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Permian Vertebrates from Oklahoma and Texas

Part I.—Vertebrates from the Flowerpot Formation, Permian of Oklahoma

by

Everett C. Olson and Herbert Barghusen

Part II.—The Osteology of Captorhinikos chozaensis Olson

bу

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The University of Oklahoma Norman July 1962

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PERMIAN VERTEBRATES FROM OKLAHOMA AND TEXAS

EVERETT C. OLSON† and HERBERT BARGHUSEN††

ABSTRACT

Part I.—Vertebrates from the Flowerpot Formation, Permian of Oklahoma. A vertebrate fauna from the basal Upper Permian Flowerpot Formation of Kingfisher County, Oklahoma, contains the new amphibian genus and species Cymatorhiza kittsi and the reptiles Rothia multidonta, Cotylorhynchus bransoni, new species, and Angelosaurus romeri, new species. The vertebrate fauna is the youngest yet described from Oklahoma Permian rocks and is comparable to that known from the San Angelo Formation of Texas.

Part II.—The osteology of Captorhinikos chozaensis. Captorhinikos chozaensis is known from the Choza Formation in Texas and from the Hennessey Formation in Oklahoma. On the basis of newly collected specimens the Hennessey form is tentatively assigned to the genus and species and hitherto unknown morphologic details of the genus are described.

PART I. — VERTEBRATES FROM THE FLOWERPOT FORMATION, PERMIAN OF OKLAHOMA*

EVERETT C. OLSON and HERBERT BARGHUSEN

INTRODUCTION

As the result of a discovery of a vertebrate-bearing locality in the middle part of the Flowerpot Formation of Oklahoma by Robert Fay of the Oklahoma Geological Survey in 1959, one of the writers (E. C. Olson) undertook a brief reconnaissance study of the Oklahoma Permian during 1960. David Kitts of The University of Oklahoma acted as guide and made possible a rapid survey of various formations. During this study some additional specimens were obtained from the locality discovered by Fay and also it was concluded that some formations other than the Flowerpot had potentialities for yielding vertebrate fossils. Thus, in 1961, with the support of the National Science Foundation and the aid and encouragement of Carl C. Branson, Director of the Oklahoma Geological Survey, a program of study that will cover several years was initiated. The principal objective of this work is the study of the Upper Permian formations of Oklahoma in the hope of obtaining additional knowledge of the Upper Permian vertebrates of North America. This work is a continuation of a similar study that has been undertaken and will be continued in the Upper Permian formations of Texas to the south.

The present report records the results of the first phase of this study. Much of the field time during the summer of 1961 was spent in a continuation of the assessment of the more profitable ways to study various formations that appeared to be possible sources of vertebrates in earlier work. Excavation of the site discovered by Fay was also undertaken and a few identifiable vertebrates were obtained from a second site which lies close by and at about the same horizon. Excellent materials were obtained from the excavation and less well-preserved, but interesting, specimens came from the second site. This first report is devoted primarily to a description of the vertebrates and an assessment of their significance. In addition, some general remarks upon significant aspects of the Flowerpot For-

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VERTEBRATE SITES

mation are included. This formation is considered as Upper Permian, as are all post-Hennessey formations up to and including the formations of the Quartermaster Group. Under this plan, a two-fold division of the Permian with the line of demarcation at the Leonardian-Guadalupean boundary is used. The earliest formation of the Upper Permian in Oklahoma thus becomes the Duncan-Flowerpot Sandstone, an equivalent of the San Angelo of Texas. As noted later, however, the Duncan-Flowerpot appears to be equivalent in age to part of the lower Flowerpot in areas of the state in which the Duncan-Flowerpot facies are not present.

All the material described herein is on deposit at the Chicago Natural History Museum (CNHM).

THE FLOWERPOT FORMATION

GENERAL CONSIDERATIONS

The name Flowerpot was first applied to beds in Kansas (Cragin, 1896) and later was extended to designate beds of equivalent age in Oklahoma and Texas. In northern and western Oklahoma beds that lie above the Hennessey Formation and below the Blaine Formation are so designated. These are, for the most part, fine clastics and are thus called Flowerpot Shale. Of the same age, in part at least, are the coarser clastic beds of the Chickasha Formation. As commonly used, this name applies to sandstone and conglomerates found in south-central Oklahoma and well exposed in Grady County and the areas immediately to the east of it. The term Chickasha was applied by Gould (1924) to much of what is now called Flowerpot, but this usage has been largely discontinued. The situation is somewhat complicated from geological and nomenclatural standpoints by the fact that a tongue of rather coarse clastics, termed the Chickasha Tongue, extends into the Flowerpot Shale, thinning to the north and west. The deposits of this tongue are well exposed in places in Kingfisher and Blaine Counties in the position in the section indicated in table 1. It is within this tongue that all currently known Flowerpot vertebrates of Oklahoma have been found.

The Flowerpot Shale, including the Chickasha Tongue without distinction, extends diagonally across the State from Woods County on the northwest, where it lies north of the Cimarron River, into Alfalfa County to the east and southeast, through Major County, south of the Cimarron River, through Blaine and Kingfisher Counties, and into Oklahoma and Cleveland Counties, where exposures

are developed west and southwest of Oklahoma City. To the south of the eastern part of the Flowerpot occur exposures of the Chickasha Formation.

In southern and south-central Oklahoma, in Beckham, Greer, Washita, and Kiowa Counties, and extending to the southern border of the State along the Salt Fork of the Red River are the Duncan-Flowerpot beds. This complex is made up of sandstones and shales, roughly equivalent in age to the San Angelo Formation of Texas and, in some sections, similar to the San Angelo beds in sedimentary characteristics. Duncan-Flowerpot and Flowerpot shales make a somewhat irregular contact, with some interfingering, much as do the San Angelo and Flowerpot beds in Texas.

Several of the areas where Flowerpot or equivalent beds are exposed show some promise of yielding vertebrate remains. Scraps of bone have been found in a number of places in the Chickasha Formation, in the upper part of the Duncan-Flowerpot near Hess*, and in several places in the middle Flowerpot in Blaine and Kingfisher Counties. In several widely scattered areas the Flowerpot beds are clearly of terrestrial origin. Rapid lateral and vertical variations are characteristic, with the irregularly bedded, rather coarse sediments of the terrestrial phases giving way to the more evenly bedded, gypsum-bearing deposits of the evaporite facies. These changes indicate a quasi-stable land and sea relationship superimposed upon a generally subsiding, broad deltaic area. The observed depositional irregularities appear to represent shifts of the strand line over relatively restricted areas throughout the period of deposition.

VERTEBRATE SITES

Two sites have yielded vertebrate remains that are sufficiently well preserved to be profitably described. Both are in Kingfisher County. One site is that discovered by Robert Fay and here designated as KF-1. The other, which lies somewhat to the east, is designated as KF-2. Fay has supplied a section compiled for Blaine County but applicable to the sites in the western part of Kingfisher County as well. This section is as shown in table 1.

Site KF-1. — The precise location of this site is NW1/4 NW1/4 NW1/4 sec. 19, T. 17 N., R. 9 W. It lies at a road intersection but a few feet east of the Blaine County line. The bone-bearing layer is described in the section as being about one foot thick.

Southeast Jackson County, Oklahoma.

TABLE 1. — GENERALIZED MEASURED SECTION OF PERMIAN ROCKS IN BLAINE COUNTY, APPLICABLE TO REPTILE SITE KF-1

	Thickness (feet)
Permian System*	
Guadalupean Series:	
El Reno Group: 750 feet thick Dog Creek Shale: 185 feet thick	
Blaine Formation: 100 feet thick	
Flowerpot Shale: 465 feet thick, with middle Chickash	a
Tongue in middle 120 feet. The reptiles are in th	
Chickasha Tongue	•
Upper part Flowerpot Shale:	
Shale, red-brown, gypsiferous; with many greenish	1-
gray beds, and portions of the Chickasha conglome	- !-
ate in lower 30 feet	160
Middle Chickasha Tongue:	
Pfc4** on Blaine County map:	
Siltstone-mudstone conglomerate, moderate reddish	1-
brown, well-indurated; with some light greenish	
gray layers; with interbedded shale, siltstone, an	
fine-grained sandstone; upper portion cross	
bedded, forming a ledge	
Unnumbered portion:	
Siltstone, and shale, reddish-brown, argillaceou	s;
covered in part	14.0
Siltstone-mudstone conglomerate, moderate reddisl	1-
brown, mottled greenish-gray, well-indurate	d,
cross-bedded, lenticular-bedded; grading in	:0
sand-size particles or smaller, in a siltstone ma	t-
rix; with interbedded cross-bedded siltstone an	
fine-grained quartzose sandstone that is micac	
ous, argillaceous, and weakly indurated	
Siltstone, moderate reddish-brown, cross-bedden	
lenticular; with some greenish-gray streaks; grac ing into fine-grained quartzose sandstone wit	1- h
subrounded to subangular grains	
	1.3
Pfc ₃ on Blaine County map: Siltstone, light-greenish-gray, quartzose, argillaceou	e
micaceous, weakly indurated, cross-bedded; forn	3,
ing a prominent light-colored streak in region	
Unnumbered portion:	
Shale, red-brown, silty	6.25
Siltstone, greenish-gray and reddish-brown, argi	
omotone, greenish-gray and reddish-brown, argi	1-

<sup>This table was supplied by Robert O. Fay of the Oklahoma Geological Survey. The map of Blaine County noted was in late stages of preparation at the time this report was being prepared.
Permian Flowerpot-Chickasha Formation as designated on Geologic Map of Blaine County, Okla. Geological Survey, 1961.</sup>

	Thickness (feet)
laceous; weathering into a light-colored band	••
Siltstone, greenish-gray, argillaceous, platy	0.5
Shale, red-brown, silty	3.0
Siltstone, greenish-gray and reddish-brown, argil-	, J.U
laceous, platy	1.0
Shale, red-brown, silty; partly covered	
Siltstone, greenish-gray, argillaceous, platy, weakly indurated	. 0.25
Siltstone, moderate- to dark-reddish-brown, argil- laceous, cross-bedded, well-indurated; with ar occasional greenish-gray band	ı
Siltstone, greenish-gray, conglomeratic, platy, well indurated	-
Shale, red-brown, well-indurated; with some green	•
ish-gray layers	3.0
Siltstone-mudstone conglomerate, mottled reddish brown and greenish-gray; grading into sandstone composed of siltstone-mudstone particles; inter bedded with siltstone, sandstone, and some shall as above.	-
This layer contains the fossil bones	. 1.0
Shale, greenish-gray, silty	
Shale, reddish-brown, silty	1.0
Siltstone-mudstone conglomerate, as above; form	-
Siltstone, light-greenish-gray, platy, cross-bedded	
lenticular	
Shale, red-brown, silty, cross-bedded	. 5.25
Siltstone, greenish-gray, argillaceous, platy	. 0.75
Siltstone, moderate- to dark-reddish-brown, platy with some greenish-gray streaks	' ;
Pfc2 on Blaine County map:	
Siltstone-mudstone conglomerate, reddish-brow and greenish-gray, cross-bedded, well-indurated as above; with interbedded siltstone	n i, 1.0
Unnumbered portion:	
Siltstone and shale, red-brown, platy to blocky	y, 10.0
argillaceousSiltstone, mottled moderate-reddish-brown an	
greenish-gray, cross-bedded, well-indurated Siltstone, greenish-gray, cross-bedded, well-indu	3.0
ated	0.25
Shale, red-brown, silty	
Siltstone, greenish-gray, cross-bedded, well-indu	r-
ated	. 1.0

VERTEBRATE SITE KF-1

	Thickness (feet)
Shale, red-brown, silty, well-indurated	3.0
Pfc1 on Blaine County map: Siltstone-mudstone conglomerate, greenish-gray, well-indurated, cross-bedded, lenticular, as above; mottled reddish brown in places; forming a light- colored bench	4.5
Lower part Flowerpot Shale: Shale, red-brown, silty, blocky; with some thin greenish-gray siltstone beds	185.0 plus
Cedar Hills Member of Hennessey Shale: (180 feet thick Siltstone, light-greenish-gray, argillaceous; mapped as Pch ₅ on map	1.0 plus

Additional work and excavation has shown that the vertebrates were distributed through a thickness of about three feet and that accompanying plant remains extended about a foot below the vertebrate remains. The bone-bearing sediments form a mass with a lenticular cross section, about ten feet across. Figure 1 represents a generalized cross section made during the course of quarrying operations. The body of sediment is linear along its major axis and trends roughly northeast and southwest. It passes under the section-line roads to the north and to the west of the area excavated. Plant remains have been found in the road ditch to the north side of the east-west road, but as yet no bones have turned up in this extension.

Small to moderate-sized fragments of bone, up to about an inch in diameter, are scattered through the sediments of the lens and are particularly characteristic of the conglomerate. Isolated bones are present as well as some articulated materials, including a vertebral column with sixteen vertebrae, a tibia, fibula and hind foot, a pelvis and femur, and a radius, ulna, and partial carpus. The fragments of bone have sharp edges and are not water worn. Single bones and articulated specimens are for the most part in an excellent state of preservation, unbroken, little distorted, and not worn by water action. It is clear that the carcasses were torn apart, perhaps by other animals, prior to deposition; but some flesh, fascia, and tendons must have been present on the articulated elements at the time of deposition. Hardening of the sediments immediately adjacent to some of the bones suggests the presence of organic matter at the time of burial.

All of the specimens probably were locally derived. Both the coarse and fine materials of the conglomerates could have been derived from the beds that this channel deposit cuts. Even the fine sandstones have clay pebbles scattered throughout them so that all

of the sediments are somewhat conglomeratic. Clay-ball conglomerate and breccia predominate but in places large fragments of sand-stone, up to three or four inches long, occur along with the finer clay fragments. Remains of plants are abundant in the sediments and, like the bones, occur in all of the types of deposits present. Remains of conifers are most abundant. Large pieces of stems or branches as much as five feet long and three inches in diameter are present. All are roughly oriented parallel to the long axis of the deposit. The following plants have been identified:* Sphenophyllum gilmorei; conifers, probably of Walchia complex.

