

terrestrial species living in open, sandy or rocky areas where excursions are made on open ground. To this group belong all bipedal species of North America as well as *Amphibolurus*, *Chlamydosaurus*, *Sitana*, *Otocryptis* and, possibly, *Varanus giganteus*. The second category includes species that live in brushy or forested areas and may be classed as semi-arboreal, semi-aquatic or both. Included in this group are *Basiliscus*, *Corythophanes*, *Physignathus*, *Hydrosaurus* and *Calotes*.

SUMMARY AND ACKNOWLEDGMENTS

The basic pattern of limb action during quadrupedal locomotion of lizards is described. *Crotaphytus c. collaris* is used as a type.

Differences between lacertilian and mammalian locomotion are indicated.

Hind leg and body action of *Amphibolurus* during bipedal progression indicates a more efficient locomotor cycle than in bipedal iguanids.

A previous listing of eight species of lizards habitually resorting to bipedal locomotion is augmented by ten others, and is subdivided into two groups based upon general habitat preferences.

The writer is indebted to Dr. F. J. Mitchell of the South Australian Museum, Adelaide, Australia, who furnished several *Amphibolurus* for study, and to the Audio-visual Department, University of Washington, for loan of photo-

graphic equipment. This study was supported in part by the Fund for Research in Biology and Medicine derived from Initiative 171 of the State of Washington.

LITERATURE CITED

- BARCLAY, O. R. 1946. The mechanics of amphibian locomotion. *J. Exp. Biol.*, 23: 177-203.
- BARRETT, CHARLES. 1950. Reptiles of Australia. Sydney, Cassell and Co.: 168 pp., 55 figs. and pls.
- EVANS, F. GAYNOR. 1946. The anatomy and function of the foreleg in salamander locomotion. *Anat. Rec.*, 95: 257-281.
- GADOW, H. F. 1901. Amphibia and reptiles. *Cambridge Natural History*. Vol. 8. London, Macmillan: xiii + 668, 181 figs.
- HOWELL, A. B. 1944. Speed in animals. Chicago, University of Chicago Press: ix + 270, 55 figs.
- LOVERIDGE, ARTHUR. 1934. Australian reptiles in the Museum of Comparative Zoology, Cambridge, Massachusetts. *Bull. Mus. Comp. Zool.*, 77: 243-383.
- SCHAEFFER, BOBB. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bull. Amer. Mus. Nat. Hist.*, 78: 395-472.
- SMITH, MALCOLM. 1935. The fauna of British India, reptilia and amphibia. Vol. II. Sauria. London, Taylor and Francis: xiii + 440, 94 figs., 1 pl.
- SNYDER, RICHARD C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. *COPEIA*, (2): 129-137.
- VAN DENBURGH, JOHN. 1922. The reptiles of western North America. Vol. I. Lizards. San Francisco, California Academy of Sciences: 611 pp., 57 pls.
- DEPARTMENT OF ZOOLOGY, UNIVERSITY OF WASHINGTON, SEATTLE, WASHINGTON.

Pliocene Lizards from Kansas

JOHN W. TWENTE, JR.

THE lizards reported in this paper were collected in the summer of 1950 from Upper and upper Middle Pliocene deposits in southwestern Kansas.

I am greatly indebted to Dr. Claude W. Hibbard and Dr. Norman E. Hartweg of the University of Michigan and to Dr. Edward H. Taylor of the University of Kansas for advice and criticism and the use of specimens under their direction. Acknowledgement is also given to Dr. Rollin H. Baker and Dr. Robert W. Wilson of the University of Kansas Museum of

Natural History for the privilege of observing specimens. The drawings were made by Mr. William L. Brudon.

Sceloporus robustus, sp. nov.

(Figs. 1, 2, 3 and 4)

HOLOTYPE.—No. 27665, University of Michigan Museum of Paleontology. Left dentary with 17 teeth and spaces for seven others.

PARATYPES.—No. 27666, a nearly complete left dentary with eight complete teeth and spaces for 14 to 16 more; No. 27668, a nearly

complete right dentary with 17 complete teeth and broken teeth or spaces for seven others; No. 27667, two fragmentary right dentaries, one with 13 and the other with nine complete teeth.

