likelihood that its range has become more restricted in the east in recent times is indicated by the isolated populations in the vicinity of Wabash County, Illinois, and in Warrick County, Indiana. *R. utricularia* may have invaded the northern parts of its present range from the south with changes in climatic conditions, possibly increasingly moist or more predictably moist. This appears to have happened along the Mississippi and Illinois rivers in Illinois. It appears likely that the Quincy and Carthage populations of *R. utricularia* are connected with the more southern populations through either Missouri or Illinois, or possibly both.

In his discussion of geographic distributions of variant leopard frog populations in Illinois, P. W. Smith (1961) stated that intergradation of *R. p. pipiens* with *R. p. sphenoccephala* [= *utricularia*] occurred across the central part of the state. This intergrading area was reportedly relatively narrow in eastern Illinois, wider along the Mississippi River, and also wider in the Illinois River valley, where intermediates were known from "Jersey to Mason County." Further, he stated that: "Individual variation in a series of *R. p. sphenoccephala* from one locality exceed geographic variation (the difference between series) displayed within Illinois. The only trend discerned in this subspecies is a tendency for individuals from the Mississippi and Ohio River floodplains at the southern tip of Illinois to have fewer dorsal spots." Series of leopard frogs from some single localities in Illinois exhibit individual variation which is as great as that between geographically distant populations in the state because these localities represent mixed species populations.

Smith discussed two intergrade samples from Illinois (from Coles County and from Mason and Morgan counties). Evidently these so-called "intergrades" between what he supposed to be two subspecies of *R. pipiens* are predominantly *R. blairi*. *R. blairi* is represented by numerous specimens in the collection of the Illinois State Natural History Survey. Most come from the northcentral part of Illinois with positively identified specimens from Coles, Mason, Edgar, Iroquois, Macon, Marshall, McLean, Menard, Shelby, and Vermillion counties in central Illinois, and from Wabash County at the confluence of the Wabash and White rivers (see Fig. 34 and Appendix I). This species is known from Indiana from Benton and Parke counties and one young specimen from Warrick County is probably also this species.

All three species of leopard frogs occurring in Illinois may be found along the Illinois River. *R. pipiens* occurs at La Salle. Downriver one would encounter *R. blairi* next, then an area in the vicinity of Havana where this species is sympatric with *R. utricularia*, then *R. utricularia* alone, then *R. blairi* alone, then again *R. utricularia* alone, and finally, between Kampsville and Grafton (at the mouth of the river) *R. blairi* and *R. utricularia* are known to occur together. Although no areas of sympatry between *R. pipiens* and *R. utricularia* are known for

Illinois, there is a strong probability that one exists in the western part of the state somewhere between Carthage (where only *R. utricularia* is known) and Gulfport, across the river from Burlington, Iowa (where only *R. pipiens* is known). The distance between these cities is less than 30 miles. There is also a possibility of sympatry involving all three species somewhere in this area or in the area between the Illinois and Mississippi rivers mentioned above.

Sympatry between *R. blairi* and *R. pipiens* was reported by Brown and Brown (1972) at 9.1 kilometers west of Ottawa, La Salle County, and I have seen specimens of both species from several localities in close proximity to one another in La Salle and McLean counties in Illinois and in Indiana.

#### R. PAPIENS AND R. BLAIRI IN NEBRASKA

Although in most cases the geographic extent of overlap between any two species in the *R. pipiens* complex is very limited, usually on the order of a few miles, there are several areas where overlap appears to be considerably greater. One of these is in the Mississippi River Valley, where *R. utricularia* and *R. blairi* appear to overlap fairly broadly. The other is in Nebraska and involves *R. blairi* and *R. pipiens*. Even in these cases, however, the area of apparent overlap is still very small relative to the entire range of either species.

*Rana pipiens* is known from adult male specimens from central Nebraska (Knox and Buffalo counties) and westward. *R. blairi* is known from adult males from Platte, Dodge, Cass, and Jefferson counties (southeastern Nebraska). Two adult males from geographically intermediate localities may represent hybrids between these species. One of these (UMMZ 67512 from Madison County) resembles typical *R. blairi* in that it has numerous small dorsal spots, rough skin on the sides of the body, and the skin overlying the internal vocal sacs is striated below the labial stripe. It lacks the snout spot which is usually found in this species, however, and has light blotches in the centers of the tympana rather than distinct spots. In these two respects it more closely resembles *R. pipiens*. Also like *R. pipiens*, it has continuous dorsolateral folds and vestigial oviducts. Another male (UMMZ 67510 from Pierce County) also has vocal sacs like *R. blairi*, but like typical *R. pipiens* males it has vestigial oviducts.

The distributions of frogs with continuous and discontinuous dorsolateral folds in eastcentral Nebraska further indicate a possibility of either broad sympatry or extensive hybridization. Because this character correlates nearly completely with diagnostic secondary sex characters (call-, vocal sac-, and vestigial oviduct-types) it is likely to be useful in assessing the genetic background of female or juvenile specimens which lack the above secondary sex characters.

In Nebraska there is considerable overlap between frogs which have both dorsolateral folds continuous and not displaced and those

which have both dorsolateral folds discontinuous and displaced. This overlap of dorsolateral fold types occurs from Boyd County to Platte County, a distance of about 100 miles, and includes the two above localities from which possible adult male hybrids were found. With the apparent intermediacy of these male specimens and the lack of information about mating calls it is difficult to determine whether this area represents one of unusually broad sympatry or of more extensive than usual hybridization. A broad area of overlap in ranges does not necessarily mean that two species are extensively sympatric for they may have relatively restricted habitats within the area of overlap.

### INTERSPECIFIC HYBRIDIZATION IN NATURE

In most areas of contact between leopard frog species that have been investigated in the field hybrids are apparently rare or absent. In the three Indiana localities where I heard *R. pipiens* and *R. utricularia* calling together at the same time there were no intermediate calls, indicating that no successful hybridization is occurring between these two species at these localities. One of the symbols in Figure 19 indicating sympatric populations of these two species is actually based on records made on different nights at two separate localities, within sight of one another, each containing one species. In two localities where *R. utricularia* and *R. blairi* were sympatric in Johnson County, Texas, Littlejohn and Oldham (1968) found no frogs with intermediate calls. At other localities in Johnson County where *R. utricularia* and *R. berlandieri* were sympatric each call heard or recorded by Littlejohn and Oldham was referable to one of these species, with no intermediates. Post and Pettus (1967) reported that in some areas in Colorado where two forms of leopard frog, corresponding to *R. pipiens* and *R. blairi*, were in contact there was no evidence of hybridization between them. In these areas the two species had different, non-overlapping, breeding seasons. In one locality, however, hybrids were present in what they termed "moderate frequencies" (Pettus and Post, 1969). They indicated that the area where hybridization was occurring between these two species was one of recent contact made possible because man had created suitable habitat for leopard frog breeding where none had existed before. The implications of this report are that divergence sufficient to prevent hybridization arises independently in different populations, that inability to hybridize can arise in a relatively short period of time, and that the genetic differences responsible for the apparent decrease in frequency of hybridization do not spread very quickly from one population to another.

At five localities (the actual total is evidently greater as some of these localities represent pooled samples) Littlejohn and Oldham (1968) reported only three probable hybrids between *R. berlandieri* and *R. blairi* among more than 50 frogs.

There appears to be some variation between mixed populations of *R. utricularia* and *R. berlandieri* with regard to the amount of hybridization occurring, at least in the relative numbers of hybrid individuals reaching adulthood. In Johnson County, in central Texas, Littlejohn and Oldham (1968) found no hybrids between these two species. In San Patricio County, near the Gulf Coast, approximately 30% of the males recorded were suspected hybrids. At two geographically intermediate localities the proportion of probable hybrids between these two species was less than 10%. Thus the proportion of hybrids appears to increase gradually between central Texas and the Gulf Coast.

The actual frequency of cross fertilizations may be considerably greater. In fact this would be so unless the hybrids were not selectively inferior or unless the inferiority was not apparent until after they mature (for example, hybrid sterility or reduced ability to attract a female). Because mating calls cannot be recorded until male frogs reach adulthood, a considerable amount of unsuccessful hybridization may not be detected by this method. Furthermore, some successful hybridization (reproductive female hybrids) also cannot be detected in this way. There is, of course, no assurance that even these males are successful hybrids since they could still be completely sterile or have reduced fertility.

In order to assess the actual amount of hybridization and the direction of selection with regard to hybridization, a combination of field and laboratory tests would be very useful. Such tests would involve female responses to calls, mating success of hybrid and non-hybrid males in the field (numbers of females attracted, egg masses fertilized, offspring produced, etc.), and assessment of allelic frequencies at different loci in several age classes, from populations within and outside the zone of overlap between species.

Salthe's (1969) study of lactate dehydrogenases in leopard frogs suggests a way in which such studies could be combined to measure the effects of occasional hybridization and selection on the evolutionary fates of two closely related groups of populations. Based on his electrophoretic and immunological studies of these proteins Salthe concluded that a single multi-allelic locus was involved in production of the different lactate dehydrogenase (hLDH) types (Fig. 35). Among 14 frogs from Ottine, Gonzales County, Texas, two had alleles at this locus which represented the two different species occurring in this locality and were therefore hybrids (at least at this locus) between the two species. Littlejohn and Oldham (1968) recorded 43 males at this same locality and found only two individuals with intermediate call characteristics which they suspected to be hybrids. These two different measures of hybridization give different frequencies. For single locus data the frequency is 14.3% and for call data the frequency is 4.7%. Salthe's samples included adults, young frogs, and even large tadpoles, however, and to the extent that the individuals in this sample represent

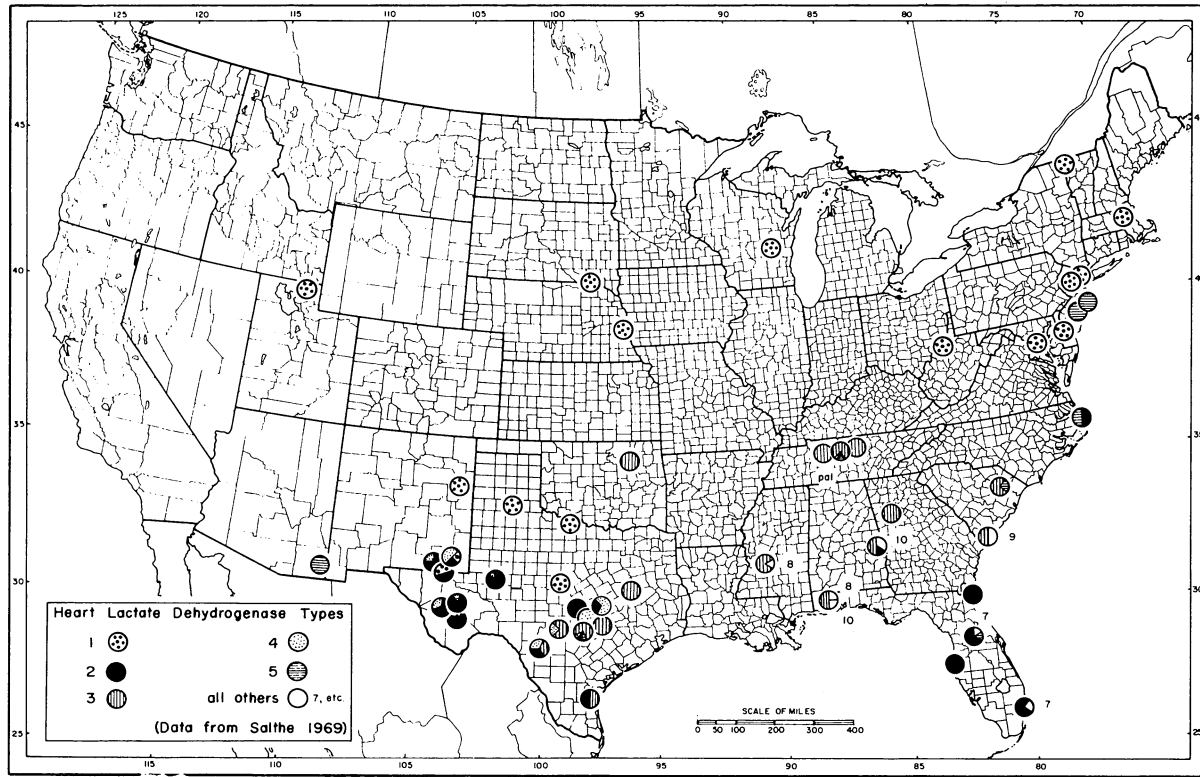


Fig. 35. Geographic distribution of electrophoretically distinguishable types of lactate dehydrogenase from the heart muscle of leopard frogs. Each pie diagram represents data from a single locality except where several localities with similar frequencies of LDH types (Salthe, 1969) were located in very close proximity (e.g., Tennessee). These LDH types evidently represent multiple alleles of a single locus. The proportion of the pie diagram therefore indicates the frequency in the population of the allele determining that LDH type. Data are derived from Salthe's table and not from his map (there are several discrepancies between the two).

young animals the difference in frequencies may be a measure of intensity of selection against hybrids in the intervening age classes.

The four hLDH alleles discovered by Salthe (1969) appeared to be segregating randomly in the Luling locality. Eleven of the 62 frogs analyzed were clearly hybrids, being heterozygous at this locus for one allele which is widespread only in the range of *R. utricularia* and another which is only widespread in the range of *R. berlandieri* and possibly other species, but not *R. utricularia*. Two of the other alleles present in this population are probably also typically *R. berlandieri* alleles since their distribution within *R. utricularia* is otherwise geographically disjunct, but these were present only in low frequencies (11.3%, the combined frequency of alleles two and five at this locality). Salthe commented that the apparent panmixia with regard to this single locus conflicted with data on presumed mating calls "from the Luling locality" (actually from the Ottine, Texas, locality) presented by Littlejohn and Oldham (1968).

Salthe concluded that no problem was presented by this population (with single locus data indicating panmixia and call data not) "unless female discrimination between different call note types can be demonstrated." He suggested that the function of calls in these two groups of frogs might "be largely one of territorial spacing of breeding males, in which case it could become polymorphic in a single population." It is difficult to imagine how any two different communicative signals, widespread in different geographic regions, could become polymorphic (with a few intermediates) in a narrow zone between the two areas and still be effective signals. This comment applies whether the call is involved in male-male interactions or in male-female interactions. Furthermore, in species which have several vocalizations (as these do) the most distinctive one is more likely to be the one involved in mate attraction and species discrimination and the more similar (between populations) calls are more likely to operate either at short ranges between the sexes or between members of the same sex (of the same or different species, for example in territoriality). In leopard frogs it is the most distinctive of several calls that have been presumed to be "mating calls."

Even if female discrimination between different call types is demonstrated, these presumably single-locus data gathered by Salthe (even if they had come from the same locality) would still present no great conflict with call data. As indicated above such results could be obtained through measuring numbers of hybrids present in different age classes. If hybrids are inferior they might be expected to decrease in frequency in successively older groups of frogs.

A further complication involved in interpreting single-locus data may be important here. If an allele is present in one population (or group of populations) and absent from another population (or group) entirely allopatric to the first, it will be easy to tell which population(s) particular individuals came from by examining that single locus. If the

ranges of the two groups of populations expand so that they come into contact with each other, they may produce hybrids. If one examines individuals from this area of contact in the first generation after contact he will be able to determine which individuals are the result of mating between individuals of the two different populations and which ones are not by looking again at this single locus. In subsequent generations, however, this becomes impossible. In the absence of mutation all that can be ascertained is whether at some point in the ancestry of that individual, members of both populations were involved (and this cannot be positively ascertained). How long ago hybridization occurred cannot be determined. If any fertile hybrids are produced in the initial cross then backcrossing could theoretically produce individuals that differ from the parental population to which they are backcrossed by only this single allele. To that parental population such a change would be like a mutation and if it conferred some advantage on the individuals possessing it, it could become widespread in that population even though all the other alleles from the second population at all other loci, and therefore hybridization *per se*, were selected against. This is an extreme example, but even examination of alleles at a large number of loci would not entirely eliminate this problem.

Differences in the apparent depth to which "alien" alleles at different loci have penetrated in European populations of two subspecies of the house mouse, *Mus musculus musculus* and *M. m. domesticus*, (Selander, Hunt, and Yang, 1969) suggest that differential incorporation of alien alleles depends on the particular relative advantage they confer. Even the combination of information from these loci does not necessarily permit any conclusion about the direction of selection regarding hybridization *per se*.

#### GROWTH RATES AND DEVELOPMENT TIME

Five leopard frogs collected in southeastern Indiana in April, 1970, were used in developmental studies involving some artificial hybridization. The numbers in parentheses below are the identification numbers assigned to these frogs at The University of Michigan Amphibian Facility where the experiments were conducted and where the frogs were housed after the experiments were begun on 16 April 1970. Differences in developmental time and rate of growth of the sort I observed may be importantly involved in determining the nature and extent of geographic overlap occurring where ranges of two species contact. For that reason I will briefly summarize these experiments and the results from them along with some other observations involving relationships between growth and developmental rates in *R. pipiens* and *R. utricularia*.

Both *R. utricularia* males (09873 and 09874) used in the crosses were collected from a population one mile east of Poland, Indiana, containing no other leopard frog species. The female *R. utricularia*

(09879) was collected from a mixed population of *R. pipiens* and *R. utricularia* three miles north of Jonesville, Indiana. She was the source of all *R. utricularia* eggs used in these crosses. One of the *R. pipiens* males (09876) also came from this locality. The other (09882) came from near the Hassmer Hill 4H Camp at Versailles State Park, Indiana, where *R. utricularia* was also found. A female *R. pipiens* collected at the same locality was also used, but her eggs were apparently overripe at the time the fertilizations were performed. Only a few eggs were fertilized and none developed to feeding stage. The two female *R. pipiens* (14343 and 14344) used in these crosses came from Whitmore Lake, north of Ann Arbor, Michigan.

Ovulation was induced in the standard way by injection of whole pituitaries into the body cavity. Sperm were obtained by surgically removing a testis from each male and preparing a sperm suspension by macerating the testis. Crosses were made using the following combinations of egg and sperm: *R. utricularia* ♀ (09879) × *R. utricularia* ♂ (09873); *R. utricularia* ♀ (09879) × *R. utricularia* ♂ (09874); *R. utricularia* ♀ (09879) × *R. pipiens* ♂ (09882); *R. utricularia* ♀ (09879) × *R. pipiens* ♂ (09876); *R. pipiens* ♀ (14343) × *R. utricularia* ♂ (09873); *R. pipiens* ♀ (14343) × *R. utricularia* ♂ (09874); *R. pipiens* ♀ (14344) × *R. utricularia* ♂ (09874); *R. pipiens* ♀ (14343) × *R. pipiens* ♂ (09876); and *R. pipiens* ♀ (14343) × *R. pipiens* ♂ (09882).

The embryos were not checked frequently enough during the very early stages of development to determine whether there was any significant effect of hybrid combinations of egg and sperm on early developmental rate. All of the embryos derived from *R. utricularia* eggs, whether fertilized with *R. utricularia* sperm or with *R. pipiens* sperm, were slightly accelerated in their development at gastrulation relative to embryos derived from *R. pipiens* eggs. However, by the end of the fourth day after fertilization, it appeared that embryos derived from *R. utricularia* sperm were developing faster than embryos derived from *R. pipiens* sperm, regardless of whether the female parent was *R. pipiens* or *R. utricularia*.

Seven weeks after fertilization the tadpoles from each cross were re-sorted by approximate size and put into one-gallon plastic jugs. The total biomass of tadpoles put into each jug was estimated by determining the amount of water they displaced in a 100-ml cylinder, and the estimated average biomass determined by dividing this value by the number of tadpoles. Since the tadpoles were grouped in jugs according to size, a very small average biomass indicates a group of tadpoles of small size and a large average biomass indicates a group of large tadpoles. For each jug the largest and smallest tadpoles were selected by inspection and measured. The group of tadpoles with the smallest average biomass (0.12 g) ranged in length from 14 to 24 mm. The group with the largest average biomass (2.05 g) ranged in length from 49 to 65 mm. At this time the control tadpoles in crosses



involving *R. pipiens* males were larger in average size than hybrids. In crosses involving the *R. utricularia* males, however, the reverse was true. In all cases where the sperm came from the same male, the tadpoles derived from *R. pipiens* eggs were larger at the same age than those derived from *R. utricularia* eggs.

The slight acceleration of developmental rate associated with the *R. utricularia* sperm and the apparent effect of *R. pipiens* egg on growth rate are evident in the rate of metamorphosis and in the relationships between size at seven weeks and the time of metamorphosis in the control crosses. The mean size of tadpoles in the seventh week is plotted against the mean age at metamorphosis in Figure 36. The mean age at metamorphosis was derived by determining the age (in weeks post-fertilization) for each tadpole that metamorphosed, totaling these for each jug (size class of tadpoles within a cross), and dividing by the total number of tadpoles from each jug that ultimately metamorphosed. *Rana utricularia* tadpoles metamorphosed approximately two weeks earlier and at a smaller size (Fig. 37) than *R. pipiens* tadpoles which were the same size approximately midway between fertilization and metamorphosis. Hybrids are apparently intermediate.

The apparent tendency of *R. utricularia* to have a faster developmental rate and slower growth rate than *R. pipiens* is reflected

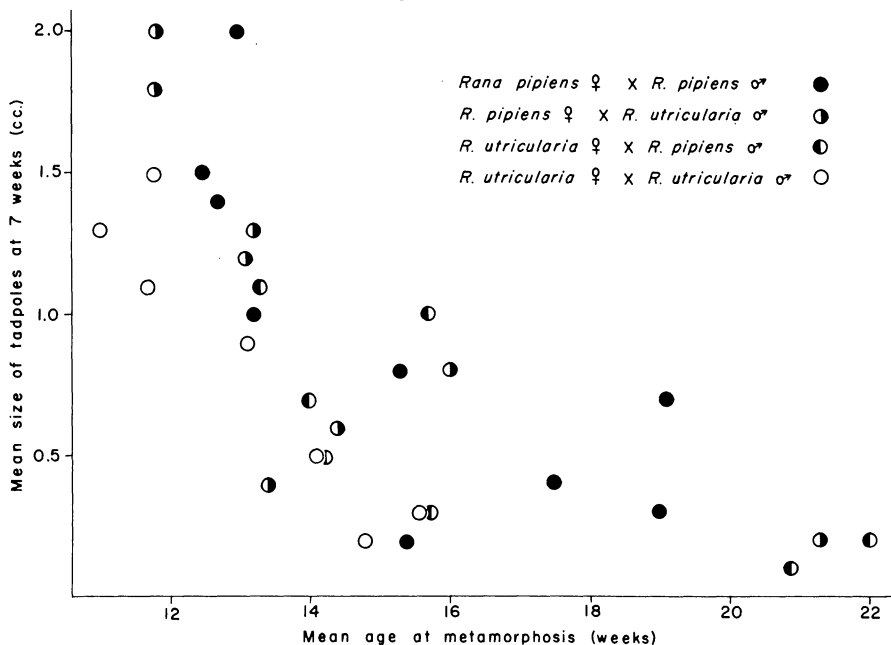


Fig. 36. Relationship between size of tadpoles when seven weeks old and the total amount of time (post-fertilization) between fertilization and metamorphosis for *Rana pipiens*, *R. utricularia* and their hybrids. Each symbol represents the mean for a group of tadpoles.

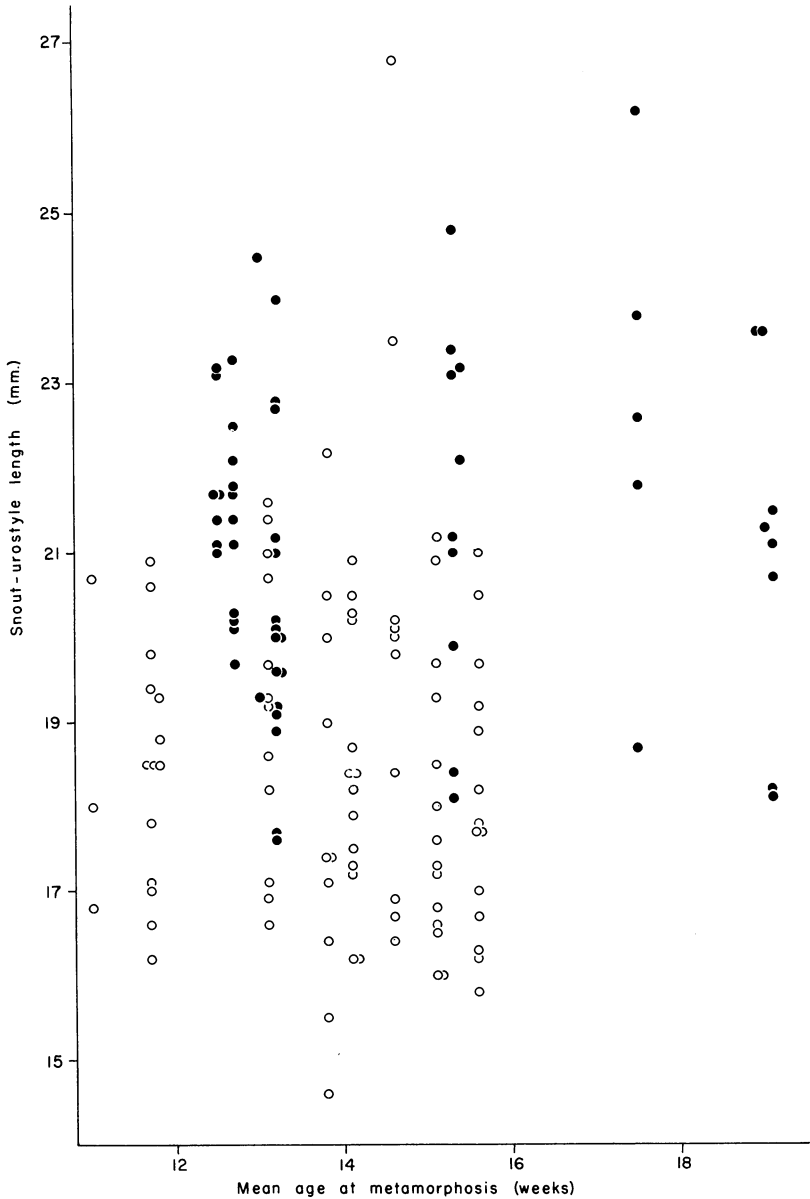


Fig. 37. Differences in size and age at metamorphosis in laboratory-reared *R. utricularia* (open symbols) and *R. pipiens* (solid symbols). Mean age at metamorphosis is for each of nine groups of *R. utricularia* and eight groups of *R. pipiens*, each group reared in a separate container. Each symbol indicates the snout-urostyle length (mm) of a single frog measured at death (some time after metamorphosis). Most frogs did not survive long past metamorphosis and the largest frogs in any group probably indicate those few individuals with the longest post-metamorphic lives.

in differences found in sizes of adult males of these two species from Indiana (Fig. 28). *Rana utricularia* not only metamorphoses at a smaller size than *R. pipiens*, but it matures at a smaller size. This information also suggests that *R. utricularia* matures at a younger age. Although there were no marked developmental incompatibilities of hybrids in the stages I examined, the fact that they appear to be intermediate in their developmental rates may mean that they are less fit than either parental type in zones of contact between the two species. Life history parameters such as age at metamorphosis and age at first breeding may be important in determining species' ranges and the amount of geographic overlap between similar species.

### LIFE HISTORIES OF LEOPARD FROGS

After locating intriguing variations in life cycle and associated attributes in *R. utricularia* along the Atlantic Coast, I re-examined the literature and my own field notes in regard to life histories of other leopard frogs and discovered striking variations among the species which seem to correlate with habitat and distributional differences among the species. In this section I will try to describe how such habitat and life history differences could have been importantly involved in speciation within this complex. My approach will be to describe briefly certain aspects of the life history of *R. pipiens*. Even though information is incomplete, this species is probably best known in this regard of all leopard frogs. Next I will consider the life history of *R. blairi*. Information on this species is more meagre and essentially restricted to populations from a small part of its total range, but the differences between the two species are particularly striking. I will then discuss how these differences may relate to habitat and historical differences between the two species before describing the more complicated situation in *R. utricularia*. Finally I will try to develop an hypothesis regarding speciation in these frogs which is consistent with these differences between species and populations within species and with the particular distributional relationships so prevalent in leopard frogs (and certain other groups as well).