Site KF-2. — This site is located east of KF-1 in NE¼ NW¼ NW¼ NW¼ sec. 34, T. 17 N., R. 9 W. Bones occur in a fine conglomerate that ranges between six inches and a foot in thickness and in a fine green sandstone that lies immediately below the con-

Identifications were made by Dr. Serge Mamay of the United States Geological Survey. We take this opportunity to express our thanks to him for this aid.

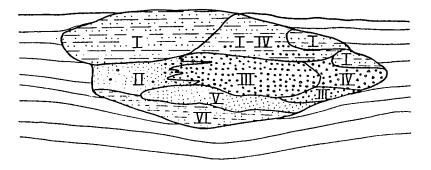


Figure 1. Cross section of the vertebrate-yielding lens at site KF-1, Kingfisher County, Oklahoma. From a sketch prepared during excavation.

- I. Brown to red sandy shale containing a few bones and some plant remains.
- Fine, soft, brown sandstone with scattered clay pebbles. Grading into green sandstone in places and becoming hard in vicinity of bones. Source of better preserved specimens.
- III. Hard brown to red conglomerate. Matrix a mixture of sand and shale, larger constituents include clay pebbles, sandstone pebbles, and small cobbles. Contains scattered fragments of bone and traces of plants.
- IV. Rounded and angular fragments of shale and sandstone in a fine, hard matrix forming a conglonierate and breccia. Red to deep brown in color and in part cemented by silica. Bone fragments, well-preserved ribs, and plant remains present.
- Soft green sandstone with few bones but abundant plant remains, some fairly well preserved.
- VI. Green shale with some sand. Plant remains but no bones.

glomerate. Above and below these beds are sandstones which are irregular, lenticular, and cross-bedded and form a broad shallow lens incised in more typical red and green Flowerpot shales. The coarse clastics are traceable for about one-half mile around the margins of a break made by a small stream. No definite channel deposits are recognizable. The sandstones thicken and thin, reaching a maximum thickness of about ten feet. They suggest deposition in a broad, shallow channel of a major stream. The conglomerate appears to be a sheet formed during a single period of flooding.

The precise stratigraphic relationships between sites KF-1 and KF-2 have not been determined, but it is virtually certain that there is no significant age difference as far as remains of organisms are concerned.

All of the bone in this site is extremely fragmentary. The largest piece, from the green sandstone, measures about three by four inches. One small partial jaw and a cast of three teeth associated with a small fragment of jaw are the only specimens worth description. Macerated plant fragments occur in the conglomerates along with the bones.

Other sites. — Two other sites in this general area have yielded traces of bone but so far have failed to produce identifiable specimens. One of these is close to KF-1, about one and one-half miles to the northwest in Blaine County. It lies on both sides of the sectionline road between sections 11 and 12, T. 17 N., R. 10 W. Here there are extensive channel deposits that cut more typical Flowerpot shales. Bone fragments were found in sandstones and in fine conglomerates. North of Hitchcock, in Blaine County, along the rangeline road between Rs. 10 and 11 W., there is a small exposure of sandstone and conglomerate. This contains fragmentary remains of bones and some plant impressions. Presumably the exposure is part of a channel deposit. Within this general area are several other exposures that contain conglomerates and cross-bedded sandstones which contrast sharply with the more evenly bedded Flowerpot shales. All are possible sources of vertebrates although as yet only those noted above have yielded remains. Study of these deposits has by no means been exhausted in the work carried out to date.

SYSTEMATIC DESCRIPTIONS

CLASS AMPHIBIA

Subclass Lepospondyli Order Microsauria Family Gymnarthridae?

Cymatorhiza, new genus

Diagnosis. — Larger than any other genus assigned to the family Gymnarthridae except for *Pantylus* and possibly some poorly known materials from the Arroyo Formation. A single row of cheek teeth reaching maximum size in the mid-tooth row and diminishing rapidly in size posteriorly. Bases of crowns of teeth roughly quadrilateral. Roots of teeth with ribbed or crenulated roots expressing a labyrinthine-like infolding of the enamel.

Cymatorhiza kittsi, new species* Figure 2

Holotype. — CNHM UR 855, part of a lower jaw with the bases of four teeth and an alveolus for a fifth.

Horizon and locality. — Middle part of the Flowerpot Formation, Upper Permian, in conglomerate at site KF-2, Kingfisher County, Oklahoma.

Diagnosis. - As for genus.

Description and discussion. — The sub-labyrinthodont nature of the roots of the teeth has provided one of the clues to probable affinities of the specimen. The feature is somewhat like that noted by Gregory, Peabody, and Price (1956) in Euryodus Olson. Along with the generally amphibian cast of the jaw, the nature and disposition of the sculpturing of the outer surface, and the sizes of the teeth relative to their positions in the jaw, form the primary basis for tentative assignment to the family Gymnarthridae. With a relatively small fragment such as this, even though it is well preserved, assignment even to class cannot be considered absolutely certain. On the basis of preserved characters, the assignment made here seems by far the most likely of the various possibilities that are open.

The fragment of jaw clearly does not pertain to any genus or species represented by other remains from the Flowerpot Formation

The name Cymatorbiza expresses the wavy character of the roots of the cheek teeth
and the specific name kittsi is given in recognition of the aid and interest of
Dr. David Kitts of The University of Oklahoma in the work of this project.

ROTHIA MULTIDONTA

of Oklahoma or Texas. It does not resemble at all closely any known genus from equivalent beds in Russia or from earlier beds in the Permian of North America. Most of its important features are shown in figure 2. Additional comment is necessary only with respect to a few specific, interrelated characters. The rather smooth, crescentic dorsoposterior termination of the specimen appears to mark the position of a suture where a more posterior bone, presumably the surangular, passed anteriorly under the posterior margin of the dentary. The dentary itself did not rise posteriorly to form part of a coronoid process as it does in some gymnarthrids. Any process that may have been present would have been formed by the coronoid(s), but there is no evidence either of presence or absence of this bone.

Below the smooth posterior termination, the dentary passes anteroventrally in a gentle curve. Much of the surface of this curve is composed of finished bone which appears to mark the dorsoanterior

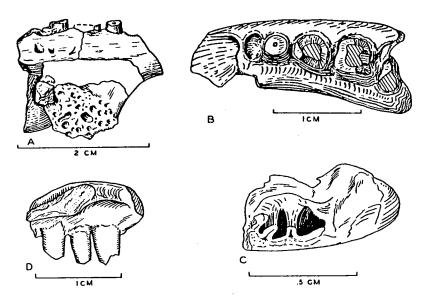


Figure 2.

- A. Lateral view of jaw of Cymatorbiza kittsi, new genus and new species, CNIIM UR 855. Anterior to the right.
- B. Same specimen enlarged to show detail. Dorsal view with anterior to the left.
- C. Same specimen, ventral view of internal structure revealed by break during preparation. The wavy character of the base of the teeth is shown. Greatly enlarged.
- D. CNIIM UR 856, unassigned specimen, see page 44. Drawing of form as shown by cast of natural mold.

margin of a lateral mandibular fossa. It is possible, of course, that there was an osseous cover that left no trace on the bone. Internal mandibular fenestrae are not uncommon in amphibians, but lateral fenestrae are rarely developed. In reptiles, in which they are a common occurrence, such fenestrae tend to be associated with elongation of the adductor muscles to form an insertion well forward of the adductor fossa. It is possibly significant in this regard that in Cymatorhiza a blind recess is medial and slightly anterior to the presumed lateral fenestra. This recess, which is within the body of the jaw, probably was continuous with the adductor fossa and lay in part at least dorsal to the Meckelian canal. It may mark the position of insertion of a somewhat extended adductor which passed forward from the adductor fossa. Entering into this pocket from the front is a small canal, probably for a blood vessel or small nerve. Specialization of the masticatory apparatus as suggested here may be related to the large, strong teeth. Until more complete materials are found, of course, this is largely speculation based on slender evidence.

The only known specimen, UR 855, was found in the sheet of brown conglomerate described in the preceding section. Only one other specimen with definitive characters was found in this bed (see p. 44). A considerable amount of scrap is scattered through the conglomerate but most of it is too broken and worn to give any indication of its identity. No remains that have been found in the conglomerate at KF-2 show resemblances to specimens found at KF-1. The large piece of bone from the green sandstone could be a part of a girdle of one of the large cascids. There is no doubt that deposits at the two sites are roughly contemporaneous and it may be that common genera will be found in the future. Present indications are to the contrary.

CLASS REPTILIA

Subclass EUREPTILIA
Infraclass CAPTORHINA

Order Captorhinomorpha Family Captorhinidae

Rothia Olson and Beerbower

Rothia multidonta Olson and Beerbower Figure 3; plate IA,B

Referred specimens. —

CNHM UR 829. A well-preserved mid-dorsal vertebra.

ROTHIA MULTIDONTA

CNHM UR 830. A partial dorsal vertebra lacking posterior zygapophyses and neural arch.

CNHM UR 831. A partial dorsal vertebra with part of spine and right posterior zygapophysis.

CNHM UR 832. Part of an anterior dorsal vertebra, possibly a posterior cervical, with part of the neural arch and spine, and part of the zygapophyses and transverse processes.

CNHM UR 833. Parts of both sides of the pelvis, lacking top of ilium and part of ischium on each side.

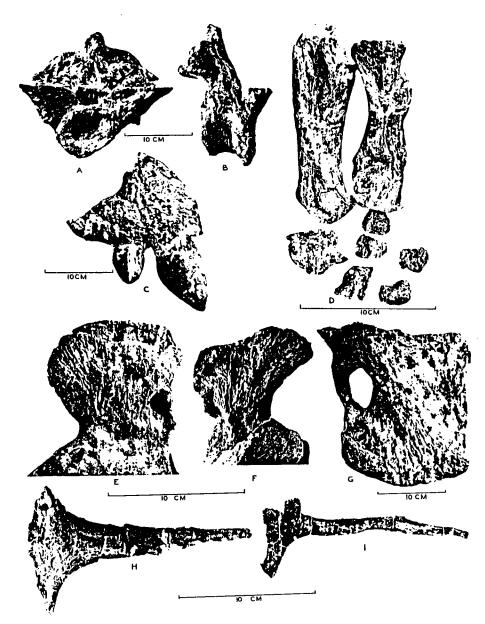
CNHM UR 834. A rib from the mid-dorsal region.

Description and discussion. — All of the specimens listed above were found scattered through various sediments at site KF-1. Specimens were not close enough together to suggest association, but it is by no means unlikely that they have come from a single individual. All of the vertebrae are of much the same size (table 2). Assignment to Rothia poses no problem, for all preserved parts resemble closely those of this genus from the San Angelo and the Flowerpot Formations of Texas. Resemblances are particularly evident in the somewhat peculiar pelvis described later in this section. The Oklahoma specimens are somewhat larger in major dimensions than are those known from Texas (table 2). Size difference, however, is certainly not beyond the range of expected variation of a species, and so cannot be used to separate the members of this genus as now known. There may be some additional differences. For example,

Explanation of Plate I

- A, B. Dorsal vertebrae of Rothia multidonta Olson and Beerbower, CNHM UR 829. A. Anterior. B. Right lateral.
- C. Premaxilla and teeth of specimen tentatively referred to Angelosaurus romeri, new species, CNHM UR 854.
- D. Radius, ulna, and partial carpus of Cotylorhynchus bransoni, new species, CNHM UR 837.
- E. Inner view of top of left ilium of *C. bransoni*, new species, CNHM UR 835.
- F. Inner view of top of right ilium of A. romeri, new species, CNHM UR 844. Compare rib insertions with E.
- G. Astragalus tentatively referred to C. bransoni, new species, CNIIM UR 838.
- H. Interclavicle of A. romeri, new species, ventral aspect, CNHM UR 846.
- Posterior cervical rib tentatively referred to A. romeri, new species, CNHM UR 852.

Plate I



LIST OF ABBREVIATIONS USED IN TABLES 2-4

ant. - anterior

CNHM -- Chicago Natural History Museum

fe — femur

HT - crown height of tooth, measured on outer side

HT_{II} — height of ilium measured from central point on dorsal margin of

HT_{sp} — height of spine of vertebra, measured from dorsal, anterior margin of neural canal

L — length

L — basal length of vertebral centrum

L_{il} — maximum length of ilium measured on dorsal plate in horizontal plane

L maximum length

L_v — ventral length of pelvis measured along medial symphysis

lf — left

mid. — middle

PIN —collection identification, Paleontological Institute, Moscow, U.S.S.R.

post. — posterior

PR — collection identification, Chicago Natural History Museum, paleontology, reptile

rt - right

tib — tibia

UR — collection identification, Chicago Natural History Museum, University (of Chicago) reptile

W - maximum width of anterior zygapophyses

W_{h1} — basal width of tooth, measured longitudinally

W_d — maximum distal width

W_{ne} — minimum width of neck of ilium

W_p — maximum proximal width

 W_{pz} — maximum width of posterior zygapophyses

W_{typ} -- maximum width of transverse processes (pair)

the deep pit on the anterior surface of the neural arch is strong in the Oklahoma specimens and, it would appear, less so in UR 263 from the Texas Flowerpot. This specimen, however, is the only one with which comparison is possible and it has been damaged by distortion and generally is rather poorly preserved. There are also possible minor differences in the pelvis, but again preservation of the Texas material is rather poor. Most of the differences probably can be accounted for either by faulty preservation or by response to increase in size of the Oklahoma specimens. It seems probable that reference to R. multidonta is the proper assignment of these specimens.

