AMPHIBIANS AND REPTILES IN THE UPPER MISSISSIPPI RIVER VALLEY: SYSTEMATIC AND DISTRIBUTIONAL PROBLEMS

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ABSTRACT

Eighteen species of amphibians and reptiles found in western Kentucky, western Tennessee, and/or eastern Arkansas display systematic problems based on their current known distributions or areas of intergradation/hybridization. Each is briefly discussed, and a biochemical approach, sometimes in combination with field work and a traditional analysis of external morphology, is proposed as a means of resolving the problem. The Mississippi River and its floodplain are shown to be a barrier to amphibian and reptile distribution.

Introduction

Interest in the biodiversity of amphibians and reptiles throughout North America has resulted in the publication of many state and regional field guides over the last three decades. More specifically, recent works are now available that contain relatively precise dot maps showing the distributions of amphibians and reptiles in states that adjoin Kentucky, Tennessee, and Arkansas (Dundee and Rossman 1989, Louisiana; Green and Pauley 1987, West Virginia; Johnson 1987, Missouri; Minton 1972, Indiana; Mount 1975, Alabama; Pfingsten and Downs 1989, Ohio; Smith 1961, Illinois; Tobey 1985, Virginia; Webb 1970, Oklahoma).

Published dot maps for the herpetofauna of Kentucky, Tennessee, and Arkansas do not exist, and information on the distribution of amphibians and reptiles in the upper Mississippi River valley remains generally unavailable to most biologists. In addition, the herpetofaunal distributions of this region are still poorly understood and in need of more voucher documentation. This lack of a more precise knowledge of the distributions of amphibians and reptiles of southwestern Kentucky, western Tennessee, and eastern Arkansas has been an historical impediment to investigating (by use of morphological criteria) the systematic relationships of a number of problematic taxa that are found there. However, new methods of data gathering and analysis may provide an opportunity to elucidate more clearly the relationships of populations of a number of taxa that inhabit the upper Mississippi River valley.

The recent redefinition of the species concept, as summarized for herpetology by Frost and Hillis (1990), leaves little doubt that the *evolutionary* species concept has replaced the *biological* species concept as an operational approach to understanding systematic relationships. It also leaves little doubt that analysis of data gathered by molecular techniques may be the only way in which the systematic relationships of many taxa will be resolved (an excellent summary of molecular systematics and its techniques is available in Hillis and Moritz 1990). Although Frost and Hillis (1990) are generally concerned with taxa at the species level only, they have, by example and implication, demonstrated that in many cases the designation of sub-

species in herpetology has been arbitrary and has lent little to our understanding of systematic relationships, and their arguments therefore raise the question of whether the continued use of subspecies is justified. It is not my intent here to debate the validity of the use of subspecies in herpetology; use of them has steadily declined over the last 35 years (see Table 3 in Collins 1990).

It is my intent to: (1) discuss some examples of subspecies that might be elevated to specific status should they be subjected to molecular analysis, and, where appropriate, analysis of external morphological characteristics, and (2) show that, in most instances, the clues that led me to question the current status of the taxa discussed below were the availability of more refined range maps and the demonstrated presence of narrow zones of intermediacy between two presumed subspecies. The maps revealed that these taxa had allopatric distributions or narrow contact zones and this, combined with their distinctive external morphologies, made their subspecific status suspect. Allopatry excludes the possibility of any gene flow between two or more presumed subspecies (obviously, intergradation cannot take place), and distinctive morphology indicates that a taxon may have its own evolutionary fate, and therefore deserves specific status. An ancillary result of my survey is the demonstrated importance of the Mississippi River and its floodplain as a barrier to distribution and/or gene flow, at least in western Tennessee and eastern Arkansas.

I herein present accounts for 18 species of amphibians and reptiles that occur in Kentucky, Tennessee, and/or Arkansas, and whose distributions imply that taxonomic investigation, combining intensive field work and/or molecular investigation in conjunction with external morphological data, might prove fruitful. The 18 species selected by me for this paper represent only the more obvious examples of taxa that might be investigated. Much of my distributional information is based on the unpublished dot maps of William H. Redmond (1985, for Tennessee amphibians) and John MacGregor (pers. comm., for Kentucky amphibians and reptiles). From both of the sets of maps supplied by them, however, I attempted to use only those records that they indicated were backed by preserved voucher specimens. Arkansas distributions are based on the maps in Conant and Collins (1991), and were derived from the many sources acknowledged therein. In all instances, literature records, which are unverifiable and (to me) unacceptable for determining the precise ranges of amphibians and reptiles (or any other organisms), were ignored. Where not otherwise attributed, the general descriptions of ranges are from Conant and Collins (1991); common names are those standardized in Collins (1990).