#### *RANA PIFIENS*

*Habitat*—This species breeds in more or less permanent water. Wright (1914), who made extensive observations on its life history in the vicinity of Ithaca, New York, remarked that, although leopard frogs sometimes lay eggs in very shallow water, they generally “prefer cattail

swamps, marshy expanses of other types, grassy overflows, and shallow dead streams. In situations other than these, they breed sparingly." Bragg (1941) observed the same species in Las Vegas, New Mexico, and found that it bred in the spring before temporary pools had formed and, therefore, only in permanent water.

*Breeding Season*—In the eastern United States *R. pipiens* is one of the first anurans to begin breeding in the spring. Wright (1914) observed that the "period of mating begins April 1, or before; but the bulk of it does not come until the middle of April, and it continues for about three weeks, extending to the first or middle of May." The time of breeding seems closely related to the rise of temperature in spring and this information can be used with moderate success to predict when breeding will occur. Olson (1956) reported the breeding season extending from late March into May for this species in Winnebago County, Illinois. In Ohio, Walker (1946) reported that breeding normally begins in mid-March. He found fresh eggs from 17 March to 28 April, but noted that most were laid from 28 March to 7 April. Zenisek (1963) said that the breeding season for this species in Columbus, Ohio, terminated in late April or early May. Fichter and Linder (1964) found breeding occurred from April to June (depending on altitude and latitude) in Idaho. In Ann Arbor, Michigan, calling usually begins in mid- to late March and is usually over before the middle of May.

Wright (1914) noted that "sometimes in summer, during showers or on cloudy days, they resume croaking; for example, July 4, 1906, followed a rainy evening, was cloudy most of the time, and *Rana pipiens* was heard throughout the day. In the autumn they are rarely heard in the swamps, e.g., September 14, 1912." Although Bragg (1941) saw one mated pair during a warm mid-August rain in New Mexico (and he did not say whether eggs were laid), the species did not call after the rains in July and August. Walker (1946) reported hearing leopard frogs calling persistently in late September in Ohio, but these may have been *R. utricularia* (Walker, pers. comm.). I have heard *R. pipiens* calling once in mid-October in Washtenaw County, Michigan. Although these records indicate *pipiens* occasionally calls in late summer and fall, no one has ever reported autumnal spawning for this species and tadpoles are not known to overwinter.

*Clutch Size*—Fichter and Linder (1964) observed that the egg masses of this species contained up to 6000 eggs per mass.

*Hatching*—Wright's (1914) field records show that 13 to 20 days are required for hatching, the actual time required depending on temperature.

*Metamorphosis*—Wright (1914) states: "The majority of the larvae transform in July, although occasional records can be found far into August . . . . The transformation-period for any one year consumes at least a month, sometimes running into August; our latest record at Ithaca is August 6, 1907 . . . . The period from egg to transformation

may be from 71 to 111 days, or a true larval period of 60 to 80 days." In the lab the mean period from fertilization to transformation ranged from about 85 to 130 days (Fig. 36). In Ohio, Walker (1946) found that most tadpoles transform in early July, the extremes being 20 June and 12 August. Oliver and Bailey (1939) found that in New Hampshire tadpoles transformed about two to two-and-a-half months after eggs were laid, in the latter part of July or in August. In Las Vegas, New Mexico, they transformed from late June to mid-July (Bragg, 1941).

*Hibernation*—Wright (1914) says: "About the middle of autumn the meadow-frogs begin to take to their places of hibernation, usually in the first of October, when the light frosts come. In the middle of October, with the approach of heavy frosts, they are rarely seen."

*Length of Juvenile Period*—Force (1933) collected a large number of individuals on a single day and assigned them to age groups based on size. She concluded from this information that in northern Michigan *pipiens* first breeds at 3 years of age. Ryan (1953) says that in Ithaca all *pipiens* probably breed at 2 years (from egg stage) and that a few may even breed during the year following transformation.

#### RANA BLAIRI

*Habitat*—Bragg (1950b) says that this species breeds in "standing or very slow flowing water of all sorts up to three feet in depth. . . ." His observations indicate that the eggs are frequently laid in temporary ponds that are subject to drying.

*Breeding Season*—Breeding records of this species are known from early February to early October. Bragg (1950a) kept records of breeding of this species in Oklahoma from 1935 to 1948 and found breeding in every month except July from February through September. Bragg and Dowell (1954) found eggs laid on 8 October by one female. Regarding within population variation in seasonality, Bragg (1950a) claims that while some leopard frogs breed in early to mid-spring irrespective of rainfall, others in the same locality await summer or fall rains.

*Clutch Size*—Smith (1956) found the egg masses of this species to be four to five inches in diameter with 4000 to 6500 eggs. Bragg (1944) observed that egg masses of this species are occasionally (10% of over 200 egg masses) small (with fewer than 200 eggs).

*Hatching*—Smith (1956) reported that eggs hatched in 5-20 days. Presumably the time required is dependent on temperature, though Smith does not provide any information relative to this question.

*Metamorphosis*—Smith (1956) reported that tadpoles transform about three months after the eggs are laid. Again, this may depend, at least in part, on temperature. Bragg's (1950b) remarks concerning transformation in this species, however, are particularly interesting:

*Rana berlandieri* [*R. blairi*] is especially interesting as well as somewhat puzzling. Elsewhere (Bragg, 1940b) I reported that in a fast evaporating

pool, half-grown tadpoles may go into metamorphosis and behave as though seeking the bank rather than deeper water still available. Since those observations were made, I have noticed many times that in deeper pools these tadpoles grow larger and remain longer in a pool before metamorphosis than in more shallow pools. This could be due to temperature differences (in general, the deeper the water the lower the temperature) or it might be an effect of salt-concentration due to evaporation in the more shallow pools. The observations reported above give evidence against temperature as the major factor, for in the deep pool under investigation the animals became large and failed to metamorphose under temperatures sufficiently high to kill some of them.

*Hibernation*—Overwintering tadpoles of this species have been found in January and February (Bragg and Dowell, 1954).

*Length of Juvenile Period*—No information is available. The range of variation in snout-urostyle lengths of adult males of this species from Iowa and Missouri, however, completely overlaps the total ranges for males of the other two species in those states (Fig. 27). Although the sample size is very small, these data suggest the possibility that there is considerable variation in the length of juvenile period or unusual variation in longevity or growth after maturity.

#### COMPARISON OF *R. PIPIENS* AND *R. BLAIRI*

As Bragg (1950b) has already noted, the breeding pattern of *R. pipiens* is that typical of anurans occurring in mesic habitats. Its breeding season is shorter and more predictable than that of *R. blairi*, correlated with differences in the predictability and dependability of rainfall in the regions where the two species are found. Consistent with the apparently unpredictable temporariness of its breeding areas, *R. blairi* appears to be a facultative early metamorphoser. Tadpoles of this species are able to overwinter and in certain situations evidently grow large before transforming.

Bragg (1950b) commented that female *R. blairi*, unlike *R. pipiens*, apparently do not have a release call. He suggested that sex recognition in these two species might therefore be different, but the possibility is also suggested that ovulation, rather than being strictly under hormonal control as in *R. pipiens*, is induced by amplexus or is to some extent under neural control in *R. blairi*. If this were so, it might be related in some way to the variations in clutch size reported by Bragg.

Some additional remarks by Bragg (1949) concerning unique features of breeding biology and behavior of *R. blairi* are included here because they may relate importantly to differences in habitat and other biological attributes related to habitat in this species:

Consistently, I found the common Oklahoma frog to differ in breeding dates, in production of eggs, and in general behavior from its counterpart to the west [*R. pipiens*] (Bragg, 1941) and to the northeast

(Bragg, 1949) and also to differ in general agility, both as juveniles and as adults. One minor observation of this sort was that the juveniles of the Oklahoma form when frightened plunged into the water, swam far out in nearly a straight line to hide on the bottom. In contrast, the northeastern frog [*R. utricularia*] at the same stage commonly plunged in and often turned sharply to one side to hide near the shore-line. In clear water with little vegetation or other cover, the latter often are easily captured while they are making frantic efforts to find concealment at or near the shore-line, whereas the Oklahoma form will come to rest on the bottom far out and is not so easily taken. . . in western Oklahoma, I found juvenile leopard frogs to be very abundant about most standing water . . . search revealed two kinds of young frogs in this county and in the Oklahoma panhandle: (1) Those whose whole behavior on approach to a pool was like the common form in Oklahoma, and (2) those in which it was not.

I have relied rather heavily on Bragg's observations in spite of the fact that they are often, sometimes appropriately, criticized as anecdotal accounts, because in every case where I have been able to gather evidence on points raised by Bragg I have found his observations to be correct. For example, he noticed that mating calls of leopard frogs from different parts of Oklahoma were different and he located areas of sympatry between species pairs which I have been able to substantiate on the basis of museum specimens.

Although Bragg's data on these variations in life history and breeding biology are sometimes poorly documented, and even yet the life history of *R. pipiens* is actually rather incompletely known, the differences are nevertheless suggestive of highly distinctive patterns, which correspond well with differences in the nature of the habitat where each species is found.

#### *RANA UTRICULARIA*

*R. utricularia* does not present the simple patterns in life history suggested by data on *R. pipiens* and *R. blairi* and I shall approach the problem of describing its life cycle and the apparent variations in life cycle within this species by first describing some of the geographic variation in morphology of adult males that initially led me to examine its life history.

Adult males of *R. utricularia* from the Atlantic Coastal Plain exhibit striking geographic variation in body size (snout-urostyle length). Contrary to what might be expected from consideration of such variation in other animals the trend in size change along this north-south line is not strictly clinal; that is, size does not consistently increase (or decrease) with increasing latitude. The populations with smallest males are not found at the northern or southern limits of the species' range but in geographically intermediate localities, while the largest males are found in the most northern (New York, New Jersey,

Pennsylvania, and Delaware) and in the most southern (Florida) localities (Fig. 38).

In female frogs, if body size is directly related to number of eggs produced, it is easy to see how selection might favor larger size. The possible advantages of larger size and the relationship between size and reproductive success may not seem as obvious in males.

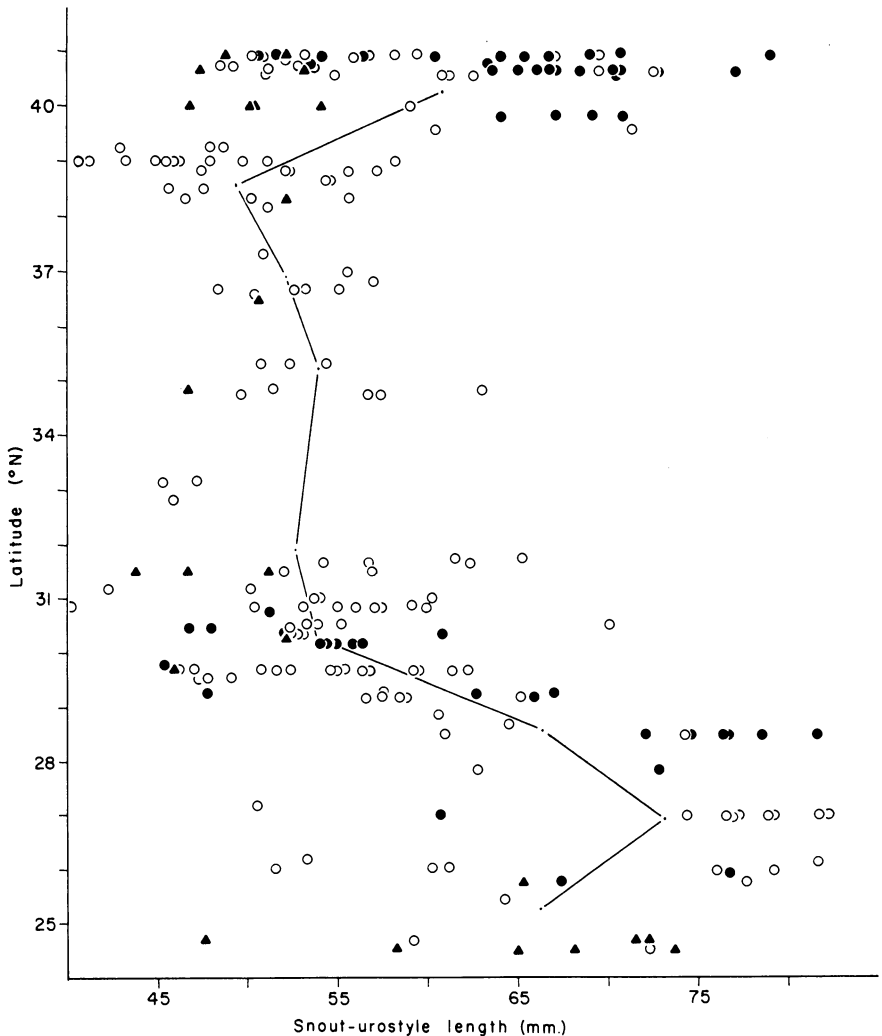


Fig. 38. Latitudinal variation in size of adult males of *R. utricularia* from the Atlantic Coastal Plain. Open circles represent males with ordinary balloon-like external vocal sacs; triangles represent males with unusually small vocal sacs that may be immature; solid circles north of  $39^{\circ}\text{N}$  represent males with unusually large external vocal sacs; solid circles south of  $31^{\circ}\text{N}$  represent males with modifications of external vocal sacs (for discussion of these variants, see pp. 43-45). The solid line joins the means for frogs at 100-minute intervals. The interval from  $32^{\circ} 45' \text{N}$  to  $34^{\circ} 25' \text{N}$  was omitted because of the very small sample size.



While examining specimens of this species from museum collections I noticed that in some males the vocal sacs were unusually large relative to body size. At the time I originally examined the specimens I made notes regarding relative vocal sac size of some frogs and subsequently sorted males arbitrarily into three groups based on these comments. The first group included all males which I had noted possessed unusually large vocal sacs. The second group included all males with unusually small vocal sacs (relatively few in number, perhaps immature or recently mature). The third group included all other males, that is those about which I had failed to note size of external vocal sacs. Presumably the vocal sacs of this last group were neither unusually large nor unusually small. The mean size of frogs with large vocal sacs was greater than mean size of males with "normal-sized" vocal sacs and the mean size of frogs with normal-sized vocal sacs was greater than the mean size of frogs with small vocal sacs (excluding frogs from Florida).

If the carrying power or effective distance of a male's call is increased relative to some other male as a result of his having larger vocal sacs it is easy to see how males with larger vocal sacs might be favored. The physical requirements of utilizing large vocal sacs in amplifying sounds may restrict their effectiveness to large males and the attainment of large size and production of unusually large vocal sacs may be developmentally linked for this reason. Large body size may also, however, be more directly related to reproductive success (for example, by increasing the likelihood of success in aggressive interactions with other males or of displacing another male from amplexus with a gravid female). Savage (1934) observed struggles between two males of *R. temporaria* that were clasping the same female. Although he never observed a second male dislodge an originally clasping male, the frequency of occurrence of these struggles in the breeding ponds suggested that such displacement of one male by another must happen occasionally, especially if the encounter occurred before the first male had firmly clasped the female.

Any reproductive advantages of large size, or correlates of large size such as increased fecundity in females, must always be measured in terms of the possibility of reproductive costs or risks involved in attaining large size (or growing larger vocal sacs, or producing more eggs, etc.). These possible costs or risks are measured in terms of the potential contrasting advantages that would be realized by maturing and breeding earlier at a smaller size. The relative magnitudes of these potential gains will depend in part on the likelihood of survival to the next breeding period.

Along the Atlantic Coast from Georgia to New York large males with unusually large vocal sacs are restricted to New York, New Jersey, and Pennsylvania. These are probably the males to which Harlan (1826) was referring when he described *Rana utricularia*, a leopard frog he distinguished by its large external vocal sacs from those of the rest of the coastal plain, south of New Jersey. Although very few recordings of

mating calls of leopard frogs were available from this area, and most of these were not correlated with specimens, the calls I have analyzed indicate no differences between mating calls of frogs from these regions and those from farther south in the coastal plain (Figs. 13, 14, and 18). As mentioned above, frogs with large vocal sacs were of large body size and males from New York and New Jersey are much larger than those from anywhere farther south in the coastal plain (excluding Florida). Interestingly the greatest difference in size occurs in populations from adjacent latitudes. Thus, males from southern New York are the largest and those from New Jersey and Delaware are only slightly smaller. Males from Maryland, however, average smaller than those from anywhere in the Atlantic Coastal states, and the maximum size increases gradually from Maryland southward (Fig. 38).

This abrupt change in size, correlated with the presence of very large vocal sacs in the largest males, suggests the possibility that there is an abrupt change in the way natural selection is operating on various behavioral and life history parameters in this species. Among the selective pressures responsible for the abruptness of this geographic change, climatic factors influencing development time are probably most important.

Even if there is no genetic variation in regard to developmental rate, breeding seasons may be prolonged southward without disadvantage because conditions are favorable for development over a longer period of time. This prolonging of the developmental period and therefore the period during which egg-laying is likely to be successful means that earlier maturing individuals may be able to breed after one winter. If size and food reserves affect the likelihood of overwintering successfully, then selection will probably favor delaying maturation and maximizing growth during the post-hatching period and during the next growing season.

Leopard frog tadpoles (at least of *R. utricularia*) probably do not commonly overwinter in the northern parts of their range, but they are likely present all year in the southernmost regions. Latitudinal differences in the length of the growing season and severity of the winter certainly affect the time during the year when attempts at reproduction would be likely to be successful. The period of egg-laying should not extend beyond that time which, on the average, allows tadpoles derived from those eggs to reach a condition in which they are likely to overwinter successfully. Egg-laying may thus cease sooner when tadpoles must metamorphose and store food in order to survive winter.

If the breeding season is thus (by climatic or any other factors, such as predators) restricted to a small portion of the total growing season this might decrease the likelihood of yearlings breeding. At the northern limits of distribution of *R. utricularia* along the Atlantic Coast the presence of huge males, and the absence of very small mature males, suggest that the growing season may be so short that even the

earliest-maturing males may not mature early enough to breed as yearlings, with selection consequently favoring those frogs which put all their energy into growth (with some of the possible advantages of large size indicated above) and delay attempts at reproduction until they are two years old. Somewhat farther south (approximately at the Delaware River), the large males disappear and males apparently mature at a smaller size, suggesting that the growing season, and that portion of the season favorable for tadpole development, is enough longer that the earliest-maturing individuals have a much greater chance of breeding successfully. At any rate there ought to be some point along the coast at which the balance shifts between selection for early maturation and selection for larger size. This change in selection must be strongly disruptive. Interruptions of gene flow are more important in a region in which such a selective reversal occurs, raising the question whether speciation may have been caused by such a phenomenon in the past, or may be in progress now (see Masaki, 1972, for a possibly parallel example in Japanese crickets). In any case, the morphological variations described here are sufficient to raise questions about the evolutionary status of populations adjacent in the region of the Delaware River, where this change appears to take place. Frogs from near the Delaware River on the south lack large vocal sacs and are mostly small; those from the north side of the Delaware River average much larger and tend to develop large vocal sacs. It may be significant that the appearance of vestigial oviducts in Florida frogs also coincides with a significant size change that probably also correlates with a life history change. Florida *R. utricularia* resemble *R. berlandieri* sufficiently to suggest that they are derived from common stock, *R. berlandieri* having speciated from *R. utricularia*, the Florida populations of *R. utricularia*, for unknown reasons, failing to do so.

Comparison of frequency of snout-spotting in leopard frogs from New York and New Jersey, that I have presumed to be conspecific, further indicates that distinct populations may be involved. Ten of 29 males of *R. utricularia* from these states with large vocal sacs, and only four of 37 males with normal or small-sized vocal sacs had snout spots.

The more northern species, *R. pipiens*, probably has a shorter breeding season than *R. utricularia*, even where the two species are sympatric. Zenisek (1963) reported that the calling season of leopard frogs (which I identified as *R. utricularia* on the basis of Zenisek's photographs) in Athens, Ohio, was about a month and a half longer than the calling season of *R. pipiens* (also identified from photographs) in the vicinity of Columbus, Ohio. Under laboratory conditions *R. pipiens* tadpoles metamorphose later and at a larger size than *R. utricularia*. Perhaps the persistence of *R. utricularia* in regions where *R. pipiens* has apparently recently invaded (probably post-hypsithermal) has been restricted partly because of the superiority of the specific developmental pattern of *R. pipiens* under prevailing environmental conditions in those regions.

Possibly genetic differences associated with developmental differences along the Atlantic Coast are, as Moore (1949) suggested, responsible for observed genetic incompatibilities, but the latitudinal changes evidently derive from selection for different life history patterns. They do not appear to be related in a simple fashion to temperature gradients, and the change is not gradual.

### DISRUPTIVE SELECTION AND PARAPATRY

The above findings suggest several possibilities in regard to relationships between modes of speciation, subsequent geographic relationships of the species involved, and the phenomenon of character displacement. These ideas, which I have developed in discussion with Dr. Richard D. Alexander, in particular by comparing data from frogs and crickets, are still highly speculative and incomplete. Nevertheless, they illustrate the kinds of biological problems that may be exposed by rather straightforward systematic work on well-known organisms. These ideas are potentially highly significant for speciation theory as a whole and I have therefore summarized them below.

As disruptive selection becomes more intense at some point within a species' range, the stringency of the requirement of extrinsic isolation for speciation is reduced, and in the extreme speciation could occur without the existence of a geographic barrier. On the other hand, most, in fact probably all, species are discontinuously distributed, and when disruptive selection occurs anywhere within a species' range it causes any interruption of gene flow at that point to assume greater significance in connection with the possibility or likelihood of speciation. In discussing regions where changes in life cycle are associated with changes in morphology and behavior in numerous crickets (Gryllidae) and katydids (Tettigoniidae), Alexander (1968b) has said: "One is led to believe that these are somehow 'fragile' connections between northern and southern components of widely ranging species, where changes in the direction of selection may make the slightest break in geographic continuity highly significant" (see also Masaki, 1972).

When speciation occurs as a result of a combination of strong disruptive selection and incomplete geographic isolation, the populations involved may be more likely to retain parapatric distributions. The reason for this is that the differences responsible for their speciation will also be related to their mode of interaction, and to the way that the particular attributes involved are affected by climatic and other factors at the geographic locations where their ranges meet. The possibility is therefore suggested that wherever extensively parapatric ranges exist between closely related species, and appear to have been persistent, one should consider the likelihood that speciation occurred

as a result of disruptive selection of the type described here as probably occurring in Atlantic Coast populations of *R. utricularia*.

When speciation occurs as a result of geographic separation, broad geographic overlap is more likely when the populations meet later. Such populations should also be more likely to hybridize, at least sporadically. This is particularly true if the separation was not unusually lengthy, and from this fact some character displacement is likely. On the other hand, disadvantages of hybridization at a point of disruptive selection should increase the likelihood of character displacement from the start of the speciation process.

Some pairs of species that formed during geographic isolation may be ecologically incompatible upon contact, and parapatry may persist on this account. In some cases the geographic separation may be so long-lasting and selection in the two locales so divergent that hybridization is not probable and ecological competition is trivial upon contact. These are reasons why character displacement may be absent in some cases.

## DISTRIBUTIONAL HISTORY AND RELATIONSHIPS WITHIN THE COMPLEX

### *R. PIPIENS* AND *R. PALUSTRIS*

In spite of the claim by Schaaf and Smith (1970) that there has never been any significant confusion of pickerel frogs (*R. palustris*) and leopard frogs, Ruthven, Thompson, and Thompson (1912) commented that earlier literature records of *R. palustris* for Michigan needed verification, "for the species is easily confused with *R. pipiens*." In every major collection of leopard frogs I examined I found specimens which I was certain (or suspected) were *R. palustris*. Many specimens from some regions were impossible to assign with confidence to either species. One such region is the northern part of the lower peninsula of Michigan (Fig. 39). This region is part of one of those labelled by Remington (1968) as a major "suture zone" in North America—regions where sibling species pairs in many unrelated groups of animals have recently come together and are hybridizing, apparently the result of recent joining of these biotas that were previously isolated. The range characterizations of *R. pipiens* and *R. palustris* (Figs. 1 and 40) are in fact very similar to those described by Remington as northern and western (*R. pipiens*) and southern and eastern (*R. palustris*) and the geographic extent of their overlap corresponds very closely to the area Remington designated as suture zone I. The distributional relationships of *R. pipiens* and *R. palustris* suggest that *R. pipiens* invaded eastern North America from the west after glaciation (since in the east it occurs only sporadically south of the glacial limit), while *R. palustris* intruded

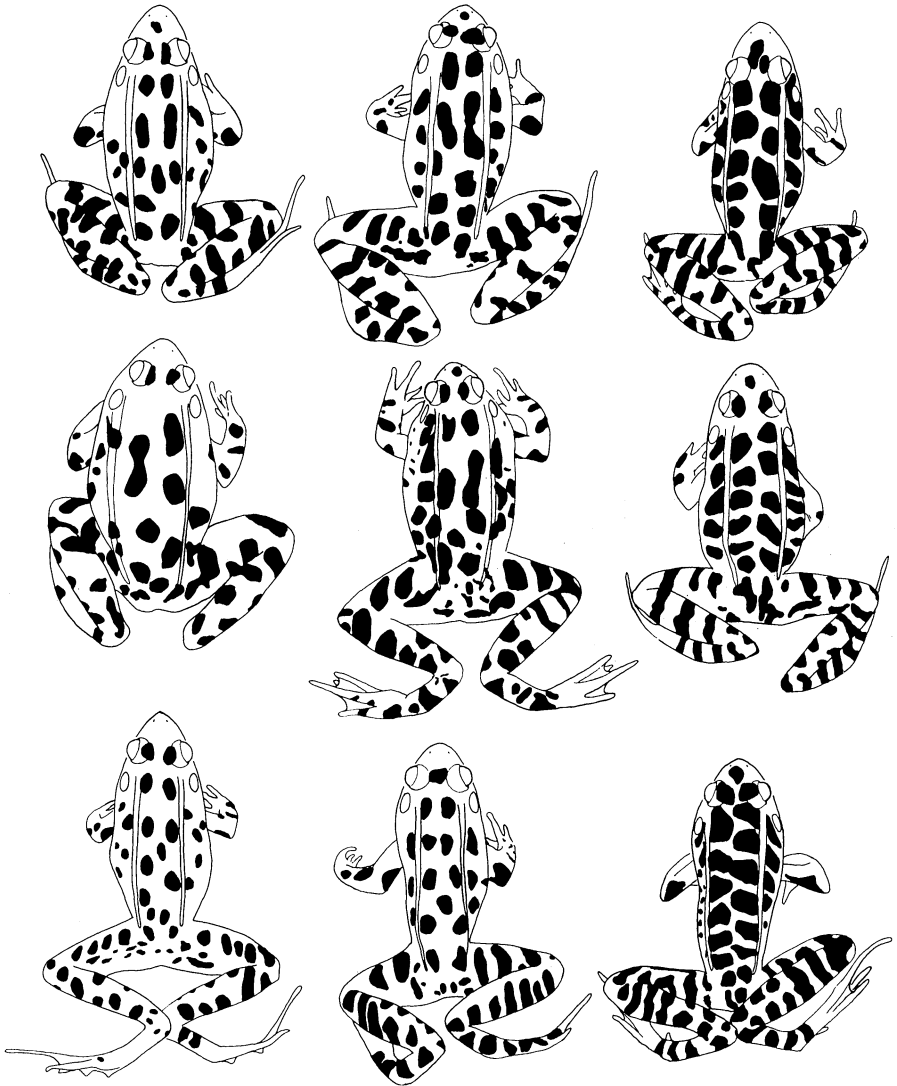


Fig. 39. North-south (top-bottom) variation in dorsal spotting of *R. pipiens* and *R. palustris* in northern Michigan. Right column is *R. palustris*; left and center columns may be *R. pipiens*. Top row, Cheboygan Co.; center row, Charlevoix Co.; bottom row, Crawford Co. Catalogue numbers of specimens, all from UMMZ, are (from left to right): top row, 42895, 47484, 61817; center row, 51791, 51790, 58664; bottom row, 59226, 59132, 59124. Drawings are not to same scale.

the glaciated region from the south. Their differences must have arisen during or prior to this period of separation.