The structures of the vertebrae are shown in figure 3 and plate IA, B, and dimensions are given in table 2. The one well-preserved rib measures about 150 mm in arc length (fig. 3C). It has a well-developed holocephalous head and a gently curved shaft. There are no features to distinguish it from the ribs of *Rothia multidonta*.

The pelvis, UR 833, gives considerable information not heretofore available. UR 263, from the Texas Flowerpot, includes a partial pelvis, but evidence was insufficient to interpret what seemed to be a very odd pattern when this specimen was studied alone. The Oklahoma specimen, although incomplete, gives a fair idea of the preserved structures and a reasonable basis for reconstruction of those that are not. After examination of this specimen, the structure of the Texas specimen could be similarly interpreted.

TABLE 2.— MEASUREMENT OF VERTEBRAE OF Rothia multidonta BASED ON SPECIMENS FROM TEXAS* AND OKLAHOMA*

(Measurements in millimeters. Numbers in parentheses refer to the number of vertebrae measured.)

		Do	rsal Veri	ebrae		Cerv	ical Vertebi	ae
	UR 831	UR 830	UR 82	9 UR 263 t	JR 502	UR 832	UR 129 U	R 503
	FPO	FPO	FPO	FPT	SA	FPO	SA	SA
W_{az}		53(1)	55 ⁽¹⁾	36-38 ⁽³⁾	36 ⁽¹⁾		27-29 ⁽³⁾	36 ⁽¹⁾
W_{pz}	50 ⁽¹⁾		53(1)	39-43 ⁽³⁾	38(1)	43 * * (1)	31-32 ⁽³⁾	30(1)
L_c		14(1)	15(1)	13-14(5)			13-14 ⁽³⁾	

^{*}Abbreviations: SA, San Angelo Formation, Texas; FPT, lower part of Flowerpot Formation, Texas; FPO, middle part of the Flowerpot Formation, Kingfisher County, Oklahoma.

^{• •} Approximate.

A reconstruction of the pelvis based on UR 833 is shown in figure 3A,B. The most striking feature is the lateral flare of the pubes, which together form a broad anteromedially facing plate. The leading edges of the pubes pass laterodorsally from the symphysis, with the lateral component greater and nearer to the horizontal than is characteristic of most tetrapods at this stage in vertebrate evolution. Ascending dorsomedially and somewhat posteriorly from this margin is the anterior rim of a large acetabulum. The entrance to the long obturator canal is present on the anteromedial face of the pubis. The canal issues through the obturator foramen beneath the anterior part of the acetabulum. Coincident with the pubic modification has been the development of a strong, deep symphysis at the junction of

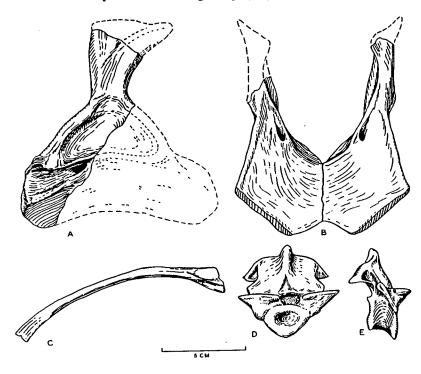


Figure 3.

- A, B. Pelvis of Rothia multidonta Olson and Beerbower, CNHM UR 833.
 Restored areas shown by dotted lines. A. Lateral. B. Anterior, showing broad pubic plate.
- C. Dorsal rib of R. multidonta Olson and Beerbower, CNHM UR 834. From about same level as vertebra in D and E.
- D, E. Dorsal vertebra of R. multidonta Olson and Beerbower, CNHM UR 829.
 D. Anterior. E. Left lateral.

thick descending ridges on the inner side of the pubes. Posterior to this, it would appear, the ischium participated in the symphysis as shown in the restoration. On the outer surface of the pubis, passing anteriorly and somewhat lateroventrally from just below the opening of the external obturator foramen is a strong ridge which more or less divides the surface of the pubis into two areas.

The acetabulum is terminated dorsally by a small, rather weak buttress. Above this rises the slender neck of the ilium. The iliac blade is not completely preserved, but it clearly was slender and probably had a rather modest posterior process. The structure of the pelvis indicates that there was a rather strong modification of the musculature, especially of the pubo-ischiatic-femoralis internus (anterior portion) and of the abdominal muscles. The femur is known in Rothia multidonta from UR 263 from the Texas Flowerpot. It is very small for an animal of the size indicated by other elements of the skeleton. From the Captorbinus-Labidosaurus level of the Arroyo Formation, through Captorhinikos, as known in specimens not as yet described, to Rothia, there appears to have been a steady and rather rapid decrease in the relative size of limb bones. This is true for the forelimb as well as for the hind, for in UR 129 from the San Angelo, the humerus is remarkably small in proportion to body size. It is probable that the modifications of musculature noted above are related to this proportional change, but the nature of the relationship is not clear from the materials at hand.

Order PELYCOSAURIA Family CASEIDAE

Cotylorbynchus Stovall

Cotylorbynchus bransoni, new species*
Figures 4A,B, 5, 6A,C; plates ID,E,G, IIA,C-E

Holotype. — CNHM UR 835. Left side of the pelvis, left femur, partial sacral rib.

Horizon and locality. — Middle part of Flowerpot Formation, Upper Permian, site KF-1, Kingfisher County, Oklahoma.

Referred specimens. --

CNHM UR 836. Right tibia and fibula, tarsus, metatarsus, phalanges except for unguals.

The species is named for Dr. Carl C. Branson, Director of the Oklahoma Geological Survey, in recognition of his aid and interest in the program of study.

CNHM UR 837. Left radius and ulna and part of carpus.

CNHM UR 838. Flattened left astragalus. Reference tentative.

CNHM UR 839. Immature left tibia.

CNHM UR 840. Poorly preserved left fibula of somewhat immature individual.

CNHM UR 841. Part of left maxilla with two cheek teeth.

CNHM UR 842. Two fragments of an ungual phalanx.

CNHM UR 843. Ungual phalanx.

Diagnosis.—A species of Cotylorhynchus of approximately the same over-all size as C. romeri Stovall, but differing in proportions, particularly proportion of limb bones (table 3). Pelvis with high iliac blade. Radius and ulna relatively slender and short. Femur with slender shaft. Astragalus with very large foramen. Maxillary teeth with distinct, longitudinal, tricuspid pattern, similar to that of C. hancocki Olson and Beerbower, but more highly developed than in comparable teeth of that species.*

Description and discussion. — Most of the referred specimens can be placed in C. bransoni with little question. It is probable that UR 835, UR 836, UR 837 and UR 841 are all parts of the same individual. They were not, however, found in articulation and thus association cannot be demonstrated. The partial forelimb, UR 837, may well be from a smaller individual, but the size difference is not sufficient to preclude the possibility that it also came from the same individual. The immature tibia, UR 839, and fibula, UR 840, are clearly from one or two other individuals. The two ungual phalanges probably belong to the species on the basis of their size and general Cotylorhynchus-like structure. Affinities with Angelosaurus are also possible. More problematic is the astragalus, UR 838, which has only a general resemblance to the astragalus of UR 836. The presence of the large foramen, which is an unusual feature in astragali, suggests that this is C. bransoni, but this can be accepted only if rather extensive crushing of a type rather difficult to envisage is assumed. Because there are no other genera or species in the deposit to which this specimen could pertain and because UR 836 is unlike the

astragalus of any other known tetrapod of this time, tentative assignment to C. bransoni has been made.

C. bransoni is readily distinguished from C. romeri of the Hennessey by the well-developed cuspate pattern of the cheek teeth and, somewhat less easily, by proportions of various parts of the skeleton. Separation from C. bancocki is similarly possible on the basis of proportions but is more readily done by the marked size difference. Bases for these differentiations can be found in table 3. Details that are of interest in themselves or applicable to species determination are presented in the following paragraphs.

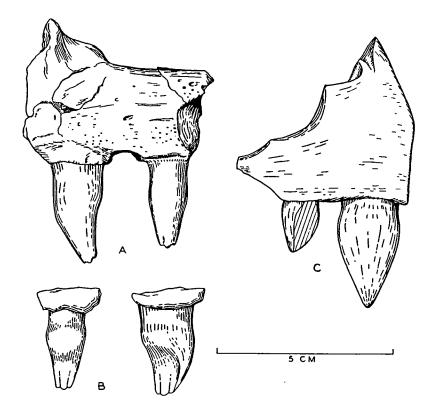


Figure 4.

- A. Lateral view of partial maxilla and two teeth of Cotylorhynchus bransoni, new species, CNHM UR 841. Anterior to left.
- B. Two teeth of C. bransoni, new species, same specimen as A but inner view with posterior tooth to left and anterior to right.
- C. Premaxilla and teeth of a specimen tentatively referred to Angelosaurus romeri, new species, CNHM UR 854.

C. hancocki Olson and Beerbower was described from a humerus from the San Angelo Formation (Olson and Beerbower, 1953). A complete description is now in press (Olson, 1962). Pertinent elements are illustrated, discussed or presented in tables in this paper.

TABLE 3.— MEASUREMENTS OF Cotylorhynchus bransoni, NEW SPECIES,
AND COMPARABLE MEASUREMENTS OF OTHER SPECIES OF
Cotylorhynchus AND Ennatosaurus AS AVAILABLE
(Measurements in millimeters)

		Теетн	Ennatosaurus tecton
	C. bransoni UR 841	C. hancocki C. hancocki C. hancocki UR 489 UR 642 UR 490	PIN
	Ant. Post.	UR 489 UR 642 UR 490 Ant. Post. Ant. Post. Ant. Post.	1580/19(1) Ant. Post.
W _{bl}	10.2 8.3	7.9 9.1 10.1 7.5 6.8	8.5 8.2
HT _e	19.1 16.9	18.0 26.0 22.0 18.1 15.0	17.0
		LIMB BONES	
		Radius	
	C. bransoni UR 837	<i>C. hancocki</i> UR 571 UR 581 UR 621 UR 622	C. romeri PR 272
L_{max}	127	195 210 231 249	137
		Ulna*	
	C. bransoni UR 837	C. hancocki UR 249 UR 567 UR 571 UR 581 UR 623	C. romeri PR 272
L_1	123	178 210 191 190 216	155
L_2	158	299 281 310	208
		Femur	
	C. bransoni UR 835	<i>C. hancocki</i> UR 581 UR 488	C. romeri PR 272
$L_{_{\mathbf{max}}}$	249	400 488	305
$W_{\mathbf{p}}$	97	188	126
$\mathbf{w}_{\mathbf{a}}^{r}$	90	120	100
W _p /L	.38	.47	.41
W_{d}^{\prime}/L	.36	.30	.33

^{*}L1 - to base of notch

(Continued on next page)

TABLE 3. — Continued

		Tibia	
	C. bransoni UR 836	C. hancocki UR 581 UR 622	C. romeri PR 272
L_{max}	155	255 250	127*
W _p	87		
$\mathbf{W}_{\mathbf{d}}^{\mathbf{r}}$	62		
L _{max} (t	(ib) .62		.42
		Fibula	
	C. bransoni UR 836	<i>C. bancocki</i> UR 581 UR 622	C. romeri PR 272
\mathbf{L}_{\max}	171	267 260	174
W**	51	63 72	40
W**	74	102	83
		Pelvis	
	C. bransoni UR 835	C. hancocki UR 581 UR 703	C. romeri PR 272
L	310 (approx)	380 390 (approx)	240
HT _{ii}	100	130	78
W _{ne}	66	123	85
L	101	210	110

^{*}This specimen has a short and broad tibia, much shorter than the fibula

L₂ - maximum length including olecranon

[•] Dimensions somewhat increased by crushing, not entirely reliable for comparisons

1. Maxilla and teeth (fig. 4A,B). — The preserved fragment of maxilla lies under the posterior margin of the naris and includes a small portion of the orbito-narial bar. It shows no features that are not common to all species of Cotylorhynchus. The two preserved teeth are separated by an alveolus for a third. The longitudinal cusp pattern is well developed on both teeth, somewhat better developed than in comparable teeth of C. bancocki. The more anterior tooth has a relatively broad base, a well-developed waist, and a slender, curved continuation of the crown. The cusp pattern resembles that of teeth that lie somewhat farther back in the cheek-tooth series of C. hancocki. The shape is somewhat more like that found in comparable teeth of Ennatosaurus tecton Viushkov of the Russian Permian. The more posterior tooth is rather comparable in shape to teeth at about the same position in the tooth row in C. hancocki. The internal grooves that pass toward the base of the crown from between the cuspules are distinctly more prominent in C. bransoni.

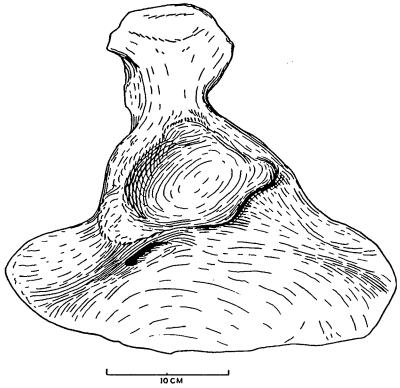


Figure 5. Left side of pelvis of Cotylorbynchus bransoni, new species, seen from outside, CNHM UR 835.

2. Forelimb (fig. 6A; pl. ID). — Only a somewhat distorted radius and ulna and a few carpal elements have been recovered. The degree of ossification of the limb bones suggests that these pertain to a mature individual. The carpal elements seem, on casual inspection, to be immature, but the lack of finished bones on some of them is the result of weathering rather than original absence. The radius and ulna, as shown in table 3, are small as compared to the tibia and fibula of the hindlimb, UR 836. This size difference is not encountered in other species and, although it may be a characteristic of C. bransoni, it seems at least as probable that the forelimb and hindlimb have come from different individuals. The radius and the ulna, as far as can be determined, are typically caseid. The sigmoid notch of the ulna has a strongly sloping surface, which passes distally toward the radial facet. Scars for insertions of tendons are well developed. There are, however, no clear distinctions from other species of Cotylorbynchus evident in these bones.

