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OSTEOLOGY AND RELATIONSHIPS OF CAPTORHINUS AGUTI (COPE) (REPTILIA: CAPTORHINOMORPHA)

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The University of Kansas Paleontological Institute

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ABSTRACT

The osteology of *Captorhinus aguti* (COPE) is discussed, and the attachment of the major appendicular muscle groups is interpreted. Speciation in *Captorhinus*, position of this genus among the Captorhinomorpha, evolution of the middle ear in captorhinomorphs and their derivatives, and the question of relationships of the captorhinomorphs to micro-saurian amphibians, seymouriamorphs, and embolomeres are analyzed. It is concluded that microsaurians have no relationship to captorhinomorphs and that a basic captorhinomorph-elycosaur stock arose from embolomeres without seymouriamorph intermediates.

INTRODUCTION

In 1882 COPE described *Ectocynodon aguti*, based on a fragmentary skull from the Lower Permian of Texas, collected by W. F. CUMMINS at Coffee Creek. The type-species of the genus, *Ectocynodon ordinatus*, had been described by COPE in 1878 from what CASE (1911a, p. 36) called "a mere fragment of a skull in very poor condition" for which it was impossible to give a meaningful list of characters. In 1888 COPE described a third ectocynodont, *E. incisivus*; in 1896a, however, he referred all ectocynodonts to *Pariotichus*, a genus named by him in 1878 on the basis of an imperfect skull of which CASE (1911a, p. 35) wrote "the type specimen is in very poor condition, showing little more than the general outline and a few maxillary teeth." Consequently, CASE designated a homotype (AMNH 4760). Along with referring the ectocynodonts to *Pariotichus* (COPE's original distinction between the genera was the supposed absence of sculpture on the roof of the skull of the type of *P. brachyops*), COPE named *P. aduncus* (1896c), and *P. isolomus* and *Captorhinus angusticeps* (1896a). Also in 1896a COPE described a

curious individual and gave it the name *Hypopnous squaliceps*. CASE (1911a) suggested that *Hypopnous* was represented by two skulls, the larger probably a species of *Captorhinus* and the smaller, a diminutive amphibian in the mouth of the larger; consequently, CASE dropped the genus and species. ROMER (1956) and SELTIN (1959) listed *Hypopnous* as a synonym of *Captorhinus*, but EATON (1964) referred both skulls to *Romeria*.

In 1909 WILLISTON described another pariotichid, *Pariotichus laticeps*, and BROOM (1910) referred *Captorhinus angusticeps* to *Pariotichus*.

In 1911, CASE revised the cotylosaurs of North America. Because COPE's type of *Pariotichus* was too poor a specimen to be useful in determining the characters of the genus (COPE's type for *Ectocynodon* had been found equally wanting, and what could be made of the specimens did not seem to pertain to the later-named species), CASE referred *P. (Ectocynodon) aguti*, *P. aduncus*, and *P. isolomus* to *Captorhinus*, and established a new family, Captorhinidae. CASE at the same time referred WILLIS-

TON's *P. laticeps* to *C. isolomus*, and COPE's *P. (E.) incisivus* to *C. aguti*.

The taxonomy of *Captorhinus* remained essentially static for the next 48 years. Then, in 1959, SELTIN reviewed the Captorhinidae and as a part of that study tested for statistical significance the characters that COPE and CASE had used in discriminating among the four then-recognized species of *Captorhinus*. These characters included size, position of the large maxillary tooth, abrupt difference in length of the median premaxillary tooth, skull shape, sculpture, angle of the premaxillary bone with the maxillary, size of orbits, proportions of bones of the skull, and number of rows of teeth. From his sample SELTIN concluded that there was no evidence for more than one species of *Captorhinus*, namely *C. aguti* (COPE), and OLSON (1962a) concurred in this view. SELTIN also (p. 470) referred CASE's (1911a) homotype of *Pariotichus brachyops* to *Captorhinus*, judging it to be an immature individual of that genus.

In addition to CASE's (1911a), major contributions to the knowledge of the morphology of *Captorhinus* have been made by SUSHKIN (1928) and PRICE (1935), though neither dealt with parts behind the skull and no complete study of the osteology of *Captorhinus* has ever been undertaken. The wealth of material presently available in museum collections, both from the classic Texas sites and, more recently, from fissure deposits near Richard's Spur, Oklahoma, fairly demands a comprehensive description of the skeleton of *Captorhinus*. Accordingly, the present study was undertaken.

SYSTEMATIC DESCRIPTIONS

Class REPTILIA Linnaeus, 1758

Subclass EUREPTILIA Olson, 1947

Order CAPTORHINOMORPHA Watson, 1917

Family CAPTORHINIDAE Case, 1911

Genus CAPTORHINUS Cope, 1896

Captorhinus COPE, 1896a, p. 443.

Pariotichus, COPE, 1878, p. 508.

Type-species.—*Captorhinus aguti* (COPE), 1882.

Occurrence.—Lower Permian, Texas, Oklahoma, New Mexico.

Diagnosis.—Small terrestrial captorhinomorph with skeleton behind skull somewhat advanced beyond primitive members of order; dentition and skull roof specialized; palate generalized, with interpterygoid vacuity, ectopterygoid bone lacking; basipterygoid joint at level of or but slightly posterior to level of pterygoid flange; tabular absent; supratemporal reduced and wedged into posterolateral corner of parietal, which is suturally united with squamosal; posterior maxillary and mandibular dentition produced in 2 to 4 irregular rows; stapes with enlarged foot-plate and heavy shaft; centrum of atlas extending ventrally to surface of column and fused to intercentrum of axis; centra of anterior vertebrae excavated, leaving ventral keel; breaking point in tail; two pairs of

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Most of the material from the fissure deposits at Richard's Spur, Oklahoma, in collections of The University of Kansas Museum of Natural History and used in this study was collected by the late Dr. FRANK E. PEABODY and to a large extent sorted and prepared by him. It was his intention, before his premature death in 1958, to carry out a thorough study of *Captorhinus*, and the present work is therefore intended to be a fulfillment of his hope.

ABBREVIATIONS

Abbreviations used to designate the museum identity of specimen numbers are: MCZ, Museum of Comparative Zoology, Harvard College; AMNH, American Museum of Natural History; UC, UR, P, Chicago Museum of Natural History; UMMP, University of Michigan, Museum of Paleontology; USNM, United States National Museum; YPM, Peabody Museum, Yale University; KU, The University of Kansas Museum of Natural History.

sacral ribs; last presacral vertebra with powerful rib directed laterally but failing to touch pelvis; propodial to epipodial ratios greater than in more primitive reptiles; manus with single proximal centrale; astragalus and navicular in pes. [Dentition suggests insectivorous habits.]

CAPTORHINUS AGUTI (Cope), 1882

Ectocynodon aguti COPE, 1882, p. 451.

Pariotichus aguti COPE, 1896a, p. 447.

Captorhinus aguti (COPE), CASE, 1911a, p. 41.

Ectocynodon incisivus COPE, 1888, p. 290.

Pariotichus incisivus COPE, 1896a, p. 446.

Captorhinus incisivus (COPE), CASE, 1911a, p. 41.

Captorhinus angusticeps COPE, 1896a, p. 443.

Pariotichus angusticeps (COPE), BROOM, 1910, p. 218.

Pariotichus isolomus COPE, 1896a, pp. 445-446.

Pariotichus laticeps WILLISTON, 1909, p. 241.

Captorhinus isolomus (COPE), CASE, 1911a, p. 43.

Pariotichus aduncus COPE, 1896c, p. 135.

Captorhinus aduncus (COPE), CASE, 1911a, p. 44.

Holotype.—AMNH 4333, poor skull crushed laterally and twisted to left; skull roof incomplete, and many of sutures present indistinct; features of palate poor and somewhat harmed in preparation.

Diagnosis.—Characters of genus.

Occurrence.—Admiral, Belle Plains and Clyde Formations, Wichita Group, and Arroyo, Vale and (?) Choza Formations, Clear Fork Group, Lower Permian, Texas; Abo Formation, Lower Permian, New Mexico; (?) Arroyo Formation, Clear Fork Group, Lower Permian, Oklahoma.

OSTEOLOGY

SKULL

In dorsal outline the skull of *Captorhinus* exhibits the triangularity found in many reptiles, both fossil and Recent; the length of the sides of the skull is roughly 1.3 of the width of the skull at the occiput (Figs. 1-5).

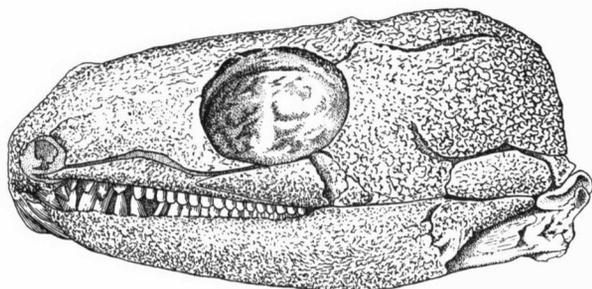


FIGURE 1. *Captorhinus aguti* (COPE). Lateral view of skull (KU 9978), $\times 1.25$.

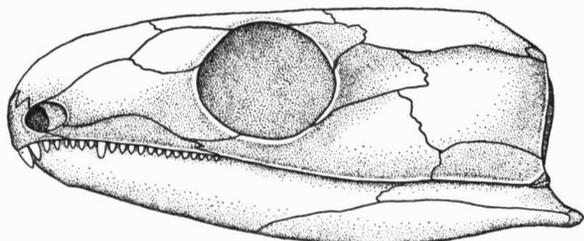


FIGURE 2. *Captorhinus aguti* (COPE). Lateral view of skull. About $\times 1.25$.

The outline of the cheeks commonly is inflated to a modest degree, causing the preorbital part of the skull to appear to be drawn out in a relatively narrow but blunt rostrum. The inflation is not expressed to the same degree in all skulls and not expressed at all in some skulls. In a skull (KU 9978) from the Richard's Spur locality that has suffered little post-mortem disturbance of the dorsal outline, the cheeks are feebly inflated; in the illustration by WATSON (1954, p. 333, fig. 7E) of *Captorhinus*, based on a specimen from Texas, the cheeks are not inflated. Another specimen (AMNH 4334) exhibits modest inflation of the cheeks, as does the illustration, presumably composite, of the skull by ROMER (1956, p. 70, fig. 36A). SELTIN (1959, p. 474) has suggested that post-depositional deformity is a major factor in the apparent variation in skull shape in *Captorhinus*.

The occipital margin of the dorsal skull roof is indented at the mid-line, but the depth of the indentation is seemingly highly variable among different individuals. The skull pictured by WATSON is nearly straight across the dorsal margin of the occiput; some specimens (KU 9978, AMNH 4334) show the mid-sagittal indentation more strongly.

The skull presents a low profile laterally. The roof

slants gently downward in a straight or weak dorsally convex line from the height of the occiput to the inception of the curve of the rostrum at the frontonasal contact. The skull terminates anteriorly in a decurved beak formed by the premaxillary and similar to that found in *Romeria*, *Labidosaurus*, and incipiently in *Limnoscelis* (VAUGHN, 1955, p. 451). The ventral margin of the skull roof is modestly convex ventrally at the level of the cheek and shallowly concave farther forward at the level of the teeth. The ventral margin of the mandible is convex ventrally. The profile of the occiput is essentially vertical; the pos-

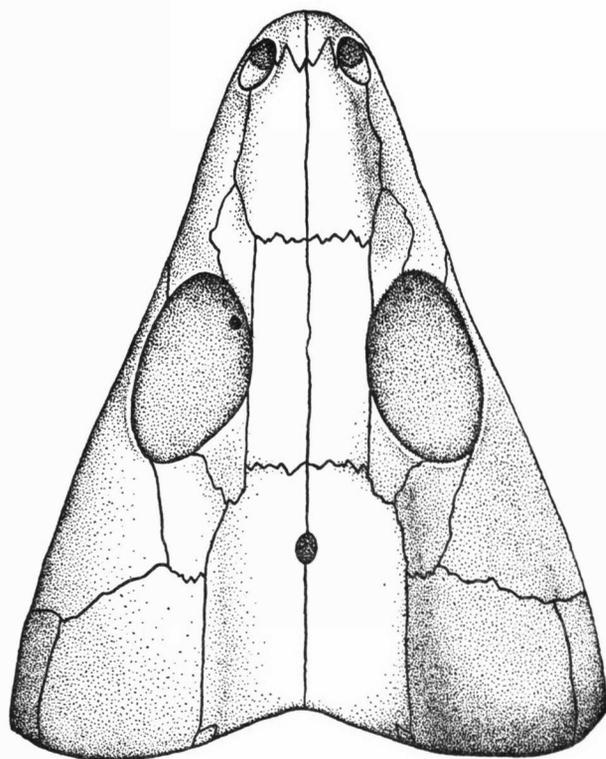


FIGURE 3. *Captorhinus aguti* (COPE). Dorsal view of skull. About $\times 1.25$.

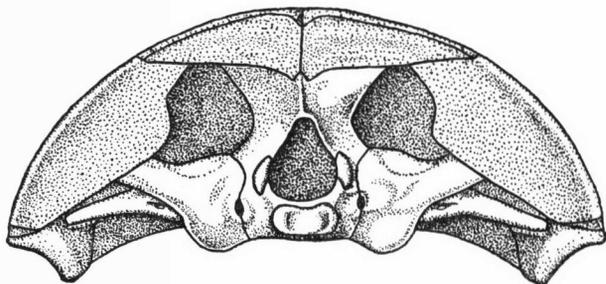


FIGURE 4. *Captorhinus aguti* (COPE). Occipital view of skull. About $\times 1.25$.

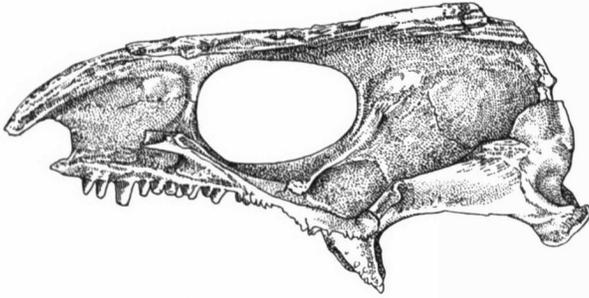


FIGURE 5. *Captorhinus aguti* (COPE). Internal view of right side of skull and right palatoquadrate, uncatalogued specimen, Clarke collection, $\times 1.6$.

terior margin of the squamosal is straight to shallowly sigmoid.

The orbits are located slightly in front of the mid-point of the length of the skull; they face laterally and slightly dorsally. The dorsal rim of the orbit is not raised above the dorsal skull table as in *Protorothyris* and as yet undescribed romeriid (MCZ 1963) (WATSON, 1954, p. 334, fig. 8A,B). The nares are in the anterior position usual among captorhinomorphs, and they face laterally and slightly anteriorly.

The skulls measured by SELTIN (1959, p. 499, table 2), yield a mean length of 57.5 mm., a mean interorbital width of 12.2 mm., and a mean orbital length of 15.9 mm.

DERMAL BONES OF SKULL ROOF

PREMAXILLARY

The premaxillary of *Captorhinus*, like that of other primitive reptiles, is a triradiate bone that sends a forked process dorsally to the nasal, and two processes posteriorly, one at the mid-line to the vomer and one externally that is overlain by the maxillary. The nasal process curves posteriorly and bears two projections separated by deep incisures for the reception of the converse system of projections and incisures of the nasal. The walls of the premaxillary incisures possess small foramina which presumably carried nutrient blood vessels brought to the bone through a passage on the internal surface of the nasal (Fig. 7).

The vomerine process of the premaxillary extends backward along the mid-line and possesses a moderate taper posteriorly. The dorsal surface of each process is beveled in such a manner that in articulation the processes form a groove between them for the reception of the anterior tips of the vomers.

The maxillary process curves backward externally and slips under the anterior projection of the maxillary, beneath the naris. The contact is again by an intricate system of grooves and ridges.

The premaxillaries are in contact with each other along the apposing broad flat surfaces of the nasal and vomerine processes. Movement of one premaxillary on the other is not suggested, however, because of the complex articulations of the premaxillaries with the neighboring bones of the skull roof.

The premaxillary most commonly bears four teeth, the

most medial one the longest, the remaining ones decreasing in height laterally. Random specimens are found with three or five teeth, but the numbers of teeth are without taxonomic significance (SELTIN, 1959).

The premaxillary forms the anterior wall of the narial opening, but little or none of the ventral rim. The septomaxillary fails to touch the premaxillary.

In articulation the premaxillary tilts downward and backward to form a beak and to cast the teeth that it possesses backward at such an angle that they overlap the apposing teeth of the dentary; before the lower jaw could be depressed, the mandible had to be pulled back slightly (Fox, 1964).

MAXILLARY

In *Captorhinus* the maxillary is a long, slender bone that extends from the naris, which it underlies, posteriorly to the anterior projection of the jugal beneath and slightly anterior to the orbit (Fig. 6). In lateral view, both anterior and posterior ends of the bone are radically tapered to finger-like projections. Slightly anterior of the mid-length of the maxillary is a pronounced dorsal swelling of the suture with the lacrimal that roughly coincides with or is slightly posterior to the level of the largest of the maxillary teeth. A similar swelling is found in the primitive romeriids *Hylonomus* and *Archerpeton* (CARROLL, 1964).

The anterior end of the maxillary forms the ventral rim of the naris by overlapping the external projection of the premaxillary. The septomaxillary apparently rested on the rim, but no evidence of this articulation in the form of scars or other marks is apparent. Dorsally the maxillary touches the lacrimal in a long suture that extends from the naris to the jugal. The posterior contact of the maxillary is with the jugal by means of an extensive overlap of the jugal on to the maxillary in which the jugal overrides the maxillary and passes forward lateral to it. The contacts of the maxillary with the premaxillary, jugal, and lacrimal seemingly have been made firm and immovable by the complex system of grooves and ridges that blanket the articulating surfaces.

The maxillary adjoins the palatine, however, in a moveable articulation. The internal surface of the maxillary bears a slender arcuate ridge posterior to the largest of the maxillary teeth that is complementary in shape to a groove borne by the lateral edge of the palatine. The surface of this ridge is of smooth, finished bone; based upon the structure of the palate, the ridge probably acted as a hinge for restricted swinging up and down of the palate upon it.

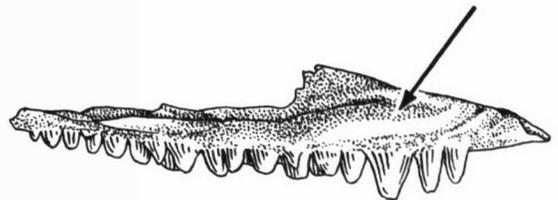


FIGURE 6. *Captorhinus aguti* (COPE). Internal view of left maxillary, uncatalogued specimen, Clarke collection, $\times 3$. Arrow indicates ridge for articulation with palatine.

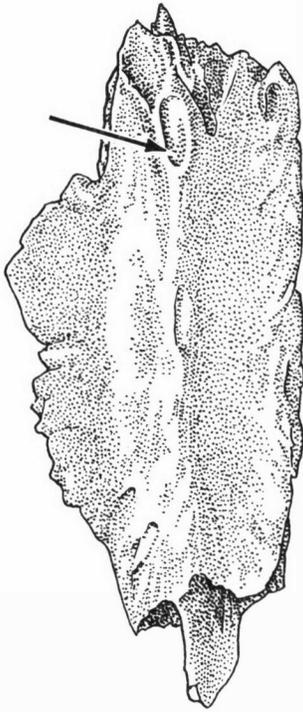


FIGURE 7. *Captorhinus aguti* (COPE). Internal view, right nasal bone, uncatalogued specimen, Clarke collection, $\times 6$. Arrow indicates opening to nutrient passage.

The marginal dentition of the maxillary reflects in length and distribution of the tooth rows the apposing dentition of the lower jaw. The multiple posterior rows of teeth in the dentary are apposed to the multiple posterior rows of teeth borne by the maxillary (KU 9978). There is a like alignment of the anterior and intermediate teeth of the dentary against the marginal, single-rowed teeth of the maxillary. The largest of the maxillary teeth are opposite the small teeth that follow upon the large anterior "tusks" of the lower jaw. The tusks are opposite the small anterior teeth of the maxillary. Anteriorly on the maxillary a series of three to five teeth occurs in a single row. Behind these are the multiple rows of laterally compressed teeth which are so characteristic of *Captorhinus*. The position of the largest of the maxillary teeth is without taxonomic significance (SELTIN, 1959). Of the maxillary dentition he has stated:

Apparently, at some stage during the growth cycle, varying in individuals, the fourth tooth becomes the dominant one. In the younger stages the third tooth is dominant. This can come about in at least two ways: (1) Replacement may take place in either the third or fourth tooth. It would appear from the scatter diagram that, if this is the case, it would have to be the third tooth that was replaced by a smaller one. (2) A new tooth may be added anterior to the third maxillary tooth, thus putting the third tooth in the fourth position so that the same tooth is actually dominant, but in a different position. The scatter diagram supports this idea. In only one individual in the Chicago Natural History Museum collections (CNHM-UR 242) have I observed the fifth tooth to be the largest. This is a large individual and therefore possibly represents a second (or later) stage in the growth process. (SELTIN, 1959, p. 473.)

SEPTOMAXILLARY

The septomaxillary in *Captorhinus* occupies most of the narial opening. In a nearly complete skull (KU 9978) the bone is thin, depressed centrally and in apparent contact with the nasal, lacrimal and maxillary bones. The residual opening into the naris is in front of the bone, and was probably circular, suggesting that the anterior border of the septomaxillary was crescent-shaped.

NASAL

The nasal in *Captorhinus* (Fig. 7) is a moderately long, slender bone that adjoins the premaxillary, septomaxillary, lacrimal, prefrontal, frontal, and (at the mid-line) the nasal of the opposite side of the skull.

Three sharp processes extend forward to the premaxillary; two of these are separated by a deep incisure and are lateral to a third (bordering the mid-line) which is separated from the others by a broad, shallow notch. The irregularity of the suture suggests a firm contact with the premaxillaries.

The line of contact of the nasals with each other is nearly straight, without any broad interfitting of processes and notches. Through at least part of the contact of the apposing edges, the fit of one nasal to the other is by a tongue-and-groove arrangement, in which a narrow thin lapet of the bone of one side fits into a shallow groove in the adjacent edge of the bone of the other side.

The contact of the nasal with the bones lateral to it is more complex. Behind the smoothly contoured rim in contact with the septomaxillary, the nasal broadens widely to meet the lacrimal. The suture is irregular; the edge of the nasal bears numerous sharp processes separated by narrow notches. In some specimens the nasal overlaps the adjacent edge of the lacrimal.

At the posterior termination of the lacrimal contact, the lateral edge of the nasal swings sharply toward the mid-line and then extends backward roughly parallel to the mid-line. This embayment marks the contact of the nasal with the prefrontal. The articulation is by means of small processes and notches that are combined with a multiple tongue-and-groove system usually involving two to three horizontal ridges and grooves extending for various distances along the edges of the respective bones.

The articulation of the nasal with the frontal bone occupies the whole of the posterior edge of the nasal. The contact is made firm by a complex interdigitation of acute processes and notches.

The single significant feature of the internal surface of the nasal is the presence of a broad, smoothly contoured ridge that extends the length of the bone. The ridge encloses a narrow passage that opens at the apex of the deepest of the notches involved in the premaxillary articulation. The passage continues into the premaxillary and presumably served as conduits of blood vessels for nourishment of the anterior bones of the snout.

LACRIMAL

In *Captorhinus* the lacrimal extends from the orbit to the naris. It forms the anterior and anteroventral borders of the orbit and limits the naris posteriorly. The bone is

longer than wide, being essentially rectangular in surface view, except for a thick posteroventral spur that contributes to the orbital rim.

Much of the bone is a relatively thin sheet. The lower edge, however, is thick and heavy. The articulating surface of this region is crossed by irregular grooves and ridges that touch the maxillary and jugal.

Internally the contribution of the lacrimal to the orbital rim rises sharply above the adjacent surface of the bone. The rim is narrowest near the prefrontal articulation and broadest at the base of the posteroventral spur. The spur overlaps both the jugal and the maxillary. Dorsal articulations of the lacrimal are with the nasal and the prefrontal; the lacrimal is overlapped slightly by both.

The posterior part of the narial rim is formed by the lacrimal alone. The lacrimal possesses no evidence of the septomaxillary articulation, although complete specimens show that such did occur. The lacrimal duct opens into the ventral part of the narial rim. The duct extends posteriorly through the thickened ventral edge of the lacrimal to the orbital rim.

PREFRONTAL

In *Captorhinus* the prefrontals are wedged between frontals and nasals dorsally and the lacrimal ventrally. The prefrontal forms the anterodorsal rim of the orbit. The contact with frontals and nasals is by a complex system of grooves and ridges on the apposing faces of the bones. Along the orbital rim the prefrontal is overlapped by the lacrimal; the remainder of the contact is simple abutment of the apposing edges made secure by grooves and ridges.

FRONTAL

In *Captorhinus* the frontals (Fig. 8) are narrow and nearly rectangular, although they taper slightly from side to side anteriorly. The bones articulate with each other along the mid-line, and with the nasals, prefrontals, postfrontals, and parietals.

The articulation of the frontals with the nasals has been described in a preceding section on the nasals. The prefrontals articulate with the frontals by means of a wide groove that is set into the lateral edge of each frontal in front of the orbit. A similar groove posterior to the orbit marks the contact of the frontal with the postfrontal. Between these grooves the frontal forms a part of the rim of the orbit.

The articulation of the frontal with the parietal is by both an interdigitating suture and, beneath this, by an onlap of the frontal onto a flange of the parietal.

The articulation between the frontals is expressed in a system of grooves and ridges that radiate upward, forward, backward, and obliquely, from a point that is opposite the contribution of the frontal to the orbital rim.

