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The Postcranial Osteology of the Lizard Shinisaurus 1. The Vertebral Column

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INTRODUCTION

During the winter of 1960 the senior author had the opportunity to study the reptilian osteological collections in the Zoologisches Museum in Berlin. These collections represent an important source of comparative material, particularly for the identification of fossil-lizard remains. Unfortunately many skeletons were improperly labeled when the specimens were reassembled after World War II. One lizard skeleton, preserved in alcohol, is distinct and characterized by a unique partial tail; it lacks, however, a skull and several other elements. Comparison with the specimen in the American Museum of Natural History shows that the partial skeleton in Berlin is that of *Shinisaurus crocodilurus* Ahl. Presumably the original describer had at one time intended to report on this specimen and during his study isolated and lost some of the elements.

Shinisaurus is rarely represented in collections. McDowell and Bogert (1954) described its cranial morphology and published an X-ray photograph of the postcranial skeleton. They placed Shinisaurus, with Xenosaurus, in the family Xenosauridae. The trigeminal musculature of Shinisaurus,

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saurus was described by Haas (1960), who concurred with McDowell and Bogert on its affinities. To clarify the relationships of *Shinisaurus* and to assist in the identification of related fossil material, a complete description of the skeleton is needed. The present paper is the first of two papers on the postcranial osteology.

Метнор

The vertebrae of the partially disarticulated skeleton were studied individually and measured with an M5 Wild microscope with the use of ocular micrometers and a goniometer. All the drawings were made by the junior author with a Wild camera lucida. Comparisons were made with material in the American Museum of Natural History collection and with dissected material donated by Hobart M. Smith of the University of Illinois.

VERTEBRAL COLUMN

The vertebral column of *Shinisaurus* consists of at least 65 procoelous vertebrae. There are 23 presacral vertebrae, five or six cervical, 17 or 16 thoracic, and one lumbar. There are two sacral vertebrae and at least 40 caudals. The vertebrae articulate by means of a ball-shaped projection on the posterior face of each centrum which fits into a socket on the anterior face of the following vertebra. Zygantra and zygosphene articulations are absent. Beneath the prezygapophyses and postzygapophyses the walls of the centra are slightly excavated to form a series of intervertebral foramina that run the entire length of the vertebral column. The diameters of these foramina do not vary uniformly throughout the presacral column. They increase in diameter to about the middle of the thoracic region, and then decrease to vertebra 19. After this point, they increase to the lumbar vertebra.

The length of the vertebrae, excluding the axis, increases steadily to vertebra 20 and then decreases up to the sacral vertebrae. Posterior to the sacrum, the vertebrae increase in length. The length of the neural spines, again excluding the axis, decreases up to vertebra 7 and then increases continually throughout the presacral column.

CERVICAL VERTEBRAE

Cervical vertebrae are defined as those anterior vertebrae lacking attachment to the sternum. In the Berlin specimen the sternum was disarticulated from the vertebral column, and it is impossible at this time to determine the exact number of cervical vertebrae. It appears, how-

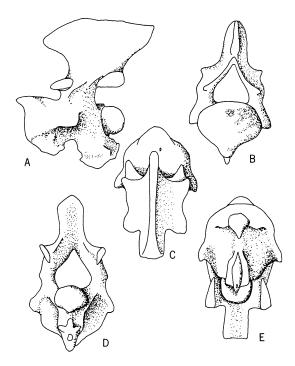


Fig. 1. Axis of *Shinisaurus*. A. Lateral view. B. Anterior view. C. Dorsal view. D. Posterior view. E. Ventral view. ×5.

ever, from our material that there are only five cervical vertebrae in *Shinisaurus*, which is corroborated by our X-ray of the single specimen (A.M.N.H. No. 44928).

The atlas of the Berlin specimen is unfortunately missing. Of the remaining four cervicals (fig. 2D), the last two, vertebra 4 and vertebra 5, bear rib articulations on the sides of the centra ventral to the prezygapophyses. The axis has short transverse processes in this region, but vertebra 3 bears a much more pronounced transverse process. The fifth cervical lacks a hypapophysis, which is present as a slight projection on the posteroventral surface of vertebra 4 and is quite prominent on vertebra 2 and the axis. The neural spines of the cervicals are at an angle of 55 to 60 degrees from a base line drawn through the most ventral part of the condyles and cotyles.