The positions and shapes of the carpal elements are shown in figure 6A. The ulnare is well preserved but the other elements are not. The positions have provided the chief basis for identification. The element identified as intermedium has little of its original shape preserved. Presumably it was considerably larger than shown. The posterior centrale is a square element and has retained a well-ossified surface. Distal 4 is large and strongly ossified. It appears to have been rotated about sixty degrees from its articular position. Distal 3 is not well preserved. The bone designated as the anterior centrale occupies a position that admits the possibility that it is distal 2, but this calls for the disappearance of the anterior centrale, an element present in other species of *Cotylorbynchus*.

- 3. Pelvis (fig. 5; pl. IIA). The left side of the pelvis is excellently preserved in UR 835. The only distortion is a slight flattening. The main features are shown in the figures and plate, and the dimensions are listed in table 3. The strong development of the ilium, which rises as a blade above the acetabulum, is the principal feature of interest. The anterior part of the iliac blade lies above the level of articulation of the sacral ribs, but posteriorly the third sacral rib was attached at the level of the top of the blade. A rather different condition is noted in Angelosaurus romeri, new species, on p. 39 of this paper. Scars for the three sacral ribs are well shown, indicating a condition somewhat more like that of C. bancocki than of C. romeri.
- 4. Femur (pl. IIC). A well-preserved femur is associated with the pelvis, UR 835. It is a rather long and slender bone and is distinctly smaller in all major dimensions than the femur of *C. romeri*.

This apparently represents a major difference between the two species and it becomes increasingly clear when comparisons to pelvic measurements are added. The femur of C. bransoni is much smaller, more slender, and longer shafted than that of C. bancocki.

Ossification is strong, and muscle and tendon scars are prominent. The intertrochanteric fossa is deep and the popliteal space is well developed. The fourth trochanter lies far down the slender shaft

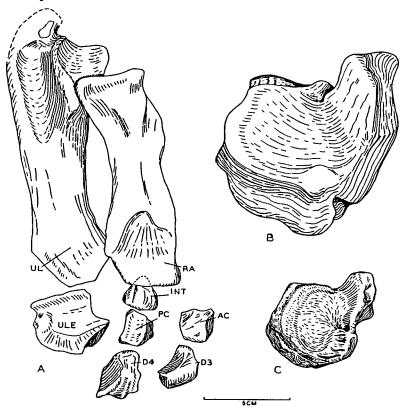


Figure 6.

- A. Radius, ulna, and part of carpus of Cotylorhynchus bransoni, new species,
- Astragalus of C. hancocki Olson and Beerbower, CNHM UR 581, dorsal
- C. Astragalus of C. bransoni, new species, CNHM UR 836. Dorsal aspect.

AC - anterior centrale D3, D4 — distals as numbered PC - posterior centrale

RA — radius INT - intermedium

UL - ulna

ULE - ulnare

and there is no appreciable adductor ridge. The distal condyles are widely spaced. As in C. romeri and C. hancocki, there is a distinct shelf developed on the proximal part of the anterior surface, and, as in C. bancocki, this platform is isolated from the dorsal surface of the femur by a slightly overhanging shelf. Presumably this flat, platform-like area marks the position of insertion of a large, but fleshy, adductor.

Distally, over the anterior part of the intercondylar groove and the posterior part of the anterior condyle, a prominent projection extends distally well beyond the level of the condyles. This is a strongly developed ridge or shelf of the type that is found in less prominent guise in other species of Cotylorhynchus and in some other caseids and edaphosaurids. Dorsally in C. bransoni it forms a flat, somewhat ovoid table that is marked by strong rugosity. This table tapers proximally into a strong, smooth ridge that passes about one-third the total length of the shaft toward the head. Presumably this projection and accompanying structures served for the origin of strong extensors of the crus.

- 5. Tibia (pl. IID). The tibia, known from UR 836 and UR 839 (immature) is typically caseid in the possession of a large, double head and a somewhat inflected distal articular surface. The length, as shown in table 3, is greater than that of C. romeri, in strong contrast to comparative femoral lengths. That this may be in part the result of poor preservation in the available specimen of C. romeri is suggested by the fact that fibular measurements for the two species do not show a similar discrepancy. The tibia of C. bransoni, even if the tibial measurement of C. romeri is distorted, is without any question proportionately great with respect to femoral length as compared to the proportional condition in C. romeri. This would not necessarily follow, of course, if the limb and foot, UR 836, and the femur, UR 835, do not actually belong to the same individual. In this particular case, however, the condylar dimensions of the femur and tibia match to produce an almost perfect articulation and individual identity is not crucial.
- 6. Fibula (pl. IID). The fibula is a rather long, slender bone, known at present from two specimens, UR 836 and UR 840 (probably immature). The proximal articular facet is extremely well ossified, so much so that it is reminiscent of the sigmoid notch and olecranon process of the ulna. Rugosities for tendon origins and insertions are prominent on the proximal part of the bone. Flexor musculature appears to have been strong and tendinous.
 - 7. Tarsus and pes (fig. 6C; pl. IID). These structures are pre-

served in UR 836. The tarsus is either complete or nearly so, possibly lacking one element. The pes, however, lacks the ungual phalanges. Two unguals, UR 842 and UR 843, probably pertain to the species as noted earlier. The foot in *C. bransoni*, like that of other species of *Cotylorhynchus*, is massive, broad, and short. Rugosities for tendons are strongly developed. Many of the important features of the foot are shown in the illustrations; some need special mention.

The articular surfaces of all of the elements are well ossified, although, of course, all carried a modest cartilaginous cap. The calcaneum had strong articulation with distal 4, but distal 5 is weak, probably vestigial. The calcaneum and astragalus probably were closely appressed in life. Neither carries the usual notch that produces a foramen between them. Instead, there is a large foramen in the astragalus. Passing near the medial margin of the bone, a strong channel leads into the foramen. This feature has not been identified in other species of *Cotylorbynchus*.

The medial centrale is fairly large, well ossified, and thin. As the elements have been identified (pl. II), no lateral centrale is present. There is, however, a space in which it might have been present, perhaps in cartilaginous state. Probably it was either unossified or was lost during preservation, for this bone is present in other species of Cotylorhynchus. Distals 1 through 4 are fairly large, with the fourth particularly strong. The metatarsals decrease in size from the fifth to the first. The first, in fact, is so short that in dorsal aspect it shows little of the dumbbell shape seen in the other toe bones.

Explanation of Plate II

- A. Left side of pelvis of Cotylorhynchus bransoni, new species, CNHM UR 835.
- B. Left femur of Cotylorhynchus romeri Stovall, CNHM PR 272, for comparison with C.
- C. Left femur of C. bransoni, new species, CNHM UR 835.
- D. Tibia, fibula, and hind foot of C. bransoni, new species, lacking terminal elements of phalanges. Shown as best preserved, in ventral aspect. CNHM UR 836.
- E. Left femur of C. bransoni, new species, in ventral aspect, CNHM UR 835.
- F. Posterior dorsal rib of Angelosaurus romeri, new species, CNHM UR 851.
- G, H, I. Dorsal ribs of A. romeri, new species, CNHM UR 848, 847, 849 respectively. (See figure 7 for head configuration.)

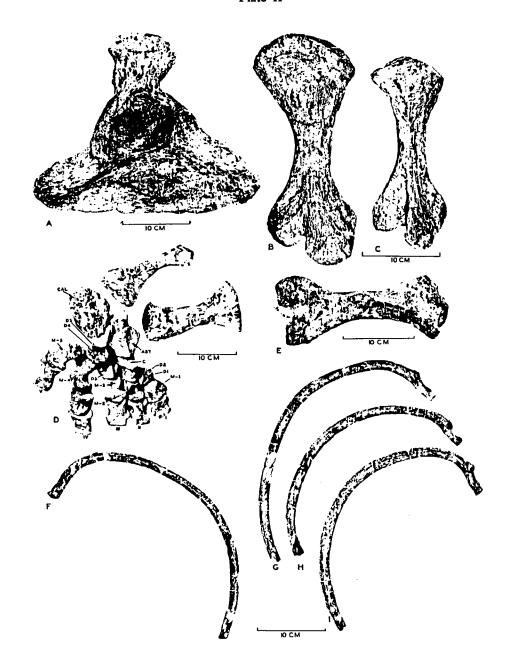
AST — astragalus
C — centrale

D1 — distals of tarsus, as numbered M-1 — metatarsals, as numbered

CAL — calcaneum

I — phlanges, as numbered

Plate II



ANGELOSAURUS ROMERI

Beyond the metatarsals only one element is preserved except in the fourth toe, in which there are two. It is, of course, not possible to be entirely certain of the phalangeal formula under this circumstance. Each of the most distal preserved elements is marked by a deep facet on the anterior and posterior margins adjacent to the articular surface for the more distal element. No such feature is present on the metatarsals or on the phalanx of the fourth toe immediately distal from the metatarsal. This structure probably is associated with strong tendons to the heavy, claw-like unguals. Adjacent to the pits, on the unguals, are strongly swelled, rugose areas marginal to the articular surfaces. If this interpretation is correct, then each of the preserved bones which contains the pair of facets lies immediately proximal to the ungual, and the phalangeal formula is 22232. The forefoot of C. romeri has a formula 22332. The hindfoot of C. bancocki shows three elements in the fourth toe and the positions of preserved elements of the second and third suggests a formula of -223-.

The unguals referred to this species are similar to those of other species of Cotylorhynchus, except for size. A prominent boss on the medioposterior part of the ventral surface, evidently marking the position of insertion of a strong tendon, presumably is part of the deep flexor system of the foot.

Angelosaurus Olson and Beerbower

The genus Angelosaurus Olson and Beerbower was based upon a partial skeleton from the middle part of the San Angelo Formation, Upper Permian, of Knox County, Texas (Olson and Beerbower, 1953). It was assigned to the family Caseidae, a placement which additional information has confirmed. CNHM UR 149 was designated as the holotype of A. dolani Olson and Beerbower. In 1954 other specimens of the genus were found in the basal part of the Flowerpot Formation, Alexander Ranch, Knox County, Texas. Remains were fragmentary, largely as the result of serious chemical decomposition after burial. The best specimen, UR 257, has been established as the holotype of a second species, described elsewhere (Olson, 1962). For the present it will be called Angelosaurus sp. In 1958, a second specimen of A. dolani was found about one hundred yards from the site of the holotype of this species. Two specimens, which proved to be Angelosaurus, were discovered in the course of reconnaissance studies of the Oklahoma Permian cited in the introduction. In 1961, additional specimens were taken from the same site, designated in this paper as KF-1. These have proved to represent a third species as described in the following paragraphs. Angelosaurus romeri, new species Figures 4C, 7A-D, 8A, 9B; plates IC,F,H,I, IIF-I, IIIA-F

Holotype. — CNHM UR 827. Pelvis, right femur, 16 presacral, 3 sacral, and 4 caudal vertebrae. Ribs associated with 5 posterior presacral vertebrae and chevrons associated with two caudal vertebrae, probably numbers 7 and 8.

Horizon and locality. — Middle part of Flowerpot Formation, Upper Permian, site KF-1, Kingfisher County, Oklahoma.

Referred specimens (horizons and localities same as for holotype).—

CNHM UR 828. Two sacral and 2 presacral vertebrae articulated in series. Associated ribs.

CNHM UR 844. Right side of pelvis with most of ischium missing.

CNHM UR 845. Right pubis.

CNHM UR 846. Interclavicle.

CNHM UR 847. Anterior dorsal rib.

CNHM UR 848. Mid-dorsal rib.

CNHM UR 849. Mid-dorsal rib.

CNHM UR 850. Anterior dorsal rib.

CNHM UR 851. Posterior dorsal rib.

CNHM UR 852. Cervical rib.

CNHM UR 853. Four anterior caudal vertebrae.

CNHM UR 854. Fragment of snout with two teeth (reference uncertain).

Diagnosis. — Pubis and ischium forming a broad, somewhat saddle-shaped plate with strong median symphysis. Sacral ribs blade-like and almost completely separated from each other at articulation with ilium. All three sacral vertebrae ankylosed. Femur with internal trochanter developed approximately halfway between proximal and distal limits of the intertrochanteric fossa. Fourth trochanter prominent, with marked drop-off to slightly developed adductor ridge.

Description and discussion. — Much of the description is based upon the holotype, which is excellently preserved and reveals much of the osteology now known. Referred specimens add some additional bones, such as the interclavical and the thoracic ribs, and give some supplemental detail to the data available from the holotype.

1. Vertebrae and ribs (fig. 7; pls. IIF-I, IIIA,B). — Vertebrae are typically caseid with sacrals, lumbars, and thoracics characterized

TABLE 4. — MEASUREMENT OF Angelosaurus romeri, New Species, and Comparable Measurements for Other Species of Angelosaurus as Available

(Measurements in millimeters)

	A. romeri (ft) UR 827	A. dolani (tt) UR 149	A. sp. (rt) UR 257
L	165	216	260
W	71	92	105
$\mathbf{W}_{\mathbf{d}}$	72	83	128
		Pelvis	
	A. romeri UR 827	A. romeri UR 844	A. dolani UR 149
HT	70	76	
\mathbb{W}_{ne}	40	43	60
L_v	144 (approx)		195

RIB-LENGTHS

	Sac	rals		Lu	mbars	i		Thorac	cics	Cervi- cal
	2	1	1	2	3	4	5	Post. Mid	Ant.	Post.
A. romeri UR 827		58	82	110	171	265	320			
A. romeri UR 828	48	50	70+	60+						
A. dolani UR 149	51	60								
A. romeri UR 851								490		
A. romeri UR 848								470	1	
A. romeri UR 847									430	
A. romeri UR 852			(Con	tinued o	n nexi	page,)			145

TABLE 4. — Continued

PRESACRAL VERTEBRAE*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
A. romeri																
UR 827 W _{pz}	50	48	38	37	33	29	28			20		20	19	21	22	
Wtvp												78				
HT _{sp}												22				
L _c						40						33				
A. romeri																
UR 828 W _{pz}	44	42														
W _{tvp}	••															
HT _{sp}	31	30														
L _c	27	31														
<i>A. dolani</i> UR 149																
W_{pz}		57		54								39				
W _{tvp}												108				
HT _{sp}																
L _c	39	39										39				

(Continued on next page)

TABLE 4. - Continued

SACRAL AND CAUDAL VERTEBRAE

	S	acra	ls					Cau	dals				
	1	2	3	1	2	3	4	5	6	7	8	9	10
A. romeri UR 827													
$\mathrm{HT}_{_{\mathrm{sp}}}$	35	32	32							21	19	18	
L _e	26	27	31							25	23	23	22
A. romeri UR 828													
HT _{sp}	30	38											
L _c	38	41											
A. romeri													
UR 853 HT _{sp}							27			20			
L _c							16	19	20	22			
A. dolani													
UR 149		27											
$\mathrm{HT}_{\mathrm{sp}}$		37											
L_{c}	35	48	}	35		33	32	30	30				25

^{*}Sacrals numbered 1-3, anterior-posterior; caudals numbered 1-10, anterior-posterior.

by short neural spines with flattened tops, moderately widely spaced zygapophyses, and short, broad centra without pronounced keels. At the anterior and posterior ends of the sacral series there are large, well-preserved intercentra. It appears probable that intercentra were fused into the sacral complex between the centra of the first and second and the second and third sacral vertebrae.

The transverse processes on the presacral vertebrae are relatively short in the lumbar region and increase slightly in length anteriorly (table 4). In the lumbar series, here considered as comprising the first five vertebrae anterior to the sacrum, the ribs are fused to the transverse processes, although the junctions of the processes and the

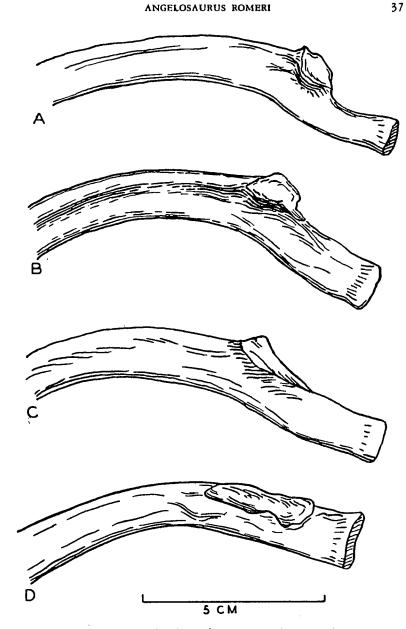


Figure 7. Four ribs of Angelosaurus romeri, new species.

- Anterior dorsal, CNIIM 847.
- B, C. Mid-dorsals, CNHM UR 849, 848 respectively.
- Posterior dorsal, CNHM UR 851.

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heads of the ribs can still be seen. Anteriorly, the transverse processes reach their maximum extent at about the eighth thoracic anterior to the lumbar series. Facets for the capituli of the ribs are developed on the anterior margins of the centra.

Caudal vertebrae decrease rather rapidly in size posteriorly. Neural spines become increasingly deflected posteriorly and zygapophyses become more closely spaced. Chevron bones occur on vertebrae identified as the seventh and eighth caudals in the holotype.

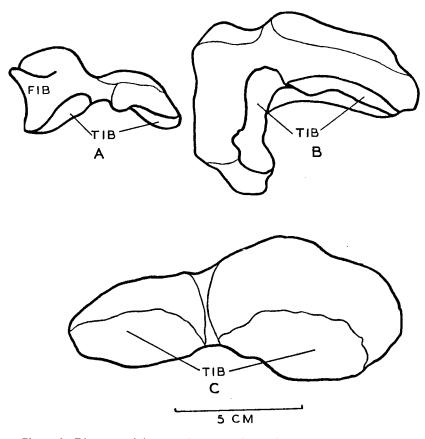


Figure 8. Diagrams of femora of species of Angelosaurus in distal aspects to show articular surfaces for tibiae.

A. A. romeri, new species, CNHM UR 827.

B. A. dolani Olson and Beerbower, CNHM UR 149.

C. A. sp., CNHM UR 257.

FIB - articulation of fibula TIB -- articulation of tibia

Presacral ribs are long and curved in typical caseid fashion. The most posterior lumbar rib is rather short and but little curved. There is rapid increase in length and curvature so that the fifth lumbar rib is nearly as long as the posterior thoracics and is strongly curved. Because the five lumbars are fused to the vertebrae, there is no problem of their identification. The other ribs that have been identified as pertaining to Angelosaurus romeri were not in direct association with the vertebrae. They are similar to ribs found in other caseids, in particular Cotylorhynchus. On the basis of size, they seem to belong to Angelosaurus romeri, but the possibility that they are actually from Cotylorbynchus remains.

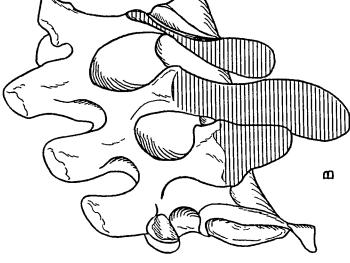
The heads and necks of the thoracic ribs, with indications of their probable positions, are shown in figure 7. Arc length measurements are given in table 4. The full ribs are shown in plate IIF-1.

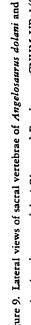
There are three large sacral ribs. The second sacral is the largest, and its articulation with the ilium is more extensive than is that of the others, reaching ventrally approximately to the level of the upper margin of the acetabulum. The anterior and posterior sacral ribs are strong and there may be slight fusion between the second and third. The lateral views of the terminations of the sacral ribs. shown in figure 9, give a basis for visual comparison of the conditions in A. dolani and A. romeri, illustrating one of the features in which they differ rather strongly.

2. Pelvis (pls. IF, IIIE,F). — The pelvis of the holotype is the best preserved specimen, but UR 844 and UR 845 add some details and give some concept of the variation. The blade of the ilium is relatively high for a caseid. It flares somewhat more posteriorly than anteriorly above the neck, but is less extended posteriorly than is the case in most non-caseid pelycosaurs. The ilium of A. dolani, in the one specimen in which it is known, is poorly ossified and thus somewhat difficult to compare with the highly ossified ilium of A. romeri. Projection of the curvature as shown in the former suggests that there was no great difference in general shape in the two species.

The ventral plate of the pelvis, formed by the pubis and ischium. is fairly broad, but considerably narrower than that of A. dolani in proportion to the height of the sacrum. The ventral symphysis is strongly ossified, whereas it was cartilaginous in A. dolani. The obturator foramen is large. Both the pubis and ischium are rather restricted longitudinally. The acetabulum is large and deep, as in A. dolani, and has a rather strong posterodorsal buttress.

Attachment of the anterior sacral rib to the pelvis is flush with the anterior margin of the blade of the ilium. The rib rests on a





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Angelosaurus dolani Olson and Beerbower, CNHM UR 149. Angelosaurus romeri, new species, CNHM UR 827. Not to scale. Figure 9. Lateral views of sacral vertebrae of Angelosaurus dolani and A. Α̈́B

strongly pitted surface. The middle, or second, sacral rib has a long ventral extension on the ilium as shown in figure 9. The ilium is thickened at the site of attachment of this rib, with the result that the areas of insertion of the first and third ribs appear to be depressions. The iliac blade rises above the position of emplacement of the dorsal margin of the second and third sacral ribs, but the first inserts essentially at the top of the blade and is somewhat less firmly attached than are the other two.

In the holotype, a rugose line passes posteriorly and somewhat dorsally along the outer surface of the ilium for about two-thirds of its total width. A ridge occurs in this position in UR 844. In both specimens the structure lies about 2.5 cm below the dorsal margin at the anterior end of the ilium and about 1.5 cm below at its posterior end. Presumably this marks the dorsal margin of the iliofemoralis muscle.

3. Femur (pl. IIIB,C). - The femus is relatively small and strongly ossified. The measurements and proportions given in table 4 describe the size and shape relationships in the known species of Angelosaurus. There is considerable variation in proportions of widths to lengths but there is no evidence of any developmental trends. It is important in this regard to recognize that distortion may have played a more or less undetectable role in altering the widths of the long bones.

The internal trochanter is strong and has a rugose surface. The intertrochanteric fossa is markedly concave. The fourth trochanter is well developed and raised slightly above the adductor ridge. The anterior distal condyle is shallow and flat and is well separated from the posterior condyle. The latter is larger and carries a well-defined surface for the articulation of the fibula. The popliteal space is prominent.

- 4. Interclavicle (pl. IH). An interclavicle, UR 846, is tentatively assigned to this genus and species. It cannot be certain that it actually pertains to Angelosaurus romeri and not to Cotylorbynchus bransoni, but the size suggests that assignment to the former is more reasonable. The bone is typically caseid with a broad, dorsally inflected, triangular anterior plate and a long, slender stem. The ventral surface of the plate is deeply grooved for reception of the clavicles. The anterior margin is somewhat irregular but is in general disposed normal to the long axis of the bone.
- 5. Skull (fig. 4c; pl. Ic). Of the two fragments of skulls found in site KF-1, one may belong to Angelosaurus romeri, UR 854. This fragment consists of a premaxilla, a blunt anterior tooth, and

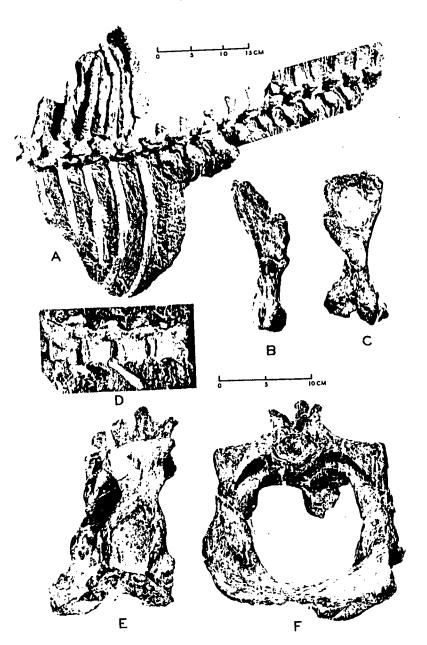
Plate III

a smaller posterior tooth. The teeth and premaxilla are different from those known in Cotylorbynchus. Little is known of the dentition of Angelosaurus. The holotype of A. dolani includes poorly preserved skull and jaw fragments that contain shattered teeth. Since the time of description of the genus, additional preparation has been attempted but with indifferent success. The cheek teeth of A. dolani appear to have been long and slender and not the type that would be expected to pass forward into the premaxillary teeth of UR 854. Two considerations, however, suggest that for the present at least reference of the latter to this genus offers the best solution. First, the accuracy of the restoration of A. dolani is far from certain and there may have been more bulbous anterior teeth than would appear to be the case. Second, there is in the deposits at KF-1 no other animal of appropriate size to which UR 854 can be assigned. It may, of course, represent a genus otherwise unknown. If this assignment is correct, it must mean that the teeth of Angelosaurus differ markedly from those of other known genera of caseids.

Comparisons of species of Angelosaurus.—There are pronounced size differences between the three recognized species of Angelosaurus, with A. sp. the largest, A. dolani intermediate, and A. romeri the smallest. Additional differences in proportions of homologous elements are also evident. These characteristics are shown in table 4.

The femur of A. romeri is easily distinguished from that of A. dolani by the prominences of its fourth trochanter and by the relationship of its distal condyles to each other. It can be distinguished from A. sp. by the position of the internal trochanter. In A. romeri and A. dolani the internal trochanter is more or less midway between the proximal and distal ends of the intertrochanteric fossa, whereas in A. sp. it lies near to the distal end of the fossa. The distal condyles of the femur of A. dolani are conspicuously different from those of A. sp. and A. romeri. In all three species the anterior distal condyle is the flatter of the two; however in A. romeri and A. sp. the posterior condyle is the larger and is well separated from the anterior. In A.

Explanation of Plate III



A. Vertebral column of A. romeri, new species, with fused lumbar ribs, CNHM UR 827.

B. Right femur of A. romeri, new species, CNHM UR 827.

C. Same as B, ventral aspect.

D. Four caudal vertebrae of A. romeri, new species, CNHM UR 827.

E, F. Pelvis and sacrum of A. romeri, new species, CNHM UR 827. E. Right side. F. Anterior.

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dolani the anterior condyle is the larger and it is not well separated from the posterior, presumably as a result of the presence of an extensive cartilaginous cap. In A. dolani the posterior condyle is oriented to face somewhat anteriorly, so that the two articular surfaces for the tibia were approximately at right angles to each other (fig. 8A-C). The tibia of A. dolani reflects this articular configuration, but there is no indication of a similar condition in either A. sp. or A. romeri.

Except for the incompletely ossified blade of the ilium and the weak symphysis, the pelvis of A. dolani is quite similar to that of A. romeri. The massiveness of the vertebral connection and the fusion of the ribs to form a single plate distally characterize and distinguish the sacral ribs of A. dolani (fig. 9). In A. romeri there is only slight, if any, fusion between the second and third sacral ribs and none between the first and second. In A. romeri, however, the centra of all three vertebrae of the sacrum are ankylosed, whereas in A. dolani apparently only the first two are fused.

INCERTAE SEDIS

A small specimen, CNHM UR 856, is evidently that of an otherwise unknown genus in the middle of the Flowerpot Formation of Oklahoma. It was found in the conglomerate sheet in locality KF-2, not far from the jaw designated as the holotype of Cymatorhiza kittsi, new genus, new species. The specimen consisted of some fragments of bone embedded in a red-brown sandy shale and impressions of three teeth in this matrix. A plaster cast was made from this natural mold and the matrix removed. As shown in figure 2D, the teeth were simple, peg-like cones. They appear to be cheek teeth and probably are uppers. The only known genus of the middle part of the Flowerpot to which they might conceivably belong is Cymatorhiza. This is highly improbable, for there seems no logical way that the teeth of the two could be fitted into a reasonable dental pattern. The only other genus from the Flowerpot or San Angelo Formations to which the teeth might pertain is a small, as yet unnamed relative of Rothia, known from the deposits in Knox County, Texas. The teeth of this genus, like those of Rothia, are more bulbous than those in the specimen under consideration, and thus assignment seems unlikely, although not clearly impossible.

Until more materials are found, it will not be possible even to determine with certainty whether this specimen is a reptile or an amphibian. Its importance at present is merely as an indicator of the diversity of the fauna.

INTERPRETATIONS

CORRELATION

The age of the vertebrate assemblages described in the previous sections, middle Flowerpot, has been determined primarily by correlations based on physical criteria. The section supplied by Fay (table 1) shows the position of the vertebrates in the middle part of the Chickasha Tongue. This tongue is about 120 feet thick and lies between the lower part of the Flowerpot Shale, 185 feet thick, and the upper part of the Flowerpot Shale, about 160 feet thick. The fossil-bearing bed lies about 46 feet from the base of the tongue and 230 feet from the base of the Flowerpot, approximately in the middle of the total section which measures 465 feet. The sequences have been established over the years by field relationships of the beds and by lithology, for there are no marine invertebrates. Plants, which are abundant in some places, have as yet been little studied. Vertebrates have been heretofore unknown above the Hennessey Formation.

To the east and southeast in Grady and Stephens Counties the Chickasha Formation occupies the stratigraphic position of the Flowerpot and, perhaps, is equivalent to much of the El Reno Group, including the Blaine and the Dog Creek Formations (Davis, 1955). Below it is the Duncan-Flowerpot Sandstone. This, on the basis of stratigraphic position and lithology, appears to be equivalent to the San Angelo Formation of Texas. The Duncan-Flowerpot overlies the Hennessey, the upper part of which is equivalent to the Choza Formation of Texas.

Where the Duncan-Flowerpot Sandstone is overlain by the Flowerpot shales, as in Carter County (Scott and Ham, 1957), relationships are similar to those encountered in Stonewall, Knox, Foard, and Hardeman Counties, Texas, where the San Angelo is overlain by the Flowerpot Formation. Differences except in names are, it would appear, slight.

The Hennessey beds, underlying the Duncan-Flowerpot Sandstone, appear to be in large part of terrestrial origin, although in places a rather high content of gypsum suggests deposition in an evaporite basin. This is in marked contrast to the Choza beds in which the sediments for two or three hundred feet below the San Angelo contact clearly were formed in an evaporite basin. In Blaine and Kingfisher Counties the Flowerpot Shale lies upon the Cedar Hills, generally considered a member of the Hennessey. If this as-

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signment is correct, as it seems to be, the lower part of the Flowerpot shales in Kingfisher and Blaine Counties is in part correlative with the Duncan-Flowerpot to the east and southwest. The Duncan-Flowerpot facies wedges out to the west and northwest, being replaced by Flowerpot shales deposited in large part under evaporite conditions. Similarly, somewhat later, the Chickasha Sandstone thins to the west and northwest to form a wedge in the Flowerpot shales.

The San Angelo vertebrates of Texas (Olson and Beerbower, 1953) lived at the time of deposition of the Duncan-Flowerpot in central and south-central Oklahoma and in the lower part of the Flowerpot shales in Kingfisher and Blaine Counties. In similar fashion, in Texas, shales were being deposited to the west of the area of accumulation of the San Angelo beds during the formation of these terrestrial deposits. Vertebrates occur in the upper twothirds of the San Angelo Formation, which ranges from about sixty to two hundred feet in thickness over the area from which vertebrates have been obtained. The Flowerpot verrebrates of Texas occur in the lowest 25 feet of the Flowerpot Formation, as it overlies the San Angelo. Thus the highest vertebrates in the Guadalupean of Texas lie about 140 feet above the contact with the Choza, the uppermost formation of the Leonardian. The Oklahoma vertebrates, as noted, lie about 230 feet from the base of the Flowerpot Formation, the first formation of the Guadalupean in Kingfisher and Blaine Counties. Thickness of this order of magnitude, developed under circumstances that involved deposition of clastic sediments under rapidly changing conditions, both laterally and vertically, is not a particularly reliable time indicator. Everything else being equal, however, it would seem likely that the vertebrates from Kingfisher County are somewhat more recent than those from the San Angelo and Flowerpot of Texas. That they might be contemporary or even older is not ruled out by the evidence from the physical circumstances alone.

The tetrapods recovered from site KF-1 give some evidence on this matter. All found to date are of North American cast, that is, they have close relatives in the Leonardian and seem to have evolved in North America. The tetrapods from KF-1 find generic counterparts in the San Angelo of Texas, the Flowerpot of Texas, and the Hennessey of Oklahoma. One species, Rothia multidonta, is known from both the San Angelo and the Flowerpot of Texas. The genus Angelosaurus occurs in the red shales of the middle part of the San Angelo and in the comparable facies of the lower part of the Flowerpot. It is not known from the coarse clastics of the upper part of the

San Angelo. The unnamed species of *Angelosaurus* from KF-1 is new, being smaller and more lightly built than are either of the other two. This may indicate a difference in age, since there is little facies difference, but mere geographic separation of the deposits may also be involved. Not enough is known of the genus to recognize evolutionary trends, and so the fact that there is a species difference gives no clue to relative ages. Even if the species difference is thought to indicate a difference in time, it is not possible to determine from morphology which species was earlier and which was later.

Cotylorhynchus is known from the Hennessey, San Angelo, and Flowerpot Formations. In addition Ennatosaurus, a genus similar to Cotylorhynchus, is known from Russia, from beds that probably belong to Zone II of the Kazanian. The temporal sequence that includes C. romeri of the Hennessey, C. bancocki of the San Angelo, and Ennatosaurus of the Kazanian is clear. One feature that shows consistent directional change within this sequence is the increasing cuspidation of the teeth. C. romeri has no terminal cuspules; C. bancocki has three small terminal cuspules, which are better expressed on the posterior than on the anterior teeth; and Ennatosaurus has three or five (possibly seven) well-expressed cuspules, with strongest expression on the posterior teeth. C. bransoni falls in this sequence between C. bancocki and Ennatosaurus, closer to the latter than to the former. It has three cuspules on the anterior teeth, more fully expressed than any known in C. bancocki but less fully developed than in Ennatosaurus. The tooth pattern of C. bransoni thus is somewhat more advanced than that of C. bancocki and suggests that the species in which it occurs was derived from the C. bancocki stage and is somewhat later in time.

Such reasoning, of course, is subject to obvious dangers. In the present case, in view of the similarities of facies and geographic proximity these seem to be minimal. That *C. bransoni* came directly from *C. hancocki* is improbable in view of the difference in size and implied reversal of an apparent trend toward large size in the line leading to *C. hancocki*. Although the evidence cannot be considered more than suggestive, it appears that the relative positions of the assemblages from the upper part of the San Angelo and the middle part of the Flowerpot in the rock sequences give a fairly accurate basis for estimation of their relative ages and that the middle Flowerpot assemblage from KF-1 is younger than the assemblage from the upper San Angelo. That no great age difference is involved is indicated by the presence of *Rothia multidonta* at all three levels, upper San Angelo, lower Flowerpot, and middle Flowerpot.

COMPOSITION OF THE FAUNAL COMPLEX

The assemblage from the sites in Kingfisher County, Oklahoma, is small and certainly incomplete. Assessments of its meanings must be considered with this in mind. It is clear that all known elements of the assemblage could have stemmed from stocks represented in earlier deposits in North America. No traces of animals related to the very primitive therapsids known in the lower beds of the Russian Kazanian and in the upper part of the San Angelo and lower part of the Flowerpot of Texas have been recovered. Rothia and Angelosaurus occur in the red shale facies of the middle part of the San Angelo and lower part of the Flowerpot, but Cotylorhynchus has not been found in this facies in Texas. The large species, C. hancocki, is known only from the coarse clastic facies of the upper part of the San Angelo Formation. The genus, however, does occur in red shale facies of the Hennessey of Oklahoma. There it is associated with Labidosaurikos, which is probably a direct ancestor of Rothia. The Hennessey Cotylorhynchus, C. romeri, could lie close to the ancestry of both C. bancocki and C. bransoni, with the latter retaining the same general ecological relationships as C. romeri. Cymatorhiza is a descendent of a family not otherwise known above the Arroyo Formation of the Clear Fork. This family also occurs in red shale facies.

The complex as now known thus appears to represent a continuation of evolutionary lines that were established in North America in the late Wolfcampian and flourished in somewhat different guises in the deltaic deposits of Texas laid down during the Clear Fork, and in the Hennessey deposits of Oklahoma. The latter appear to have been deposited somewhat farther from the marine-nonmarine interface of the delta, in a somewhat different deltaic regime than age-equivalent beds in Texas. Roots of the Flowerpot stock are evident in the Hennessey in the presence of Labidosaurikos and Cotylorbynchus romeri. The oldest known source of Angelosaurus is the middle part of the San Angelo of Texas. As yet, however, equivalent beds in Oklahoma have not been studied in any detail. The absence of more "progressive" elements from the complex bears out an apparent relationship between "archaic" faunal elements and red shale facies and "progressive" elements and coarse clastic facies.

PART II. — THE OSTEOLOGY OF CAPTORIUNIKOS CHOZAENSIS OLSON*

EVERETT C. OLSON

INTRODUCTION

Captorhinikos chozaensis Olson, a member of the family Captorhinidae, was described on the basis of rather fragmentary materials from the Choza Formation of Foard County, Texas. Specimen CNHM UR 97, lower jaws and part of a skull, was designated as the holotype. In the course of the last 10 years several specimens of a medium-sized captorhinid were found in the Hennessey Formation, Early Permian, near Norman, Oklahoma. The resemblance of these specimens to Captorhinikos is unmistakable and Vaughn (1958) referred one of them, USNM 21275 collected in 1953 by David Dunkle, to Captorhinikos chozaensis Olson. Seltin (1959) referred another specimen, CNHM UR 183, to Labidosaurikos meachami Stovall. This specimen consists of a small skull and one lower jaw, both rather poorly preserved. The diagnostic features of the dentition, not completely available to Seltin, leave little doubt, as Vaughn (1958) pointed out, that these specimens pertain to Captorhinikos rather than to Labidosaurikos.

Specific reference here, as in the case of most fossil reptiles and amphibians, poses a problem because of the difficulties of ascertaining appropriate morphological characters and of assessing their variability. If the operational rule, that within a genus recognition of "significant" morphological differences constitutes the sole basis for separation of species, is applied, then Vaughn's assignment of the Hennessey Captorhinikos to C. chozaensis Olson is proper. The available materials do not provide a morphological basis for separation. It would be dangerous, however, to draw inferences from such an assignment with respect to such matters as species duration, variability, or evolution. Rarely can species distinctions based on such ma-

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terials be sufficiently precise to contribute significantly to detailed considerations in these areas.

Collections from the Oklahoma Permian made by the writer and his party in 1961 include three new specimens of Captorhinikos chozaensis. These were found together in a sandy shale exposed in a ditch along a secondary road in the NE1/4 NW1/4, sec. 29 T. 9 N., R. 2 W. One (CNHM UR 857) consists of a partial skull, lower jaws, and much of the skeleton. During excavation, when it was not realized that a full skeleton was present, a break was made between two blocks, each of which included part of the specimen. Water, carried in the road-side ditch and seeping into the shales, not only had damaged all of the specimens rather badly but also made it difficult to see the bone in the shale. On the slab that contains the posterior part of the skeleton, CNHM UR 857, are a poorly preserved partial skull and fragments of an associated skeleton (CNHM UR 859). CNHM UR 858 is a third specimen, which consists of fragments of a partially preserved vertebral column and ribs, parts of girdles, a fairly well-preserved forelimb and partial front foot and a few isolated bones. These new materials, combined with CNHM UR 183 and USNM 21275, make it possible to gain a fair idea of much of the osteology of the genus Captorbinikos.

As Vaughn (1958) has emphasized, the family Captorhinidae is extremely uniform in most morphological features throughout its full temporal range, which encompasses all of the Early Permian and the initial part of the Late Permian. The osteology of Captorhinus and Labidosaurus is well known from studies of Williston (1910, 1917), Case (1911), Price (1935), and, more recently, Seltin (1959). More advanced members of the family, Captorhinoides Olson, Labidosaurikos Stovall, Captorhinikos Olson, Rothia Olson and Beerbower (part I, this report), Kahneria Olson, and Hecatogomphius Vjushkov have been described during the last decade and a half. For none of these is the osteology of more than a relatively small part of the animal (usually the skull and jaws) well known. Captorhinikos thus serves to fill an important gap, by providing information on the morphology of a stage intermediate between the earlier forms, particularly Captorhinus and Labidosaurus and the genera in the initial part of the Late Permian (San Angelo and Flowerpot Formations) in North America and the middle or late Kazanian of the Soviet Union. Much of what is known can best be presented by illustration, supplemented by short descriptions and analyses. Vaughn (1958) has already given a verbal description of a number of the pertinent items in his brief but lucid report on USNM 21275.

OSTEOLOGY

SKULL AND JAWS

Most of what is known of the skull and jaws of Captorbinikos chozaensis has come from the rather fragmentary Choza specimen CNHM UR 97, and from Hennessey specimens CNHM UR 183, CNHM UR 857, and USNM 21275. A poorly preserved skull is also present in CNHM UR 859. Measurements of a few aspects of these individuals are presented in tables 5, 6, and 7 and in figures 10 and 12 and portray much of the known detail.

Vaughn (1958) emphasized the stability of cranial morphology throughout the family Captorhinidae, pointing in particular to Captorhinus, Labidosaurus, Captorhinikos and Labidosaurikos. Slightly greater range is introduced by genera from the very Early Permian, such as Paracaptorhinus Watson (1954), and from the Late Permian, in particular Rothia (part I, this report; Olson, 1962). Nevertheless, this family is remarkably stable, with the principal differences between genera to be found in the dentitions.

It is difficult to differentiate Captorhinus, Labidosaurus, Captorhinikos, and Labidosaurikos from features of the dorsal and lateral surfaces of the skulls and structures of the lower jaws. Were structural patterns known in great detail and were the variability liable to assessment, it is probable that many bases for separation would be found. At present, however, the main generic difference appears to relate to certain skull proportions.

Measurements and ratios of various skull measurements pertinent to these proportional distinctions are given in tables 6 and 7. In none of the cases is the number of individuals large enough to warrant statistical analysis. Two sets of the ratios show differences of magnitudes of the mean ratios that may be of some significance. The mean of the orbital length:interorbital width ratio (O_1/Io_w) ranges from 0.93 in Labidosaurikos to 1.22 in Labidosaurus stovalli Seltin (1.21 in Captorhinus aguti). Arrayed in order of increasing skull length (mean value where possible), this ratio shows a fairly consistent decrease with increase in skull length. An exception is found in Captorhinikos chozaensis in which the ratio is 1.01 with mean skull length of 103 mm. The ratio for Labidosaurus hamatus, with mean skull length of 147 is larger, 1.12. In this case, however, one skull of Captorhinikos chozaensis is small, compared to the other known skulls. The ratio for USNM 21275, with skull length 124,

is 0.98. The change of ratio noted in this pair of characters is probably related to size and, as such, is not of great significance as a generic character.

The orbito-snout length:postorbital length ratio (O-S₁/Po₁) shows a range from 1.09 to 1.50. It does not give any evidence of size dependency. The highest ratio, 1.50, is in *Captorbinikos* and the next highest in *Labidosaurikos*. *Labidosaurus hamatus* with a skull length about equal to that of *Captorbinikos*, USNM 21275, shows a ratio of 1.10. *Captorbinus aguti* has a comparable ratio, 1.09. Values for *Labidosaurus stovalli*, run rather high and the mean is 1.22 if the somewhat abberant specimen, MUO 3-1-S5 is included. Without this specimen the ratio is 1.16. There appears to be a tendency for the length of the snout to increase relative to the postorbital length from the earlier forms to the later. This presumed trend probably can be related to the increased development of the multiple rows of teeth on the maxilla and dentary.

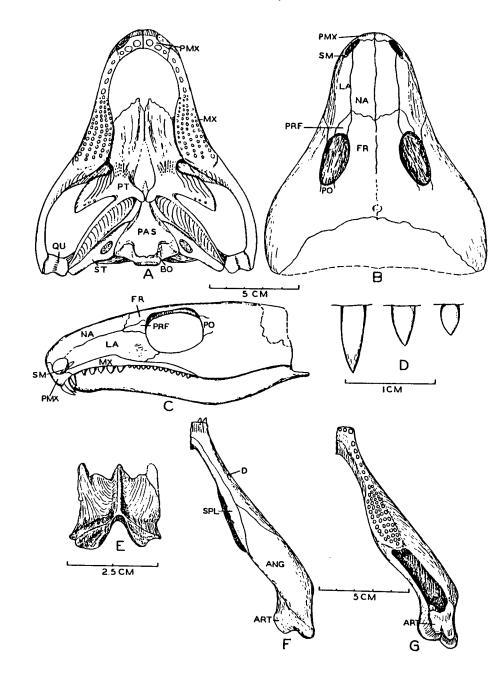
The differences noted are slight and are far outweighed by the common captorhinid features of the skull surface, the basicranium, the stapes, and the palate, as illustrated in figure 10. Lower jaws, likewise, show common features throughout the captorhinids, such as the broadly expanded articular region; the swollen, somewhat bowed ramus; and the strongly sloped, short symphysial area (fig. 10F,G). The dental surface of the dentary is somewhat expanded in the genera with highly developed multiple rows of teeth, Captorhinikos, Labidosaurikos, Rothia, Kahneria, and Hecatogomphius. The retroarticular process is rather prominent in all captorhinids. In Captorhinikos and Labidosaurikos it is elongate and considerably more prominent than in earlier genera such as Captorhinus and

Figure 10. Skull and jaws of Captorbinikos chozaensis Olson

F, G. Lower jaw in ventral and dorsal aspects respectively.

ANG — angular	PAS — parasphenoid
ART — articular	PMX — premaxilla
BO — basioccipital	PO — postorbital
D — dentary	PRF - prefrontal
FR — frontal	PT — pterygoid
LA — lacrimal	QU — quadrate
MX — maxilia	SM — septomaxillary
NA — nasal	SPL — splenial

ST — stapes



A, B, C. Reconstructions of the skull in palatal, dorsal, and lateral aspects respectively.

D. Upper teeth, from left to right: large premaxillary tooth, large maxillary tooth, tooth typical of those in multiple rows.

E. The supraoccipital bone drawn from USNM 21275.

Labidosaurus. The elongation may well be related to modifications of the dentition, expressed in some way, not at present determinable, in modification of the depressor mechanism. Whether or not this character was present in the heavily toothed genera of the Late Permian is not certain, although there is a suggestion of it in Rothia.

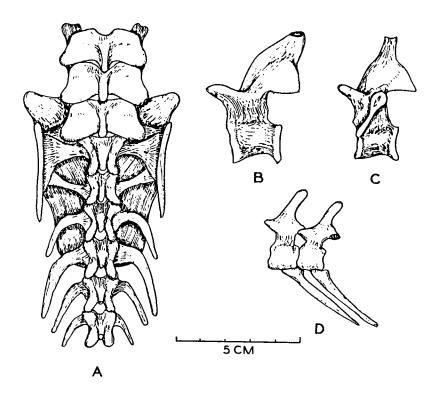


Figure 11. Vertebrae and sacrum of Captorbinikos chozaensis Olson

- A. Vertebrae and sacrum reconstructed from CNHM UR 857.
- B. Lumbar vertebra based on USNM 21275.
- C. Anterior dorsal vertebra based on USNM 21275.
- D. Caudal vertebrae, about numbers 8 and 9, showing very large haemal arches, based on CNHM UR 857.

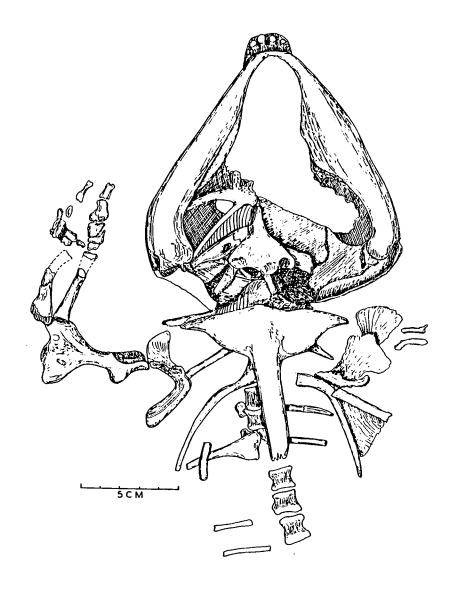


Figure 12. Ventral view of anterior part of specimen of Captorhinikos chozaensis Olson, drawn from CNIIM UR 857 as preserved. Note in particular the long, heavy, but unexpanded ribs in the vicinity of the shoulder girdle, the humerus, and posterior part of the skull and the interclavicle.

USNM

ABBREVIATIONS USED IN TABLES 5-7

anterior dorsal vertebra
- collection designation: American Museum of Natural History
— width of anterior zygapophyses
height of vertebral centrum
length of vertebral centrum
.— collection designation, Chicago Natural History Museum, University Reptile
length of femur
- length of fibula
— total height of vertebra, base of centrum to top of spine
— interorbital width, minimum
- length of lower jaw
mid-dorsal vertebra
-collection designation: Museum, The University of Oklahoma
— number of individuals
— orbital length, maximum parallel to axis of skull
- distance from anterior margin of orbit to tip of snout
— posterior dorsal vertebra — distance from posterior margin of orbit to back of skull
— width of posterior zygapophyses
— length of radius
— length of skull along dorsal midline
— length of tibia
— length of ulna

- collection designation: United States National Museum

DENTITION

The principal differences between Captorhinikos and Labidosaurikos, as originally defined, are in the dentitions: in the number and disposition of the rows of maxillary and dentary teeth, the nature of the transitions from the tooth plates to the more anterior teeth, and the number and form of the anterior teeth above and below. The dentition of USNM 21275 was the basis for its assignment to Captorhinikos by Vaughn (1958). The new materials, plus CNHM UR 183, provide an essentially complete picture of the pattern of upper dentition and most of the detail of the lower.

The pattern of the upper dentition is shown in figure 10A. Five rows of maxillary teeth form a more or less crescentic tooth plate. The curvature of the rows conforms roughly to the outlines of this plate. All of the teeth are subconical, with slightly bulbous waists,

TABLE 5.— MEASUREMENTS OF Captorhinikos chozaensis OLSON (Measurements in millimeters)

SKULL AND JAWS USNM **CNHM UR CNHM UR CNHM UR** 857 859 21275 183 Sk, 124 83 -----150 +LJ, 135 96 134 VERTEBRAE c, PZ_w AZ_w Ht, USNM 21275 (ad) 8.2 9.2 19.5 18.5 27.0 22.8 23.0 27.0 USNM 21275 (pd) 8.0 12.0 CNHM UR 857 (md) 22.0 CNHM UR 858 (pd) 24.0 LIMB BONES Fi, Ti, R, U 57.0 41.0 40.0 USNM 21275 ----29.0 CNHM UR 858 40.0 54.0 32.0 CNHM UR 857 38.0 ---- --

17

as shown in figure 10D. There is a slight tendency toward reduction in size anteriorly along the rows. Anterior to the tooth plate are four or five single teeth, rather large and not flanked by smaller teeth, as in *Labidosaurikos*. They pass forward more or less from the middle row of the dental plate. There are two large, strongly recurved premaxillary teeth and a third smaller lateral tooth of the same general shape.

There are four rows of teeth on the dentary (fig. 10g). Although details are less clear, it is evident that these lead forward into a single row of six or seven rather small teeth. Anteriorly there are two or three somewhat larger teeth that slope strongly anterodorsally. The second or third, as the case may be, is the largest and is shaped much like the upper premaxillary teeth.

This dentition, while similar to that of Labidosaurikos in general aspects, differs in details as described by Olson (1954) and Vaughn (1958). The most critical differences are the general shape of the tooth plate, which is more quadrilateral in Labidosaurikos; the numbers of rows of teeth, less in Captorhinikos; and the manner of transition from the tooth plate to the more anterior teeth. This is particularly striking in the lower jaw in which the single row of teeth which passes forward from the dental plate in Captorhinikos contrasts with the rather abrupt termination of the tapering dental plate in the large, tusklike tooth in Labidosaurikos.

AXIAL SKELETON

1. Vertebrae. — The principal types of vertebrae are illustrated in figure 11. All of the presacrals are very much in the captorhinid mold. Dorsals and lumbars possess broad arches; flat, broad, horizontal zygapophyses; and a single transverse process for attachment of a holocephalous rib. Centra are deeply amphicoelous, unkeeled, and without distinguishing characteristics. The neural spines, however, are quite high in Captorhinikos, as contrasted with those of Captorhinus and Labidosaurus. The nature of the spines is somewhat uncertain in Labidosaurikos, although the known vertebrae do not suggest strong development. Neural spines are not well developed in Rothia but those of Kahneria are similar to the spines of Captorhinikos.

No accurate count of the number of presacrals is possible. The column in CNHM UR 857 was complete when found, but the anterior vertebrae are obscured by the interclavicle and some vertebrae were lost during collection, as was noted earlier. The number of presacrals appears to be about 25, but this may be one or two less than the actual number.

There is one fully developed sacral vertebrae and a second, more posterior, which carries a somewhat modified rib. This is typical of the family. There is an abrupt change of vertebral form with the first caudal, for the arch is much reduced in width and the zygapophyses are narrowly spaced and have limited articular surfaces. The second sacral has the form of the anterior caudals.

TABLE 6.— MEASUREMENTS OF SPECIMENS OF Captorhinus, Labidosaurus, Captorhinikos, AND Labidosaurikos

(Measurements in millimeters)

			Сар	torbinus agu	ti			
	CNHM P 12757	AM 43		AMNH 4410	AMNI 4338	ł	AMNH 6790	
Sk ₁	57	60)	60	65		68	
O-S ₁	19	2	i	25	27		26	
Po	20	2	3	20	21		24	
Io _w	14	13	3	14	13		16	
O ₁	18	10	5	16	18		17	
	Captorb	Captorhinikos chozaensis			Labidosaurikos meachami			
	USNM 21257	CN	HM UR 183		MU(3-1-S			
Sk ₁	124		83		295	i		
O-S ₁	55		43		138			
Po_1	38		28	107				
Io _w	29		17	54				
O	28		18	50				
	Labido	Labidosaurus hamatus			Labidosaurus stovalli			
	AMNH 4414	AMNH 4341	AMNH 4460	MUO 3-1-S7	MUO 3-1-S5	MUO 3-1-S3	MUO 3-1-S4	
Sk ₁	155	145	142	63	59	78	60	
O-S ₁	69	60	59	25	25	31	23	
Po	53	55	64	21	18	27	20	
Io _w	29	30	28	14	15	14	12	

33

30

34

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TABLE 7.— SELECTED RATIOS OF SKULL MEASUREMENTS OF GENERA LISTED IN TABLE 6

Captorhinus aguti

Mean skul	length	(Sk)	for	sample	= 62
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Ratios	CNHM P 12757	AMNH 4334	AMNH 4410	AMNH 4338	AMNH 6790	Mean
O-S ₁ /Po ₁	0.95	0.91	1.25	1.28	1.08	1.09
O ₁ /Sk ₁	0.32	0.26	0.26	0.27	0.25	0.27
O _l /Io _w	1.29	1.19	1.17	1.35	1.06	1.21
Io _w /Sk ₁	0.25	0.22	0.23	0.20	0.24	0.23

Captorbinikos chozaensis

Labidosaurikos meachami

Mean skull leng	th (Sk _l) for	Skull length = 295		
Ratios	USNM 21275	CNHM UR 183	Mean	MUO 3-1-S2
O-S ₁ /Po ₁	1.45	1.55	1.50	1.29
O_{l}/Sk_{l}	0.23	0.22	0.23	0.17
O_l/Io_w	0.97	1.06	1.01	0.93
Io_w/Sk_1	0.23	0.20	0.21	0.17

Labidosaurus hamatus

Mean skull length (Sk₂) for sample = 147

Ratios	AMNH 4414	AMNH 4341	AMNH 4460	Mean
O-S ₁ /Po ₁	1.30	1.09	0.92	1.10
O ₁ /Sk ₁	0.21	0.21	0.24	0.22
O_1/Io_w	1.14	1.00	1.21	1.12
Io _w /Sk ₁	0.19	0.21	0.20	0.20

(Continued on next page)

TABLE 7. -- Continued

Labidosaurus stovalli

Mean skull length (Sk,) for sample = 65

Ratios	MUO 3-1-\$7	MUO 3-1-S5	MUO 3-1-S3	MUO 3-1-S4	Mean
O-S ₁ /Po ₁	1.19	1.39	1.15	1.15	1.22
O ₁ /Sk ₁	0.27	0.31	0.26	0.28	0.28
O_l/Io_w	1.21	1.20	1.05	1.42	1.22
Io _w /Sk ₁	0.22	0.25	0.24	0.20	0.23

Mean Ratios for Genera in Summary Form

Ratio	Captorhinus aguti	Labidosaurus bamatus	Labidosaurus stovalli	Labidosaurikos meachami	Captorhinikos chozaensis
	(N=5)	(N=3)	(N=4)	(N=1)	(N=2)
· O-S ₁ /Po ₁	1.09	1.10	1.22	1.29	1.50
O _i /Sk,	0.27	0.22	0.28	0.17	0.22
O'/Io'	1.21	1.12	1.22	0.93	1.01
Iow/Sk	0.23	0.20	0.23	0.17	0.21
Mean Sk	62.0	147.0	65.0	295.0	103.0

Caudal vertebrae have narrow arches, somewhat compressed centra, and narrow zygapophyses with surfaces inclined from the horizontal. Haemal arches, which appear on about the seventh or eighth caudal, are long and rather massive proximally. CNHM UR 857, upon which knowledge of the caudals is based, includes a series of about 15 caudal vertebrae and, within this series, the overall size is reduced by approximately one-half. There was a rather long tail with certainly no less than 45 vertebrae.

2. Ribs. — The presacral ribs are simple and, for the most part at least, holocephalous. The heads of the ribs on the atlas, axis, and anterior cervicals are not known. The ribs that underlie the shoulder girdle are heavy and fairly massive, as shown in figure 12, but lack expansion of the shafts or distal ends. More posteriorly the ribs are long and rather slender, as shown in figure 13. The most posterior lumbars may have lacked ribs, but evidence is not conclusive.

One sacral rib is fully developed, being thick and strongly ex-

panded laterally into a plate-like articulation. The second sacral rib is much smaller and passes forward and laterally to abut against the first at the junction with the sacrum. The first four caudal ribs are flat and strongly recurved posteriorly. As shown in figure 11A, there is rapid decrease in size from the first to the fourth. Thereafter caudal ribs are either small or nonexistent.

FORELIMB AND GIRDLE

Much of what is known of the forelimb is illustrated in figures 12, 13, and 14. In no specimen is the shoulder girdle complete. Figure 14c shows the girdle drawn from data from specimens CNHM UR 857 and USNM 21275. Two coracoids and part of the scapula are indicated, with considerable lack of ossification in the acetabulum and along the base of the scapula-coracoid junction. This assumption is based primarily upon the condition in USNM 21275 and the poor ossification may merely represent the condition of this specimen, which shows various signs of being somewhat immature. The upper part of the scapula is poorly known, but there is no reason to suppose that it is unlike that in *Captorbinus* and *Labidosaurus*.

The humerus, radius and ulna, and front foot are as shown in figures 12 and 14A as preserved, and in figure 14B, as reconstructed. The condition of the foot in CNHM UR 85B, on which the reconstruction is based, is rather poor, and, as is evident, considerable interpretation has been necessary. There is, however, no suggestion of marked differences from other captorhinids. The humerus is fairly well preserved in CNHM UR 857 and the reconstruction as shown is reliable. This aspect is the only orientation in which this bone can be studied. The descriptions of the radius and ulna are based primarily upon CNHM UR 85B, but some details have been added or confirmed from other specimens. The forelimb, like the hind limb as noted later, is small and lightly built and provides supplemental evidence of a general trend in this direction noted earlier in *Rothia* and *Kahneria* (Olson, 1962).

Figure 13. A specimen of Captorbinikos chozaensis Olson, CNHM UR 857, shown in ventral view as preserved. The nature of the ribs is not well shown.

CL - clavicle

ICL — interclavicle

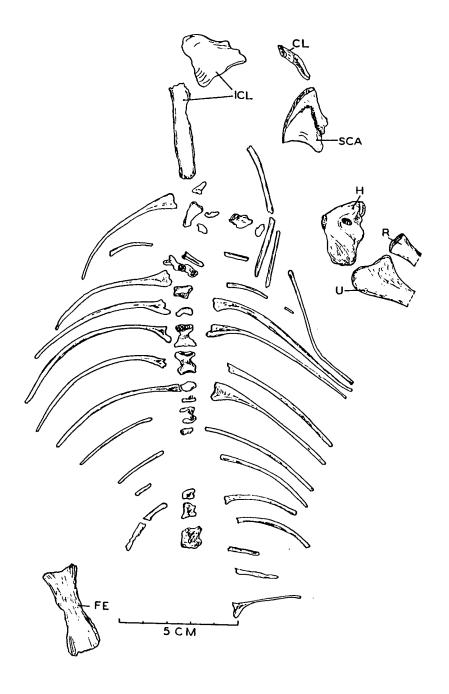
FE - femur

R — radius

H — humerus

SCA — scapula

U --- ulna



HIND LIMB AND GIRDLE

The pelvis is preserved only in CNHM UR 857 and in this specimen can be studied only in dorsal and internal aspects. Thus a considerable amount of detail is missing. The principal features that can be determined are shown in figures 11A and 15F. There are some points of some special interest. First, as shown in figure 15F. it has a strong buttress which passes ventrally from the level of the ilium and forms the thick central part of the symphysis. This is a feature common to other captorhinids and strongly emphasized in later forms, such as Rothia (part I, this report). The pubic plate shows a slight anterior flare, a more or less incipient development of the strongly forward-facing pubic plate in Rothia. The ilium is slender and projected posteriorly in a long caudal process. This is a condition rather distinct from that in Labidosaurus, but reminiscent of that in Captorhinus. Finally, the pelvis as a whole is light, narrow, and small in relation to the size of the animal as a whole.

The femur in figures 15D and 15E has been drawn from that of USNM 21275. It is poorly ossified and suggests that the individual was immature. A poorly preserved but more mature femur is present in CNHM UR 857 (fig. 15A), and from this the dashed lines showing the outline of the more mature bone have been added. The tibia and fibula show no special features except that neither is fully ossified. They are typically captorhinid.

The structure of the hind foot (fig. 15c), is based upon CNHM UR 857, shown as preserved in the enlarged sketch (fig. 15A), and upon USNM 21275. The astragalus is shown as being composed of three parts, corresponding to the immature astragalus of Captorhinus described by Peabody (1951). In the preserved foot of CNHM UR 857, the "intermedium" portion of the astragalus is detached and rotated somewhat out of position. The "proximal centrale"

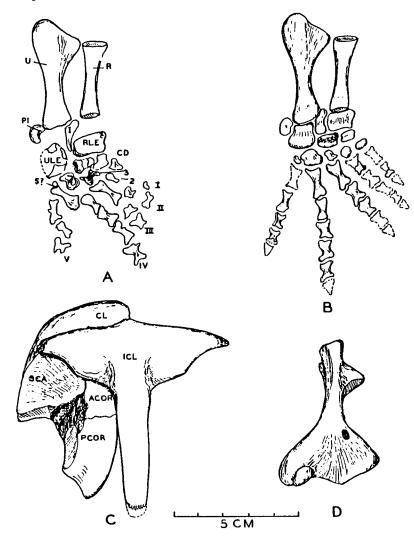
Figure 14. Shoulder girdle and forelimb of Captorhinikos chozaensis Olson

D. Humerus in ventral aspect, based on CNHM IIR 857 and 858

and the remain aspect, based on Civilla	OR O)/ and o)
ACOR — anterior coracoid	Pl pisiform
CD — distal centrale	R radius
CL — clavicle	RLE radiale
I — intermedium	SCA — scapula
ICL — interclavicle	U — ulna
PCOR — posterior coracoid	ULE - ulnare
1.5 — distals of carpus and	tarsus

I-V -- phalanges of front and hind feet

portion is only partially fused to the "tibiale" portion. The condition in USNM 21275 is shown in figure 15B, in which it may be seen that the "proximal centrale" portion is joined by an open suture and the "tibiale" and "intermedium" portions are more firmly fixed. The foot, on this basis as well as other morphological features, shows a strong resemblance to that of Captorhinus and, so far as is known, is typical of the hind foot pattern common to the family Captorhinidae.



A. Forefoot as preserved in CNHM UR 858.

B. Reconstruction of forefoot based largely upon specimen shown in A.

Interclavicle, clavicle, coracoids, and scapula in ventral aspect. Based largely upon CNHM UR 857 and USNM 21275.

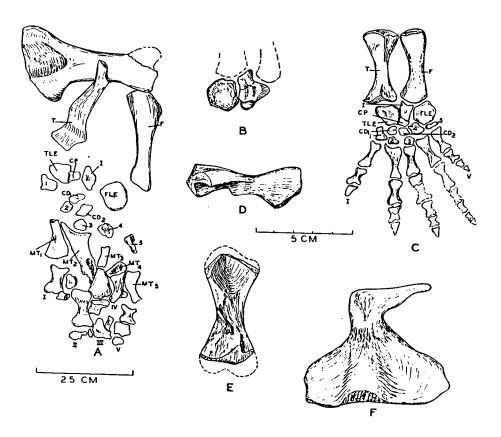


Figure 15. Pelvis and hind limb of Captorhinikos chozaensis Olson

- A. Left hind limb as preserved in CNHM UR 857, enlarged to show detail.
- B. Calcaneum and "astragalus" of USNM 21275 showing separate "centrale" and position of fracture along plane of weakness between what appears to be "intermedium" and "tibiale."
- C. Reconstruction of hind foot from conditions shown in A and B.
- D. Right femur of USNM 21275, anterior aspect.
- E. Same as D, but in ventral aspect with dashed lines indicating shape in more mature femur, from CNHM UR 857.
- F. Right side of pelvis viewed internally.
 - CD1 second distal of amphibian (as Trematops)
 - CD. third distal of amphibian

CP — proximal centrale F — fibula

MT — metatarsal T — tibia

FLE --- fibulare

re TLE — tibiale
1-5 — distals of carpus and tarsus

I-V - phalanges of front and hind feet

SUMMARY AND CONCLUSION

New materials confirm Vaughn's (1958) determination that the medium-sized captorhinid from the Hennessey Formation is Captorhinikos and that the species is most probably C. chozaensis Olson. Captorhinikos is known from the Vale Formation from a primitive species C. valensis Olson and from the Choza Formation of Texas, but has not been found in older rocks. The Hennessey species is comparable in level of advancement to C. chozaensis, to which it has tentatively been referred, and, as Vaughn (1958) has indicated, suggests that the part of the Hennessey Formation from which it comes, near Norman, Oklahoma, is an approximate age equivalent of the Choza.

The morphology of Captorhinikos chozaensis Olson, as described herein, is based largely on the Hennessey specimens. Its resemblances to that of other captorhinids confirms Vaughn's observation concerning the conservative nature of the skeletal features of members of this family. Except for size, which is by no means a safe criterion, the dentitions provide the principal means of separating genera. Details of dentition characteristic of the genus differ from those of Labidosaurikos to which Captorbinikos shows the closest resemblances. Principal differences are the numbers of rows of teeth, arrangement of the rows relative to each other, and the mode of transition from multiple rows to a single row, particularly in the lower dentition. The only evident differences in the skulls and jaws of the four best known genera, Captorbinus, Labidosaurus, Labidosaurikos, and Captorhinikos, if size is disregarded, are the relative lengths of the snouts and of the retroarticular processes. Both snouts and retroarticular processes tend to be relatively long in Captorbinikos and Labidosaurikos and both modifications from the more primitive pattern may be related to changes in dentition.

The postcranial morphology of Captorbinikos is basically similar to that known in Labidosaurus and Captorbinus. There are minor differences in the shapes of elements, for example in the heights of vertebral spines and in the length of the posterior process of the ilium, but proportional differences appear to be more important than those of form. The forelimbs, hind limbs, and girdles are proportionately small and lightly constructed compared with those of specimens of Labidosaurus of comparable size. This is a reflection of a trend in the evolution of the family, carried to a considerably greater degree in Rothia and Kahneria of the San Angelo and the Flowerpot Formations.

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