A Succession of Pliocene and Pleistocene Snake Faunas from the High Plains of the United States

BAYARD H. BRATTSTROM

Over 11,000 skeletal elements of snakes from a series of fossil deposits ranging from the Lower Pliocene to the Recent from Kansas and adjacent areas were studied. Each local fossil fauna is relatively distinct, containing as few as one and as many as 15 species of snakes. Glacial and interglacial faunas differ in kind, number, and size of snakes present.

Many, but not all, of the Pliocene and Interglacial snake species occur in Kansas today. The greatest overlap of the ranges of all of the species of snakes represented in the fossil deposits occurs today in southwestern Texas, in the Balconian Biotic Province.

In contrast to the mammal fauna and other herpetofaunas, the snake faunas from the high plains have no extinct forms in the Pleistocene deposits (though extinction or change in two forms occurred in the Mid and Upper Pliocene) and further indicate that most genera and species of Recent snakes go back, almost unchanged, to at least the Upper, and in some cases Lower Pliocene.

INTRODUCTION

DR. Claude W. Hibbard of the Museum of Paleontology, University of Michigan, initiated studies in 1936 on the Pliocene and Pleistocene geology and paleontology of southwestern Kansas and adjacent areas. With the perfection of washing and screening techniques (Hibbard, 1949; McKenna, 1962) a fantastic number of macro- and microfossils have been collected over the years. Numerous reports on the geology and paleontology have been presented by Hibbard. Other workers have reported on special taxonomic groups. This report presents studies on the fossil snakes.

The geology and mammalian faunas from these deposits have been summarized by Hibbard (1958), D. W. Taylor (1960), and Hibbard and Taylor (1960). The latter two references are used as the basis for the geological ages presented here. Each new field season adds to the understanding of the area. Thus, Hibbard has recently suggested (pers. comm.) that the correct Illinoian through Wisconsin sequence of local faunas might be: Doby, Rezabek, Nye, Cragin Quarry, Jinglebob, Bar M, Jones, and that the Kentuck may be Illinoian.

Herpetological studies on the Pliocene and Pleistocene of North America have been reviewed by Gehlbach (1965) and Auffenberg and Milstead (1965). Only two papers are specifically concerned with the fossil snakes of Kansas (Gilmore, 1938; Peters, 1953).

MATERIALS AND METHODS

The fossil snake material is, unless otherwise specifically mentioned, in the collection of the Museum of Paleontology, University of Michigan. The fossil snake material in the Field Museum of Natural History, U. S. National Museum, and Museum of Vertebrate Paleontology, University of California, Berkeley has been examined and some comments are based on that material.

In addition to my own osteological collection (now in the collections of California State College at Fullerton), I have examined snake skeleton collections in the Field Museum of Natural History, American Museum of Natural History, Museum of Vertebrate Zoology, University of California, Berkeley, as well as specimens sent to me on loan (see acknowledgments in Brattstrom, 1954, 1964). The identifications were mostly done while I was living in New York, and fossil specimens were often compared with the extensive skeletal material at the American Museum of Natural History (a list of which can be found in McDowell and Bogert, 1954).

Terminology used is that of Auffenberg (1963), Gilmore (1938), or Brattstrom (1964). Scientific and common names for snakes follow common usage or American Society of Ichthyologists and Herpetologists checklists. Geological, stratigraphic, and age determinations are as reported in Taylor (1960) and Hibbard and Taylor (1960). A summary of the fossil material is presented in Table 1. Catalog numbers, specific collection data, itemized lists of skull elements, etc., are available in the catalog of the Museum of Paleontology, University of Michigan. Measurements, subsample means and modes, and skull element measurements are not presented herein except in a summary manner or where important to a specific identification or discussion.

Identification of Fossil Snakes

Dissociated vertebrae are by far the commonest fossil specimens. Skull elements are occasionally recovered and are of considerable aid in identification. Identification of fossil snakes based on vertebrae is relatively easy, though little appreciated. The characters used may be clear and obvious for the higher taxon, but specific identification is often based on subtile characters (Fig. 1). Most of these characters have been diagrammed or quantified (Auffenberg, 1963; Brattstrom, 1954, 1964; Dowling, 1958; Holman, 1962, 1963; etc.). Final identification must, of course, be based on direct comparison with Recent specimens or with other fossil specimens of known identity.

A special note must be made of the problem of identification of natricine snakes. Many species of *Natrix* and *Thamnophis* can be identified on the basis of skull elements, but identification even to genus on the basis of vertebrae alone is difficult, if not impossible. Generic characters of natricine snakes based on external morphology are somewhat confused at present (Smith and Huheey, 1960; Rossman, 1963; Malnate, 1960; Lowe, 1955). This is due to the fact that many species of *Natrix* (*sensu lato*) are small and slender (i.e., *Thamnophis*-like) and some species of *Thamnophis* are large and broad like many water snakes.

I have been unable to find vertebral characters to identify *Thamnophis* and *Natrix* vertebrae consistently and correctly. In general, *Thamnophis* vertebrae are elongate when viewed from above, while *Natrix* vertebrae are almost square. Small species of *Natrix* (*s.l.*), however, have elongate vertebrae and some large *Thamnophis* have almost squarish vertebrae. I have therefore always divided natricine vertebrae into squarish *Natrix*-like vertebrae and elongate

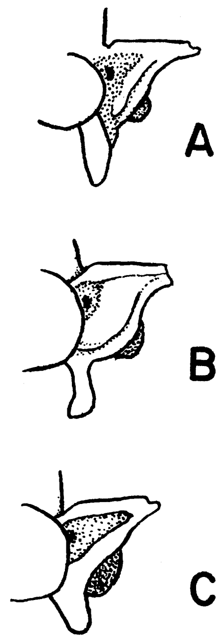


Fig. 1. Diagrams showing differences in the anterior lateral face of vertebrae of A, *Agkistrodon contortrix*; B, *Sistrurus catenatus*; and C, *Crotalus viridis*.

Thamnophis-like vertebrae and cataloged the former as *Natrix* and the latter as *Thamnophis*. Hence some material listed herein as *Thamnophis* might well be *Natrix* and vice versa. Calling the vertebra *Natrix*-like or *Thamnophis*-like at least allows the use of the data of size and shape of the snakes for paleoecological interpretation. *Storeria* vertebrae are fairly easily identified to genus, though I, like Holman (1962) cannot separate vertebrae of *S. dekayi* and *S. occipitomaculata*. In contrast, vertebrae of a few, distinct, Late Pleistocene fossil natricines (e.g., *Natrix sipedon, N. erythrogaster*) can occasionally be identified to species on unique characters (see Holman, 1962, 1963, and herein).

Pliocene

Quarry E, Long Island, Phillips County, Kansas

Elaphe kansensis.—Gilmore (1938) described *Paleoelaphe kansensis*, Type U. S. National Museum 13500, from the Lower Pliocene, Republican River Formation. I have examined the type material and find no basis for maintaining the genus *Paleo-*

TABLE 1. CENTRUM LENGTHS OF FOSSIL SNAKES IN HIGH PLAINS DEPOSITS. Measurements in 0.1 mm in the following order: maximum, average, minimum, and then sample size. Maximum only is given for Recent specimens. For a few occurrences, simply indicated "present," vertebral dimensions were not available. Under *Heterodon*, asterisk denotes *H. plionasicus*.

Fauna	*Thamnophis*	*Natrix*	*Lampropeltis*		*Heterodon*	
			doliata	*getulus*	*platyrhinos*	*nasicus*
Recent	69	87	55	65	49	33
Jones	39-26-26-73					
Nye	x-48-x-1					
Rezabek		55-x-x-18				
Cragin, UM	28-x-24-2					x-26-x-1
Cragin, Q	46-33-15-650	50-29-15-82		61-43-16-25	present	
Jinglebob	57-30-17-70	56-31-15-256	52-48-40-7	60-54-36-6	52-39-13-25	64-55-19-68
Doby Spr.	46-43-43-8	62-32-x-50				
Bar M		49-39-19-150				
Berends	46-44-40-4					x-38-x-1
Butler	55-50-40-4	49-40-28-9				
Kentuck		52-46-29-38	54-46-41-5		x-62-x-1	
Borchers			43-31-19-18	55-46-24-5		56-43-22-49
Cudahy	55-32-14-37	48-32-16-209				
Sanders	32-x-18-22					
Deer Park						
Dixon	50-44-42-26					
Sand Draw	41-35-19-6	62-48-35-47			x-17-x-1	
Fox Canyon	40-33-18-130	43-34-26-256	36-28-18-44	44-35-25-41	46-39-27-39	53-33-17-165*
Wend. Fox	55-41-28-139	73-40-18-1596	29-25-20-6	48-30-20-29		60-31-18-49*
Loc. 3	60-52-18-592	63-48-18-2912	44-30-20-34	47-38-27-26	37-28-23-50	57-38-19-70*
Saw Rock	58-34-17-483	62-32-15-1867				
Buis Ranch	41-29-24-4		31-30-29-12			x-45-x-1*
L. Pliocene						

elaphe as distinct from *Elaphe*. The characters of the species suggest that it is a distinct member of the genus *Elaphe*, closest perhaps to *E. obsoleta* (Fig. 2). Drawings of some of the type material are presented in Gilmore (1938). Diagrams of those thoracic vertebrae without hypapophyses which either have a flat subcentrum keel which stops before the central cup (= cotyle) (8 vertebrae) or have a keel that is rounded and continuous with the edge of the cup (2 vertebrae) are presented in Fig. 2.

Driftwood Creek, Hitchcock County, Nebraska

Coluber constrictor.—Six vertebrae (AMNH 7186) from the Lower Pliocene of Driftwood Creek do not differ markedly from Recent *C. constrictor*.

Buis Ranch Local Fauna, Beaver County, Oklahoma

Thamnophis sp., *Heterodon plionasicus*, *Coluber constrictor*, *Crotalus* cf. *viridis*, *Elaphe* near *obsoleta*, *Lampropeltis doliata*.

A single *Elaphe* vertebra is much like *E. obsoleta* in zygosphene and subcentrum keel characters. It is not like *E. kansensis*.

The *L. doliata* vertebrae are much the same size and shape as Recent material, though the neural spine is missing from all. Though the posterior part of the post-

TABLE 1. *Continued.*

	Elaphe obsoleta	*Pituophis catenifer*	*Coluber constrictor*	*Agkistrodon contortrix*	*Sistrurus catenatus*	*Crotalus viridis*	Others present
Recent	65	79			41	73	
Jones	x-58-x-2						
Nye							
Rezabek							
Cragin, UM							*Storeria, L. calligaster*
Cragin, Q			71-x-52-3	x-40-x-1		65-43-28-27	*Storeria, ?Diadophis*
Jinglebob	74-57-19-68	60-55-37-15	54-44-27-73				*L. calligaster*
Doby Spr.		70-67-64-29	47-44-39-3				
Bar M							
Berends							
Butler							
Kentuck	67-x-60-2						
Borchers	56-35-26-22	64-38-24-84	64-48-30-16	53-36-24-30	50-36-25-11	64-47-24-44	*Rhinocheilus lecontei,* Snake sp.
Cudahy							*Storeria*
Sanders							
Deer Park	x-43-x-1		66-60-51-8				
Dixon	present						
Sand Draw							
Fox Canyon	60-42-19-92	63-37-27-47	80-45-23-154	43-32-24-6	44-34-25-4	50-45-38-3	
Wend. Fox	60-46-28-19	58-44-26-18	67-50-36-49	41-38-29-11		56-x-47-2	
Loc. 3	80-45-21-102		65-47-27-59	50-41-26-8	46-36-29-10	present	
Saw Rock	69-59-25-34		44-35-24-6	54-30-18-9			
Buis Ranch	x-61-x-1		32-30-27-5			37-x-29-2	
L. Pliocene			present	present		present	*Elaphe kansensis*

zygosphene is curved more than usual for *L. doliata* and hence approaches the smooth curve found in *L. calligaster,* the characters of the subcentrum keel and the area lateral to the keel clearly indicate that the material belongs to *L. doliata.*

Saw Rock Local Fauna,
Seward County, Kansas

Natrix sp., *Thamnophis* sp., *Elaphe obsoleta, Coluber constrictor, Agkistrodon contortrix.*

Rexroad Local Faunas
Location 3, Meade County, Kansas

Natrix sp., *Thamnophis* sp., *Coluber constrictor, Lampropeltis getulus, Elaphe obsaleta, Heterodon plionasicus, H. platyrhinos, Agkistrodon contortrix, Crotalus viridis, Sistrurus catenatus.*

Natrix basisphenoids from this location are most similar to *N. sipedon* and *N. cyclopion.* The proportions of basioccipitals of *Natrix* and *Thamnophis* are shown in Fig. 3. An anterior portion of a right pterygoid and a single fang (measuring 9.0 $\times$ 2.3 mm) are tentatively referred to *Crotalus viridis.*

In addition to 50 *Heterodon platyrhinos* vertebrae there is a single left articular. The articular appears to be most like *H. platyrhinos* when compared with American Museum material. It is definitely not *H. nasicus,* which has a narrow Meckelian foramen opening. The fossil has a foramen rounder than the slit-like one of Recent *H. platyrhinos.* The characters of the vertebrae

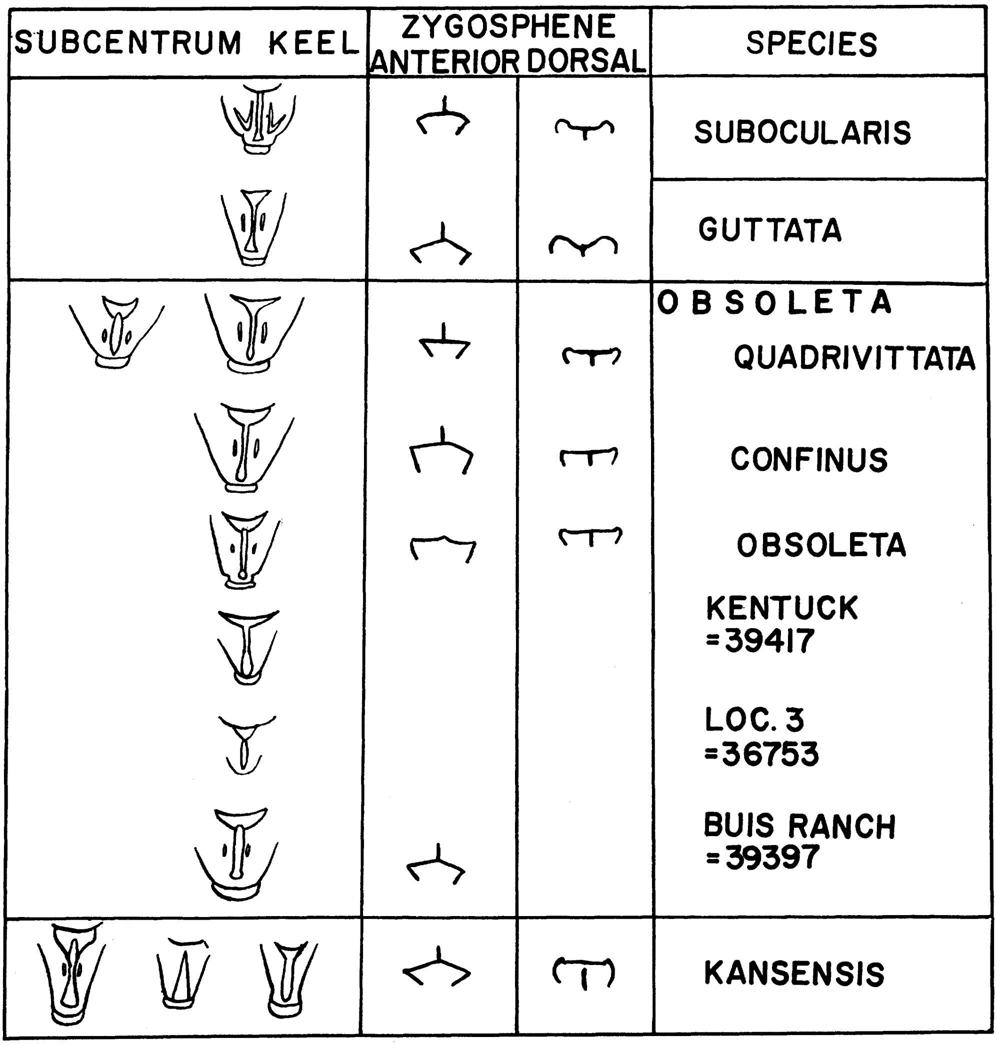


Fig. 2. Diagrams of a few vertebral characters of fossil and Recent *Elaphe*.

and the articular do not seem distinct enough to me to warrant the naming of a new species presumably ancestral to *H. platyrhinos*.

Wendell Fox Pasture, Meade County, Kansas

Natrix sp., *Thamnophis* sp., *Heterodon plionasicus, Pituophis catenifer, Elaphe obsoleta, Lampropeltis getulus, L. doliata, Coluber constrictor, Agkistrodon contortrix, Crotalus viridis.*

Wendell Fox and Saw Rock *Natrix* quadrate measurements are presented in Fig. 4. The Wendell Fox *Natrix* ectopterygoids are much like recent *N. sipedon*, though the quadrates suggest that at least two species might be represented in this material. A worn quadrate, 8.5 × 4.0 mm, is most like *Pituophis catenifer*. It is not like the larger and narrower quadrate of *P. melanoleucus*. A single left *Heterodon* quadrate, 6.1 × 3.7 mm, is tentatively referred to *H. plionasicus* on the basis of its similarity to *H. nasicus* and because it comes from a Pliocene deposit. *H. plionasicus* quadrates have heretofore been unknown.

Fox Canyon, Meade County, Kansas

Natrix sp., *Thamnophis* sp., *Elaphe obsoleta, Heterodon plionasicus, H. platyrhinos,*

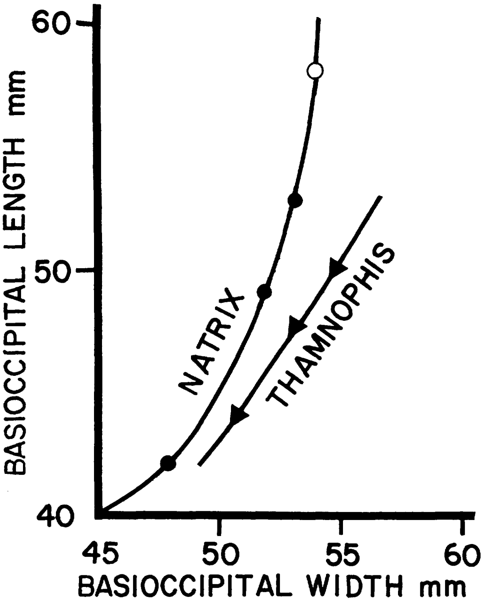


Fig. 3. Graph showing relationship between basioccipital length and width measurements of Pliocene (Rexroad) *Natrix* and *Thamnophis*. Open circle, a single basioccipital from the Pleistocene (Bar M).

Lampropeltis getulus, L. doliata, Pituophis catenifer, Coluber constrictor, Agkistrodon contortrix, Crotalus viridis, Sistrurus catenatus.

Peters (1953) described *Heterodon plionasicus* from Fox Canyon, Location UM-K1-47, on the basis of maxillary and palatine elements. The *Heterodon* vertebral elements found in the various deposits (Fig. 5, Table 1) represent three or possibly four types: those like Recent *H. nasicus* (from several of the Pleistocene deposits), those like Recent *H. platyrhinos* (from several deposits, both Pliocene and Pleistocene, though those from Location 3 and Fox Canyon are slightly different from Recent *platyrhinos*), and those not like *platyrhinos* or *nasicus* (nor like *simus* or *brevis*, Auffenberg, 1963). Because these latter vertebrae are most like *nasicus* and are found only in Pliocene deposits, including this one, I am calling them *H. plionasicus*. Those *H. plionasicus* from the Fox Canyon locality seem more variable than samples from Buis Ranch, or Location 3. A few of them seem to be like *H. nasicus* and perhaps the transition from *plionasicus* to *nasicus* took place in the uppermost Pliocene and early Pleistocene. The next occurrence of

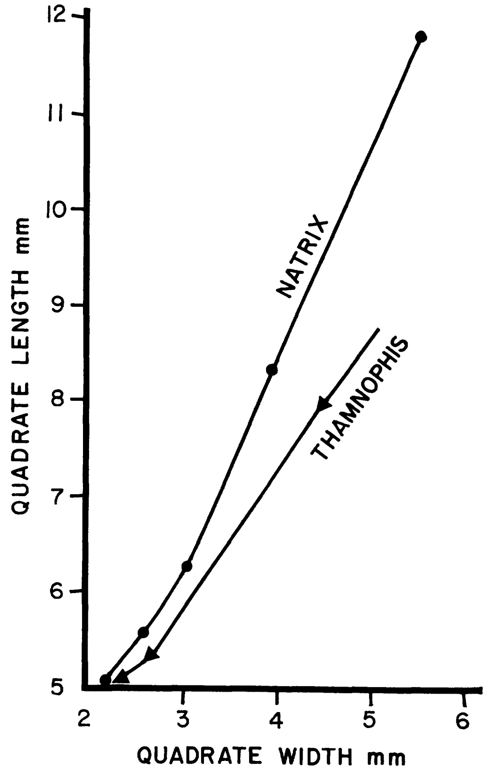


Fig. 4. Graph showing relationship between quadrate length and width measurements for Pliocene *Natrix* (N = 5) and *Thamnophis* (N = 3).

this lineage is in the Borchers Local Fauna (Yarmouth Interglacial) and those specimens are clearly *H. nasicus* (Fig. 5).

Pleistocene

Sand Draw Local Fauna,
Brown County, Nebraska

Natrix sp., *Thamnophis* sp., *Heterodon platyrhinos.*

Dixon Local Fauna,
Kingman County, Kansas

Thamnophis sp., *Elaphe* sp. The *Elaphe* is represented by a single, worn vertebra that is much like *E. obsoleta.*

Deer Park Local Fauna,
Meade County, Kansas

Coluber constrictor, Elaphe obsoleta.

Sanders Local Fauna,
Meade County, Kansas

Thamnophis sp., near *T. sauritus.*

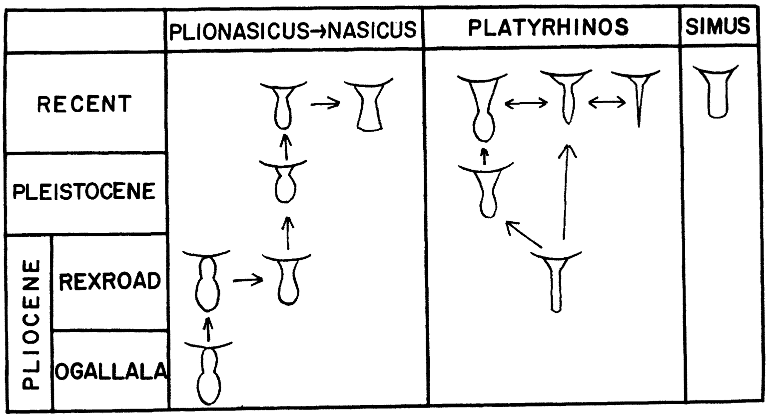


Fig. 5. Diagrams and possible evolutionary relationship of the shape of the subcentrum keel of *Heterodon*. *H. simus*, not represented in any high plains fossil fauna, drawn from Auffenberg, 1963.

Cudahy Fauna, Sunbright Mine,
Meade County, Kansas

Natrix sp., *Thamnophis* sp., *Storeria* sp.

Borchers Local Fauna,
Meade County, Kansas

Heterodon nasicus, Coluber constrictor, Pituophis catenifer, Elaphe cf. *obsoleta, Lampropeltis getulus, L. doliata,* ?*Rhinocheilus lecontei, Agkistrodon contortrix, Crotalus viridis, Sistrurus catenatus,* ?ground snake.

The *Heterodon nasicus* vertebrae are typical of this species except that the anterior dorsal edge of the zygosphene is flat as in *H. plionasicus* rather than slightly upturned at the sides. The *Rhinocheilus* material consists of four vertebrae. They are much like the vertebrae of *Pituophis catenifer*, but are small and the subcentrum keel is low and reduced, especially anteriorly, as in *R. lecontei*.

Four small vertebrae from this deposit are unidentifiable. Two of them are somewhat like the vertebrae of young *Heterodon*. They have been compared with the young or adults of all North American colubrids (including such forms as *Sonora, Chionactis, Phyllorhynchus, Carphophis, Diadophis, Cemophora, Tantilla,* etc.) and they do not appear referable to any. They are perhaps most like the genus *Sonora* but are not assigned to that genus.

All the crotalid vertebrae from this deposit are badly worn, suggesting transport to the deposition site.

Kentuck Assemblage,
McPherson County, Kansas

Natrix sp., *Heterodon platyrhinos, Elaphe obsoleta, Lampropeltis doliata.*

Butler Springs Local Fauna,
Meade County, Kansas

Natrix sp., *Natrix* cf. *sipedon, Thamnophis.*

Berends Local Fauna,
Beaver County, Oklahoma

Thamnophis sp., *Heterodon nasicus.*

The garter snake material consists of four large vertebrae similar to *T. sirtalis* in hypapophyseal characters, but distinct in characters of the zygosphene and parapophyses. The vertebrae probably represent a new species, but diagnosis on the basis of vertebral characters within the genus *Thamnophis* seems unwise.

Bar M Local Fauna, Loc. 1,
Harper County, Oklahoma

Natrix sp. perhaps near *N. cyclopion.*

Doby Springs Local Fauna,
Harper County, Oklahoma

Natrix sp., *Thamnophis* sp., *Coluber constrictor, Pituophis catenifer.*

Jinglebob Local Fauna,
Meade County, Kansas

Natrix sp., *Thamnophis* sp., *Heterodon nasicus, H. platyrhinos, Coluber constrictor, Pituophis* cf. *catenifer, Elaphe* cf. *obsoleta, Lampropeltis getulus, L. doliata, L. calligaster, Lampropeltis* sp.?

There are three and possibly four species of *Lampropeltis* represented in this deposit. A single vertebra with a centrum length of 2.8 mm is not assignable to the other three species nor is it like *L. pyromelana* or *zonata* (*L. alterna* and *blairi* not seen). The vertebra is also similar to *Arizona elegans* but not enough so to add *Arizona* to the fauna.

Cragin Quarry Local Fauna,
Meade County, Kansas

Natrix sp., *Thamnophis* sp., *Storeria* sp., *Heterodon* sp., probably near *platyrhinos, Coluber constrictor, Lampropeltis getulus,* ?*Diadophis* sp., *Agkistrodon contortrix, Crotalus viridis.*

A very small vertebra (centrum L : 0.9 mm) with a smooth, rounded subcentrum "keel" is much like *Diadophis* but is only tentatively assigned to that genus.

Cragin Quarry Local Fauna, Loc. UM-K3-59,
Meade County, Kansas

Thamnophis sp., *Storeria* sp., *Heterodon nasicus, Lampropeltis calligaster.*

Rezabek Local Fauna,
Lincoln County, Kansas

Natrix cf. *sipedon.*

Nye Sink, Beaver County, Oklahoma

Thamnophis sp.

Jones (Ranch) Local Fauna,
Meade County, Kansas

Thamnophis sp., *Elaphe obsoleta.*

Tutsman County, North Dakota

Thamnophis sp. Twenty vertebrae sent to me by Dr. Wilson M. Laird, North Dakota Geological Survey from Late Pleistocene deposits at the mouth of Minneapolis Flats Creek (where it enters Pipestem Creek), SW¼, NW¼, Sec. 24, T. 141 N, R. 65 W, Tutsman County, North Dakota appear referable to *Thamnophis* sp. An articular and a few ribs are also so referred.

Composition of Snake Faunas

The snakes found in each of the deposits are summarized in Table 1. Fig. 6 presents an analysis of the snake faunas in terms of per cent of composition of fauna. It is apparent from these data that natricine snakes are the most abundant forms. They are most abundant during, just preceding, and just following glacial periods. *Natrix* is usually the most abundant of the natricine snakes present except in presumedly very cold (Berends) or very warm (Deer Park, Borchers) times. The abundance of natricine snakes is probably due in large part to their membership in the community proximal to the deposition site. Non-natricine colubrids and crotalids are most abundant during the interglacial periods, though strangely no crotalids are known from the Aftonian interglacial.

Table 2. Summary of Glacial Snake Faunas of the High Plains.

	Nebraskan	Kansan	Illinoian	Wisconsin
Thamnophis sp.	×	×	×	×
Natrix sp.	×	×	×	
Storeria sp.		×		
Elaphe obsoleta	×			
Heterodon platyrhinos	×			
H. nasicus			×	
Pituophis catenifer			×	
Coluber constrictor			×	
Total	4	3	5	1

Table 2 presents a summary of the glacial snake faunas and Table 3 summarizes the interglacial snake faunas. These tables show that each of the interglacial periods are sometimes markedly different from each other.

Certain species now occurring in Kansas (Smith, 1950) or nearby areas are not found in the various fossil deposits. Some of the possible reasons for "missing" these snakes are: too small for effective fossilization or recovery (*Leptotyphlops, Carphophis, Diadophis, Opheodrys, Sonora, Tantilla, Hypsiglena*), wrong habitat (*Leptotyphlops, Tantilla*), too cold for—generally occurring today to the southeast (*Opheodrys aestivus, Elaphe guttata, Haldea striatula* and *valeriae, Agkistrodon piscivorus, Crotalus horridus*), too cold for—generally occurring today to the southwest (*Arizona, Hypsiglena, Crotalus atrox*). Two fairly widely distributed forms are not found in the deposits: *Masticophis flagellum* and *Tropidoclonion lineatum.*

Comparison of Snake Faunas with Other Vertebrate Faunas

The extensive studies on fossil mammals, lizards, and turtle remains from the Pliocene and Pleistocene deposits of the high plains, or for that matter from most of North Amer-

TABLE 3. SUMMARY OF INTERGLACIAL SNAKE FAUNAS OF THE HIGH PLAINS. X = present; E = eastern Kansas only; * = *H. plionasicus.*

Species	Upper Pliocene	Aftonian	Yarmouth	Sangamon	Recent Kansas
Thamnophis sp.	X	X		X	X
Natrix sp.	X		X	X	X
Storeria				X	X
Lampropeltis doliata	X		X	X	X
L. getulus	X		X	X	X
L. calligaster				X	X
Heterodon nasicus	X*		X	X	X
H. platyrhinos	X			X	X
Elaphe obsoleta	X	X	X	X	XE
Pituophis catenifer	X		X	X	X
Coluber constrictor	X	X	X	X	X
?*Rhinocheilus lecontei*			X		X
?*Diadophis*				X	X
?ground snake sp.			X		X
Agkistrodon contortrix	X		X	X	XE
Sistrurus catenatus	X		X		X
Crotalus viridis	X		X	X	X
Total	12	3	12	14	17+

ica, show that these faunas are composed of: 1, many forms that are extinct today; 2, Tertiary forms that were dying out; and 3, forms that were appearing for the first time (Auffenberg and Milstead, 1965; Tihen, 1964; Hibbard, *et al.*, 1965). The high plains snake faunas are quite different from the above: 1, no forms became extinct during the Pleistocene; and 2, the snake faunas are modern, composed of extant forms (i.e., most genera and species of Recent snakes have existed, almost unchanged, since at least the Upper, and in some cases the Lower Pliocene).

EVOLUTIONARY CHANGES

Two evolutionary changes are evident in the faunas studied. One is the transition of *Heterodon plionasicus* into modern *H. nasicus* that took place near the end of the Pliocene and beginning of the Pleistocene (Fig. 5). The other is the elimination of *Elaphe kansensis* and its replacement by *E. obsoleta.* Whether this represents a geographic or ecological replacement or a transition from one form to the other cannot be determined with the available material.

BIOGEOGRAPHIC AND PALEOECOLOGICAL CONSIDERATIONS

Two approaches to the paleoecology of the snake faunas at hand are presented here. It should be noted that terrestrial amphibians and reptiles are especially important and useful in determining past climates. Their usefulness for paleoecological considerations is enhanced by the following: 1, they are ectotherms, and hence are markedly responsive to the environment and its changes; 2, they are often ecologically, behaviorally, or perhaps physiologically restricted to specific microhabitats and environments; 3, many forms have restricted geographic ranges; and 4, many forms are territorial or have relatively restricted movements and none is migratory.

Biogeography of High Plains Snakes

One of the methods for estimating the climate of a fossil deposit is to plot the area of greatest overlap of all the modern ranges of extant species represented in the fossil deposit (Etheridge, 1958). Ideally this should be done for each local fauna. The relative level of completeness of the herpetofauna hinders accurate interpretation. The paleoecological interpretation of the glacial faunas (Table 2) should be rather apparent. Unfortunately the three primary glacial forms (*Natrix, Thamnophis, Storeria*) occur sympatrically over eastern or northeastern North America. In addition, these wide ranging genera have many thermophilic

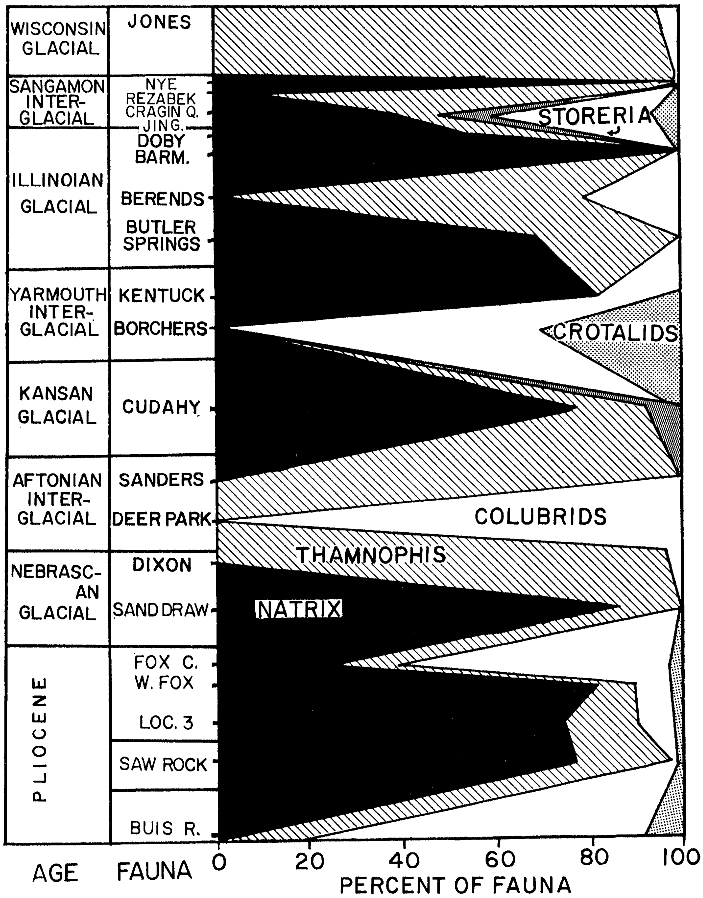
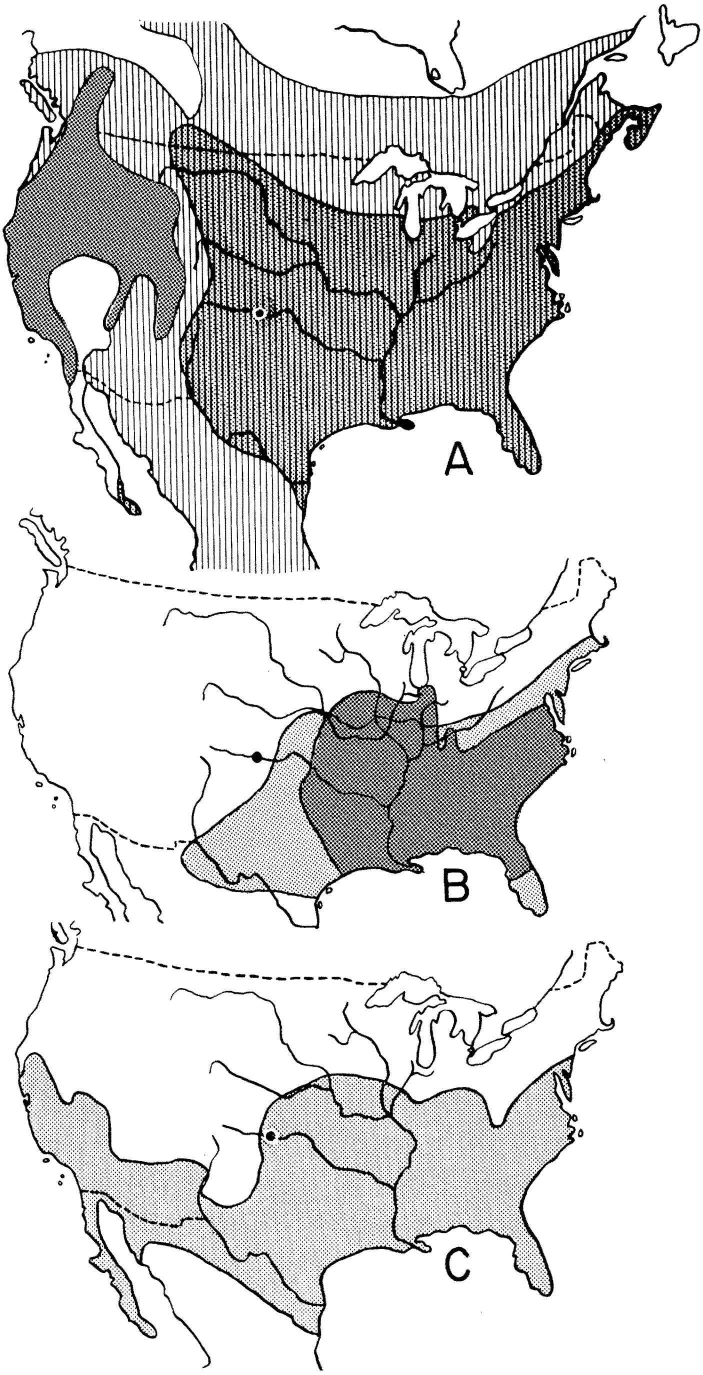


Fig. 6. Chart showing composition of fossil snake faunas from the high plains. Data from Table 1.

members, though northern species tend to have lower thermal tolerances (Brattstrom, 1965). Species identification of the fossil material is almost impossible except in a few rare cases. It is apparent, however, that these genera are often the only forms present in glacial deposits and are the most abundant in periglacial times (Table 2, Fig. 6).

Fig. 7 presents and summarizes the ranges of a warm snake fauna, and thus is representative of the Sangamon interglacial and most of the Upper Pliocene faunas (Table 1, 3, Fig. 6). The other interglacial periods and local faunas would be expected to differ from the summary given by virtue of omission of certain forms.

Certain forms have relatively wide geographic ranges (Fig. 7A, *Coluber constrictor, Thamnophis*). Others range today generally to the east (Fig. 7D, *Elaphe obsoleta, Lampropeltis doliata, Natrix, Storeria, Heterodon platyrhinos*), to the southeast (Fig. 7B, *Lampropeltis calligaster, Agkistrodon contortrix*), to the south (*Lampropeltis getulus*, Fig. 7C), to the west (Fig. 7E, *Pituophis catenifer, Rhinocheilus lecontei, Crotalus viridis*), or southwest (Fig. 7E, *Rhinocheilus lecontei, Sistrurus catenatus, Heterodon nasicus, Sonora*). Fig. 7A–E shows the current overlapping ranges of the snakes just listed, all of which occur in the fossil deposits. When all these ranges are superimposed, the greatest overlap of ranges occurs in southwestern Texas (Fig. 7F). This would seem to imply that the Upper Pliocene and Sangamon interglacial climates of Kansas and adjacent areas was similar to that of southwestern Texas today. Etheridge (1958) found a similar overlap area, though


A
B
C

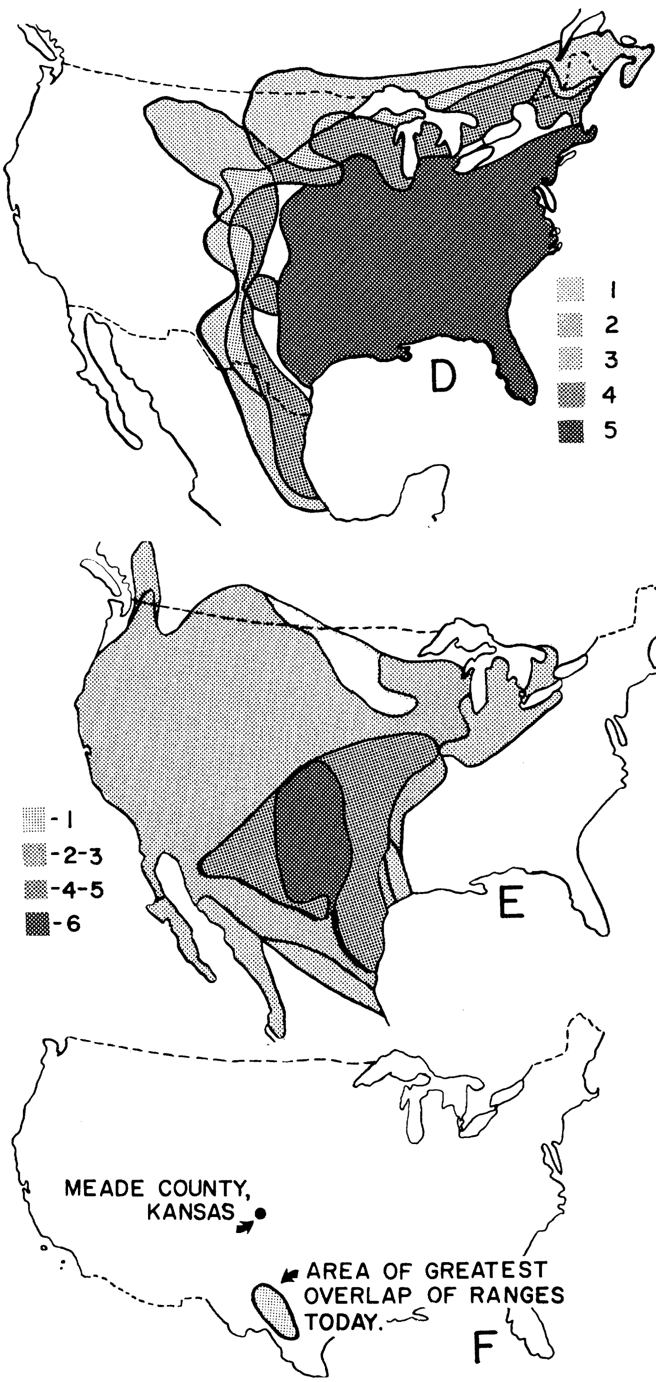


Fig. 7. Present ranges of snake species and genera found in fossil deposits of the high plains of the United States. Map A is of two taxa with very wide ranges. Other maps show two taxa generally ranging to the southeast (B), one to the south (C), five to the east (D), and six to the west and southwest (E). F shows the area of greatest overlap of ranges (A–E) of all extant snake taxa represented in warm period fossils deposits (see text, p. 197).

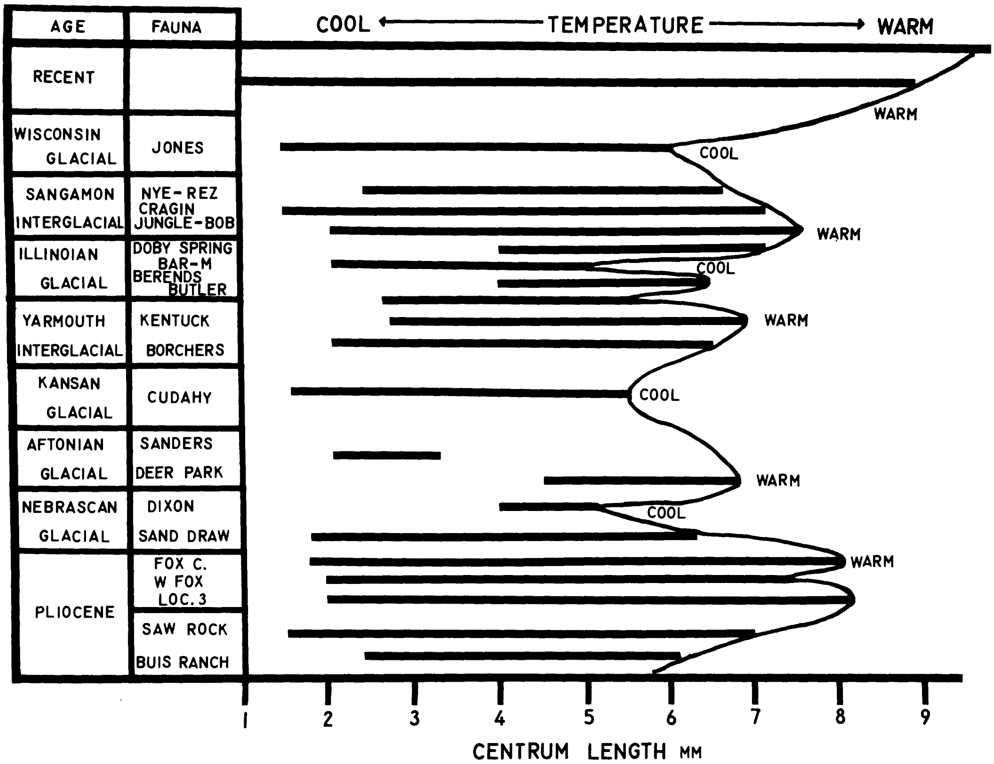


Fig. 8. Chart showing minimum, maximum, and range of vertebral size (based on length of centrum) of all species from the various deposits from the high plains which suggest (see text) the climates indicated. Data from Table 1.

slightly to the west in western Texas and northeastern Mexico, for five species of Cragin Quarry, Sangamon interglacial, lizards. The area of overlap of the snake ranges corresponds for the most part with the Balconian Biotic Province of Blair (1950). According to Blair (1950) the most characteristic plant association of the Balconian is a scrub forest of *Juniperus mexicana*, *Quercus texana*, and *Q. virginiana* with such forms as *Taxodium distichum* invading the province in the southeast along streams while others (*Nolina*, *Agave*, and *Pinus edulis*) invade from the west. Blair (1950) lists the following snakes as characteristic of or common in the Balconian: *Leptotyphlops dulcis*, *Masticophis flagellum*, *M. taeniata*, *Elaphe obsoleta*, *Salvadora lineata*, *Arizona elegans*, *Sonora episcopa*, *Thamnophis marcianus*, *T. sauritus*, *Hypsiglena torquata*, *Natrix erythrogaster*, *N. rhombifera*, *Crotalus atrox*, while the following invade the province from the Austroriparian to the east: *Opheodrys aestivus*, *Diadophis punctatus*, *Heterodon platyrhinos*, *Coluber constrictor*, *Storeria dekayi*, *Haldea striatula*, *H. valeriae*, *Micrurus fulvius*, *Agkistrodon contortrix*, *A. piscivorus*, while others invade the province from the Chihuahuan to the west: *Ficimia cana*, *Thamnophis eques*, and *Crotalus molossus*. Many of the forms cited occur in the fossil deposits and many occur in Kansas today (Smith, 1950). Still others, found in the fossil deposits, are neither represented in the Balconian Biotic Province nor in Kansas today.

Paleoecology

In contrast to Bergmann's rule for endotherms, ectotherms tend to follow just the opposite, i.e., the smaller forms occur in the north and the larger forms to the south (Cowles, 1945; Brattstrom, 1956, 1961, 1964, 1965). This is true for ectotherms because their heat source comes from without (Cowles and Bogert, 1944; Bogert, 1949; Fitch, 1956; Brattstrom, 1963, 1965) and in more northern or alpine climates, only the small forms, with their greater surface area to volume, can absorb enough solar radiation to heat their bodies to operational levels. In addition, more northern ectotherms seem to have lower thermal tolerances and preferences (Brattstrom, 1965). I have accordingly used size of snakes as a clue towards an interpretation of past climates. Fig. 8 summarizes the range in centrum length (as a measure of snake size, see Auffenberg, 1963) for all the snakes in each of the faunal deposits (data from Table 1). As can be seen from Fig. 8, smaller snakes occur during the glacial periods while larger snakes, often of the same species (Table 1), occur during the interglacial periods. If the comments above are correct, this would imply, along with other geological and paleontological evidence (Taylor, 1960; Hibbard, 1960; Hibbard and Taylor, 1960; Hibbard, *et al.*, 1965) the coolness of the glacial and the warmness of the interglacial periods in the high plains.

Clearly this technique has its limitations, as for example with completely fossorial forms, but it does allow a first approximation of past climates using known information on surface-volume relationships, incoming radiation, and the thermal requirements of ectotherms. This technique does not allow for interpretation of humidity or rainfall, though others might (Brattstrom, 1956, 1961). Attempts to associate specific physiological requirements with distribution will fail by virtue of the diversity of evolutionary adaptations to specific environments already achieved by organisms (Bartholomew, 1958), or are now in progress (Brattstrom, 1965).

Acknowledgments

I am most grateful to the curators of the paleontological and herpetological collections cited for being allowed to examine material in their care. Aspects of this paper have been discussed in person or through correspondence with several people. I would especially like to thank Drs. Walter Auffenberg, Charles Bogert, Richard Etheridge, Fred Gehlbach, Max Hecht, Jay M. Savage, and Hobart M. Smith. Thanks are due to the various field parties and laboratory assistants under the leadership of Dr. Claude Hibbard for the collecting, screening, sorting, cataloging, and shipping snake material to me. Special thanks are due to Dr. Hibbard whose enthusiasm and hard work seem only to be exceeded by his patience.

Portions of this work, or collection of data and ideas for its interpretation, were supported by the American Philosophical Society (G-2241 and G-237, Johnson Fund), The California Institute of Technology, and The National Science Foundation (G-8394, GB-2307).

Literature Cited

Auffenberg, W. 1963. The fossil snakes of Florida. Tulane Stud. Zool. 10:131–216.

——— and W. M. Milstead. 1965. Reptiles in the Quaternary of North America. *In:* The Quaternary of the United States. H. E. Wright, Jr. and D. G. Frey, eds., pp. 557–568. Princeton Univ. Press, Princeton, N. J.

Bartholomew, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates. *In:* Zoogeography. Carl L. Hubbs, ed., pp. 81–95. Am. Assoc. Adv. Sci., Wash., D. C.

Blair, W. F. 1950. The biotic provinces of Texas. Texas J. Sci. 2:93–117.

Bogert, C. M. 1949. Thermoregulation in reptiles: a factor in evolution. Evolution 3:195–211.

Brattstrom, B. H. 1954. The fossil pit-vipers (Reptilia: Crotalidae) of North America. Trans. San Diego Soc. Nat. Hist. 12:31–46.

———. 1956. The climate of the past. Eng. Sci. Month. 19:22–23.

———. 1961. Some new fossil tortoises from western North America with remarks on the zoogeography and paleoecology of tortoises. J. Paleontol. 35:543–560.

———. 1963. A preliminary review of the thermal requirements of amphibians. Ecology 44:238–255.

———. 1964. Evolution of the pit vipers. Trans. San Diego Soc. Nat. Hist. 13:185–268.

———. 1965. Body temperatures of reptiles. Am. Midl. Nat. 73:376–422.

Cowles, R. B. 1945. Surface-mass ratio, paleoclimate, and heat sterility. Am. Nat. 79:561–567.

——— and C. M. Bogert. 1944. Preliminary study of the thermal requirements of desert reptiles. Bull. Am. Mus. Nat. Hist. 83:261–296.

Dowling, H. G. 1958. Pleistocene snakes of the Ozark Plateau. Am. Mus. Novit. No. 1882, pp. 1–9.

Etheridge, R. 1958. Pleistocene lizards of the Cragin Quarry fauna of Meade County, Kansas. Copeia 1958(2):94–101.

Fitch, H. S. 1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. Univ. Kans. Pub. Mus. Nat. Hist. 8:417–476.

Gehlbach, F. R. 1965. Amphibians and reptiles from the Pliocene and Pleistocene of North America: a chronological summary and selected bibliography. Texas J. Sci. 17:56–70.

Gilmore, C. W. 1938. Fossil snakes of North America. Spec. Pap. Geol. Soc. Am. 9:1–96.

Hibbard, C. W. 1949. Techniques of collecting

microvertebrate fossils. Univ. Mich. Contrib. Mus. Paleontol. 8:7–19.
———. 1958. Summary of North American Pleistocene mammalian local faunas. Pap. Mich. Acad. Sci., Arts, Lett. 43:3–32.
———. 1960. An interpretation of Pliocene and Pleistocene climates in North America. Ann. Rep. Mich. Acad. Sci., Arts, Lett. 62:5–30.
——— AND D. W. TAYLOR. 1960. Two late Pleistocene faunas from southwestern Kansas. Univ. Mich. Contrib. Mus. Paleontol. 16:1–223.
———, C. E. RAY, D. E. SAVAGE, D. W. TAYLOR, AND J. E. GUILDAY. 1965. Quaternary mammals of North America. *In:* The Quaternary of the United States. H. E. Wright, Jr. and D. G. Frey, eds., pp. 509–525. Princeton Univ. Press, Princeton, N. J.
HOLMAN, J. A. 1962. A Texas Pleistocene herpetofauna. Copeia 1962(1):255–261.
———. 1963. Late Pleistocene amphibians and reptiles of the Clear Creek and Ben Franklin local faunas of Texas. J. Grad. Res. Cent. So. Methodist Univ. 31:152–167.
LOWE, C. H., JR. 1955. Generic status of the aquatic snake *Thamnophis angustirostris.* Copeia 1955(4):307–309.
McDOWELL, S. B., JR. AND C. M. BOGERT. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Am. Mus. Nat. Hist. 105:1–142.
McKENNA, M. C. 1962. Collecting small fossils by washing and screening. Curator 3:221–235.
MALNATE, E. V. 1960. Systematic division and evolution of the colubrid snake genus *Natrix,* with comments on the subfamily Natricinae. Proc. Acad. Nat. Sci. Phila. 112:41–71.
PETERS, J. A. 1953. A fossil snake of the genus *Heterodon* from the Pliocene of Kansas. J. Paleontol. 27:328–331.
ROSSMAN, D. A. 1963. Relationship and taxonomic status of the North American natricine snake genera *Liodytes, Regina,* and *Clonophis.* La. State Univ. Occ. Pap. Mus. Zool. 29:1–29.
SMITH, H. M. 1950. Handbook of amphibians and reptiles of Kansas. Univ. Kans. Pub. Mus. Nat. Hist., Misc. Pub. No. 2, 336 pp.
——— AND J. E. HUHEEY. 1960. The watersnake genus *Regina.* Trans. Kans. Acad. Sci. 63:156–164.
TAYLOR, D. W. 1960. Late Cenozoic molluscan faunas from the high plains. U. S. Geol. Surv. Prof. Pap. No. 337, 94 pp.
TIHEN, J. A. 1964. Tertiary changes in the herpetofaunas of temperate North America. Senck. Biol. 45:265–279.

DEPARTMENT OF BIOLOGY, CALIFORNIA STATE COLLEGE, FULLERTON, CALIFORNIA 92631.

Variation and Distribution of the Iguanid Lizard *Sceloporus bulleri*, and the Description of a Related New Species

ROBERT G. WEBB

Study of the little-known *Sceloporus bulleri* of mountainous areas in western Mexico indicates two distinct populations. *Sceloporus insignis,* a new species of the *torquatus* group from the Sierra de Coalcomán, Michoacán, and the Nevada de Colima and Volcán de Colima in southern Jalisco, shows most differentiation in color and pattern from its closest relative, *S. bulleri.* The two species are allopatric. *S. bulleri* and *S. insignis* seem most closely related to *S. torquatus.*

As currently recognized, *Sceloporus bulleri,* a large, black-collared species of the *torquatus* group, occurs in mountainous habitats of western Mexico from southern Sinaloa and southwestern Durango south to Michoacán. Comparison of living and preserved specimens from near the southern and northernmost limits of the range indicates two taxonomically distinct populations. Lizards in Sinaloa, Durango, and most of Jalisco are referable to *Sceloporus bulleri,* whereas those to the south in southern Jalisco and Michoacán represent an apparently undescribed species.

Sceloporus bulleri Boulenger

Sceloporus bulleri Boulenger, 1894:729–730, pl. XLVII, Fig. 3, 1894.

Type and type locality.—Lectotype, by present designation (see p. 207), Brit. Mus. (Nat. Hist.) No. 1946.8.29.90 (Fig. 1); obtained by Dr. A. C. Buller from La Cumbre de los Arrastrados, Jalisco, México. There seems to be no specific locality in the Mexican state of Jalisco known as La Cumbre de los Arrastrados. Dr. Hobart M. Smith (pers. comm.) stated "No, I never found the type locality of *bulleri.* I doubt very much