

HERPETOLOGICAL EVIDENCE FOR THE POSTGLACIAL EASTWARD EXTENSION OF THE STEPPE IN NORTH AMERICA

KARL P. SCHMIDT

Field Museum of Natural History, Chicago

The westward extension of the characteristic steppe fauna of central Asia into central Europe in Pleistocene times, with numerous persistent influences on the modern fauna, is one of the best documented zoogeographic explanations of a faunal relation. It was at first highly surprising to find fossil evi-

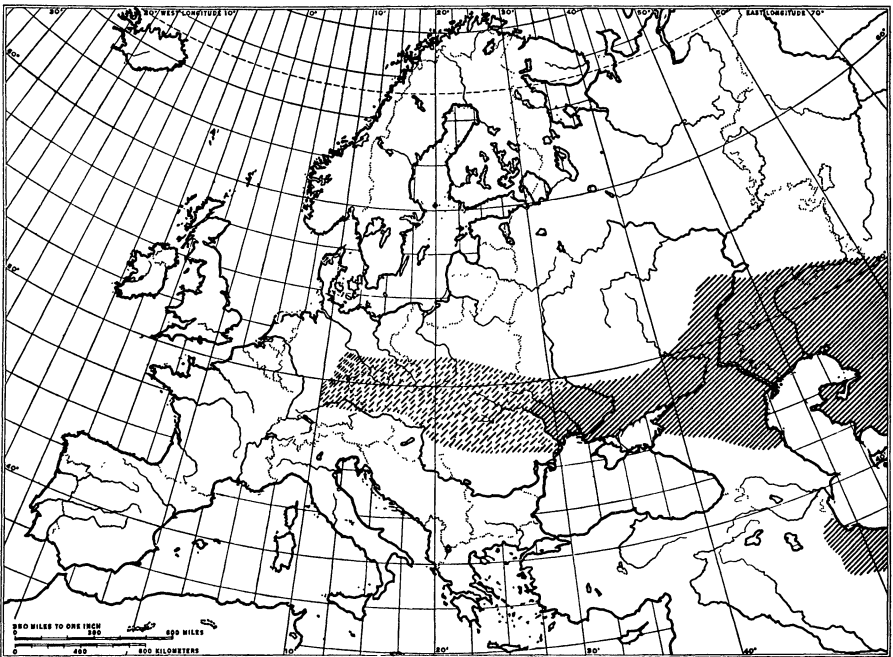


FIG. 1. Pleistocene westward extension into Europe (shown by dashes) of the range of the jerboa (from Scharff). Numerous animals have a similar range and history. Existing range in diagonal lines.

dence of the relatively recent existence of the lion and hyena in England, and of the saiga antelope and jerboa (Fig. 1) in Germany; but as these data accumulated, they shed a clear light on the origin of an important element of the existing fauna of western Europe. Boyd Dawkins (1880) set forth the

evidence which had been accumulating for some time. Alfred Nehring (1890) amplified this material, and interpreted it as due to a peninsular westward extension of steppe conditions, correlated with the retreat of the continental glaciers. The range of certain well known forms of central Europe, such as the hamster, whose principal home is in central Asia, falls into its proper relation with the evidence from fossils. The information with respect to mammals is well summarized and illustrated with maps by Scharff (1907). Invertebrate evidence from the modern fauna strongly supports the steppe peninsula hypothesis. Burr's report of more than eighty species of Orthoptera from small open areas in Moravia, wholly unlike those of the adjacent territory, and allied to forms in the Russian steppe in the Volga valley, has been cited repeatedly (Taylor, 1913, p. 275).

Without further examination into the European relict steppe fauna the question arises as to whether this set of relations is paralleled in North America, by the extension of animals otherwise characteristic of the Great Plains into the eastern forested region. The subject is especially interesting to the herpetologists of the Middle West, and I have long thought that the distributions of a number of the species of reptiles and amphibians in the Illinois fauna are explainable in varying degrees by a climatic history similar to that known for Europe. Our knowledge of the details of the distribution of these forms is still far from complete, but I believe that in their general outlines the ranges are sufficiently defined for the purpose of the present essay.

The geographic relations of steppe, glaciated region, and existing forest, with the directions reversed, are roughly similar. The plains and deserts of the American west and southwest correspond to the steppe and desert of central Asia, while wooded eastern North America corresponds to forested western Europe. The parallel is somewhat strengthened by the fact that the extent of glaciation was greatest in Europe and in eastern North America, and least in Asia and western North America. The importance to zoogeographic speculation of this curiously little known feature of the glacial eras has been discussed in a former essay (Schmidt, 1931). In both central Asia and western North America the steppe conditions and fauna long antedate the glacial period.

In North America the great southeastern forest, which likewise dates far back into Tertiary times, undoubtedly persisted with little modification through the Pleistocene climatic cycles. Gleason (1922), for example, in a paper bearing directly on the prairie peninsula question, does not think that the southeastern forest retreated beyond the Ohio at any stage of glaciation. By analogy with the situation in Europe, and indeed on theoretic grounds, there must have been a broad belt of tundra, succeeded by steppe, parallel to the retreating front of the great glacier in eastern North America. This belt of open country, broadly connected with the plains region to the west, and extending eastward to Pennsylvania, and sometimes even to the Atlantic coast, to the north of the southeastern hardwood forest, obviously afforded a natural

highway for the eastward spread of a part of the western steppe fauna. This must especially have been the case since the area was for a time relatively empty of animal life, so that the normal barrier of a saturated fauna was temporarily absent.

The base of our postglacial steppe¹ peninsula coincides with what is familiar in American botanical literature as the "prairie peninsula." This lies between the Ozark highland of Missouri and central Minnesota, and extends eastward in Illinois to the Indiana line. The more ancient steppe peninsula extended farther eastward between the Ohio and the Great Lakes to western New York and Pennsylvania, with a more hypothetical extension as a "Steppe Corridor" through the Mohawk Valley to southern New England and New Jersey.

With the northward advance of the hardwood forests and reestablishment of a continuous forest habitat, the steppe forms would either retreat westward to the plains; be exterminated by their inability to compete with forms long adjusted to the forest habitat; persist as relicts in isolated areas either naturally suited to them, like sandy regions, or less favorable to the forest fauna proper (like the sphagnum bogs); or, finally, in some few cases, adjust themselves completely to the forest habitat, and spread to the south and north to varying distances. It is an essential element in the hypothesis as a whole that the southeastern states are occupied by a "saturated" fauna and flora, essentially old, rich, and stable (its animal life therefore well adjusted to the environment), which offers an effective barrier to the spread of steppe plants and animals. Thus all of the animals which have an eastward range north of the Appalachian region, and are absent from the southeastern states, may be scrutinized for an origin from the west.

The botanical evidence for the existence of a postglacial steppe stage has been accumulating, and in some respects has been much more carefully sifted than the faunal evidence. Gleason (1922) sets forth the theoretic postglacial floral succession. With regard to the prairie peninsula he states: "An advance of the prairie vegetation toward the east and northeast followed immediately behind the coniferous forests, displacing the rearguard of the forest by successional processes. . . . The eastern migration of the prairie proceeded as a wedge-shaped extension between the coniferous vegetation at the north and the deciduous forests at the south and reached limits considerably beyond the eastern margin of modern continuous prairies." Sears (1926) places a tongue of relict prairie in eastern Ohio, extending into Beaver County, Pennsylvania. Transeau (1935), in a paper entitled "The Prairie Peninsula," summarizes the botanical aspects of the problem. Its present extent is well shown by Goode (1923, p. 34), and its eastward extension corresponds rather closely, in Goode's map, to the "oak-hickory" area. Renewed studies based on pollen analysis of vertical sections of bogs are now actively in progress. It is disappointing to find that Sears (1935) in a recent review of this topic,

¹ "Steppe" is used in this paper in an inclusive sense for all grassland.

makes no direct mention of the hypothetical steppe stage, or of the extremely factual fossil and other evidence in Europe which bears upon the subject.

As in so many zoogeographic questions, much of the available evidence is obscure. Thus I would like to interpret the former eastward range of the bison as connected with a postglacial steppe period; but its entry into and persistence in the forests, and its relatively wide range in the east, make for uncertainty in this supposition. Bison remains are reported from the interglacial Toronto deposits. The common eastern woodchuck, whose relatives are so clearly steppe animals in Asia, has likewise entered the forest too freely to afford clear evidence for the steppe highway; but its complete absence in the southeastern states is nevertheless an indication that it is not primarily a forest form, and its original eastward spread to the Atlantic coast may well have taken place via the steppe corridor. The range of the heath hen, so clearly allied to the prairie chicken of the great plains, is much more directly derivable from the steppe hypothesis.