Axis: The axis of *Shinisaurus* (fig. 1) has a very large, compound centrum, the anteriormost part of which represents the atlantan pleurocentrum. This portion is fused without visible suture lines to the axial

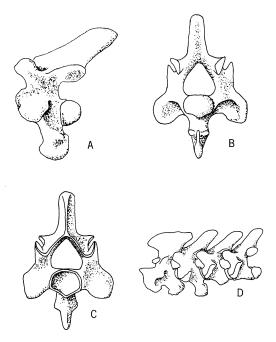


Fig. 2. A-C. Third cervical vertebra of *Shinisaurus*. A. Lateral view. B. Posterior view. C. Anterior view. D. Axis and posterior cervical series of *Shinisaurus*, lateral view. \times 5.

intercentrum and forms the odontoid process which projects into the atlas. The centrum of the axis ends posteriorly in a ball-shaped condyle which articulates with the cotyle of the third cervical vertebra. Anteriorly the odontoid process bears a pointed prominence. The distance from this prominence to the posterior condyle is 6.01 mm.

Two hypapophyses are present on the ventral surface of the axis. The anterior one associated with the odontoid is a small, somewhat flattened structure projecting posteriorly. The second hypapophysis is much larger. It bears prominent anterior and posterior as well as laterally projecting processes. These lateral processes are also present on the third cervical (fig. 2A-C). The axis bears a short, posterolaterally directed, ribless, transverse process. The prezygapophyses are small, ovoid, dorsolaterally projecting processes on the neural arch. The postzygapophyses are somewhat elongated, narrow, ventrolaterally projecting surfaces on the posterior border of the neural arch. The neural spine is developed into a large, elongated crest, poleax in shape, projecting anteriorly as well as posteriorly, with a maximum length of 6.2 mm.

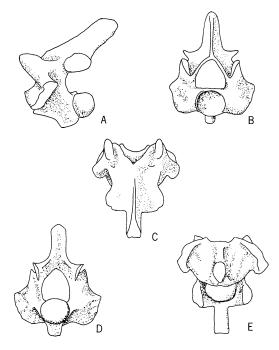


Fig. 3. Fourth cervical vertebra of *Shinisaurus*. A. Lateral view. B. Anterior view. C. Dorsal view. D. Posterior view. E. Ventral view. ×5.

FOURTH CERVICAL: The fourth cervical (fig. 3) can be considered as a typical cervical vertebra. It has a prominent, posteriorly directed, neural spine which overhangs a posterior condyle for articulation with the cotyle of the fifth cervical. Anteriorly it bears a cotyle for articulation with the condyle of vertebra 3. This cotyle is almost round and has a dorsal flattening. The articulating surfaces of the prezygapophyses are nearly vertical in orientation and face toward the medial plane of the vertebra, whereas the postzygapophyses face downward and outward at an angle of about 45 degrees.

Laterally the centrum bears a process, the synapophysis, for articulation with the capitula of the single-headed, short, movable ribs. Ventrally the centrum bears a small blunt hypapophysis which is immediately anterior to the posterior condyle. The hypapophysis is shorter than the diameter of the condyle and bears no lateral processes. A deep groove is present which clearly separates the condyle and the hypapophysis. This is the last cervical vertebra to bear a hypapophysis and the first to bear ribs.

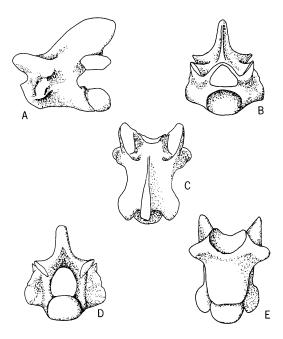


Fig. 4. Typical thoracic vertebra (vertebra 15) of *Shinisaurus*. A. Lateral view. B. Anterior view. C. Dorsal view. D. Anterior view. E. Ventral view. × 5.