These two species are very similar in both morphology and behavior. All of the calls in their acoustical repertoires are structurally, and apparently functionally, very similar (Fig. 11). Their life histories are basically similar. The breeding season of *R. palustris* is somewhat

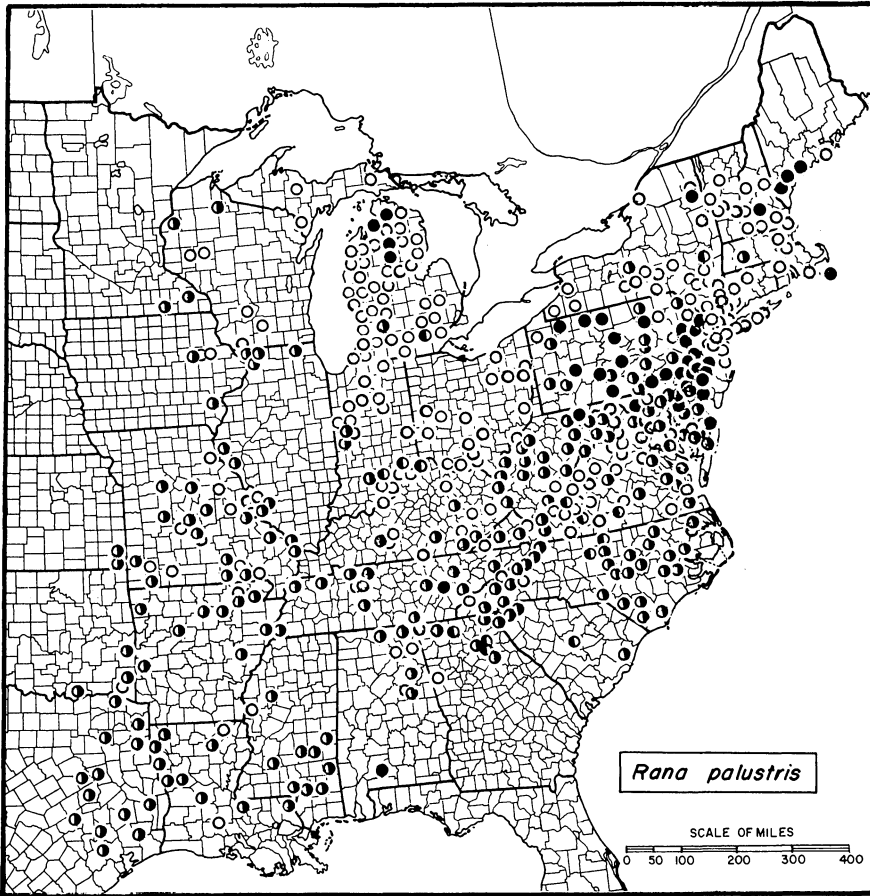


Fig. 40. Geographic distribution of *Rana palustris* in the United States. Solid dots represent specimens in museum collections examined by me; circles shaded on the right side present records from Schaaf and Smith (1970) (transferred directly from their map); circles shaded on the left side represent my field records (mostly listening records) that are additions to the above two kinds of records; open circles represent unverified records based on information in museum catalogues.

later than that of *R. pipiens* but often overlaps it. It has been suggested that this is a "partial isolating mechanism" between these two species. The absence of any evident character displacement, however, suggests that this difference arose while they were allopatric and, while it may have something to do with how they now co-exist, was not selected in the context of reproductive isolation.

#### THE PRAIRIE PENINSULA AND DISTRIBUTIONAL RELATIONSHIPS IN THE MIDDLE WEST

It is unclear where *R. blairi* survived glaciation, if it was indeed distinct at that time, but its intrusion into the midwest evidently

coincided with or followed the postglacial expansion of the Prairie Peninsula (Smith, 1957). The curious question is the geographic relationships of *R. pipiens* and *R. utricularia*. These two species now meet in the general vicinity of the glacial limit. I speculate that *R. utricularia* invaded from the south, meeting *R. pipiens* somewhere north of their present zone of interaction. Frogs from Miami County, Indiana (Indiana University, Department of Zoology Collection, Nos. 6809, 6812, and two unnumbered specimens), east of the present known range of *R. blairi* (Fig. 9), seem intermediate between that species and *R. pipiens*. Some eastern and southern populations of *R. blairi* in Illinois and Indiana appear to be distinct relicts (Figs. 9 and 34). This evidence, together with that from isolated northern populations of *R. utricularia* in southeastern Ohio (Zenisek, 1963), suggests that *R. pipiens* has moved across the former eastern range of *R. blairi* and, after contacting *R. utricularia*, has shifted its zone of interaction with that species southward. In view of this hypothesis it will be especially interesting to discover whether or not the small region just east of the present distribution of *R. blairi* (compare Figs. 1, 4, and 9) is indeed without leopard frogs.

Some problems in understanding the present distribution of *R. pipiens* in the east remain. Certain populations, for example those in northern New Jersey and in western Maryland, appear to be disjunct from more northern populations of that species (for example, those in the Mohawk River Valley). The population at Lily Pons, Maryland, may be a result of human activities at the fish hatchery there. The origin of the other populations is uncertain. The question is raised whether *R. pipiens* has receded northward along the Atlantic Coast while penetrating southward in the midwest.

#### *RANA BERLANDIERI* AND FLORIDA POPULATIONS OF *R. UTRICULARIA*

The leopard frogs of peninsular Florida are different in a number of significant ways from conspecific individuals from other areas. Adult male *R. utricularia* from peninsular Florida usually have vestigial oviducts whereas *R. utricularia* males from all other localities are without these ducts. Males of these Florida frogs (which I refer to as *R. u. sphenoccephala*) also have a higher frequency of further differentiation of the external vocal sacs than in other members of this species (Figs. 6a and 22). Furthermore the males with oviducts in Florida are significantly larger than the adult males from Florida (primarily northern Florida) without vestigial oviducts. The hLDH allele which is most common here is found in much lower frequency in other populations of this species that have been examined and the allele which is most common in the central United States part of the species' range is not found at all in southern Florida (Salthe, 1969 and Fig. 35). In all of these characteristics and in some others which will be mentioned later, these frogs resemble *R. berlandieri* in Texas.



*R. berlandieri* males characteristically (always?) have vestigial oviducts. Their external vocal sacs are not simple balloon-like bags, but are modified with texturings and foldings (Fig. 8) somewhat similar to those found on some of the Florida frogs (Fig. 6a). The hLDH common within the range of *R. berlandieri* is electrophoretically indistinguishable from the most common one in Florida. The hLDH of Florida frogs is not identical with that of *berlandieri*, however, since they can be distinguished immunologically. The mean size of adult males with vestigial oviducts from Texas (*berlandieri*) is significantly greater than the mean size of male *utricularia* from Texas or of male *utricularia* without oviducts from Florida. Males of *berlandieri* are not significantly different in size from the *u. sphenoccephala* males that have oviducts.

The prevalence of ventral melanism in both *u. sphenoccephala* and *berlandieri* is another characteristic which they share and in which both differ from most *utricularia*.

In some of his early hybridization experiments with members of the *pipiens* complex, Moore crossed frogs from Monahans, Texas (*berlandieri*) with *utricularia* from Ocala, Florida, and from Mt. Ephraim, New Jersey. He remarked at the time (Moore, 1946) that the genomes of the Texas and Florida individuals were more compatible with each other than either one was with the New Jersey individuals. This was a surprising observation to him because of the "pronounced morphological and embryological differences that separate the Florida and Texas forms," but one that accords well with my hypothesis (stated below) concerning the origin of the Florida *u. sphenoccephala*.

The fact that *berlandieri* hybridizes with Texas *utricularia* so little as to be considered a distinct species, yet resembles Florida populations of *u. sphenoccephala* which intergrade with *u. utricularia*, raises questions about the distributional history of this part of the complex. There seems to be no alternative to postulating that the ancestors of Florida *u. sphenoccephala* and Texas *berlandieri* were once connected along the Gulf Coast. The hybridization pattern today and the similarity of Gulf Coast and more northern *u. utricularia* reduces the likelihood that all of these populations evolved more or less in their present locations. It seems necessary to postulate that *u. utricularia* was once geographically isolated from the ancestor of *berlandieri* and of Florida *u. sphenoccephala*. Furthermore the patterns of hybridization and morphological variation today, giving no evidence of intergradation toward Florida or Texas morphological forms across the Gulf Coast, suggest that Gulf Coast ancestors of *berlandieri* and Florida *u. sphenoccephala* disappeared along the coast before non-Florida *u. utricularia* invaded that region. Where did non-Florida *u. utricularia* survive this period of isolation? Today *utricularia* is most abundant along the Atlantic and Gulf Coastal areas and in the Mississippi River Valley. If the eastern coast represents the geographic origin of this form, then as it invaded to the south and west while assuming its present distribution, on the basis of distance alone it would have

encountered Texas *berlandieri* much later than Florida *u. sphenoccephala*, and probably after more change. This hypothesis, while extremely tenuous in several regards, nevertheless accounts for the present patterns of distribution and hybridization. As this reconstruction was developed, it was pointed out to me by Dr. R. D. Alexander that in the cricket genus *Miogryllus*, one species (*verticalis*) occupies approximately the present range of *utricularia*, and intergrades with a variant in Florida that resembles in both song and morphology a separate species in Texas (*lineatus*).

### SUMMARY AND CONCLUSIONS

1. Populations of leopard frogs from the United States are comprised of numerous separate species. Four of these (*Rana pipiens*, *R. utricularia*, *R. berlandieri*, and *R. blairi*) have been distinguished by their vocalizations. Male specimens can also be distinguished unequivocally by certain morphological characters, in particular the structure of the external vocal sacs.

2. Each species produces several vocalizations. These were analyzed for *R. pipiens*. Playback experiments with males led to the following hypotheses regarding functional significance of some of these vocalizations: The long trill is a long-distance female-attracting call; the short trill with a faster pulse rate is a short-distance direction signaler; the third sound heard most frequently in a chorus of this species is aggressive or territorial, used primarily in male-male interactions in this species. The latter call may be the signal from which the presumed mating calls of species like *R. utricularia*, which lack the long, many-pulsed trill of *R. pipiens*, were derived.

3. Distributions of different dorsolateral fold types, of vocal sac types, and of males with and without vestigial oviducts were plotted independently and ranges of each type found to correspond closely with distributions of species as known from information on mating calls, though some species were alike in some of these morphological characters.

4. Other morphological variation, such as in frequency of snout-spotting or tympanal-spotting, or in ventral melanism, or in body proportions, may be different between species on the average, but species cannot usually be distinguished on these bases alone.

5. Geographic ranges of species are in general mutually exclusive with essentially contiguous boundaries (except in the case of *R. pipiens* and *R. palustris*, which overlap broadly, and of *R. pipiens* and *R. utricularia*, which contact one another in only a few localities).

6. Morphological variation along the Atlantic Coast in what appears to be a single species on the basis of available call data suggests that such (parapatric) distributional relationships might arise and persist

whenever disruptive selection in a geographic region has been significant in producing divergence.

7. Morphological and behavioral similarities of *R. palustris* and *R. pipiens* suggest that they are closely related and their distributional relationships suggest that geographic isolation was probably a significant factor in their divergence.

8. Genetic and morphological evidence suggests that Florida populations of *R. utricularia* and Texas populations of *R. berlandieri* are derived from the same ancestral stock, Texas populations having speciated from *R. utricularia* and the Florida populations for unknown reasons failing to do so.

## APPENDIX I: LOCALITIES OF SPECIMENS EXAMINED

All specimens in the *Rana pipiens* complex (including *R. palustris*) from the United States that have been examined during the course of this study are listed below. The species are arranged alphabetically. Localities and specimens are given in the following order: state (alphabetical order); county (alphabetical order); specific locality; letters indicating museum in which material is located (AMNH, American Museum of Natural History; INHS, Illinois Natural History Survey; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum); numbers immediately following indicate catalogue or other identifying numbers of specimens; numbers in parentheses indicate number of specimens examined from each collection for that locality. Number of male specimens examined is indicated separately. For example, (1♂, 2) indicates that a total of three specimens was examined from that locality: one was a male; the remaining two may have been females or juveniles of unknown sex. Localities that have not been located to county are listed immediately after the name of the state. Specimens with data giving only the state are listed first in that political unit under "No specific locality." Specimens located only to county are listed first in that political unit; specimens with specific localities follow. Specimens which could not be identified with confidence are listed together at the end of this appendix. Specimens of *R. utricularia* from Florida, in the private collection of S. N. Salthe at Brooklyn College, are listed separately at the end of the list for that species.

### *Rana berlandieri* Baird

TEXAS—Bexar Co.: 4 mi N of San Antonio, Highway 1604, USNM 160630 (1♂), USNM 160668 (1♂), USNM 160681 (8♂). Cameron Co.: Brownsville, USNM 3293 (1♂), USNM 131513 (1♂), AMNH 85 (1♂), AMNH 87-88 (2), AMNH 90-102 (1♂, 12); 20 mi ESE of Harlingen, near Brownsville, AMNH 51872 (2); 10 mi N of Brownsville, UMMZ 115828 (1). Comal Co.: New Braunfels, USNM 17706 (1♂). Duval Co.: San Diego, USNM 15679 (1♂). Hays Co.: San Marcos, USNM 33774 (1♂); San Marcos, Cypress Creek, AMNH 22677-22678 (1♂, 1). Kinney Co.: Fort Clark (Bracketville), USNM 20879 (1♂). Maverick Co.: Eagle Pass, AMNH 5641 (1). Tom Green Co.: Spring Creek, San Angelo, AMNH 51875 (1♂). Travis Co.: Austin, AMNH 44214-44215 (1♂, 1); Austin, Municipal Golf Links, AMNH 68341 (2♂, 1). Uvalde Co.: 2 mi N of Uvalde, AMNH 69039 (1). Ward Co.: Monahans, AMNH 58864-58881 (10♂, 8); Pyote, AMNH 58977 (1♂).

*Rana blairi* Mecham, Littlejohn, Oldham, Brown, and Brown

COLORADO—Yuma Co.: Wray, AMNH 3995 (1).

ILLINOIS—5 mi NE of Mohamet, UMMZ 79945 (1). Alexander Co.: Horseshoe Lake Dam, UMMZ 84301 (1). Calhoun Co.: 1 mi S of Hamburg, INHS 7245 (1). Champaign Co.: Fisher, INHS 2798 (1♂); Ogden, INHS 2561 (1); Okaw Creek from Copper Slough to Sadorus, INHS 1161 (1); Saint Joseph, INHS 6139 (1); 2 mi S of Urbana, INHS 3723 (1). Coles Co.: Fox Ridge State Park, INHS 2407-2408 (1♂, 1), INHS 6136 (1♂), INHS 6138 (1); Fox Ridge State Park, Charleston, INHS 1639 (1); 7 mi S of Mattoon, INHS 3827 (1); Ridge Lake, INHS 1845 (1). De Witt Co.: Farmer City, INHS 7336 (1). Douglas Co.: Chesterville, INHS 7217 (1 [hermaphrodite?]); Villa Grove, INHS 7856-7857 (1♂, 1). Edgar Co.: 3 mi W of Chrisman, INHS 8826 (1♂). Greene Co.: 3 mi S of Eldred, INHS 3606 (1). Iroquois Co.: 1 mi NE of Cissna Park, INHS 5584-5585 (1♂, 1). Jersey Co.: Saaw Island Slough, 2 mi N of Grafton, INHS 2819 (1). La Salle Co.: UMMZ 67515 (1). Logan Co.: Lincoln, T 19 N, R 3 W, Sec 2, INHS 1145 (1); Lincoln, Kickapoo Creek, T 20 N, R 3 W, Sec 20, INHS 1149 (1). Macon Co.: Decatur, INHS 8883 (1♂); Decatur, Sangamon River, 1/4 mi below Disposal Plant Outlet, INHS 1164 (1). Marshall Co.: 4 mi W of Sparland, INHS 9313 (1♂). Mason Co.: West Spillway, Chautauqua Lake, USBS Wildlife Refuge, INHS 1165 (1); Chautauqua Lake, Havana, INHS 1842 (1♂). McLean Co.: Leroy, INHS 2602 (1♂); 3 mi NW of Saybrook, INHS 8671 (1♂). Menard Co.: 2 mi E of New Salem State Park, INHS 4445-4447 (2♂, 1). Morgan Co.: Meredosia Bay, INHS 1159 (1); 4 mi E of Meredosia, INHS 4679 (1♂). Moultrie Co.: 6 mi E of Sullivan, INHS 8995-8996 (1♂, 1). Pike Co.: 1 1/2 mi NE of Summer Hill, INHS 9232 (1♂). Tazewell Co.: 5 mi NW of San Jose, INHS 8669-8670 (2); Spring Lake, INHS 8677 (1♂). Vermillion Co.: 2 mi N of Fairmount, INHS 5786 (1♂), INHS 6679 (1); Hillery, INHS 1148 (1); Kickapoo State Park, INHS 2564 (1). Wabash Co.: 2 mi N of Mount Carmel, INHS 4732 (1♂).

INDIANA—Benton Co.: Freeland Park, UMMZ 103360 (1♂). Parke Co.: Turkey Run State Park, UMMZ 98493 (1). Warrick Co.: Scales Lake, near Boonville, UMMZ 106583 (1).

IOWA—Greene Co.: Cedar Creek, UMMZ 95046 (1♂); East Buttrick Creek, UMMZ 95042 (1♂); Hardin Creek, UMMZ 95045 (1♂); Raccoon Creek, UMMZ 95044 (1♂). Taylor Co.: 1/2 mi E of Bedford, UMMZ 93172 (3♂, 1). Woodbury Co.: Brown's Lake, UMMZ 93171 (4).

KANSAS—Missouri Valley, UMMZ 52198 (1). Barber Co.: Kiowa, USNM 45379 (1♂). Bourbon Co.: Xenia, USNM 89035 (1). Cowley Co.: Near Winfield, UMMZ 75973 (1♂). Dickinson Co.: Near Herington, USNM 90791-90792 (2). Ellsworth Co.: Near Carneiro, USNM 90790 (1♂). Franklin Co.: UMMZ 67536 (1); 4 mi SE of Ottawa, UMMZ 86387 (1♂, 4). Labette Co.: Near Parsons, USNM 90320 (1♂). Marshall Co.: UMMZ 67542-67549 (41). McPherson Co.: Inman, USNM 90322-90323 (1♂, 1). Meade Co.: Meade County State Park, UMMZ 121469 (3), UMMZ 107967 (1); 3 mi E of Meade County State Park, Crooked Creek, UMMZ 107968 (1); 14 mi SW of Meade, UMMZ 91515 (1♂); 7 mi S and 2 mi W of Meade, UMMZ 96093 (2). Phillips Co.: UMMZ 67541 (2). Pratt Co.: Pratt, UMMZ 84004 (1). Reno Co.: Medora, USNM 89041-89043 (1♂, 13). Riley Co.: Manhattan, UMMZ 64405 (2). Wabaunsee Co.: Near Maple Hill, USNM 90793-90794 (2). Wallace Co.: Sharon Springs, UMMZ 68621 (1♂, 1). Washington Co.: UMMZ 67532-67535 (2♂, 3); UMMZ 67539 (4♂, 4).

MISSOURI—Mineola, AMNH 32292 (1). No Specific Locality: AMNH 57782-57786 (4♂, 1). Boone Co.: 12 mi E of Boonville, AMNH 32267-32268 (1♂, 1). Buchanan Co.: Easton, USNM 93728 (1). Cooper Co.: 4 mi E of Boonville, AMNH 32272-32273 (2), AMNH 32275-32277 (3). Daviess Co.: Grand River 1 mi S of Jameson, UMMZ 95506 (1). Holt Co.: Little Tarkio River, UMMZ 95508 (1). Jackson Co.: USNM 57951 (1); 20 mi E of Kansas City, AMNH 32286 (1); 5 mi NE of Oak Grove, AMNH 32294 (1). Jefferson Co.: Pacific, USNM 93099 (1). Lafayette Co.: Concordia, AMNH 32284-32285 (2). Macon Co.: Lingo, USNM 93726 (1♂). Mercer Co.: Sandy Creek, UMMZ 95507 (1). Pettis Co.: Shaw's Cave at Lamonte, 68939 (1). Saint Charles Co.: USNM 57942 (1♂); 6 mi E of Wentzville, AMNH 32269-32271 (3). Saint Louis Co.: Saint Louis, USNM 3431 (1), USNM 17090 (1). Saline Co.: Blackwater River, 11 mi S of Marshall, UMMZ 98005 (1).

NEBRASKA—Boyd Co.: UMMZ 67509 (1). Hall Co.: 9 mi E of Grand Island, USNM 82027 (1). Hitchcock Co.: Trenton, Republican River, USNM 150942 (1). Holt Co.: 1 mi SE of Bristow Dam, USNM 82036 (1). Jefferson Co.: Near Thompson, USNM 90787-90789 (3♂). Pierce Co.: UMMZ 67510 (1). Platte Co.: UMMZ 67513 (2♂, 1). Valley Co.: Ord, USNM 82028 (1).

NEW MEXICO—Guadalupe Co.: Santa Rosa, USNM 45368 (1♂). Union Co.: Near Gladstone, USNM 87079-87080 (2).

OKLAHOMA—2 mi N of Mullhall, AMNH 32621-32622 (2); Wichita Mountains, Mount Scott, USNM 45987 (1). No specific locality: AMNH 32608 (1); USNM 89040 (1). Beckham Co.: UMMZ 82805 (3). Cimarron Co.: UMMZ 63503 (1♂, 1); UMMZ 63504 (1♂); UMMZ 77087 (1♂). Cleveland Co.: UMMZ 77086 (1); Little River, 10 mi E of Norman, UMMZ 82799 (2). Comanche Co.: UMMZ 77594 (1); UMMZ 82802 (1); UMMZ 82804 (2). Harmon Co.: UMMZ 63502 (1). Marshall Co.: East Branch of Brier Creek, AMNH 83636 (1). Noble Co.: 12 mi N of Perry, AMNH 32607 (1). Payne Co.: 9 mi S and 1 mi W of Stillwater, UMMZ 84284 (1). Texas Co.: UMMZ 77595 (1). Woods Co.: Waynoka, UMMZ 81514 (1♂).

TEXAS—Brown Co.: Brownwood, AMNH 52848-52849 (2♂). Castro Co.: Dimmitt, USNM 46177 (1♂). Crosby Co.: Silver Falls Lake, USNM 92784 (1♂). Dickens Co.: South Wichita River, near Dickens, USNM 92739-92747 (5♂, 4), USNM 92751 (1). Donley Co.: South of Clarendon, ANSP 13646 (1). Foard Co.: Crowell, USNM 92668-92669 (2♂). Hemphill Co.: Canadian, USNM 45835-45837 (3). King Co.: Guthrie, USNM 92726-92731 (6). Lubbock Co.: Lubbock, USNM 92801-92802 (2♂). Potter Co.: 6 mi W of Amarillo, UMMZ 68976 (1♂, 3); 20 mi NW of Amarillo, UMMZ 68974 (1♂). Swisher Co.: Tule Canyon, UMMZ 68979 (8♂, 3).

### *Rana onca* Cope

NEVADA—No specific locality: USNM 57679 (1). Clark Co.: Vegas Valley, USNM 18957-18959 (3); Las Vegas, AMNH 5949-5955 (1♂, 6), AMNH 5957 (1), USNM 18961-18962 (2), USNM 18964 (1), ANSP 17873-17875 (3); Tule Springs, 12 mi W of Las Vegas, USNM 118664 (1♂).

UTAH—No specific locality: USNM 25331 (1).

### *Rana palustris* LeConte

CONNECTICUT—Hartford Co.: Scantic River, UMMZ 65392 (1).

DELAWARE—Newcastle Co.: Near Newark, ANSP 18511-18513 (3). Sussex Co.: Millsboro, ANSP 18502 (1).

MAINE—Cumberland Co.: Baldwin, Sand Pond, ANSP 19860-19863 (4). Sagadahoc Co.: Bowdoinham, ANSP 19864 (1). York Co.: Limington Sac Valley, ANSP 19858-19859 (2).

MARYLAND—No specific locality: USNM 33682 (1); USNM 48866 (1). Cecil Co.: Big Bohemia Creek, ANSP 18505 (1); Stony Run, ANSP 18529 (1); Stoney Creek at Northeast, ANSP 16396-16397 (2). Garrett Co.: Jennings, ANSP 17822 (1). Kent Co.: Chestertown, ANSP 17751-17754 (4).

MASSACHUSETTS—Middlesex Co.: Framingham, USNM 3422 (2). Nantucket Co.: Nantucket, ANSP 16163 (1).

MICHIGAN—Barry Co.: Thornapple River Drainage, UMMZ 60897 (1). Cass Co.: Marcellus Township, UMMZ 61118 (1). Charlevoix Co.: UMMZ 56647 (2); Thumb Lake, UMMZ 58664 (1). Cheboygan Co.: UMMZ 61815, 61817 (2). Chippewa Co.: Whitefish Point, UMMZ 42757, 42760 (2♂). Crawford Co.: N branch AuSable River, dam 4, UMMZ 59124 (1). Ontonagon Co.: Carp Lake, UMMZ 30758, 30760 (2).

MISSOURI—Crawford Co.: Onondaga Cave, near Leasburg, UMMZ 70693 (1).

NEW HAMPSHIRE—Merrimack Co.: ANSP 20912 (1).

NEW JERSEY—No specific locality: ANSP 14497-14505 (9). Burlington Co.: Kinkora Creek, SE of Bordentown, ANSP 17639 (1); Newton's Bridge, ANSP 19309 (1). Camden Co.: Pensauken, ANSP 19216-19220 (5). Cape May Co.: Belleplain, USNM 127330 (1). Cumberland Co.: Bridgeton, ANSP 2873 (1). Gloucester Co.: Pitman, ANSP 19086 (1). Passaic Co.: Post Brook, UMMZ 65385 (1). Sussex Co.: West Branch Papakatung Creek, near Plumbrook, ANSP 27520 (1). Warren Co.: White Pond, ANSP 4211-4215 (5).

NEW YORK—No specific locality: USNM 13409 (1). Essex Co.: Long Pond, ANSP 26636 (1). Madison Co.: Peterboro, USNM 28318 (1). Orange Co.: Highland Falls, USNM 23303-23306 (4). Oswego Co.: Oswego, USNM 131521 (1).

PENNSYLVANIA—No specific locality: ANSP 17376-17388 (13). Blair Co.: Altoona, ANSP 18638 (1). Bucks Co.: Eddertan, ANSP 18619 (1); Tributary to Core Creek, near Longhouse, ANSP 17370 (1); Tinicum Creek, 1 1/2 mi E of Yosts, ANSP 22006 (1). Chester Co.: Chadd's Ford Junction, ANSP 15850 (1); Nottingham, ANSP 16300-16304 (5). Clarion Co.: Foxburg, ANSP 17719 (1). Clinton Co.: Near Round Island, ANSP 4583-4584 (2). Delaware Co.: Addingham, ANSP 18929 (1); Near Collar Brook, tributary to Darby Creek, ANSP 17103 (1); Durlly Creek, Near Collingdale, ANSP 17149-17150 (2); Near Lansdown, ANSP 18494 (1); Markham, ANSP 17671 (1). Fulton Co.: ANSP 16178 (1). Indiana Co.: Rock Run, Green Township, ANSP 18613 (1); Simpson's Run ANSP 18615 (1). Lancaster Co.: Ephrata, ANSP 19233-19234 (2). McKean Co.: Alleghany River at Port Alleghany, ANSP 17360-17363 (4); Hemlock Forest W of Port Alleghany, ANSP 17368-17369 (2); Port Alleghany, ANSP 16218-16230 (13). Mifflin Co.: Sugar Valley Run, ANSP 18520-18522 (3). Monroe Co.: Mount Pocono, ANSP 16168 (1); Taylor's Lake, ANSP 19388 (1). Montgomery Co.: Centerville, ANSP 18618 (1); Gladwyne, ANSP 18531 (1); Jenkintown, ANSP 17367 (1); Mill Creek, ANSP 18490 (1), ANSP 18504 (1); Valley Forge, ANSP 18612 (1); Walnut Hill,

ANSP 18637 (1). Northampton Co.: Belfast, ANSP 18617 (1). Philadelphia Co.: Byberry Creek, ANSP 19087 (1); Holmesburg, ANSP 19062 (1), ANSP 19279-19281 (3); Pennypack Creek, Holmesburg, ANSP 16298 (1); Philadelphia, ANSP 2881 (1), ANSP 2883-2884 (2), ANSP 2886-2891 (1♂, 5), ANSP 2893-2894 (2); Near Philadelphia, ANSP 2874 (1). Potter Co.: Genesee Valley, near Gold, ANSP 17364-17366 (3). Sullivan Co.: Colley Township, Rouse Pond, ANSP 22765 (1); 3 mi E of Lopez, ANSP 22702-22707 (6), ANSP 22709-22711 (3); 1 mi SE of Lopez, ANSP 22712-22718 (7); Little Loyalsock Creek, 1 mi S of Dushore, ANSP 22708, 22719 (2); Ganoga Lake, ANSP 12411-12414 (4); Shady Nook, ANSP 14562 (1). Warren Co.: Warren, ANSP 17717 (1). York Co.: York Furnace, ANSP 17372-17388 (17).