REFERRED MATERIAL.—No. 27669 consists of fragments of 17 dentaries referred to this species. These specimens were collected by the University of Michigan, Museum of Paleontology field party under the direction of Dr. Claude W. Hibbard.

HORIZON AND TYPE LOCALITY.—Upper Pliocene, Rexroad formation, Rexroad fauna.

are typically iguanid in character, the trilobation being more evident in those in the posterior part of the jaw. The teeth appear to be well-worn in that the median cusp is worn down to the level of the lateral cusps in most instances. However, the replacement teeth show the median cusp to extend well above the lateral cusps. The teeth are compressed transversely and are approximately twice as thick at the base as at the tips and are strongly ankylosed to the outer dentary wall. The teeth in the anterior part of the dentary do not show the evidence of trilobation as do those in the

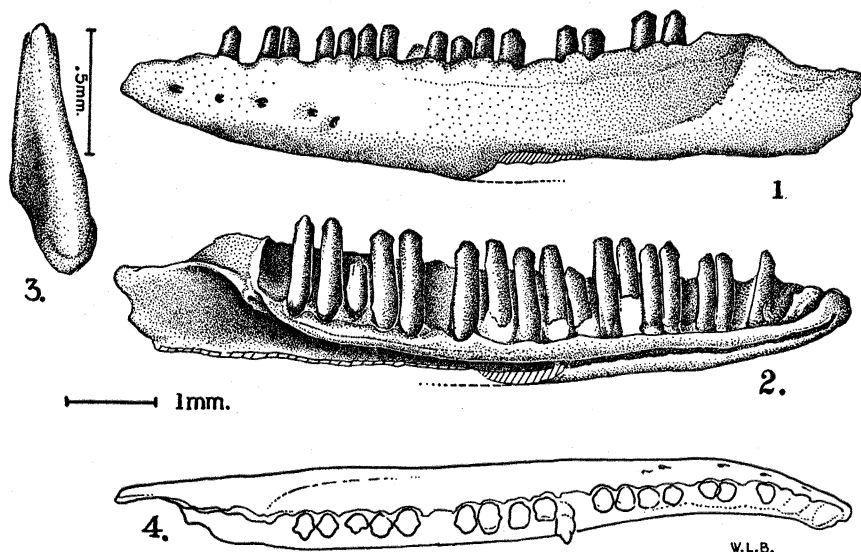


Fig. 1. Labial view of left dentary of *Sceloporus robustus* (No. 27665).

Fig. 2. Lingual view of same.

Fig. 3. Tooth showing trilobation and transverse compression at the base.

Fig. 4. Occlusal view of same.

Locality UM-K1-47, Fox Canyon, XI Ranch, Sec. 35, T. 34S., R. 30W., Meade County, Kansas.

DIAGNOSIS.—A *Sceloporus*, apparently approximately the same size as a large *Sceloporus undulatus garmani* Boulenger, but the dentary is more robust and possesses a deep excavation on the posterior lateral surface for the insertion of what is interpreted to be the adductor mandibularis muscle. The teeth are relatively heavy and are somewhat transversely compressed at the base.

DESCRIPTION OF HOLOTYPE.—The holotype is a nearly complete left dentary 8 mm. in length bearing 15 complete teeth, 2 replacement teeth and spaces for 7 others. The teeth

posterior part (the first 13 tooth spaces counting from the most posterior). The tooth row is $6\frac{1}{2}$ mm. in length and there are 20 teeth per half centimeter.

The meckelian groove (Fig. 2) is deep and well-developed extending to the symphysis. The shelf above is relatively heavy and protrudes a short distance mesially from the bases of the teeth. The part of the dentary ventral to the meckelian groove is very strong and forms the ventral part of the jaw. The meckelian groove faces ventrally at the symphysis and a short distance posterior to this it turns ventromesially becoming gradually mesial in position towards the posterior part of the dentary.

The labial face of the dentary (Fig. 1) shows

four prominent foramina in the anterior one-third and a fifth foramen slightly below and behind the fourth which is situated at the level of the ninth tooth space from the symphysis. At the region of the last tooth, a distinct ridge extends downward and obliquely towards the anterior part of the jaw. This ridge forms the boundary of a deep excavation which extends to near the middle part of the dentary. This depression is interpreted to serve as the insertion of the adductor mandibularis muscle and is more prominent in *S. robustus* than in any of the recent scelopori surveyed. When viewed from the labial side, therefore, the dentary is slightly concave at its posterior half and becomes convex towards the anterior.