THORACIC VERTEBRAE

There are 17 thoracic vertebrae, all bearing movable ribs. In lateral outline the neural spines vary in an anterior to posterior direction. The more anterior vertebrae tend to have neural spines with anterior surfaces that are straight up to the maximum height of the neural spine, where they form a clearly discernible rounded angle with the extreme dorsal border of the spine. This grades into a condition in the more posterior thoracic vertebrae in which the neural spines are broader in the anterior posterior direction and have curved anterior surfaces which join the flat dorsal ridge of the spine without forming a sharply discernible angle. The height of the neural spines decreases posteriorly. The neural spines are at an angle of approximately 70 degrees to the base line drawn through the condyle and cotyle.

The processes for rib articulation (synapophyses) show a marked decrease in prominence posteriorly. The more anterior thoracics have rib articulations that are large, convex, long ridges of bone which protrude markedly from the sides of the centra. These synapophyses are oriented at a fairly constant angle of about 75 degrees from the base line. They

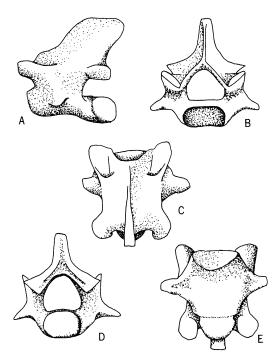


Fig. 5. Lumbar vertebra of *Shinisaurus*. A. Lateral view. B. Anterior view. C. Dorsal view. D. Anterior view. E. Ventral view. ×5.

are ventral, lateral, and posterior to the prezygapophyses. The more posterior rib-articulating surfaces tend to be less prominent, shorter, and slightly rounder elevations. The zygapophyses do not show any major variation throughout the thoracic region.

TYPICAL THORACIC VERTEBRA: Vertebra 15, which is the tenth thoracic vertebra, was chosen as a typical thoracic vertebra of *Shinisaurus* and as such is described here (fig. 4). The vertebra is procoelous and bears a broad neural spine, with a slightly curved anterior border which joins the dorsal border without forming a well-defined angle. The faces of the prezygapophyses are oriented diagonally, facing the medial plane of the vertebra, and are not placed vertically as in the cervical vertebrae. The postzygapophyses face away from the midline of the vertebra and downward. The synapophyseal surfaces are directly posterior, lateral, and ventral to the prezygapophyses and are prominent. They are ovoid, rounded surfaces. Immediately dorsal and posterior to the synapophyses is a mound with an irregularly shaped surface for muscle attachment. The vertebra lacks ventral processes.

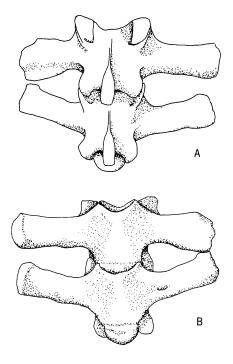


Fig. 6. Sacrum of Shinisaurus. A. Dorsal view. B. Ventral view. ×5.

Lumbar Vertebra

A single lumbar vertebra is present in *Shinisaurus*. It is anterior to the sacral vertebrae, bears laterally projecting, short pleuropophyses which are fused to the synapophysis, and has a neural spine which is shorter than the last thoracic vertebra immediately preceding it. In general form, the lumbar is similar to the last thoracic (fig. 5).

SACRAL VERTEBRAE

There are two completely separate sacral vertebrae. These lack hemal arches and have neural spines that are higher and narrower than those of the more posterior thoracic and lumbar regions. Both sacrals bear large, prominent diapophyses. The diapophyses of the first sacral are thicker than those of the second and are projected more or less at right angles from the centrum. The diapophyses of the second sacral vertebra are less stout and project slightly anteriorly. The diapophyses of both sacrals join distally, but without fusion, for articulation with the pelvic

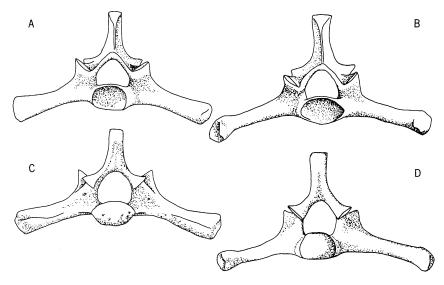


Fig. 7. Sacral vertebra of *Shinisaurus*. A. Anterior view of first sacral vertebra. B. Anterior view of second sacral vertebra. C. Posterior view of first sacral vertebra. D. Posterior view of second sacral vertebra. × 5.

girdle. The condyle of the first sacral is ovoid, rather than round, probably to decrease the possibility of rotation between the two sacrals. The condyle of the second sacral is normally rounded (figs. 6, 7).

CAUDAL VERTEBRAE

The caudal portion of the *Shinisaurus* skeleton is not complete in our material. The first three postsacrals articulate. Following a gap of unknown length there are seven more articulated vertebrae. These are continuous with a series of 13 vertebrae remaining in a segment of undissected tail. The vertebrae in this segment were counted and studied in an X-ray photograph, which revealed that the posterior end of the tail had lost a posterior segment of vertebrae and was undergoing regeneration. This was obvious because of the abrupt termination of the caudal series and the complete lack of vertebrae in the regenerated apex which extends about a centimeter beyond the vertebrae.

We estimate, on the basis of comparisons with X-rays of A.M.N.H. No. 44928, that three or four vertebrae are missing from the gap described after the first three postsacrals. Such an estimate places the typical anterior caudal described below as tenth or eleventh in the post-

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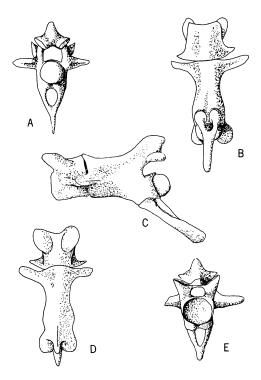


Fig. 8. Typical anterior caudal vertebra of *Shinisaurus* A. Posterior view. B. Ventral view. C. Lateral view. D. Dorsal view. E. Anterior view. × 5.

sacral series. In all, our specimen has 23 caudals, in comparison with the more than 40 caudals of the complete American Museum specimen.

Typical Anterior Caudal: In dorsal view the typical caudal (fig. 8) bears a short, caudally projecting, neural spine. Projecting ventrally and laterally from the neural spine are the postzygapophyses, the facets of which articulate with the upper sides of the prezygapophyses of the succeeding vertebra. Just anterior and ventral to the posterior condyle is a pair of flat facets which articulate with the posteriorly directed, V-shaped, chevron bones. Conspicuous features of the caudal vertebrae are the planes of fracture situated anteriorly on each vertebra. The plane of fracture is one-third of the distance from the anterior end of the vertebra to the posterior end, and completely encircles the vertebra passing through the laterally projecting pleuropophysis. When the vertebra is broken along this point, the craniad portion bears a small anterior piece of the pleuropophysis, and the caudad portion of the vertebra bears the majority of the process, including the area of its greatest width. The neural arch

forms a small spine, the pseudospine, at the plane of fracture. The first three postsacrals lack fracture planes (fig. 11A, B).

Our X-rays show that the tail of the specimen was broken off at the intervertebral joint and not at the plane of fracture, probably because in older lizards the fracture planes ossify and fuse. According to Etheridge (1967) such a fusion occurs in a posterior to anterior direction, so that in an old individual only the anterior part of the tail is capable of autotomy. Thus tension placed on a part of the tail with fused fracture planes could lead to intervertebral separation.

RIBS

Shinisaurus apparently has 19 pairs of movable ribs, none of which was articulated in our specimen. The first two pairs are cervical, and the remaining 17 are thoracic. The cervical ribs are short. Their medial ends are laterally compressed and bear a groovelike concavity on the posterior surface. The anterior surface is convex. The articulating facet on the medial end of the rib is an ovoid, shallow concavity. The thoracic ribs are similar to the cervicals except for their progressive increase in length. Posteriorly the articulating facets of the thoracic ribs become progressively rounder, following the change in shape of the synapophyses on the vertebrae.

COMPARISON OF THE VERTEBRAL COLUMNS OF SHINISAURUS AND XENOSAURUS

CERVICAL VERTEBRAE

According to Barrows and Smith (1947), *Xenosaurus* has six cervical vertebrae, whereas *Shinisaurus* appears to have five. The atlas is missing from *Shinisaurus*, so no comparison can be made with that of *Xenosaurus*. A comparison of the remaining cervicals as well as of the remaining vertebral column leads, however, to some interesting observations.