The most positive faunal evidence bearing on this subject is to be found among the reptiles and amphibians. The species of these groups whose distribution I believe to be correlated with the steppe peninsula appear to be the following eleven:

- Ambystoma tigrinum tigrinum* (Green)
- Rana pipiens pipiens* (Schreber)
- Heterodon nasicus* Baird and Girard
- Coluber constrictor flaviventris* Say
- **Elaphe vulpina* (Baird and Girard)
- **Natrix kirtlandii* (Kennicott)
- **Thamnophis butleri* (Cope)
- **Sistrurus catenatus catenatus* (Rafinesque)
- **Emys blandingii* (Holbrook)
- Terrapene ornata* (Agassiz)
- **Chrysemys picta marginata* Agassiz

No less than six of these indicated by an asterisk (*) above are endemic, either wholly confined to the steppe peninsula like *Natrix kirtlandii*, or centered in it and not widely distributed toward the southwest. In spite of the great amount of work on American reptiles in recent years, the ranges of these forms can still be only approximately outlined. The accompanying maps are intended to be suggestive and to represent the general relations. I believe that the argument here presented will be strengthened rather than weakened when these ranges are worked out in greater detail. I am indebted to Dr. E. B. S. Logier for correction of the ranges of *Emys* and *Sistrurus* in Ontario.

THE MIDDLE WESTERN ENDEMIC

Atkinson and Netting (1927) have interpreted the eastward "peninsular" range of the massasauga (*Sistrurus catenatus catenatus*) (fig. 2) as associated

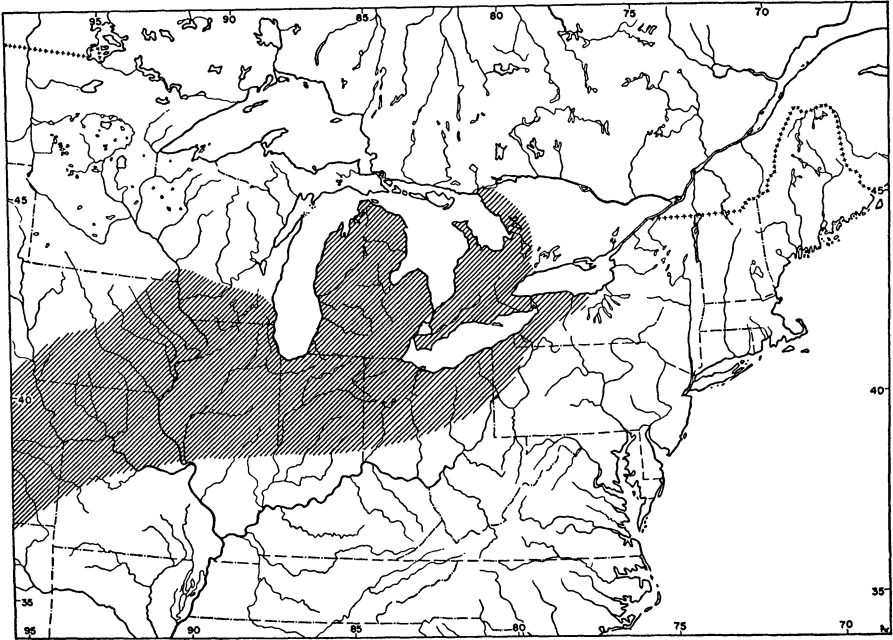


FIG. 2. Range of the massasauga, *Sistrurus catenatus catenatus*.

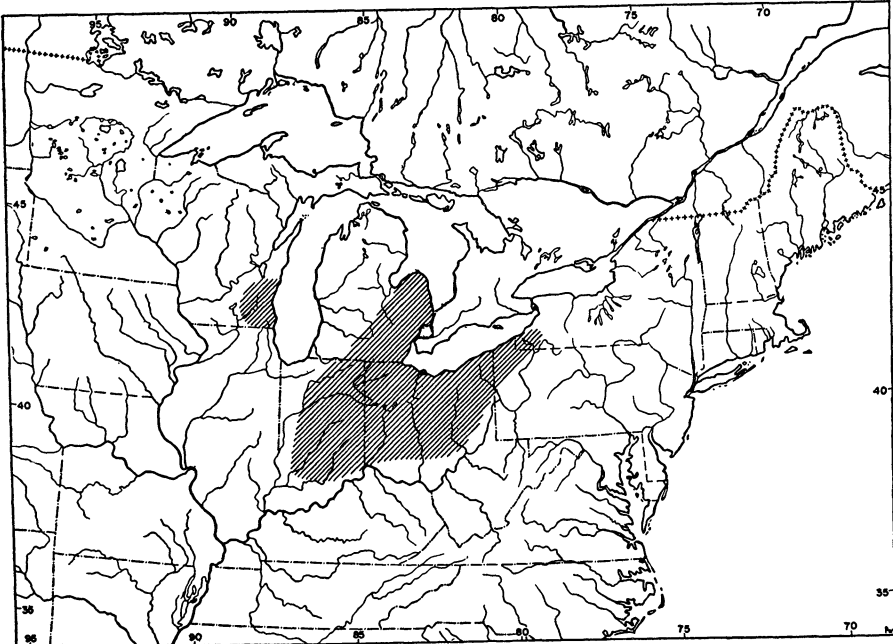


FIG. 3. Range of Butler's garter snake, *Thamnophis butleri*.

with a prairie stage antecedent to the present forest formation in Ohio and Pennsylvania. The great range of the massasauga on the plains has an extension through Indiana and Ohio to western New York and Pennsylvania, fitting almost exactly into our hypothetical steppe peninsula. In Missouri it is abundant in the prairie north of St. Louis, and absent in the Ozarks. In the eastern part of its range the massasauga is decidedly local in its distribution, tending to be confined to the vicinity of sphagnum bogs; it is fairly evident that its populations were declining before the advent of man, and that this decline may be associated with the change of habitat conditions which has overtaken the subspecies.

Butler's garter snake (*Thamnophis butleri*) has almost the same range (fig. 3) and is directly derived from the vastly abundant *Thamnophis radix* of the plains. The decline in abundance of Butler's garter snake toward the east, and the degenerative characters of the species as compared with the dominant parent plains form, appear to be significant, and this form accordingly illustrates the fact that partial isolation in our steppe peninsula may have been a factor in the origin of various distinct subspecies of western

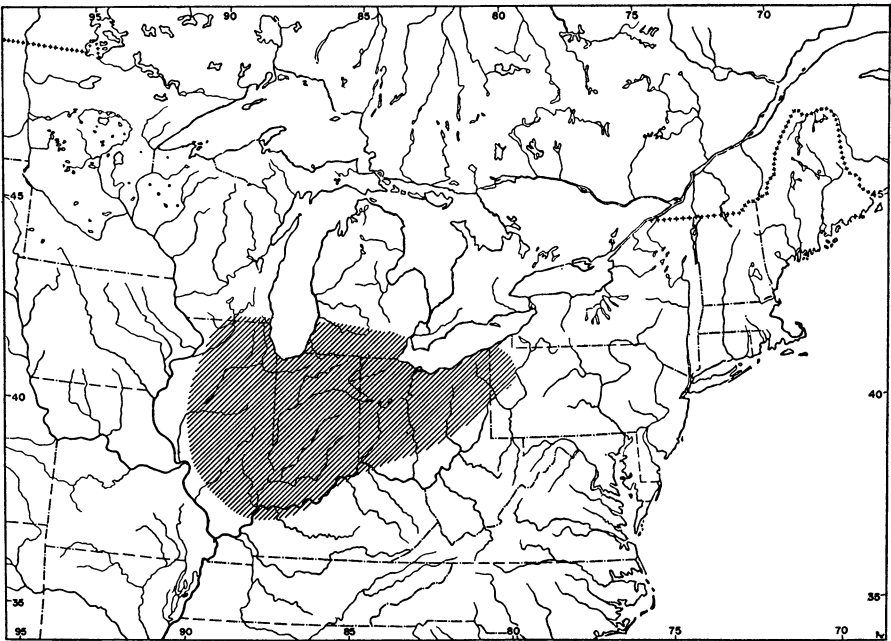


FIG. 4. Range of Kirtland's water snake, *Natrix kirtlandii*.

forms, and, under other circumstances, may preserve species from the competition of plains forms. *Thamnophis butleri*, for example, might represent the *T. radix* of some interglacial stage, the present contact of *radix* and *butleri*

being of post-Wisconsin date. Ruthven (1908a, p. 87) and Davis (1932, p. 113) have dealt with the distribution of this highly interesting garter snake.

Natrix kirtlandii is a strikingly distinct species, without any very direct relationship with other American species of *Natrix*. Its range (fig. 4) is typical of the steppe peninsula endemics. With most of Illinois as a base, it ranges eastward through Indiana and Ohio to western Pennsylvania.

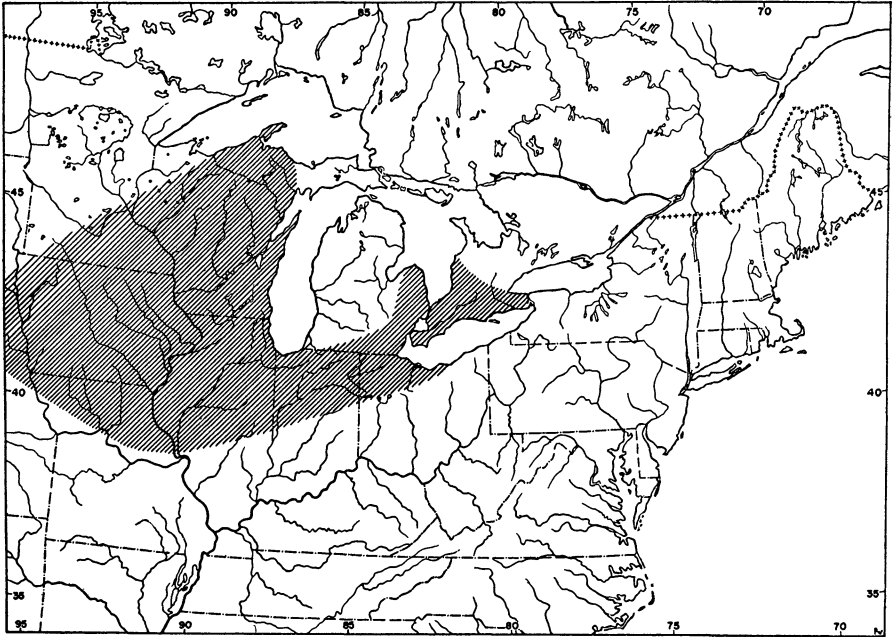


FIG. 5. Range of the fox snake, *Elaphe vulpina*.

Elaphe vulpina (the "pine snake" of Wisconsin, "spotted adder" of Illinois, and the "fox snake" of books) is another mid-western endemic, with a slightly greater amplitude of range to the north (fig. 5), where it enters the Wisconsin forests. I interpret this as a postglacial spread, favored by the impoverishment of the fauna of the coniferous forest during the glacial retreat. Another distinctively plains species, *Chrysemys picta bellii*, ranges throughout the forest region of Wisconsin and the Upper Peninsula of Michigan, an invasion obviously postglacial, and obviously independent of the dispersal of *Chrysemys picta marginata*. The absence of *E. vulpina* in most of the Lower Peninsula of Michigan seems to be significant. Morse (1912), in recording this species from Ohio, remarks on other western faunal elements associated with it.

Although with a range of slightly greater amplitude, Blanding's turtle (*Emys blandingii*) is obviously a "Middle Western endemic" (fig. 6). It is

found as far west as Nebraska, but does not range southward in the Great Plains; and to the east it reaches the Atlantic coast. From Ohio eastward its range is broken into isolated areas, a typical relict distribution. The single record from the Upper Peninsula of Michigan may represent a similarly isolated station. The New Jersey and Long Island records do not appear to

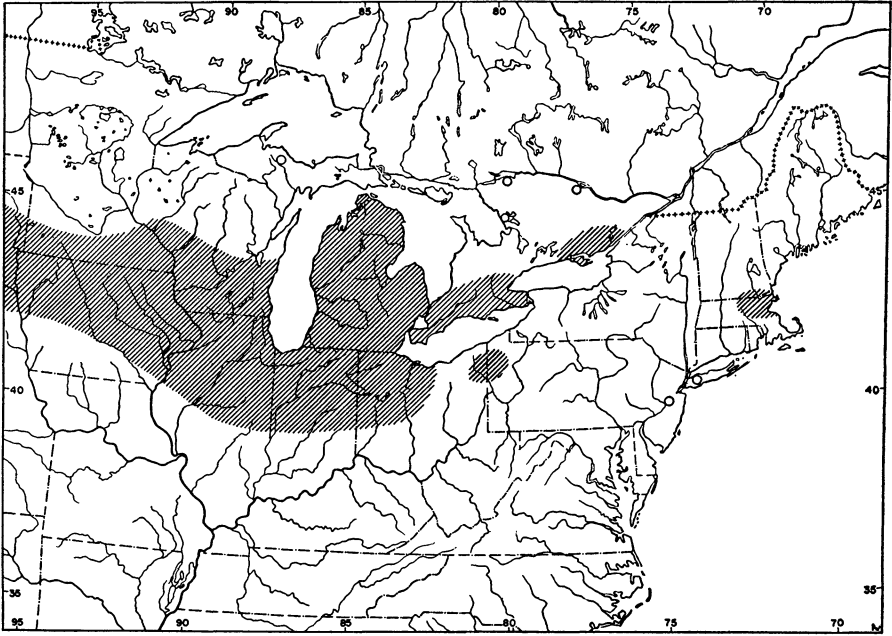


FIG. 6. Range of Blanding's turtle, *Emys blandingii*.

represent existing populations. The range of the European *Emys orbicularis* suggests a parallel dispersal westward from Central Asia, essentially comparable to the dispersal of the genus *Clemmys*.

The painted turtles are so extremely wide-spread on the Great Plains that I have no hesitation in correlating the restriction of *Chrysemys picta marginata* to the steppe peninsula, with an eastward dispersal. The genus *Chrysemys* may well have reached the Atlantic coast by this highway, but if this be true, it must have been at a preglacial, or, at the latest, early interglacial period. The present intergradation of the mid-western *marginata* with the Atlantic coast *picta* in the Hudson valley and with the western *bellii* in the Chicago area seems to be at renewed contacts of populations separated during the Wisconsin advance of the glaciers (Bishop and Schmidt, 1931, p. 134). This is especially evident in the east, where the forms *marginata* and *picta* would be separated on the two sides of the Alleghenies by a southward displacement of their ranges.

Among amphibians, the tiger salamander (*Ambystoma tigrinum tigrinum*) has very much the "steppe peninsula" distribution, with a broad contact with the plains population of a fairly distinct subspecies, to the west.

THE NON-ENDEMIC STEPPE ELEMENT

The species which correspond in the eastward part of their range with the steppe peninsula endemics, but without specific or subspecific differentiation from their Great Plains population, may either be later entrants or forms which have been relatively stable during postglacial time. These are connected with such isolated species as *Natrix kirtlandii* or *Emys blandingii* by the forms which exist in the steppe peninsula as subspecies of wide-spread western forms, like *Sistrurus catenatus catenatus* with *S. c. tergeminus*, or *Chrysemys picta marginata* with *C. picta bellii*.

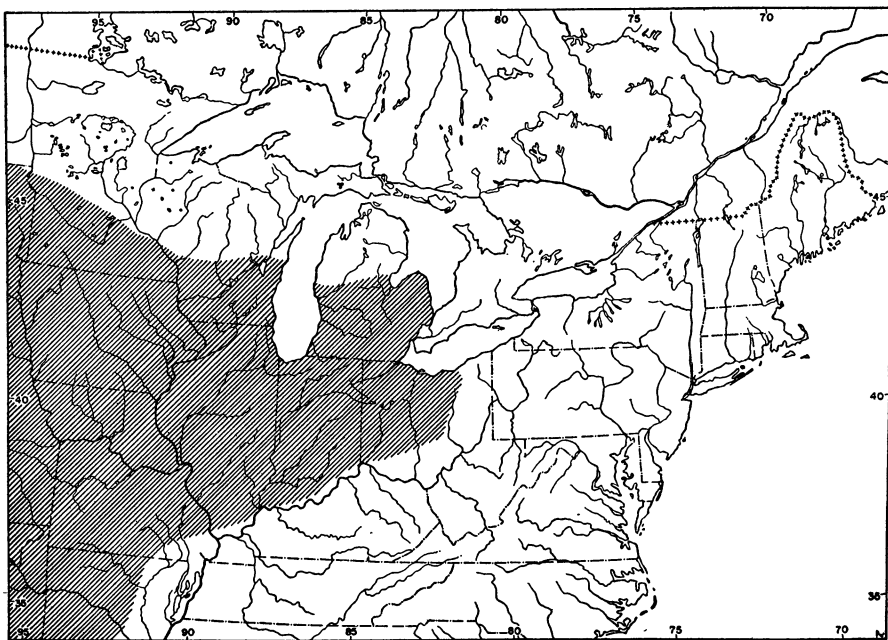


FIG. 7. Range of the blue racer, *Coluber constrictor flaviventris*.

The range of the blue racer (fig. 7), *Coluber constrictor flaviventris*, is instructive. The species has been exhaustively studied (Ortenburger, 1928, p. 184, fig. 33). While it is quite clearly a post-Wisconsin entrant into the prairie peninsula, its continuous range extends eastward beyond central Ohio. There could scarcely be a better example of correlation between existing range and the steppe peninsula hypothesis.

Much the same may be said of the western hog-nosed snake, *Heterodon*

nasicus, but this species, instead of being wide-spread and dominant like the blue racer, is plainly on the decline, wholly restricted throughout its present range east of the Mississippi to limited sandy areas. While there may well be other stations for this species in Illinois, the only one known to me is that reported by Vestal (1913, p. 61), namely the sand area at Havana.

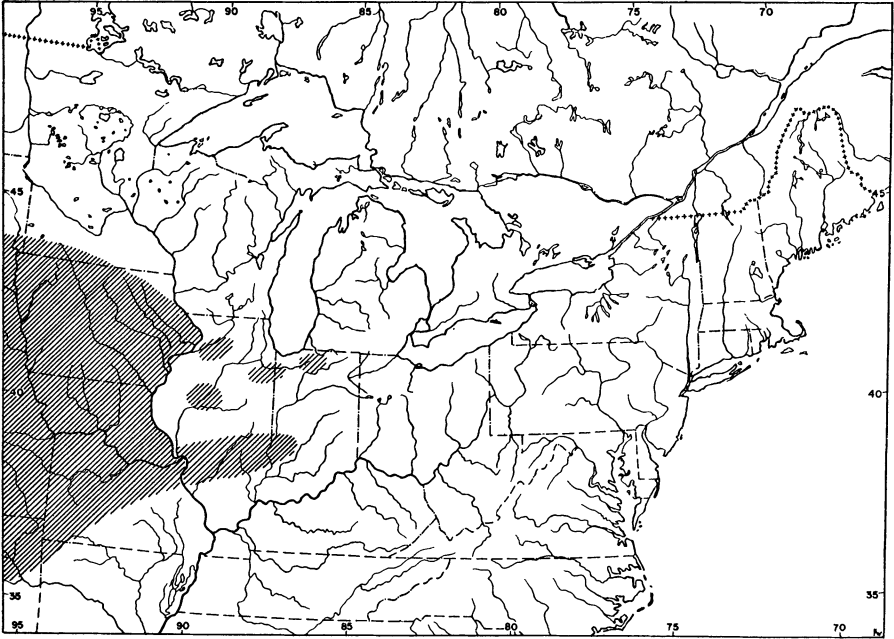


FIG. 8. Range of the ornate box turtle, *Terrapene ornata*.

Among the turtles, the western box turtle, *Terrapene ornata*, is a relict form (fig. 8), strictly confined to sandy areas. Its range is strikingly like that of *Heterodon nasicus*. Its presence in Lee and Kankakee Counties in Illinois, and at various stations in northern Indiana has recently been discussed (Grant, 1935).

In its complete absence from the southeast and vast range on the Great Plains, *Rana pipiens* (as usually distinguished from *Rana sphenoccephala*) appears to agree in part with the criteria for the series of forms here set up.

A few forms are doubtfully referred to the steppe peninsula series. Fowler's toad (*Bufo fowleri*) is directly allied to the Great Plains species, *woodhousii*; the range of *fowleri* in the east is far more extensive and complicated than that of the species considered above. The same is true of *Pseudacris triseriata*, whose relations with the southern *nigrita* are not yet clear. The western ring-necked snake is reported by the "Check-list" (Stejneger and Barbour, 1933, p. 90) to reach Ohio, which would give it a typical prairie

peninsula range. Mr. Necker and I have entertained some doubt about the Illinois records of this species (Schmidt and Necker, 1935, p. 61). The middle western bull snake (*Pituophis sayi sayi*) enters the prairie peninsula as far as the Kankakee dune area (Schmidt and Necker, 1935, p. 70) and reaches Door County, Wisconsin. The geographic turtle somewhat vaguely follows the prairie peninsula, but with a broad entry into the southeastern forest region.

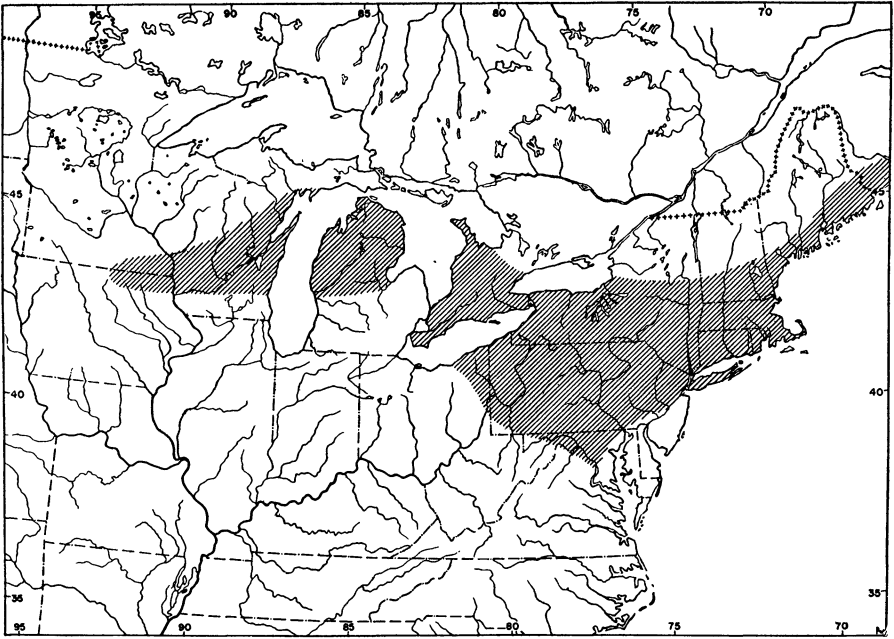


FIG. 9. Range of the wood turtle, *Clemmys insculpta*.