From an occlusal view (Fig. 4) the dentary is straight from the posterior border to approximately 2 mm. from the symphysis where the angle of curve occurs. The tangent of the angle whose opposite side is the chord connecting the symphysis and the beginning of the curve in the dentary has a value of four. The width of the dentary at the region of the most posterior tooth is 1 mm. The dentary gradually narrows toward the region of the angle where the measurement is $\frac{3}{4}$ mm.

DESCRIPTION OF PARATYPES.—These agree essentially with the holotype although the fifth foramen is better developed (except in No. 27666 where it is lacking) and is directly in line with the other foramina. A great amount of variation is evident in the degree of trilobation of the teeth, but this is presumably due to the amount of wear. No replacement teeth are present in any of the paratypes.

The depth of the excavation on the labial surface of the dentary is also variable, but the presence of this characteristic is always evident to the naked eye.

COMPARISONS.—These dentaries have been compared with those of all of the species of *Sceloporus* living in Kansas, Oklahoma, Texas, New Mexico, Arizona, Colorado and many of the forms living in México. Although the dentary is approximately the same size as that of the *Sceloporus undulatus* living in Kansas today, in *Sceloporus robustus* it is decidedly heavier. The teeth are transversely compressed at the base in the fossil form whereas those of *S. undulatus* are nearly conical at the base.

The meckelian groove is much more pronounced than in the living species and the part

of the dentary above the groove is much thicker and heavier forming a definite shelf. In the recent forms studied only a very slight shelf is formed separating the base of the teeth from the mesial border of the dentary.

The labial surface of the dentary in the recent form is convex throughout showing little evidence of the excavation so prominent in *S. robustus*.

An occlusal view of the recent species shows that the curve towards the symphysis begins very near the middle part of the tooth row. In *S. robustus* this angle begins until very near the symphysis.

DISCUSSION.—These specimens were referred to the family Iguanidae on the basis of the trilobate teeth. All of the living genera of this family which have members falling in this size group were studied and the fossil specimens could only be ascribed to the genus *Sceloporus*. This comparison was made on the basis of the type of teeth, the degree of trilobation and the number, and on the general characters of the dentary itself. Differences found in the fossil species were not deemed sufficient to warrant generic rank since a great amount of variation in characters of the dentaries and teeth occurs in the living species of *Sceloporus*.

Although *S. robustus* is a relatively small species it possesses weight and ruggedness of the dentary not found in living species of a similar size. *Eumeces striatulus* Taylor found in the same beds shows a similar degree of robustness in comparison to the species living today.

As far as I can determine, this is the first fossil record of the genus *Sceloporus*.

Eumeces striatulus Taylor

Eumeces striatulus Taylor, 1941. *Kans. Geol. Surv. Bull.* 38: 171-72.

No. 27674 consists of a nearly complete right dentary with 19 complete teeth and spaces for four more; the anterior tip of a right dentary with ten teeth and spaces for two more; and a right maxillary containing 16 complete teeth and spaces for six more. These specimens were collected in association with the upper Middle Pliocene Saw Rock Canyon fauna (Hibbard, 1949) University of Kansas locality No. 6, Saw Rock Canyon, Sec. 36, T. 34S., R. 31W., Seward County, Kansas.

This is the first record of *Eumeces striatulus* Taylor from beds other than the type locality

(Rexroad formation, Upper Pliocene, Locality 2 [Taylor, 1941]). Although from beds somewhat older than the type locality, these specimens agree with the holotype in detail except that they are somewhat smaller. The complete right dentary is approximately one-half the size of the holotype and of other individuals of this species referred to in this paper, but it has been found that young individuals of living *Eumeces* differ from the adults (in characters of the jaws) only in size and the degree of wear on some of the teeth.

Hibbard (1949) has discussed the relationship of the Saw Rock fauna to the Rexroad fauna as follows:

From a study of the vertebrates it is evident that the forms are younger than the Edson Quarry fauna (Hemphillian) from Sherman County, Kansas. A closer relationship is shown between the Rexroad fauna and the Saw Rock fauna than between the Saw Rock fauna and the Edson Quarry fauna, as indicated by the rodents. For this reason the fauna could be assigned either to the upper part of the Middle Pliocene or to the lower part of the Upper Pliocene.