SOUTH CAROLINA—Greenville Co.: USNM 72374 (1).

TENNESSEE—No specific locality: ANSP 4395 (1). Clay Co.: Near Celina, USNM 87173 (1). Roane Co.: Harriman, ANSP 4336-4337 (2).

TEXAS—Kleberg Co.: Kingsville, USNM 102667 (1).

VIRGINIA—Arlington Co.: USNM 13307 (1).

WEST VIRGINIA—Pendleton Co.: Mouth of Seneca River, USNM 33671 (1). Pocahontas Co.: Durbin, Greenbrier River, USNM 33679 (1). Randolph Co.: Mingo, Valley River, USNM 33684-33686 (3).

### *Rana pipiens* Schreber

ARIZONA—"Tuba" [probably = Tuba City, Coconino County], AMNH 3101 (1). No specific locality: USNM 16195-16197 (2♂, 1); USNM 53101 (1); USNM 60435 (1); USNM 73722-73725 (4). Apache Co.: 4 mi N of Alpine, AMNH 74522 (1♂); Alpine, 8000 ft, USNM 53100 (1♂); about 4 mi S of Alpine, AMNH 65800, 65803 (2). Coconino Co.: Tappen Springs, Cameron, USNM 79683 (1); Tuba City, USNM 45553 (1).

[ARKANSAS—Lawrence-Randolph Cos.: Imboden, AMNH 44245 (1♂). This record is probably an error. See text for explanation.]

CALIFORNIA—Eldorado Co.: 4 mi from Myer's [probably = Meyers] P.O., USNM 54967-54973 (3♂, 4).

COLORADO—"Near Valmont," AMNH 624-625 (2), AMNH 544 (1), AMNH 871 (1♂); St. Louis Valley, USNM 8251 (1♂). No specific locality: USNM 125722 (2♂); USNM 125723-125726 (4); AMNH 627 (1). Archuleta Co.: Piedra, AMNH 55962-55963 (2). Boulder Co.: Boulder, USNM 34577-34579 (3), USNM 28429 (1), AMNH 774 (1♂); 4 mi N of Boulder, AMNH 872-873 (2); about 4 mi N of Boulder, AMNH 541-543 (3), AMNH 626 (1); about 4 mi W of Boulder, AMNH 546 (1); E of Boulder, AMNH 606-607 (2); Musky Lake, near Science Lodge, Boulder, 8300 ft, AMNH 58928-58936 (9♂). Costilla Co.: Fort Garland, USNM 9944 (1). Delta Co.: Near Delta, USNM 87081 (1). Denver Co.: Denver, USNM 17654 (1♂), USNM 16661-16662 (2), USNM 8236 (2), USNM 8237 (3), AMNH 18665 (1). Eagle Co.: Gypsum, Eagle River, USNM 16364-16369 (6). El Paso Co.: Colorado Springs, 5988 ft, AMNH 52346 (12). Garfield Co.: Glenwood Springs, AMNH 6928 (1). Gunnison Co.: Meridian Lake, 20 mi N of Gunnison, USNM 137305 (1). La Plata Co.: Electra Lake, AMNH 6929 (1). Mesa Co.: Gill Creek, 1/4 mi above junction with West Creek, USNM 123586 (1). Moffat Co.: Craig, USNM 118599 (1♂); Ladore, USNM 40203 (1). Montrose Co.: Roubideau Creek, USNM

125721 (1). Sedgwick Co.: Julesburg, AMNH 6198-6199 (1♂, 1). Weld Co.: AMNH 41675-41677 (3).

CONNECTICUT—Hartford Co.: Simsbury, USNM 134412 (1♂).

[FLORIDA—Dade Co.: Miami, AMNH 38292 (1♂), AMNH 37452-37456 (5♂, 1). These records are probably erroneous. See text.]

IDAHO—2 mi W of Massacre Rock, AMNH 55992 (1); Lower Salmon Falls (probably Twin Falls County), USNM 39801 (1). Bear Lake Co.: Bear Lake, AMNH 8160 (1♂). Blaine Co.: 9.3 mi NE of Carey, AMNH 63563 (1). Bonner Co.: Sandpoint, USNM 20922 (1); Hope, Lake Pend d'Oreille, USNM 39706-39707 (2). Canyon Co.: Boise River, Caldwell, USNM 21469 (1). Elmore Co.: Mountain Home, ANSP 18011-18014 (4). Franklin Co.: Cub River Canyon, AMNH 55993 (1). Fremont Co.: 5 mi W of St. Anthony, AMNH 45946 (1). Washington Co.: Man Creek, 10 mi from Weiser, USNM 39739-39740 (2).

ILLINOIS—Boone Co.: Caledonia, INHS 2193 (1). Carroll Co.: Mt. Carroll, INHS 3441 (1); 2 mi S of Thompson, INHS 3219 (1); Carroll-Whiteside Co. line, 2 mi S of Thompson, INHS 3423 (1). Cook Co.: Barrington, Flynn Creek, concrete bridge on golf course, INHS 1163 (1). Dekalb Co.: Sandwich, INHS 6740-6743 (2♂, 2), INHS 6745-6746 (2♂). Henderson Co.: 1 mi E of Burlington, UMMZ 71533 (1♂, 1); Oquawka, INHS 2393-2403 (2♂, 9), INHS 5371-5372 (2). Jo Daviess Co.: Apple River Canyon State Park, INHS 4285-4286 (2). Kankakee Co.: Goodrich, INHS 9302 (1). Lake Co.: Antioch, INHS 7405-7406 (2); Sand Lake, INHS 1143 (1), INHS 8750-8752 (2♂, 1). LaSalle Co.: UMMZ 67515 (1♂); LaSalle, UMMZ 64437 (1♂, 1); 10 mi N of LaSalle, Spring Creek, AMNH 36652 (1). McHenry Co.: Chemung, INHS 2194 (1♂); Lake Pistakee, INHS 1700 (1♂); Marengo, Kishwaukee River, INHS 1151 (1). McLean Co.: Bloomington, UMMZ 32334 (1). Ogle Co.: Grand Detour, USNM 3429 (1♂, 4). Rock Island Co.: East Moline, INHS 4265 (1); Moline, INHS 4108-4110 (3♂); Rock Island, INHS 3707-3708 (2). Winnebago Co.: Rockford, INHS 1160 (1), INHS 3188-3190 (2♂, 1), 8753-8756 (3♂, 1); Rockford high bridge, INHS 1162 (1); 7 mi NE of Rockford, INHS 6902-6903 (2); Rock River, above Rockford, INHS 1150 (1♂); Pecatonica, INHS 1152 (1); Rock River, below Rockford, INHS 1153 (1♂); Rock River, Franklin's Spring, INHS 1154 (1); Rock Cut Forest Preserve, INHS 7285 (1♂); Rockton, INHS 3170-3172 (1♂, 2); Rock River, Pipersville Rapids, INHS 1157 (1); Kinnikinnik Creek at Meridian Highway N of Roscoe, INHS 1158 (1); Rock River, Dell Creek above route 2 bridge, INHS 1156 (1♂).

INDIANA—Miami River, ANSP 2868 (1♂). No specific locality: USNM 35991 (1). Adams Co.: 5 mi NE of Decatur, UMMZ 103494 (5); Decatur, St. Mary's River, USNM 21679 (1). Allen Co.: 4 1/2 mi NW of Arcola [Whitley County?], UMMZ 110264 (1); Fort Wayne, Old Wabash and Erie Canal, USNM 50923 (1). Benton Co.: 2 mi N of Freeland Park, UMMZ 108123 (1). Carroll Co.: 2 1/2 mi W of Deer Creek, UMMZ 101626 (2); Wild Cat Creek, Burlington, USNM 42911-42912 (2). Cass Co.: USNM 89059 (1); Lake Cicott, UMMZ 55376 (1); Mud Creek, UMMZ 68729 (1); Georgetown, UMMZ 55374-55375 (2). Decatur Co.: St. Paul, UMMZ 110270 (2). De Kalb Co.: 1/4 mi S of Auburn, UMMZ 110557 (1); 2 mi S of Auburn, UMMZ 110558 (1); Waterloo, Cedar Creek, USNM 21672-21678 (7). Delaware Co.: 2 1/2 mi N of Gaston, UMMZ 100405 (3♂, 2). Elkhart Co.: 2 1/2 mi E of Wakarusa, UMMZ 108119 (2♂). Fayette Co.: 1 mi N of Columbia, UMMZ 103558 (2♂). Floyd Co.: 1 mi NW of Georgetown, UMMZ 99116 (1). Franklin Co.: Brookville, ANSP 14564 (1♂, 1). Fulton Co.: Bruces Lake, USNM 33412-33413 (2); 4 mi W of Akron, UMMZ 101830 (1♂, 1). Grant Co.: Point Isabel, UMMZ 101629 (1♂); Sims, USNM 33778-33779 (2♂). Hamilton Co.: Fox Prairie between Noblesville and Cicero,



UMMZ 101836 (4♂). Hancock Co.: Eden, UMMZ 105549 (1♂, 1); Greenfield, UMMZ 103356 (1♂). Henry Co.: 1 1/2 mi S of Cadiz, UMMZ 105548 (2♂). Huntington Co.: West of Monument City, UMMZ 68938 (1). Jasper-Pulaski Cos.: Jasper-Pulaski State Park, West Point, UMMZ 103496 (1). Jay Co.: 3 mi NW of Bryant, UMMZ 108124 (2). Kosciusko Co.: Lake Tippecanoe, USNM 50925 (1). La Grange Co.: 2 mi SE of Mongo, UMMZ 69282 (1). Madison Co.: 1/2 mi S of Elwood, UMMZ 101632 (1). Marion Co.: Bacon's Swamp, UMMZ 100296 (1♂); Indianapolis, UMMZ 76907 (2♂, 1). Marshall Co.: Green Flat SW of Lake Maxinkuckee, UMMZ 122499 (1); Lake Maxinkuckee, USNM 33225 (1), USNM 33231 (1), USNM 33234 (1), USNM 33379 (1), USNM 33435-33437 (3), USNM 35448-35455 (6♂, 2), USNM 42619-42620 (2); Lost Lake, USNM 33390-33391 (2), USNM 33243-33246 (4). Newton Co.: 3 1/2 mi NW of Morocco, UMMZ 108122 (3♂). Noble Co.: 2 mi NE of Wilmot, UMMZ 101631 (1♂, 1). Ohio Co.: 4 mi W of Rising Sun, UMMZ 100584 (2). Pulaski Co.: 4 mi N of Winamac, UMMZ 105551 (2♂). Randolph Co.: 4 mi E of Lynn, UMMZ 101835 (1♂). Ripley Co.: Versailles State Park, UMMZ 110554 (1). Shelby Co.: Conn's Creek near Waldron, UMMZ 106586 (4). Starke Co.: W side of Bass Lake, UMMZ 122498 (1); Bass Lake Beach, UMMZ 103495 (1). Steuben Co.: Fremont, AMNH 74517-74519 (3); Hamilton, Fish Lake, USNM 21669-21671 (3). Switzerland Co.: 1 mi W of Vevay, UMMZ 101634 (1). Tippecanoe Co.: 6 mi NE of Lafayette, UMMZ 101625 (1♂). Tipton Co.: Hobbs, UMMZ 101831 (2); New Lancaster, USNM 89057-89058 (1♂, 1). Wabash Co.: 1 1/2 mi NE of Urbana, UMMZ 101630 (1). Warren Co.: 3 mi S of Pine Village, UMMZ 100302 (1♂, 1). Wayne Co.: 2 1/2 mi SE of Milton, UMMZ 103357 (4♂); Hayes Arboretum near Richmond, UMMZ 126835-126836 (2); 1 1/2 mi S of Richmond, UMMZ 101834 (1); 1 1/2 mi N of Richmond, UMMZ 105547 (1♂,1).

IOWA—Hottes Lake, UMMZ 93173 (1); Township of Spirit Lake, UMMZ 55133 (6). Black Hawk Co.: UMMZ 67552 (1); 2 mi E of Cedar Falls, UMMZ 93169 (7♂, 12). Clayton Co.: Guttenberg, UMMZ 93170 (9♂, 3). Dickinson Co.: Near Swan Lake, UMMZ 76036 (2). Johnson Co.: Iowa City, USNM 25863 (1♂). Polk Co.: Des Moines, USNM 13925 (9), USNM 14756 (1♂). Story Co.: Ames, USNM 19841-19843 (3). Woodbury Co.: Brown's Lake, UMMZ 93171 (9).

KENTUCKY—No specific locality: USNM 6283 (7). Boone Co.: Florence, UMMZ 75907 (5♂, 2). Fayette Co.: Near Lexington, UMMZ 75908 (6♂, 1). Nicolas Co.: Vicinity of Carlisle, UMMZ 81221 (1♂), UMMZ 81222 (1♂, 1).

MAINE—East Harpswell, AMNH 36661, 36663 (2); Camp Wigwam, AMNH 51725 (1); Laurentian National Park, AMNH 45734 (1); Old Beaver Pond, near St. Croix River, Woodland Township (atypical), "Selected from 36,000 frogs of which 96% are atypical or intergrades," AMNH 51343-51346 (1♂, 3). No specific locality: USNM 36322 (1); USNM 36325 (1). York Co.: Kittery, ANSP 19675 (2).

MARYLAND—Frederick Co.: Lily Pons, USNM 141003 (1), USNM 165697 (18♂).

MASSACHUSETTS—Cuttyhunk Island, Elizabeth Islands, AMNH 3380 (1♂), AMNH 3381, 3383, 3385 (3); Monterey, Lake Garfield, UMMZ 123869 (1). Hampshire Co.: Near Amherst, UMMZ 53813 (1); Northampton, UMMZ 46628 (2♂, 1), UMMZ 47225 (7); South Hadley, AMNH 7523-7525 (3). Middlesex Co.: Framingham, USNM 3422 (7); Medford, USNM 63299 (1♂). Worcester Co.: USNM 57968 (1♂).

MICHIGAN—Pine River, 3 mi above mouth, USNM 39711-39712 (2); Sheheon Creek, tributary to Saginaw Bay, Sheheon (probably Huron or Tuscola County) USNM 39726 (1). Alcona Co.: UMMZ 61800 (1); Black River, UMMZ

56582 (2); Greenbush, UMMZ 51845-51849 (5), UMMZ 51844 (1); Harrisville, UMMZ 51843 (1); Hubbard's Lake, UMMZ 56583 (1). Alger Co.: Onata Township, UMMZ 48544-48546 (1♂, 2), UMMZ 48571 (1); Otter Lake, beach pools, UMMZ 103703 (2); Near Shingleton, T45N R17W, UMMZ 103693 (2); Silver Lake, UMMZ 48572 (1); Trout Lake, UMMZ 100201 (1). Allegan Co.: Kalamazoo River, UMMZ 42111 (1); Thornapple River Drainage, UMMZ 60898 (1); Wayland, UMMZ 84196 (2♂, 3). Alpena Co.: Upper S branch Thunder Bay River, Sec 24, T31N R5E, UMMZ 63103 (1); Long Lake, UMMZ 63137 (1); Big Raisin Creek, Sec 22, T29N R7E, UMMZ 63138 (2); Devil River, UMMZ 63139 (3). Antrim Co.: UMMZ 63397 (2); Intermediate Lake, T30-31N R7-8W, UMMZ 118861 (1). Arenac Co.: UMMZ 42632 (2); UMMZ 42633 (5); Charity Island, UMMZ 41298 (1), UMMZ 42042 (6), UMMZ 42053-42058 (6), UMMZ 42077 (1); 5 mi N of Pinconning, UMMZ 95374 (1). Baraga Co.: Sturgeon River, just S of Pelkie, UMMZ 62576 (4). Barry Co.: UMMZ 41909 (1); Wall Lake, UMMZ 53816 (27), UMMZ 53817-53823 (1♂, 6), UMMZ 53824 (1♂), UMMZ 53825-53828 (4), UMMZ 53829 (1♂), UMMZ 53830 (1); Leonard's Pond, Wall Lake, UMMZ 53831 (1♂); Thornapple River Drainage, UMMZ 60897 (1♂, 4). Bay Co.: Bay City, Menona Beach, USNM 39795 (1); Bay State Park, UMMZ 63489 (1); about 2 1/2 mi W of Bay City, UMMZ 96192 (1); 3 mi N of Bay City, UMMZ 96300 (2); 1 mi N of Kawkawlin, UMMZ 96418 (2). Benzie Co.: Near Platte Lake, UMMZ 58568 (1); Manistee Drainage, UMMZ 61681 (1). Berrien Co.: Harbert, UMMZ 51175-51176 (2); Painter's Creek, Oronoko Township, UMMZ 61103 (1); Tributary to Blue Creek, UMMZ 61117 (1); 3 mi N of Three Oaks, Warren's Woods, UMMZ 99242 (1). Branch Co.: 1 1/4 mi E of Gilead, UMMZ 52011 (1♂); Marble Lake, UMMZ 52012-52013 (1♂, 1); St. Joe River, Union City, UMMZ 52014 (1). Calhoun Co.: Homer Township, S branch of Kalamazoo River, UMMZ 96191 (1♂); Marengo Township, Rick Creek, UMMZ 99727 (1♂). Cass Co.: UMMZ 41887-41893 (1♂, 6); Goose Lake, UMMZ 40916 (1), UMMZ 40920-40921 (2); Long Lake, UMMZ 40914-40915 (2), UMMZ 40917-40919 (3); Calvin Township, UMMZ 40922 (1). Charlevoix Co.: Beaver Island, 2 mi S of Antrim Iron Works, UMMZ 86004 (1); Beaver Island, 9 mi S of St. James, Millers Marsh, UMMZ 86005 (1); Beaver Island, 2-3 mi S of St. James, UMMZ 86006 (3); Beaver Island, 3 mi SW of Barney's Lake, UMMZ 86007 (17); High Island, UMMZ 125770 (1); Pine Lake, UMMZ 51792 (1); Thumb Lake, UMMZ 58663 (1). Cheboygan Co.: UMMZ 61815 (10); Douglas Lake, UMMZ 39792 (1♂), UMMZ 47483-47486 (3♂, 2), UMMZ 47488-47489 (1♂, 2), UMMZ 42895 (1); Pigeon River, E of Wolverine, UMMZ 76056 (1). Chippewa Co.: Sugar Island, Sec 26, UMMZ 103724 (1); Vermillion, UMMZ 46074, 46077-46078 (2♂, 5); Whitefish Point, UMMZ 42780 (1). Clare Co.: UMMZ 95372 (3♂, 9); Harrison, UMMZ 53832 (2); Beebe Lake, UMMZ 95043 (1). Clinton Co.: UMMZ 47442 (2); 2 mi NNE of DeWitte, UMMZ 96195 (1), UMMZ 96424 (3); 1 mi W of DeWitte, UMMZ 96196 (1); 3 mi E of Bath, UMMZ 96429 (6); Rose Lake, UMMZ 96430 (4). Crawford Co.: N branch of AuSable River, at mouth, UMMZ 30711-30713 (2); N branch of the AuSable River, Dam 4, UMMZ 59123 (1); AuSable River, just below Grayling, UMMZ 59130 (1); AuSable River, near Jones Lake, UMMZ 59131 (1); Kile Lake, 14 mi N of Wakeley's Bridge, UMMZ 59218 (1); Wakeley's, Grayling, UMMZ 59226 (1); Duck Lake, UMMZ 99645 (1); Grayling, UMMZ 30716. Delta Co.: Round Lake, UMMZ 81943 (1). Dickinson Co.: Iron Mountain, UMMZ 40325 (11♂, 1); Sturgeon River, UMMZ 40318 (1♂). Emmett Co.: Cecil Bay, UMMZ 59186 (1); Round Lake, UMMZ 56659 (1♂). Genesee Co.: Lake Fenton, UMMZ 89512 (2♂, 1); 2 mi W of Linden, UMMZ 110488 (2♂). Gladwin Co.: 7 mi W of Gladwin, UMMZ 96294 (1); 5 mi NNW of Gladwin, UMMZ 96426 (4); 1 3/4 mi NNE of Gladwin, UMMZ 96428 (5); Ross Lake, UMMZ 63444 (1). Gogebic Co.: Crooked Lake, 10 mi SW of Watersmeet, UMMZ 83774 (1); Beaver Creek, Sec 15, T44N R38W, UMMZ 113521 (1♂); Tenderfoot Creek, T45N R42W, Sec 23, UMMZ 120374 (1); Wakefield, USNM

51929 (1♂). Grand Traverse Co.: Boardman, UMMZ 61676 (2); Kilmer Creek, UMMZ 58677 (4); Kingsley, UMMZ 63401 (1); Marion Island, UMMZ 58566 (3); Mayfield, UMMZ 58675 (1), UMMZ 59116 (1); Mitchell Creek, UMMZ 58674 (1); Paradise Township, near Kingsley, UMMZ 90520 (1); Twenty Two Creek, UMMZ 58673 (1); Walton, UMMZ 90521 (1). Gratiot Co.: Alma, UMMZ 56679 (1), UMMZ 56318-56319 (2♂); 1 1/4 mi SW of Ithaca, UMMZ 96290 (1); 2 3/4 mi SW of Ithaca, UMMZ 96291 (1); 3 1/2 mi SW of Ithaca, UMMZ 96423 (3). Hillsdale Co.: Amboy Township, junction of Territorial and Woodbridge roads, UMMZ 99598 (1♂); Cambria Township, 2 mi S of Hillsdale, UMMZ 99596 (1♂); Amboy Township, Sec 4, W of Hagman Lake, UMMZ 99597 (1♂); North Sand Lake, UMMZ 52048 (1♂); Woodbridge Township, 1 mi S of Cub Lake, UMMZ 99595 (3♂). Houghton Co.: UMMZ 32917 (1); UMMZ 62589 (3); Otter River, UMMZ 76055 (1); Winona, UMMZ 32818 (1). Huron Co.: UMMZ 33752 (1♂); UMMZ 33753-33755 (3); UMMZ 33756, 33758 (2♂); UMMZ 33759 (1); Bay Port, USNM 39799 (1♂); Mud Creek, tributary of Wild Fowl Bay, Bay Port, USNM 39730 (1♂); Caseville, Pigeon River, USNM 39758 (1); Little Oak Point, UMMZ 37870 (3); Point aux Barques, UMMZ 42818 (8); Port Austin, USNM 39781 (1); Rush Lake, UMMZ 37874 (1), UMMZ 37858-37859 (2), UMMZ 37862 (1♂), UMMZ 37871 (2), UMMZ 37868 (6); Grass Lake, Sand Point, UMMZ 37872 (1); Sand Point, UMMZ 37863 (1♂, 5), UMMZ 37866 (1), UMMZ 37873, 37875-37876 (6), UMMZ 37855-37856 (2); Stony Island, UMMZ 37864 (1♂), UMMZ 37869 (10). Ingham Co.: UMMZ 63445 (1); 2 1/2 mi NW of Webberville, UMMZ 96425 (3); Zimmer Road, below Williamston, UMMZ 96431 (4). Ionia Co.: 2 mi N of Portland, UMMZ 96419 (2); 3.2 mi N of Portland, Grand River, UMMZ 96200 (1); 6 mi N of Muir, UMMZ 96422 (3). Iosco Co.: East Tawas, USNM 39728 (1); Tawas, UMMZ 61963 (1). Iron Co.: Golden Lake, Sec 26 T44N R37W, UMMZ 113523. Isabella Co.: UMMZ 63398 (1). Jackson Co.: Francisco, UMMZ 56573 (1♂); Grand River Drainage, UMMZ 60896 (2); Wolf Lake, USNM 42706-42707 (1♂, 1). Kalamazoo Co.: Kalamazoo River, UMMZ 42109 (3), UMMZ 42110 (1); Head Portage River, near Kalamazoo, UMMZ 88893 (2); Outlet to Gull Lake, near Kalamazoo, UMMZ 96190 (1). Kalkaska Co.: UMMZ 45652 (1); UMMZ 68834 (1♂, 4); UMMZ 69342 (1); Big Twin Lake, UMMZ 69544 (1); Near Rapid City, Round Lake Swamp, UMMZ 122733 (1). Kent Co.: Nelson Township, UMMZ 61110 (3); Reed Lake, Grand Rapids, UMMZ 51868-51871 (4). Keweenaw Co.: Phoenix, Eagle River, UMMZ 88474 (1♂, 1); 2.2 mi SE of Copper Harbor, Keweenaw Point (= Clark Mine), UMMZ 98432 (4♂, 21). Lake Co.: UMMZ 61114 (1♂); Ellsworth Township, UMMZ 60894-60895 (2♂); Twin Lakes, near Sauble Corners, UMMZ 96297 (2). Lapeer Co.: UMMZ 64289 (1♂). Leelanaw Co.: Duck Lake, UMMZ 56207 (3), UMMZ 56208 (8), UMMZ 56209 (2♂), UMMZ 82961 (1♂, 3), UMMZ 89499 (7). Lenawee Co.: Devil's Lake, UMMZ 61683 (1♂); 1/4 mi E of Morenci, UMMZ 99258 (1♂); Seneca Township, NE corner, Sec 31, UMMZ 99257 (1); Seneca Township, SE quarter, Sec 31, UMMZ 99256 (1♂); Tiffin River, S of Hudson, UMMZ 61697 (1). Livingston Co.: Brighton, UMMZ 32321-32322 (2), UMMZ 31606 (1), UMMZ 46449 (1), UMMZ 46456-46457 (2); Edwin S. George Reserve, UMMZ 100045 (3); Iosco Township, UMMZ 74529 (1). Luce Co.: UMMZ 72437 (2); Taquamenon Drainage, UMMZ 61707 (5); Kilhane Lake, UMMZ 61774 (1♂). Mackinac Co.: Mouth of Carp River, tributary to St. Martin's Bay, 12 mi from Straits of Mackinac, USNM 39791 (1); Bois Blanc Island, UMMZ 91430 (4♂, 9); Hendricks Quarry, UMMZ 52272-52274 (3). Macomb Co.: Dollar Lake Outlet, Section 5, T4N R12E, UMMZ 122801 (1); Utica, Messmore's Pond, UMMZ 77882 (1♂); 2 mi SW of New Baltimore, UMMZ 96194 (1); 2 1/2 mi SW of Romeo, UMMZ 96193 (1); 2 mi S of Utica, UMMZ 96197 (1). Manistee Co.: UMMZ 61104 (5); East Lake, UMMZ 46038-46048 (1♂, 10), UMMZ 46050-46053 (4); Above Highbridge, UMMZ 45650 (1♂); Little Manistee Drainage, UMMZ 61107 (2); Stronach Township, UMMZ 63400 (1♂, 2); Bar