The axes of Shinisaurus and Xenosaurus are basically alike in general appearance, but they bear several clearly distinguishable differences. The neural spines on each of the axes are hatchet-shaped, with the anterior process of the Shinisaurus spine being more produced anteriorly and projecting beyond the level of the prezygapophyses. In Xenosaurus (fig. 9) the anterior limit of the neural spine reaches just to the level of the middle of the prezygapophyses. The transverse processes of the Xenosaurus axis are more prominent than those of the Shinisaurus axis. Both axes bear two hypapophyses. In Xenosaurus both are equally prominent, with the posterior one bearing a suture line. In Shinisaurus, however, the

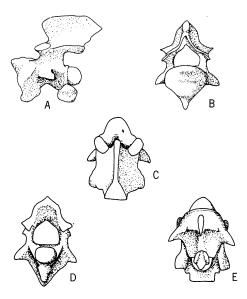


Fig. 9. Axis of *Xenosaurus*. A. Lateral view. B. Anterior view. C. Dorsal view. D. Posterior view. E. Ventral view. × 5.

posterior one is much more prominent and bears no suture line, whereas the anterior hypapophysis is quite flat and has a suture line. Posteriorly, the second hypapophysis of both axes bear transverse processes. In *Xeno-saurus* these are in the form of indistinct swellings; on *Shinisaurus* the processes are well developed into clear projections.

The third cervical of *Shinisaurus* has a large, prominent hypapophysis bearing lateral projections as in the axis, whereas the third cervical of *Xenosaurus* has only a slight keel ending in a small enlargement at the base of the condyle. The transverse processes of the *Shinisaurus* third vertebra are broad and rounded at their ends; the processes of *Xenosaurus* are thinner and come to a point.

The fourth cervical of *Shinisaurus* bears a prominent keel that ends in a definite, knoblike hypapophysis, but the *Xenosaurus* fourth cervical has none. The fourth cervicals of both bear ribs. The fifth cervicals of both species appear to be similar.

THORACIC VERTEBRAE

The number of thoracic vertebrae in our specimen of *Xenosaurus* is 22, agreeing with the description of Barrows and Smith (1947). The number of these vertebrae in the *Shinisaurus* material is 17, a number that ap-

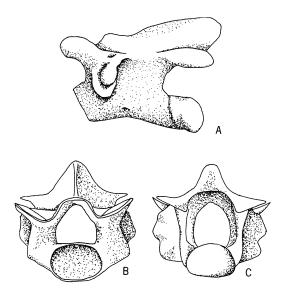


Fig. 10. Typical thoracic vertebra (vertebra 17) of *Xenosaurus*. A. Lateral view. B. Anterior view. C. Posterior view. × 10.

parently disagrees with the roentgenogram published by McDowell and Bogert (1954), which shows 20 thoracic vertebrae. Because our material was already disarticulated, the possibility exists that three thoracics were lost by the original preparator. Our measurements and comparisons of vertebrae, however, do not indicate any gap in the presacral series. The number of vertebrae may possibly vary.

In a comparison of vertebra 15 of Shinisaurus and vertebra 17 of Xenosaurus, the following differences were observed. The neural spine of the Xenosaurus vertebra (fig. 10) is considerably flatter than that of Shinisaurus, which is prominent and angular. The synapophyses of Shinisaurus consist of one large, ovoid mound, dorsoventral in orientation. At its dorsal limit there is a small, valley-like depression above which lies an irregular projection. The synapophyses of Xenosaurus are more complex. They are almost hemispherical in form. The dorsal projection described in Shinisaurus is more prominent, and not as clearly separated from the synapophysis as in Xenosaurus. Below and encircling the ventral half of the synapophysis is a flattened prominence (which may be an articulating surface) which is completely lacking in Shinisaurus (fig. 10A).