Many specimens of *Eumeces striatulus* were also collected by Hibbard and party in 1950 from the same locality as *Sceloporus robustus*. A complete right dentary, No. 27659, has 21 teeth and spaces for two others. This is a better specimen than the holotype (Kansas University Museum of Vertebrate Paleontology No. 5079). Five fragmentary dentaries, No. 27661, and nine fragmentary maxillaries, No. 27660 were recovered with specimen No. 27659.

Although from a different locality than the holotype, these specimens, members of the Rexroad fauna, agree with the specimens described by Taylor (1941).

Eumecoides hibbardi Taylor

Eumecoides hibbardi Taylor, 1941. *Kans. Geol. Surv. Bull.* 38: 173-74.

The posterior part of a right dentary, No. 27663, containing the last ten teeth belongs to the above species. This specimen was found associated with *Sceloporus robustus*. It agrees with the holotype of *E. hibbardi* in the character of the teeth and the fact that the labial face of the dentary is concave. No other specimens of this species were found.

Eumecoides mylocoelus Taylor

Eumecoides mylocoelus Taylor, 1941. *Kans. Geol. Surv. Bull.* 38: 174-76.

The posterior part of a right dentary, No.

27664, containing seven teeth and spaces for three more of *E. mylocoelus* was found associated with the other lizards from the Fox Canyon locality. Only one fragment of this species was collected. The labial face of the dentary in this form is convex as opposed to the concave condition found in *E. hibbardi*. (See Taylor, 1941, for a key and figures of both of these species of *Eumecoides*.)

The saurian members of the Rexroad fauna now include four genera and five species. One form, *Cnemidophorus bilobatus* Taylor has not been found to date at the Fox Canyon locality.

The Rexroad fauna is one of the best known fossil faunas in North America. Taylor (1941 and 1942) has studied the lizards and amphibians; Wetmore (1944) and Tordoff (1951) the birds; and Hibbard and Riggs (1949) and Hibbard (1941 and 1950) the mammals. Baker (1938) and Franzen and Leonard (1947) have recorded the mollusks. The paleoecology of the Rexroad fauna is discussed by Hibbard (1950: 175-178).

This paper is a contribution from the Museum of Paleontology, University of Michigan.

LITERATURE CITED

- BAKER, F. C. 1938. New land and freshwater Mollusca from the Upper Pliocene of Kansas and a new species of *Gyraulus* from early Pleistocene strata. *Nautilus*, 51: 126-131.
- FRANZEN, D. S., AND A. B. LEONARD. 1947. Fossil and living Pupilidae (Gastropoda-Pulmonata) in Kansas. *Univ. Kans. Sci. Bull.*, 31: 311-411.
- HIBBARD, C. W. 1941. Mammals of the Rexroad fauna from the Upper Pliocene of southwestern Kansas. *Trans. Kans. Acad. Sci.*, 44: 265-313.
- . 1949. Pliocene Saw Rock Canyon fauna in Kansas. *Contrib. Mus. Paleo. Univ. Mich.*, 7: 91-105.
- . 1950. Mammals of the Rexroad formation from Fox Canyon, Meade County, Kansas. *Ibid.*, 8: 113-192.
- HIBBARD, C. W., AND E. S. RIGGS. 1949. Upper Pliocene vertebrates from Keefe Canyon, Meade County, Kansas. *Bull. Geol. Soc. Amer.*, 60: 829-860.
- TAYLOR, E. H. 1941. Extinct lizards from Upper Pliocene deposits of Kansas. *Kans. State Geol. Surv. Bull.*, 38: 165-176.
- . 1942. Extinct toads and frogs from the Upper Pliocene deposits of Meade County, Kansas. *Univ. Kans. Sci. Bull.*, 28: 199-235.
- TORDOFF, H. B. 1951. Osteology of *Colinus hibbardi*, a Pliocene quail. *Condor*, 63: 23-30.
- WETMORE, A. 1944. Remains of birds from the Rexroad fauna of the Upper Pliocene of Kansas. *Univ. Kans. Sci. Bull.*, 30: 89-105.

MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN