

ROMERIID REPTILES FROM THE LOWER PERMIAN

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ABSTRACT. The Family Romeriidae, ancestral to most major reptilian groups, is represented by numerous specimens in the Lower Permian of Texas, West Virginia, and Oklahoma. Two lineages can be recognized. One, characterized by the genus *Protorothyris archeri*, is a continuation of the main Pennsylvanian stock in which the upper tooth row is horizontal. A species from West Virginia, originally placed in a distinct genus, *Melanothyris morani*, is here considered as only specifically distinct from *P. archeri*. A second group, in which the premaxilla is hooked, is typified by *Romeria texana*. Within this group, a new species, *Romeria primus*, and a new genus, *Protocaptorhinus pricei*, are named. A sequence of forms within this group demonstrates an almost complete transition between the families Romeriidae and Captorhinidae. The Captorhinidae can be differentiated from the Romeriidae by the conspicuous lateral expansion of the cheek region. In the late Belle Plains and Clyde Formations of Texas, captorhinids are represented by a genus closely resembling *Captorhinus*, but having only a single marginal tooth row. In Texas, *Captorhinus aguti* is not known with assurance prior to the Arroyo Formation. A primitive antecedent of *Labidosaurus hamatus* is known from the Clyde Formation, an indication that this genus evolved directly from the romeriids, rather than from the immediate ancestor of *Captorhinus aguti*. The following groups must have evolved from romeriids prior to the Permian: pelycosaurs, mesosaurs, *Bolosaurus*, araeoscelids, and eosuchians. Turtles may have evolved from Lower Permian romeriids. Procolophonoids probably diverged from the ancestral reptilian stock separately from romeriids, as did limnoscelids.

¹ John Clark began this work in the early 1950's, but died before the paper was completed.

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Introductory note. Much of the careful and thorough preparation of the romeriids described in this paper was accomplished by John Clark while he was a graduate student at Harvard between 1948 and 1954. He also made many preliminary drawings of the specimens and had begun description of several species as a basis for his Ph.D thesis. This work was continued by Mr. Clark at Marietta College where he taught for a number of years. Study of these specimens was interrupted by Mr. Clark's death in 1967. In 1968, Dr. Romer asked me to prepare this material for publication. In general, the scope of this paper corresponds with that of John Clark's preliminary work. Because research on the origin of reptiles and the anatomy of Pennsylvanian romeriids has been published by other authors since the initiation of Mr. Clark's thesis, some of the broader phylogenetic problems that he was considering are not discussed in this paper. Nevertheless, his extensive work with this material fully justifies his recognition as senior author.

Robert L. Carroll

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INTRODUCTION

The earliest known reptiles and the ancestors of most, if not all, advanced members of the class are included within the Family Romeriidae. This family was first recognized by L. I. Price (1937) in his description of skulls from the Lower Permian of Texas. Other specimens, also discovered by Price, were assigned to this group by Watson (1954). Subsequently, a number of species from the Pennsylvanian have been described as members of this family (Carroll, 1964, 1969a; Carroll and Baird, 1972). Despite their great taxonomic significance, the Permian romeriids have never been thoroughly described. The palates and postcranial skeletons have never been illustrated and their relationships to contemporary and derivative groups have been considered only in a cursory manner. The excellent preservation of these specimens enables very detailed illustrations and descriptions to be made, and these in turn provide a basis for specific comparisons with other groups of primitive reptiles.

The Lower Permian romeriids are the youngest known members of a family that can be traced back to the early Pennsylvanian. Although several lineages of Pennsylvanian romeriids can be recognized, the genera described in this paper appear to have a common ancestry within the Permian. This, together with the fact that most are represented primarily by very well-preserved skulls, makes it practical to discuss them separately from the Pennsylvanian members of the family.

Among the material collected by Price, two lineages may be recognized. The more conservative, represented by *Protorothyris*, is a continuation of the main Pennsylvanian lineage of *Hylonomus* from the Westphalian B and *Paleothyris* from the Westphalian D. The number of marginal teeth is large, the upper tooth row is horizontal and there are two pairs of "canines" near the front of the maxilla. The other assemblage is first recognized in the Moran Formation (see Figs.

21 and 22 for stratigraphic position of the specimens), contemporary with *Protorothyris*. It is represented by one specimen from that horizon, *Romeria texana* from the Putnam, and others from the Admiral and Belle Plains. This stock demonstrates a transition toward the Family Captorhinidae. The premaxilla is hooked, the tooth row becomes progressively shorter and the canines less pronounced.

The Texas Redbeds, from which most of these specimens have come, represent an area of essentially continuous deposition over some 15 million years of the Lower Permian. The predominant environment is deltaic, but with many subenvironments representing rivers, streams, swamps, and small lakes. It is apparent that few really upland forms are preserved. Reptiles are relatively rare in the early beds, but attain complete dominance by the end of the sequence.

Although individuals are rare, the known romeriids apparently represent quite well the total range of diversity of the group; at least, all the specimens can be fitted into a simple and consistent phylogenetic pattern. Despite the diversity and numerical dominance of their descendents, the romeriids themselves were apparently very rare elements of the Lower Permian fauna, in contrast with their local abundance in the Pennsylvanian.

The species will be described in taxonomic and stratigraphic sequence, beginning with the more primitive of the two genera from the Moran Formation.

ACKNOWLEDGMENTS

We wish to thank Dr. Romer for encouraging us to study these members of the Family Romeriidae and for setting a high standard by his own work with other groups of Paleozoic vertebrates. Dr. Romer further contributed to this paper by preparing the map and stratigraphic section showing the geographical and geological distribution of the specimens described.

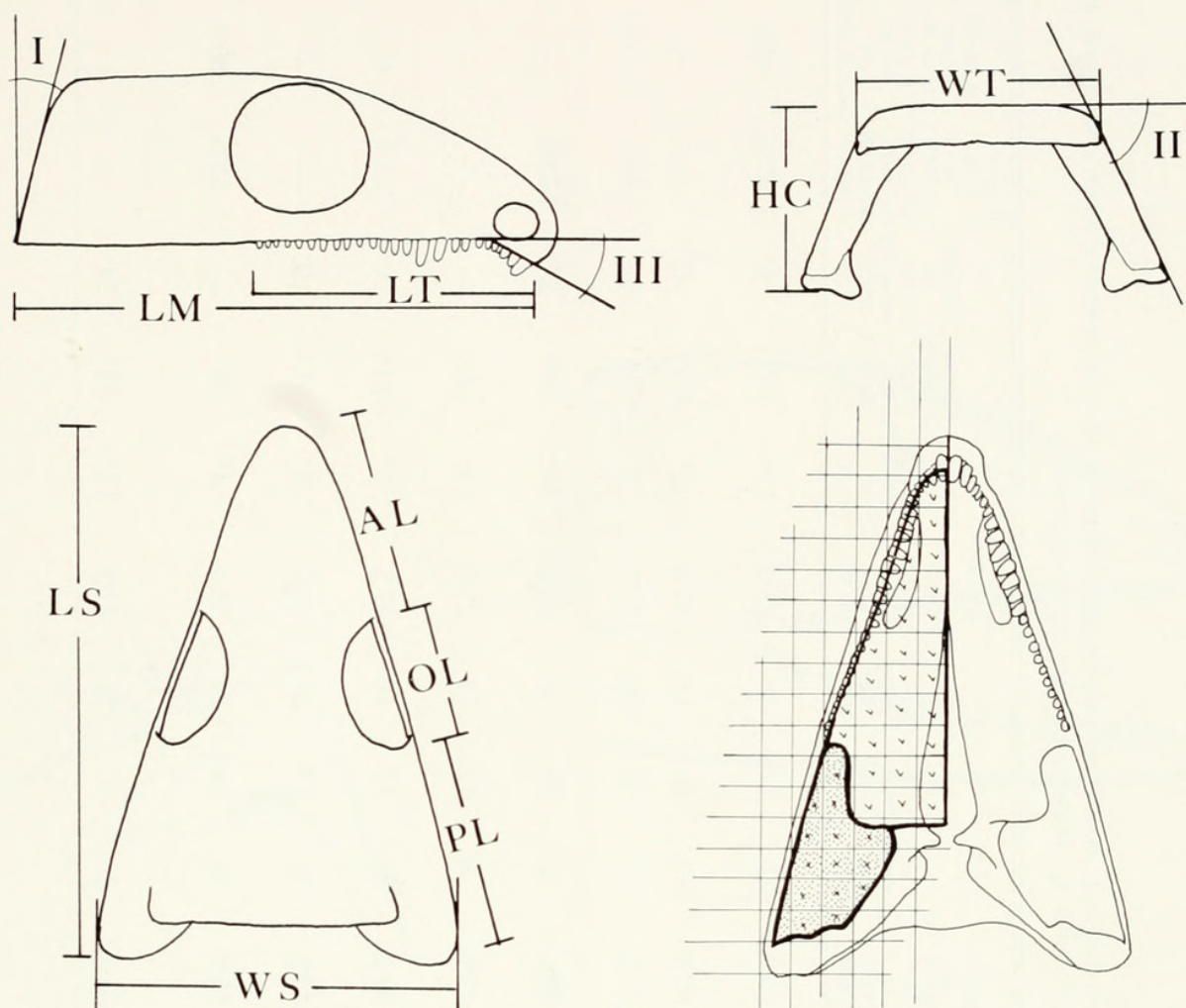


Figure 1. Sketches of romeriid skull showing position of measurements given in Table I. LS—length of skull; WS—width of skull; HC—height of cheek; WT—width of skull table; LM—length of skull margin; LT—length of tooth row; LO—length of orbit; PL—postorbital length; AL—antorbital length; I—angle of posterior margin of cheek; II—angle between cheek and skull table; III—angle of premaxillary tooth row. Area with heavy lines indicated by checks and crosses is measured as total palatal area. Shaded portion is measured as cross section of subtemporal fossa.

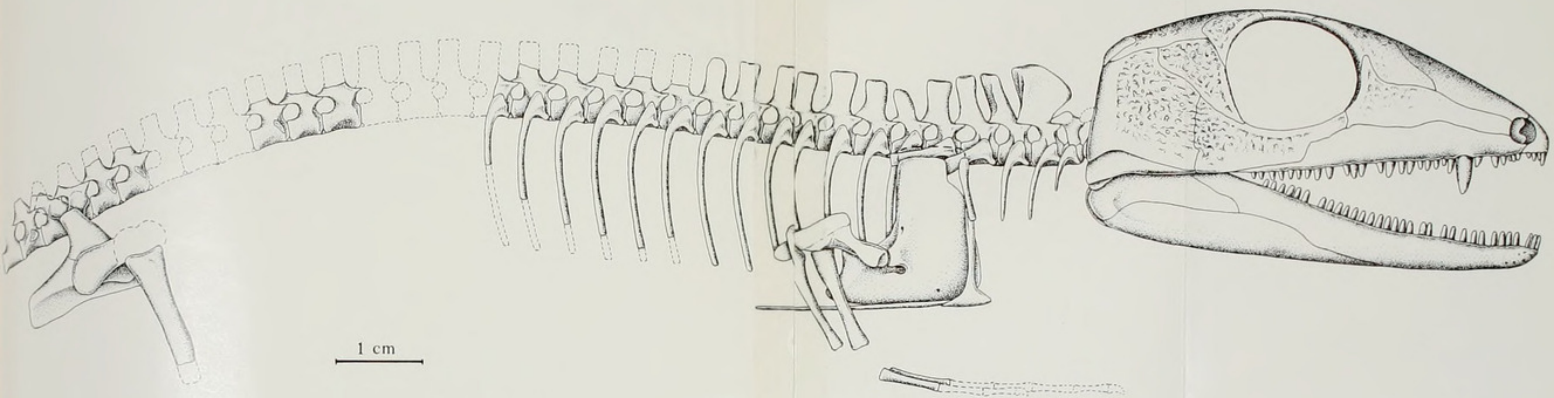
In addition to the material from the Harvard collections, specimens were loaned by Dr. Zangerl of the Field Museum, Chicago; Dr. Langston of the University of Texas, Austin; Dr. Dawson, Carnegie Museum, Pittsburgh; and Dr. Russell, Natural History Museum, Ottawa; for this help we are grateful. Dr. Olson has contributed much information on the romeriids and captorhinids from Oklahoma. Special credit should be given to Mr. L. I. Price, whose keen vision enabled him to discover nearly all of the Lower Permian romeriids from Texas. The illustrations were made by Mrs. Pamela Gaskill; without her careful work, several

more years would have been necessary before this paper could have been completed. Mrs. D. Alison assisted with many technical aspects of the preparation of this paper. This work was supported by grants from the National Research Council of Canada.

Specimens described in this paper are identified by the following museum abbreviations: CM, Carnegie Museum, Pittsburgh; MCZ, Museum of Comparative Zoology, Harvard; UC-CNHM, Field Museum of Natural History, Chicago, including specimens from the University of Chicago; UT, University of Texas, Austin.

TABLE I. MEASUREMENTS OF THE SKULL OF ROMERIDS AND CAPTORHINIDS, MADE PRIMARILY ON THE BASIS OF THE RESTORATIONS. POSITIONS OF MEASUREMENTS INDICATED ON FIGURE 1. MEASUREMENTS IN MILLIMETERS.

	Length of skull	Width of skull	Height of cheek	Width of skull table	Length of skull margin	Length of tooth row	Ratio of tooth to margin	Length of orbit	Antorbital length	Postorbital length	Ratio of orbit length to skull length	Angle of posterior margin of cheek	Angle between cheek and skull table	Angle of premaxillary tooth row	Proportion of palate occupied by subtemporal fenestrae	Area of lower jaws as a proportion of palatal area
<i>Protorothyris archeri</i>	56	31	20	21	56	37	66%	16	22	18	28%	17°	67°	0°	27%	45%
<i>Protorothyris morani</i>	35	21	13	13	35	21	60%	13	12	10	37%	8°	68°	0°	—	—
<i>Romeria primus</i>	57	38	22	24	53	29	51%	17	17	22	30%	5°	70°	26°	31%	43%
<i>Romeria texana</i> type	58	38	19	25	55	31	56%	15	20	23	26%	14°	66°	25°	33%	—
<i>Romeria texana</i> juvenile	33	21	12	16	32	15	47%	9	11	13	27%	13°	68°	—	—	—
<i>Protocaptorhinus pricei</i> type	52	37	15	24	49	29	59%	14	17	19	27%	2°	61°	19°	37%	60%
<i>Protocaptorhinus pricei</i> MCZ 1160	57	38	17	24	57	28	49%	13	17	26	23%	5°	61°	19°	—	—
Type of "Parioticus laticeps"	69	58	20	31	72	38	55%	19	24	29	28%	4°	56°	—	38%	60%
Clyde "Labidosaurus" CNHM-UC 183	121	79	38	42	122	62	51%	26	47	52	21%	14°	61°	34°	—	—



(Fold out). Restoration of the skeleton of *Pratorothyris rcheri*, based primarily on the type. $\times 1\frac{1}{2}$.

SYSTEMATIC DESCRIPTIONS

Class REPTILIA

Subclass ANAPSIDA

Order Cotylosauria

Suborder Captorhinomorpha

Family ROMERIIDAE

Genus *Protorothyris* Price 1937

Type species *Protorothyris archeri* Price

Melanothyris Romer, 1952: 92.

Revised generic diagnosis. Large romeriid captorhinomorph. Primitive pattern of bones of skull roof. Both tabular and supratemporal retained. Bones marked by uniformly distributed shallow pits. Posterior margin of the parietal deeply embayed for postparietal and tabular. Postorbital does not extend onto skull roof. Premaxilla not down-turned. Primitive marginal dentition. Twenty-four to 30 maxillary teeth, two pairs of enlarged "canines." The ventral margin of the transverse flange of the pterygoid bears a row of large denticles. Ectopterygoid present. Ossified portion of the opisthotic does not reach squamosal. No retroarticular process. Axis intercentrum not a separate ossification. Skull equal in length to 12 to 14 trunk vertebrae. Neural spines tall and narrow, not sculptured. Two sacral vertebrae. Humerus lacking supinator process and entepicondylar ridge. Scapulocoracoid ossified as a single unit. Two species known, *P. archeri* from the Lower Permian of Texas and *P. morani* from the Dunkard of West Virginia.

Protorothyris archeri Price

Figures 2-6 and fold-out

Protorothyris archeri Price, 1937: 98.

Specific diagnosis. Same as for genus, except that there are 29 to 30 maxillary teeth. The length of the teeth increases behind the canines but none in this series is especially larger than those immediately adjacent. Jugal is wide beneath orbit. There are apparently no denticles on the parasphenoid.

Horizon and locality. Moran Formation, Wichita Group, Lower Permian, Cottonwood Creek, Archer County, Texas, about 50 feet below the Sedwick limestone equivalent.

Holotype. MCZ 1532—skull and anterior portion of postcranial skeleton. Referred specimens: MCZ 2149—laterally compressed skull. MCZ 2148—laterally compressed skull lacking snout region. Pectoral girdle and anterior vertebrae. MCZ 2150—dorsoventrally compressed skull and postcranial elements. MCZ 2147—dorsoventrally compressed skull; this specimen could not be located during this study.

Protorothyris archeri is represented by five specimens, all from a single locality in the Moran Formation, Lower Permian of Texas. All were collected by L. I. Price, who described the first specimen in 1937 as a member of a new family, Protorothyridae. One specimen (MCZ 2150) is very poorly preserved and has been only partially prepared. The description of the species is based primarily on the remaining animals. Two skulls are compressed laterally and two dorsoventrally. All are substantially the same size. The restoration is based primarily on the type, with details contributed from the other specimens.

Skull. The skull, like those of *Hylonomus* and *Paleothyris*, is long and narrow. The significance of this feature will become more evident when the lineage including the genus *Romeria* is discussed. The height of the cheek region is roughly equal to the width of the skull table. The width at the quadrates is approximately 50 percent greater than that of the skull table. The total length of the type skull is 56 mm, the width at the quadrates, 31 mm. The orbits are situated slightly posterior to the middle of the skull. The cheek region and skull roof are uniformly sculptured with a pattern of evenly distributed pits and grooves. The pattern is more pronounced than in any of the Pennsylvanian romeriids. The anterior portions of the nasal and the lacrimal, as well as the maxilla and premaxilla, are

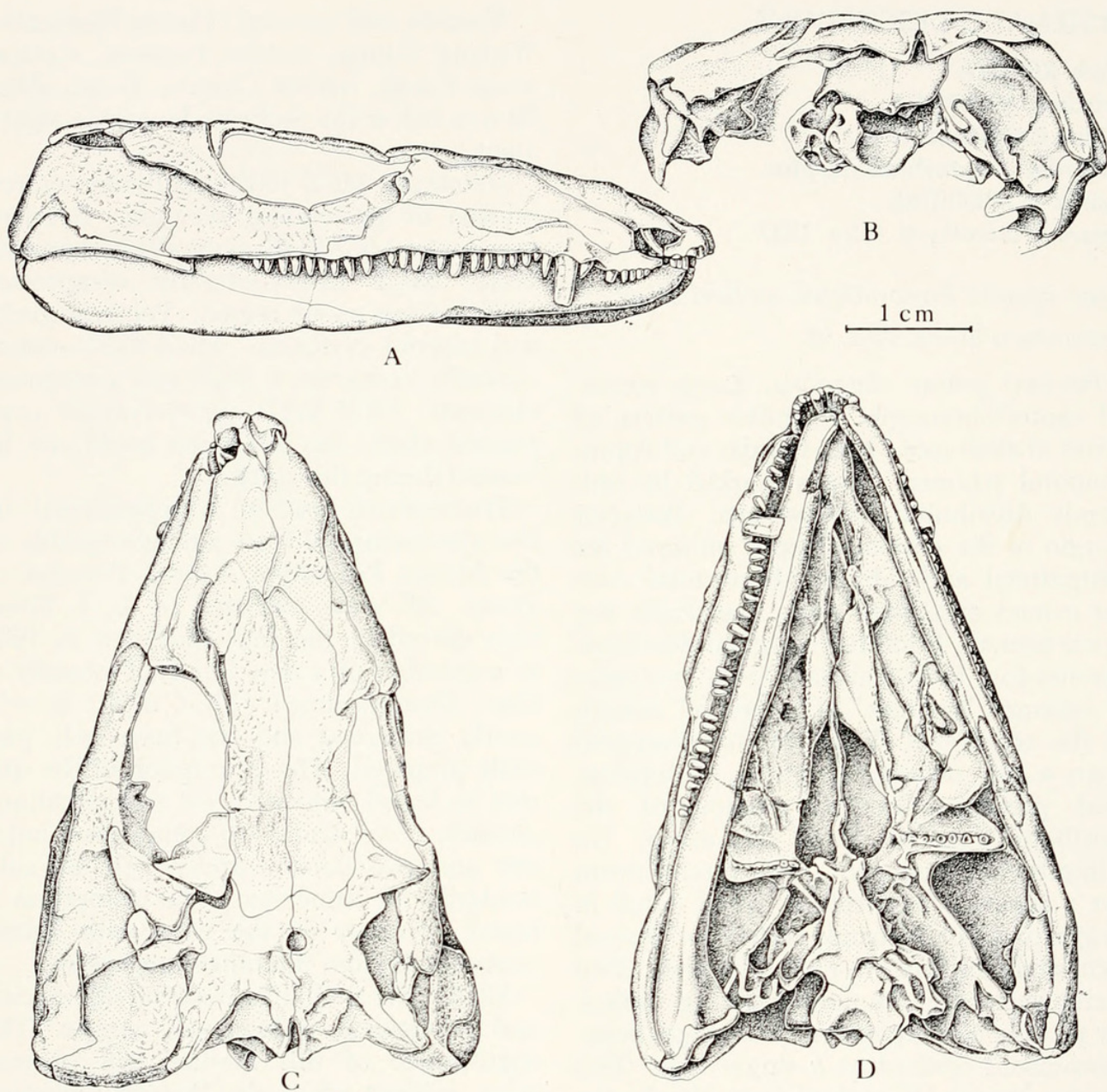


Figure 2. *Protorothyris archeri*. Skull is A, lateral; B, occipital; C, dorsal; and D, palatal views. Type MCZ 1532. $\times 1\frac{1}{2}$.

nearly smooth. The pattern of the bones of the skull roof is very similar to that noted in *Paleothyris* and *Brouffia*. The configuration of the individual elements is somewhat different, however. The parietals are very deeply embayed posteriorly for the postparietals, with the dorsal surface of the bone extending posterolaterally as a narrow process to the corner of the skull table. The parietal embayment is presumably developed to accommodate a forward extension of the axial musculature.

The tabulars and postparietals are themselves insubstantial bones of little structural significance. For most, if not all, of their extent they are underlain by the parietals. The postparietals are thin sheets of bone that are readily displaced. The tabular has no connection with the braincase, nor does it serve to strengthen the attachment of the skull roof to the cheek region. It appears to be little more than a relict from an earlier stage of evolution. The supratemporal is a narrow strip of bone, supported dorsally

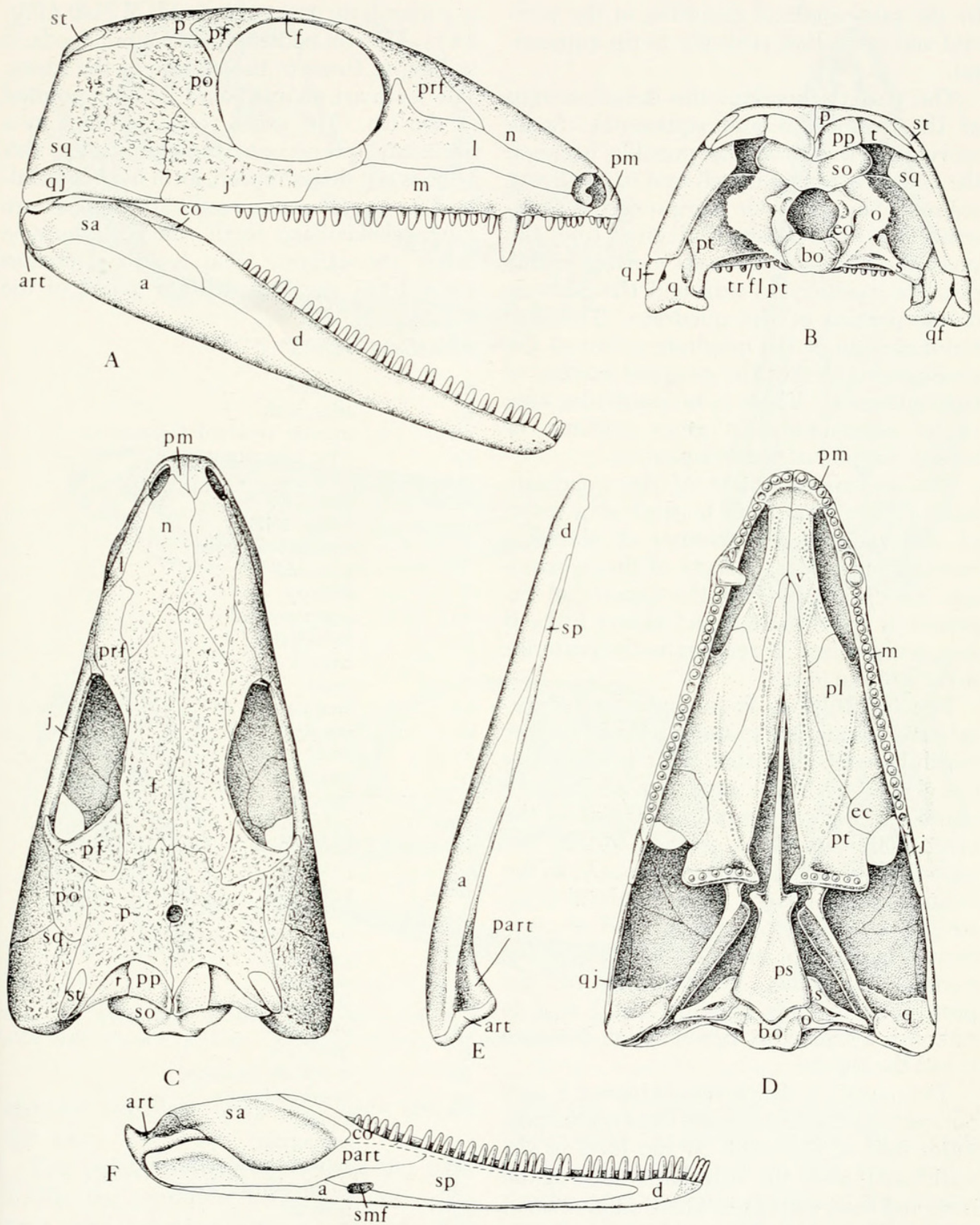


Figure 3. *Protorothyris archeri*. Restoration of skull, based primarily on the type. A, lateral; B, occipital; C, dorsal; and D, palatal views of the skull. E and F, ventral and medial views of lower jaw. $\times 1\frac{1}{2}$. Abbreviations indicated on page 360.

by the posterolateral extension of the parietal and extending ventrally to the squamosal.

The parietal overlaps the dorsal margin of the postorbital and squamosal. Some movement was probably possible between the cheek region and skull roof in the living animal. The posterior margin of the squamosal is no more than 17 degrees from the vertical. The bone extends a considerable distance medially to surround the posterodorsal portion of the quadrate. The posterior margin of the quadrate ramus of the pterygoid underlies the occipital portion of the squamosal. There is no particular area of the squamosal that gives evidence of having supported the tympanum.

The superficial extent of the quadratojugal differs from skull to skull as a result of the variable preservation of the thin overlapping ventral margin of the squamosal. Except posteriorly, the superficial exposure is quite limited and shows little, if any, sculpturing. It reaches to the posterior margin of the jugal.

The jugal differs from that of all Pennsylvanian romeriids in the relatively greater width beneath the orbit. This is related to the absolutely larger skull size of *Protorothyris* and the relatively smaller size of the orbit. The bone also extends further anteriorly than in the smaller forms. As in the Pennsylvanian genera, the postorbital is restricted to the cheek region and is overlapped by, but not suturally attached to, the parietal. In other Permian genera, the postorbital extends onto the skull roof to establish a somewhat firmer union between it and the cheek.

The maxilla is distinctive in having a very narrow superficial exposure beneath the posterior half of the orbit. At the level of the sixth tooth from the rear, the width of the bone suddenly increases. There are five small teeth at the front of the maxilla, two much larger "canines," and room for 23 "cheek teeth"; the length of these teeth is greatest in the middle of the series and decreases gradually, anteriorly and posteriorly. This

is particularly noticeable in MCZ 2149 (Fig. 4A). The immediate post-canine tooth is as long as those in the middle of the series. The teeth are simple cones, bluntly pointed at the tip. The tooth row continues in a horizontal plane onto the premaxilla; this bone is not down-turned, as in more specialized Lower Permian romeriids. There are four premaxillary teeth, the anteriormost being the largest. The length decreases toward the maxilla, with the length of the

ABBREVIATIONS

a	angular
aa	atlas arch
acf	anterior coracoid foramen
ap	atlas pleurocentrum
art	articular
axa	axis arch
bo	basioccipital
cf	coracoid foramen
co	coronoid
d	dentary
ec	ectopterygoid
eo	exoccipital
f	frontal
j	jugal
l	lacrimal
m	maxilla
n	nasal
o	opisthotic
p	parietal
part	prearticular
pf	postfrontal
pl	palatine
pm	premaxilla
po	postorbital
pp	postparietal
prf	prefrontal
proa	proatlas
ps	parasphenoid
pt	pterygoid
q	quadrate
qf	quadrate foramen
qj	quadratojugal
s	stapes
sa	surangular
sgf	supraglenoid foramen
smf	submeckelian fossa
sp	splénial
sq	squamosal
SR	sacral rib
st	supratemporal
t	tabular
tr fl pt	transverse flange of pterygoid
v	vomer

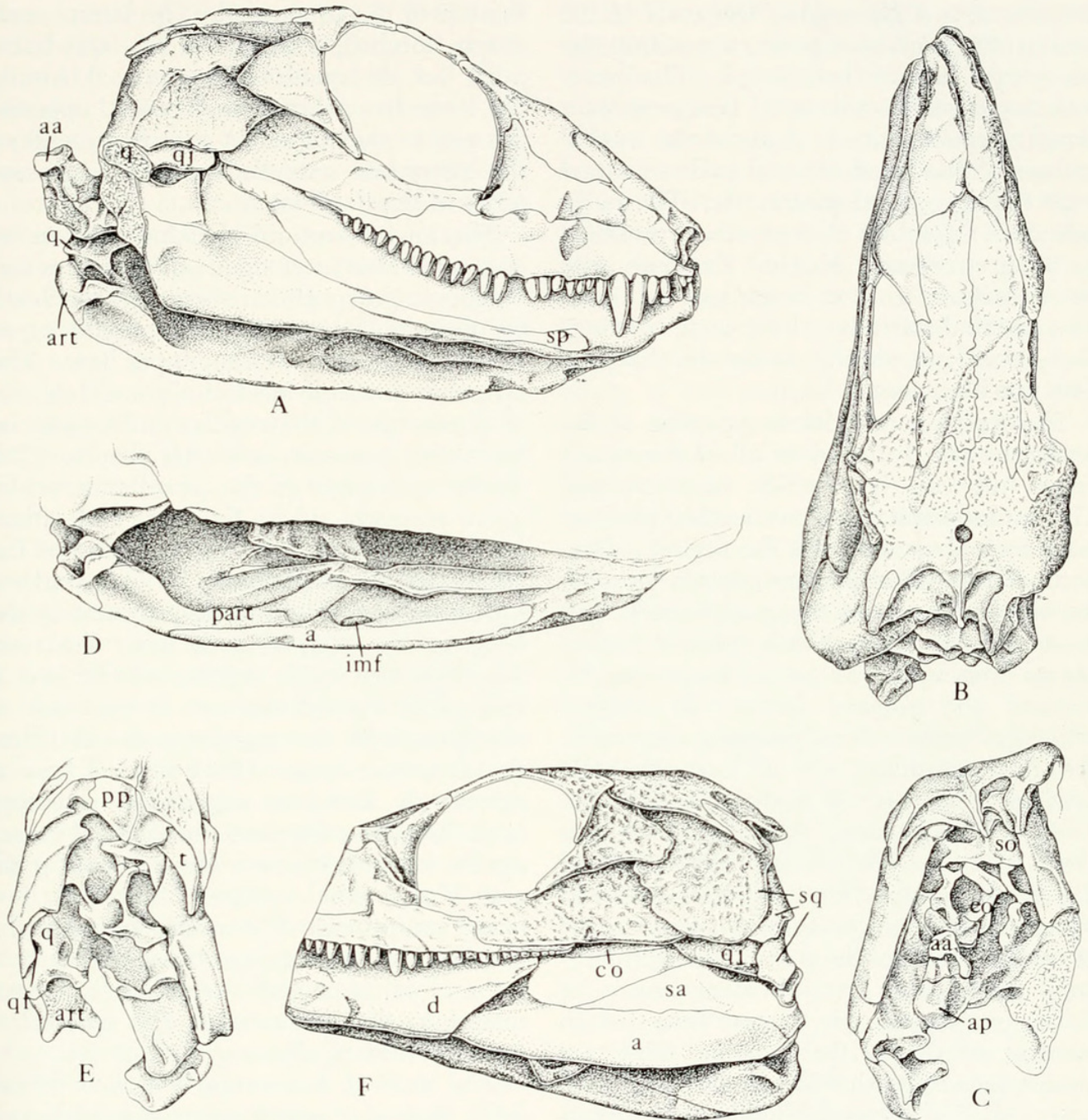


Figure 4. *Protorothyris archeri*. A–D, lateral, dorsal, and occipital views of skull and medial view of lower jaw, MCZ 2149. E and F, occipital and lateral views of skull, MCZ 2148. $\times 1\frac{1}{2}$.

anterior maxillary teeth increasing toward the rear.

The palate is well exposed in the type. Unlike the condition in *Captorhinus*, a distinct oval ectopterygoid is retained. The transverse flange of the pterygoid bears a row of large teeth. Finer rows of denticles extend from the basicranial articulation obliquely laterally toward and onto the

palatine. A second row runs anteriorly, near the midline toward the vomers. The vomers carry a continuation of this row and a further row along the margin of the internal nares. There are narrowly triangular interpterygoid vacuities which extend for one-half of the length of the pterygoids. Anteriorly, the portion of the pterygoid medial to the longitudinal row of denticles extends

dorsally at a slight angle. The ends of the pterygoids come to a point, separating the vomers for half of their length. The quadrate ramus of the pterygoid continues as a broad vertical plate to support the medial surface of the quadrate and makes contact with the squamosal posteriorly. The parasphenoid resembles that of other romeriids in its proportions. Neither the body nor the cultriform process bears any denticles. The internal nares are long oval openings that extend posteriorly to the level of the 14th maxillary tooth.

The occiput and posterior portion of the braincase are distorted in all of the specimens but can be readily reconstructed. The supraoccipital is a wide, thin plate of bone incised ventrally for the foramen magnum. The ossified portion extends laterally beyond the limits of the postparietals, but does not make contact with either the tabular or squamosal. There are large, but ill-defined posttemporal fossae. In contrast with the known Pennsylvanian romeriids, the otic capsules are at least partially ossified. They appear incomplete laterally. They extend toward the squamosal, but there is no evidence that they reached the cheek region. Ventrally, the opisthotic forms the posterior margin of a large fenestra ovalis. Neither the proötic nor epipterygoid can be seen in these specimens.

The exoccipitals are narrow bones, each bearing a facet for the proatlas. They are almost indistinguishably fused to the basioccipital. The stapes follow the typical pattern in early reptiles, with a broad footplate fitting into the large fenestra ovalis and braced by the parasphenoid ventrally. There is an oblong stapedial foramen just proximal to the dorsal process. The stem extends as a stout rod toward the quadrate.

The quadrate, like that of other romeriids, has a broad articular surface, separated into a large lateral condyle and a transversely elongate oval medial knob. The anterior portion of the surface is obscured in all the specimens. Dorsally, the bone narrows to a thin blade that extends nearly to

the top of the squamosal. The lateral margin is notched, adjacent to the quadratojugal, for the quadrate foramen. Medially the bone has a broad depression, opposite the end of the stapes. A narrow process of the pterygoid extends ventrally, just anterior to this depression.

The lower jaws are clenched shut in all specimens, but most significant features can be seen. No specimen shows all the teeth in place, but a count of 35 would agree closely with that in the upper jaw. The articular is visible posteriorly and laterally at the margin of the angular and surangular but there is no retroarticular process. The medial extension of the articular provides space ventrally, where this bone is sheathed by the prearticular, for the insertion of the pterygoideus musculature. The prearticular extends anteriorly to approximately the level of the eighth tooth from the rear. Much of the inside surface of the jaw is formed by the splenial. At the junction of this bone with the angular is the small in-frameckelian fossa. The coronoid area is not clearly visible in any specimen, except laterally, where the posterior element makes up the margin of a very low coronoid process. The external surface of the lower jaw is not sculptured. The suture between the angular and surangular is very difficult to see and so its course can only be approximated in the restoration. The splenial is not exposed laterally.

The skull of *Protorothyris archeri* differs from that of Pennsylvanian romeriids primarily by its greater size (compare with Table I in Carroll and Baird, 1972). The greater extent of the jugal beneath the orbit is a consequence of the relatively smaller size of the orbit. The deep posterior embayment of the parietals for the greater anterior extent of the axial musculature is a further distinguishing characteristic. On the basis of the current fossil record, this genus is the last known member of this particular romeriid lineage.

Postcranial skeleton. Postcranial elements are known for three specimens of *Protoro-*

thyris archeri: the type, MCZ 2149, and MCZ 2150. Much of the skeleton is represented, except for the feet and the tail. The anterior 18 vertebrae are preserved in the type, as well as a series of three from the more posterior trunk region and two from immediately anterior to the sacrals. The minimum number of 23 presacrals may well be too short. The column is restored as having 29, the number in the largest of the Pennsylvanian romeriids, *Coelostegus*. As was noted in the earlier members of the family, the ratio of head to trunk increases in proportion to the total body size. In *Protorothyris* the head was approximately 50 percent the length of the presacral column.

The basic structure of the vertebrae resembles that of *Paleothyris*. Neither the proatlas nor the atlas intercentrum is visible, but the remainder of the atlas-axis complex is typical of romeriids. The left atlas arch in the type is crushed down on the axis arch. The posterior portion of the right is present in MCZ 2149, atop a broken pleurocentrum. Although not well preserved, these elements can be restored according to the pattern in other romeriids. The axis is well shown in the type. The spine is a large, hatchet-shaped structure, very similar in configuration to that of the pelycosaur *Ophiacodon*. The anterior margin overhangs the atlas arch. The posterior edge tips slightly posteriorly from the vertical and shows a series of grooves for attachment of the interspinous ligaments. The arch is indistinguishably fused to the centrum. As can be seen in dorsal view (Fig. 5), the transverse processes of the axis and other anterior vertebrae are very long. Their total lateral extent is nearly twice the width of the zygapophyses. All of the preserved trunk vertebrae have much longer neural spines than those of other romeriids. They are not expanded anteroposteriorly as in *Anthracodromeus*, however.

The elongation of the anterior spines can be associated with the need for additional support of the disproportionately large

skull. The spine of the sixth vertebra in the type is shorter and rounded dorsally, rather than having a constant width. This modification would have allowed greater dorsal flexure of the neck. Such specialization is noted in other romeriids as well, but may affect different vertebrae (e.g., the third in *Anthracodromeus*). In MCZ 2148, the atlas and axis are not preserved. Judging from the configuration of the ribs, the first vertebra preserved in the third. The spine is almost nonexistent. This may be a peculiarity of this particular specimen, or indicate a range of variability in which one of the cervical vertebrae is specialized to allow flexure. None of the more posterior cervicals in this specimen is so modified.

The length of the transverse processes decreases posteriorly. Throughout the column the arches and centra are firmly attached without evidence of suture. Small crescentic intercentra are in place throughout the column.

Several vertebrae are associated with the pelvic girdle. The two presacrals are badly crushed, obscuring the structure of the neural spines. The sacrals resemble those of *Paleothyris*, in that the more anterior bears the principal sacral rib and the second has a smaller supporting role. These vertebrae in *Protorothyris archeri* are too poorly preserved to distinguish them from those of the trunk region. Two poorly preserved vertebrae are present behind the sacrum. The spine of the first is apparently complete but is half the length of those in the cervical region. As in most romeriids, the major portion of the tail is missing.

All the ribs have clearly separated heads. This is particularly conspicuous in the cervicals, in which the transverse processes are particularly long. The first three ribs have narrow shafts that probably extended ventrolaterally, as do those in pelycosaurs, although their original orientation is difficult to reconstruct from the crushed specimens. The fourth and fifth ribs have wide shafts and definitely extended posterolaterally to form extensive supports for the endo-

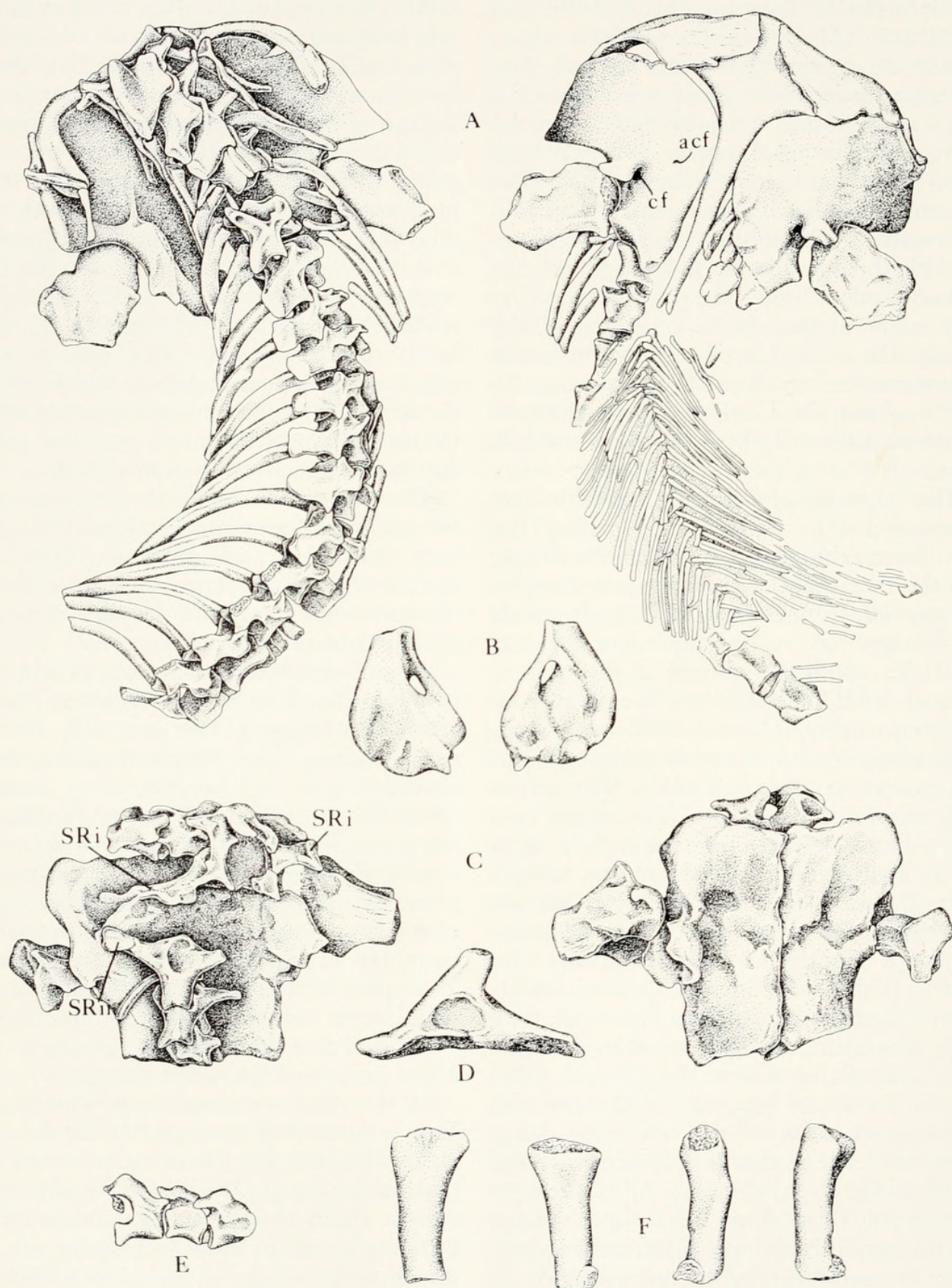


Figure 5. *Protorothyris archeri*. Postcranial elements of type, MCZ 1532. A, shoulder girdle and anterior axial skeleton in dorsal and ventral views. B, dorsal and ventral views of distal end of left humerus. C, dorsal and ventral views of sacral vertebrae and pelvis. D, lateral view of left side of pelvic girdle. E, three posterior trunk vertebrae. F, left tibia in anterior, posterior, medial, and lateral views. $\times 1\frac{1}{2}$.

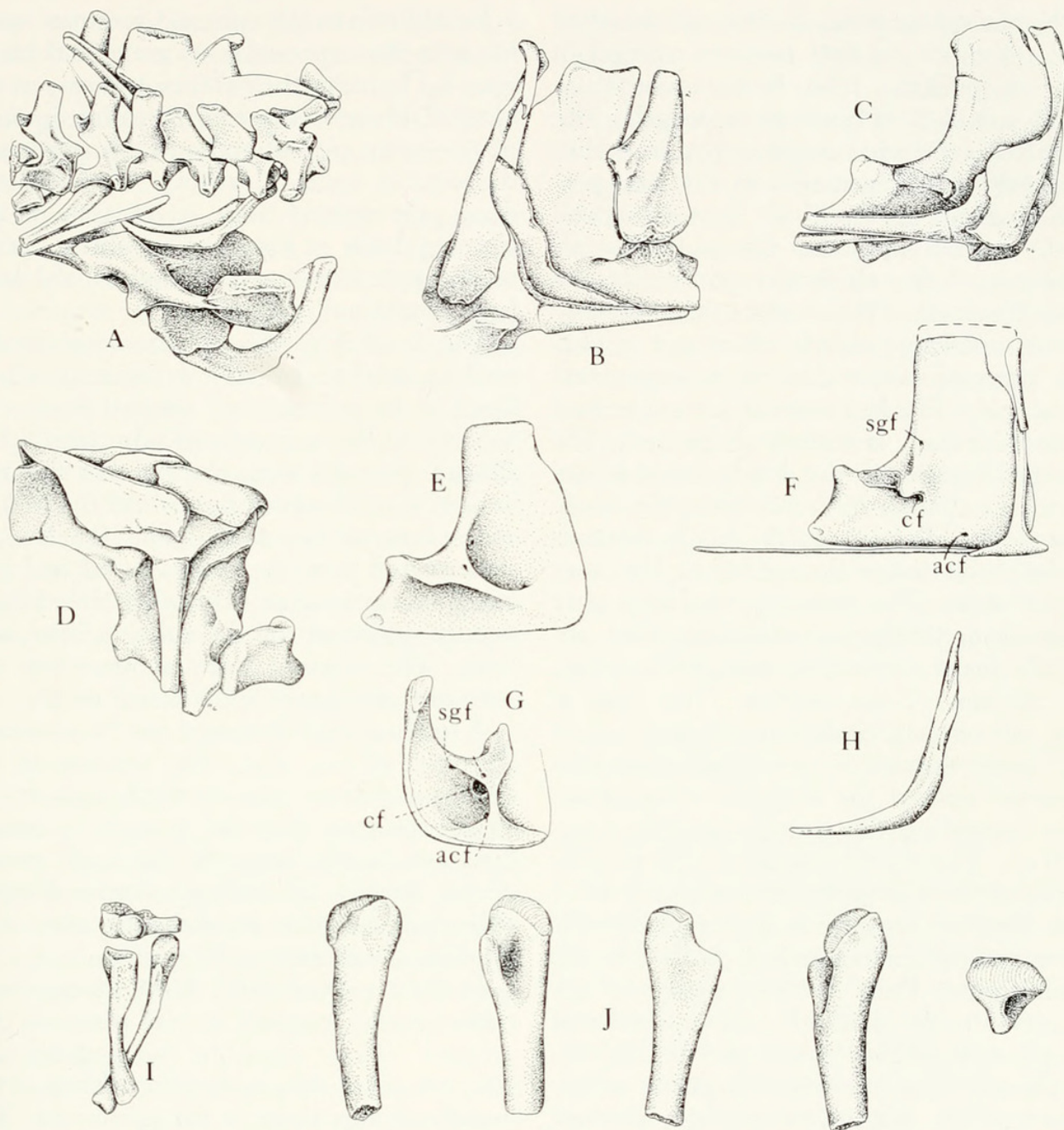


Figure 6. *Protorothyris archeri*. Postcranial elements. A, B, C, and D, various views of shoulder girdle, MCZ 2148. E and F, restoration of shoulder girdle in medial and lateral views. G, obliquely anterodorsal view of the scapulocoracoid showing position of foramina on medial surface. H, anterior view of left clavicle. I, ventral view of distal end of humerus, ulna, and radius, MCZ 2150. J, dorsal, ventral, anterior, posterior, and proximal views of femur, MCZ 2150. $\times 1\frac{1}{2}$.

chondral shoulder girdle. Most, if not all, of the ribs in the trunk region are incomplete distally. The pattern shown in the skeletal restoration is based on the maximum length of the ribs preserved. No ribs are present between the eighteenth trunk vertebra and the sacrum. The pattern of the sacral ribs is evidently similar to that described in *Paleothyris*, although the preservation here

is too poor for further elaboration. No caudal ribs are preserved.

The shoulder girdle is superbly shown in the type and MCZ 2149 (Figs. 5 and 6). It does not differ substantially from that of *Paleothyris*, but some details are more clearly shown. The cleithrum is a simple, compressed rod of bone fitting into a well-defined groove at the anterolateral margin

of the clavicular stem. It was not attached to the scapula, as that bone is ossified in these specimens. The lateral margin is gently rounded throughout its length. The clavicle is somewhat simpler than in earlier romeriids and pelycosaurs in that the posterior margin of the shaft does not swell out to form a superficial flange for the attachment of the clavicular portion of the deltoid muscle. The entire shaft is very narrow anteroposteriorly. It is not noticeably grooved posteriorly to accommodate the scapula, but lies entirely lateral to that bone. The blade is slightly sculptured. The anterior margin of the blade extends anteriorly at about a 15° angle from the transverse plane. Posteriorly the blade expands to about six times the width of the very narrow stem. The interclavicle has a very wide, diamond-shaped plate, recessed anteriorly for the clavicles, except for a narrow isthmus at the midline. The stem is long, narrow, and forked at the tip.

The scapulocoracoid is ossified as a single element, without the slightest trace of sutures separating the scapula and the coracoid(s). The dorsal margin of the scapula as preserved was probably continued for a short distance dorsally in cartilage, but this portion of the endochondral girdle remains much shorter than its counterpart in any pelycosaur. As ossified, the anterodorsal margin of the blade is recessed behind the cleithrum. The posterior margin is essentially vertical. Anteroventrally, the coracoid portion bulges beyond the clavicular stem. The coracoid regions curve strongly medially from each side to approach each other at the midline, at least anteriorly. The glenoid is short, with the anterior margin slightly below the posterior, but otherwise similar to that of other romeriids and pelycosaurs. Behind it there is a prominent process for the attachment of the coronoid head of the triceps. This structure is common in pelycosaurs, but not reported in other romeriids. The supraglenoid foramen opens just anterior to the supraglenoid buttress, near its apex.

In addition to the coracoid foramen opening (for the supracoracoid nerve and blood vessels) beneath the anterior buttress of the glenoid, there is a second, smaller opening on the more ventral and anterior portion of the anterior coracoid region. As in ophiacodont pelycosaurs, there is an area of unfinished bone at the posteroventral corner of the posterior coracoid that would have been continued in cartilage.

The medial surface of the scapulocoracoid is marked by two prominent ridges. One, as in pelycosaurs, extends vertically, medial to the supraglenoid buttress. The second diverges from the base of the first and runs anteroventrally toward the middle of the anterior coracoid region. It is sharply demarcated from the more ventral and posterior coracoid area. Dorsally, the ridge is deeply undercut for the subcoracoscapular fossa. The coracoid foramen opens into this area just anterior to the vertical ridge.

A further, small foramen can be seen near the apex of the ridge, just anterior to the divergence from the vertical support. A small opening for the anterior coracoid foramen can be seen at the base of the dorsal surface of the anteriorly directed ridge, just posterior to where it merges with the flat anterior coracoid region.

In the type and MCZ 2149, the proximal ends of the humeri are in place in the glenoid. They resemble the general pattern of romeriids and *Captorhinus*. The middle of this shaft is not preserved. The distal end is present in the type and in MCZ 2150. There is apparently neither an ectepicondylar ridge nor a supinator process. In lacking these features the humerus resembles that of *Hylonomus* rather than *Paleothyris* or *Captorhinus*. The preservation is not good in either specimen, however.

The ulna and radius in MCZ 2150 are very lightly built, but not well enough preserved for detailed comparison with other romeriids. The olecranon is ossified and the distal articulating surface is narrow. The carpals are not preserved. Judging

from other romeriids, they were probably ossified, but no evidence is afforded by these specimens. Metacarpals and/or proximal phalanges are preserved in MCZ 2150, but their specific identity cannot be established.

Except for the iliac blades, the entire pelvic girdle is preserved in the type. The basic pattern resembles that of *Hylonomus*, *Paleothyris*, and *Brouffia*, but few surface details are evident. The base of the iliac blade is narrow, but there is no indication of its normal length. The badly crushed heads of both femora are present in each acetabulum. Details can be seen much more readily in MCZ 2150. It resembles closely that of *Paleothyris*. The distal end is not known. The isolated proximal end of a tibia is associated with the type. The general configuration of the femur and tibia suggests that the proportions of the rear limbs were similar to those of *Paleothyris*. Neither tarsals nor any elements of the rear foot are known.

A great many ventral scales are preserved in more or less their natural association in the type. They have the usual open lattice, chevron pattern of primitive reptiles. The proximal end of the medial scales is expanded to overlap with the scale from the opposite side. Each scale is very long and narrow. Two or three ranks are visible posteriorly.

Discussion. *Protorothyris archeri* is the last known member of a conservative romeriid stock going back to the Lower Pennsylvanian. Except for a slight increase in size, it shows a continuation of the basic pattern established by *Hylonomus* and *Paleothyris* in the Lower and Middle Pennsylvanian. The conservative skull proportions and the nature of the dentition indicate a similar diet and manner of catching and consuming the prey throughout this entire period of time. Throughout the skeleton there are sufficient differences to recognize a series of genera, but the basic way of life must have remained nearly constant. The larger body size is the culmination of

a general trend to increased size within the family as a whole. Judging from the body proportions of Pennsylvanian species, the disproportionately large head to trunk ratio is a direct consequence of the overall size increase. Despite the considerable longevity of the lineage, it does not seem to have survived past the earliest Permian. Fossils of a wide range of reptiles and amphibians are common in the later Redbeds of Texas, but no survivors of this particular lineage have been described. Romeriids and their successors are known throughout the Lower Permian but the primitive central stock apparently become extinct prior to the deposition of the Putnam Formation.

Although lepidosaurs and archosaurs probably arose from this particular lineage, these groups apparently evolved from genera of a slightly more primitive morphology than the known Permian forms.

Protorothyris morani (Romer), new combination

Figure 7

Melanothyris morani Romer, 1952: 92.

In a preliminary report, Romer (1952) described a new species of romeriid from the Dunkard Group of West Virginia, *Melanothyris morani*, based on a number of small skulls. No illustrations were included, but he compared the form to the Texas genus *Romeria*. Preparation of this material indicates that the skulls are no more than specifically distinct from *Protorothyris archeri*.

Specific diagnosis. *Protorothyris morani* resembles the type species, *P. archeri*, except for the smaller number of maxillary teeth (24–26 rather than 29–30) and the presence of two teeth noticeably larger than the remainder in the series posterior to the canines. The cultriform process bears a row of small denticles, apparently not present in the type species. All known specimens are small (the skull length ranging from 31 to 34 mm), and are apparently immature. The jugal is narrow beneath the orbit, but

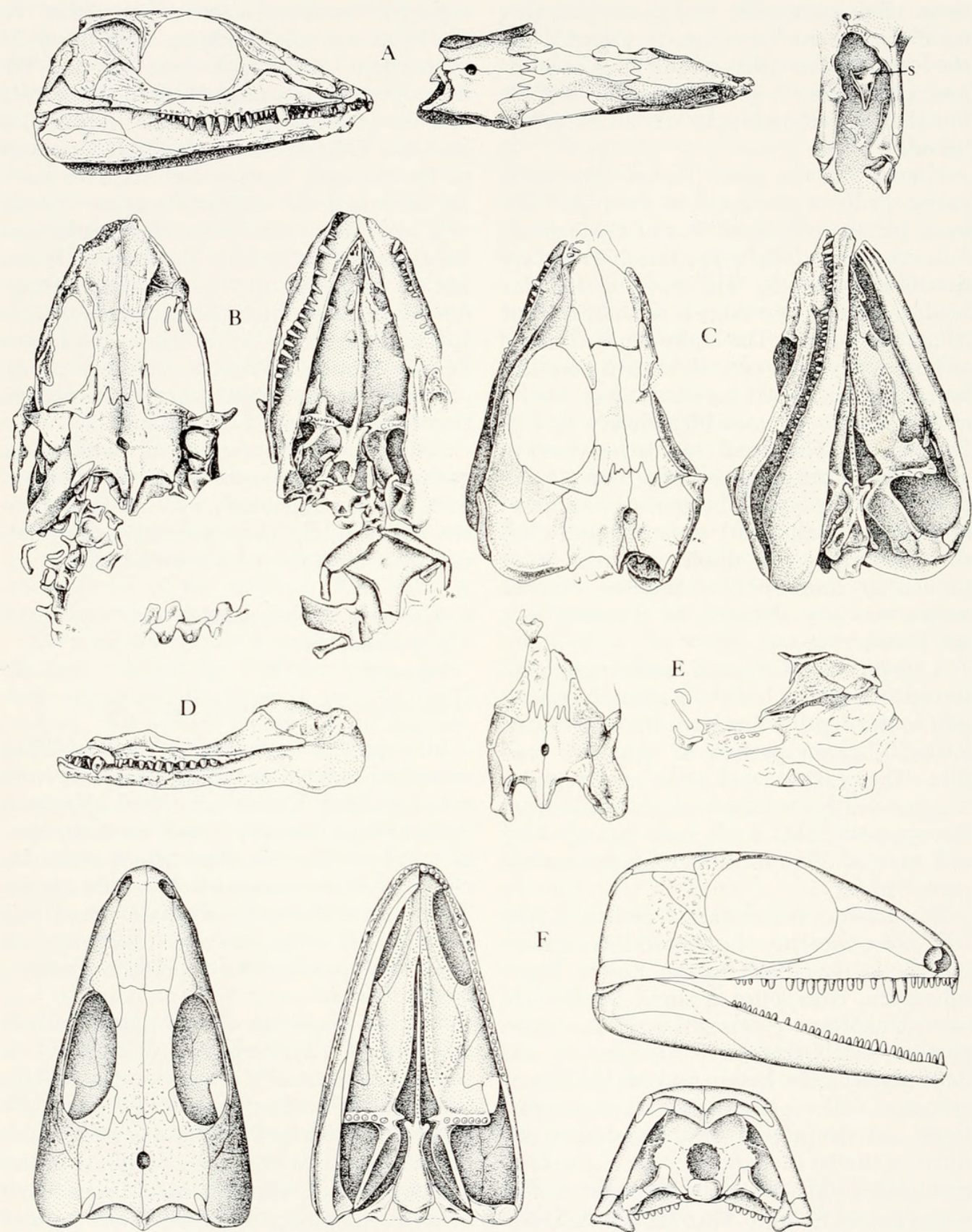


Figure 7. *Protorothyris morani*. A, type, CM 8617, skull in lateral, dorsal, and occipital views. B, MCZ 2151, skull in dorsal and palatal views with associated postcranial elements, anterior neural arches in lateral view. C, MCZ 2152, skull in dorsal and palatal views. D, MCZ 4111, crushed skull. E, MCZ 4110, back of skull in dorsal view and portion of left cheek region. F, restoration of skull, dorsal, palatal, lateral, and occipital views. $\times 1\frac{1}{2}$.

this may be a result of immaturity and not a distinguishing feature from *P. archeri* in the adult.

Locality and horizon. Dunkard locality 9 (see Romer, 1952) near Blacksville, West Virginia. Equivalent to the lower Wichita Group of Texas.

Type. CM 8617. Skull, laterally compressed.

Referred specimens. MCZ 2151, dorso-ventrally compressed skull and associated postcranial material. MCZ 2152, well-preserved skull. MCZ 4110, posterior portion of skull roof and left cheek region. MCZ 4111, badly crushed skull. MCZ 4112, dorsoventrally crushed skull. MCZ 4113, incomplete skull associated with MCZ 2151. Other specimens in the collection of the Carnegie Museum.

The Dunkard species is represented by seven skulls, ranging from 31 to 34 mm in length. All are substantially smaller than the adult specimens of other Permian romeriids. The skulls show some evidence of immaturity (see subsequent discussion), but the adults may have been small as well.

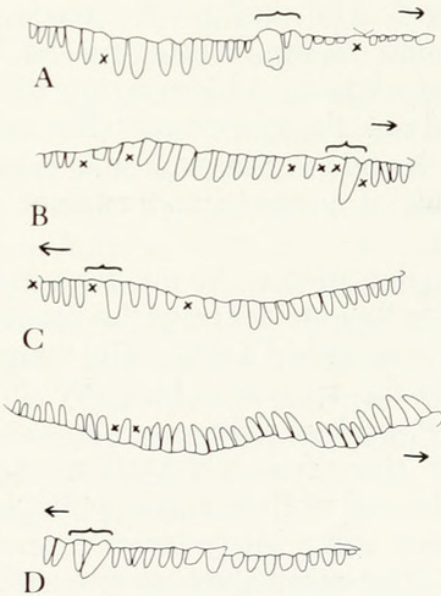
Important similarities seen in *Protorothyris archeri* and the Dunkard form, but not shared with other Permian romeriids, include: tooth-bearing margin of the premaxilla in same plane as that of maxilla. Similar pattern of sculpturing. Canines very prominent. Second peak in length of maxillary teeth behind canine. Ectopterygoid retained. Long teeth on ventral margin of transverse flange of pterygoid. Tabulars present and parietals deeply embayed for reception of postparietals and tabulars. Only the last feature distinguishes *P. archeri* from such Pennsylvanian romeriids as *Paleothyris* and *Brouffia*.

Were the skulls not so well preserved, or had they come from Texas rather than West Virginia, it would be difficult to justify even specific differentiation from *P. archeri*.

Except for the small size and slightly different proportions, the skull is basically similar to that of the type species of *Protorothyris*. One clear-cut difference is the con-

TABLE II. DENTITION OF ROMERIIDS AND CAPTORHINIDS. A-D, *PROTOROTHYRIS MORANI*—SIMPLIFIED DRAWINGS OF DENTITION TO SHOW POSITION OF TEETH BEING REPLACED (X) AND RELATIVE LENGTH OF TEETH IN DIFFERENT REGIONS OF THE JAW. BRACKETS INDICATE POSITION OF CANINES, ARROW INDICATES ANTERIOR END OF JAW. A, MAXILLA AND PREMAXILLA OF CM 8617; B, MAXILLA OF MCZ 2151; C, MAXILLA AND DENTARY OF MCZ 2152; D, MAXILLA OF MCZ 4111. $\times 2$.

	No. of premaxillary teeth	No. of maxillary teeth	Position of canine(s)
<i>Paleothyris acadiana</i>	6	35	8 & 9
<i>Protorothyris archeri</i>	4	29-30	6 & 7
<i>Protorothyris morani</i>	5	24-26	6 & 7
<i>Romeria primus</i>	4	26	26 & 7
<i>Romeria texana</i>	5	20	5 & 6
<i>Protocaptorhinus pricei</i> 1478	5	22	5
<i>Protocaptorhinus pricei</i> 1160	4	18	4
" <i>Parioticus laticeps</i> " type	4	16	4
UC 181 Clyde " <i>Labidosaurus</i> "	4	20	6



sistently smaller number of maxillary teeth (see Table II). This is not simply a result of immaturity, since the small skull of *Romeria texana* has only one less tooth than does the adult, although the size difference is equivalent to that between the Dunkard skulls and *Protorothyris archeri*. Another

difference between the Dunkard skulls and *Protorothyris archeri* is the relatively narrower exposure of the jugal beneath the orbit in the former. This difference is certainly related to size, with all of the circumorbital bones being small in the Dunkard species. Larger individuals might well resemble the Texas species in this feature. *Protorothyris morani* has denticles extending along the cultriform process of the parasphenoid. These are missing on the Texas species, but are present in *Paleothyris* and also in some individuals of *Captorhinus*.

Mechanical preparation of the Dunkard specimens has resulted in the loss of much of the very thin bone from the surface of the skulls. Except on the occipital surface, this has not greatly interfered with determination of the extent of the bones. Although quite delicate, the pattern of sculpturing resembles that of the Texas species. Except for the accommodation of the relatively large orbits, the configuration of the skull bones is very similar to that of *Protorothyris archeri*. The skull table extends posteriorly almost to the level of the back of the jaw articulation. As Parrington (1959) has pointed out, the greater posterior extent of the cheek region in larger forms is probably a result of allometric adjustment during growth.

Since the dentition is the one feature that distinguishes this species from the genotype, it will be described in detail. The marginal dentition of this species is basically similar to that of *P. archeri*. There are apparently five rather than four premaxillary teeth, although the end of the snout is damaged in all specimens and a lower count cannot be ruled out. The most anterior premaxillary tooth is conspicuously larger than the remainder. The first five maxillary teeth are also of small size. These are followed by two very large canines. In most specimens, one or the other is either absent or represented by a very small, immature tooth. The length of the teeth gradually increases behind the canines, to reach a maximum in the area of the sixth to ninth tooth. Two teeth

in this series are noticeably larger in diameter than those adjacent. Such distinctive teeth are not seen in *P. archeri*. The length gradually decreases to the end of the tooth row. The tooth count, the position of gaps in the tooth row, and the position of the longest teeth is shown in Table II. The complete complement of postcanine teeth apparently varies from 17 to 19; the total of maxillary teeth from 24 to 26. This is four to six teeth less than in *Protorothyris archeri*. All of the teeth are cylindrical, with conical, sharply pointed tips.

In only a single specimen, MCZ 2152, is the dentition of the lower jaw well exposed. Twenty-nine teeth are in place; there is room for two additional teeth. As in the upper jaw, the length of teeth is variable. Although there are none as long as the canines, and the overall differentiation is not as clear, peaks are noted at the very front of the jaw, at the ninth and tenth teeth, and to a lesser extent in the area of the 16th and 22nd.

Fragments of at least six vertebrae are in place behind the skull of MCZ 2151. They are badly crushed and too delicate for complete preparation. The neural spines of the third and fourth are tall and narrow, as in the type species, and the transverse processes extend a considerable distance laterally. The total length of the four most completely preserved vertebrae in natural articulation is 10.5 mm from the anterior end of the anterior zygapophyses to the posterior end of the posterior zygapophyses. The skull is thus equal in length to approximately 12 trunk vertebrae. In *Protorothyris archeri* the skull is equal in length to almost 14 complete vertebrae. The measurement of only four vertebrae is probably not sufficient to stress this possible proportional difference, however.

Much of the shoulder girdle is preserved in MCZ 2151. The dermal elements differ from those of the type species only in their smaller size and generally imperfect preservation. The margins of the scapulo-coracoid are broken or obscured by other

bones. The glenoid area resembles that of *P. archeri* in indicating only a single area of ossification. The supraglenoid and coracoid foramina are in the same relative position. Although the dorsal margin of the scapular blade was probably extended in cartilage, its relative height is as great as in *P. archeri*. Only an uninformative fragment of the humerus is present. Nothing is known of the more posterior portion of the skeleton.

Discussion. The chief problem in dealing with *Protorothyris morani* is in determining whether the small size is indicative of immaturity, or whether the specimens represent adults.

Fortunately, a standard of comparison is provided by another romeriid species in which both an adult and a juvenile are known. Only two specimens of the species *Romeria texana* are known; both are figured and described in a subsequent section of this paper. The type is presumably an adult, very similar in size to the several specimens of *Protorothyris archeri*. The second specimen, from a different locality but the same horizon in Texas, has a skull that is only 57 percent the length of the type. Except for the absence of the postparietals, the braincase, and the lower jaw in the type, the skulls are very similar in structure, including the number of teeth in the upper jaw. The smaller skull has relatively larger orbits and a more rounded snout, but no other significant differences. Although incompletely exposed, the endochondral shoulder girdle of the small specimen is ossified as a single unit, in contrast to the obviously juvenile romeriids from the Pennsylvanian, *Cephalerpeton ventriarmatum*, *Brouffia orientalis*, and *Coelostegus*, that show multiple centers of ossification of the endochondral shoulder girdle. The stem of the stapes of the smaller skull of *Romeria texana* is as fully ossified as that of the mature specimens of *Protorothyris archeri*.

Although the skulls of *Protorothyris morani* are as large or larger than that of the

juvenile *Romeria texana*, the orbits are significantly larger, both absolutely and relatively. This feature might be accentuated in a form with a small-sized adult, although it is not noted in *Paleothyris acadiana*. As in the juvenile *Romeria texana*, the scapulo-coracoid of *P. morani* is ossified as a unit. In contrast with that specimen, the stem of the stapes is incompletely ossified. This feature suggests that the specimens of *Protorothyris morani* are at least as immature as the juvenile *Romeria texana* and that the adult might be as large as the adult of that species.

Romeria Price

Type species *Romeria texana* Price, 1937: 97.

Revised generic diagnosis. Large Lower Permian romeriid. Premaxillary tooth row inclined at an angle from the maxillary tooth row. Four to five premaxillary teeth. Twenty to twenty-five maxillary teeth. Fifth and sixth teeth slightly larger than remainder. No tabular, no ectopterygoid. No retroarticular process. Opisthotic incompletely ossified and not extending to squamosal. Cheek region forming an angle of more than 65° with the skull roof. Parietal deeply embayed for postparietals. Where known, short denticles scattered on anterior face of transverse flange of pterygoid rather than long denticles on ventral margin. Low neural spines on anterior vertebrae. Two species are known, *R. texana* from the Putnam Formation and *R. primus* from the underlying Moran Formation, Lower Permian of Texas.

Romeria primus, new species

Figures 8, 9, and 10

From the same locality as the five specimens of *Protorothyris* has come a single skull (MCZ 1963) of a distinct genus that indicates the initiation of a new trend in the evolution of romeriid reptiles—one that culminates in the origin of the distinct family Captorhinidae and may even presage the evolution of turtles. Whereas the tooth

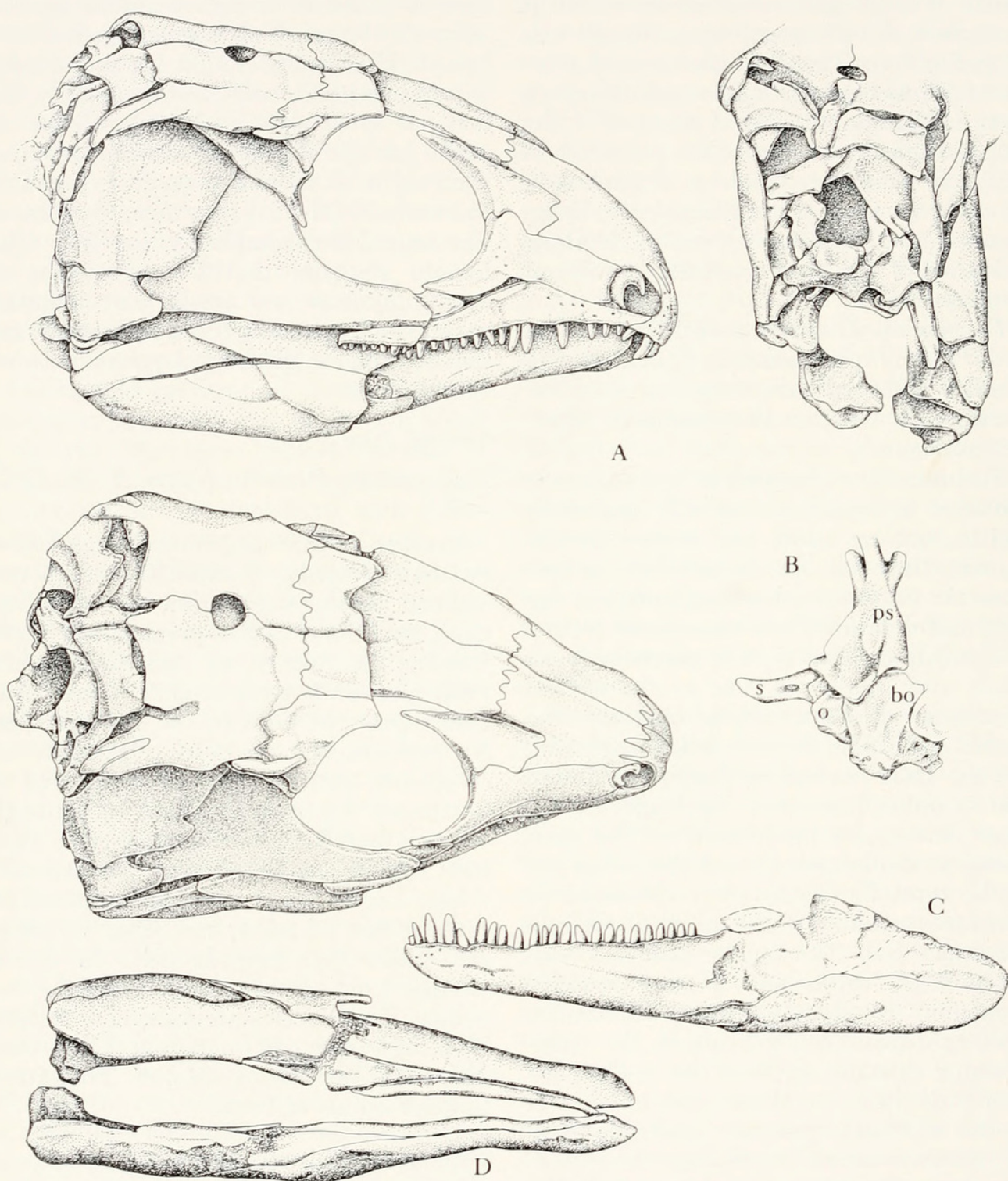


Figure 8. *Romeria primus*, n. sp. Type, MCZ 1963. A, skull in lateral, dorsal, and occipital views. B, braincase in ventral view. C, left lower jaw in lateral view. D, lower jaws in ventral view. $\times 1\frac{1}{2}$.

row in all Pennsylvanian romeriids and *Protorothyris* is straight, the premaxilla of this species and subsequent members of this lineage is down-turned to form a "beak." The canines are less emphasized

and the entire tooth row becomes relatively shorter. The size of the skull remains essentially the same. The changes in dentition indicate that the appearance of this genus was related to a change in prey spe-

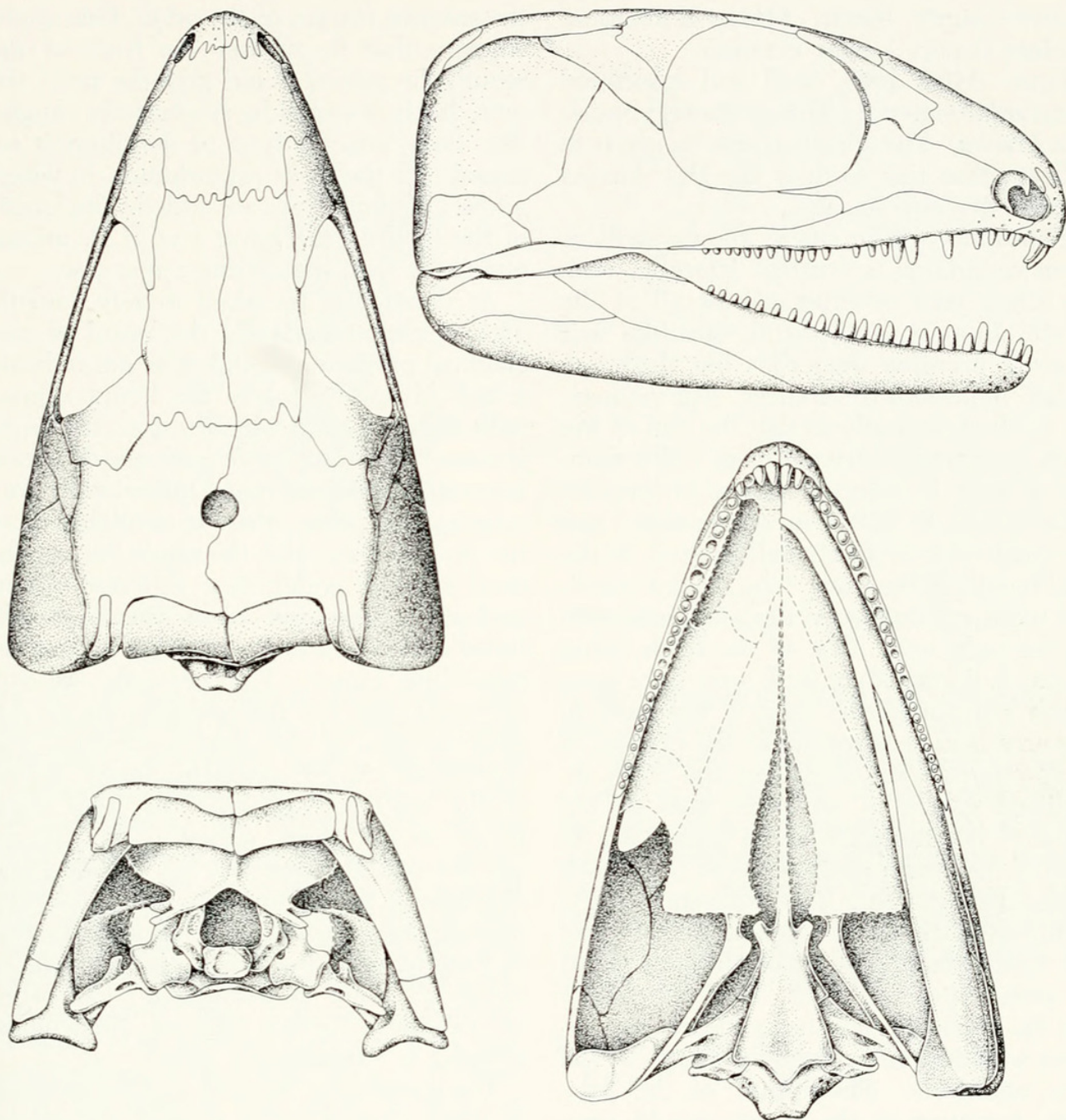


Figure 9. Type of *Romeria primus*, n. sp., MCZ 1963. Restoration of skull in dorsal, lateral, occipital, and palatal views. Smooth appearance of skull roof is not natural. Sculpturing was removed during preparation. Tabulars are missing. There is no evidence for ectopterygoid. $\times 1\frac{1}{2}$.

cies and/or a shift in the way prey was captured and ingested.

The specimen from the Moran is clearly closely related to *Romeria texana* from the overlying Putnam Formation. Although we are limited to comparisons of only one adult specimen from each horizon, the difference in age and dentition seems sufficient to recognize two species. Despite the taxonomic

priority, the new species will be described prior to a redescription of the type species in order to emphasize the phylogenetic and taxonomic sequence of the specimens.

Specific diagnosis. Similar to type species, *R. texana*, except for having five rather than four premaxillary teeth and 23–25 rather than 20 maxillary teeth.

Horizon and locality. Cottonwood Creek,

Archer County, Texas. Moran Formation, Wichita Group, Lower Permian.

Type. MCZ 1963, skull and associated postcranial material. This is the only specimen known. The specific name is given to indicate that this form is the first known member of a new lineage.

Description. The single known skull of *Romeria primus* is crushed laterally, with the lower jaws covering almost all of the palate. In general, the skull resembles that of more primitive romeriids but there are certain important differences. The premaxilla is tilted ventrally so that the end of the tooth row forms a hooked "beak." The number of teeth is reduced to four in the premaxilla and to 23–25 in the maxilla, and the tooth row is shortened relative to the total length of the skull. The longest maxillary tooth, nominally a canine, is the seventh on the right side. One of the teeth being replaced, the fourth or sixth, may have been longer but apparently none of the teeth in this area is as conspicuous as the canines in *Protorothyris*. The length of the teeth diminishes gradually on either side of the "canine" but increases again posteriorly to reach a maximum at the level of the eighth tooth from the rear. The difference in the dentition of these two genera seems relative to the position at which the prey could be most efficiently held. In *Protorothyris* and its Pennsylvanian antecedents, the canines would serve to block the escape of the prey anteriorly. The center of the prey held crossways in the mouth would have been about half way between the anterior margin of the orbit and the external nares. A shallow notch in the tooth row is also evident directly beneath the external nares with the anterior premaxillary teeth elongate to block the egress. The efficiency of this trap is greatly improved in *Romeria primus* by the down-turning of the entire premaxilla. The relative position of the canines now becomes more posterior and would serve as the posterior barrier for the main insect trap and the anterior barrier of a less well-developed notch beneath

the anterior margin of the orbit. One might suppose that the nearer the front of the mouth the animal could grip the prey, the more likely it would be successfully caught. The same general type of dentition is retained into the early captorhinids, in which additional tooth rows are added. The length of the teeth in the lower jaw of *R. primus* alternates with that in the upper jaw.

As illustrated, the skull is very smooth. This is almost certainly the result of mechanical preparation, and does not indicate a lack of sculpturing in the living animal. Although it is difficult to restore the angle between the skull table and cheek region accurately without more information concerning the palate than is available from the skull as preserved, the whole back of the skull appears wider than in *Protorothyris* and earlier romeriids. There are a few additional differences in the configuration of the individual bones. The parietals are still embayed, but the postparietals do not extend anterior to the supratemporals. The postorbital extends onto the dorsal surface of the skull roof to bind the table more firmly to the cheek region. The tabulars are lost and the postparietals extend laterally toward the squamosals. The quadratojugal appears shorter and higher than that of *Protorothyris*, but this is probably not an important point of distinction. The orbits are relatively further forward. The pineal opening is considerably larger.

The crushing of the skull and the presence of lower jaws obscures most of the palate. The posterior portion of the braincase, the parasphenoid, and stapes can be seen at an oblique angle between the jaws (Fig. 8B). This area is substantially similar to that of both other romeriids and *Captorhinus*.

In occipital view, the opisthotics can be seen to be more fully ossified than in *Protorothyris*, but the exposure of the ventrolateral portion of the supraoccipital suggests that the otic capsule was still not completely ossified. The supraoccipital is a broad plate of bone, possibly reaching as far as the squamosal laterally, restricting the

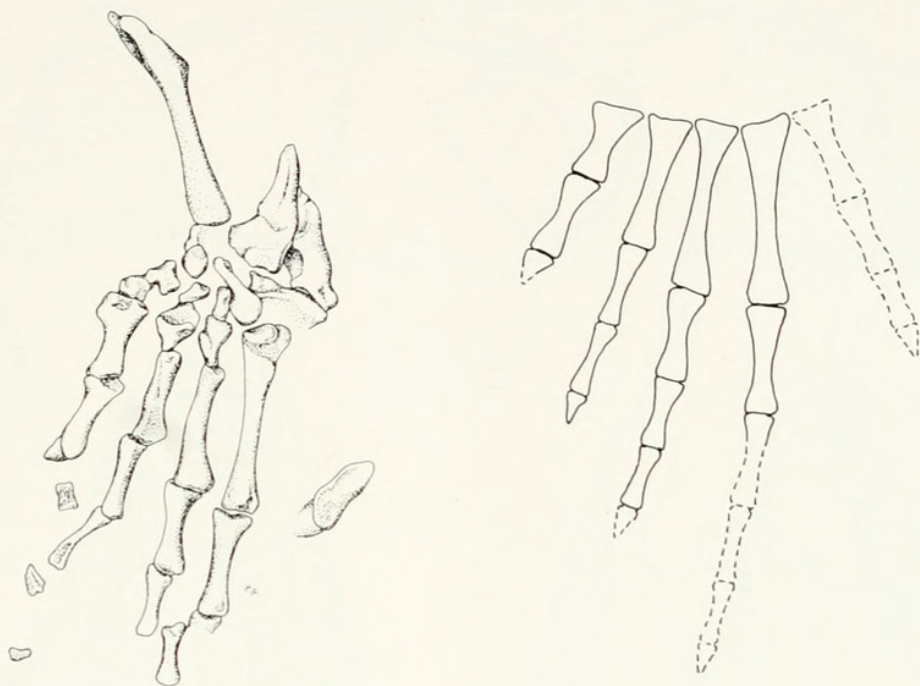


Figure 10. *Romeria primus*, n. sp., type, MCZ 1963. Hand as preserved and as restored. $\times 1\frac{1}{2}$.

size of the posttemporal fenestrae. The basicranial tubera for the insertion of axial musculature are readily seen at the back of the parasphenoid, beneath the otic capsule. The relationship and configuration of the quadrate is as in other romeriids. As restored, the lower jaws resemble in general those of *Protorothyris archeri*, although the splenial extends further forward, and the entire jaw is thicker, relative to its length. Jumbled postcranial remains accompany the skull. The anterior vertebrae have low neural spines, quite unlike those of *Protorothyris*, but more or less similar to those of *Captorhinus*. They are not well enough preserved for further description. Broken and incomplete bones of the forelimb are present, but give very little evidence of their original structure or even proportions. The carpals are broken and jumbled, but were evidently well ossified. Their specific configuration cannot be restored. The proximal portions of the first four digits are present in nearly their normal position. The configuration is obviously reptilian and the proportions similar to those of the better known Pennsylvanian romeriids. The claws are short and pointed. Nothing is known

of the posterior portion of the vertebral column or the rear limb.

Discussion. *Romeria primus* clearly evolved from the main romeriid stock. Since the two species are contemporary, it could not have evolved from *Protorothyris archeri* itself, but it may have evolved from a very similar antecedent form. The cranial differences are clear cut, but may not have required much time to develop.

Romeria texana Price

Figures 11, 12, and 13

Specific diagnosis. The same as for genus. This species may be distinguished from *R. primus* by the smaller number of maxillary teeth and the greater number of premaxillary teeth.

Horizon and locality. Archer City Bone Bed, Archer County, Texas. Putnam Formation, Wichita Group, Lower Permian of Texas.

Holotype. MCZ 1480, skull lacking braincase, lower jaws, and postparietals.

Referred specimen. UT 40001-4, skeleton of juvenile individual from Zott Pasture, southwest corner, section 55, block 3, Clark

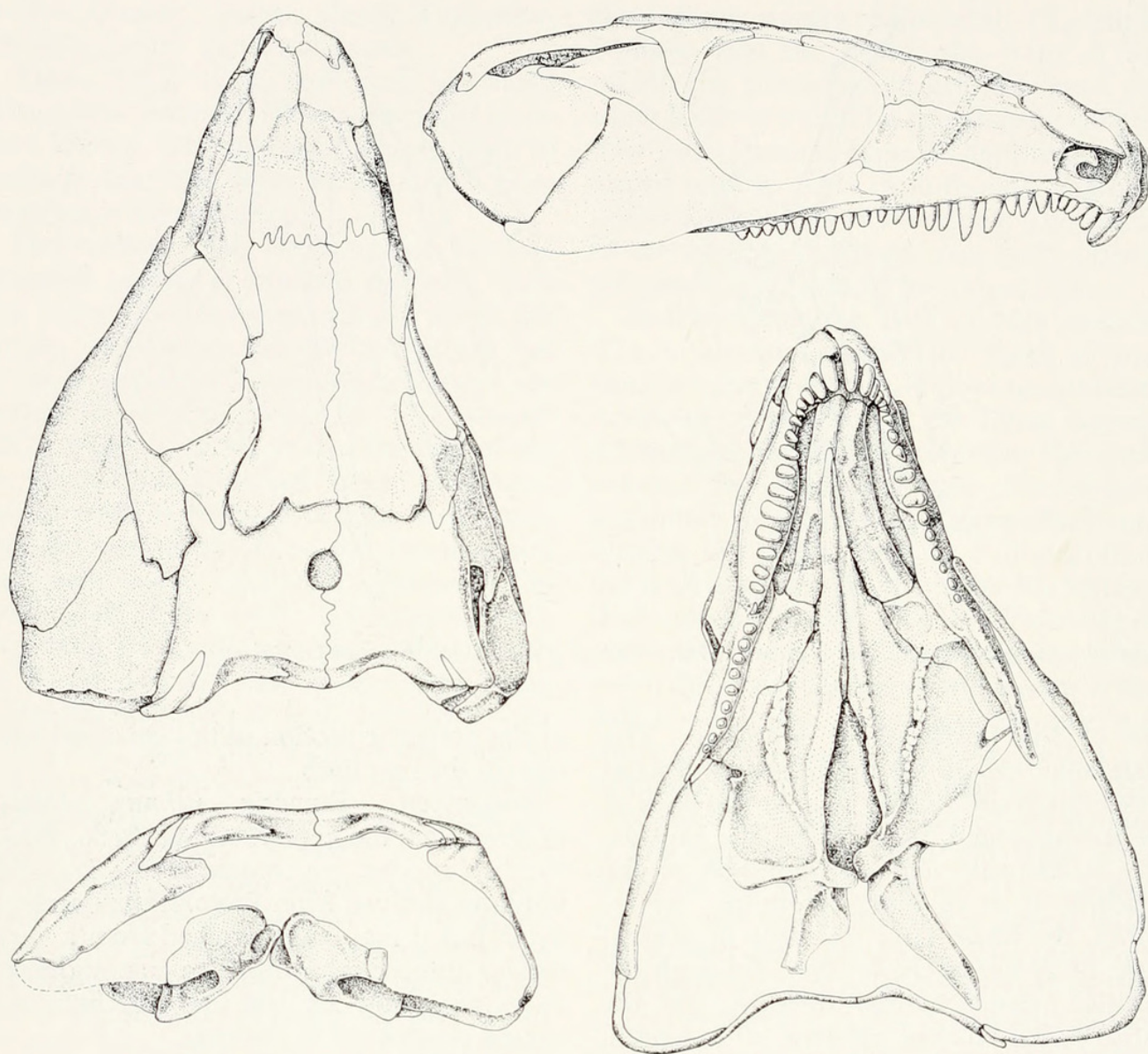


Figure 11. *Romeria texana*. Type, MCZ 1480, in dorsal, lateral, occipital, and palatal views. Braincase, lower jaws, and postparietals are missing. $\times 1\frac{1}{2}$.

and Plumb Survey, 3 miles north of Windthorst, Archer County, Texas, Putnam Formation.

Description. Price based the family Romeriidae on a single specimen of the species *Romeria texana*. Only the skull, minus the low jaws, braincase, and postparietals is preserved. The original description was based on the skull roof alone, but the palate has since been exposed.

The general pattern of the skull roof follows that of other romeriids. The specimen shows almost no sculpturing of the dermal bones. This is almost certainly the result of

polishing in the course of mechanical preparation. A pattern of shallow, scattered pits can be dimly perceived in the remaining bone surface. The pineal opening of this species, like that of *Romeria primus* and the next species to be described, is relatively and absolutely larger than in other romeriids. The postparietals are missing from the skull but their position and relative width can be judged from the emargination of the parietals. Although readily perceived, this emargination is not as marked as that of *Protorothyris*. As can be seen in the second, juvenile skull of *Romeria texana*,

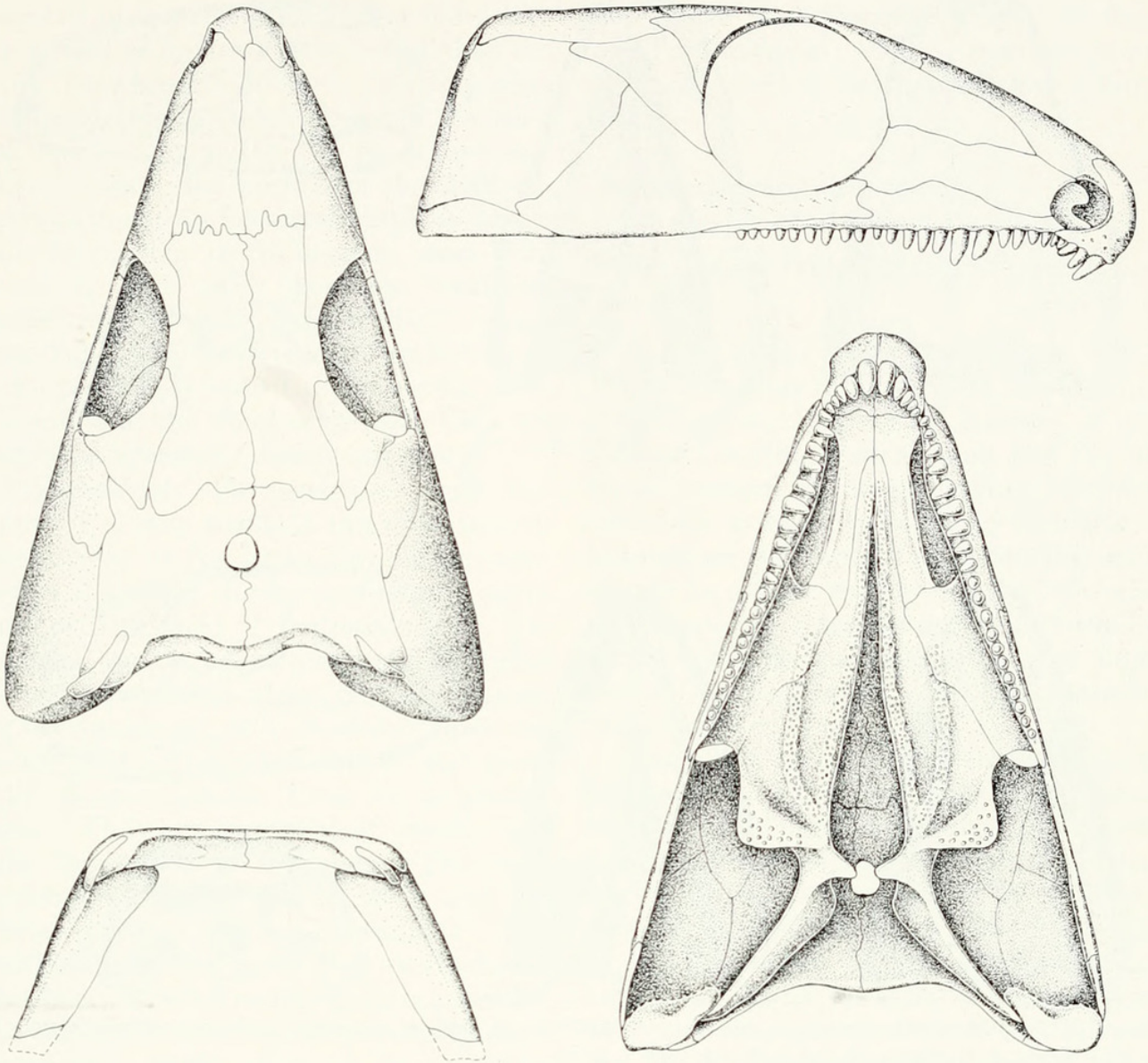


Figure 12. *Romeria texana*. Type, MCZ 1480. Restoration of skull in dorsal, lateral, occipital, and palatal views. Post-parietals and braincase are missing. There is no ectopterygoid. Smooth appearance of skull roof is an artifact, sculpturing was removed during preparation. $\times 1\frac{1}{2}$.

there is no tabular. The postorbital extends very slightly onto the dorsal surface of the skull roof to strengthen its attachment to the cheek region.

The lateral exposure of the portion of the maxilla extending beneath the orbit is very narrow. There are twenty teeth in the right maxilla, with no empty sockets. The posterior portion of the left maxilla has been damaged, precluding determination of the exact tooth count. The anterior 12 teeth are all in place. The fifth and sixth teeth are sufficiently longer than the remainder to

be designated "canines." The next five teeth are progressively shorter. The length of the next three teeth increases slightly and the remainder are all short. The tooth-bearing surface of the premaxilla is at an angle of 25° to the maxillary tooth row. The most anterior of the premaxillary teeth are the longest, roughly equal to the canines. The more posterior are progressively shorter.

Since the lower jaws are missing the palate is well exposed. The surface detail has, unfortunately, been blunted by mechanical

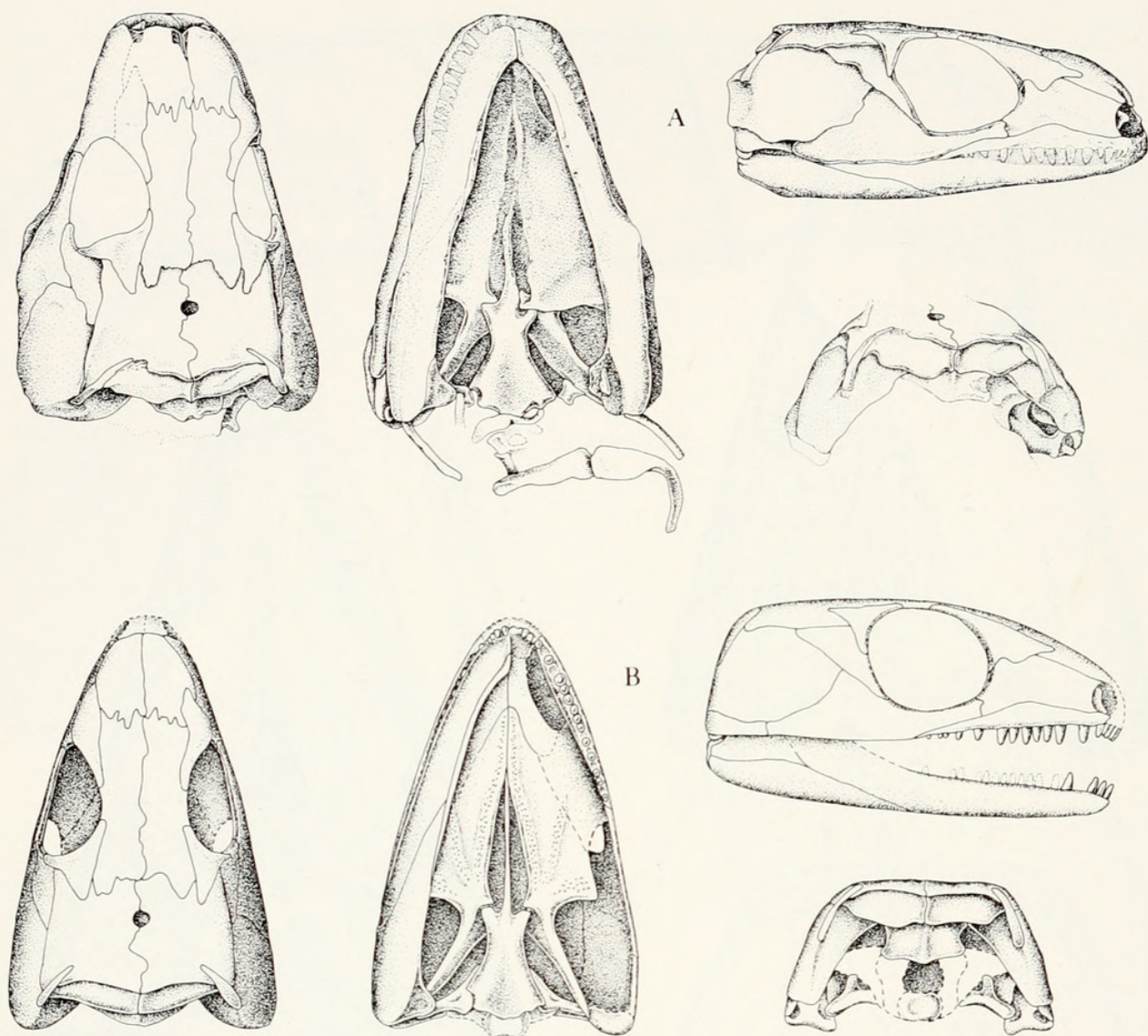


Figure 13. *Romeria texana*. Immature specimen, UT 40001-4. A, skull as preserved in dorsal, ventral, lateral, and occipital views. B, restoration of skull in similar views. $\times 1\frac{1}{2}$.

preparation. There is apparently no ectopterygoid. The palatine extends from the internal nares to the subtemporal fossa. The transverse flange of the pterygoid apparently does not have a row of large teeth on its margin, but rather a scattering of smaller denticles along its anterior face. Two ridges, certainly bearing denticles, extend along the palatal ramus of the pterygoid, one along the medial margin and the other obliquely laterally toward the palatine. Another ridge, possibly topped with denticles, borders the lateral margin of the vomer. The pterygoids extend between the vomers, nearly to the premaxillae. In occipital view, the squamosal can be seen to

extend medially to underlie the postparietals. The quadrates and the posterior portion of the quadratojugal are missing.

In addition to the type skull, *Romeria texana* is represented by a second, juvenile specimen, from the University of Texas collection UT 40001-4. It was collected together with a great deal of material of the microsauro *Pantylus*. This locality is in the Putnam Formation as is that from which the type was collected. Except for the smaller size and slight difference in proportions, the juvenile skull is very similar to the type. It is more complete in retaining the postparietals and the braincase in their natural positions. The presence of the post-

parietals makes this skull appear more similar to that of *Romeria primus* than does the type. Between the juvenile and the adult of this species the relative size of the parietal opening increases, the snout becomes more elongate, the portion of the skull anterior to the orbits becomes relatively longer and the canine teeth become more pronounced. The orbit becomes relatively smaller and the tooth row relatively longer (See Table I). There is room for five teeth in the premaxilla and 19 in the maxilla. This suggests that the number of teeth does not change substantially during ontogeny.

Unfortunately the specimen was preserved in a very resistant ironstone matrix. The surface of the bone was almost completely destroyed during preliminary preparation with acid (?hydrochloric). The occipital area is preserved but little preparation is possible without severely damaging the specimen. It is clear that there are broad postparietals that extend just short of the supratemporals. There are no tabular bones. The supraoccipital is about one-third the width of the skull. The posttemporal fossae open between it and the medial portion of the squamosal. The opisthotic appears quite well ossified and must have extended nearly to the squamosal. The stapes are small but of essentially adult proportions, unlike that of the juvenile specimen of *Coelostegus* (Carroll and Baird, 1972) or *Protorothyris morani*. The stem is long and abuts against the quadrate. The lower jaw shows no retroarticular process.

Much of the postcranial skeleton is preserved in a nodule behind the skull. Unfortunately, the extremely small size and fragility of the bones combined with the hardness of the matrix render it impractical to prepare the remainder of the specimen at the present time. It is hoped that techniques will be developed which will make this preparation practical. Elements that are exposed include a series of neural arches that are broad and show little development of a spine. A series of three arches extends for 9 mm. The elements of the shoul-

der girdle are generally similar to those of *Protorothyris*. The scapulocoracoid, although small, is clearly ossified as a single unit.

Protocaptorhinus, new genus

Figures 14, 15, 16, and 17

Type species *Protocaptorhinus pricei*, new species

Only a single romeriid specimen (MCZ 1478) has been discovered in the Admiral Formation that overlies the Putnam. It consists of a well-preserved skull and the anterior portion of the postcranial skeleton. Although generally similar to *Romeria*, it approaches the captorhinid condition more closely in several respects. It was included in the species *Captorhinus aguti* by Seltin (1959) but the presence of only a single row of marginal teeth definitely precludes this assignment.

Generic diagnosis. Large romeriid captorhinomorph. Skull roof deeply sculptured with uniformly distributed oval pits. Tabulars lost. Posterior margin of parietals shallowly concave. Supratemporal extending down along top half of the posterior margin of the squamosal. Posterior margin of the squamosal nearly vertical. Postorbital large and extending onto skull roof. Pineal opening large. Premaxilla down-turned. Four to five teeth in premaxilla, 18 to 22 in maxilla; fourth or fifth is enlarged "canine." No evidence of more than a single tooth row. Ossified portion of opisthotic not reaching squamosal. Supraoccipital constricted laterally to form margins of large posttemporal fenestrae. Very slight retroarticular process. Neural arches in trunk region approaching configuration noted in *Captorhinus*. Zygapophyses nearly horizontal.

Protocaptorhinus pricei, new species

Specific diagnosis. Same as for genus.

The specific name honours Mr. L. I. Price, who found this and most of the other

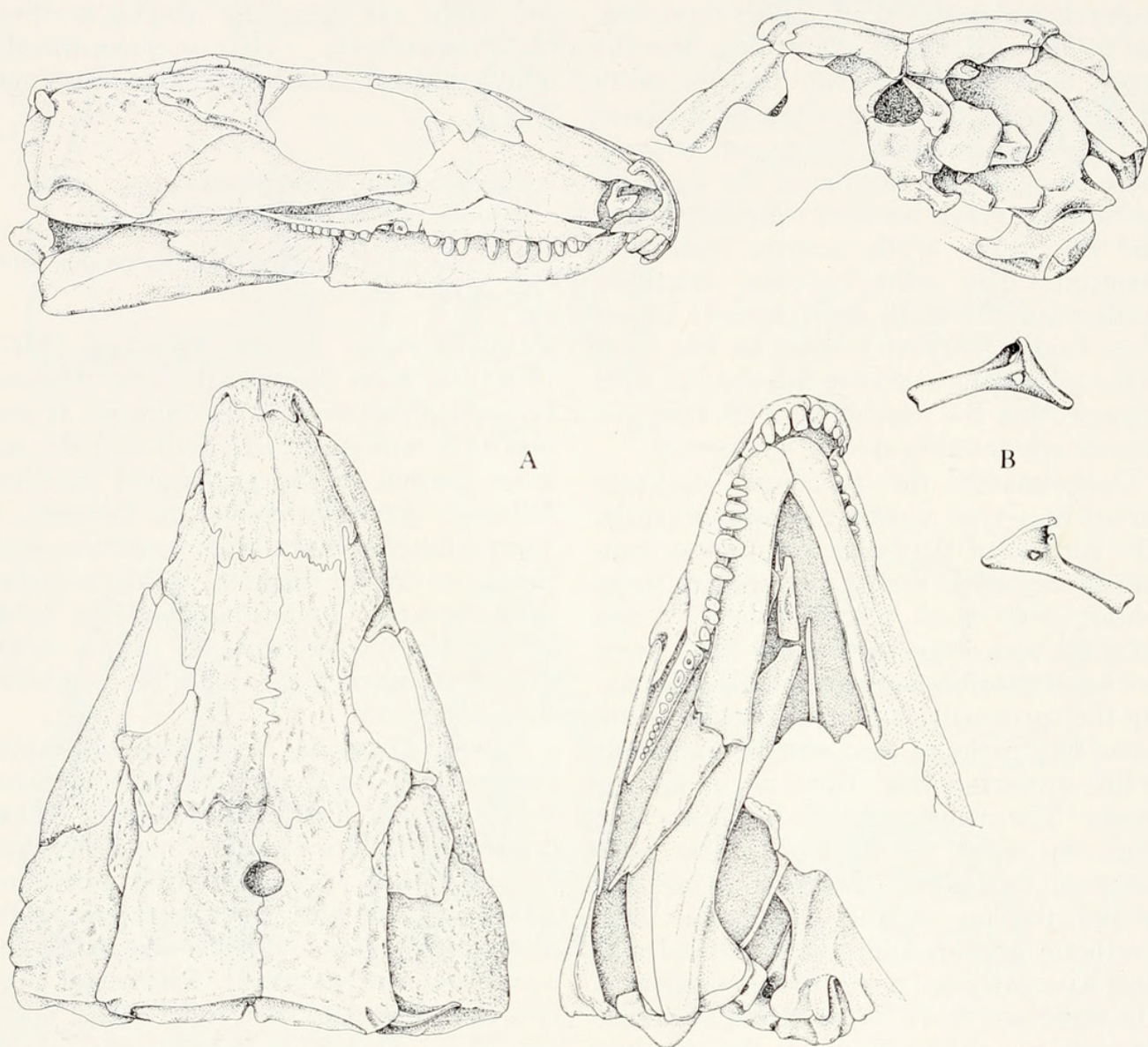


Figure 14. *Protocaptorhinus pricei*, n. gen. and n. sp. Type, MCZ 1478. A, skull in lateral, occipital, dorsal, and ventral views. White areas show position of overlying postcranial elements that appear in a different plane than the skull. B, left stapes in posterior and anterior views. $\times 1\frac{1}{2}$.

romeriid specimens from the Lower Permian of Texas.

Horizon and locality. Rattlesnake Canyon, Archer County, Texas. Uppermost Admiral Formation, Wichita Group, Lower Permian.

Holotype. MCZ 1478. Skull and associated elements of anterior postcranial skeleton.

Questionably referred specimen, MCZ 1160. Badly crushed skull from the Belle Plains Formation.

Description. The size and general con-

figuration of the skull resemble those of the previous genus. The surface is deeply pitted, more like *Captorhinus* than earlier romeriids, although the individual pits are noticeably wider than in that genus. The pineal foramen, as in *Romeria*, is larger than in most Lower Permian reptiles. The posterior margin of the two parietals is shallowly concave; unlike the condition in *Romeria*, these bones are shortest at the midline. The postparietals are thin, narrow bones, exposed primarily in occipital rather than dorsal view. The supratempo-

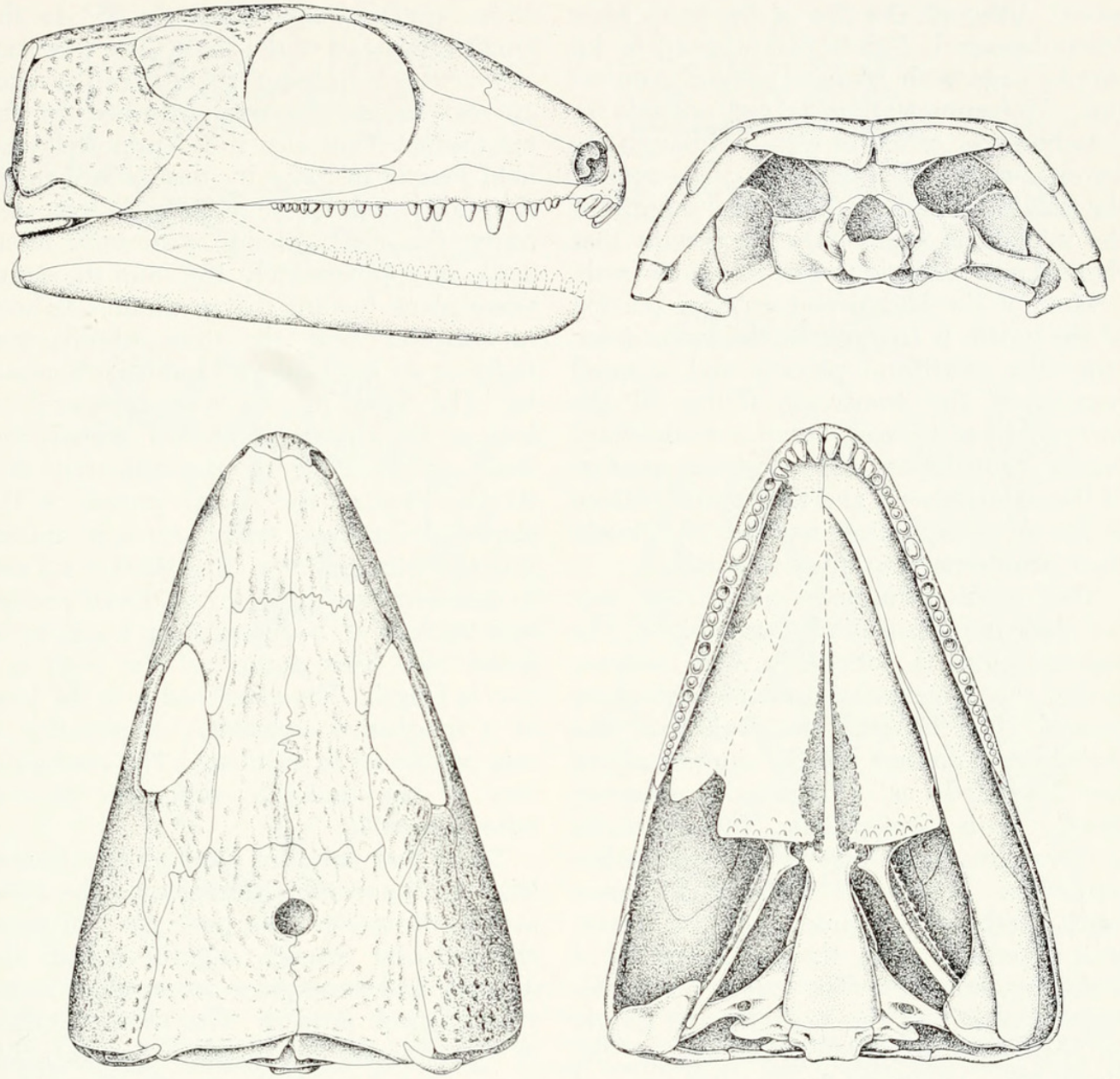


Figure 15. *Protocaptorhinus pricei*, n. gen and n. sp. Restoration of type, MCZ 1478. Skull in lateral, occipital, dorsal, and ventral views. $\times 1\frac{1}{2}$.

rals are supported dorsally by very shallow notches in the parietals. Distally, they extend ventrolaterally over the dorsal half of the posterior margin of the squamosal. The posterior margin of the squamosal is nearly vertical. The dorsal margin of the post-orbital extends onto the skull roof.

The dentition resembles that of *Romeria*. The premaxilla is tilted down from the horizontal and bears five teeth; the anterior one is the largest and the length of the remaining teeth decreases gradually.

The most anterior maxillary teeth are also short. The length increases rapidly to the sixth, which may be considered a canine although it is not as prominent as the canines in earlier romeriids. Only a single tooth can be so designated on each side, in contrast with the condition in *Romeria*, *Protorothyris*, and the Pennsylvanian genera that always have two pairs of canines. The length of the teeth decreases steadily behind the canines. On the right side, 14 teeth are in place in this area, with room for three

more. Although the tips of the teeth have been damaged slightly, all appear to be simple pegs with bluntly pointed, conical tips. Unfortunately, it is not possible to determine the extent of wear. Although the lower jaws are clenched into place against the palate, enough of the ventral margin of the maxilla is exposed to be certain that there is only a single row of marginal teeth.

Most of the lateral and anterior portion of the palate is covered by the lower jaws. Only the cultriform process and a small portion of the transverse flange of the pterygoid can be seen anterior to the basicranial articulation. The posterior portion of the parasphenoid and the ventral surface of the otic-occipital region resemble closely their counterparts in other romeriids.

The occipital surface demonstrates several differences from earlier romeriids. The supraoccipital is noticeably more narrow, so that very large posttemporal fenestrae are formed. Just beneath the skull roof, the dorsolateral corners of the supraoccipital are extended as cylindrical processes, exactly as in *Captorhinus*. The opisthotic is more completely ossified than in earlier romeriids. It extends laterally to cover much of the dorsal process of the stapes. It is separated from the squamosal by a wide gap, however. The extent of the occipital portion of the squamosal is nearly parallel with the lateral margin of the cheek. The exoccipitals bear well-developed facets for articulation with the proatlas and are indistinguishably fused to the basioccipital. The cheek region meets the skull roof at an angle of 61° .

The right stapes is in place, but much of the stem has been lost. The left stapes has fallen out of the skull and lies adjacent to the cervical vertebrae. Although it cannot be removed completely without damage to the adjacent bones, it can be drawn from several angles to disclose the most important structures. In its large relative size and in most structural details it resembles the stapes of other romeriids and *Captorhinus*. There is a large oval footplate, set

at an angle of approximately 55° to the longitudinal axis of the shaft. The posterior end of the footplate rests against the margin of the fenestra ovalis formed by the opisthotic. Ventrally it is supported and held loosely in place by the parasphenoid. Anteriorly it abuts the proötic. As seen ventrally, the shaft extends posteriorly at an angle of approximately 18° from the transverse plane toward the quadrate. As seen in occipital view, the stem extends ventrally at an angle of 20° from the horizontal. The dorsal process is approximately as long as the shaft is thick and extends medially at an angle of approximately 45° . At the base of the dorsal process is the stapedia foramen, which extends antero-dorsally from the rear. The shaft is 1.5 mm in diameter just distal to the dorsal process and thickens to a diameter of 3 mm at its distal end. This portion of the shaft is 6 mm in length. The distal end is in the form of a roughened concavity. Presumably it was continued in cartilage. The configuration of the quadrate resembles that of other romeriids.

The lower jaws are considerably thicker than in *Protorothyris*, continuing the trend seen in *Romeria*. The posterior margin of the articular extends slightly behind the angular and surangular as an abbreviated retroarticular process. The ventral surface of the articular and supporting prearticular are extended medially to provide a large area for the insertion of the pterygoideus jaw musculature that originates on the back of the transverse flange of the pterygoid. The splenial extends forward to the symphysis. The tooth-bearing margin of the lower jaw is completely covered by the skull roof. In contrast with *Protorothyris*, the dentary is lightly sculptured.

Postcranial skeleton. Accompanying the skull are a series of seven anterior vertebrae, ribs, much of the shoulder girdle, and the right forelimb. The elements of the atlas-axis complex resemble in general those of *Paleothyris* and *Protorothyris*, but the relative proportions of the bones differ widely

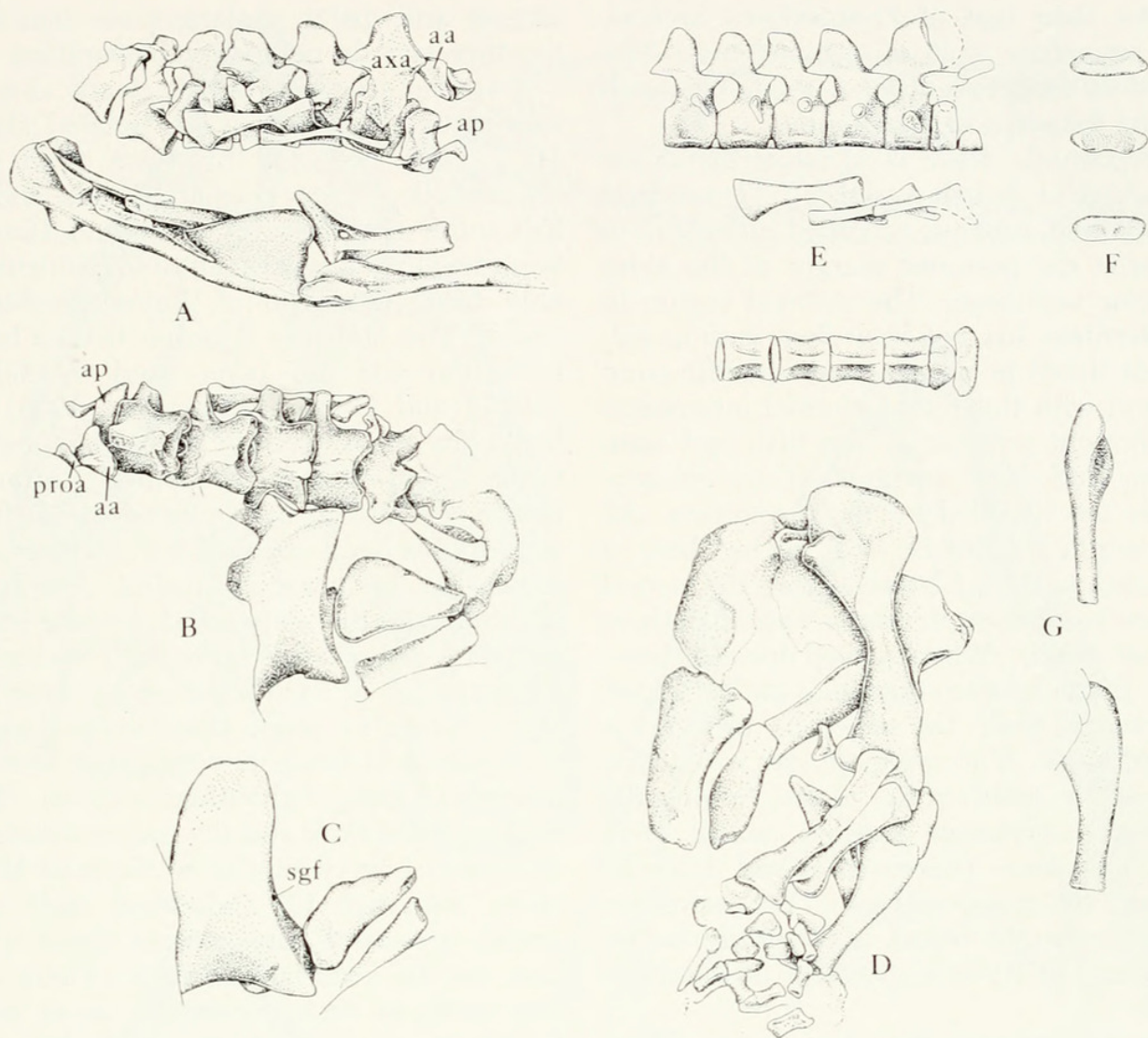


Figure 16. *Protocaptorhinus pricei*, n. gen and n. sp. Type, MCZ 1478. Postcranial elements. A, anterior vertebrae in lateral view, humerus, ulna, and stapes. B, anterior vertebrae in dorsal view, scapula and proximal end of left humerus. C, left scapula and broken proximal end of humerus. D, shoulder girdle and right forelimb. E, restoration of anterior vertebrae in lateral and ventral views, cervical ribs. F, atlas intercentrum in anterior, dorsal, and ventral views. G, right ulna in posterior and medial views. $\times 1\frac{1}{2}$.

in the three genera. A piece of the oval proaltas may be seen emerging from the left posttemporal fenestra. The posterior portion is flattened ventrally and rounded dorsally. The atlas intercentrum has fallen from its normal position and lies below the other cervicals. It is a wide crescent, marked ventrally by a longitudinal ridge. It presumably bore the capitulum of the first rib, but the facet for its articulation is not visible. The atlas arch is a small, paired structure without a neural spine. It is loosely articulated with a short, cylindrical

pleurocentrum that is notched dorsally for the nerve cord. There is no separate axis intercentrum; presumably it is indistinguishably fused to the base of the atlas pleurocentrum. The axis centrum is only slightly longer than the atlas centrum and not appreciably larger than the remaining cervicals. It is indistinguishably fused to the arch. The axis neural spine is broken anteriorly, but was clearly larger than those of the other cervicals; presumably, as in other romeriids, the anterior margin overhung the atlas arch. The spine is much

shorter than that of *Protorothyris archeri*, but resembles that of *Captorhinus*. The length of the axis centrum is relatively much shorter than that of *Paleothyris*.

Surprisingly, there is no intercentrum for the third or fourth vertebra. The ventral lip of these centra is extended anteriorly to underlie the posterior margin of the more anterior vertebrae. The cervical region in *Captorhinus* has not been described in sufficient detail to permit more specific comparison with this form. Normal intercentra are present anterior to the fifth and sixth centra and both margins of the pleurocentra are bevelled for their reception. All the centra in the cervical region bear a rounded keel. In lateral view, the neural arches in *Protocaptorhinus* resemble those of *Paleothyris*. When viewed dorsally, however, it can be seen that they are expanded laterally in much the same way as those in *Captorhinus*. The zygapophyses extend far beyond the width of the centra, to form the "typical" cotylosaur swollen neural arch. The transverse processes extend laterally beyond the zygapophyses. The alternation in spine height noted in *Captorhinus* by Vaughn (1970) is not evident in this short series.

Several cervical ribs are present. Those associated with the first three vertebrae are shown in Figure 16. They have clearly separated heads to bridge the wide gap between the anterior transverse process and the base of the centra, and spatulate shafts that evidently extended posteriorly alongside the column, rather than ventrally.

The shoulder girdle is badly jumbled, but most of the elements are present. Their preservation is such that no more than general similarities with other romeriids can be noted. The humerus, ulna, and radius are all somewhat distorted and broken. They resemble their counterparts in *Captorhinus* in being considerably more stoutly built than those of earlier romeriids. In as much as the preservation permits comparison, the humerus in particular is nearly identical with that of *Captorhinus*. The

carpals and distal phalanges are jumbled together and do not permit restoration.

A further specimen that is clearly closely related to MCZ 1478 is an isolated skull, MCZ 1160, collected by Price from the lower Belle Plains Formation, one and a half miles northwest of Woodrum House. Superficially it appears almost indistinguishable from the type of *Protocaptorhinus pricei*. The fact that it comes from a later formation and has been cited by Seltin (1959) and Fox and Bowman (1966) as belonging to the genus *Captorhinus* makes it deserving of special notice. Unfortunately, the skull is not well preserved. The skull roof is badly cracked and much of the palate and braincase is missing. The bone is softer than the matrix and delicate preparation is not possible. Although the superficial surface of the skull roof has been removed in earlier preparation, the pattern of the individual bones is very easily seen as a result of their slight disarticulation. The outline of the skull and the configuration of the bones is very similar to those of MCZ 1478. Although the individual teeth are poorly preserved, the general dental pattern can be readily discerned. There are four teeth in each premaxilla, as in most specimens of *Captorhinus aguti*, but one less than the count in the type of *Protocaptorhinus pricei*. There is definitely only a single row of maxillary teeth. In *Captorhinus* the fourth maxillary tooth is usually the largest and the terminal member of the first diagonal row. The next tooth is smaller and clearly more medial in position. In MCZ 1478 the fifth tooth is the largest, but those more posterior are clearly in the same row. In MCZ 1160 the fourth tooth is the largest, but again, all of the marginal teeth are in a single, straight row. Neither maxilla is sufficiently well preserved to establish the tooth count accurately. There are approximately 18 teeth, intermediate between the number of marginal teeth in MCZ 1478 (22) and *Captorhinus* (approximately 16). A further factor in which MCZ 1160 resembles the type of *Protocaptorhinus*

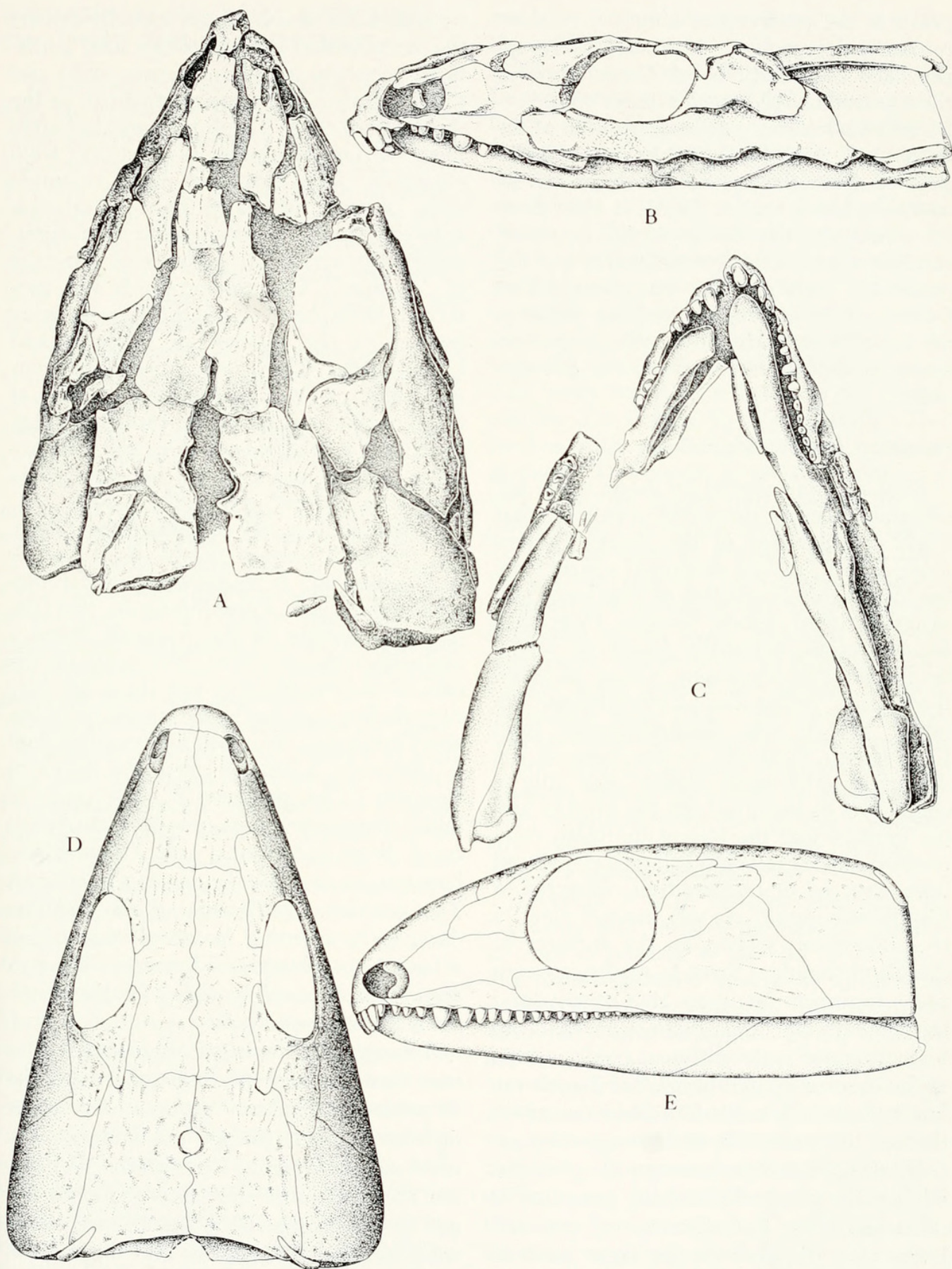


Figure 17. *Protocaptorhinus pricei*. MCZ 1160. Skull as preserved in A, dorsal, B, lateral, and C, ventral views. Restoration of skull in D, dorsal and E, lateral views. $\times 1\frac{1}{2}$.

pricei is the presence of only a very short retroarticular process. It more closely approaches the condition of *Captorhinus* in the extension of the jugal anterior to the orbit and the relatively anterior position of the orbit, but can be unequivocally distinguished from that genus by the relatively narrower cheek region. In MCZ 1160, as in all romeriids, the skull margin is nearly straight between the external nares and the quadrate. Although this specimen differs from the type of *Protocaptorhinus pricei* in the number of teeth and in other minor respects, it will be included here in the species.

Pleuristion brachycoelous Case

Brief mention should be made of an additional, recently described specimen that might be included in the family Romeriidae. In 1970, Olson described a skull from the Wellington Formation of Oklahoma and assigned it to Case's species *Pleuristion brachycoelous*, originally based on vertebrae from that formation. Olson included the species within the Captorhinidae. He noted that it was distinguishable from *Captorhinus* primarily on the basis of the dentition. The skull clearly has only a single row of teeth in both the maxilla and the dentary and the tips of the teeth were pointed rather than chisel-shaped or blunted with wear as in *Labidosaurus hamatus* or *Captorhinus aguti*. As will become clear in the subsequent section on the ancestry of the Captorhinidae, there is an almost complete transition between that family and the Romeriidae. One distinction that can be maintained is the different configuration of the cheek region. The skull of *Pleuristion brachycoelous* described by Olson resembles that of the romeriids in having an essentially straight margin between the posterior edge of the premaxilla and the quadrate, as determined by the structure of the left lower jaw. Because of the large mass of the jaw muscle, the common captorhinid genera *Captorhinus* and *Labidosaurus* have

expanded the cheek region laterally so that the ventrolateral margin of the skull is distinctly concave between the premaxilla and the quadrate. There are no features in the skull described by Olson that are definitely those of captorhinids as distinct from romeriids. The individual teeth resemble those of romeriids more than captorhinids in having sharply pointed rather than chisel-shaped tips and in the presence of two pairs of "canines." The premaxilla is not preserved. Olson has restored this bone as being hooked in the manner of *Romeria* and *Captorhinus*. The small number of marginal teeth, as well as the configuration of the posterior margin of the skull roof, suggests that it is advanced over the *Protorothyris* pattern and so might be expected to have a specialized premaxilla as well.

Although it is not illustrated by Olson, the posterior portion of the skull roof is well preserved. It resembles that of *Protocaptorhinus* and *Captorhinus* in that the posterior margin of the parietals forms a shallowly concave recess. The postparietals face entirely posteriorly and there are only very shallow notches in the parietals for the supratemporals. In these features the skull is definitely advanced over the level of *Romeria*. The presence of two pairs of fairly conspicuous canines distinguishes it from *Protocaptorhinus* and *Captorhinus*, however, as does the very narrow lower jaw. The peculiar distribution of the palatine denticles is a further feature distinguishing it from *Captorhinus* and *Romeria*. The palate is not exposed in either of the specimens of *Protocaptorhinus*.

Apparently *Pleuristion* represents a lineage that has evolved in parallel with the *Romeria-Captorhinus* group. No other members of this lineage are known. The exact age equivalence between the Wellington Formation and the Texas sequence has not been determined. It has been equated with both the Belle Plains and the Arroyo. In either case, *Pleuristion* is one of the latest romeriids.

CHANGES IN THE SKULL STRUCTURE OF LOWER PERMIAN ROMERIIDS

In contrast with the Pennsylvanian romeriids, in which the postcranial skeleton of most genera is known in considerable detail, our current knowledge of the Lower Permian members of the family is based primarily on a series of excellently preserved skulls. These skulls show progressive changes in the palate, jaws, and dentition that culminate in the origin of the family Captorhinidae.

The significance of the changes in the structure of the jaws and their musculature in the origin of reptiles has recently been emphasized (Carroll, 1969b). The basic pattern achieved by the early romeriids is retained in the primitive members of many advanced reptilian lineages, notably lepidosaurs and archosaurs. All of the Pennsylvanian romeriids retain the primitive configuration in which the tooth-bearing margin of the skull is in a single plane and the canines are very conspicuous. Except for *Cephalerpeton*, the remaining maxillary teeth are small and numerous.

The entire jaw apparatus in small, primitive reptiles was probably evolved to capture, hold, and ingest small insects. In most Pennsylvanian romeriids, the skull is small and the marginal teeth are typically small so that they would serve primarily to hold the prey. The larger teeth in *Cephalerpeton* may have been more efficient in piercing. The canine teeth in the typical genera, *Hylonomus* and *Paleothyris*, may have served to pierce the prey as well, but more likely their primary function was to keep small fusiform insects from escaping at the front of the mouth. They would be most effective if the prey were held crossways in the jaws, as may be observed in living lizards. The canines are approximately midway between the anterior margin of the orbits and the posterior margin of the external nares. The longer anterior premaxillary teeth would have served a similar function, but there is little space between them

and the canines to accommodate any but the smallest prey.

The two species of *Protorothyris* from the Lower Permian continue the pattern established by *Hylonomus* and *Paleothyris*. *Romeria* and *Protocaptorhinus* initiate a distinct departure that culminates in the specialized dentition of the family Captorhinidae. The trend is first recognizable in *Romeria primus* from the Moran Formation. This species resembles more primitive romeriids in many respects, but the tooth-bearing margin of the premaxilla bends ventrally at an angle of 26° to the horizontal. The tooth count is reduced to 25 in the maxilla and four in each premaxilla. The canines shift to a slightly more posterior position. This results in the formation of a very effective insect trap anterior to the canines, just beneath the external nares. This is significantly further forward than the primary trap in *Protorothyris*. The canines are less conspicuously larger than the remaining cheek teeth, although they remain easily recognizable in this genus. The shorter teeth behind the canines form a secondary food trap. The teeth in the lower jaw also contribute to the effectiveness of the system. In both *Protorothyris* and *Romeria primus* the length of the dentary teeth alternates with that of the premaxillary teeth. A basically similar pattern is seen in *Protocaptorhinus*.

Although it is of obvious advantage in capturing prey to have the holding surface as close as possible to the end of the jaws, this places the lever system of the jaw at a considerable mechanical disadvantage. More force must be applied by the muscles the further the prey is from the fulcrum. Not surprisingly, the change in tooth and jaw structure seen in the sequence *Protorothyris*-*Romeria*-*Protocaptorhinus* is accompanied by a progressive enlargement of the subtemporal fenestrae and the width of the lower jaw (see Table I). The areas in question were measured by the use of a grid, with squares being counted as zero if less than half was covered and as one if

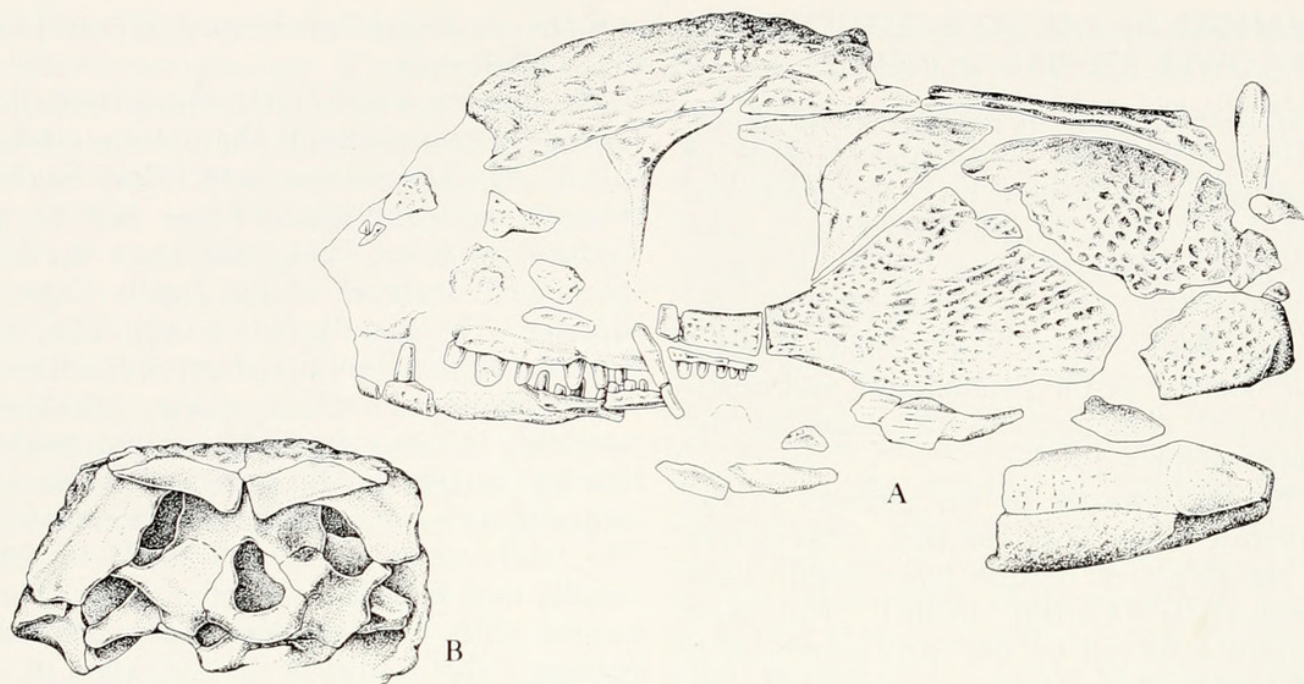


Figure 18. A, lateral view of skull of the earliest identifiable captorhinid, MCZ 1483, from the middle of the Belle Plains Formation. Cheek region is expanded and posterior teeth have chisel-shaped tips. There is only a single row of marginal teeth. B, occiput of *Captorhinus* pattern, UC 1119, Wichita River, near Vernon Crossing, Clyde Formation. $\times 1\frac{1}{2}$.

more than half was covered. These measures are not meant to correspond strictly to functional units, but simply to give a standard for discussing the relative size of the areas available for jaw musculature. In *Protorothyris archeri*, the subtemporal fenestrae occupy approximately 27 percent of the palatal surface, in *Romeria primus* 31 percent, *Romeria texana* 33 percent, and *Protocaptorhinus pricei* 37 percent. Other measurements demonstrate a similar widening of the lower jaws to accommodate a greater mass of the adductor musculature. These changes set the stage for a second, even more radical organization of the dentition which occurred in the origin of the Captorhinidae (see subsequent section).

A further series of changes, occurring simultaneously with those noted in the lower jaw, are seen in the occiput. One, which has no immediately obvious structural or functional advantage, is the ossification of the otic capsule. This structure is only questionably recognizable in the Pennsylvanian members of the group. In *Paleothyris* the exoccipital appears to have

occupied some of the area later recognized as opisthotic. In *Protorothyris* the exoccipital is clearly recognized, but little is evident of the opisthotic. In *Romeria primus* the medial and ventral portions of the otic capsule are ossified, but the dorsal and lateral areas were apparently cartilaginous. In *Protocaptorhinus* all of the medial part is ossified, but the distal ends stop short of the squamosals. In *Captorhinus* the capsule extends to the cheek. This changed pattern of ossification seems to have little significance within the romeriids, but may be very important in the evolution of at least one group of advanced reptiles. Of more obvious significance is the change in the overall proportion of the occiput. As may be noted in Table I, the Permian romeriids show a progressive widening of the skull so that the height-width ratio changes from 1:1.5 to 1:2.5 from *Protorothyris* to *Protocaptorhinus*. The length of the skull is essentially unchanged and the height is only slightly reduced. One reason for the relative increase in the width of the cheek region is to accommodate the increased jaw

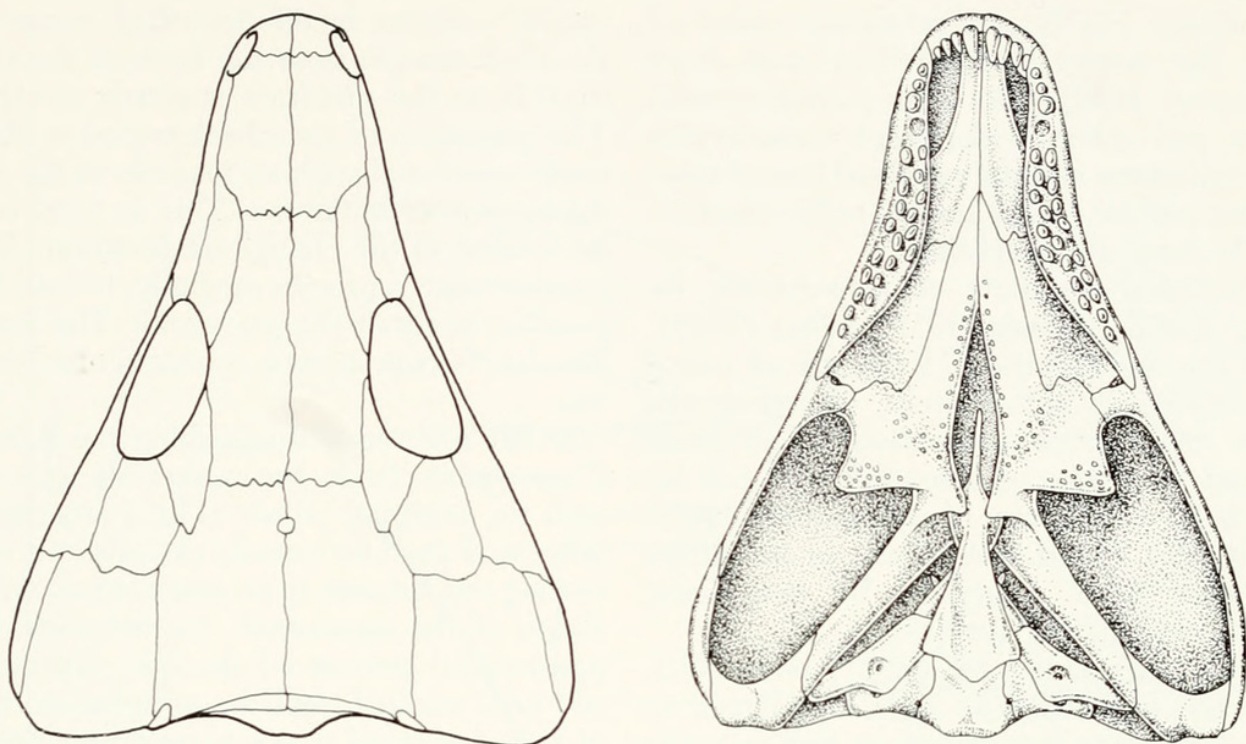


Figure 19. *Captorhinus aguti*. Skull in dorsal and palatal views. Approximately $\times 1$.

musculature. The widening of the occiput also results in a reorganization of the cervical musculature and the direction of the major forces that move the skull. The occipital condyle forms a fulcrum that allows movement in both the vertical and horizontal planes. The degree of control and mobility in each species is dependent on the placement and orientation of the major muscles. Judging from modern lizards, the muscles moving the skull of *Protorothyris* were probably located in an arc above the occipital condyle extending no more than about 15 degrees from the vertical. Control of the head would have been primarily in a vertical plane. In *Protocaptorhinus* the muscles could occupy much more lateral positions, enabling greater force to be applied in moving the skull from side to side. In modern lizards much of the force in crushing the prey is achieved by pushing the jaw along the ground on one side or the other. This would be facilitated by the distribution of muscles seen in the advanced romeriids. As a result of the lateral shift of the cervical musculature, the postparietal

extends laterally to usurp the position occupied by the tabular in *Protorothyris* and other primitive romeriids. The supratemporal narrows to give a greater surface for the attachment of the spinalis capitis muscles, attaching to the margin of the posttemporal fossa.

THE ORIGIN OF THE FAMILY CAPTORHINIDAE

As Watson (1954) and others have observed and as has been further demonstrated in this paper, the Lower Permian romeriid lineage including the genus *Romeria* forms a more or less continuous transition from the primitive romeriid pattern to that of the Captorhinidae. If these two families are to be distinguished taxonomically, it is necessary to determine the specific phylogenetic relationship between them and establish what significant morphological features can be used to differentiate the assigned species.

Among captorhinids, only the genera *Captorhinus* and *Labidosaurus* need concern us here. The many genera described

by Olson (1970 and references therein) and the newly discovered African form (Taquet, 1969), all with multiple tooth rows and other evidence of considerable specialization, certainly evolved from *Captorhinus* and/or *Labidosaurus*, rather than directly from any romeriids.

Published accounts of *Captorhinus* by Price (1935), Romer (1956), Seltin (1959), and Fox and Bowman (1966) are all based essentially, if not entirely, on specimens from the Arroyo Formation, Clear Fork Group in Texas, or from the Fort Sill locality in Oklahoma of apparently equivalent age. These specimens can be differentiated from romeriids by significant differences in the dentition.

Both the maxilla and dentary bear multiple rows of teeth. The teeth are aligned in three or four (depending on the maturity of the specimen) overlapping rows, roughly parallel to each other, but set at a slight angle to the long axis of the jaw. The presence of more than a single row of teeth can be determined even in specimens with the jaws closely clenched because the "marginal" tooth row is not straight, but "stepped" where one tooth row is succeeded by the next.

In well-preserved and carefully prepared specimens, the rear teeth can be distinguished from those in typical romeriids by the lateral compression of the tips and their termination in a flat, chisel edge, in contrast to a sharpish point. Except for recently erupted teeth, most show considerable wear.

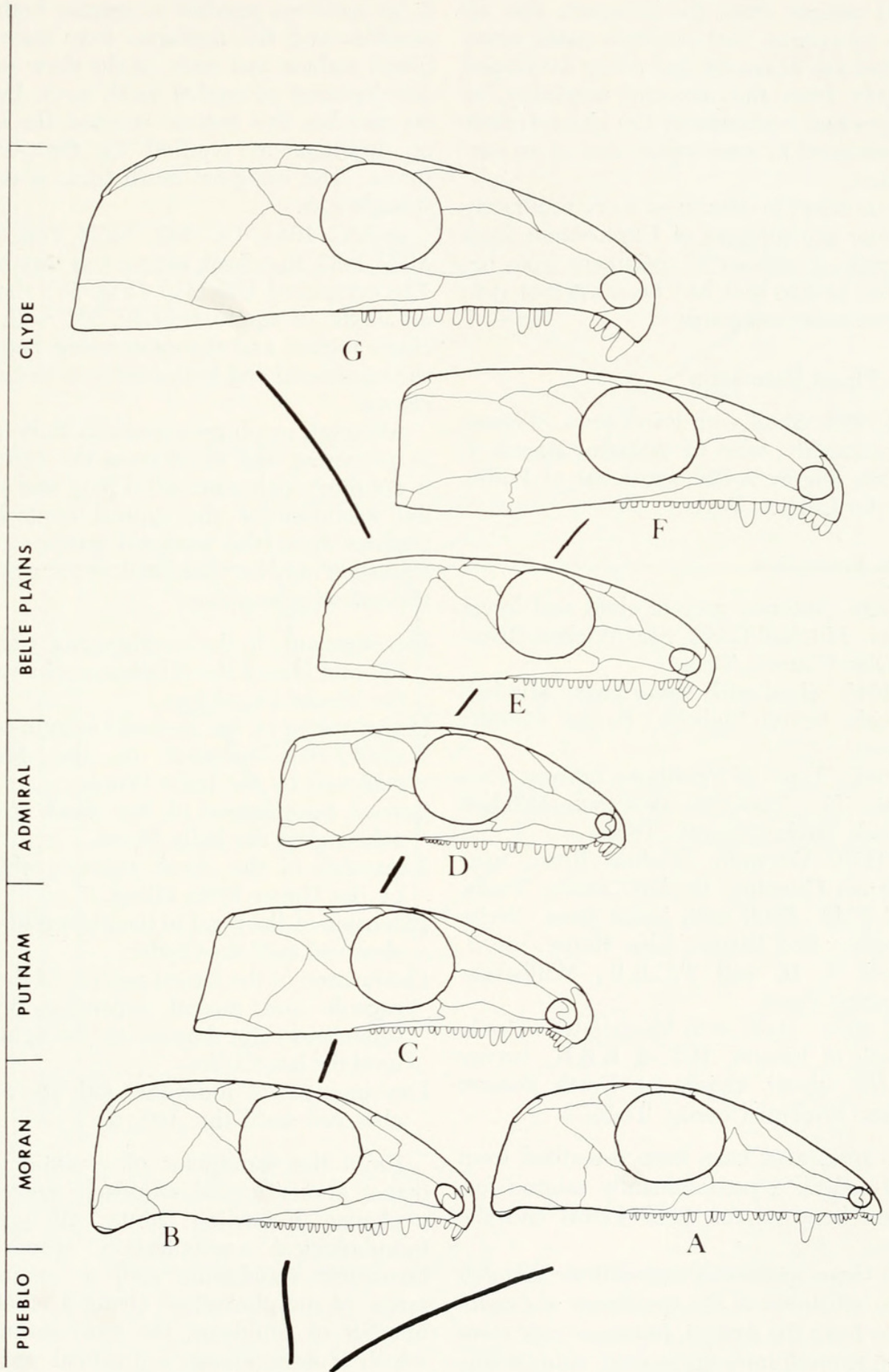
In dorsal view, the skulls of the Arroyo *Captorhinus* can be distinguished from those of any romeriids by the lateral expansion of the cheek region. A line drawn along the skull margin and extending back to the quadrate is distinctly concave out-

wards, whereas in all described romeriids the skull margin from the back of the premaxilla to the quadrate is nearly straight. The expansion of the cheek region is obviously associated with an increase in the adductor jaw musculature. This, in turn, may be related to the change in dentition. The jugal extends a process medially, behind the maxilla, to reach the pterygoid. The lower jaw has a conspicuous retroarticular process.

Other features distinguishing the Arroyo *Captorhinus* from the romeriids can be seen in occipital view. The paroccipital process of the otic capsule extends as a narrowing rod anterior to an extensive occipital flange of the squamosal. In romeriids, the paroccipital process of the otic capsule is not fully ossified, and the occipital portion of the squamosal is not as extensive [compare Fig. 15 of *Protocaptorhinus pricei* and Romer's fig. 36F (1956) of *Captorhinus*]. In association with the expansion of the jaw musculature, the angle between the skull roof and the cheek region decreases substantially (from approximately 70° to 60°). Although these specimens of *Captorhinus* can readily be derived from the known romeriids, particularly *Protocaptorhinus pricei*, there is no problem of differentiating the two groups or of accepting the familial distinction. The latter is further justified by the considerable subsequent differentiation of the known captorhinids.

In addition to the specimens from the Arroyo, *Captorhinus* has been recognized in diminishing numbers from as early as the Admiral or Belle Plains Formation. According to Seltin (1959) and Fox and Bowman (1966) all of the earlier members of the genus can be included in the same species, *C. aguti*, as the Arroyo form. Since they were placed in the same species, one

Figure 20. Pictorial phylogeny illustrating the origin of the Captorhinidae from Permian romeriids. A, *Protorothyris archeri*, $\times 1$; B, *Romeria primus*, $\times 1$; C, *Romeria texana*, $\times 1$; D and E, two specimens of *Protocaptorhinus pricei*, $\times 1$; F, type of "*Parioticus laticeps*," a possible ancestor of *Captorhinus aguti*, $\times 1$; G, UC 183, possible ancestor of *Labidosaurus hamatus*, $\times \frac{2}{3}$.



would assume from the literature that all these specimens had multiple tooth rows, and that this character had either developed abruptly from the romeriid condition, or that gradual evolution of the characteristic had occurred in some other area at an earlier time.

In an effort to determine more accurately the time of evolution of *Captorhinus* from romeriids, a number of specimens from below the Arroyo that had been attributed to *C. aguti* were examined:

Belle Plains Formation

MCZ 1483. Skull with lower jaws. *Trematops* locality, west of Williams Ranch, J. Gibbs Survey A-566, southeast of Fulda, Baylor County, Texas.

Clyde Formation

UC 196. Anterior part of skull and lower jaws. Mitchell Creek, near Wichita River, Baylor County, Texas.

UC 1043. Skull with lower jaws. Mitchell Creek, below Mabelle, Baylor County, Texas.

UC 642. Type of *Parioticus laticeps* (see Plate I). Complete skeleton. Mitchell Creek, Baylor County, Texas.

UC 1119. Occiput. Wichita River, near Vernon Crossing, Baylor County, Texas.

MCZ 1740. Skull with lower jaws. Weiss locality, Red Pasture Line House, sec. 7, block 5, H. and T.C.R.R., Willbarger County, Texas.

MCZ 2804. Skull with lower jaws. 1 mile south of Electra, H.T. & B.R.R., survey A-137, about middle of North Section lines, Wichita County, Texas.

No specimens have been described from the Lueders, a predominantly marine formation between the Belle Plains and the Arroyo.

All these specimens showed one or more of the attributes of the specimens of *Captorhinus* from the Arroyo, *but in no case were multiple tooth rows discovered*. Admittedly,

it has not been possible to prepare both the maxillae and the dentaries from their occlusal surface and some might show initial development of medial tooth rows, but in no case has this feature reached the stage of development typified by the Arroyo forms. The marginal teeth form a single, straight row.

In UC 1043, UC 642, MCZ 1740, and MCZ 1483, the cheek region was expanded. The occiput of UC 1119 (Fig. 18) showed an angle of approximately 60° with the cheek region, and the relationship between the squamosal and braincase is as in *Captorhinus*.

Although much more remains to be done in preparing and illustrating the material, it definitely demonstrates a long and gradual evolution of the typical captorhinid features from the romeriid pattern. This transition may be visualized as occurring in the following sequence:

Development of the overhanging premaxilla and loss of the tabulars—achieved in the Moran Formation.

Straightening of the posterior margin of the skull roof—initiated in the Moran, achieved by the Belle Plains.

Lateral compression of the cheek teeth—achieved in the Belle Plains.

Expansion of the cheek region—achieved by the Upper Belle Plains.

Extension of the jugal to the pterygoid—not observed until the Clyde.

Ossification of the lateral portion of the otic capsule and medial expansion of the squamosal—not known to be achieved until the late Clyde.

Development of multiple tooth rows—not observed until the Arroyo.

From the standpoint of evolution, this makes a very logical sequence, suggesting a change in feeding habits with gradual morphological specialization. From the taxonomic standpoint such a continuous series of morphological changes creates a number of problems, the most serious of which is determining a practical point of

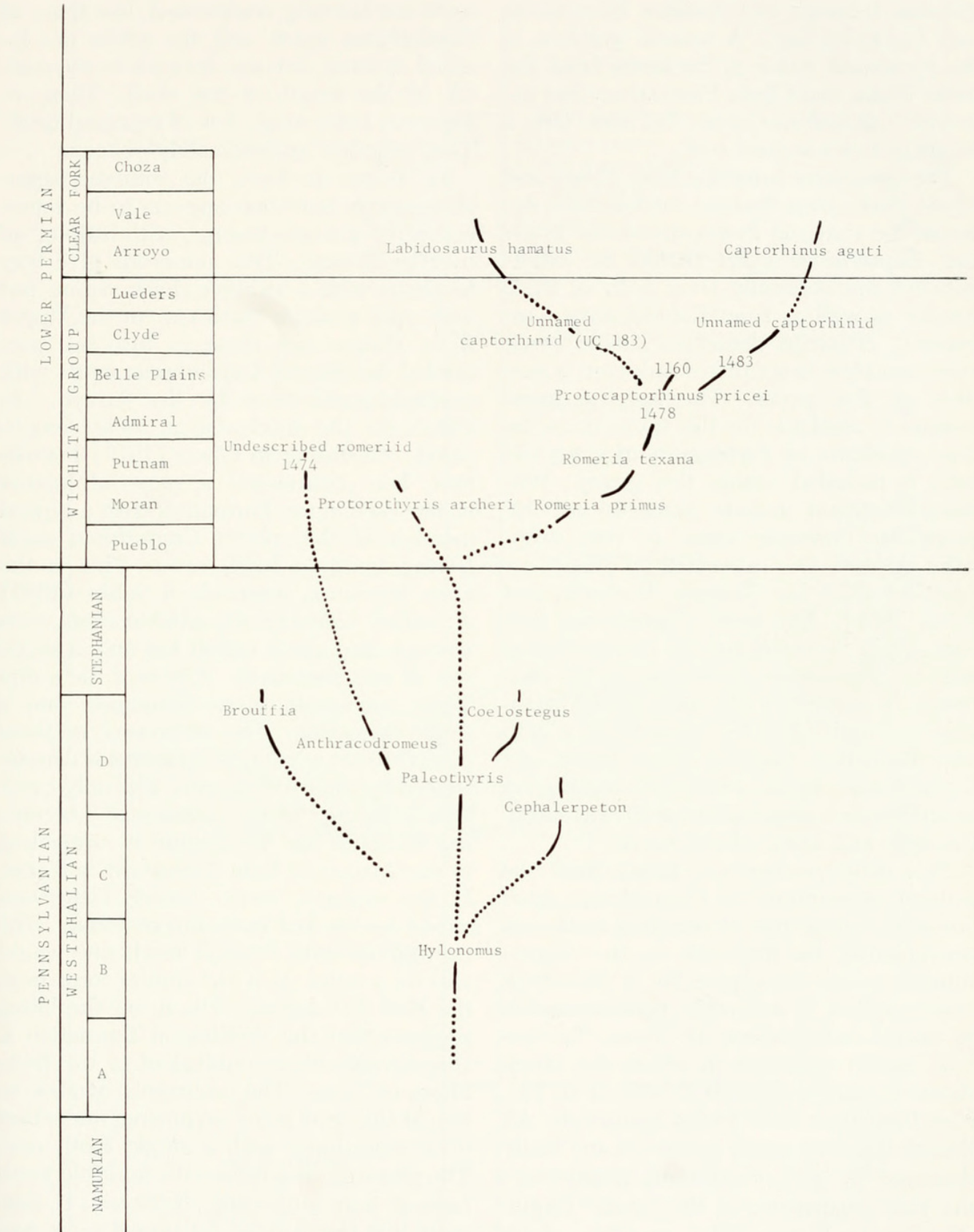


Figure 21. Phylogeny of romeriids. 1160, 1483, 1478, and 1474 are MCZ numbers.

division between the families Romeriidae and Captorhinidae. A second problem is the taxonomic status of the forms from the Belle Plains and Clyde Formations that resemble *Captorhinus aguti*, but have only a single row of marginal teeth.

The specimens from the Belle Plains and Clyde Formations that are intermediate between the romeriid *Protocaptorhinus pricei* and *Captorhinus aguti* should be differentiated taxonomically from both of these species as well as from *Labidosaurus* (see below). A formal definition should await more complete descriptive work than is possible in this paper. The specific name *laticeps* is available for this taxon since the type specimen of *Parioticus laticeps* (UC 642) is included within this group. Williston's original generic name is not appropriate, however, since it was originally applied to a gymnarthrid microsaure (AMNH 4328, see Gregory, Peabody, and Price, 1956). The name *Captorhinus laticeps* might be used, but the morphological and developmental significance of the evolution of multiple tooth rows should probably be emphasized by establishing a generic distinction between these forms and *Captorhinus aguti*. Formal designation awaits further preparation of the presumptive type and other related forms.

This newly recognized genus, with the general appearance of *Captorhinus aguti* but only a single row of marginal teeth, can conveniently be included in the Captorhinidae since the expansion of the cheek region makes it separable from romeriids by casual examination. In Texas, the earliest known specimen in which the cheek region is expanded is MCZ 1483 (Fig. 18), from the Upper Belle Plains Formation. Although it is very poorly preserved and badly damaged by acid preparation, it illustrates the first occurrence of the family Captorhinidae in Texas. The posterior cheek

teeth are laterally compressed, like those of *Captorhinus aguti*, and the orbits are located at some distance anterior to the middle of the length of the skull. There is, however, but a single row of marginal teeth. They number approximately sixteen.

In Texas, at least, the romeriid-captorhinomorph transition appears to be represented by a single lineage, with little or no overlap in time. True romeriids give way to forms with a swollen cheek region but with only a single tooth row in the Upper Belle Plains, and these in turn are succeeded by typical *Captorhinus aguti* with multiple tooth rows by the Arroyo. In Oklahoma the succession is more complicated. According to Olson (1970) *Pleuristion*, here considered a romeriid, occurs in the Wellington Formation with a typical member of the species *Captorhinus aguti* having multiple tooth rows. This is the same formation from which Seltin (1959) described *Labidosaurus oklahomensis*, with an expanded cheek region but only a single row of marginal teeth. It is as if the entire Texas succession were telescoped into a single formation. The occurrence of these diverse forms in a single formation is demonstrated by the fossil record. The only question is the age of the occurrence. According to Seltin the Wellington is equivalent to the Arroyo or Vale Formation in Texas. If this estimate were correct, *Pleuristion* would be the last surviving romeriid. The captorhinid with a single tooth row would also be a relict, as is the similar form from the Fort Sill deposit. Olson, on the hand, suggests that the Wellington Formation is considerably older, equivalent to the Belle Plains of Texas. The occurrence of *Pleuristion* at this level is not surprising, nor is that of a captorhinid with a single tooth row. The presence of a form with multiple tooth rows is very surprising, however. It suggests that this feature developed some two

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		LUEDEERS		
		Talpa limestone		
UC 196; UC 1043; UC 642; UC 183 UC 1119	X	Mitchell Creek (? and Vernon Crossing)		⑨
		CLYDE		
MCZ 2804	X	S. Electra		⑧
MCZ 1740	X	Weiss locality-Red Pasture Line House		⑦
		Bead Mountain limestone-Beaverburk		
MCZ 1483	X	Trematops locality		⑥
		BELLE PLAINS		
MCZ 1160	X	NW of Woodrum's		⑤
Type of Protocaptorhinus pricei	MCZ 1478	X	Elm Creek horizon Rattlesnake Canyon	④
		ADMIRAL		
Type of Romeria texana	X	Coleman Junction horizon		③
Juvenile Romeria texana	X	Archer City bonebed Zott Pasture		②
		PUTNAM		
All material of Protorothyris archeri and Romeria primus	X	Sedwick horizon Cottonwood Creek		①
		MORAN		
		Camp Colorado horizon		
No romeriids		PUEBLO		
		Saddle Creek horizon		

formations earlier in Oklahoma than in Texas. This is possible, but it would be surprising that the more primitive forms survived so much longer in Texas, with so far no substantiated reports of *C. aguti* before the Arroyo.

Olson admits that the stratigraphic basis for assigning any particular age to the Wellington is still very weak. His faunal arguments for comparison with the earlier beds of Texas are reasonable, but are subject to other interpretations. The significance of the occurrence of these three captorhinomorphs in the Wellington Formation cannot be established until the age of the beds can be determined with greater accuracy.

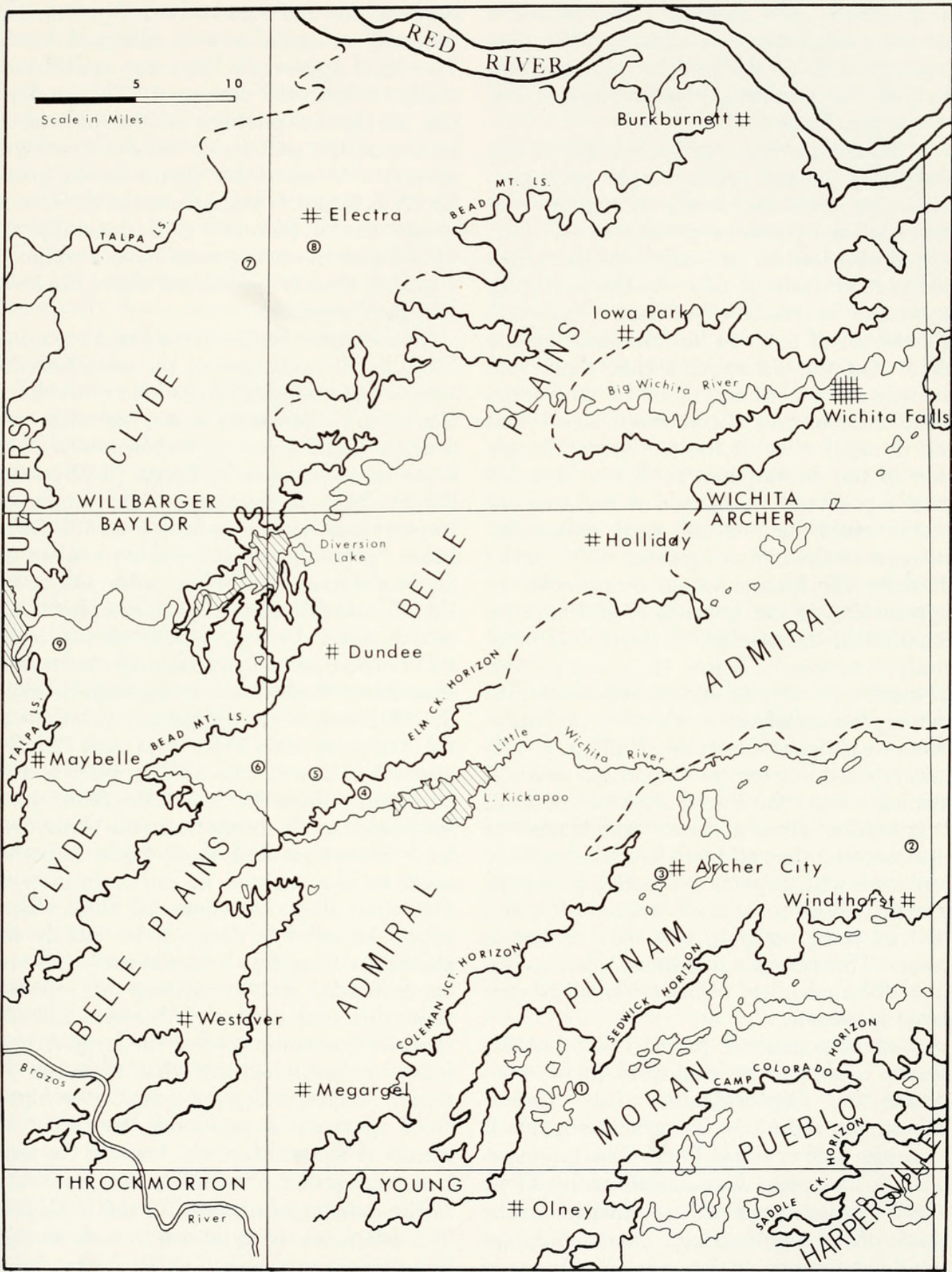
Captorhinus aguti has also been reported from the Abo Formation in New Mexico (Seltin, 1959). The specimen on which this identification was based, UC 735, does not include the skull, however, and so there is no evidence for distinguishing it from a romeriid such as *Romeria* or *Protocaptorhinus*.

Whatever the evidence from Oklahoma, the evolutionary picture in Texas is quite clear. Through the transition to captorhinids, the romeriids dwindle in importance. In terms of both numbers and taxonomic diversity, romeriids are much less important than they were in the Pennsylvanian. With the development of a laterally expanded cheek region, the early captorhinids of the Clyde quickly became much more common, and in the Arroyo started to differentiate taxonomically. It would appear that some change had occurred that provided a great selective advantage for this group. Although the evidence is limited, there do not appear to be any fundamental modifications in the postcranial skeleton between *Protorothyris* and *Captorhinus*. Modification in the vertebral struc-

ture and limb proportion evidenced by *Protocaptorhinus* indicates that the *Captorhinus* pattern had been achieved within the romeriids. As with the earlier romeriid dichotomy in the lowermost Permian, the final phase in the romeriid-captorhinomorph transition is best explained by consideration of the jaw mechanism and dentition. A notable feature in all well-preserved and carefully prepared specimens of *Captorhinus aguti*, and the captorhinid jaws with a single tooth row from Fort Sill, is the severe wear of the teeth. The crowns are flattened and even chipped, apparently as the result of force from the occlusal surface. There is a variety of possible causes for the great amount of wear observed in these teeth. The animals may have been crushing hard-shelled molluscs, arthropods, or annelids; they may have eaten tough plant food; or eaten either plant or animal food dug from the ground and ingested with a great deal of soil grit. Whatever the food source or sources, it was apparently very plentiful to provide for the enormous number of individuals recorded from the Fort Sill locality. Judging from the proliferation of other captorhinid genera with multiple tooth rows, it would appear that the facility to have evolved extra crushing surfaces was of considerable survival value.

Interestingly enough, the success of the captorhinids was initiated (in Texas at least) prior to the development of the extra rows of teeth. A genus with a single row is already fairly common in the Clyde. The romeriid genera *Romeria* and *Protocaptorhinus* show a preadaptation for the development of multiple tooth rows as a result of changes in the lower jaws. Because of the mechanical disadvantages of holding and crushing prey near the anterior end of the jaws in this lineage, the mass of jaw

Figure 23. Geological map of North Central Texas showing geographic position of specimens described in this paper. Drafted from a map prepared by Dr. Romer. Relative stratigraphic positions of numbered localities shown in Figure 22. Harpersville in Uppermost Pennsylvanian. Conspicuous "islands" in Pueblo, Moran, Putnam, and Admiral formations are outliers from overlying formations.



musculature must increase. This placed a selective advantage on widening the posterior portion of the jaw for the insertion of both the vertical adductor muscles and the pterygoideus.

Although we have no knowledge of the system of genetic control, it is quite possible that selection, acting to increase the width of the posterior portion of the jaw, would also lead to an increase in the width of the tooth-bearing area. As this occurred, it would be possible for more than one generation of teeth to be functional at one time. On the assumption that there had already been a dietary shift in the immediate ancestors of *Captorhinus aguti* that led to rapid wear of the teeth, any disruption of the developmental pattern that led to the premature eruption of replacement teeth would have a selective advantage. Because of the initially greater width of the dentary, this feature would be expected to appear first in the lower jaw, and later be manifest in the maxilla. A great deal more study is necessary before the exact pattern of tooth replacement and its relationship to the expression of the tooth rows in *Captorhinus aguti* are determined. This is certainly possible from the wealth of material available from the Fort Sill fissure deposit. It is evident from a casual examination of this material that all teeth are continuously replaced, with gaps in the tooth pattern approximately as common as in romeriids, and that all tooth positions can show extensive wear. The functional pattern remains essentially unchanged from very small to very large specimens.

The phylogenetic position of *Labidosaurus* must also be evaluated in order to define the Captorhinidae. Like *Captorhinus*, the definitive form of this genus is from the Lower Clear Fork. The type species, *L. hamatus*, was described by Cope (1896) from the Arroyo Formation. The skulls of the type species are commonly approximately twice the size of those of *Captorhinus aguti* (see Seltin, 1959: 502), have an even more conspicuously expanded

cheek region and a down-turned premaxilla, but only a single row of marginal teeth. The jugal apparently does not extend medially to reach the pterygoid. The similarities in the morphology of the individual teeth and the pattern of the skull roof are adequate to unite this genus in the same family as *Captorhinus*, despite the difference in the dental pattern. It is generally assumed that the two genera have a common ancestor, already specialized above the level of typical romeriids.

The situation has been confused taxonomically by the extension of the term *Labidosaurus* to forms with a skull size and shape similar to *Captorhinus aguti*, but with only a single tooth row, e.g., *Labidosaurus oklahomensis*, described by Seltin (1959) from the Wellington Formation, and numerous *Captorhinus*-sized jaws from Fort Sill, Oklahoma, generally considered equivalent in age to the Arroyo of Texas. Seltin suggested that *L. oklahomensis* was a morphological intermediate between *Captorhinus aguti* and *Labidosaurus hamatus*, and structurally antecedent to the former, although he cited the Wellington Formation as equivalent to the Arroyo or even Vale. The term *Labidosaurus* has hence come to be applied to two or possibly three different categories: both large and small forms from the Arroyo or later formations and small forms hypothesized to have existed in earlier formations that were true antecedents of *Captorhinus aguti*. In order to define more clearly the taxonomic boundary between romeriids and captorhinids, it is necessary to separate these different usages of the term *Labidosaurus*. Re-examination of the large Arroyo forms makes it evident that they can be readily segregated from any *Captorhinus*-sized species. In particular, the great increase in the width of the back of the skull has necessitated a complete reorganization in the manner of support for the braincase. The braincase is, relatively, much smaller in *Labidosaurus hamatus*. The paroccipital process does not extend to the middle of the squamosal, but rather is supported by

the posterolateral margin of the parietal (see Case, 1911, plate 12, fig. 2). The paroccipital process and the stapes both have very much longer stems than is the case in *Captorhinus*. Since these features are primarily an adjustment to the greater size of this particular species, it is clear that it would not occur in smaller forms. The increase in size, together with the necessary adjustment of the braincase, seems sufficient to separate *Labidosaurus hamatus* generically from currently known animals the size of all known specimens of *Captorhinus aguti*.

The necessity of differentiating between the ancestors of *Captorhinus aguti* and *Labidosaurus hamatus* is emphasized by the anatomy of an additional specimen from the Clyde Formation. With one exception, all the specimens that have been assigned to *Labidosaurus hamatus* have come from the Arroyo Formation. One skull, attributed to this species by Seltin, CNHM-UC 183, comes from the earlier Clyde Formation of Mitchell Creek, Texas. This skull (Plate I) is smaller than those of most described specimens of *Labidosaurus hamatus*, but far larger than any described for *Captorhinus aguti*. Its general anatomy suggests that it is a reasonable antecedent for the Arroyo specimens of *Labidosaurus hamatus*, although it differs in several respects.

This skull has a single tooth row, with four premaxillary teeth and twenty in the maxilla, the sixth of which is considerably larger. The posterior cheek teeth are not laterally compressed, but show considerable wear. Detailed comparison with *Labidosaurus hamatus* would require extensive preparation and description of that species that is beyond the scope of this work. Some general features can be noted, however, based on the published descriptions and CNHM-UR 161, illustrated by Seltin (1959). The tooth count and position of the "canine" are identical. The distance between the orbits is relatively greater in the more primitive skull; the snout is considerably

less acuminate anteriorly. The cheek region may be somewhat expanded, but not as much as in the Clyde specimens that resemble *Captorhinus aguti*. The cheek and skull table meet at a sharp angle. The configuration and nature of support for the braincase appear like that of advanced romeriids, rather than having the peculiarities of *Labidosaurus hamatus*. The skull roof is notably shorter than the posterior margin of the cheek. Except for this last feature, these characteristics resemble those of *Protocaptorhinus pricei*. The relatively narrow cheek region, noncompression of the posterior cheek teeth, and absence of a medial extension of the jugal suggest that this specimen evolved directly from romeriids such as *Protocaptorhinus*, possibly in the late Admiral or during the Belle Plains, rather than from the immediate ancestor of *Captorhinus aguti*. This specimen may reasonably be placed in a species distinct from *Labidosaurus hamatus*, but formal description must await further work on that species.

The establishment of an almost continuous sequence between romeriids and captorhinids complicates the definition of both groups. Since both names are widely used in the literature and encompass the approximate bounds of two distinct patterns of morphological and taxonomic diversification, it is of obvious advantage to retain the accepted usage as closely as possible. Phylogenetically, the most practical point of division would be at the dichotomy between the typical romeriids, such as *Paleothyris* and *Protorothyris* that have a straight tooth row, and the Lower Permian genera that have evolved a hooked premaxilla. The two lineages are readily separable morphologically and presumably had adapted to different manners of feeding. This point of division has, however, the lamentable taxonomic implication of removing the type genus from the family Romeriidae. Since the name Romeriidae has long been associated with the phylogenetically most important family of Paleozoic reptiles and also

honours one of this century's greatest contributors to vertebrate paleontology, an alternative point of separation should be considered. In order to include the common ancestors of both *Captorhinus aguti* and *Labidosaurus hamatus* within the Captorhinidae, the division must be made below the Clyde. On the basis of the presently available material it is fairly easy to differentiate the romeriid *Protocaptorhinus pricei* from the ancestors of *Captorhinus* by the configuration of the cheek region and from the ancestors of *Labidosaurus* on the basis of size. From an evolutionary standpoint this is a logical point of division, since the taxonomic diversification and numerical success of the Captorhinidae both occur subsequent to this division.

RELATIONSHIPS OF ROMERIIDS WITH OTHER REPTILES

Although much of this paper has been devoted to the close relationship between a particular group of Lower Permian romeriids and the family Captorhinidae, the additional information on romeriids provides a basis for discussing the origin of other reptilian groups as well. During the past ten years, all of the specimens that might be included in the Family Romeriidae have been studied. Two or three incomplete specimens from the Lower Permian of Texas remain to be described, but they do not substantially alter the picture provided by the descriptions already published.

Of all known groups of Paleozoic reptiles only romeriids are sufficiently generalized to be ancestral to any of the subsequent lineages. All of the members of this family that have been described conform to a single, basic morphological pattern, showing progressive modification of a series of skeletal features, but within rather narrow limits. On the assumption that the known record is representative of the total differentiation of the family, it is possible to specify both the time and particular phylogenetic position of the derivation of a

large proportion of the advanced reptilian orders. The position of several groups has been discussed in previous papers (Carroll, 1969a; Carroll and Gaskill, 1971; Carroll and Baird, 1972), primarily on the basis of the Pennsylvanian romeriids. The progressive evolution of all known members of the family in the Lower Permian places an apparent upper limit on the derivation of some groups whose earliest known appearance might otherwise have allowed derivation in the earliest Permian.

Pelycosaurs. On the basis of both their early appearance and generalized morphology, pelycosaurs have long been accepted as diverging from the main reptilian stock at a very early stage. Evidence of pelycosaurs from the Westphalian B of Joggins, Nova Scotia (Carroll, 1964), and the Westphalian D of Florence, Nova Scotia (Reisz, 1972), emphasizes the close relationship of pelycosaurs and romeriids and indicates that the two groups diverged from one another shortly before the appearance of the earliest member of either lineage in the Lower Pennsylvanian. The definition of the family Romeriidae could easily be extended to include the earliest Pennsylvanian and/or the latest Mississippian forms that were ancestral to both known romeriids and pelycosaurs. Such forms would, in fact, be barely distinguishable from *Hylonomus lyelli*.

Mesososaurs. The mesosaurs are also certainly direct romeriid derivatives. Members of this group are known only from the Pennsylvanian-Permian boundary, by which time they are already highly specialized in their cranial anatomy. Their postcranial skeleton is less specialized and suggests derivation from romeriids at about the level of development exemplified by *Paleothyris* in the Westphalian D.

Aclisterhinus, *Batropetes*, *Bolosaurus*, and *Eunotosaurus*. Although many details of the anatomy of the genera *Aclisterhinus* (Daly, 1969), *Batropetes* (Carroll and Gaskill, 1971), and *Bolosaurus* (Watson, 1954; Carroll and Gaskill, 1971) remain to be

studied and their interrelationships are not firmly established, these forms have a number of peculiarities in common. All may have evolved from rather primitive romeriids in the early Pennsylvanian or from one or more persistently primitive lineages in the middle or late Pennsylvanian. The primitive expression of a single pair of sacral ribs and the reduced number of vertebrae make *Eunotosaurus* a possible member of this ill-defined assemblage. As emphasized by Cox (1969), it is clearly a derivative of the primitive captorhinomorph assemblage.

Araeoscelidae. The *Araeoscelidae* (Vaughn, 1955), known from the North American genus *Araeoscelis* and the European *Kadaliosaurus*, resemble most closely *Paleothyris* among known romeriids and presumably evolved from forms of approximately that level of development, in the middle part of the Pennsylvanian.

*Lepidosaur*s. The ancestry of the lepidosaurs can be closely associated with the romeriids. Watson (1957) made a very plausible case for accepting the millerosaurs as ancestors for the typical eosuchians, including younginids and prolacertids, themselves ancestral to the living lepidosaur orders. Although Watson suggested that the millerosaurs had evolved from a group other than the captorhinomorphs, Parrington (1958) demonstrated the overwhelming similarities between millerosaurs, romeriids, and pelycosaurs. The known millerosaurs are all from the middle and late Permian and suggest that both the lateral and dorsal temporal openings appeared fairly late in the evolution of this group. Both the skull and the postcranial anatomy of the millerosaurs indicate derivation from romeriids in the middle to late Pennsylvanian, prior to the evolution of the cranial specialization seen in *Coelostegus*, *Protorothyris*, or the *Romeria-Captorhinus* lineage. The skull is noticeably small relative to the length of the trunk region. The tabular remains large and the paroccipital process does not extend to the squamosal.

An alternate ancestry for the typical eosuchians was suggested by Peabody (1952) in his description of *Petrolacosaurus* from the Upper Pennsylvanian of Kansas. He claimed that this animal had two temporal openings and so was ancestral to later diapsids, despite the primitive nature of the remainder of the skeleton. The presence of two temporal openings has been disputed by other workers and Stovall *et al.* (1966) suggested that this genus was an edaphosaur pelycosaur. Additional material of *Petrolacosaurus*, discovered by Peabody and Eaton, is currently being studied by Eaton and Reisz. These specimens show that there are indeed two temporal openings. The remainder of the cranial anatomy resembles that of primitive romeriids, while the girdles and limbs bear marked resemblance to those of the araeoscelids. The region of the quadrate and otic capsule are not well preserved, but there is no compelling evidence of the tympanum being supported by the quadrate in the manner of both millerosaurs and typical eosuchians.

Whether advanced lepidosaurs evolved from millerosaurs or from *Petrolacosaurus* or some other, as yet undetermined, intermediate forms, their ultimate derivation evidently lies with Middle Pennsylvanian romeriids such as *Paleothyris*.

Archosaurs. Our current knowledge of the romeriids adds little to our understanding of the ancestry of archosaurs. The earliest known members of that group, from the uppermost Permian, are already far advanced in most aspects of their skeletal anatomy from the primitive reptilian pattern. Clearly, the ancestors of these forms originally arose from romeriids, but whether via primitive eosuchians (Watson, 1957), varanopsid pelycosaurs (Reig, 1970), or some group as yet unreported (Romer, 1967), cannot be determined. Among romeriids, the greatest similarity to archosaurs is found in *Protorothyris*. This is mainly due to the large size of the skull and the large skull to trunk ratio. Although

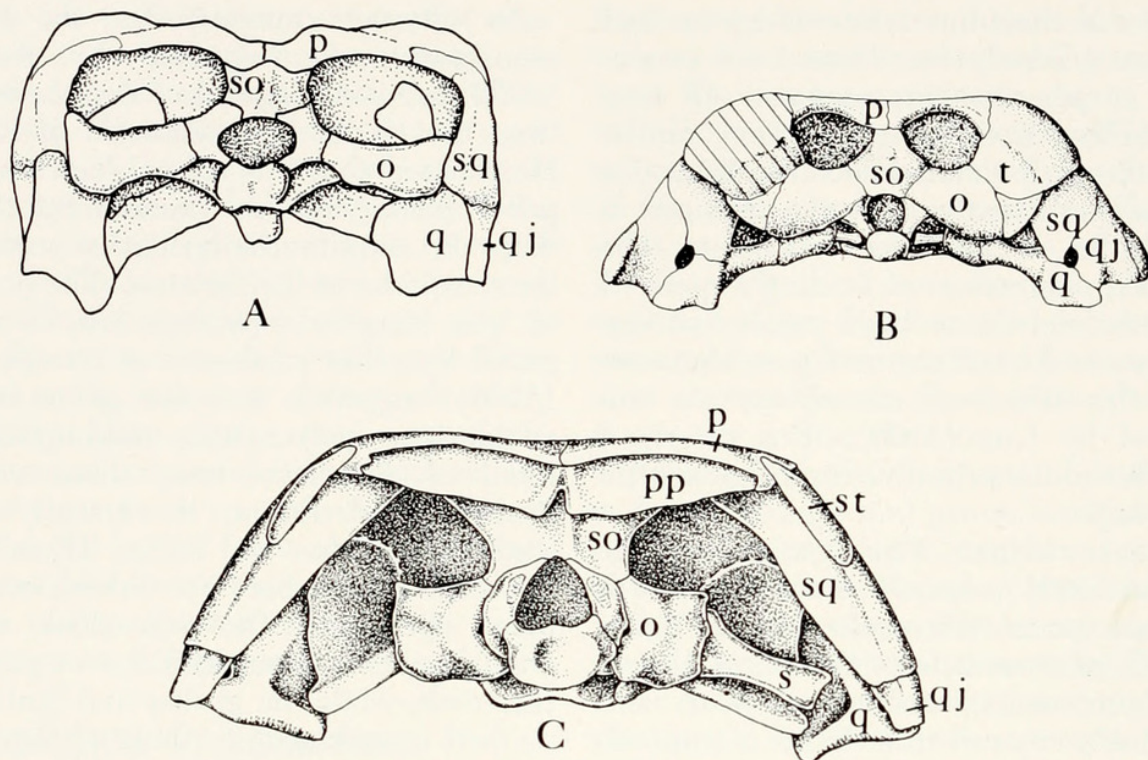


Figure 24. A, occiput of the Triassic turtle, *Proganochelys*, sketch based on photographs in Parsons and Williams (1961). B, occiput of *Procolophon*. C, occiput of *Protocaptorhinus pricei*.

this genus might be slightly closer to archosaurs than are other known romeriids, the similarities are not even close enough to differentiate between romeriids and pelycosaurs as potential archosaur ancestors. At present it does not seem appropriate to specify romeriids as any more than the *ultimate* ancestors of archosaurs.

Chelonian ancestry. The ancestry of turtles remains one of the greatest unsolved problems in reptilian phylogeny. Since they lack lateral or dorsal temporal openings, it can be safely assumed that they did not evolve from any of the advanced reptilian groups with synapsid, diapsid or parapsid skull configurations. If phyletically reptilian, they could have evolved only from primitive anapsid forms. Although no real intermediate forms are known, relationship with various "cotylosaurs" has been suggested: pareiasaurs (Gregory, 1946); diadectids (Olson, 1947); and procolophonoids (Romer, 1964 and 1966). The interrelationship of these groups and their phylogenetic position relative to other

primitive reptiles is subject to continuing dispute. None seem to have evolved from romeriids as such. If turtles had evolved from any of these groups, they would be only distantly related to the remaining reptilian subclasses, all of which may be reasonably traced to the romeriids.

In working with *Protocaptorhinus* and *Captorhinus*, one is struck by the similarities in the occiput to the primitive chelonian *Proganochelys* (Fig. 24). In both the captorhinomorphs and the turtle there are large posttemporal fossae, separated by a narrow supraoccipital. The paroccipital processes extend laterally toward the squamosal and are braced against this bone in *Captorhinus*. The tabular is missing.

The significance of the occipital structure is apparent if one considers the nature of the jaw musculature in turtles. As Gaffney (1971) has emphasized, the specialized jaw musculature in turtles is nearly as significant as the armor in differentiating this group from other reptiles. The main adductor muscle extends posteriorly from the

normal reptilian subtemporal fossa over the otic capsule (or a special process of the pterygoid in pleurodires) in the fashion of a pulley, and inserts on the supraoccipital. In both groups of turtles and their common ancestor, a strong union between the paroccipital process and the cheek region is necessary. This is already established in *Proganochelys*. This relationship between the paroccipital process and the cheek region is also developed in both lepidosaurs and archosaurs, in association with the development of an otic notch in the quadrate and the establishment of temporal openings. The only anapsid groups in which there are large posttemporal fossae above the paroccipital process are the advanced romeriids and captorhinids.

Pareiasaurs and procolophonoids seem particularly inappropriate ancestors for turtles because they have a totally different configuration of the occiput. Comparison of procolophonoids with both *Proganochelys* and early captorhinomorphs is relatively simple since they are of similar size (Fig. 24). The paroccipital processes of the braincase in procolophonoids are directed dorsolaterally toward the *tabulars*, as in anthracosaurs and the primitive genus *Limnoscelis* (Carroll, 1970). In the well known primitive genus *Procolophon*, the attachment of the braincase to the skull roof is loose, and the two are easily separated. The quadrate ramus of the pterygoid retains a primitive configuration, effectively separating the jaw musculature from the occipital surface. The main adductor musculature is essentially vertical in orientation and the posterior margin of the orbit is emarginated in order to provide a larger area for its expansion.

Although *Procolophon* is not the most primitive of procolophonoids, the primitive features of the jaw musculature that it exhibits would effectively bar both it and its immediate ancestors from giving rise to turtles. Consideration of pareiasaurs is difficult because of the great size and corresponding modification of the skull in all the

described genera. As in procolophonoids, the jaw musculature is effectively separated from the occipital surface by the quadrate ramus of the pterygoid and the quadrate itself. The paroccipital processes are oriented dorsolaterally, effectively preventing their attachment to the squamosal or the development of large posttemporal fossae.

It is certainly more difficult to envision the development of chelonian jaw musculature from pareiasaurs, procolophonoids, or their immediate ancestors than from advanced romeriids. Such a derivation for turtles has the aesthetic advantage of relating them to the main stream of reptilian evolution, although at a much later point of derivation than has typically been assumed.

One can argue that many of the factors involved in the origin of the chelonian jaw musculature are comparable with the changes that occurred in the origin of *Captorhinus* from romeriids. In both cases some factor in the relative abundance or nature of the food supply placed a premium on the development of a greater amount of, and more efficient use of, the jaw musculature. From a basic romeriid skull configuration, the cross-sectional area of the subtemporal fossa has increased, resulting in a lateral expansion of the cheek region. Some time between the Lower Permian and the Upper Triassic the jaw musculature of the ancestors of turtles expanded medially and posteriorly over the quadrate ramus of the pterygoid and took origin on the margins of the posttemporal fossae—on the upper surface of the paroccipital process and the lateral face of the supraoccipital. This is easily conceived from an advanced romeriid or a primitive captorhinid pattern.

The relatively short cheek region in *Proganochelys* and presumably its ancestors would have placed a premium on the evolution of some compensatory change in the jaw musculature. The posterior prolongation of the squamosal and supraoccipital would have provided for an even larger amount of jaw musculature than

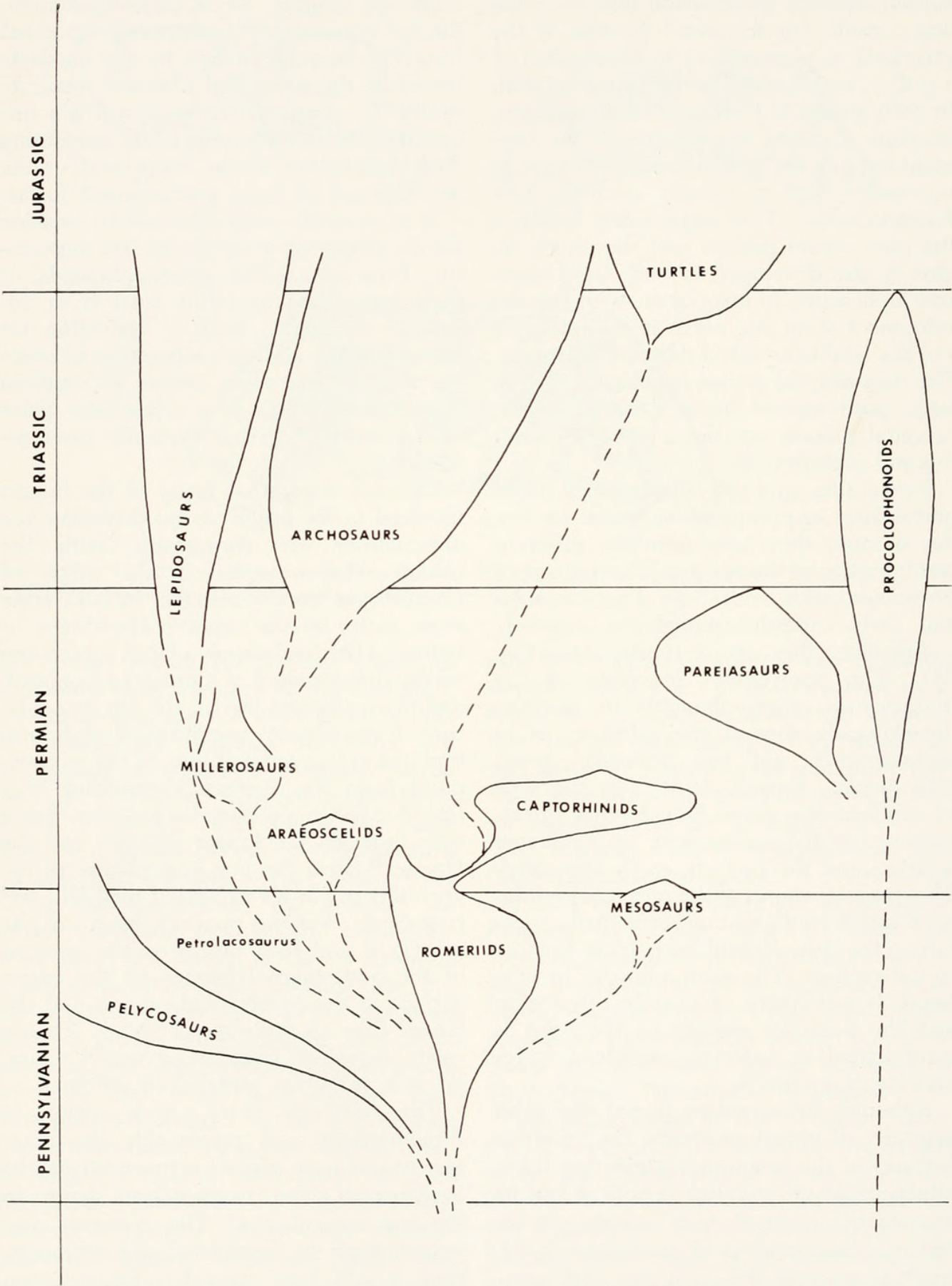


Figure 25. Phylogeny of romeriid descendants.

could be present in a captorhinomorph with a much longer cheek region. Presumably the otic notch, little developed in *Proganochelys*, evolved secondarily beneath this process.

Ichthyopterygia and Euryapsida. Unfortunately, elucidation of the anatomy of the Lower Permian romeriids casts little light on the origin of the specialized aquatic reptilian subclasses Ichthyopterygia and Euryapsida. We would prefer to accept Romer's (1971) assumption that they share a common ancestry with other reptilian subclasses, rather than Kuhn-Schnyder's (1967) suggestion of multiple, separate origins from amphibians, but an obvious point of departure of any of these forms from the romeriids cannot yet be established.

Procolophonoids and pareiasaurs. Further groups that are usually considered to be among the reptiles should be discussed in connection with the romeriids. Despite the apparently primitively anapsid condition shared by procolophonoids and pareiasaurs, neither group can be readily derived from any romeriids. Although restricted to the Middle and Upper Permian, all known pareiasaurs are large, highly specialized animals. The specializations of the skull, in association with their large size, preclude simple comparison with any of the groups of small, primitive reptiles. It is generally accepted that they are most closely related to the procolophonoids, but the similarities are primarily confined to the common absence of temporal openings and the presence of other strictly primitive features. The dorsolateral orientation of the opisthotic, common to the pareiasaurs, may, as in *Labidosaurus hamatus*, be a result of the great lateral extent of the cheek region and may not be a primitive trait. If so, this eliminates one of the few bases of comparison with procolophonoids, without providing any evidence of other possible relationships.

Because of their small size, procolophonoids are more readily compared with romeriids. As was mentioned recently in a

separate paper (Carroll and Gaskill, 1971), the configuration of the occipital region in procolophonoids is distinctly more primitive than is that of romeriids or their immediate derivatives. In this characteristic they more closely resemble *Limnoscelis* and the anthracosaurian ancestors of romeriids. Unless it can be shown that the procolophonoid condition can be derived from that observed in the romeriids, it must be assumed that the two groups have a separate ancestry, prior to the appearance of the earliest known romeriids. The highly specialized nature of the pareiasaurs make it more difficult to preclude the possibility of romeriid ancestry, but at present it cannot be established.

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