SPECIES ACCOUNTS

Salamanders

Dusky Salamander (Desmognathus fuscus). This salamander is found throughout southwestern Kentucky and occurs in western Ten-

nessee east of the Mississippi River floodplain (there is an isolated colony in northeastern Arkansas, but it is probably extirpated). It is composed of two subspecies, the northern dusky salamander (D. f. fuscus) and the spotted dusky salamander (D. f. conanti), which are presumed to intergrade in a relatively narrow band from southwestern Kentucky (where the Indiana and Illinois borders meet) southeastward to the Fall Line along the Georgia-South Carolina border. However, these two taxa are strikingly different in appearance, and they may represent two distinct species. Further investigation by molecular techniques, correlated with a detailed evaluation of pattern and color characteristics, might reveal that these two races deserve specific status.

Longtail Salamander (Eurycea longicauda). This salamander is currently composed of three very distinct races: (1) the longtail salamander (E. l. longicauda), which occurs in southwestern Kentucky (John MacGregor pers. comm.) and extreme northwestern Tennessee; (2) the three-lined salamander (E. l. guttolineata), which occurs in the remainder of western Tennessee (Redmond 1985) and south along the eastern bank of the Mississippi River, and (3) the dark-sided salamander (E. l. melanopleura), which is found to the west, but is absent from the floodplain of the Mississippi River in Arkansas. Specific status has been proposed for E. l. guttolineata, but the evidence is in dispute, depending on whether intermediate specimens are considered hybrids (from a narrow zone of hybridization between E. l. longicauda and E. l. guttolineata) or intergrades. I favor treating the intermediate specimens as hybrids, because so few have been found and there is no evidence of intergradation over a broad portion of the range. But most investigators have been reluctant to follow this arrangement. To the west, the race E. l. melanopleura may exhibit a similar situation. Although there are apparently a number of intermediate specimens between E. l. melanopleura and E. l. longicauda, all are from a narrow band in southeastern Missouri (Johnson 1987). All three taxa are excellent candidates for systematic analysis by molecular technique to determine whether each might be accorded specific status.

Mudpuppy (Necturus maculosus). The nominate race of this salamander, the mudpuppy, is apparently absent from much of the western part of the Jackson Purchase in southwestern Kentucky (John MacGregor pers. comm.) and the upper Mississippi River floodplain of Tennessee (Redmond 1985). If the distributional hiatus is not an artifact of insufficient collecting, its western subspecies, the Red River mudpuppy (N. m. louisianensis), of Arkansas and neighboring states, is allopatric. Because N. m. louisianensis is allopatric and also morphologically distinct, it is probably a distinct species and is an excellent candidate for further investigation by molecular technique.

Zigzag Salamander (*Plethodon dorsalis*). The nominate race of this salamander, the eastern zigzag salamander, is found throughout southwestern Kentucky (John macGregor pers. comm.) and adjacent extreme northwestern Tennessee, but is apparently absent from much of the rest of western Tennessee (Redmond 1985). A western subspecies, the Ozark zigzag salamander (*P. d. angusticlavius*), is distributed in north-central Arkansas and adjacent southern Missouri and eastern Oklahoma. Because *P. d. angusticlavius* is allopatric and also morphologically distinct, it is probably a distinct species, and is an excellent candidate for systematic investigation by molecular technique.

Mud Salamander (*Pseudotriton montanus*). Although distributed somewhat to the east of southwestern Kentucky and western Tennes-

see, the distribution of the western race of this salamander, the midland mud salamander (*P.m. diastictus*), extends west to Caldwell County, Kentucky (Scott et al. 1984) and throughout much of central Tennessee. If the distributional hiatus between this subspecies and its presumed races to the east and south is not an artifact of insufficient collecting, *P. m. diastictus* is allopatric. In addition, it is strikingly different in color and pattern than its other races. Because *P. m. diastictus* is allopatric and morphologically different, it is probably a distinct species, and is a good candidate for systematic investigation by molecular technique.