The turtles of the genus *Clemmys* require separate consideration. The wood turtle (*Clemmys insculpta*) has the east-west distribution (fig. 9) characteristic of the steppe peninsula, but its range in the west is strongly displaced northward, while its optimum area is eastern instead of western. It is evidently neither truly a mid-western endemic nor a member of the older southeastern fauna. The westward peninsula of its range may well be due to a westward dispersal during the most recent steppe peninsula period, now displaced northward. The spotted turtle (*Clemmys guttata*) has a still wider north-south range in the east, with a narrow westward extension; while the third eastern species of the genus, *muhlenbergii*, is confined to sphagnum bogs, ranging southward to North Carolina only in the mountains. These turtles with their Pacific coast ally (*C. marmorata*) seem to represent a pre-glacial dispersal from northern Asia, but to post-date the major elements in the southeastern fauna.

The hypothesis of a postglacial eastward extension of the steppe in North America appears to be amply supported by the evidence set forth. More detailed examination of the ranges of the species and other problems involved is obviously desirable. Evidence from other groups of animals, insects in particular, should have an important bearing on the whole matter. It is hoped that the present essay, by an integration of the herpetological evidence, may stimulate the discussion of the problem.

LITERATURE CITED

- Davis, D. Dwight.** 1932. Occurrence of *Thamnophis butleri* Cope in Wisconsin. *Copeia* (1932): 113-118.
- Dawkins, W. Boyd.** 1880. Early man in Britain and his place in the Tertiary period. *MacMillan, London*,
- Gleason, H. A.** 1922. The vegetational history of the Middle West. *Ann. Assoc. Amer. Geog.* 12: 39-85.
- Goode, G. Paul.** 1923. Goode's School Atlas. *Rand McNally, Chicago*. xii + 96 + 41 pp.
- Grant, Chapman.** 1936. The "eastward migration" of *Terrapene ornata* (Agassiz). *Copeia* (1935): 186-188.
- Kauffeld, Carl F.** 1937. The status of the leopard frogs, *Rana brachycephala* and *Rana pipiens*. *Herpetologica* 1: 84-87.
- Morse, Max.** 1902. The range of the fox snake. *Science* 15: 1035.
- Nehring, Alfred.** 1890. Ueber Tundren und Steppen der Jetzt- und Vorzeit mit besonderer Berücksichtigung ihrer Fauna. *Dümmler, Berlin*, viii + 257 pp.
- Ortenburger, A. I.** 1928. The whip snakes and racers genera *Masticophis* and *Coluber*. *Mem. Univ. Mich. Mus.* 1, xviii + 243 pp.
- Ruthven, Alexander G.** 1908a. Variations and genetic relations of the garter-snakes. *Bull. U. S. Nat. Mus.* 61, xii + 201 pp.
- . 1908b. The faunal affinities of the prairie region of central North America. *Amer. Nat.* 42: 388-393.
- Scharff, R. F.** 1907. European animals: their geological history and geographical distribution. *Dutton, London*. xiv + 258 pp.
- Schmidt, Karl Patterson.** 1931. On the zoogeography of the holarctic region. *Lingnan Sci. Jour.* 10: 441-449.
- Schmidt, Karl P., and Necker, Walter L.** 1935. Amphibians and reptiles of the Chicago region. *Bull. Chicago Acad. Sci.* 5: 57-77.
- Sears, Paul B.** 1926. The natural vegetation of Ohio. II. The prairies. *Ohio Jour. Sci.* 26: 128-246.
- . 1935. Glacial and postglacial vegetation. *Bot. Rev.* 1: 37-51.
- Stejneger, Leonhard, and Barbour, Thomas.** 1933. Check-list of North American amphibians and reptiles. *Harvard, Cambridge*. xiv + 185 pp.
- Transeau, E. N.** 1935. The Prairie Peninsula. *Ecology* 16: 423-437.
- Vestal, Arthur G.** 1913. An associational study of Illinois sand prairie. *Bull. Ill. State Lab. Nat. Hist.* 10: 1-96.
- Taylor, John W.** 1913. Geographical distribution and dominance in relation to evolution and phylogeny. *Trans. 2nd. Int. Congr. Entom., Oxford, 1912*, pp. 271-294.