LUMBAR VERTEBRAE

Both Shinisaurus and Xenosaurus have a single lumbar vertebra. These

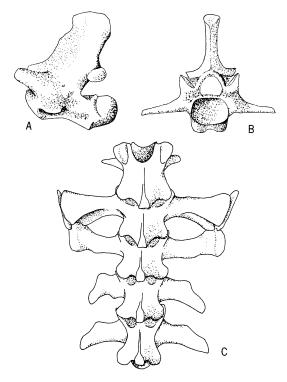


Fig. 11. A, B. Second caudal of *Shinisaurus*. A. Lateral view. B. Anterior view. C. Lumbar, sacral, and anterior caudals of *Xenosaurus*, dorsal view. × 5.

are similar except for the neural spine which is quite prominent in *Shini-saurus* but reduced to a small ridge in *Xenosaurus* (fig. 11C).

SACRAL VERTEBRAE

Both forms have two sacral vertebrae. The sacrum of *Xenosaurus* shows more fusion than that of *Shinisaurus* in that it has the sacral diapophyses well fused distally. The *Xenosaurus* sacrum (fig. 11C) also continues the trend of small neural spines, in contrast to the higher neural spines of *Shinisaurus*. The first sacral diapophysis of *Xenosaurus* is expanded distally and bears a strong dorsal ridge which is not present in *Shinisaurus*. The second sacral dispophysis of *Xenosaurus* is at right angles to the axis of the centrum, whereas in *Shinisaurus* the diapophysis points anteriorly.

Caudal Vertebrae

The number of caudals in Xenosaurus is 37; in Shinisaurus it exceeds 40.

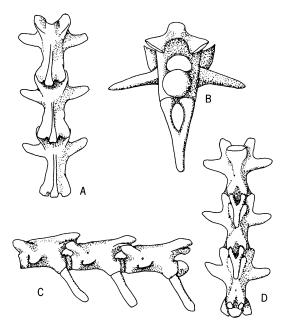


Fig. 12. Caudals of *Xenosaurus*. A, C, D. Vertebrae 8-10. A. Dorsal view. C. Lateral view. D. Ventral view. B. Vertebra 10, posterior view. A, C, D, $\times 5$; B, $\times 10$.

The postsacral vertebrae of the two forms differ in the greater height of the neural spines in *Shinisaurus* and the greater development of the transverse processes in *Xenosaurus* (fig. 12).

A typical caudal vertebra is one that is defined as having a fully developed hemal arch. A comparison of vertebrae so defined reveals striking differences between *Xenosaurus* and *Shinisaurus*. The most important is the presence of autotomous planes of fracture in the vertebrae of *Shinisaurus*. These have previously been reported erroneously as not being present (Etheridge, 1967). An examination of figure 8 reveals that *Shinisaurus* belongs to that group of lizards in which the plane of fracture is anteriorly placed and passes through the transverse process. It is apparent that Etheridge made his determination from the X-ray published by McDowell and Bogert (1954, pl. 7). This plate does not clearly indicate the presence of the fracture plane. Another X-ray taken by us from a different view (fig. 13) clearly indicates that the fracture planes occur in both specimens.

Further differences include the neural spines, which are higher in



Fig. 13. X-ray photograph of the tail of Shinisaurus.

Shinisaurus than in Xenosaurus, and the posterior border of the hemal arches, which come into contact with the posterior condyle in Xenosaurus but not in Shinisaurus.

RELATIONSHIP BETWEEN SHINISAURUS AND OTHER GROUPS OF THE ANGUIMORPHA BASED ON VERTEBRAL MORPHOLOGY

McDowell and Bogert (1954), on the basis of cranial morphology, concluded that Xenosaurus and Shinisaurus are more closely related to each other than either is to other genera of the Anguimorpha. A comparison of Xenosaurus and Shinisaurus reveals significant differences in vertebral plan. Etheridge (1967) has pointed out that caudal vertebral morphology is a good family character and, in the case of large families, an indicator of phyletic lines. We demonstrate above that this vertebral character can be used to differentiate between the genera of the Xenosauridae. As a result, we have attempted a re-evaluation of the systematic position of Shinisaurus based on vertebral morphology alone. An examination of table 1 reveals that, within the Anguimorpha, the lack of tail autotomy and the presence of nine cervical vertebrae remove from consideration the two living families of the Platynota, the Varanidae and the Lanthanotidae. The Helodermatidae may also be eliminated because of the lack of autotomy, although the count of their cervical vertebrae is closer to normal. The mosasaurs and their other marine allies are precluded by their lack of autotomy, their obvious marine adaptations, and their closer relationship to the Varanidae. It is clear that the basic relationship of Shinisaurus should lie within the Diploglossa.