Six species of salamanders, although not discussed here with regard to their taxonomy, show an apparent distributional hiatus caused by the Mississippi River, or avoidance of all or at least a major part of the Mississippi River floodplain in Tennessee. They are the tiger salamander (Ambystoma tigrinum), hellbender (Cryptobranchus alleganiensis), southern two-lined salamander (Eurycea cirrigera), cave salamander (Eurycea lucifuga), four-toed salamander (Hemidactylium scutatum), and red salamander (Pseudotriton ruber). Whether this is an artifact of insufficient collecting is not known.

FROGS AND TOADS

American Toad (Bufo americanus). A diminutive race of this species, the dwarf American toad (B. a. charlesmithi), occurs in the upper Mississippi River valley. This subspecies has been the subject of some controversy because the external morphological characteristics that presumably separate it from the nominate race are so poorly defined. Smaller average snout-vent length is supposedly an important diagnostic character of the subspecies B. a. charlesmithi, but is not much use when only small specimens are at hand for comparison. If, indeed, there are populations of B. americanus in southwestern Kentucky and western Tennessee that exhibit statistically significant differences in snout-vent length, then they probably represent different species. Systematic investigation by molecular technique would clarify the status of the two races of B. americanus.

Eastern Spadefoot (Scaphiopus holbrookii). The nominate race of this spadefoot is generally confined east of the Mississippi River, having breached that river only in the Missouri bootheel, northeastern Arkansas, and extreme southeastern Arkansas. A second distinctive race, Hurter's spadefoot (S. h. hurterii), is distributed west of the Mississippi River, and is found from western Arkansas southwestward to the Rio Grande Valley of Texas, with an isolated colony in north-central Arkansas. If the distributional hiatus between its two races is not an artifact of insufficient collecting, the western subspecies is allopatric. Because S. h. hurterii is allopatric and also morphologically different from S. h. holbrookii, it is probably a distinct species and is an excellent candidate for systematic investigation by molecular technique.

Four species of frogs and toads, although not discussed here with regard to their taxonomy, have ranges that suggest the Mississippi River as an apparent distributional barrier, either preventing their spread eastward into western Tennessee, or preventing their spread westward into eastern Arkansas. They are the southern cricket frog (Acris gryllus), bird-voiced treefrog (Hyla avivoca), barking treefrog (Hyla gratiosa), and Strecker's chorus frog (Pseudacris streckeri). Whether this is an artifact of insufficient collecting is not known.

Turtles

Spiny Softshell (Apalone spinifera). In the upper Mississippi River valley, this turtle has two subspecies: one east of the river (the

eastern spiny softshell, A. s. spinifera), and one west of the river (the western spiny softshell, A. s. hartwegi). Presumably, these two races intergrade in eastern Arkansas and western Tennessee, but the area of intergradation is apparently narrow. A systematic analysis of data from these two taxa gathered by molecular technique, combined with a sophisticated analysis of external characteristics, may reveal that they are distinct species exhibiting a narrow hybrid zone.

False Map Turtle Complex (Graptemys kohnii and G. pseudogeographia). The taxonomic status of map turtles in the upper Mississippi River valley has been controversial for over a decade. Two species, the Mississippi map turtle (G. kohnii), and the false map turtle (G. pseudogeographica), are currently recognized and known from the region, and are quite distinctive in their external head morphology. Despite their distinctive appearance and the fact that no recent published analysis of their systematic relationship has been done, many herpetologists feel they are the same species and should be, at most, accorded subspecific status. An analysis of data gathered by molecular technique from these two taxa would be helpful in resolving this argument. Apparently data analysis based on head morphology alone will not suffice.

Eastern Mud Turtle (Kinosternon subrubrum). In the upper Mississippi River valley, this turtle has two subspecies: one west of the river (the Mississippi mud turtle, K. s. hippocrepis), and one east of the river (the eastern mud turtle, K. s. subrubrum). Presumably, these two races intergrade in eastern Arkansas and western Tennessee, but the area of intergradation is apparently narrow. A systematic analysis of data gathered by molecular technique from these two taxa may reveal that they are distinct species exhibiting a narrow hybrid zone.

Eastern Box Turtle (Terrapene carolina). In most of the upper Mississippi River valley, this turtle has two subspecies: one west of the river (the three-toed box turtle, T. c. triunguis), and one east of the river (the eastern box turtle, T. c. carolina). The former apparently crosses the Mississippi River in extreme southwestern Tennessee. No area of intergradation has been shown between these two subspecies in Arkansas, Kentucky, or Tennessee, but intergradation over a large area has been reported from northern Georgia south and west along the Gulf Coast to southeastern Louisiana. A systematic analysis of data gathered by molecular technique from specimens of these two taxa on either side of the upper Mississippi River valley may reveal that they are distinct species exhibiting a narrow hybrid zone. If so, reevaluation of the data from Georgia and other states to the south may be needed.

Two species of turtles, although not discussed here with regard to their taxonomy, have known distributions that suggest the Mississippi River and/or its floodplain as an apparent distributional barrier, either preventing their spread eastward into western Tennessee, or preventing their spread westward into eastern Arkansas. They are the common map turtle (*Graptemys geographica*) and chicken turtle (*Deirochelys reticularia*). Whether this is an artifact of insufficient collecting is not known.

Lizards

Six-lined Racerunner (*Cnemidophorus sexlineatus*). The western race of this lizard, the prairie racerunner (*C. s. viridis*) is found west of the Mississippi River, and the nominate race, the six-lined racerunner, is found east of the river. These two races have been shown to intergrade from eastern Missouri (St. Louis area) south along the

Mississippi River in eastern Arkansas and south through Louisiana to the Gulf, but this area of intergradation is apparently narrow. No evidence of the western race crossing the Mississippi River south of St. Louis has been detected. A systematic analysis of data gathered by molecular technique from these two taxa may reveal that they are distinct species exhibiting a narrow hybrid zone.

Slender Glass Lizard (Ophisaurus attenuatus). The nominate race of this lizard, the western slender glass lizard, is found west of the Mississippi River, but is apparently absent from all territory adjacent to the western bank of that river in an area extending from southern Illinois south to the Gulf of Mexico. An eastern subspecies, the eastern slender glass lizard (O. a. longicaudus), is distributed east of the Mississippi River but is absent from its floodplain, except in southern Tennessee, southern Mississippi, and adjacent Louisiana. At no point anywhere in their range do these two subspecies make contact. Because they are allopatric and morphologically distinct, both may be distinct species; thus both are excellent candidates for systematic investigation by molecular technique.

Two species of lizards, although not discussed here with regard to their taxonomy, have ranges that suggest the Mississippi River and/or its floodplain as an apparent distributional barrier, either preventing their spread eastward into western Tennessee, or westward into eastern Arkansas. They are the southeastern five-lined skink (*Eumeces inexpectatus*) and coal skink (*E. anthracinus*). Whether this is an artifact of insufficient collecting is not known.

Snakes

Worm Snake (Carphophis amoenus). Two very poorly defined races of this snake, the eastern worm snake (C. a. amoenus), and the midwest worm snake (C. a. helenae), are generally found east of the Mississippi River, but C. a. helenae apparently has invaded extreme eastern Arkansas along the west bank of the Mississippi River. A presumed western subspecies, the western worm snake (C. a. vermis), is distributed west of the Mississippi River, but is absent from its floodplain, except in central Illinois. An isolated colony of Carphophis in southeastern Arkansas and another such colony in northeastern Louisiana appear to be relictual hybrid populations between taxa found east of the Mississippi River and those to the west. At no point anywhere in their ranges do helenae and vermis intergrade. Because it is allopatric and morphologically distinct from helenae, vermis is probably a distinct species and thus an excellent candidates for systematic investigation by molecular technique. Recently, Conant and Collins (1991) treated *vermis* as a distinct species.

Pine Snake (*Pituophis melanoleucus*). This species is enigmatic in the upper Mississippi River valley. The nominate subspecies, the eastern pine snake has been documented from Land Between The Lakes (LBL) and eastern Calloway County in Kentucky (John MacGregor pers. comm.), and the portion of LBL in Tennessee. In addition an isolated colony exists in extreme southwestern Tennessee. But no records for this snake exist for most of the Jackson Purchase of southwestern Kentucky, the Mississippi River floodplain of western Tennessee (with the exception noted above), nor eastern Arkansas. Is this sporadic distribution an artifact of lack of collecting? If not, then the hiatus between this subspecies and the bullsnake (*P. m. sayi*) to the north and west is real, and *sayi* should be considered the eastern race of a distinct western species, *Pituophis catenifer*, as recently proposed by Lynch (1985) and adopted by Collins (1990).

Corn Snake (Elaphe guttata). The nominate subspecies, the corn snake, is found in two isolated colonies in eastern and central Kentucky, and in Tennessee from the eastern mountains west along the southern border to the Mississippi River floodplain at Memphis. West of the Mississippi River, the Great Plains rat snake (E. g. emoryi) occurs as far east as southeastern Missouri (exclusive of the bootheel), north-central Arkansas, southeastern Arkansas, and central Louisiana. At no point do the ranges of these two races meet, although some workers consider the populations in southeastern Arkansas, central Louisiana and eastern Texas to be intermediate between the presumed races guttata and emoryi. Nonetheless, because they are allopatric and morphologically distinct, they may be distinct species and thus are excellent candidates for systematic investigation by molecular technique.

Milk Snake (Lampropeltis triangulum). The milk snake (L. triangulum) in Kentucky and Tennessee is a complex systematic problem (Conant and Collins 1991) that, more than any other presented in this paper, lends itself to exploration by biochemical means. As currently defined, this species has been divided into nine races in the United States, creating an unwieldy, and probably unnatural, arrangement. The upper Mississippi River valley is purported to harbor at least two subspecies, the red milk snake (L. t. syspila) and the scarlet kingsnake (L. t. elapsoides), while the eastern milk snake (L. t. triangulum) is found just to the east. No statistically significant morphological evidence exists to show that the extremely distinctive scarlet kingsnake is anywhere a race of L. triangulum, but because of historical inertia, most systematists continue to recognize it as such. An investigation by molecular technique, correlated with a detailed evaluation of pattern and color characteristics, will probably reveal that the scarlet kingsnake deserves specific status.

Timber Rattlesnake (Crotalus horridus). Pisani et al. (1973) synonymized the southern race of this well-known rattlesnake. Investigators have since attempted to resurrect the southern race, but their attempts, which have not met with acceptance, were focused on small, geographically restricted samples and based on highly variable external characteristics such as pattern and color. Indeed, Conant and Collins (1991) illustrated four distinct color and pattern variants for this highly variable species, including a previously unknown variant found in the western part of the range. Most range maps for C. horridus show it as continuous across the upper Mississippi River valley, but closer scrutiny of the distribution based on actual vouchers reveals that this reptile has never been verified in the Jackson Purchase of southwestern Kentucky (John MacGregor pers. comm.). Further, Collins and Knight (1980) showed no records for western Tennessee, although numerous vouchers were mapped by them for eastern Arkansas close to the Mississippi River. Much field work is needed in western Kentucky and Tennessee to determine the presence or absence of this large snake. Given its variability, coupled with its possible absence from large areas throughout its range, this snake invites investigation by molecular techniques to determine its status. Is it a single wide-ranging, highly variable species? Or is it composed of a number of isolated (allopatric),

morphologically distinct taxa that might be recognized at the species level?

Ten species of snakes, although not discussed here with regard to their taxonomy, have ranges that suggest the Mississippi River and/or its floodplain as an apparent distributional barrier, either preventing their spread eastward into ewestern Tennessee, or preventing their spread westward into eastern Arkansas. They are the coachwhip (Masticophis flagellum), northern water snake (Nerodia sipedon), Graham's crayfish snake (Regina grahamii), queen snake (R. septemvittata), pigmy rattlesnake (Sistrurus miliarius), southeastern crowned snake (Tantilla coronata), flathead snake (T. gracilis), eastern ribbon snake (Thamnophis sauritus), (but not the western ribbon snake, T. proximus), rough earth snake (Virginia striatula), and smooth earth snake (V. valeriae). Whether this is an artifact of insufficient collecting is not known.

ACKNOWLEDGMENTS

Many individuals supplied me with data that helped in revealing the taxonomic problems presented here. In particular, John MacGregor (U.S. Forest Service, Berea, Kentucky) and William H. Redmond (Division of Land and Forest Resources, Tennessee Valley Authority, Norris, Tennessee) supplied me with unpublished distribution maps for Kentucky and Tennessee, respectively. To them both I am most grateful. A. Floyd Scott, symposium coordinator (Austin Peay State University, Clarksville) provided support and encouragement.

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