Lake, UMMZ 96295 (1). Marquette Co.: UMMZ 64278 (2); Mountain Lake, UMMZ 64297 (1); 1 mi W of Five Forks, UMMZ 88432 (1); Head of Mountain Stream, UMMZ 88433 (1). Mason Co.: UMMZ 61116 (1); UMMZ 63073 (1); Custer Township, Sec 9, Pere Marquette River, UMMZ 100065 (1); Ludington State Park, UMMZ 101348 (1). Mecosta Co.: Green Township, Sec 14, UMMZ 61685 (1♂); Sheridan Township, UMMZ 63399 (1). Menominee Co.: UMMZ 63443 (1♂); Menominee River, Chappel Rapids, UMMZ 83989 (1); 7 mi E of Stephenson, UMMZ 88467 (3). Midland Co.: Bullock's Creek, UMMZ 63490 (2); 2 mi N of Midland, UMMZ 96199 (1); 16 mi SW of Midland, Pine River, UMMZ 96292 (1); 2 mi N of Sanford, Midland Game Refuge, UMMZ 96293 (1); 5 mi W of Sanford, UMMZ 96420 (2); 3.5 mi S of Sanford, UMMZ 96427 (5). Missaukee Co.: UMMZ 64337 (4). Monroe Co.: Grape, UMMZ 44650 (1); 1 mi E of Grape, UMMZ 44660 (1♂); Plum Creek, UMMZ 44648-44649 (2), UMMZ 44658 (1); Raisin River, Grape, 14 mi from mouth, UMMZ 44652 (1♂); Raisin River, 8 mi from mouth, UMMZ 44651 (1); N of Raisin River, UMMZ 44653 (1); woods, 1 mi S of Raisin River, UMMZ 44654 (1); Raisin River, 8 mi from mouth, UMMZ 44655-44656 (2); 0.5 mi N of Raisin River, UMMZ 44657 (1), UMMZ 44659 (1); Monroe Piers, 4 mi from Monroe, UMMZ 44643 (1); Monroe Piers, UMMZ 44638-44641 (1♂, 3), UMMZ 44644-44647 (1♂, 3), UMMZ 44663 (1♂), UMMZ 44667 (1); N of Monroe Piers, UMMZ 44664-44666 (2♂, 1); Sand Beach, N of Monroe Piers, UMMZ 44642 (1♂). Montmorency Co.: UMMZ 62590 (1); UMMZ 62593 (1♂, 2); King's Camp, UMMZ 58567 (1♂, 2); Tributary to Black River, Vienna Township, Sec 30, UMMZ 61784 (1). Muskegon Co.: UMMZ 66770 (1). Newaygo Co.: UMMZ 63442 (1); UMMZ 63446 (1♂). Oakland Co.: 2 mi E of South Lyon, UMMZ 84292 (1); Walnut Lake, UMMZ 36825 (3♂, 3), UMMZ 32986-32987 (1♂, 1), UMMZ 36828 (1). Oceana Co.: Fogg Lake, UMMZ 56667 (1♂); Pentwater, UMMZ 57678 (1); Shelby, UMMZ 30620 (1), UMMZ 30625 (1); W of US route 31 at the Mason-Oceana county line, UMMZ 96299 (2). Ogemaw Co.: Edward's Lake, UMMZ 63488 (1); Sec 14, T23N R3E, UMMZ 106524 (1). Ontonagon Co.: UMMZ 32844 (1); Carp Lake, UMMZ 30755 (1), UMMZ 30761-30762 (2); Porcupine Mountains, UMMZ 32311 (1♂), UMMZ 32315 (3). Osceola Co.: UMMZ 64376 (1); 4.5 mi N and 1 mi E of Reed City, UMMZ 96298 (2♂). Otsego Co.: UMMZ 61804 (1♂, 4); UMMZ 62587 (1); Pigeon River Trout Research Area, Sec 10 and 15, T32N R1W, UMMZ 110522 (1). Ottawa Co.: UMMZ 66706 (2); Port Sheldon, UMMZ 102799 (1). Presque Isle Co.: Sunken Lake, UMMZ 63102 (1); 2.2 mi E of Mulky Crossroads on road to Rogers City, UMMZ 99321 (1); 3 mi SE of Cheboygan County, on highway along Lake Huron, UMMZ 99322 (1). Roscommon Co.: Beaver Creek, UMMZ 59151 (1); Houghton Lake, UMMZ 46443 (9), UMMZ 56655, 56657-56658 (3), UMMZ 56662 (1); Beaver Creek, near Roscommon, UMMZ 61821 (3); Robinson Creek, 1 mi above Roscommon, UMMZ 59219 (1♂). Saginaw Co.: Bow of Tittabawassee River, UMMZ 63101 (3); Saginaw River near Stilwaukee, UMMZ 82082 (1); 1.5 mi N of Swan Creek, UMMZ 95373 (1). St. Clair Co.: Port Huron, USNM 3413 (3), USNM 39804 (1), UMMZ 42639 (6). St. Joseph Co.: Klinger Lake, UMMZ 38896 (1). Sanilac Co.: Black River, UMMZ 83012 (1); Minden City Game Refuge, UMMZ 96421 (3). Schoolcraft Co.: UMMZ 62577 (1); Floodwood, UMMZ 47374-47377 (5); Seney Refuge, Germfask, UMMZ 95376 (1). Shiawassee Co.: Byron, UMMZ 68725-68726 (3). Tuscola Co.: Cass River, UMMZ 63491 (2); Juniata Township, UMMZ 82107 (5); 6 mi W of Unionville, UMMZ 96198 (1). Van Buren Co.: UMMZ 96189 (1); South Haven, Black River, UMMZ 103666 (2♂, 3); Wolf Lake Hatchery, UMMZ 116305 (1♂); Sec 10, T4S R13W, UMMZ 118466 (1). Washtenaw Co.: UMMZ 30623 (1); UMMZ 34246 (1); Ann Arbor, UMMZ 41904 (1), AMNH 32714-32715 (2), UMMZ 34399 (1♂), UMMZ 34247 (1), UMMZ 31455-31456 (2), UMMZ 30643-30645 (3); Ann Arbor, Hamilton Park, UMMZ 32586 (1); Ann Arbor, overflow, UMMZ 30401 (1♂, 1); 3 mi E of Ann Arbor, UMMZ 30464 (1); Ann

Arbor, Three Sisters Lakes, USNM 35601 (1), UMMZ 30396 (2); Three Sisters Lakes, UMMZ 30473 (4); First Sister Lake, UMMZ 51909 (1♂); Third Sister Lake, UMMZ 33040 (1♂), UMMZ 31357 (1), UMMZ 30808 (1♂), UMMZ 30806 (2♂, 7), UMMZ 36078 (1); Dowd Creek, UMMZ 60899 (1); Fleming Creek, UMMZ 51907-51908, 51910 (3); Fiegals Creek, UMMZ 41987 (2); Chelsea, UMMZ 34754 (1♂, 3), UMMZ 34892-34893 (1♂, 1); Lima Center, UMMZ 30500 (1♂); Portage Lake, UMMZ 30628-30629 (2), UMMZ 30631-30632 (2), UMMZ 30634 (1), UMMZ 43936-43937 (2). Wayne Co.: Grosse Isle, UMMZ 51906 (1), UMMZ 95375 (1); Detroit River, Grosse Isle, USNM 39735-39736 (2); Detroit, Fox Creek, USNM 39798 (1). Wexford Co.: UMMZ 45651 (1); Fife Lake Forest, S tributary to Manistee River, UMMZ 90519 (1); Poplar Creek, N of Lake-Wexford county line, UMMZ 96296 (1).

MINNESOTA—No specific locality: USNM 37941-37945 (1♂, 4); USNM 6472-6476 (5). Chisago Co.: Colby Lake, Taylors Falls, USNM 64854-64855 (2); Lindstrom, North Lake, USNM 64856-64858 (3); Lindstrom, Lake Chisago, USNM 64685-64723 (39); Green Lake, Chisago City, USNM 64727 (1); Stacy, Tamarack Lake, USNM 70452 (1). Hennepin Co.: Vicinity of Fort Snelling, USNM 32054-32055 (2♂); Fort Snelling, AMNH 875-882 (1♂, 7), AMNH 11710-11716 (2♂, 5). Lake Co.: Hare Lake, 7 mi W and 4 mi N of Schroeder, AMNH 77315 (1♂). Nicollet Co.: West Newton, USNM 81994-81996 (1♂, 2). Renville Co.: 1.2 mi W of Hector, route 212, USNM 141963 (1♂), USNM 134045 (1♂). Sherburne Co.: Elk River, Birch Lake, USNM 70453-70455 (3). Stearns Co.: Koronis Lake, Paynesville, USNM 70456-70457 (1♂, 1).

MONTANA—Indian Creek, USNM 59298 (1); 5 mi SW of Oka, USNM 61578-61579 (2); Post Creek, USNM 20917-20919 (3); Yellowstone River, collected by Dr. F. V. Hayden, USNM 3363 (1♂, 1); Sioux National Forest, USNM 54536 (1). No specific locality: USNM 62315 (1). Beaverhead Co.: Dillon, Beaver Head River, USNM 17572 (1). Big Horn Co.: Crow Agency, USNM 59785-59786 (2). Carter Co.: Capitol, USNM 54576 (1♂); 5 mi S of Sand Creek, USNM 54543-54544, 54546 (3♂); Ekalaka, USNM 54539-54540 (2), USNM 54541 (1). Custer Co.: Miles City, USNM 61560-61567 (8). Fergus Co.: 8 mi W of Lewistown, on Beaver Creek, USNM 61584, 61586 (1♂, 1); Moccasin Mountains, 5 mi NW of Hilger, USNM 62472 (5); 7 mi NE of Hilger, USNM 62393, 62396-62397, 62399 (4♂). Hill Co.: Box Elder Creek, USNM 54542 (1). Lake Co.: Swan River, near Swan Lake, USNM 17573 (1). Lewis and Clark Co.: Missouri River, Wolf Creek, USNM 11926 (3♂). Meagher Co.: Martinsdale, S fork of the Musselshell River, USNM 61571-61577 (7). Phillips Co.: Zortman, Ruby Creek, USNM 62391 (1♂). Powder River Co.: Powderville, USNM 54537 (1), USNM 51583 (1). Prairie Co.: Yellowstone River, USNM 61549-61559 (11). Rosebud Co.: SW of Ashland, USNM 59301-59304 (4); Lane Deer, USNM 59299 (1), USNM 61367 (1). Stillwater Co.: Head of Valley Creek, 10 mi N of Park City, USNM 60286 (1). Sweet Grass Co.: Big Timber, USNM 60331 (1♂), USNM 60437-60438 (1♂, 1); 10 mi N of Plateau (probably Sweet Grass County), USNM 60434 (1♂). Valley Co.: Glasgow, USNM 62385 (1). Wheatland Co.: Judith Gap, USNM 61580 (1). Wibaux Co.: 17 mi S of Wibaux, USNM 54547-54550 (4♂). Yellowstone Co.: Billings, USNM 45500-45504 (1♂, 4), USNM 82323-82324 (2).

NEBRASKA—No specific locality: USNM 4794 (2). Antelope Co.: UMMZ 67511 (3). Boyd Co.: UMMZ 67507 (2♂); UMMZ 67508 (5); UMMZ 67514 (2♂). Brown Co.: Ponds, 17 mi S of Long Pine, USNM 21288-21292 (1♂, 4). Buffalo Co.: Ravenna, USNM 19824 (1♂). Cass Co.: South Bend, USNM 19826 (1). Cherry Co.: Kennedy, UMMZ 66752 (2). Dawes Co.: Chadron, USNM 21367 (1). Dakota Co.: 4 mi N of Homer, USNM 83958 (1). Douglas Co.: Omaha, UMMZ

46454-46455 (2). Holt Co.: UMMZ 67506 (1♂, 9); Atkinson, USNM 82037-82039 (1♂, 2). Howard Co.: 6.5 mi W of St. Paul, USNM 82030 (1). Knox Co.: Niobrara, USNM 21281-21283 (1♂, 2). Madison Co.: UMMZ 67512 (1); 6 mi SW of Norfolk, USNM 82032-82035 (4). Platte Co.: UMMZ 67513 (1). Pierce Co.: UMMZ 67510 (1). Valley Co.: Ord, USNM 82028 (1).

NEVADA—Carson City: AMNH 5900-5906 (3♂, 4). Churchill Co.: Fallon, USNM 118604 (1); Near Fallon, USNM 87076-87078 (3). Elko Co.: 3 mi S of Halleck, USNM 71189 (1), 71218-71235 (19). Lincoln Co.: Pahrnagat Valley, USNM 18927 (1♂). Washoe Co.: Pyramid Lake, The Willows, USNM 50694-50695 (2).

NEW HAMPSHIRE—Second Connecticut Lake, USNM 134408-134411 (1♂, 3). Coos Co.: 7 mi NE of Pittsburg, UMMZ 86299 (1); 15 mi NE of Pittsburg, USNM 131903, 131905 (2♂); First Connecticut Lake, USNM 36456 (1♂). Grafton Co.: 1.75 mi SW of Haverhill, UMMZ 86301 (2♂, 1); Hanover, USNM 131902 (1♂); Ammonoosuc River, Woodsville, UMMZ 86297 (1). Hillsboro Co.: 3 mi NE of Amherst, UMMZ 84568 (1♂); Near Nashua, UMMZ 84570 (1♂). Merrimack Co.: Near Penacook, UMMZ 84569 (1♂). Sullivan Co.: 2 mi S of Charlestown, UMMZ 86300 (1♂).

NEW JERSEY—Sussex Co.: Newton, AMNH 13114 (1), AMNH 35138-35139 (2). Warren Co.: Jenny Jump State Park, AMNH 51720 (5).

NEW MEXICO—Lake Burford, USNM 63057-63060 (4). No specific locality: USNM 87066-87074 (9). Bernalillo Co.: Albuquerque, USNM 3294 (1). Colfax Co.: Philmont Ranch, 18 (1.8?) mi SSW of Cimmaron, AMNH 46206 (1). McKinley Co.: Chusca Mountains, USNM 63054-63056 (3). Otero Co.: Mescalero, USNM 25441 (1♂). Rio Arriba Co.: Abiquiu, USNM 8499 (1♂, 1); Chama, AMNH 45780-45785 (6). San Miguel Co.: Near Las Vegas, USNM 87075 (1). Santa Fe Co.: Santa Fe USNM 8500 (1).

NEW YORK—No specific locality: AMNH 51042-51045 (4♂, 6); USNM 38352-38353 [could be 28352-28353] (2). Bronx Co.: Van Cortlandt Park, AMNH [field tags read 198, 197; data as for AMNH catalogue number 52342] (1♂, 1). Broome Co.: Castle Creek, UMMZ 78904 (1). Chautauqua Co.: Panama, UMMZ 82061 (1♂, 1); Chautauqua Lake, USNM 51227-51228 (2). Chenango Co.: Near South Otselic, UMMZ 78906 (1). Clinton Co.: 4 mi NE of Au Sable Forks, UMMZ 71704 (2). Cortland Co.: Near Homer, UMMZ 78905 (1). Essex Co.: 2.9 mi W of Wilmington, AMNH 68336 (1); 0.5 mi W of Wilmington, AMNH 68337 (6); Near Severance, AMNH 24337-24340 (1♂, 3). Hamilton Co.: Raquette Lake, USNM 82503 (1). Jefferson Co.: Grenadier Island, USNM 17653 (1); Cape Vincent, USNM 39815 (1♂), USNM 62750 (1); Stony Island, USNM 39807 (1). Madison Co.: Peterboro, USNM 28352 (1♂). Monroe Co.: Irondequoit Bay, UMMZ 71696 (2). Niagara Co.: 2 mi E of Lewiston, UMMZ 71705 (2). Oneida Co.: 1 mi S of Westernville, UMMZ 71693 (8); 3 mi E of Vienna, UMMZ 71695 (2). Orleans Co.: 1 mi W of Murray, UMMZ 71700 (1). Oswego Co.: Salmon River estuary, near Pulaski, UMMZ 74310 (10); Oswego, USNM 131520 (1), USNM 131522 (1). Otsego Co.: Near Edmeston, UMMZ 78907 (1). St. Lawrence Co.: Madrid, USNM 3403 (1). Thompsons Co.: Ithaca, AMNH 255 (1); Fall Creek, Etna, UMMZ 71365 (1♂). Wayne Co.: Wallington, UMMZ 71701 (1).

NORTH DAKOTA—Goodall, USNM 53091-53094 (4); Grinell, USNM 53096 (1); Lost Wood, USNM 53089 (1♂); Spring Lake, USNM 53086 (1); Tenman, USNM 50001 (1); Wood Lake, USNM 53087-53088 (2). No specific locality: USNM 52454-52455 (2♂). Barnes Co.: Moon Lake, Valley City, USNM

66613-66615 (3). Benson Co.: Tokio, USNM 53095 (1); Fort Totten, USNM 53099 (1). McLean Co.: Washburn, USNM 45505-45506 (2). Ramsey Co.: Devil's Lake, USNM 38093 (1). Richland Co.: Wahpeton, USNM 53090 (1♂), USNM 53133 (1).

OHIO—Maumee Basin, USNM 21660-21664 (5). Allen Co.: Lima, Sugar Creek, USNM 21666 (1). Ashtabula Co.: Ashtabula River, Geneva, Cowles Creek, USNM 39734 (1). Auglaize Co.: Moulton Township, Sec 36, UMMZ 98031 (1♂). Champaign Co.: Cedar Swamp, UMMZ 111976 (1♂). Fayette Co.: Washington Court House reservoir, UMMZ 111980 (1♂). Franklin Co.: USNM 25987 (1); Columbus, USNM 3418 (1♂, 2). Greene Co.: Yellow Springs, Glen Helen, UMMZ 111974 (2♂); 1 1/2 mi NE of Xenia, UMMZ 112215 (1♂). Huron Co.: Monroeville, Huron River, USNM 39796 (1). Lorain Co.: Black River, USNM 39809 (1♂). Lucas Co.: Toledo, USNM 5453 (1); Toledo, Cedar Point, USNM 39777 (1); Toledo, Maumee River, USNM 21665 (1). Miami Co.: 1/4 mi S of West Milton, UMMZ 111982 (4♂). Montgomery Co.: Germantown Dam, UMMZ 111988 (1♂). Ottawa Co.: Put in Bay, USNM 39721 (1♂). Putnam Co.: Cloverdale, Sugar Creek, USNM 21667-21668 (2). Scioto Co.: Near Franklin Furnace, AMNH 51629 (1♂). Shelby Co.: 7/8 mi NNW of McCartyville, UMMZ 111970 (1♂). Warren Co.: 1 mi W of Waynesville, UMMZ 111977-111979 (6♂). Wayne Co.: Chippewa Township, Sec 18, UMMZ 123235 (1♂). Wood Co.: Grand Rapids, Beaver Creek, USNM 21659 (2).

OKLAHOMA—Caddo Co.: 6 mi E of Hydro, UMMZ 68754 (1).

OREGON—John Day River, USNM 12585 (1). Malheur Co.: Ontario, USNM 38391-38392 (1♂, 1). Umatilla Co.: Umatilla, USNM 53097-53098 (1♂, 1). Wasco Co.: Fort Dalles, USNM 3375 (1).

PENNSYLVANIA—Crawford Co.: Pymatuning Swamp, UMMZ 71918 (4♂). Cumberland Co.: Carlisle, USNM 3419 (1♂, 5). Indiana Co.: Cherry Run, ANSP 19265 (1); Indiana, ANSP 19828 (1♂). Jefferson Co.: Brookville, USNM 4830 (1♂). Sullivan Co.: 1 mi S of Dushore, Little Loyalsock Creek, ANSP 22720-22724 (5). Warren Co.: UMMZ 67118 (1).

RHODE ISLAND—Newport Co.: Newport, ANSP 2822-2842 (21); Newport, Peat Pond, USNM 28744-28749 (2♂, 4), USNM 30055-30057 (1♂, 2). Providence Co.: Providence, AMNH 287 (1♂), AMNH 257-259 (1♂, 2).

SOUTH DAKOTA—No specific locality: USNM 21279 (1); USNM 21380 (1); USNM 63053 (1). Brookings Co.: Brookings, USNM 68717 (1). Fall River Co.: Ardmore, USNM 63052 (1), USNM 19823 (1♂); Hot Springs, USNM 19817-19822 (4 ♂, 2). Hamlin Co.: Lake Norden, USNM 140726 (1♂). Lake Co.: 4 mi S of Winfred, USNM 140727 (1♂). Marshall Co.: West Sieche Hollow, USNM 140728 (1). McCook Co.: Montrose, USNM 140729 (1). Pennington Co.: Rapid City, USNM 19816 (1♂). Roberts Co.: Bullhead Lake, USNM 140730 (1♂).

UTAH—Provo River, USNM 13987 (1); Salt Lake Valley (probably Salt Lake County), USNM 3341 (1). No specific locality: USNM 14011 (7); USNM 8101 (1). Beaver Co.: Beaver Creek, USNM 36363 (1); Beaver Creek, Beaver City, AMNH 36644-36650 (7). Garfield Co.: Panguitch, USNM 46095 (1♂). Kane Co.: Kanab, USNM 89872 (1). Salt Lake Co.: Murray, AMNH 6169-6174 (4♂, 2); Salt Lake City, AMNH 6157-6168 (1♂, 11). Uintah Co.: Near Jensen, USNM 66176-66177 (2). Utah Co.: Near Colton, USNM 87082-87083 (2); Provo, USNM 121478-121483 (6). Washington Co.: Springdale, AMNH 63564 (1).

VERMONT—No specific locality: AMNH 14377-14385 (2♂, 7); AMNH 43803-43804 (2); UMMZ 52293 (1). Addison Co.: Shoreham Center, Richville, AMNH 14390-14394 (5). Franklin Co.: St. Albans, AMNH 14376 (1); Swanton, UMMZ 52301 (1♂). Grand Isle Co.: Alburg, AMNH 43796-43802 (7). Lamoille Co.: Stowe, USNM 103313 (1); 4 mi NE of Stowe, Joe's Pond, USNM 108708 (1). Washington Co.: 1 mi E of Middlesex, UMMZ 71698 (1).

WASHINGTON—Walla Walla Co.: Fort Walla Walla, USNM 10922 (3); Touchet, USNM 45367 (1), USNM 45380 (1).

WEST VIRGINIA—Wood Co.: Williamston, AMNH 78337-78358 (13♂, 9).

WISCONSIN—Root River, USNM 3427 (1♂). Bayfield Co.: Bayfield, Pike River, USNM 39720 (1); 3.5 mi N and 4.5 mi W of Iron River, AMNH 77323 (1). Chippewa Co.: Stanley, AMNH 6842-6847 (6). Racine Co.: Racine, USNM 3421 (1♂, 3). Winnebago Co.: Oshkosh, AMNH 51294 (1).

WYOMING—No specific locality: USNM 21366 (1♂). Albany Co.: USNM 57971-57972(2); Laramie, USNM 9353 (1), USNM 9356 (1). Big Horn Co.: Grey Bull, USNM 48173 (1♂). Teton Co.: Beaver Dick Lake, Grand Teton Park, AMNH 45746 (1). Uinta Co.: Fort Bridger, USNM 46214-46217 (4); Fort Bridger Reservation, USNM 5456 (1♂). Washakie Co.: Ten Sleep, USNM 48119-48120 (2).

*Rana utricularia* Harlan

ALABAMA—Baldwin Co.: Bayou Minette, UMMZ 90099 (1). Barbour Co.: Bethel, 2 1/2 mi E of Pine Hill, USNM 62350 (1). Limestone Co.: Near Athens, USNM 92433 (1). Mobile Co.: USNM 42550 (1); USNM 57510-57513 (4); Mobile, USNM 80122 (1); Mobile Bay USNM 46144 (1). Randolph Co.: 3.8 mi NW of Wadley, UMMZ 122172 (1). Talladega Co.: 6.5 mi ENE of Talladega, UMMZ 99404 (1♂); Howell's Cove, UMMZ 122171 (1♂).

ARKANSAS—No specific locality: AMNH 24271-24276 (3♂, 3); USNM 9261 (1). Boone Co.: Harrison, Harrison Spring, AMNH 52057 (4♂, 3). Greene Co.: Cache River, 93174-93175 (1♂, 1). Lawrence-Randolph Cos.: Imboden, AMNH 44246 (1♂), AMNH 22718-22731 (14♂). Logan Co.: Booneville, USNM 99485 (1). Miller Co.: 4 mi N of Texarkana, AMNH 32623 (1). Montgomery Co.: 1/4 mi E of Oden, USNM 99536 (1).

DELAWARE—Fort Miles, USNM 121219 (1). Kent Co.: Brown's Bridge, near Harrington, ANSP 18514 (1♂). Newcastle Co.: Delaware City, ANSP 18627-18628 (2), ANSP 15901-15903 (1♂, 2), USNM 118278-118279 (2♂).

DISTRICT OF COLUMBIA—Washington, USNM 9257 (1♂), USNM 11967 (1), USNM 13310-13311 (2), USNM 17366 (1), USNM 19253 (1), USNM 36100 (1), USNM 45977 (1♂), USNM 49672-49673 (1♂, 1), USNM 80126-80129 (1♂, 3).

FLORIDA—Braden River (probably Manatee County), USNM 61340-61341 (2); Kissimmee River at Alligator Bluff (probably Okeechobee County), USNM 29003 (1); Kissimmee River, Fort Gardner, USNM 28864 (2); Kissimmee River at Whidden's Landing, USNM 36495 (1); Acklewaha [= Oklawaha River?], UMMZ 44945-44952, 44955, 44958 (6♂, 4); Lake Okechobee, UMMZ 77193 (2); Near camp at Okochobee, AMNH 44197 (1); Ozona, AMNH 106-116 (12); Caloosahatchie River, ANSP 2862 (1); Southwestern Florida, ANSP 3081-3087 (7). No Specific Locality: AMNH 49896-49897 (2); AMNH 51046 (1♂); AMNH



65709 (1♂); AMNH 15176-15181 (2♂, 4); AMNH 16908 [= AMNH 16098 from Eastport ?] (1); USNM 57058 (1); USNM 57509 (1); USNM 29004 (1). Alachua Co.: UMMZ 56615 (1♂, 1); UMMZ 56546-56547 (2); Gainesville, UMMZ 57773 (2), UMMZ 84465 (1), AMNH 34393-34395 (12♂), AMNH 38282 (1♂), AMNH 38284 (1♂); Near Gainesville, UMMZ 77192 (3); 8 mi S of Gainesville, USNM 107259-107260 (2); Micanopy, USNM 4747 (1♂). Brevard Co.: Canaveral, AMNH 3879 (1), AMNH 6480-6482, 6484-6489 (7♂, 3); Eau Gallie, AMNH 3843-3844, 3847-3848, 3850 (5); Indian River, USNM 3692 (1♂). Broward Co.: 1.6 mi W of Hollywood, UMMZ 108400 (1♂, 1); 2.2 mi W of Hollywood, UMMZ 108401 (1). Collier Co.: 5.1 mi N of Carnestown, UMMZ 109412 (1); 8 mi W of Carnestown, UMMZ 109409 (1); Marco Island, UMMZ 108398 (1), UMMZ 111417 (5); Marco Island, 10.1 mi SW of Royal Palm Hammock, UMMZ 109403 (1); Marco Island, 10.6 mi SW of Royal Palm Hammock, UMMZ 109407 (1); Marco Island, 2.3 mi S of Marco Post Office, UMMZ 109411 (1); 2.4 mi SE of Marco Post Office, UMMZ 109404 (2); 22 mi S of Marco Post Office, UMMZ 109408 (1); Everglades, UMMZ 109410 (1); 3 mi SE of Naples, UMMZ 109414-109415 (2♂, 2); 5 mi SE of Naples, UMMZ 109405 (1♂), UMMZ 108396 (1♂); 8.5 mi SE of Naples, UMMZ 109406 (1); 9.4 mi SE of Naples, UMMZ 108395 (1); 10.2 mi SE of Naples, UMMZ 108394 (1♂); Royal Palm Hammock, UMMZ 103354 (1); 7.9 mi E of Royal Palm Hammock, UMMZ 108397 (1); 13.6 mi NW of Royal Palm Hammock, UMMZ 109413 (1♂); 2.5 mi W of Ochopee, UMMZ 106117 (1). Dade Co.: 2 mi E of Florida City, UMMZ 108402 (1♂), UMMZ 103837 (1); Lemon City, USNM 26313 (1), USNM 30952-30954 (3); Miami, AMNH 38291, 38293-38397 (6), UMMZ 108403 (1♂), [untagged, data same as AMNH 37452] (1♂, 7); 16.9 mi W of Miami, UMMZ 106120 (1); 17.5 mi W of Miami, UMMZ 106116 (2♂); 19 mi W of Miami, UMMZ 102532-102533 (2); 19 mi W and 3 mi S of Miami, UMMZ 108399 (1); 21.2 mi W of Miami, UMMZ 108405 (1); 36 mi W of Miami, UMMZ 108146 (5); Paradise Key, USNM 85353 (1); 1.3 mi N and 5.2 mi NE of Paradise Key, UMMZ 108145 (1♂, 2); 2.1 mi E of Paradise Key, UMMZ 110670 (1); 1.5 mi SW of Paradise Key, UMMZ 110671 (1); 15.9 mi SW of Paradise Key, UMMZ 110672 (1). DeSoto Co.: Orange Hammock, USNM 22342 (1). Duval Co.: Arlington, AMNH 15041 (1), AMNH 15251-15253 (1♂, 2); Goodby's Creek, AMNH 16005 (1); Jacksonville, AMNH 15174-15175 (1♂, 1), AMNH 15473-15476 (4); Jacksonville, 5 mi N of Riverview, AMNH 11499-11500 (1♂, 1); Near Jacksonville, AMNH 16629-16632 (2♂, 2), AMNH 16634-16639 (6), USNM 145370 (1); South Jacksonville, AMNH 11468-11471 (4), AMNH 15974-15975 (2). Escambia Co.: Pensacola, USNM 3428 (6). Glades Co.: Palmdale, UMMZ 56129 (1). Hamilton Co.: 3 mi N of Genoa, UMMZ 86433 (2♂). Hendry Co.: Labelle, UMMZ 56123-56128 (8), UMMZ 56174 (1). Hillsborough Co.: UMMZ 61753 (1); Palm River, UMMZ 91391 (1♂); Tampa, AMNH 49895 (1); Ponds near Tampa, USNM 39833 (1); Takoma, USNM 78463 (1). Jackson Co.: Marianna, UMMZ 73973 (1♂). Jefferson Co.: UMMZ 56717-56718 (2). Jefferson-Taylor Cos.: Aucilla River, USNM 63244 (1). Lake Co.: Eustis, USNM 19996 (1), USNM 19976 (1); Near Esmeralda, USNM 69647-69649 (3). Lee Co.: 4 mi S of Naples, UMMZ 97221 (4); Fort Myers, UMMZ 56172-56173 (2), UMMZ 56122 (1), AMNH 118-121 (4); Kissimmee Billy Swamp, USNM 63243 (1). Leon Co.: ANSP 16313 (1); Ochlochee [= Ochlokonee ?] River, AMNH 49899 (1); Tallahassee, AMNH 67492-67496 (4♂, 1). Marion Co.: Candler, UMMZ 46935 (1♂, 1); Lake Kerr, UMMZ 95548 (2); Ocala, AMNH 51443-51448 (7♂, 3); Silver Springs, UMMZ 95546 (2♂, 2). Martin Co.: 12 mi WSW of Jupiter, ANSP 27087 (1). Monroe Co.: Big Pine Key, USNM 85339-85342 (4), USNM 95830-95843 (1♂, 12), UMMZ 108404 (1), UMMZ 108148 (3), UMMZ 108150 (12), UMMZ 108151 (2♂, 4); Key West Graveyard, UMMZ 108147 (5♂, 5); Little Torch Key, UMMZ 108149 (2♂, 4); Ramrod Key, UMMZ 108152 (1); 40 mi W of Miami, UMMZ 102534 (1). Okeechobee Co.: Vicinity of Okeechobee, AMNH 54348-54349 (2), AMNH

54351 (1). Orange Co.: Orlando, AMNH 3859 (1); Wekiva Springs, USNM 124128 (1♂). Palm Beach Co.: Ritta, USNM 61656 (1). Pinellas Co.: UMMZ 61751-61752 (3); St. Petersburg, USNM 28631 (1). Polk Co.: 3 mi E of Lakeland, UMMZ 79180 (1). Putnam Co.: Near Welaka, University of Florida Conservation Reserve, UMMZ 100716 (2), UMMZ 100721 (2); Near Welaka, fish hatchery ponds, UMMZ 100720 (2♂, 1). Saint Lucie Co.: Eden, USNM 46196 (1). Saint John's Co.: St. Augustine, USNM 3442 (1). Santa Rosa Co.: Blackwater River, AMNH 49898 (1); Santa Rosa Sound UMMZ 91392 (1). Sarasota Co.: "Miaka" Lake, USNM 61337-61338 (1♂, 1); Englewood, AMNH 51456-51460 (5♂), UMMZ 95547 (3); 6.1 mi NW of Englewood, UMMZ 109258 (4♂). Seminole Co.: Sanford, USNM 82580-82581 (2). Taylor Co.: 1 1/2 mi W of Hampton Spring, UMMZ 98720 (5♂, 2). Volusia Co.: ANSP 14549-14552 (4); Deland, UMMZ 43950 (2); Enterprise, UMMZ 56130-56133 (1♂, 3). Walton Co.: 63 mi E of Pensacola, UMMZ 97222 (2♂, 2).

GEORGIA—No specific locality: AMNH 35508 (1); ANSP 2785 (1♂). Appling Co.: 2 mi S of Baxley, UMMZ 67774 (1). Berrien Co.: Nashville, USNM 11907 (2) (specimens with this catalogue number are included in Cope's 1889 list for *Rana virescens virescens*), USNM 11916 (1) (this specimen is illustrated in Cope's 1889 figure 99 of *Rana virescens sphenoccephala*). Bryan Co.: Ogeechee Lake, W of Savannah, UMMZ 73974 (1♂); Near Roding, USNM 92397 (1). Burke Co.: Brier Creek, UMMZ 72704 (1). Charlton Co.: Okefenokee Refuge, USNM 129980, 129982, 129984-129990 (9♂); 20 mi N of Folkston, UMMZ 58081 (1♂). Clinch Co.: 2 mi W of Homerville, UMMZ 71590 (1); 4 mi W of Homerville, UMMZ 71593 (1). Columbia Co.: Near Evans, USNM 92039 (1). Dade Co.: 3 1/2 mi SE of Trenton, UMMZ 103355 (1). DeKalb Co.: Near Atlanta, UMMZ 98060 (2); Near Decatur, UMMZ 67834-67836 (3). Glynn Co.: Near Brunswick, USNM 92155-92158 (4); Saint Simon's Island, USNM 11477 (1). Houston Co.: UMMZ 67802 (1). Lanier Co.: Lakeland, AMNH 35547 (1♂), AMNH 37227-37231 (2♂, 3). Liberty Co.: USNM 3689 (2♂, 1) (these specimens were collected by Dr. E. Coues, although Cope, 1889, indicates they were collected by Dr. W. L. Jones); Riceboro, USNM 3414 (1♂), USNM 46213 (1). Lowndes Co.: 1 mi W of Naylor, UMMZ 71552 (1♂). McIntosh Co.: Sapelo Island, AMNH 77265-77272 (6♂, 2). Mitchell Co.: North of Camilla at Big Slough, UMMZ 110409 (1♂). Thomas Co.: Thomasville, ANSP 16336 (1). Turner Co.: Ashburn, AMNH 34390 (1♂), AMNH 41293-41296 (2♂, 2). Walker Co.: LaFayette, USNM 92110-92112 (3). Ware Co.: Near Manor, USNM 92197 (1); Satilla River, UMMZ 67773 (1♂); Near Waycross, USNM 92233 (1♂). Wilcox Co.: 2 mi E of Bowens Mill, State Fish Hatchery, UMMZ 98061 (1♂, 1).

ILLINOIS—Wood Slough, INHS 1141 (1). No specific locality: USNM 12028 (1); USNM 3450 (1♂); Southern Illinois, USNM 2560 (1), USNM 9419 (1♂), USNM 8079 (a series including several males). Adams Co.: Quincy, INHS 2662-2663 (1♂, 1), INHS 2779-2785 (5♂, 2). Alexander Co.: Cairo, USNM 9673 (2); Horseshoe Lake, UMMZ 84301 (1), INHS 5115-5116, 5119-5120 (1♂, 3), INHS 5759-5760 (2); 3 mi NE of McClure, INHS 8736 (1). Bond Co.: Greenville, INHS 7214 (1). Calhoun Co.: 1 mi S of Hamburg, INHS 7244 (1♂); 1 mi S of Michael, INHS 7103 (1). Cass Co.: 3 mi E of Beardstown, INHS 5673 (1♂); 1 mi S of Beardstown, INHS 6150 (1); Chandlerville, INHS 5721-5725 (4♂, 1). Clark Co.: Rocky Branch, INHS 2584 (1♂). Coles Co.: Charleston, UMMZ 44972 (1); Ridge Lake, INHS 1843-1844 (1♂, 1); Fox Ridge State Park, INHS 6135 (1♂), INHS 6137 (1); 7 mi S of Mattoon, INHS 3828 (1). Cumberland Co.: Greenup, INHS 1975-1976 (2♂); Neoga, INHS 3841 (1♂), INHS 5740-5741 (1♂, 1); Toledo, INHS 2171 (1♂). Edgar Co.: 6 mi N of Oliver, INHS 8104 (1♂). Effingham Co.: Near Effingham, UMMZ 74572 (1); 3 mi NE of Mason, INHS 8064, 8066-8067 (3). Fayette Co.: 8 mi SW of Vandalia, INHS 5783-5784 (1♂,

1); 7 mi N of Vandalia, INHS 8999 (1). Gallatin Co.: Pounds Hollow Lake, INHS 4253 (1♂); 4 mi above Shawneetown, UMMZ 79946 (1♂, 1). Greene Co.: 3 mi S of Eldred, INHS 3607-3608 (2♂) INHS 3964 (1); 3 mi W of Eldred, INHS 7215 (1♂). Hancock Co.: Carthage, INHS 7337-7338 (2♂). Hardin Co.: Eichorn, INHS 4870-4871 (2♂); Elizabethtown, INHS 2911-2917 (3♂, 4); Spring Branch, T 11 S, R 8 E, Sec 20, INHS 1146 (1♂). Jackson Co.: 4 mi S of Carbondale, AMNH 32295-32297 (3); Dowell, AMNH 32299 (1); Fountain Bluff, INHS 5881-5882 (2); Murphysboro, INHS 1978 (1); 10 mi W of Murphysboro, INHS 1902 (1); 11 mi SSW of Murphysboro, UMMZ 95274 (1♂). Jasper Co.: 3 mi W of Rose Hill, INHS 1901 (1♂); Wheeler, INHS 8766 (1). Jefferson Co.: 2 mi S of Divide, INHS 8884 (1); Woodlawn, INHS 9280 (1♂). Jersey Co.: Chickahomeney Slough, Illinois River, Grafton, INHS 1658-1659 (2). Johnson Co.: Forman, INHS 2501 (1); Vienna, INHS 2326 (1). Macoupin Co.: 2 mi N of Shipman, INHS 7247-7248 (1♂, 1). Marion Co.: 2 mi S of Helm, INHS 8987 (1♂); 4 1/2 mi S of Kinmundy, INHS 5033 (1♂). Mason Co.: 5 mi S of Bath, INHS 6262-6263 (2♂); Chautauqua Lake, USBS Wildlife Refuge, INHS 1116 (1); Havana, INHS 1142 (1♂). Massac Co.: 18 mi S of Renshaw, INHS 4872-4874 (3♂). Monroe Co.: 1 mi S of Chalfin Bridge, INHS 4419-4420 (2); 4 mi N of Prairie du Roche, INHS 4093 (1); 3 mi NE of Valmeyer, INHS 3469 (1♂), INHS 5842-5843 (2); 3 mi N of Redbud, UMMZ 58758 (1). Pike Co.: 3 mi NW of Pearl, INHS 3644-3645 (1♂, 1). Pope Co.: SE of Eddyville, INHS 6995 (1); 1 mi NW of Herod, INHS 4868 (1♂); SW of McCormick, INHS 6994 (1♂). Pulaski Co.: 4 1/2 mi N of Grand Chain, INHS 4999 (1). Randolph Co.: 10 mi NW of Chester, UMMZ 58757 (1); 3 mi W of Modoc, INHS 8394 (1). Richland Co.: 8 1/2 mi S of Boos, INHS 5213 (1); Calhoun, UMMZ 43991-43996 (6), UMMZ 44474-44480 (1♂, 6), UMMZ 44482-44496 (3♂, 12); 6 mi E of Clay City, INHS 8105-8106 (2♂); "Bird-Haven" near Olney, USNM 38424 (1♂); Olney, USNM 14173 (1), USNM 52144 (1). Saint Clair Co.: USNM 57966 (1); Millstadt, INHS 7216 (1). Saline Co.: 3 mi E of Stonefort, INHS 9437 (1♂). Sangamon Co.: Springfield, INHS 4111-4119 (9♂). Shelby Co.: 3 mi W of Tower Hill, INHS 4661-4665 (5♂). Union Co.: Aldridge, INHS 2532 (1); 4 mi SE of Aldridge, INHS 5844 (1); 5 mi SE of Aldridge, INHS 3079 (1); 2 mi N of Anna, AMNH 32278-32280 (1♂, 2); 7 mi S of Anna, AMNH 32246-32251 (2♂, 4); Cobden, INHS 6071 (1); Wolf Lake, INHS 3303, 3306 (2). Wabash Co.: Mt. Carmel, INHS 3241 (1), USNM 12081 (1♂, 1), USNM 10046 (1); 3 mi NE of Mt. Carmel, UMMZ 55386 (1♂). Washington Co.: USNM 3447 (3). White Co.: Carmi, INHS 8786 (1); Norris City, UMMZ 74573 (1). Williamson Co.: 4 mi E of Energy, INHS 6794 (1♂).

INDIANA—No specific locality: UMMZ 55382 (1♂). Bartholomew Co.: Stoney Lonesome, UMMZ 99114 (1). Brown Co.: 2 mi N of Beanblossom, UMMZ 101832 (5). Clark Co.: Silver Creek at Fourth Dam, UMMZ 98494 (4♂). Clay Co.: 4 1/2 mi S of Clay City, UMMZ 101628 (2♂, 2). Crawford Co.: 1 mi E of Pilot Knob, UMMZ 55383 (1). Daviess Co.: 3 mi E of Odon, UMMZ 108121 (1♂, 1). Dubois Co.: 1 mi E of Huntingburg, UMMZ 106585 (1). Floyd Co.: 1.5 mi W of New Albany, UMMZ 95805-95807 (1♂, 2); Silver Hills, UMMZ 95808-95809 (2♂). Fountain Co.: 3 mi E of Kingman, UMMZ 101717 (1). Gibson Co.: Foot's Pond, UMMZ 89734 (5), UMMZ 91420 (4). Harrison Co.: 1 1/2 mi W of New Boston, UMMZ 103497 (1); 2 mi NW of Corydon, UMMZ 55384 (1). Jackson Co.: 1 mi SW of Chestnut Ridge, UMMZ 55387-55388 (2); Muscatatuk Swamps S of Tampico, UMMZ 100303 (2♂, 1). Jefferson Co.: Hanover College, ANSP 2789 (1). Jennings Co.: 2 mi W of Weston, UMMZ 55385 (4). Johnson Co.: 1.5 mi S of Amity, UMMZ 99117 (1); Trafalger, UMMZ 98502 (1♂). Knox Co.: Near Decker Chapel, UMMZ 98492 (1♂, 1); Near Orrville, UMMZ 101692 (2♂, 1); Wheatland, USNM 13372 (1♂); 2 mi E of Wheatland, UMMZ 100300 (1). Marion Co.: 1 1/2 mi NE of Broad Ripple, UMMZ 101636

(2♂); Indianapolis, Fall Creek, UMMZ 99115 (1). Monroe Co.: Bloomington, AMNH 51474-51479 (+ 14 untagged specimens) (8♂, 12); Dolan, UMMZ 100299 (1♂); Mount Vernon, AMNH 52510 (1). Montgomery Co.: 3 mi N of Waveland, UMMZ 103359 (1♂). Morgan Co.: Link Observatory, 1 1/2 mi SW of Brooklyn, UMMZ 101703 (1♂, 1). Orange Co.: 3 mi SW of Orleans, UMMZ 101833 (1♂). Owen Co.: 1 1/2 mi SW of Freedom, UMMZ 100297 (2♂); Spencer, UMMZ 100298 (2). Perry Co.: 8 mi W of Rome, UMMZ 105550 (1), UMMZ 105552 (2♂). Pike Co.: Patoka River, 3.5 mi N of Oakland City, UMMZ 100301 (1♂); 1 1/2 mi N of Pikeville, UMMZ 106584 (1). Posey Co.: UMMZ 60957 (2♂, 2); Hovey Lake, UMMZ 89731 (4). Scott Co.: 1 mi N of Scottsburg, UMMZ 101633 (2♂). Sullivan Co.: 5 mi W of Carlisle, UMMZ 55381 (1); 1 1/2 mi S of Hymera, UMMZ 101627 (2♂, 2). Vanderburgh Co.: UMMZ 60956 (1♂, 8). Vermillion Co.: 1 1/2 mi NW of Perrysville, UMMZ 101718 (1). Vigo Co.: 3 mi NE of Farmersburg, UMMZ 98501 (1); 3 1/2 mi SW of Prairietown, UMMZ 55379 (1); 3 1/2 mi NW of Middletown, UMMZ 55380 (1♂). Washington Co.: 3 mi N of Campbellsburg, UMMZ 101635 (1♂).

KANSAS—Salt Creek, USNM 3346 (1♂). Labette Co.: Near Parsons, USNM 90321 (1♂). Miami Co.: UMMZ 66884 (3♂, 2); Pigeon Lake, USNM 89036 (1), USNM 89038-89039 (2♂). Wilson Co.: 3 1/2 mi N of Neodesha, USNM 73317 (1).

KENTUCKY—Ballard Co.: La Center, AMNH 32290 (1). Calloway Co.: 12 mi NE of Murray, AMNH 32291 (1). Clay Co.: Big Creek (Post Office), UMMZ 97986 (1♂). Clinton Co.: Near Albany, USNM 87657 (1), USNM 88045 (1). Hickman Co.: Murphy's Pond, 4 mi SE of Milburn, UMMZ 98531 (1). Owsley Co.: 1 mi E of Booneville, UMMZ 97985 (1). Powell Co.: Red River, UMMZ 81220 (1♂, 1). Todd Co.: Near Clifty, USNM 87177-87178 (2). Trigg Co.: 4 mi E of Cadiz, AMNH 32266 (1).

LOUISIANA—Pride, AMNH 44348 (1), AMNH 44694-44698 (5). No specific locality: AMNH 84164 (1♂); AMNH 18718-18725 (1♂, 7). Beauregard Parish: 15 mi N of Longville, AMNH 32618 (1). Calcasieu Parish: Lake Charles, USNM 35395-35396 (2♂); 6 miles S of Vinton, AMNH 32609-32610 (2). East Baton Rouge Parish: Baton Rouge, AMNH 44692-44693 (2). Grant Parish: Selma, USNM 100606 (1♂). Madison Parish: Singer Wildlife Refuge, USNM 118392-118393 (2). Morehouse Parish: Mer Rouge, USNM 45519 (1); Prairie Mer Rouge, USNM 3426 (3♂, 9). Orleans Parish: New Orleans, USNM 53181 (1), USNM 13086-13089 (3♂, 2), USNM 13103-13106 (4), USNM 13273 (1), USNM 5192 (1♂), AMNH 496 (1). Ouachita Parish: Rilla, USNM 100604 (1). Saint Bernard Parish: Chalmette, AMNH 51449-51455 (5♂, 2). Saint James Parish: Lutchter, USNM 64145-64146 (1♂, 1). Saint Landry Parish: Grand Coteau, USNM 9342 (1). Saint Mary Parish: Morgan City, USNM 73801-73804 (4). Saint Tammany Parish: Pearl River, AMNH 68346 (1♂); Between Mandeville and Covington, USNM 113248-113250 (1♂, 2); Slidell, USNM 35345-35346 (2). Tangipahoa Parish: Tickfaw, USNM 9869 (1♂). Vermillion Parish: Perry, USNM 35347-35348 (2), USNM 35350-35352 (3), USNM 35353 (1♂), USNM 35355 (1). Vernon Parish: 6 mi N of Hornbeck, AMNH 32649 (1).

MARYLAND—Anne Arundel Co.: Fort George G. Meade, USNM 140999 (1). Calvert Co.: Chesapeake Beach, USNM 62751 (1♂); Cove Point, AMNH 45163-45171 (1♂, 8); Long Beach, along Chesapeake Bay, USNM 141000-141002 (3); North Beach Park, USNM 101229-101246 (4♂, 14); Solomons Island, USNM 100824-100828 (1♂, 4). Caroline Co.: Federalsburg, AMNH 55036 (1♂). Charles Co.: Zekiah Swamp, 5 mi from La Plata, USNM 101223 (1). Dorchester Co.: 4 mi S of Federalsburg, AMNH 55037 (1); World's End Creek,

USNM 129572 (1). Kent Co.: Chestertown, ANSP 16546 (1), ANSP 17747-17750 (4). Prince Georges Co.: Cherry Hill Road, Berwyn, USNM 141004 (1♂); College Park, USNM 141005-141017 (7♂, 6), USNM 141492-141493 (2); College Park, Paint Branch, USNM 64918-64919 (2). Queen Anne's Co.: Near Centerville, USNM 104445 (1); Opposite Chestertown, ANSP 17742-17746 (5). Saint Mary's Co.: Saint George's Island, USNM 17387 (1); Near Ridge, USNM 141021-141022 (1♂, 1). Somerset Co.: Near Marion Station, UMMZ 95685 (1♂); 1 mi S of Marion Station, USNM 141018-141020 (3); Route 13, near Princess Anne, USNM 144277-144279 (3). Talbot Co.: 5 mi N of Easton, USNM 141023-141024 (1♂, 1). Wicomico Co.: Hunting Park, southwest of Salisbury, USNM 141025-141027 (2♂, 1); Hunting Wood, USNM 141028 (1). Worcester Co.: Newark, UMMZ 95672 (1♂); Ocean City, USNM 104412-104413 (2), USNM 19055 (1); Pocomoke, USNM 75267-75269 (3); Pocomoke State Forest, USNM 102182-102183 (2); 8 mi NW of Snow Hill, UMMZ 95670 (1♂).

MISSISSIPPI—Magnolia State Park, USNM 125539 (1♂). No specific locality: AMNH 50941 (1). Covington Co.: 3 mi E of Collins, USNM 99271 (1). Greene Co.: Plave, USNM 99242 (1). Hancock Co.: Bay St. Louis, USNM 46027 (1), USNM 46239 (1). Harrison Co.: Biloxi, AMNH 41287-41290 (1♂, 3), AMNH 40263-40264 (2♂), USNM 51114 (1).

MISSOURI—Camp Crowder, USNM 119122-119123 (2); 7 mi W of Williamsburg [= Williamsville, Wayne County?], AMNH 32281 (1). Barry Co.: Exeter, UMMZ 81518 (2♂); Washburn, USNM 81005 (1). Butler Co.: USNM 57939 (1); Near Neelyville, UMMZ 77619 (1); Near Poplar Bluff, UMMZ 77759 (1♂). Camden Co.: Cave Near Hahatonka, UMMZ 68940 (1). Carter Co.: Big Spring State Park, USNM 93179 (1). Crawford Co.: Onondaga Cave, near Leasburg, UMMZ 70380 (1). Holt Co.: Little Tarkio River, UMMZ 95508 (1). Iron Co.: UMMZ 75835 (1). Jasper Co.: USNM 57947 (1). Lawrence Co.: UMMZ 82817 (1). Linn Co.: Laclede, USNM 93748-93751 (4). McDonald Co.: USNM 57940 (1). Miller Co.: Eldon, UMMZ 84852 (1). Miller and Pulaski Cos.: Rubidoux Creek, UMMZ 68739 (5). Montgomery Co.: USNM 57954 (1♂). New Madrid Co.: USNM 57946 (1). Newton Co.: Neosho, UMMZ 60121 (1); Shoal Creek, UMMZ 79965 (1). Oregon Co.: USNM 57955 (1). Ozark Co.: UMMZ 57952-57953 (2). Pemiscot Co.: SE of Portageville, UMMZ 58755 (2). Saint Charles Co.: USNM 57943 (1). Saint Francis Co.: Near Farmington, UMMZ 77757 (1♂). Saint Louis Co.: USNM 57937 (1♂); Creve Cour Lake, Saint Louis, UMMZ 58792 (1); Saint Louis, USNM 3431 (2♂, 12). Saline Co.: 15 mi E of Sweet Springs, AMNH 32283 (1). Shannon Co.: Current River at Welch's Cave, UMMZ 90479 (2); Banks of the Current River, UMMZ 90482 (3). Stoddard Co.: USNM 57941 (1). Stone Co.: USNM 57944 (1♂); vicinity of Marvel Cave, AMNH 40315-40323 (1♂, 8). Vernon Co.: Nevada, UMMZ 43946 (1). Wayne Co.: 3 mi N of Patterson, UMMZ 95273 (1); Sam Baker State Park, UMMZ 95810 (1). Webster Co.: Near Fordland, USNM 85591-85592 (2♂).

NEW JERSEY—Alton, AMNH 35115 (1); Arlington, AMNH 14266 (1); Ocean City Point, ANSP 17621 (1); Spray Beach, ANSP 27098 (1). No specific locality: AMNH 77415 (1♂); AMNH 84181 (2♂); AMNH 84220 (1). Atlantic Co.: May's Landing, ANSP 3969 (1♂). Bergen Co.: Alpine, AMNH 52344 (1♂); Closter, AMNH 63848-63851 (4♂); Englewood, AMNH 12855 (1♂); Edgewater, AMNH 1719-1721 (2♂, 1); Fairview, AMNH 67491 (1); Ridgefield (Meadowlands S of Hendrick's Causeway), AMNH 70365 (1); NE edge of Old Tappan Reservoir, AMNH 81337-81340 (3♂, 1); 1 mi N of Leonia, AMNH 35503-35505 (3♂). Burlington Co.: SE of Bordentown, Kinkora Creek, ANSP 17640 (1); Jennings Mill, Marlton, ANSP 27110 (2); Near Taunton Lakes, UMMZ 116352 (2♂, 1). Camden Co.: Atco, ANSP 19286 (1♂); Delair, ANSP 19084 (1); Mount Ephraim,

AMNH 51467-51470 (4♂). Cape May Co.: Belleplain, USNM 127331-127338 (8); Cold Spring, ANSP 17606-17610 (1♂, 4); 0.3 mi N of Cold Spring, AMNH 79625 (1♂); Ocean City, ANSP 19268 (1), ANSP 17622-17625 (4); Dennisville, ANSP 17600 (1); Palermo Pool at Tide Marsh, ANSP 17355 (1♂), ANSP 17357-17359 (3♂); 1 mi S of Erma, AMNH 79623-79624 (2); 10 mi SW of Ocean City, UMMZ 86408 (1♂); Pond W of Sea Isle City, UMMZ 86409 (1). Cumberland Co.: USNM 127339 (1); 1 mi S of Delmont, AMNH 79620 (1♂); 1 mi S of Heislerville, AMNH 79621-79622 (2♂). Hudson Co.: North Bergen (Meadow Lands), AMNH 67900 (+ 1 untagged) (2). Middlesex Co.: Helmetta, AMNH 5671-5672 (2); South River, Sayreville, AMNH 35130 (1). Monmouth Co.: Allaire, UMMZ 74447 (1); Sea Bright, AMNH 36658 (1). Morris Co.: Great Swamps, Green Village, AMNH 51018-51022 (+ 3 untagged) (4♂, 4); Lincoln Park, AMNH 79579-79581 (2♂, 1). Ocean Co.: Near Barnegat, UMMZ 78902-78903 (3♂, 12); 8 mi W of Barnegat, UMMZ 78908 (1); Lakehurst, AMNH 6911 (1♂), AMNH 16111 (1), AMNH 6797-6798 (2), AMNH 35140-35141 (2), AMNH 3537-3540 (2♂, 2), AMNH 12898 (1), AMNH 36659 (1), AMNH 23051 (1), AMNH 16622 (1♂), AMNH 16954 (1♂); Lakewood, AMNH 58925 (1); Mount Hurricane Brook at route 40, AMNH 51652 (1♂); Stafford's Forge, ANSP 16395 (1♂); Toms River, ANSP 19239 (1). Passaic Co.: Garfield, AMNH 35509-35512 (2♂, 2); Haskell, near Wanaque River, AMNH 70296 (1); Wayne Township, Pompton River, AMNH 70366-70367 (2); Wayne Township, Pompton River, near route 23, AMNH 79391 (1). Sussex Co.: Waterloo Village (Morris-Essex Canal), AMNH 72588 (1♂).

NEW YORK—Long Island, Point O'Woods, AMNH 18674 (1♂); Long Island, North Hills, AMNH 41292 (1). No specific locality: AMNH 21016 (1). Bronx Co.: Van Cortlandt Park, AMNH 52342 (+ 4 untagged) (1♂, 4). Queens Co.: Bayside, AMNH 38193-38197 (4♂, 1); Cornell Creek, Jamaica, AMNH 51471-51472 (2♂); Cunningham Park, AMNH 51501-51502 (1♂, 1); Elmhurst, AMNH 14515-14522 (3♂, 5); Justice Street, near Junction Avenue, Elmhurst, AMNH 14386 (1); Flushing, AMNH 51461-6 (6♂); Jamaica, AMNH 36651 (1). Richmond Co.: Staten Island, AMNH 581 (1♂), AMNH 636 (1♂); Staten Island, Arlington, AMNH 3699-3700 (1♂, 1); Staten Island, Green Ridge, AMNH 3542-3543 (2), 23029-23032 (2♂, 2). Suffolk Co.: Long Island, Easthampton, AMNH 5368-5369 (1♂, 1).

NORTH CAROLINA—No specific locality: USNM 87180 (1). Brunswick Co.: 3.3 mi N of Supply, AMNH 73531 (1). Camden Co.: 2 mi SE of South Mills, USNM 127775 (1). Carteret Co.: Near Beaufort, UMMZ 116608 (3); 8 mi W of Morehead City, AMNH 73529 (1♂). Chowan Co.: Edenton, USNM 50892 (1). Currituck Co.: 2.6 mi E of Barco, USNM 127781 (1♂); 1 mi SW of Sligo, USNM 124523 (1♂). Edgecombe Co.: Tarboro, USNM 3436 (1). Gates Co.: 5 mi E of Sunbury, AMNH 73530 (1♂). Gates-Hertford Cos.: Winton (Gates City), AMNH 36643 (1). Lee Co.: Near Sanford, USNM 87179 (1). Lenoir Co.: Kinston, AMNH 52341 (7). Moore Co.: Southern Pines, AMNH 22407 (1). New Hanover Co.: Near Wilmington, AMNH 21348 (1). Pasquotank Co.: Elizabeth City, north edge, AMNH 75788 (1). Robeson Co.: Hayes City, USNM 144448-144455 (2♂, 6); Maxton, USNM 144327 (1). Tyrell Co.: Lake Phelps, AMNH 36654-36657 (4). Union Co.: Near Monroe, USNM 91764 (1). Wake Co.: 10 mi E of Raleigh, AMNH 33310 (1). Wayne Co.: Near Goldsboro, USNM 87176 (1♂); Goldsboro, Little River, USNM 15985 (1).

OHIO—Scioto Co.: Near Franklin Furnace, AMNH (untagged, data same as 51629) (1♂).

OKLAHOMA—Cherokee Co.: Scraper, UMMZ 81517 (8). Creek Co.: Lagoon, UMMZ 90214 (1♂); Sapulpa, AMNH 7565-7566 (2). Love Co.: 5 mi N

of Thackerville, AMNH 32602 (1). Mayes Co.: Vicinity of Choteau, UMMZ 81516 (1♂); 5 mi E of Locust Grove, AMNH 68347 (1♂). McCurtain Co.: 1 1/2 mi E of Harris, AMNH 59706 (1♂). Okmulgee Co.: UMMZ 64208-64210 (3♂). [Polk Co.: UMMZ 82803 (1).] Rogers Co.: 9 mi NW of Claremore, AMNH 32614-32615 (2). Tulsa Co.: Tulsa, AMNH 51023-51025 (3♂), AMNH 51047-51049 (3♂).

PENNSYLVANIA—No specific locality: ANSP 2784 (1♂). Bucks Co.: Emelie, ANSP 18602 (1); Cut off, Tullytown Creek, tributary of the Delaware River, near Tullytown, ANSP 17675 (1♂). Philadelphia Co.: Philadelphia, ANSP 2879 (1), ANSP 2892 (1♂), ANSP 2786-2788 (1♂, 2), ANSP 2803-2804 (2♂); Philadelphia, Port Richmond, ANSP 19222 (1♂).

SOUTH CAROLINA—No specific locality: ANSP 2816-2821 (6); AMNH 44206 (1); AMNH 44209 (1). Berkeley Co.: 16 mi NNE of Charleston, UMMZ 105089 (1♂, 1); Oakley, USNM 10312 (2♂, 2). Charleston Co.: Charleston, ANSP 2858 (1♂), USNM 3425 (3), USNM 67351 (2); Near Charleston, ANSP 14471-14486 (1♂, 15); 33 mi NE of Charleston, AMNH 44205 (1); Bull's Island, UMMZ 97197 (1♂); Fr. Marion National Forest, 4.7 mi WSW of Awendaw, UMMZ 129513 (1); Christ Church Parish, Mount Pleasant, USNM 48305-48311 (1♂, 6). Chester Co.: Near Chester, USNM 91414 (1). Georgetown Co.: Pee Dee Game Management Area, 9 mi NE of Georgetown, UMMZ 129461 (1). Greenville Co.: UMMZ 98886 (1); Greenville (collected by A. C. Pickens), USNM 71765-71767 (3♂). Horry Co.: Myrtle Beach, UMMZ 94184 (3), UMMZ 94186 (1); Vicinity of Collins Creek Church, 2 air mi E of Garden City Beach, UMMZ 129440 (2). Jasper Co.: Ridgeland, AMNH 76457 (1). Lexington Co.: Near Lexington, USNM 91363 (1). Richland Co.: Hopkins, USNM 63286-63288 (3). Saluda Co.: Murray Lake, USNM 91472 (1). York Co.: Rock Hill, UMMZ 44574 (1).

TENNESSEE—Blount Co.: Near Louisville, USNM 88044 (1). Bradley Co.: About 4 mi ESE of Cleveland, UMMZ 125281 (1♂). Cumberland Co.: Grassy Cover, UMMZ 113412 (1). Davidson Co.: AMNH 68343 (1). Dickson Co.: 2 mi E of White Bluff, AMNH 68345 (1♂, 3). Dyer Co.: Lane, UMMZ 53179 (1); Maxey, USNM 28380-28383 (1♂, 3), USNM 28385-28386 (2). Fayette Co.: Fisherville Lake, AMNH 68342 (3♂); Moscow, UMMZ 53176 (1). Henry Co.: Henry, UMMZ 53406 (1), UMMZ 53312-53314 (2♂, 1), UMMZ 53373-53374 (1♂, 1), UMMZ 53497 (1), UMMZ 53577 (1), UMMZ 53474-53484 (11). Knox Co.: Knoxville, UMMZ 55295 (1♂). Madison Co.: Jackson, UMMZ 72343 (1). McMinn Co.: Athens, Matlock Spring, USNM 21143 (1). Obion Co.: Reelfoot Lake, UMMZ 53177-53178 (2), UMMZ 53180 (1); Samburg, Reelfoot Lake, ANSP 4450 (1♂). Obion-Lake Cos.: Reelfoot Lake, UMMZ 77622 (1), UMMZ 74570-74571 (1♂, 1). Robertson Co.: AMNH 68344 (1♂, 1). Rutherford Co.: 5 mi NW of Murfreesboro, UMMZ 67775 (1). Sequatchie Co.: Near Dunlap, USNM 87174-87175 (2). Shelby Co.: Raleigh, ANSP 4404 (1), ANSP 4421 (1). White Co.: Sparta, UMMZ 56369 (1♂).

TEXAS—1 mi W of Archard, AMNH 32626 (1); 4 mi N of Wagoner, AMNH 32606 (1). Aransas Co.: S of Saint Joseph Island, UMMZ 115832 (1). Brazoria Co.: Sycamore Creek, Near Columbia, USNM 45434 (1♂); Lost Lake, UMMZ 115825 (1). Cass Co.: 1 mi NW of Atlanta, AMNH 32605 (1). Dallas Co.: Dallas, ANSP 13649 (1♂), USNM 14552 (1♂). Fayette Co.: 2 mi W of Flatonia, AMNH 32613 (1). Fort Bend Co.: 1 mi S of Sugarland, AMNH 32612 (1); 1 mi N of Sugarland, AMNH 32627-32628 (2). Galveston Co.: 7.1 mi NE of Galveston, UMMZ 115826 (1♂); Hitchcock, AMNH 124-130 (7). Gregg Co.: 3 mi S of Longview, AMNH 54684-54686 (3♂), Hardin Co.: 3 mi W of Saratoga, UMMZ 115827 (1), UMMZ 115829 (1♂, 2); 7 mi NW of Saratoga, UMMZ

115830-115831 (1♂, 1). Harrison Co.: Lake Caddo, AMNH 12892 (1). Kendall Co.: Dead Man's Cave, 11 mi E of Boerne, AMNH 54672 (1). McLennan Co.: USNM 57507 (1♂). Montgomery Co.: 2 mi N of Spring Creek, UMMZ 115824 (1). Sabine Co.: 5 mi NE of Milam, UMMZ 115833-115834 (1♂, 1). Tarrant Co.: 8 mi N of Fort Worth, AMNH 32616-32617 (2). Victoria Co.: USNM 42385-42386 (2).

VIRGINIA—No specific locality: USNM 16326 (1). Accomack Co.: Assateague Island, USNM 139392 (1); Upper Chincoteague Island, ANSP 18485 (1); Chincoteague Island, ANSP 18532 (1♂), UMMZ 95679 (1♂). Caroline Co.: Hygeia Farm, Chilesburg, USNM 48891 (1). Fairfax Co.: Great Falls, USNM 55441 (1♂); Mount Vernon, USNM 55098 (1). Greenville Co.: 9 mi SE of Emporia, USNM 135117-135118 (2). Lancaster Co.: Mollusk, USNM 139328-139330 (3); 1 mi ENE of Monaskon, AMNH 71519 (1); Morattico, AMNH 59878 (1), AMNH 63597 (1). Nansemond Co.: 1 mi W of Drivers, USNM 127724 (1♂). Norfolk Co.: Dismal Swamp, USNM 26275 (1♂), USNM 23948 (1); Dismal Swamp, Lake Drummond, USNM 35757 (1); Lake Drummond, USNM 46171 (1); Dismal Swamp, Wallaceton, USNM 46172 (1). Northampton Co.: Nassawadox, UMMZ 95677 (1♂). Orange Co.: 4 mi S of the Rapidan River, route 522, USNM 137498 (1). Prince Edward Co.: Buffalo Creek, Darlington Heights, USNM 98853 (1); Farmville, USNM 132406 (1♂). Princess Anne Co.: Pungo, USNM 127740-127746 (4♂, 3); Near Sigma, USNM 124862 (1). Wythe Co.: Wytheville, USNM 21235 (1♂).

Locality data for male specimens collected by D. B. Means and others. These specimens are in the private collection of S. N. Salthe. Numbers in parentheses are individual numbers associated with specimens from the locality indicated.

FLORIDA—Calhoun Co.: 5 mi S of Blountstown (Florida route 20) on Florida route 71 (F6, F7). Jackson Co.: Chipola River floodplain at bridge on Florida route s162, 5 mi W of Greenwood (D5, the other ♂); Florida route 69, 1 mi N of US highway 90 (Grand Ridge) at site with extensive cypress swamp to E (D1). Leon Co.: Chaires Crossroad from US 27 to railroad tracks, 1.0 mi N of road is adjacent to eastern limit of old Lake Lafayette (A7); Meridian Road north of Tallahassee between two bridges at Lake Iamonia outlet (B5). Liberty Co.: Florida route 65 from 1 mi long stretch beginning 7.0 mi and ending 8.0 mi S of Telogia (also, 1 mi portion of Florida route 65 S of Apalachicola National Forest Road 10) (C1); Florida route 65 from 4-5 mi S of Hosford (1-2 mi S of Telogia) (F4); Florida route 12 from 10 mi to 11 mi S of Bristol (E6, F2). Taylor Co.: Florida route s14 from 3.0 mi S of Aucilla River bridge to 4.0 mi S of same bridge (A4, A6). Wakulla Co.: Florida route s59 from Goose Field to Refuge officer's (Culver Gidden) residence along freshwater impoundment) (D9, E2).

*Rana* spp., probably distinct from previously listed spp.

ARIZONA—Fort Verde, AMNH 463 (1). No specific locality: AMNH 10796 (1♂); AMNH 50898-50899 (2); USNM 11896-11897 (2♂); USNM 21806-21807 (2); USNM 61509-61510 (2); AMNH 60329-60330 (2); USNM 60436 (1); USNM 14811(1). Apache Co.: Alpine, USNM 53125 (1♂); 4 mi N of Alpine, AMNH 74520-74521 (2), AMNH 74523 (1); 4 mi S of Alpine, AMNH 65801-65802 (2♂); 4 mi SSW of Alpine, AMNH 62427 (1♂), AMNH 62430 (1♂), AMNH 62433 (1); Black River, Buffalo Crossing, Apache National Forest, AMNH 55059-55065 (2♂, 5). Cochise Co.: Fort Huachuca, USNM 17796-17797 (2♂), USNM 21814 (1); San Pedro River (tributary to Gila River), Fairbank, USNM



118964 (1♂); Swisshelm Mountains, Leslie Canyon, AMNH 65804-65805 (1♂, 1); Chiracahua Mountains, Herb Martyr Dam, Cave Creek, AMNH 56311 (2♂), AMNH 62588-62594 (7); Garden Canyon, Huachuca Mountains, AMNH 55057 (1); On Garden Canyon Road, Ranch west of Divide, AMNH 55058 (1); 2 mi NE of Rucker Lake, Chiracahua Mountains, AMNH 65799 (1♂). Coconino Co.: Sabine Canyon, USNM 118562-118568 (7). Gila Co.: East Verde River at Angora, USNM 118970 (1♂). Maricopa Co.: Fish Creek, USNM 54524 (1); Phoenix, USNM 45377 (1); Tempe, USNM 15971 (1). Mohave Co.: Trout Creek, near Hubbard Ranch, USNM 125636-125637 (2); 13 mi N of Trout Creek Store, USNM 125622 (1). Pima Co.: Mouth of Bear Canyon, USNM 61508 (1); Fort Lowell, at foot of Santa Catalina Mountains, 6 mi NE of Tucson, USNM 21815 (1); 3 1/2 mi E of Tanque Verde, AMNH 49800 (1); Sabino Canyon, Santa Catalina Mountains, AMNH 51400-51404 (+ 8 untagged) (1♂, 12), AMNH 361-362 (2♂); Tucson, AMNH 5837 (1), USNM 16617 (1♂); Santa Cruz River at Tucson, USNM 118957 (1♂), AMNH 340 (1♂); Santa Cruz River at Saint Xavier Mission, USNM 118959-118961 (2♂, 1). Pinal Co.: Boyce Thompson Southwestern Arboretum, 4 mi W of Superior, AMNH 52215 (1♂). Santa Cruz Co.: Calabasas, USNM 45445 (1); Sonoita Creek, near Calabasas, USNM 15720-15722 (1♂, 2); Sonoita Creek, Patagonia, USNM 118965 (1♂); Ruby, UMMZ 91636 (4♂, 12); 6 mi NE of Lochiel, Shehe Spring, UMMZ 105696 (6). Yavapai Co.: 9 mi SE of Kirtland Junction, USNM 125654-125655 (2).

CALIFORNIA—Imperial Co.: San Felipe Creek, AMNH 68213-68214 (2♂); Fort Yuma, USNM 21876 (1♂).

TEXAS—Presidio Co.: Cibolo Creek at Shafter, AMNH 77438-77440 (3♂); Paisano, USNM 45384 (1♂).

#### Uncertain identification

ILLINOIS—Adams Co.: Quincy, INHS 2786 (1). Alexander Co.: Horseshoe Lake, INHS 5114, 5117 (2). Coles Co.: Fox Ridge State Park, INHS 2409 (1♂). Cumberland Co.: Greenup, INHS 2292 (1). Effingham Co.: 5 mi S of Effingham, INHS 8767 (1). Gallatin Co.: Pounds Hollow Lake, INHS 2328 (1). Grundy Co.: 1 mi N of Braidwood, INHS 8474 (1). Johnson Co.: Vienna, INHS 2327 (1). La Salle Co.: UMMZ 67515 (1). Mason Co.: 5 mi NE of Havana, INHS 1619 (1). Pope Co.: 3 mi S of Rock, INHS 4764 (1). Randolph Co.: 10 mi NW of Chester, UMMZ 58757 (1).

IOWA—No specific locality: UMMZ 71546 (3). Monroe Co.: 2 mi W of Albia, UMMZ 71702 (1♂). Wapello Co.: 2 mi E of Ottumwa, UMMZ 71544 (3). Woodbury Co.: Brown's Lake, UMMZ 93171 (9).

KANSAS—Ellsworth Co.: USNM 89055-89056 (2♂). Kiowa Co.: 4 mi N of Belvedere, UMMZ 85587 (1). Miami Co.: UMMZ 66884 (1); Pigeon Lake, USNM 89037 (1). Wilson Co.: UMMZ 67537 (1).

MAINE—No specific locality: USNM 36323-36324 (2).

MICHIGAN—Charlevoix Co.: UMMZ 56647 (1); Pine Lake, UMMZ 51790-51791 (1♂, 1), UMMZ 51793 (1). Cheboygan Co.: Douglas Lake, UMMZ 39791 (1), UMMZ 39793 (1♂); Vincent Lake, UMMZ 39822 (1). Chippewa Co.: Sugar Island, Sec 26, UMMZ 103723 (1); Whitefish Point, UMMZ 42781 (1). Crawford Co.: E Branch of the Au Sable River, UMMZ 59132 (1♂). Delta Co.: Round Lake, UMMZ 83810 (1♂). Gogebic Co.: T 44 N, R 38 W, Sec 16, UMMZ 113522 (1). Houghton Co.: Winona, UMMZ 32816-32817, 32819 (3). Huron

Co.: Sand Point, UMMZ 37857, 37860 (2). Iosco Co.: Tawas, UMMZ 42631 (1). Kalamazoo Co.: UMMZ 42109 (1). Kent Co.: Nelson Township, UMMZ 61110 (1). Leelanaw Co.: Duck Lake, UMMZ 56209 (1), UMMZ 89499 (1). Manistee Co.: Stronach Township, UMMZ 63400 (1). Monroe Co.: Sand Beach, north of Monroe Piers, UMMZ 44661 (1). Montmorency Co.: King's Camp, UMMZ 58567 (1).

MISSOURI—Mineola, AMNH 32293 (1). Dunklin Co.: USNM 57948 (1). Jackson Co.: USNM 57950 (1). Saline Co.: 15 mi E of Sweet Springs, AMNH 32282 (1). Shannon Co.: Welch's Spring, UMMZ 90481 (1).

NEBRASKA—Antelope Co.: UMMZ 67511 (5). Cass Co.: South Bend, USNM 19825 (1♂). Garfield Co.: Devere, USNM 82029 (1). Holt Co.: UMMZ 67506 (2). Madison Co.: UMMZ 67512 (1♂). Pierce Co.: UMMZ 67510 (1♂). Platte Co.: UMMZ 67513 (1).

NEW JERSEY—Morris Canal, Little Falls, AMNH 18730 (1). No specific locality: AMNH 64499 (1♂). Bergen Co.: Edgewater, AMNH 1570 (1). Cape May Co.: Road at Green Creek, ANSP 17620 (1). Union Co.: Plainfield, near Stony Brook, AMNH 14291 (1).

NEW MEXICO—McKinley Co.: Fort Wingate, USNM 16760 (1).

NEW YORK—Jefferson Co.: Mill Creek, Sacket Harbor, USNM 39719 (1). Madison Co.: Peterboro, USNM 28314 (1), USNM 28319 (1♂), USNM 28320 (1). Westchester Co.: Sing Sing, USNM 80125 (2), USNM 84328-84330 (3).

OKLAHOMA—Fort Sill, UMMZ 52433 (1). Le Flore Co.: UMMZ 82801 (1). Tulsa Co.: Tulsa, AMNH 36773-36774 (2).

SOUTH CAROLINA—Charleston Co.: Charleston, ANSP 2857 (1).

TEXAS—Between San Antonio and Fort Inge, USNM 3303 (4); Sycamore Creek, USNM 45832-45833 (2). No specific locality: AMNH 82409-82411 (3). Bell Co.: 2 mi S of Belton, AMNH 32603 (1). Brewster Co.: Big Bend National Park, Rio Grande Village Campground, AMNH 77437 (1); Big Bend National Park, Tornillo Creek near Hot Springs, AMNH 80111-80115 (5♂); Chisos Mountains, Chilicotal Mountain, USNM 103661 (1). Brooks Co.: 2 mi S of Encino, USNM 83386 (1). Cameron Co.: Brownsville, USNM 3298 (1), USNM 45382 (1). Crosby Co.: Silver Falls Lake, USNM 92785-92789 (5). Culberson Co.: 2 mi E of Nickel, AMNH 55984-55988 (5). Duval Co.: San Diego, USNM 15680 (1). El Paso Co.: El Paso, Rio, USNM 164933 (1). Jeff Davis Co.: Near Fort Davis, USNM 92899-92908 (10). Kinney Co.: Fort Clark (Brackettville), USNM 20878, 20880 (2). Maverick Co.: Eagle Pass, USNM 45381 (1), USNM 159536 (1). Randall Co.: Palo Duro Canyon, UMMZ 68977 (1). San Patricio Co.: 2 mi N of Sandia, USNM 83382 (1). Swisher Co.: Tule Canyon, UMMZ 68978-68979 (4).

WISCONSIN—Racine Co.: Racine, USNM 3421 (1).

## APPENDIX II: LOCALITIES OF FIELD AND CALL RECORDS

The localities in Figures 21, 22, and 37 are based on all available information of calls of leopard frogs from the United States which can be correlated with particular morphologically distinct leopard frogs, including pre-

viously published information (calls described by Mecham, 1968 have not been included because it is not possible at this time to determine which of the several kinds of leopard frogs from the southwestern United States were recorded). Localities from which these records were derived are listed below for each species, arranged by state and county. Unless otherwise indicated these are my field records. Localities of tape recordings of leopard frogs from the Cornell Laboratory of Ornithology (CLO), the American Museum of Natural History Department of Herpetology (AMNH), and the University of Michigan Museum of Zoology Sound Laboratory (UMMZ) are included. Previously published records included in my figures are indicated with authors and date of publication. My field localities include listening records and observation and collecting records. These are indicated by the following categories: heard; seen; recorded; collected; or some combination of these. If a particular specimen was both taped and collected this locality is indicated as (specimen recorded).

*Rana berlandieri* Baird

TEXAS—Brown Co.: Brownwood (Littlejohn and Oldham, 1968); 12 mi W of Brownwood (Littlejohn and Oldham, 1968). Coleman Co.: Coleman area (Littlejohn and Oldham, 1968). Erith and Hamilton Cos.: Hico area (Littlejohn and Oldham, 1968). Gonzales Co.: Ottine (recorded, Littlejohn and Oldham, 1968). Johnson Co.: Cleburne area (recorded, Littlejohn and Oldham, 1968). San Patricio Co.: Big Lake, Welder Wildlife Refuge (recorded, Littlejohn and Oldham, 1968). Travis Co.: 20 mi E of Austin (recorded, Littlejohn and Oldham, 1968).

*Rana blairi* Mecham, Littlejohn, Oldham, Brown, and Brown

ILLINOIS—LaSalle Co.: 9.1 km W of Ottawa (heard, Brown and Brown, 1972). Mason Co.: 11.1 km S of Bath (heard, Brown and Brown, 1972). McLean Co.: 14.2 km N of Normal (recorded, Brown and Brown, 1972). Piatt Co.: Camp Creek, Sangamon Township (collected).

KANSAS—Cowley Co.: (recorded, Littlejohn and Oldham, 1968).

TEXAS—Brown Co.: Brownwood (Littlejohn and Oldham, 1968); 12 mi W of Brownwood (Littlejohn and Oldham, 1968). Coleman Co.: Coleman area (Littlejohn and Oldham, 1968). Dallam Co.: (recorded, Littlejohn and Oldham, 1968). Erith and Hamilton Cos.: Hico area (Littlejohn and Oldham, 1968). Johnson Co.: Cleburne area (recorded, Littlejohn and Oldham, 1968). Martin Co.: (recorded, Littlejohn and Oldham, 1968).

*Rana palustris* LeConte

DELAWARE—Sussex Co.: Hudson Pond, 20 mi N of Millsboro (recorded).

GEORGIA—Banks Co.: Near Homer (recorded). Gilmer Co.: about 1 mi E of Cartecay (recorded). Jackson Co.: About 3 mi SW of Jefferson (recorded). Rabun Co.: Just N of Dillard (recorded).

INDIANA—Jackson Co.: 3 mi S of Dudleyton (heard). Ripley Co.: 2 mi E of Napoleon (recorded).

KENTUCKY—Boone Co.: About 1 mi S of Florence (recorded).

MARYLAND—Saint Mary's Co.: Just S of Leonardtown (recorded); 9 mi S of Leonardtown (recorded). Wicomico Co.: Powellville, Adkins Mill Pond (recorded).

MICHIGAN—Washtenaw Co.: Ann Arbor (recorded).

NEW JERSEY—Bergen Co.: (audiospectrogram, Schaaf and Smith, 1971).

NORTH CAROLINA—Alamance Co.: About 3 mi N of Burlington (heard); about 6 mi NNE of Burlington (heard). Avery Co.: Near Pineola (heard). Buncombe Co.: North Fork, NW of Black Mountain (recorded). Caswell Co.: 2 mi SE of Anderson (heard). Guilford Co.: About 10 mi SW of Greensboro (heard); 1 mi E of Pole Cat Creek, S of Greensboro (heard); near Climax (heard). McDowell Co.: 15 mi E of Black Mountain (heard); Catawba River, 16 mi E of Black Mountain (recorded).

SOUTH CAROLINA—Richland Co.: Columbia (heard).

VIRGINIA—Caroline Co.: 1 mi S of Mattaponi River and Polecat Creek (recorded). Charlotte Co.: 4 mi W of Madisonville (recorded). Craig Co.: About 10 mi W of New Castle, near Craigs Creek (recorded). Franklin Co.: Near Dickinson (heard); about 5 mi NW of Mountain Valley (Henry County) (recorded). Prince Edward Co.: Bush River, about 7 mi E of Farmville (heard).

*Rana pipiens* Schreber

COLORADO—Elbert Co.: (recorded, Littlejohn and Oldham, 1968). Larimer Co.: (recorded, Littlejohn and Oldham, 1968).

ILLINOIS—La Salle Co.: 9.1 km W of Ottawa (recorded, Brown and Brown, 1972). Ogle Co.: 9.0 km N of Grand Detour (recorded, Brown and Brown, 1972).

INDIANA—Bartholomew Co.: 4 mi N of Columbus (heard); about 1 mi N of Columbus, just S of Bethel Holiness Church (recorded); about 3 mi N of Jonesville (recorded, collected). Decatur Co.: Near Forest Hill (recorded). Hancock Co.: about 6 mi E of Eden (recorded). Hamilton Co.: Fox Prairie, 3 mi N of Noblesville (recorded). Henry Co.: About 3 mi NE of Kennard (recorded). Franklin Co.: 5 mi SE of Andersonville (recorded, collected 1 ♂). Jefferson Co.: 10 mi E of Madison (recorded). Johnson Co.: About 4.5 mi E of Franklin (recorded); about 4.5 mi W of Franklin (recorded). Ripley Co.: Hassmer Hill Road, about 5 mi NNW of Versailles (recorded specimen); about 2 mi E of Napoleon (recorded, collected). Rush Co.: about 6 mi S of Rushville (heard). Switzerland Co.: about 3.5 mi E of Florence (recorded); Pond just W of Markland Dam, 3 mi W of Florence (recorded?).

KENTUCKY—Boone Co.: About 1 mi S of Florence (recorded).

MICHIGAN—Livingston Co.: University of Michigan, E. S. George Reserve, Pinckney (recorded). Washtenaw Co.: Numerous localities in the vicinity of Ann Arbor (recorded, collected).

NEW YORK—Thompkin Co.: Ithaca (CLO). Albany Co.: E. N. Huyck Preserve near Rensselaerville (seen).

*Rana utricularia* Harlan

FLORIDA—Alachua Co.: Gainesville, Lake Alice (recorded); Gainesville, near the air port (recorded); about 6 mi NE of Gainesville on Florida route 24, near Fairbanks (recorded); Florida route 232 E of Gainesville, about 4 mi from

the junction with Florida route 24 (recorded); between Gainesville and I 75 on Florida route s232 NW of Gainesville (heard); NE 39th Avenue and Florida route s232 NW of Gainesville (recorded); about 8 mi E of Gainesville on Florida route 20, E of junction with road to Cross Creek (recorded); about 6 mi E of Gainesville on Florida route 20, near Prairie Creek (recorded, collected); about 10 mi E of Gainesville (recorded); Collier Co.: About 5 mi S of Immokalee, near entrance to Immokalee Ranch (recorded); about 3 mi S of Immokalee (heard); Lake Trafford (recorded); about 5 mi E of Immokalee (recorded); about 7 mi E of Immokalee (recorded); Tarpon Lake (AMNH # 41). Dade Co.: Nine Mile Pond, Everglades National Park (recorded); US route 41 just W of the junction with Florida route 27, about 15 mi W of Miami (heard); Road to Card Sound (collected); Florida route 27 just N of junction with US 41, about 15 mi W of Miami (heard); Homestead (heard). Dixie Co.: Near Fletcher (recorded); about 10 mi NE of Cross City (heard); Florida route 358 just N of junction with US 98-19, about 1 mi NW of Shamrock (recorded); about 5 mi SE of Clara (Taylor County) (heard). Gilchrist Co.: 3 mi E of Trenton (recorded). Glades Co.: Just W of Moore Haven (recorded). Hendry Co.: about 8 mi E of Immokalee (recorded). Highlands Co.: Near Hicoria (AMNH # 34). Lafayette Co.: Near Cooks Hammock (recorded); about 5 mi S of Cooks Hammock (recorded). Levy Co.: 2 mi SW of Bronson (recorded); 5 mi SW of Bronson (recorded); 6 mi SW of Bronson (collected); 7 mi SW of Bronson (recorded); 9 mi SW of Bronson (heard); about 0.5 mi N of Otter Creek (recorded, collected); about 5.5 mi N of Otter Creek (heard). Marion Co.: Silver Springs (CLO). Palm Beach Co.: about 12 mi W of Boca Raton (collected). Polk Co.: about 7 mi N of Lakeland (recorded); about 10 mi N of Lakeland (heard). Putnam Co.: Just past Alachua County line, east of Hawthorne (recorded); between Orange Mills and Hastings (recorded); near Federal Point (recorded, collected). Saint John's Co.: 5 mi N of Hastings (recorded); 2 mi N of Tocoï (heard). Sarasota Co.: Near Englewood (collected); Warm Mineral Springs (collected). Seminole Co.: Near Wagner (recorded).

GEORGIA—Berrien Co.: About 2 mi SE of Nashville (recorded). Bulloch Co.: Statesboro (CLO). Burke Co.: Shell Bluff (heard); just W of Shell Bluff (recorded). Emmanuel Co.: Across river from Midville (recorded). Glascock Co.: Gibson (recorded). Hart Co.: About 0.5 mi N of Hartwell (recorded). Jefferson Co.: Just W of Wrens (recorded). Morgan Co.: About 5 mi N of Madison (recorded). Richmond Co.: about 5 mi S of Augusta (recorded). Walton Co.: Near Monroe (heard).

ILLINOIS—Mason Co.: 11.1 km S of Bath (recorded, Brown and Brown, 1972).

INDIANA—Bartholomew Co.: 4 mi N of Columbus (recorded); about 3 mi N of Jonesville (recorded, collected). Decatur Co.: about 1.5 mi S of Sardinia (heard). Jackson Co.: 1 mi N of Muscatatuk River, S of Tampico (heard); 3 mi S of Dudleyton (heard); 4 mi S of Seymour (heard). Jackson-Washington Cos.: Muscatatuk Swamps, S of Tampico (heard). Jennings Co.: 4 mi S of Sardinia (recorded). Monroe Co.: 6 mi E of Bloomington (recorded, collected); 4.5 mi N of Bloomington (heard); 6 mi E of Spencer (Owen County) (recorded). Morgan Co.: About 2 mi E of Martinsville (heard). Owen Co.: 1 mi E of Poland (Clay County) (recorded, collected); 7 mi S of Cloverdale (recorded, collected). Ripley Co.: Road to Hassmer Hill 4-H Camp, about 5 mi NNW of Versailles (recorded); about 2 mi E of Napoleon (recorded).

MARYLAND—Saint Mary's Co.: 9 mi S of Leonardtown (recorded).

MISSOURI—Barry Co.: Monett (AMNH # 32). Jefferson Co.: (UMMZ # 71).

NORTH CAROLINA—Guilford Co.: 5 mi NE of Julian (recorded).

NEW JERSEY—Cape May Co.: Cold Spring (AMNH # 150, recording of specimen, AMNH cat. no. 79625).

SOUTH CAROLINA—Berkeley Co.: Mount Holly (CLO). Lexington Co.: Near West Columbia (heard). Richland Co.: Columbia (heard). York Co.: 3 mi S of McConnells (recorded); 5 mi S of York (recorded, collected).

TEXAS—Bastrop Co.: (recorded, Littlejohn and Oldham, 1968). Gonzales Co.: Ottine (recorded, Littlejohn and Oldham, 1968). Johnson Co.: Cleburne area (recorded, Littlejohn and Oldham, 1968). San Patricio Co.: Big Lake, Welder Wildlife Refuge (recorded, Littlejohn and Oldham, 1968). Travis Co.: 20 mi E of Austin (recorded, Littlejohn and Oldham, 1968).

VIRGINIA—Lancaster Co.: (AMNH # 83); Morattico (AMNH # 26, 73).

### APPENDIX III: CATALOGUE NUMBERS OF FROGS WITH UNUSUAL DORSOLATERAL FOLDS

Figure 24 shows the geographic distribution of leopard frogs having both dorsolateral folds both continuous and not displaced (Fig. 23a) or having both dorsolateral folds both discontinuous and displaced (Fig. 23d,e). I have listed below the various combinations of conditions of dorsolateral folds found only rarely in leopard frogs and, by state, the museums (abbreviations as in Appendix I) and catalogue numbers of frogs possessing that combination of types of dorsolateral folds. Numbers in parentheses indicate numbers of specimens (if more than one).

Both sides discontinuous, but neither side displaced (Fig. 23f): Arizona: AMNH 51404. Florida: AMNH 112. Georgia: AMNH 41293. Illinois: INHS 5117, 6136, 7248, 9313; UMMZ 44484. Maryland: USNM 165697. North Carolina: AMNH 22407, 21348. North Dakota: USNM 53099, 66614. Oklahoma: UMMZ 81517.

Both sides continuous and displaced (Fig. 23b,c): California USNM 125654. Colorado: USNM 125724; AMNH 872. Idaho: USNM 20922. Illinois: INHS 1843, 4661, 5968, 8474. Iowa: UMMZ 93169, 93171 (2). Kansas: USNM 89036. Maryland: USNM 141006. Michigan: UMMZ 33754, 86004, 113521. Montana: USNM 54550, 59785, 61576, 61583. Nebraska: USNM 19824, 83956. New Jersey: AMNH 35503, 81338. New York: AMNH 5369. Oklahoma: UMMZ 77087. South Dakota: USNM 19817, 63053.

One side continuous and not displaced (Fig. 23a), the other side continuous and displaced (Fig. 23b,c): Arizona: UMMZ 91636. California: AMNH 68214. Colorado: USNM 125722, 125724. Florida: USNM 30953. Illinois: INHS 3649, 6746, 6794. Indiana: UMMZ 101631 (2). Iowa: UMMZ 71544, 93169 (2), 93171 (3). Kansas: UMMZ 67544. Michigan: UMMZ 32844, 37859. Missouri: AMNH 40318. Montana: USNM 61856. New Jersey: AMNH 77415, 79579. New Mexico: USNM 87069, 87074, 87075. New York: AMNH 14516, 51463, 51465, 51371. Ohio: AMNH 51629. Oklahoma: UMMZ 64208. South Dakota: USNM 140726.

One side continuous and not displaced (Fig. 23a), the other side discontinuous and not displaced (Fig. 23f): Arizona: USNM 45553, 60435. Georgia: AMNH 34390. Illinois: INHS 2403, 3607, 7337, 2916, 5760; UMMZ 44486.

Indiana: AMNH 51474, 51479. Iowa: UMMZ 93169; USNM 13925. Kansas: UMMZ 66884 (2). Louisiana: USNM 35350. Maine: AMNH 36661. Maryland: USNM 141004. Michigan: UMMZ 95373, 96297, 96291. Missouri: USNM 85592, 3431. Nebraska: UMMZ 67514; USNM 83958. New Jersey: AMNH 79581. North Carolina: AMNH 73529. North Dakota: USNM 66613. Oklahoma: AMNH 68347. Virginia: AMNH 63597, 71519. Tennessee: AMNH 68345.

One side continuous and not displaced (Fig. 23a), the other side discontinuous and displaced (Fig. 23d,e): Iowa: UMMZ 95045. Kansas: UMMZ 67547, 66884, 67544; USNM 89039. Massachusetts: USNM 2422. Nebraska: UMMZ 67506. Oklahoma: USNM 45987; AMNH 32621. Texas: USNM 92784.

One side continuous and displaced (Fig. 23b,c), the other side discontinuous and not displaced (Fig. 23f): Colorado: USNM 125721. Florida: USNM 95833. Illinois: INHS 8826. Iowa: UMMZ 93171. Kansas: USNM 89037. Nebraska: UMMZ 67511. Oklahoma: UMMZ 64209.

One side continuous and displaced (Fig. 23b,c), the other side discontinuous and displaced (Fig. 23d,e): Arizona: USNM 53125. Colorado: USNM 125721. Illinois: INHS 1149, 3606, 6679; UMMZ 67515. Iowa: UMMZ 93172. Kansas: UMMZ 67547. Missouri: USNM 57950, 17090. New Mexico: USNM 45368. Oklahoma: AMNH 83636; UMMZ 52433. Texas: AMNH 69039; USNM 45832, 92747, 92789, 92899, 160681.

One side discontinuous and not displaced (Fig. 23f), the other side discontinuous and displaced (Fig. 23d,e): Illinois: INHS 1639, 8995; UMMZ 67515. Texas: AMNH 52849; USNM 83386.

Dorsolateral folds indistinct, especially posteriorly (Fig. 23g); or short: Arizona: AMNH 65800, 65802, 55062, 55060, 10796, 74521, 74520, 74523, 65805, 56311, 62433, 55061, 65801, 55059, 62427; UMMZ 105696 (6), 91636 (6). Kansas: UMMZ 67549. Nevada: AMNH 5955, 5951, 5953, 5957; USNM 18927, 18957. Oklahoma: UMMZ 81517. Texas: AMNH 77440, 77438, 77439.

## LITERATURE CITED

- Alexander, R. D. 1960. Sound communication in Orthoptera and Cicadidae. *In*: W. E. Lanyon and W. N. Tavolga (eds.) *Animal Sounds and Communication*, AIBS Publ., 7: 38-92.
- . 1968a. Arthropods, pp. 167-216. *In*: T. Sebeok (ed.), *Animal Communication*. Univ. Indiana Press, Bloomington.
- . 1968b. Life cycle origins, speciation, and related phenomena in crickets. *Q. Rev. Biol.*, 43: 1-41.
- Alexander, R. D., and T. E. Moore. 1958. Studies on the acoustical behavior of seventeen-year cicadas (Homoptera: Cicadidae: *Magicicada*). *Ohio J. Sci.*, 58: 107-127.
- . 1962. The evolutionary relationships of 17-year and 13-year cicadas with three new species (Homoptera: Cicadidae: *Magicicada*). *Misc. Pubs Mus. Zool. Univ. Mich.*, no. 121: 1-59.
- Baird, S. F. 1859. Reptiles, p. 1-35. *In*: *United States and Mexican Boundary Survey*.
- Baker, J. J. W., and G. A. Allen. 1971. *The study of biology*, 2nd. ed. Addison-Wesley Publishing Company, Reading, Massachusetts. 973 pp.
- Blair, W. F., ed. 1961. *Vertebrate speciation*. Univ. Texas Press, Austin. 642 pp.

- Bragg, A. N. 1941. Some observations on Amphibia at and near Las Vegas, New Mexico. *Gt Basin Nat.*, 2: 109-114.
- 1944. Egg laying in leopard frogs. *Proc. Okla. Acad. Sci.*, 24: 13-14.
- 1949. The status of the leopard frogs of Oklahoma. *Wasmann Club Collect.*, 7: 211-214.
- 1950a. Salientian breeding dates in Oklahoma. *Res. Amphib. Okla., U. Okla. Press, Norman*: 34-38.
- 1950b. Observations on the ecology and natural history of Anura. XVII. Adaptations and distribution in accordance with habits in Oklahoma. *Res. Amphib. Okla., U. Okla. Press, Norman*: 59-100.
- 1950c. Further notes on range extensions of Salientia. *Proc. Okla. Acad. Sci.*, 31: 42-44.
- Bragg, A. N., and V. E. Dowell. 1954. Leopard frog eggs in October. *Proc. Okla. Acad. Sci.*, 35:41.
- Bresler, J. B. 1964. Pigmentation characteristics of *Rana pipiens*: Tympanum spot, line on upper jaw, and spots on upper eyelids. *Am. Midl. Nat.*, 72: 382-389.
- Brown, L. E., and J. R. Brown. 1972. Call types of the *Rana pipiens* complex in Illinois. *Science*, 176: 928-929.
- Brown, L. E. 1973. Speciation in the *Rana pipiens* complex. *Amer. Zool.*, 13: 73-79.
- Brown, W. L., Jr. 1957. Centrifugal speciation. *Q. Rev. Biol.*, 32: 247-277.
- 1958. General adaptation and evolution. *Syst. Zool.*, 7: 157-168.
- Catesby, M. 1742. *Natural History of Carolina, Florida and the Bahamas*.
- Cochran, D. M. 1961. Type specimens of reptiles and amphibians in the U. S. National Museum. *Bull. U. S. Natn. Mus.*, 220: pp. xv + 291.
- Cope, E. D. 1889. *The Batrachia of North America*. *Bull. U. S. Natn. Mus.*, 34: 1-525.
- Daudin, F. M. 1802. *Histoire naturelle des rainettes, des grenouilles et des crapauds*. Levrault, Paris. 108 pp.
- DeBenedictis, P. A. 1970. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: An experimental field study. PhD dissertation, The University of Michigan, pp. iv + 72.
- Deckert, R. F. 1920. Note on the Florida gopher frog, *Rana aesopus*. *Copeia*, no. 80: 26.
- Dickerson, M. C. 1906. *The Frog Book*. Doubleday, Page & Company, New York. pp. xvii + 253.
- Duellman, W. E. 1955. Notes on reptiles and amphibians from Arizona. *Occ. Paps Mus. Zool. Univ. Mich.*, no. 569:1-14.
- Duellman, W. E., and A. Schwartz. 1958. Amphibians and reptiles of Southern Florida. *Bull. Fla St. Mus. biol. Sci.*, 3: 181-324.
- Dumas, P. C. 1964. Species-pair allopatry in the genera *Rana* and *Phrynosoma*. *Ecology*, 45: 178-181.
- Fichter, E., and A. D. Linder. 1964. The amphibians of Idaho. *Spec. publ. Idaho St. Univ. Mus.*, 34 pp.
- Force, E. R. 1933. The age of the attainment of sexual maturity of the leopard frog *Rana pipiens* (Schreber) in Northern Michigan. *Copeia*, 1933: 128-131.
- Garman, H. 1890. Notes on Illinois reptiles and amphibians, including several species not before recorded from the northern States. *Bull. Ill. St. Lab. nat. Hist.*, 3: 185-190.
- 1892. A synopsis of the reptiles and amphibians of Illinois. *Bull. Ill. St. Lab. nat. Hist.*, 3: 215-388.
- Garman, S. 1888. The Batrachia of Kalm's "En Resa til Norra America." *Bull. Essex Inst.*, 20: 90-100.
- Gillespie, J. H., and J. W. Crenshaw. 1966. Hemoglobin variation in *Rana pipiens* (Amphibia: Anura). *Copeia*, 1966: 889-893.



- Gloyd, H. K. 1928. The amphibians and reptiles of Franklin County, Kansas. Trans. Kans. Acad. Sci., 31: 115-141.
- Green, N. B. 1941. Amphibians and reptiles of the Huntington region. Marshall Rev., 4: 33-40.
- 1949. The herpetological collections of the West Virginia biological survey. Proc. W. Va. Acad. Sci., 20: 57-64.
- Green, N. B., and B. Dowler. 1966. Amphibians and reptiles of the Little Kanawha River basin. Proc. W. Va. Acad. Sci., 38: 50-57.
- Gunther, A. C. L. G. 1900-1902, 1885-1902. Biologia Centrali-Americana: Reptilia and Batrachia, 1-326 (Batrachia, 197-309).
- Hallowell, E. 1856. [No title]. Proc Acad. nat. Sci. Philad., 8: 141-143.
- Hardy, J. D., Jr. 1964. A new frog, *Rana palustris mansuetii*, subsp. nov., from the Atlantic coastal plain. Chesapeake Sci., 5: 91-100.
- Harlan, R. 1826. Descriptions of several new species of batrachian reptiles, with observations of the larvae of frogs. Am. J. Sci. Arts, 10: 53-65.
- Heilman, R. A. 1951. A list of the amphibians and reptiles of Lebanon County, Pennsylvania. Proc. Pa Acad. Sci., 25: 44-46.
- Hudson, R. G. 1956. The leopard frog *Rana pipiens sphenoccephala* in south-eastern Pennsylvania. Herpetologica, 21: 148-150.
- Hutchinson, V. H. 1956. An annotated list of the amphibians and reptiles of Giles County, Virginia. Va J. Sci., n. ser., 7: 80-86.
- Kalm, P. 1761. En resa til Norra Amerika, 3: 45-46.
- Kauffeld, C. F. 1937. The status of the leopard frogs, *Rana brachycephala* and *Rana pipiens*. Herpetologica, 1: 84-87.
- Keeton, W. T. 1967. Biological Science, 1st ed. W. W. Norton & Company, Inc., New York, 955pp.
- Key, K. H. L. 1968. The concept of stasipatric speciation. Syst. Zool., 17: 14-22.
- King, W. 1939. A survey of the herpetology of Great Smoky Mountains National Park. Am. Midl. Nat., 21: 531-582.
- Linnaeus, C. 1766. Systema Naturae, 12th edition.
- Littlejohn, M. J. 1969. The systematic significance of isolating mechanisms, pp. 459-493. In: Systematic Biology, Natn. Acad. Sci. Publ. no. 1692.
- Littlejohn, M. J., and R. S. Oldham. 1968. *Rana pipiens* complex: Mating call structure and taxonomy. Science, 162: 1003-1005.
- Liu, C. C. 1935. Types of vocal sac in the Salientia. Proc. Boston Soc. Nat. Hist., 41: 19-40.
- Masaki, S. 1972. Climatic adaptation and photoperiodic response in the band-legged ground cricket. Evolution, 26: 587-600.
- Maynard Smith, J. 1966. The theory of evolution, 2nd ed. Penguin Books, Baltimore, Maryland. 325 pp.
- Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Massachusetts. 813 pp.
- McAlister, W. H. 1962. Variation in *Rana pipiens* Schreber in Texas. Am. Midl. Nat., 67: 334-363.
- Mecham, J. S. 1968. Evidence of reproductive isolation between two populations of the frog, *Rana pipiens*, in Arizona. SWest. Nat., 13: 35-44.
- 1969. New information from experimental crosses on genetic relationships within the *Rana pipiens* species group. J. exp. Zool., 170: 169-180.
- 1971. Vocalizations of the leopard frog, *Rana pipiens*, and three related Mexican species. Copeia, 1971: 505-516.
- Mecham, J. S., M. J. Littlejohn, R. S. Oldham, L. E. Brown, and J. R. Brown. 1973. A new species of leopard frog (*Rana pipiens* complex) from the plains of the central United States. Occ. Pap. Mus. Texas Tech. Univ., 18: 1-11.
- Merrell, D. J. 1968. A comparison of the estimated size and the effective size of

- breeding populations of the leopard frog, *Rana pipiens*. *Evolution*, 22: 274-283.
- Mittleman, M. B., and H. T. Gier, 1942. Notes on leopard frogs. *Proc. New Engl. zool. Club*, 20: 7-15.
- Moore, J. A. 1939. Temperature tolerance and rates of development in the eggs of Amphibia. *Ecology*, 20: 459-478.
- 1941. Developmental rates of hybrids between *Rana pipiens* and *Rana sphenocephala*. *Proc. Soc. exp. Biol. Med.*, 47: 207-210.
- 1942. Study of embryonic temperature tolerance and rate of development in *Rana pipiens* from different latitudes. *Yb. Am. phil. Soc.*, 1942: 175-178.
- 1944. Geographic variation in *Rana pipiens* Schreber of eastern North America. *Bull. Am. Mus. nat. Hist.*, 82: 345-370.
- 1946. Incipient intraspecific isolating mechanisms in *Rana pipiens*. *Genetics*, Princeton, 31: 304-326.
- 1949. Patterns of evolution in the genus *Rana*, pp. 315-338. *In*: G. L. Jepson, et. al., eds., *Genetics, Paleontology and Evolution*, Princeton Univ. Press, Princeton, New Jersey.
- Necker, W. L. 1934. Contribution to the herpetology of the Smoky Mountains of Tennessee. *Bull. Chicago Acad. Sci.*, 5: 1-4.
- Neill, W. T. 1958. The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. *Bull. mar. Sci. Gulf Caribb.*, 8: 1-97.
- Netting, M. G. 1933a. The amphibians of Pennsylvania. *Proc. Penn. Acad. Sci.*, 7:1-11.
- 1933b. The amphibians of West Virginia. Part II. Toads and frogs. *West Virginia Wildlife*, 11:4-5.
- Oliver, J. A., and J. R. Bailey. 1939. Amphibians and reptiles of New Hampshire. *Biol. Sur. Connecticut Watershed*, Report no. 4, Concord: 1-23.
- Olson, R. E. 1956. The amphibians and reptiles of Winnebago County, Illinois. *Copeia*, 1956: 188-191.
- Ortenburger, A. I., and B. Freeman. 1930. Notes on some reptiles and amphibians from western Oklahoma. *Publs Univ. Okla. biol. Surv.*, 2: 175-188.
- Pettus, D., and D. D. Post. 1969. Genetic discontinuity of leopard frogs of Colorado. *J. Herpetol.*, 3: 193-194. [Abstract].
- Pickens, A. L. 1927. Amphibians of upper South Carolina. *Copeia*, no. 165: 106-110.
- Platz, J. E. 1972. Sympatric interaction between two forms of leopard frog (*Rana pipiens* Complex) in Texas. *Copeia*, 1972: 232-240.
- Platz, J. E., and A. L. Platz. 1973. *Rana pipiens* complex: Hemoglobin phenotypes of sympatric and allopatric populations in Arizona. *Science*, 179: 1334-1336.
- Porter, K. R. 1942. Developmental variations resulting from various associations of frog cytoplasm and nuclei. *Trans. N. Y. Acad. Sci.*, ser. 2, 4: 213-217.
- Post, D. D., and D. Pettus. 1966. Variation in *Rana pipiens* (Anura: Ranidae) of Eastern Colorado. *SWest. Nat.*, 11: 476-482.
- 1967. Sympatry of two members of the *Rana pipiens* complex in Colorado. *Herpetologica*, 23: 323.
- Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. *Evol. Biol.*, 2: 321-428.
- Ross, H. H. 1962. *A synthesis of evolutionary theory*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 387 pp.
- Ruibal, R. 1955. A study of altitudinal races in *Rana pipiens*. *Evolution*, 9: 322-338.
- Ruthven, A. G., C. Thompson, and H. Thompson. 1912. The herpetology of Michigan. *Mich. geol. biol. Surv.*, Publ. 10, Biol. Ser. 3: 1-190.

- Ryan, R. A. 1953. Growth rates of some ranids under natural conditions. *Copeia*, 1953: 73-80.
- Salthe, S. N. 1969. Geographic variation in the lactate dehydrogenases of *Rana pipiens* and *Rana palustris*. *Biochem. Genet.*, 2: 271-303.
- Sanders, O., and H. M. Smith. 1971. Skin tags and ventral melanism in the Rio Grande leopard frog. *J. Herpetol.*, 5: 31-38.
- Savage, R. M. 1934. The breeding behaviour of the common frog, *Rana temporaria* Linn., and of the common toad, *Bufo bufo bufo* Linn. *Proc. zool. Soc. Lond.*, Pt. 1, 1934: 55-70.
- Schaaf, R. T., Jr., and P. W. Smith. 1970. Geographic variation in the pickerel frog. *Herpetologica*, 26: 240-254.
- 1971. *Rana palustris*. *Cat. Amer. Amphib. Rept.*: 117.1-117.3.
- Schmidt, K. P. 1925. New Chinese amphibians and reptiles. *Am. Mus. Novit.*, No. 175: 1-3.
- Schmidt, K. P. 1953. A check list of North American amphibians and reptiles. 6th ed. ASIH, Univ. Chicago Press, Chicago. viii + 280 pp.
- Schmidt, R. S. 1966. Central mechanisms of frog calling. *Behavior*, 26: 251-285.
- Schoepf, J. D. 1911. *Travels in the Confederation 1783-1784*, translated and edited by A. J. Morrison. William J. Campbell, Philadelphia. pp. x + 426.
- Schreber, H. 1782. *Beitrag zur Naturgeschichte der Frösche*. *Der Naturforscher*, Johann Jacob Gebaur, Halle, 18: 182-193.
- Selander, R. K., W. G. Hunt, and S. Y. Yang. 1969. Protein polymorphism and genic heterozygosity in two European subspecies of the house mouse. *Evolution*, 23: 379-390.
- Shaw, G. 1802. *General Zoology, or Systematic Natural History*. Vol. III, Part I, Amphibia. Printed by Thomas Davison, for G. Kearsely, London. pp. vi + 312.
- Smith, A. 1849. *Illustrations of the zoology of South Africa*. Smith, Elder and Co., London. No pagination.
- Smith, H. M. 1956. *Handbook of amphibians and reptiles of Kansas*, 2nd ed. *Misc. Publs Mus. nat. Hist. Univ. Kans.*, 9: 1-356.
- 1969. Parapatry: Sympatry or allopatry? *Syst. Zool.*, 18: 254-255.
- Smith, P. W. 1957. An analysis of post-Wisconsin biogeography of the Prairie Peninsula region based on distributional phenomena among terrestrial vertebrate populations. *Ecology*, 38: 205-218.
- 1961. The amphibians and reptiles of Illinois. *Bull. Ill. St. nat. Hist. Surv.*, 28: 1-298.
- Springer, S. 1938. On the size of *Rana sphenoccephala*. *Copeia*, 1938: 49.
- Stebbins, R. C. 1951. *Amphibians of western North America*. Univ. Calif. Press, Berkeley. pp. xviii + 539.
- Stejneger, L. 1893. Annotated list of the reptiles and batrachians collected by the Death Valley Expedition in 1891 with descriptions of new species. *North American Fauna*, No. 7: 159-228.
- Surface, H. A. 1913. The amphibians of Pennsylvania. *Zool. Bull. Div. Zool. Pa. Dep. Agric.*, 3: 66-152.
- Tanner, V. M. 1931. A synoptical study of Utah Amphibia. *Proc. Utah Acad. Sci.*, 8: 159-198.
- Trapido, H., and R. T. Clausen. 1938. Amphibians and reptiles of eastern Quebec. *Copeia*, 138: 117-125.
- Walker, C. F. 1946. The amphibians of Ohio. Part I. The frogs and toads (Order Salientia). *Sci. Bull. Ohio St. Mus.*, 1: 1-109.
- Weed, A. C. 1922. New frogs from Minnesota. *Proc. biol. Soc. Wash.*, 35: 107-110.
- Wright, A. H. 1914. *Life-histories of the Anura of Ithaca, New York*. Carnegie Inst. Publ., No. 197: 1-98.

- Wright, A. H., and A. A. Wright. 1949. Handbook of frogs and toads of the United States and Canada. Comstock Publ. Co., Ithaca, N. Y. pp. xii + 640.
- Yarrow, H. C. 1875. Report upon the collections of batrachians and reptiles made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 1871, 1872, 1873, and 1874. *In*: G. M. Wheeler, Report upon geographical and geological explorations and surveys west of the one hundredth meridian. U. S. Govt. Print. Off., Washington. 5.
- Zenisek, C. J. 1963. A study of the natural history and ecology of the leopard frog, *Rana pipiens* Schreber. PhD Dissertation, The Ohio State University, 153 pp.

Accepted for publication April 1, 1974