Table 1 shows the great similarity of *Shinisaurus* to the families Anguidae and Xenosauridae. If a numerical analysis is made, comparing the living, limbed groups of the Anguimorpha, it is clear that in vertebral resemblances *Shinisaurus* is closest to the Gerrhonotinae. In fact, if complete resemblances to *Shinisaurus* are scored as 100, and each vertebral character is weighted equally for all the limbed anguimorphs, the following index of resemblance results:

Shinisaurus	100
Gerrhonotinae	73%
Diploglossinae	65
Lanthanotidae	63
Xenosaurus	61
Helodermatidea	59
Mosasauridae	44
Varanidae	36

Limbless groups such as the Annielidae (31%) and the Anguinae

Character a	Shini- saurinae	Xeno-saurinae	Com. Diplo- glossinae	Gerrho-notinae	Comparison of Shinisaurus with the Anguimorpha Gerrho- Anguinae Anniellidae Va	H THE ANGUIMOR	RPHA Varaninae	Heloder- matidae	Lantha- notidae	Mosa- sauridae
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4	+	+	I	ı	I	ı	ı	ı	ı	I
5	S	L	S	S	S	S	S	L	S	ı
9	+	+	+	+	+	I	ı	I	+	+
7	V4	V3	V8+	V4-5	V5	V12	V7-8	V3	9Λ	77
8	V5	V4	V4	V4	V4	V3	V6-7	V4	V4	V_2
6	17	22	26	23	۵.	۵.	19	23–26	26	22-44
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TABLE 1—(Continued)

	Mosa- sauridae	1	*	I	1	۵.
	Lantha- notidae	۵.	۵.	1	I	٠.
	Heloder- matidae	2	+	I	I	1
	Varaninae	1	+	•	1	2
	Anniellidae	Ι	*	+	2	2
(Anguinae	I	*	+	2	2
1	Gerrho- notinae	1	ı	+	2	1
	Diplo- glossinae	-1	+	+	-	2
	Xeno- saurinae	-	+	1	I	1
	Shini- saurinae	2	1	+	2	2
	Character a	15	16	17	18	19

a Characters and symbols: 1. Number of cervical vertebrae. 2. Number of hypapophyses on axis. 3. Largest hypapophysis on axis: A, the first, or B, the second; C, both of equal size. 4. Processes on hypapophysis: +, present; -, absent. 5. Size of transverse processes on axis: S, small;

L, large. 6. Anterior process on axis neural spine: +, present; -, absent. 7. Last cervical vertebra with a hypapophysis. 8. First cervical vertebra with ribs. 9. Number of thoracics. 10. Shape of zygapophyses: R, round; O, oval. 11. Similarity of neural spine series to that of Shini-

saurus: NS, not similar; S, similar. 12. Protuberance above synapophysis: +, present; -, absent. 13. Number of lumbars. 14. Degree of sacral fusion: 1, unfused; 2, slightly fused; 3, strongly fused; -, no sacrum distinguishable. 15. Angle of second sacral diapophysis: 1, rib at right angle to centrum; 2, rib pointing anteriorly; -, sacrum not distinguishable. 16. Enlargement of distal end of first sacral diapophysis: +, present;

-, absent; *, sacrum not distinguishable. 17. Caudal fracture planes: +, present; -, absent. 18. Position of fracture planes: 1, anterior to transverse processes; 2, through transverse processes; --, no fracture planes. 19. Position of hemal arches: 1, touching condyle; 2, not touching condyle. Question marks indicate that the information is not determinable. (52%) score low because of their obvious specialization.

Many of the unique features of the vertebrae of *Shinisaurus* can be found scattered among the Iguania and Scincomorpha, but these are certainly the result of convergence due to adaptations in form and habit.

CONCLUSIONS

The vertebral column of *Shinisaurus* has caudal vertebrae with fracture planes, a short cervical series, and unique hypapophyses and synapophyses. The vertebral morphology is consistent with an anguimorph and diploglossine relationship, but it presents a problem in regard to familial and subfamilial affinities.

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