The inner surface of the frontal bears a conspicuous ridge that is highest and most narrow anteriorly. It extends backward from below the mid-point of the prefrontal contact to about the mid-point of the postfrontal contact. The ridge is gently arched medially, curving away from the orbit and toward the mid-line of the skull. The ridge may have functioned to provide increased support to the skull

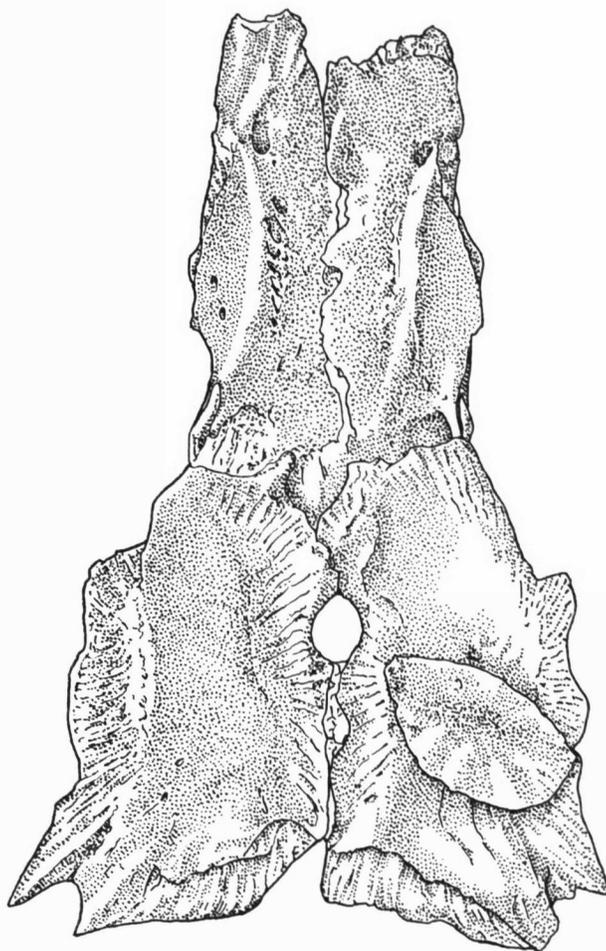


FIGURE 8. *Captorhinus aguti* (COPE). Internal view of articulated frontals and parietals, uncatalogued specimen, Clarke collection, $\times 3.75$.

roof in compensation for the weakness in the skull roof caused by the presence of the orbits.

The anterior-most part of the inner surface possesses a short ridge directed forward that is incised at its summit by a narrow groove. The groove is the precursor of the nutrient passage within the nasal bone.

JUGAL

The jugal in *Captorhinus* is a large, triangular element articulating with the maxillary and lacrimal anteriorly, the quadratojugal and squamosal posteriorly, the postorbital above, and the pterygoid and palatine internally. Between the postorbital and lacrimal articulations the jugal forms the lower rim of the orbit. Behind the orbit the jugal fans out into a broad plate. Beneath the orbit the bone extends forward as a finger-like projection to its preorbital articulations. Much of the ventral edge of the jugal is free and with the edge of the quadratojugal forms the lower border of the cheek.

The postorbital overlaps the jugal both on the surface

of the cheek and the surface of the orbital rim. Both the squamosal and the quadratojugal overlap the jugal. The anterior projection of the jugal is both dorsal and external to the maxillary. The lacrimal, in turn, rests on the dorsal edge of the anterior projection.

The jugal sends an anteromedially directed process from beneath the orbit to the palate. The end of this process is forked. The posterior tine articulates with the lateral flange of the pterygoid; the anterior tine adjoins the lateral edge of the palatine.

QUADRATOJUGAL

In *Captorhinus* this posteroventral component of the skull roof is a minor element. Dorsally it is overlapped by the squamosal; anteriorly it overlaps the jugal; posteriorly it articulates with the quadrate by means of a medially directed lappet that rests on the foot of the quadrate. The bone is convex in both vertical and horizontal sections and curves slightly around the posterior corner of the skull. The free ventral border is straight except posteriorly where the lappet for articulation with the quadrate extends obliquely inward and upward. The internal surface of the bone bears no marks of any kind.

The edge of the lappet that rests on the quadrate is slightly concave along its length, resulting in a shallow trough exposed on the occiput; presumably, the trough is the anterior wall of the external auditory meatus.

POSTORBITAL

The postorbital is roughly triangular in *Captorhinus*. Its greatest width is at the orbit, which it borders posteriorly. Articulations are with the postfrontal and parietal dorsally, the squamosal posteriorly, and the jugal ventrally. The postorbital is overlapped by the parietal and postfrontal and overlaps the squamosal and the jugal. The contribution of the postorbital to the rim of the orbit is the thickest part of the bone. The remainder is thin, plate-like and slightly convex in cross section.

POSTFRONTAL

The postfrontal in *Captorhinus* is a small triradiate bone that touches the frontal and parietal dorsally and the postorbital posteroventrally. The postfrontal furnishes the posterodorsal part of the orbital rim.

The dorsal edge of the bone is straight and thickened for its contact with the frontal and parietal. The surface of the posteroventral edge is beveled obliquely inward toward the orbital rim and overlaps the postorbital broadly. The suture that externally marks this contact is anteriorly concave.

The postfrontal has no such projection into the orbit from the anterior edge such as VAUGHN (1955, p. 319) has reported in *Labidosaurus*.

SQUAMOSAL

The squamosal of *Captorhinus* is the largest of the cheek series of dermal bones. It is overlapped externally by its dorsal neighbors, the parietal and the postorbital. Anteriorly the squamosal overlaps the jugal and ventrally the quadratojugal.

The squamosal sends a thin flange of unornamented

bone around the posterior corner of the skull to the occiput. Here the flange overlaps the posterior edge of the quadrate and is also possibly in contact with the cartilaginous extension of the paroccipital process, although this is uncertain. The lateral ascending process of the supraoccipital is said by PRICE (1935, p. 380) to meet the skull roof at the parietosquamosal suture. The occipital flange of the squamosal also overlaps the tip of the postparietal along its ventral edge.

The portion of the squamosal that forms the cheek is gently convex in both horizontal and vertical sections; the occipital flange meets the cheek at an angle that is slightly greater than a right angle.

Internally, the surface of the squamosal is smooth, except for a ridge that extends across its length. The ridge passes upward and forward from the posteroventral corner of the bone and parallels the articulation of the squamosal with the parietal. The ridge presumably marks the upper limits of the origin of the masseter from the squamosal (Fox, 1964).

PARIETAL

The parietals (Fig. 8) in *Captorhinus* are nearly rectangular, although they are slightly wider posteriorly than anteriorly. The central position of the bones in the posterior dermal roof results in articulations with the postparietals, supratemporals, squamosals, postfrontals, postorbitals, and supraoccipital.

The posterolateral corner of the parietal possesses a small notch for reception of the supratemporal. Medial to the notch, the postparietal is attached to the parietal by means of a lappet that fits under a shelf of heavily striated bone extending along the posterior edge of the parietals. The supraoccipital sends its ascending process forward between the postparietals and beneath the parietals into a groove at the junction of the parietals at the midline.

The frontals and postfrontals both overlap onto the parietal; the postorbital fits into a notch on the anterolateral corner of the parietal next to the frontal articulation.

The parietals articulate with each other by a complex system of interdigitating processes, grooves, and ridges. The parietal foramen is of a diameter usual among reptiles of this size. WATSON (1954, p. 342) states that the foramen in *Captorhinus* may be larger than that in romeriids; EDINGER (1955, p. 29) reports that the relative sizes of the parietal foramen and the foramen magnum appear to be essentially the same in *Protorothyris*, *Romeria*, and *Captorhinus*. The parietal foramen is located anterior of the mid-point of the length of the interparietal suture.

The parietal overlaps the squamosal broadly; although the articulation may have been weak, as suggested by the frequency of breakage along this line in preserved skulls, there is no indication that this articulation was moveable in *Captorhinus* or that the parietal merely rested on the cheek, as in *Hylonomus* (CARROLL, 1964, p. 63) or *Protorothyris* (WATSON, 1954, p. 339). The articulating areas of the squamosal and parietal show such a profusion of grooves and ridges that a sutural connection is indicated and immobility of the joint immediately suggests itself.

The inner face of the parietal reflects in two ways the attachment of the adductor muscles of the lower jaw. On the surfaces bordering the interparietal contact are numer-

ous striae directed toward the center of the bone but stopping short of that area. The central part is concave throughout much of the length and width of the parietal. Bordering the concavity is a ridge just within the attachment of the parietal and squamosal. The ridge probably marks the outer extent of the origin of the temporal muscle. The medial striae may be the scars of tendinous attachments of the temporal adductors. Lateral to these, in the concavities, the temporal mass possessed a fleshy origin.

SUPRATEMPORAL

The supratemporal in *Captorhinus* is a small bone inserted into a notch at the posterolateral corner of the parietal (Fig. 8). Distally, the lateral edge of the supratemporal articulates with the squamosal; distally, the ventral surface articulates with the postparietal.

The reduction of the supratemporal from the comparatively large size it possessed in such primitive captorhinomorphs as *Limnoscelis* and *Protorothyris* is well documented, particularly in the romeriid-captorhinid morphological sequence analyzed by WATSON (1954). The sequence removes any remnants of doubt concerning the proper identity of the supratemporal in *Captorhinus*.

Parenthetically, note should be taken of the presence of the supratemporal in *Labidosaurus*. Both WATSON (1954, p. 350) and VAUGHN (1955, p. 451) report that apparently the bone is absent in *Labidosaurus*, an error that seems to be derived from WILLISTON (1925). A skull of *Labidosaurus* at hand (AMNH 4427) clearly shows supratemporals in the expected position at the posterolateral corners of the parietals, and SELTIN (1959, p. 482) states that the difference in dentition is the major feature that distinguishes the two genera. The absence of the supratemporal in this regard is not noted by him.

POSTPARIETAL

In *Captorhinus* the postparietals are very nearly limited to the occiput. These small, roughly sickle-shaped bones may bear a dorsal ridge that borders the posterior edge of the parietals; the ridge is the sole expression of the postparietals on the dorsal table of the skull. It is not at all uncommon, however, for the ridge to be absent and the postparietals to be entirely limited to the occiput.

In occipital aspect the postparietals barely meet in the mid-line. Much of what would be their common suture is taken up by a notch for the receipt of the dorsal process of the supraoccipital in its passage to its parietal contact. From the mid-line, the occipital face of each postparietal extends laterally in a gentle curve that matches the curvature of the posterior edge of the skull roof above and the contact with the supraoccipital below.

The contacts of the postparietal with the parietal and the supraoccipital are complex and extensive enough to seem to preclude movement of the occiput upon the skull roof. The parietals abut against the dorsal limiting ridge of the postparietals when that is present, and are underlain by a broad shelf bearing extensive grooves and ridges that suggest a firm joint with the postparietals.

Similarly the postparietals send down a flange from their ventral edge that wedges tightly into a corresponding groove on the occipital face of the supraoccipital. Conse-

quently, the postparietals were in firm contact with both dorsal skull table and the central bones of the occiput. Lateral contact of the postparietals to the occipital flange of the squamosal was limited. It consisted only of the slender lateral termination of the postparietals overlapped by the squamosals. In none of the specimens examined is this contact extensive.

The internal surface of the postparietals is entirely unmarked. The surface is smoothly concave, the bone being thinnest at the edges and thickest at the junction of its parietal and occipital flanges.

VAUGHN (1955, p. 418) reports the presence of paired postparietals in *Protorothyris*, *Romeria*, and *Captorhinus*; in *Limnoscelis*, recorded by ROMER (1946) as having a median unpaired element, VAUGHN reports that ROMER (1954, personal communication to VAUGHN) states that the sutures are too indistinct to determine the nature of the postparietal.

OCCIPUT

The occiput of *Captorhinus* has been illustrated by WATSON (1954, p. 335, fig. 9E), and PRICE (1935) has described and illustrated bones of the braincase that are exposed on the occipital surface. In general outline the occiput (Fig. 4) resembles a trapezoid, the oblique sides of which are bowed gently outward.

The postparietals, the paired dorsal-most components of the occiput, extend widely to the sides from the mid-line. At the sides each adjoins the occipital flange of the squamosal, which meets the postparietal in a limited overlap. Contact of the postparietal and the parietal is along a shelf inset into the dorsal edge of the postparietal; the posterior edge of the parietal rests on this shelf.

The ventral edge of the postparietal is inserted into a broad groove that extends across the occipital face of the supraoccipital.

The supraoccipital is widest at its articulation with the postparietals. Below this contact the sides of the supraoccipital constrict toward the mid-line to form a neck, then abruptly widen before meeting the opisthotics. The occipital outline of the supraoccipital consequently resembles that of an hourglass. Along the mid-line and extending upward from the foramen magnum to the postparietals, the supraoccipital bears a crest, presumably reflecting the attachment of the dorsal axial musculature.

The supraoccipital forms the dorsal rim of the foramen magnum. On either side of the foramen the exoccipitals intervene. These are wing-shaped bones that curve upward around the foramen magnum from the basioccipital and form the dorsolateral and lateral rims of the foramen. At their tips the exoccipitals are backed by the supraoccipital.

The opisthotics are broadly Y-shaped bones in occipital view and possess a horizontal or nearly horizontal orientation. The dorsal ramus of each bone abuts against the foot of the supraoccipital and the ventral ramus against the basioccipital. The area between the rami articulates with the exoccipital and basioccipital and in this suture is pierced by a foramen for the passage of cranial nerves IX and XI (PRICE, 1935). The paroccipital process of the opisthotic extends laterally toward the quadrate and articulates with the quadrate by a cartilaginous extension.

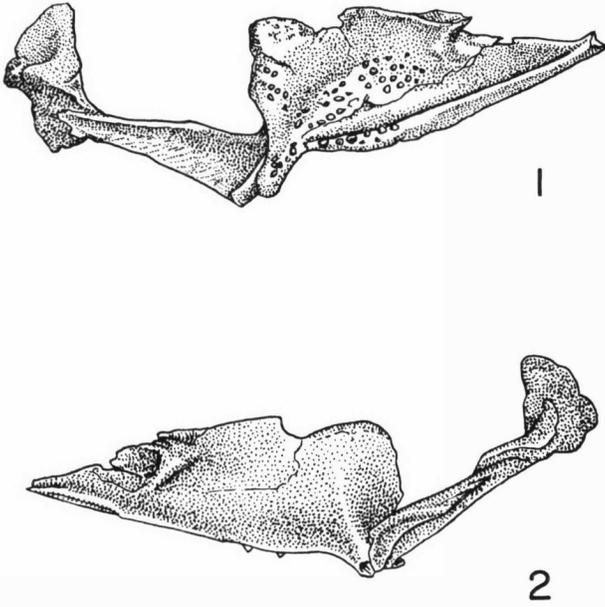


FIGURE 9. *Captorhinus aguti* (COPE). Right palatoquadrate, uncatalogued specimen, Clarke collection, $\times 1.75$. —1. Ventral view. —2. Dorsal view.

The post-temporal fenestrae are relatively large, subtriangular openings bounded by the occipital flange of the squamosal, postparietal, supraoccipital, and opisthotic. The size of the fenestrae is distinctly greater than that in *Protorothyris* (WATSON, 1954) and *Limnoscelis* (ROMER, 1956). The size of the fenestrae in *Captorhinus* is at least partly attributable to the loss of the tabulars (ROMER, 1956: 93). As WATSON has noted, the transition from the primitive romeriids to *Captorhinus* has resulted in a flattening of the skull and a spreading of the cheeks away from the mid-line. The change from the primitive proportions of height to width of the occiput has brought the occipital condyle down nearly to the level of the condyles of the quadrates. The change is not due so much to decrease in depth of the cheek or increase in height of the bones above the foramen magnum as to movement of the quadrates and lower edge of the cheek away from the condyle. The consequent increase in breadth of the occiput carried with it an increase in breadth of the post-temporal fenestrae.

The occipital flange of the squamosal is a flat sheet of bone that provides the lateral border of the temporal fenestra. The width of the flange is constricted for a short distance at its upper end; below the constriction the bone increases in width by about a fourth of its narrowest point. Ventrally the flange contacts the quadrate lappet of the quadratojugal. The latter achieves its expression on the occiput as a narrow band intervening between the ventral termination of the occipital flange of the squamosal and the posterior edge of the foot of the quadrate. WATSON (1954, p. 335, fig. 9E) is in error in showing the quadratojugal with a distinct occipital flange extending upward from the articulation of quadrate and quadratojugal. Such a flange does not exist.

The narrowness of the supraoccipital has been mentioned by VAUGHN (1955, p. 451); WATSON (1954, p. 427) discussed the nature of the supraoccipital of *Captorhinus vis-a-vis* the ancestry of lizards, but regarded suggestions of relationship of lizards with *Captorhinus* that rest on similarities in the supraoccipital as baseless.

DERMAL BONES OF PALATE

ROMER (1956, p. 71) has presented a general description of the palate of *Captorhinus*, in which he pointed out that it is of a generalized type, appearing in such widely diverse reptiles as pelycosaurs and *Sphenodon* (Fig. 9). ROMER reported that (1) the vomers are long and narrow, as are the choanae lateral to them, (2) the ectopterygoid is reduced or lost entirely among members of the suborder, (3) a small palatine fenestra is present, (4) the pterygoids are large and laterally bound the narrow interpterygoid vacuities, (5) the pterygoid flange is well developed and bears a row of teeth on its crest, (6) the basiptyergoid joint is moveable, (7) the palate is arched, although it remains below the sphenoid region, (8) the concave medial surface of the quadrate ramus of the pterygoid lodges the stapes (see below, however), (9) the expanded foot of the epipterygoid forms at least part of the basiptyergoid joint and bears a dorsally ascending slender rod, and (10) the bony quadrate may articulate with the paroccipital process. COPE (1896a, p. 443) reported:

In *Pariotichus aguti* the vomers are elongate posteriorly and the palatines send an acute anterior process between them. The palatines are separated by a fissure which is narrow anteriorly and becomes wider posteriorly. Each interior border bears on its posterior two-thirds a row of small teeth. The suture between the palatines and the ectopterygoid is not easily made out, but this region descends below the maxillaries to oppose the middle of the inside of the mandible. Just anterior to the oblique angle which makes this descent, a ridge of the palatine extends forward and outwards, and for a short distance bears a row of teeth. The posterior border of the ectopterygoid supports a patch of teeth in several rows.

The pterygoids are slender and diverge from the interior part of the palatines outward, backward and upward, to the inner side of the quadrate. They bear no teeth.

CASE (1911a, p. 44), paraphrasing BROILI, reported that:

The pterygoid is tripartite, the anterior portion bears small teeth and the inner edges of the two bones are united anteriorly; posteriorly the edges are separate and between them can be seen the slender parasphenoid rostrum. The posterior portion is extended as a broad plate back to the quadrate. The third (ectopterygoid) portion is truly only a thickening of the posterior border of the anterior portion behind, though it joins it gradually in front. . . .

CASE based his description of the skull in his morphological revision upon at least four specimens (AMNH 4334, 4338, 4424, and UC 642). He illustrated AMNH 4334 and AMNH 4338 in palatal views. His description (1911a, p. 96-97) is as follows:

The prevomers are long and slender, meeting in the median line and inclosing anteriorly the posterior ends of the premaxillaries; posteriorly they diverge and receive between them the anterior ends of the pterygoids. There is no trace of teeth on the prevomers. On either side are the elongate oval openings of the posterior nares.

The palatines lie in the normal position, but the sutures cannot be readily made out; the posterior end seems to be marked

by a suture extending inward and backward from a point about opposite the middle of the orbit. A short row of small teeth extending outward and forward from the median vacuity seems to be confined to the palatine.

The *pterygoids* have the usual tripartite form. The posterior process is a thin, nearly vertical, plate extending back to the quadrate and is applied to its inner surface. A strong basisphenoid process joins the basiptyergoid process of the basisphenoid. In the type specimen of *C. aguti* the palate has been very slightly crushed together from the sides, so that the basisphenoid processes lie between the basiptyergoid processes of the basisphenoid and the interptyergoid vacuity is narrowed. This may also account for the loss of the parasphenoid rostrum in this specimen. The external processes of the pterygoid extend out to the maxillary and there is no trace of an ectopterygoid bone. The posterior edge of the external process is prominent and the outer end is lower and presents a terminal face to the lower jaw, as in the Crocodylia, *Sphenodon*, and the Pelycosauria. The outer portion of this process supported a small cluster of minute teeth. The anterior processes are long and slender and extend far forward between the palatines and the prevomers. The inner edges anterior to the basisphenoid processes are concave and surround a considerable interptyergoid vacuity; opposite the anterior end of the orbit the inner edges of the pterygoids come in contact. From a point opposite the palatine suture the inner edge of the pterygoid supports a single row of small teeth.

WILLISTON (1925) did not comment upon the palate of *Captorhinus*.

PARRINGTON & WESTOLL (1940, p. 312), in comparing the palate of *Captorhinus* to that of *Seymouria*, reported that:

In *Captorhinus* the structural pattern is only slightly modified; the prevomers are laterally compressed, but still separate the internal nares and retain the old relations to premaxillae, palatines and pterygoids.

These authors showed (fig. 2D) *Captorhinus* in palatal view and indicated that an ectopterygoid is present. Later (p. 239) they reported that in comparison with *Seymouria*

The most obvious modification in the palate is the reduction of the ectopterygoid, and the great development of the transverse bar of the pterygoid, which terminates in a deep flange applied to the interior of the mandible. Both these changes were probably connected with a change in angle of the jaw muscles indicated by the more nearly vertical position of the quadrate. The ectopterygoid is small, and situated on the pterygoid flange.

The considerable historical interest in the palate of *Captorhinus* is reflected by the number of descriptions of it that have appeared in the literature. The most important of these have been reviewed above. These accounts, however, vary widely in detail and for the most part have been limited to the ventral surficial features of the palate, including the shape of its component bones and the distribution of the teeth they bear. Some attention recently has been paid to the articulation of the palate to the braincase (e.g., WARREN, 1961); no comparable discussion on the attachment of the palate to the dermal bones of the skull and to the quadrate or the possibility of movement of the palate on these bones is known. The features of the dorsal surface of the palate are unknown and a detailed description of the more commonly exposed ventral surface is lacking.

At the outset, it should be pointed out that no ectopterygoid bone occurs in *Captorhinus*. The element labeled ectopterygoid by PARRINGTON & WESTOLL (1940, p. 311, fig. 2D) is a process of the jugal directed medially to an attachment with the transverse flange of the pterygoid and

the most posterolateral tip of the palatine. The process delimits the postpalatine fenestra posteriorly.

VOMER

The most anterior components of the palate, the vomers, possess in cross section a horizontal I-beam construction. The medial and lateral edges of the bones are vertically oriented expansions that form, with the horizontal sheet that lies between and connects them, two troughs, one on the dorsal surface and opening dorsally, the other and shallower on the ventral surface and opening ventrally. The dorsal trough extends the length of the bone; the ventral trough has a comparable posterior extent, but anteriorly it disappears at the premaxillary articulation.

The medial limits of the palatal openings of the internal choanae are provided by the vomers. At this level the bones are slender and act as a bridge reaching between the choanae from the more platelike parts of the palate to the premaxillaries. The slenderness is restricted to the anterior fifth of the bone; backward from this point the lateral border of the vomer swings abruptly out and away from the mid-line. The vomer continues to broaden posteriorly until it reaches the palatine. The trough exhibited on the ventral surface is restricted to the expanded part of the vomer.

At the level of the expansion two changes in the orientation of the plane of the bone are seen. First, a faint outward twisting of the bone anteriorly causes the lateral edge to be somewhat lower than the medial edge. Second, the slender anterior region is bent downward, with result that the vomer is gently arched dorsally along its antero-posterior axis.

Both the peculiar I-beam construction and the arching of the vomer may be interpreted reasonably as adaptations to protect the vomers from fracture. These bones in *Captorhinus* are delicate. Because of their position within the palate they presumably received a variety of shocks. Stresses were applied to the vomers from the pterygoids and palatines, and additional and more varied stresses were applied to the vomers from below when food items were seized, chewed, and swallowed. The strength of the I-beam construction is axiomatic and its efficiency in structural steel framework well known. Although the significance of the arching of the vomers probably should not be taken out of its morphological context and discussed apart from the remainder of the palate, one apparent result of the arch is to lift the delicate vomers up and away from food. The vertical distance embraced by the arch is small, but it may well have been significantly effective in this regard.

The vomerine bridge is anchored posteriorly to the pterygoids and palatines in a system of articulations that assures a firm and stable connection to these more posterior components of the palate. The pterygoid sends a long, slender splinter of bone from its anterior process forward along the inner vertical face of the vomer. The joint is strengthened materially by an interlocking and closely spaced system of grooves and ridges on the apposing surfaces. Its rigidity is further enhanced by a ventral overlap of the vomer on to the pterygoid splint that is visible in palatal view in articulated specimens.

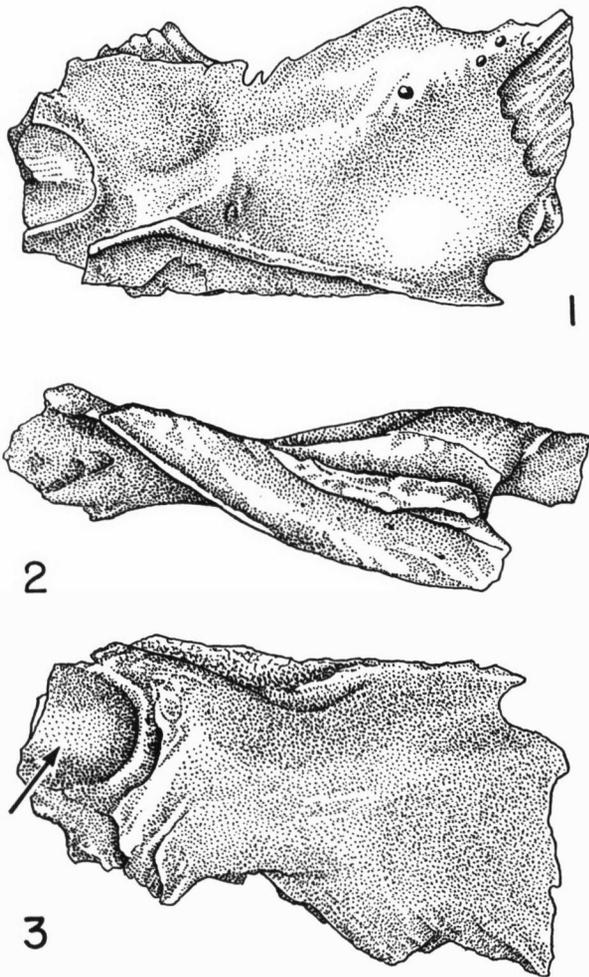


FIGURE 10. *Captorhinus aguti* (COPE). Right palatine bone (KU 14746), $\times 5$. —1. Ventral view. —2. Lateral view. —3. Dorsal view. Arrow indicates recess for olfactory bulb of the brain.

The horizontal surface of the vomer adjacent to its inner vertical face meets the pterygoid in a tongue-and-groove contact; the edge of this part of the vomer fits into a groove in the adjacent part of the pterygoid. Lateral to this area, the vomer is overlapped by the pterygoid for the remainder of the articulation of the two bones.

The palatine supplants the pterygoid in the postero-lateral articulations of the vomer and dorsally overlaps the vomer in their contact. The bone involved in the articulation of these elements is thin and is usually partially destroyed in fossils. It appears probable, however, that the palatine sent a short splint forward, like that of the pterygoid, but one which extended along the inner face of the lateral expansion of the vomer.

The articulations of the vomer with the pterygoid and palatine are thus complex. The integrated systems of these articulations seem to suggest that the vomerine relationship to the pterygoid and palatines was that of a firmly welded unit, with no movement possible between the anterior and posterior components.

The contact between the vomers and premaxillaries is limited and simple. The ventral trough of the vomer is filled in anteriorly; the surface of the bone is swollen and forms a pad directed ventrally and without features other than a faint groove extending along its medial edge. The dorsal trough is still present above, so that in cross section the region resembles the letter U.

Each premaxilla sends a spine backward along the mid-line that articulates closely with its fellow. When in contact with each other the spines in cross section resemble the letter V. They are beveled dorsally in such manner as to form a shallow groove that receives the anterior tips of the vomers. The lining bone of the groove, like that of the vomerine pads, is smooth. The articulation of the vomers with the premaxillaries, therefore, appears to have been nothing more intricate than resting of the tips of the vomers within the groove formed by the posterior spines of the premaxillaries.

PALATINE

If the vomers are viewed as an anteriorly extending bridge from the major part of the palate to the premaxillaries, the palatines (Figs. 9, 10) perform a more central supporting role, joining the components anterior and posterior to them and bonding them to the maxillaries laterally. This function is significant, because the palatine-maxillary contact is the only substantial support the palate receives between its premaxillary and quadrate articulations.

The articulation of the palatine with the pterygoid is divided into a suture extending along the anterior process of the pterygoid, and a second suture, transverse in orientation, with the transverse process of the pterygoid. The articulation of the palatine with the anterior process of the pterygoid can be divided in turn into three regions. The most posterior of these, extending along the mesial side of the palatine teeth, consists of an overlapping dorsally of the pterygoid onto the palatine. The suture anterior of this overlap changes to a groove in the edge of the palatine that receives a bony slip of the pterygoid. Beyond this, the palatine dorsally overlaps the anterior process of the pterygoid.

The posterior articulation of the palatine with the transverse process of the pterygoid is no less complicated. At the posteromedial corner of the palatine and continuous with the most posterior part of the articulation with the anterior process of the pterygoid, the pterygoid overlaps the palatine. As the suture passes laterally through the patch of pterygopalatine teeth it possesses a complex interdigitating pattern, with spinelike processes of the pterygoid and palatine extending deeply between each other. Lateral to this area and extending out to the postpalatine fenestra, the palatine rides up and over the transverse process of the pterygoid to the top of the pterygoid flange.

The palatine has yet another articulation, a lateral one, with the maxillary bone. Extending a short distance laterally from the body of the palatine is a dorsoventral expansion of the bone that is limited posteriorly by the postpalatine fenestra. The lateral face of the expansion is hollowed to form an attenuated, tear-shaped depression, broad anteriorly and narrow posteriorly. The whole of the depression is twisted slightly on its long axis with the result that anteriorly it faces more ventrally than it does pos-

teriorly. This peculiar groove fits over a correspondingly shaped, smoothly rounded ridge on the inner face of the maxillary, immediately above the anterior part of the maxillary dentition. In articulation the palatine groove is essentially horizontal, throwing the whole of the palate to the basiptyergoid joint downward posteriorly and toward the mid-line.

PTERYGOID

Posterior to the palatine the pterygoid has but three connections. The first of these is with the process of the jugal mentioned above. This process is a short dorsoventrally flattened spur that bears several stubby and rounded projections at its tip. The process is turned anteriorly and the projections are divided into two clusters. The more anterior of these just touch the palatine between the postpalatine fenestra and the groove that articulates with the maxillary. The posterior portion fits into a small group of pits on the side of the pterygoid immediately in front of the anteriormost part of the pterygoid flange. The smooth rim between the two articulating tines of the spur of the jugal encloses a small fenestra (Fig. 11).

The remaining articulations of the pterygoids are with the basiptyergoid processes and the epiptyergoid, described completely by OLSON (1951, p. 100) and WARREN (1961), and with the quadrate. The latter consists of a broad overlap of the expanded quadrate wing of the pterygoid upon the medial face of the dorsal plate of the quadrate, impressed upon the quadrate in faint outline.

The quadrate process of the pterygoid is a broad vertical plate of bone extending posteriorly and slightly laterally from the basiptyergoid articulation. The process terminates on the medial side of the quadrate in an overlap that is sizeable but which may have been loose enough to permit the pterygoid to pull slightly away from the quadrate when the palate moved.

The ventral edge of the process is rounded and of hard, finished bone. The dorsal edge is a shelf, broad anteriorly, narrow posteriorly, for the articulation of the foot of the epiptyergoid. The shelf is grooved medially and along its edges, suggesting the presence of a cartilaginous pad between the bony surfaces of the epiptyergoid and pterygoid. Anteriorly the continuity of the dorsal edge is interrupted by a deep cleft for reception of the spur of the epiptyergoid and the basiptyergoid process.

The dorsal shelf of the quadrate process hangs out over the medial surface of the process but not the lateral surface. Consequently, the medial surface is concave in cross section and the lateral surface is flat. The concavity of the medial surface is particularly pronounced anteriorly. Posteriorly the concavity progressively diminishes; at the level of the quadrate the concavity is absent and the medial surface is flat.

The medial surface of the quadrate process possesses no marking to indicate its role in the definition of the cavity of the middle ear. However, the posterior part of the process must surely have been involved in limiting the cavity laterally because of the close proximity of the process to the stapes. ROMER (1956, p. 71) is correct in suggesting this, but in error in supposing that the quadrate process of the pterygoid lodged the stapes in the concavity of the medial surface of the process. The concavity is well for-

ward of the level of the stapedial shaft; at the level of the shaft the process is flat, but there can be little doubt of ROMER's suggestion of the participation of the process in the cavity of the middle ear, if only because of the close proximity of the process to the stapes.

The remaining articulation of the palate is between its two halves, along the mid-line anterior to the interptyergoid vacuity. Commonly, in specimens in which other post-mortem distortion is at a minimum, one of the halves of the palate is slightly displaced in relation to the other, indicating that the connection between the two was weak. The expanded medial faces of the anterior processes of the pterygoids and the medial expansions of the vomers participate in this articulation, which may have been by nothing more than ligaments.

The character of the vomerine articulation with the premaxillary, the palatine articulation with the maxillary, and the pterygoid articulation with the epiptyergoid and basiptyergoid processes suggests that some kind of movement of the palate of *Captorhinus* was possible. It does not seem probable, however, that anteroposterior sliding of the palate could have occurred. The spur of the jugal braces both the palatine from behind and the pterygoid from the side to prevent any forward or backward movement of the palate.

A capacity for bending of the halves of the palate up and down seems to be a more plausible explanation of the apparent movable character of these joints. Presumably, in this kind of movement the medial spur of the jugal and the palatine-maxillary joint acted as fulcrum, placed laterally, so that the greatest swing of the palate occurred along the junction of the two halves. The apparent looseness of the medial connection of the palatal halves anterior of the interptyergoid vacuity seemingly would permit this kind of movement. The only factor that could be called upon to prevent the palate from swinging up and down is the character of the pterygoquadrate joint, but this factor must be consistently faced regardless of the nature of the palatal movement. There can be no question but that the quadrate remained firmly in place; the extent and complexity of its articulation with the roofing bones of the skull lead to no other conclusion than that the quadrate could not move. Nor does the quadrate wing of the pterygoid seem thin enough to have permitted it to be twisted in response to the ventrodorsal movement of the palate anterior to it. What seems most probable, although not entirely satisfactory, is that the pterygoquadrate joint could yield slightly to the pressures exerted on it by the movement of the anterior palate. Downward movement of the palate would tend to pull the pterygoid away from the quadrate; upward movement would bring the apposing surfaces of the two bones into contact again.

All of the teeth of the palate arise from areas that are raised above the relief of the surrounding tooth-free bone. The most ventral parts of the pterygoid flange bear teeth, as do the medial ridge of the anterior process of the pterygoid and the oblique pterygopalatine swelling between the anterior pterygoid process and the transverse pterygoid process. The teeth, therefore, arise from areas of bone that are more ventral than the neighboring bone and more likely to have come into contact with items of food than if they arose from nonswollen areas. The vomers are eden-

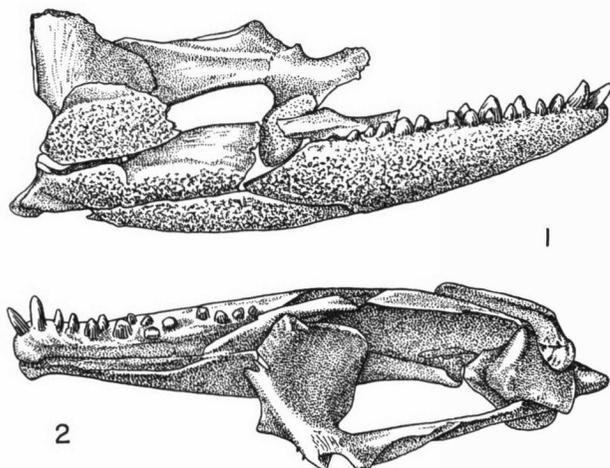


FIGURE 11. *Captorhinus aguti* (COPE). Right mandibular ramus and incomplete palatoquadrate, $\times 1.7$ —1. Dorsolateral view. —2. Dorsomedial view.

tate in *Captorhinus*. The entire palate in the toothed areas slopes obliquely downward and backward; the teeth slant obliquely to the palate at an angle to cause them to be essentially vertically oriented when the palate was articulated. Movement of the palate in the manner suggested above could satisfy three ends: (1) to relieve undue pressure against the palate from food held in the mouth; (2) to hold and release food as it moved backward in the throat during swallowing; (3) to aid in pushing food down the throat, particularly by movement of the pterygoid flanges. The ventral position of the teeth materially aids in the performance of the second and third functions.

The features of the dorsal surface of the palate (Figs. 9, 10) have yet to be described. The components of the palate anterior to the pterygoid flange consist of little more than a sheet of bone that is gently convex from front to back and which is limited medially by a ridge that decreases in height posteriorly. However, the dorsal surface of the palatine (Fig. 10) exhibits a large and deep depression that is surrounded laterally and posteromedially by a wall, and which opens anteriorly to the dorsal groove of the vomer that adjoins it in front. This structure held

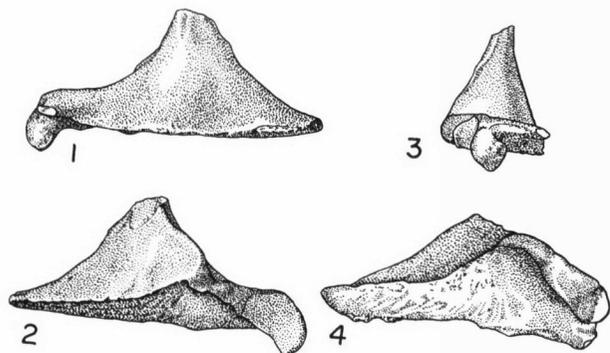


FIGURE 12. *Captorhinus aguti* (COPE). Left epipterygoid, KU 14755, $\times 3.1$. —1. Lateral view. —2. Medial view. —3. Anterior view. —4. Ventral view.

the olfactory bulb of the brain; the neurons from the olfactory receptors ran through the dorsal channel of the vomer to the olfactory bulb. The size of the depression suggests that the olfactory bulbs, and thus the olfactory sense, were well developed in *Captorhinus*, for the diameter of the essentially circular receptacle is more than three-quarters of the width of the palate at this level, and the width of the adjoining vomerine channel is equally impressive.

Dorsally on the pterygoid flange there extends a transverse line that has been interpreted by Fox (1964) as marking the anterior limit of the origin of the anterior pterygoid muscles from the dorsal surface of the palate.

OSSIFICATIONS OF PALATOQUADRATE CARTILAGE

EPIPTERYGOID

The epipterygoid (Fig. 12) possesses three regions that are morphologically distinct: a vertical bar, a foot plate, and an anterior spur. WARREN (1961) has shown these clearly.

The vertical extent of the bar is not known, and its termination presumably was in cartilage. Attachment to the skull roof may have been by ligaments, as ROMER (1956, p. 64) has suggested for primitive reptiles generally, but there are no scars to indicate such an attachment. The bar arises from a broad base on the dorsal surface of the foot plate; its medial face is shallowly concave in horizontal section and its lateral face convex. The bar possesses a flange with a hooked process, which may have provided attachment for a palatal levator, on its anterolateral face.

The foot plate is broadly wedge-shaped in dorsal view, and is three to four times wider anteriorly than posteriorly. Dorsally, the foot plate grades insensibly into the vertical bar. The medial surface of the foot plate is gently concave, in tune with the bar above, and possesses at its antero-basal corner a small, posteriorly directed spur, possibly anchoring a muscle slip, but otherwise of unknown function.

The anterior edge of the foot plate bears a hook that forms a notch on its inner curve and that descends below the base line of the foot plate proper. The hook inserted into the basipterygoid joint between the notch of the pterygoid and the inserting spur of the basipterygoid.

The epipterygoid rested on the expanded dorsal edge of the quadrate process of the pterygoid. The nature of the joint is not certain; the apposing surfaces are grooved posteriorly but are smoothly finished anteriorly. The whole suggests a cartilaginous pad between the pterygoid and the epipterygoid permitting slight movement, perhaps bending, between the two bones.

QUADRATE

The quadrate (Fig. 13) of *Captorhinus* is a pivotal element of the skull in the sense that it must anchor the palate, the stapes, the mandible and the skull roof to itself. Consequently, the quadrate acts as a bridge for the reception and distribution of the stresses transmitted to it by each of these functionally diverse components of the skull.

The bone, as WATSON (1954, p. 359, fig. 15) has illus-

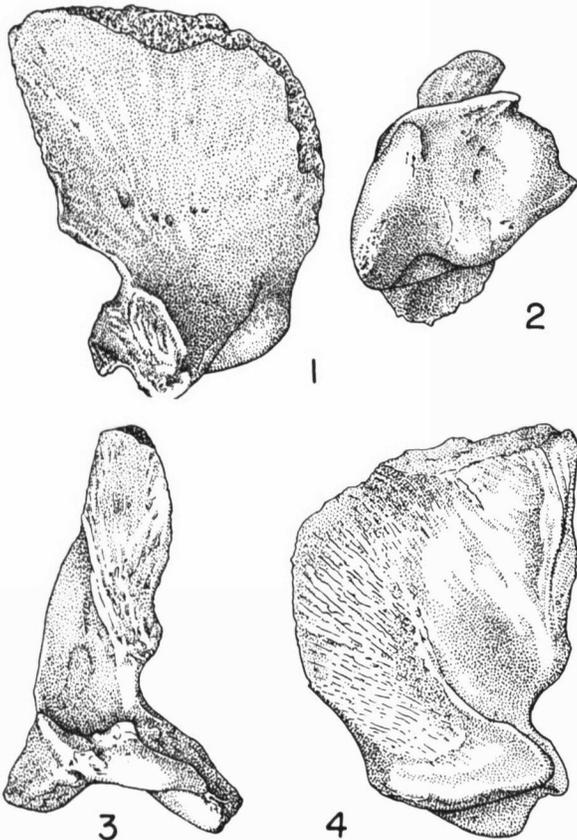


FIGURE 13. *Captorhinus aguti* (COPE). Right quadrate (KU 14754), $\times 4$. —1. Lateral view. —2. Ventral view. —3. Posterior view. —4. Medial view.

trated, consists of three morphologically distinct regions: a vertical dorsal plate, a ventral foot, and a connecting neck. The plate is roughly triangular in outline; its apex is directed ventrally toward the neck. Except for the anterodorsal corner, the plate is ossified throughout. The corner is commonly lacking in preserved specimens, suggesting that the bone was very thin here, if there were bone at all, or that, in at least some individuals, the corner was constructed of cartilage.

The upper border of the plate is nearly straight in lateral view, but when looked at from above, the border transcribes a gentle arc that lends to it a slight lateral convexity. The border lacks grooves or ridges of any kind, but is slightly swollen above the adjacent area of the plate. This thickening is most evident on the lateral surface of the plate; here the border overhangs the face of the plate below. WATSON (1954, p. 359, fig. 15) is in error in indicating that the dorsal border of the quadrate articulated with the squamosal. The border was free of any contact with the skull roof.

The posterior border of the plate flares out into a broad flange, oriented at right angles to the plane of the plate. A system of minor grooves and ridges that passes obliquely across the ventral parts of the flange suggests the extent of the articulation of the quadrate with the occipital flange

of the squamosal. As in the case of the dorsal ridge, most of the flare of the flange is directed laterally rather than medially. The flange tapers to a delicate feather edge laterally; medially the flange is only slightly swollen above the surface of the medial face in small or moderately sized individuals. In large specimens, the swelling may become a pronounced boss bearing grooves and ridges for the attachment of the paroccipital process of the opisthotic.

The anterior edge of the dorsal plate requires little comment. It is not swollen; below the anterodorsal corner its ossification is complete.

The features of the lateral face may also be dismissed with little comment. It is a smooth and unbroken surface of bone that is slightly hollowed owing to the lateral extent of the dorsal border and posterior flange beyond its surface. The medial face, in contrast, possesses a remarkable suite of morphological characters. It is upon this face that several of the functions of the quadrate are focused.

A dramatic feature of the medial face is a broad and irregular scar imprinted on its anterior half. The topography of the scar is extremely irregular; grooves and ridges are abundantly present in a complex arrangement. The borders of the scar mark the extent of the overlap of the quadrate wing of the pterygoid on the quadrate. The probable nature of this joint is discussed fully in the description of the palate.

A second feature of the medial face of the plate is the stapedial recess, described by WATSON (1954). The recess is a broad groove that extends from the pterygoid scar to the constricted neck of the quadrate. As the recess nears the neck, the ventral lip of the recess becomes increasingly prominent and the corresponding dorsal lip becomes progressively weaker and ill-defined. The recess terminates at the neck in the posterior notch of the quadrate. The flare of the ventral lip of the stapedial recess provides a shelf for the support of the stapes as it enters the recess. The depth of the penetration of the stapedial shaft into the recess is defined by the presence of a small, irregular patch of porous bone within the floor of the recess. The patch was in contact with an apposing plaque of porous bone on the stapedial shaft. The tip of the shaft abuts against the bottom rim of the posterior notch of the quadrate (Fig. 14) when the surfaces of porous bone are in articulation.

WATSON (1954) labeled the posterior notch of the quadrate a part of the quadratojugal foramen, a feature that ROMER (1956) called the quadrate foramen, an opening between the quadrate and the quadratojugal on the occiput for the passage of a vein draining the upper jaw. The posterior notch of the quadrate probably was not involved in the passage of a vein from the upper jaw through the quadrate foramen of Romer. The quadrate foramen is small in *Captorhinus* and is located to the side of the posterior notch of the quadrate. The plane of the notch is perpendicular to the plane of the occiput and medial to the quadrate foramen. The quadrate foramen seems to be an opening into the adductor chamber rather than into the notch of the quadrate.

A final feature of this region is to be noted. Above the stapedial shaft as it enters the stapedial recess roughly paralleling the shaft is an extremely thin and straight groove extending approximately the length of the stapedial recess. The groove curves laterally with the dorsal plate at

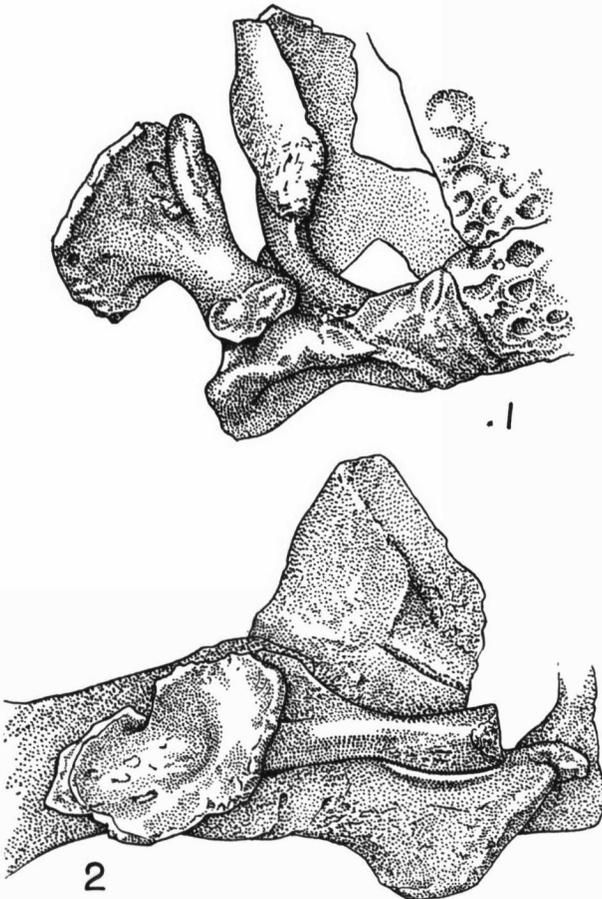


FIGURE 14. *Captorhinus aguti* (COPE). Right stapes and quadrate in articulation, uncatalogued specimen, Clarke collection, $\times 5$. —1. Occipital view. —2. Internal view.

the entrance to the posterior notch and terminates above the termination of the stapedial shaft. The identity of the groove is uncertain. It may be the imprint of the facial nerve on the quadrate prior to the nerve's split into its chorda tympani and hyoid branches.

The remainder of the quadrate bone consists of a broad, expanded foot, the ventral surface of which articulates with the articular bone of the lower jaw. The foot of the quadrate is asymmetrical in that it extends farther laterally beyond the plane of the dorsal plate than medially. The lateral extension was overlapped dorsally by the quadrate lappet of the quadratojugal. In ventral view the foot is irregularly rhomboidal in outline with its wider end directed anteriorly. The articular surface of the foot possesses a shallow groove that extends the length of the foot and which is bordered on either side by a low rounded swelling. Presumably the jaw could slide back and forth along the quadrate but could not move from side to side on it (WATSON, 1954; FOX, 1964).

In articulation with the pterygoid, the skull roof and the occiput, the quadrate was not oriented vertically but leaned in toward the mid-line. In consequence, the foot of the quadrate faced not only ventrally but slightly laterally

as well. The apposition of the articular bone to the foot of the quadrate in this position effectively braced the rami of the lower jaw, preventing them from being pulled toward each other when the jaw was adducted.

BRAINCASE

The details of the braincase of *Captorhinus* have been clear since PRICE'S (1935) concise and exact report. Because little new has been discovered about the braincase since PRICE'S work, and because the present study is intended to be a complete description of the morphology of *Captorhinus*, we have repeated verbatim his description of the bones of the braincase, with exception of the stapes. Evidence found to supplement that of PRICE follows upon his remarks (Figs. 15, 16).

BASIOCCIPITAL AND EXOCCIPITAL

No features are known to supplement PRICE'S description of the braincase which follows.

The basioccipital and exoccipitals are completely fused, no indication of suture remaining to delineate the extent of the exoccipital on the cranial base.

Anteriorly the basioccipital is separated from the basisphenoid by a comparatively broad area which was filled with cartilage. At this point the continuity of the bony cranial base is effected by the ventrally ensheathing parasphenoid which extends along the basioccipital to an apex not far from the condyle. The posterior margin of the parasphenoid rests along the crest of the quite shallow basioccipital tubera.

The basioccipital is bounded laterally by the very large stapedial foot. Along this boundary, on either side, there is a pronounced recess or outpouching from the otic capsule, the floor of which is very thin. This recess contained the lagena. Posterior to the recess the opisthotic joins the basioccipital by a broad smooth faceted surface which is continued dorsally on the occipital aspect of the brain case by the former element and the exoccipital, to the top of the foramen magnum; the only interruption being that of the large jugular canal between the opisthotic and exoccipital for the vagus, glosso-pharyngeus, and accessorius nerves.

Posteriorly the basioccipital supports a strong condyle semi-circular in cross section and bearing a deep notochordal pit. On either side of the condyle are a pair of foramina, the outlets for the canals which contained the hypoglossal nerves.

Dorsally the basioccipital has a pronounced median longitudinal ridge on the sides of which, just posterior to the recess for the lagena, a marked depression received the ventral surface of the anterior portion of the medulla.

The exoccipitals are roughly triangular in horizontal section and do not meet dorsally to close the foramen magnum, whose dorsal rim is completed by the supraoccipital. Mesially at the floor of the brain cavity, a canal for the hypoglossal nerve begins by traversing the exoccipital to the postero-lateral outlet mentioned on the basioccipital. Just posterior to the inception of this canal and slightly above there is a small protuberance whose function is undetermined.

Anteriorly the exoccipital forms the posterior surface of the jugular canal above which continues the opisthotic suture and more dorsally the supraoccipital, the suture with the latter being a broad facet. Leaving the jugular canal and entering the exoccipital itself there is a second canal whose exit has been mentioned as lateral to the condyle. This canal in all probability carried the anterior fibers of the hypoglossal nerve.

The latero-posterior exoccipital face bears an elongate vertical facet for articulation with the pre-zygapophysis of the proatlas.

OPISTHOTIC

The opisthotic meets the supraoccipital in a suture that is laterally concave in at least some specimens. In other

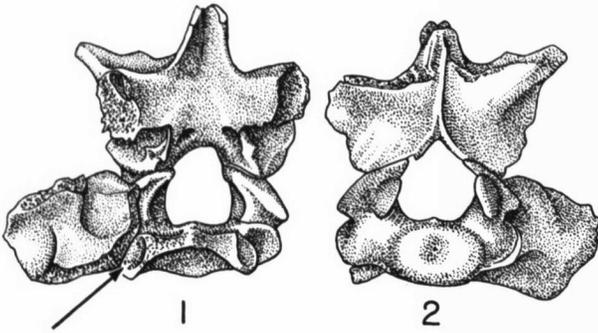


FIGURE 15. *Captorhinus aguti* (COPE). Incomplete braincase, uncatalogued specimen, Clarke collection, $\times 3$. —1. Internal view. —2. Occipital view. Arrow indicates lagenar recess.

external features the opisthotic agrees with the description by PRICE.

The opisthotic is joined dorsally to the supraoccipital. The exact limits of these bones are obscured as early fusion has to a great extent destroyed the sutural indications between the prootic, opisthotic, and supraoccipital.

Anteriorly it is united to the prootic, the suture in this case being quite definable. Mesially the opisthotic forms the floor of the subarcuate fossa, forms a portion of the sinus utriculus and posterior to this is depressed into two concavities the lowermost being a ganglionic recess at the proximal end of the jugular canal. The opisthotic forms the dorsal and posterior rim of the very large internal auditory meatus whose borders are ill-defined, presumably due to lack of ossification of cartilage.

Ventro-laterally the opisthotic receives the large stapedial foot and beyond this is produced into a short powerful opisthotic process whose tip was continued by cartilage to an attachment with the occipital flange of the squamosal.

The opisthotic contains the posterior half of the posterior and horizontal semicircular canals with their common posterior ampulla. The positions of all the semicircular canals are evident on the lateral surface of the otic capsule.

Internally the opisthotic bears a broad groove that is parallel to the ventral and posterior rim of the fenestra ovalis formed by the opisthotic and that appears to extend from the anterior end of the bone (although this is uncertain because of breakage) backward to at least the level of the paroccipital process. The groove presumably provided a part of the floor and posterior wall of the perilymphatic cistern. A second groove lies medial to the first, is confluent with the first posteriorly but is separated from the first throughout most of its length by a thin ridge. The medial groove opens toward the lagenar recess and presumably housed a part of the sacculus or the proximal part of the lagena (Fig. 15) itself.

PROOTIC

PRICE's description, to which we have no information to add, it as follows.

The prootic is a comparatively small element bounded posteriorly by the supraoccipital and the opisthotic. It borders the stapedial foot ventrally thus forming the dorsal rim of the fenestra ovalis. It is united anteriorly to the basisphenoid and along this suture in its mesial aspect is situated the foramen for the palatine branch of the facial nerve. The canal for this nerve runs diagonally outward, its exit from the brain case being entirely in the basisphenoid.

Mesially the prootic forms the anterior wall of the subarcuate fossa; more ventrally the anterior rim of the internal auditory meatus. The dorsal prootic region encloses the anterior half of the anterior semicircular canal; the lateral region encloses the anterior half of the horizontal semicircular canal as well as the anterior and horizontal ampullae.

The anterior surface of the prootic forms the posterior outline of the prootic incisure and bears a buttressed shelf in a slightly mesial position. The shelf to all appearances was the base for a cartilage in support of the orbitosphenoid elements. A comparable shelf is found in iguanas today. Above the shelf on the supraoccipital-prootic suture there is a small oval area also for cartilage attachment, probably an accessory to the former cartilage.

The prootic is produced into a short shelf overhanging the stapes; this curves down slightly to meet an ascending "process" from the stapes. Just ventral to this shelf a shallow groove marks the position of the vena capitis lateralis on the prootic. Wedged between the groove and the shelf a small foramen permits the exit of the hyomandibular branch of the facial nerve.

SUPRAOCCIPITAL

As described by PRICE,

The supraoccipital is an extensive element resting mainly on the opisthotics and abutted antero-ventrally by the prootics. Posteriorly it is supported by the exoccipitals where it completes the dorsal rim of the foramen magnum.

Laterally, rising toward the "occipital crest," there are stout processes which were continued to the parieto-squamosal suture on the occipital ridge by cartilage masses. These lateral ascending processes are obviously means of bracing the brain case to the dermal roof. The posterior edge of these processes carries a continuous indentation or groove into which the ventral edge of the dermosupraoccipitals rest. Between the two lateral processes and directed forward over the cranial cavity the supraoccipital is produced into a stout median ascending process which fits dorsally into a groove formed by the parietals. This median process with an inverted V cross section extends nearly to the pineal foramen. Its posterior limit is seen on the occiput of the articulated skull wedged between the mesio-ventral borders of the dermosupraoccipitals.

The otic portion of the supraoccipital contains the posterior half of the anterior semicircular canals and encloses the dorsal portion of the sinus utriculus. Mesially it forms the roof of the subarcuate fossa, proceeds posteriorly around the utriculus and finally meets the exoccipitals.

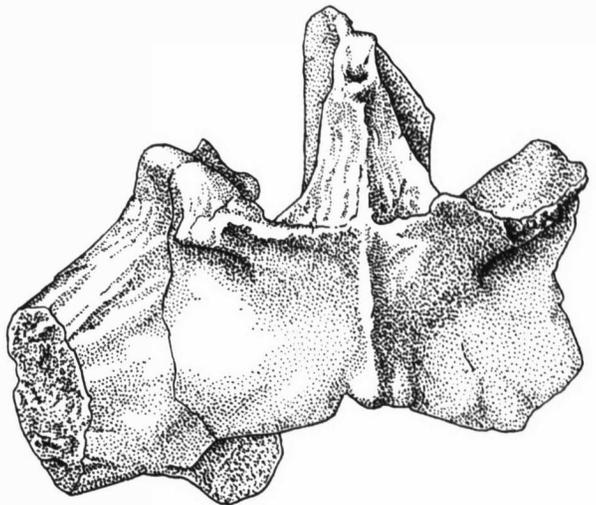


FIGURE 16. *Captorhinus aguti* (COPE). Occipital view, incomplete braincase, uncatalogued specimen, Clarke collection, $\times 5$.

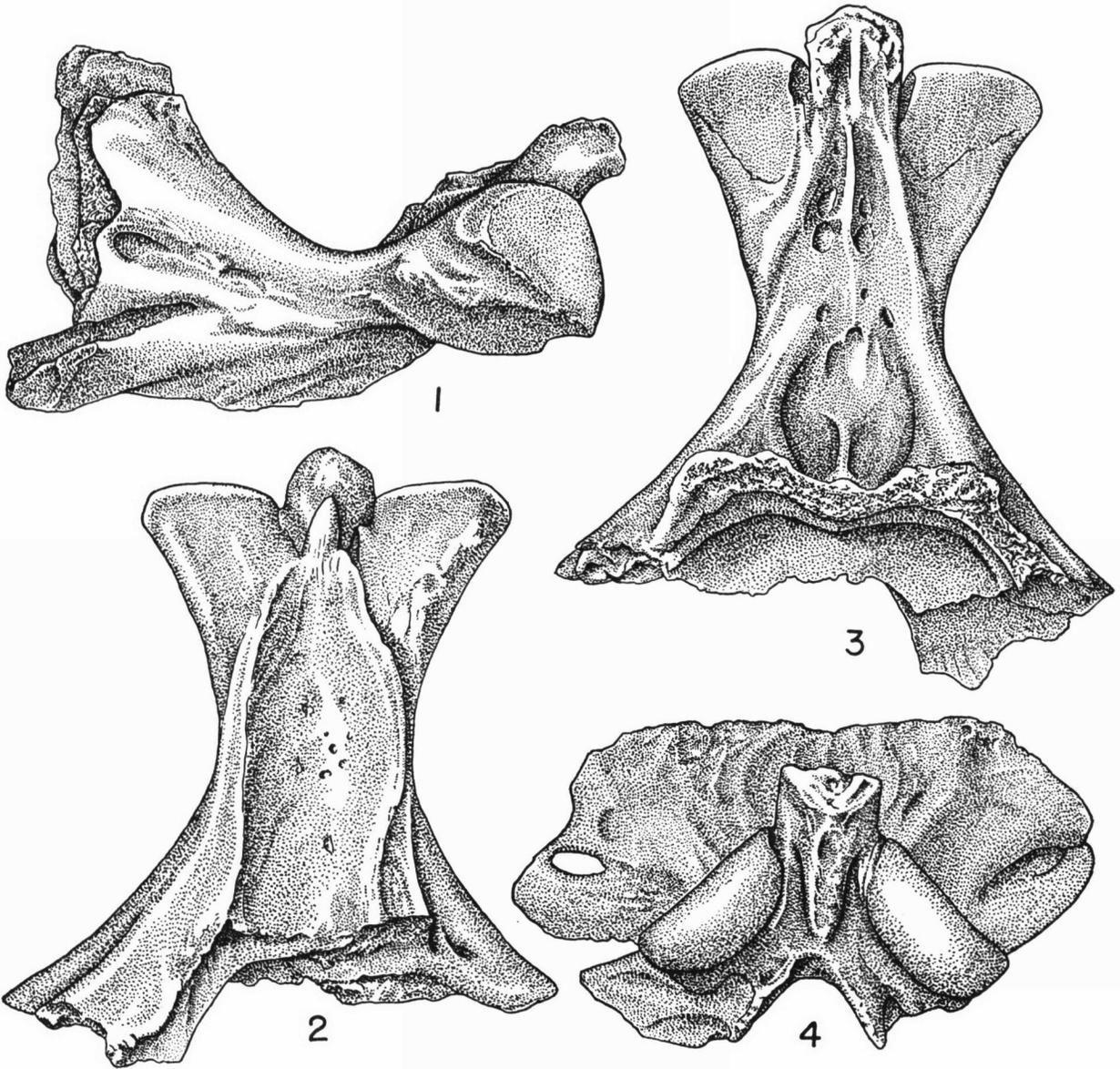


FIGURE 17. *Captorhinus aguti* (COPE). Incomplete basiparasphenoid, uncatalogued specimen, Clarke collection, $\times 4.5$. —1. Lateral view. —2. Ventral view. —3. Dorsal view. —4. Anterior view.

No indication of an exit for the endolymphatic duct was found. In all probability the duct made its exit from the otic capsule through the cartilage rim of the internal auditory meatus.

The notch in the ventral edge of the supraoccipital that forms the dorsal border of the foramen magnum normally appears to be shallower than pictured by PRICE.

The posterior rim of the internal auditory meatus, formed by the supraoccipital, bears a shallow transverse notch, crossing the rim between the otic capsule and the brain. This may represent the passage for the endolymphatic duct, in which case the anterior limits of the passage were formed by cartilage.

BASISPHENOID

According to PRICE (Fig. 17, 18),

The basisphenoid is a rather large and involved element. As has been noted it does not reach the basioccipital posteriorly, the intervening space having been filled with cartilage. Ventrally it is united to the occipital base by means of a well developed parasphenoid whose edges rise to overlap its lower limits.

The basisphenoid supports a very high dorsum sella which inclines forward to a slight degree. The dorsum sella itself is a very thin transverse sheet of bone strengthened laterally by thicker columns, the prootic pillars, which rise far toward the top of the brain case and form the anterior margin of the prootic incisure. The dorsal margin of the transverse wall sags below the tops of the pillars. The prootic incisure was obviously the outlet for all of the branches

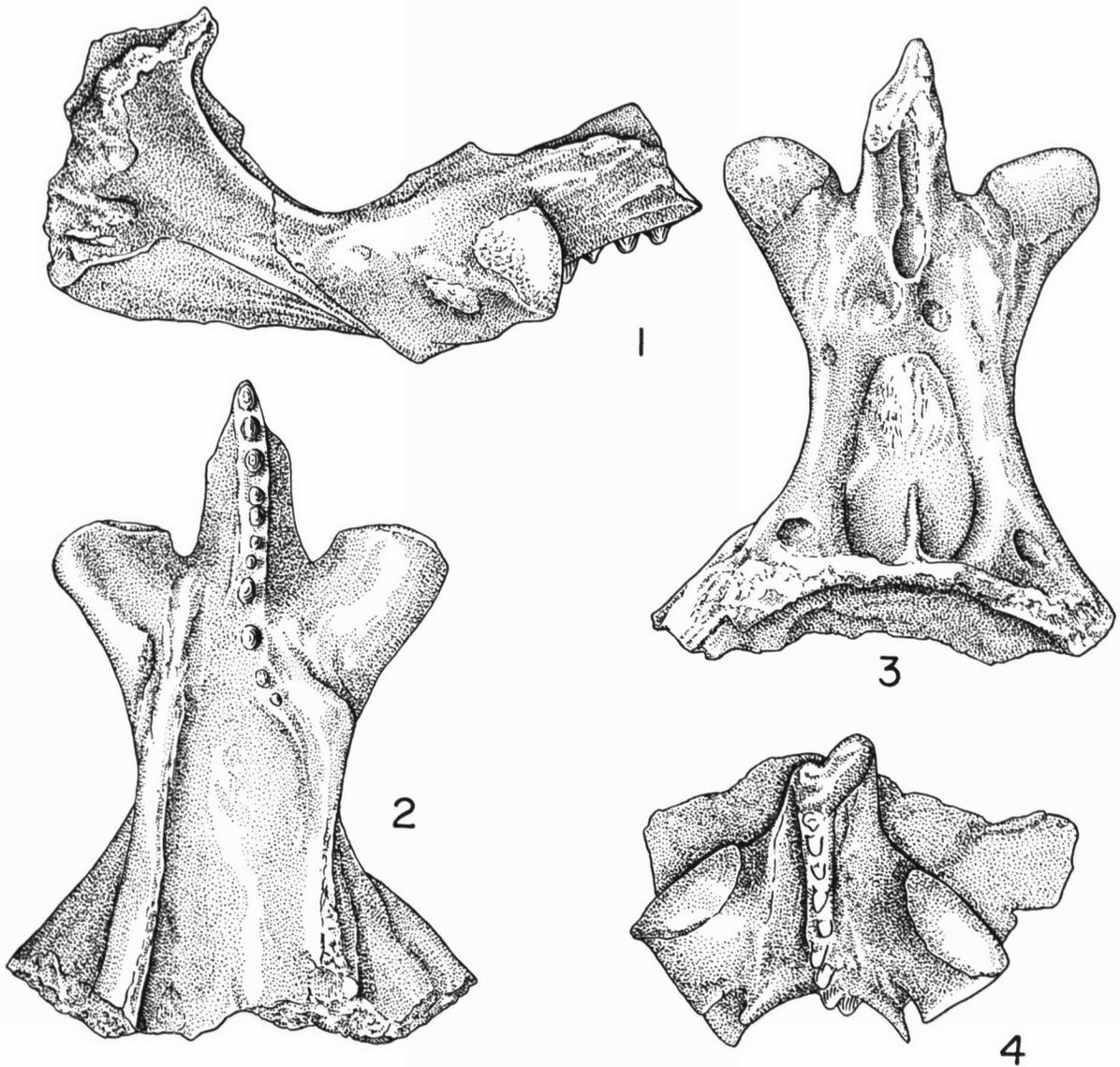


FIGURE 18. *Captorhinus aguti* (COPE). Incomplete basi-parasphenoid (KU 14749), $\times 12$. —1. Lateral view. —2. Ventral view. —3. Dorsal view. —4. Anterior view.

of the trigeminus including the profundus and also for the maxillary and mandibular branches of the facial nerve.

Posterior to the dorsum sella the basisphenoid forms a shelf with lateral walls. In this concavity rested the anterior body of the medulla. The lateral walls unite with the prootics dorsally, and more ventrally form the anterior rim of the fenestra ovalis. Along the prootic-basisphenoid suture the exterior surface of the brain case is well ossified, but within the cranial cavity the ventromesial surface of the prootic shows a comparatively large area of unfinished bone surface. The cartilage which limited the anterior rim of the internal auditory meatus appears to have extended over this unfinished portion of prootic and attached itself to the basisphenoid.

It was in the cartilage mass mentioned above that the canal for the palatine branch of the facial nerve had its inception, then angling through the posterior wall of the basisphenoid it finally appears deeply incised on the lateral face of that element and continues forward and downward as a pronounced groove, on the lateral wall of the brain case.

Close to the floor level the prootic pillars are pierced by canals for the abducens nerves which ran out over the rostral portion of the basisphenoid.

The rostral portion of the basisphenoid narrows rapidly to a strong "pre-sphenoidal" process. Near the tip two stout basiptyergoidal processes diverge pointing forward and slightly downward. The dorsal surface of the rostral tip has a strong medial ridge in the middle of which a longitudinal groove, deeply incised, presumably received a cartilage support for the median ethmoid.

There is some indication that the basisphenoidal rostrum may have been continued by a well-developed "pre-sphenoid" extending far into the interptyergoidal vacuity.

Laterally to the median ridge and just above the basiptyergoids there are two pairs of openings, the exits for the canals for the internal carotids and (slightly anterior to these) exits for the common trunk of the ophthalmic (sic) and cerebral arteries branching from the internal carotid, apparently, while still in the bony mass of the rostrum. Posterior to the median ridge the dorsal surface

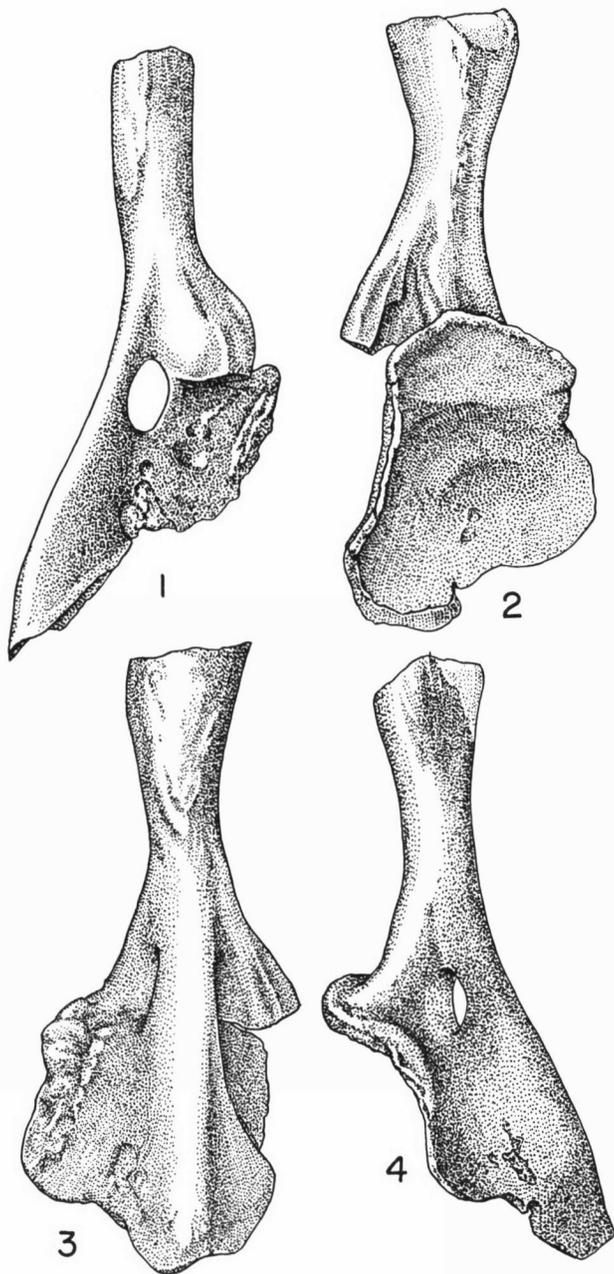


FIGURE 19. *Captorhinus aguti* (COPE). Right stapes, uncatalogued specimen, Clarke collection, $\times 7$. —1. Dorsal view. —2. Internal view. —3. External view. —4. Ventral view.

gives way to a longitudinal depression, the sella turcica. This depression becomes divided posteriorly into two lateral pockets which are partly embedded in the anterior wall of the dorsum sella. The division of these two pockets is accentuated by a perpendicular median septum on the anterior vertical face of the dorsum sella. This septum does not quite reach the floor of the sella turcica.

The median septum of the sella turcica extends forward to about half the length of the depression and reaches its floor. This is particularly evident in one of five basisphenoids from the Richard's Spur locality (UMMP

50985), but is also found in various uncatalogued basisphenoids from the same locality in The University of Kansas collections.

Another specimen (UC 1702) shows the continuation of the basisphenoid rostrum in ventral view anteriorly to a level that is about at the mid-point of the length of the palate, and another (AMNH 4338) shows the rostrum extending nearly the length of the interpterygoid vacuities.

The presence of basisphenoid-parasphenoid teeth has been reported by WARREN (1961). Among five fragments otherwise referable to *Captorhinus* in the collections of the Chicago Museum of Natural History, two are without teeth; one has four teeth restricted to the rostrum; one has one tooth, posterior to the rostrum; and one has at least six teeth, found both on the rostrum and posterior to the rostrum. Similar variation in the presence and distribution of teeth is found among the basisphenoid-parasphenoid fragments of the collections of The University of Kansas. Consequently, the character, as WARREN (1961) has suggested, is not of phylogenetic significance, and is without taxonomic significance as well.

PARASPHENOID

The following description is given by PRICE.

The parasphenoid is an extensive sheet covering the ventral aspect of the cranial base. Anteriorly this thin sheet of bone is wedged between the basiptyergoids and runs forward as a sharp cultriform process. Its exact anterior limit has not been determined since very few specimens show this delicate structure. Specimen AMNH 4338 has been figured with a long cultriform process; just how far the parasphenoid followed this is not known, however, and the bulk of this process may well be the "presphenoid" mentioned before. Wedged between the parasphenoid and the mesial surface of the basiptyergoid processes there are two small foramina, probable openings for the palatine branches of the internal carotids. Paralleling the edges of the parasphenoid in the same region well defined grooves mark the paths of the palatine branches of the facial nerve as they coursed underneath the basiptyergoid processes.

While still between the basiptyergoids the parasphenoid becomes concave in its midline. This concavity broadens and becomes deepest at the posterior limits of the basisphenoid then gradually shallows out until its walls are nearly flat as they rest on the basioccipital tubera. The lateral walls rise sharply to overlap the basisphenoid and just posterior to the basiptyergoid processes they are pierced by the canals for the internal carotids whose course has before this been embedded in deep grooves. The artery then continues through the basisphenoidal rostrum, to the outlets already mentioned. In the region of the stapes the lateral wall is shallow and overlaps the medial limits of the stapedia foot.

STAPES

PRICE (1935) described the stapes of *Captorhinus* briefly but accurately. The following description is a composite of PRICE's report and additional information on the stapes which has been discerned in this study (Fig. 14, 19).

The stapes of *Captorhinus* has commonly been characterized as being a massive bone, and perhaps it may properly be considered so when compared to that of modern reptiles, but in absolute size, as pointed out by HORTON (1960), the bone is small.

The foot plate of the stapes resembles a shallow, elongate cup or bowl with irregular borders, but it seems to be a general characteristic that the foot plate is slightly broader anteriorly than posteriorly. Some of the rim of the foot plate must have borne a strip of cartilage or was at least apposed to a cartilaginous cushion, particularly along

its basisphenoid and prootic articulations, for these parts of the rim are made up of porous, unfinished bone of a delicate nature. The more posterior and ventral articulations of the foot plate, those that it makes with the opisthotic and parasphenoid, are composed of finished bone and are comparatively robust.

Posteriorly and dorsally the foot plate is flat in internal aspect, providing a surface that is liplike in relationship to the anterior depression. The latter feature occupies more than half of the internal area of the foot plate and protrudes outward beneath the base of the bridge that defines the stapedia foramen.

The shaft is short and stout, although the thickness that it exhibits is by no means uniform. Its greatest width is at the foot plate. The bridge of the stapedia foramen spreads out over the foot plate and acts as a backing for the outpocketing of the foot plate beneath. The main ramus of the shaft, in back of the stapedia foramen, joins the foot plate on its posterior lip, but without any increase in diameter. Slightly distal from the level where the shaft is again imperforate and where the dorsal process arises, the shaft exhibits its minimal width, narrowing in its dorsoventral dimensions to about two-thirds of its usual width, but without any change in its anteroposterior diameter.

The extent of the shaft beyond the waist is thicker dorsoventrally, but thinner anteroposteriorly, thereby causing the shaft to be bilaterally flattened. Associated with this part of the shaft is a triangular plaque of porous bone located on the anteroventral face of the shaft and oriented in such manner that its base is adjacent to the termination of the shaft and its apex is directed toward the foot plate; it extends proximally nearly to the origin of the stapedia

bridge from the shaft. The plaque marks the articulation of the shaft with the stapedia recess of the quadrate.

The dorsal process of the stapes in *Captorhinus* is a prominent, flat flange that springs from the shaft at approximately the level of genesis of the bridge of the stapedia foramen. The process bends posteriorly so as to enclose a groove beneath for the passage of the vena capitis lateralis and also the stapedia artery as it leaves the stapedia foramen (PRICE, 1935, p. 383). The curvature of the process also directs its dorsal surface toward a groove of the prootic where the two bones articulated.

The distal tip of the shaft consists of porous bone and bears in its center a nubbin raised slightly above the surrounding surfaces. Extending proximally from the tip and contiguous with it as an obliquely oriented beveled edge on the posterodorsal surface of the shaft is a short triangular plaque of unfinished bone, presumably associated with the cartilaginous tympanic process of the stapes.

PARRINGTON (1946, p. 196) stated:

PRICE (1935) has shown the presence of a dorsal process to the columella of *Captorhinus* but figures the distal end if [sic] this bone as a featureless structure. A specimen in the Museum of Zoology at Cambridge, however, shows that in adults at least the bone terminates in a slightly flattened process which reaches forwards and slightly outwards and, more ventrally, a somewhat swollen boss. The former process almost certainly contacted the quadrate while the boss probably marks the position of the attachment of the hyoid and, possibly, the site of a cartilaginous extra stapes (fig. 9C).

None of the specimens examined for this study reflect the morphology of the distal end of the stapes that PARRINGTON describes; PRICE's presentation is essentially accurate, with modifications that are added above.

MANDIBLE

The mandible of *Captorhinus* has been illustrated by WILLISTON (1925, p. 39, fig. 25) fairly accurately, and has been described by CASE (1911a) and FOX (1964). When in articulation the rami were probably vertically oriented, for in a nearly perfect skull from the Richard's Spur locality (KU 9978), the rami are vertical and not tilted medioventrally, as PEABODY (1952) has suggested they were in *Captorhinus*. The rami are of moderately heavy build, extend the length of the skull, and are gently convex ventrally in lateral outline (Fig. 20).

The descriptive morphology of the mandible can be conveniently divided into two areas, one anterior, associated with the teeth, and the other posterior, associated with the adductor muscles of the jaw. The anterior half of the mandible is roughly wedge-shaped in lateral outline. The apex of the wedge, the anterior end of the mandible, is blunt and possesses a dorsal border that bulges slightly upward at the level of the large anterior teeth; immediately behind the anterior bulge is a more narrow neck region. Backward from the neck to the posterior half of the jaw, the dorsal and ventral margins of the mandible diverge slightly but continuously to lend the wedge-shaped aspect to the profile.

The outer surface of both anterior and posterior parts of the mandible is laterally convex in cross section and

sculptured; the medial surface is flat and free of ornamentation. The sculpture extends upward from the ventral edge of the jaw to the base of the teeth, implying that in life the skin bordered on the tooth row. Anteriorly, at the

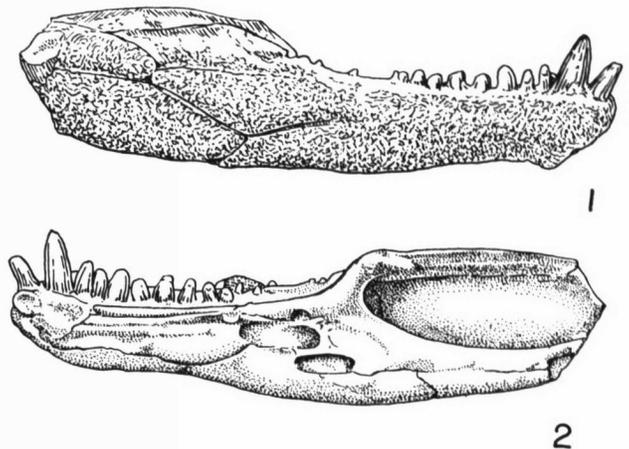


FIGURE 20. *Captorhinus aguti* (COPE). Incomplete right mandibular ramus (KU 8963), $\times 1.6$. — 1. External view. — 2. Internal view.

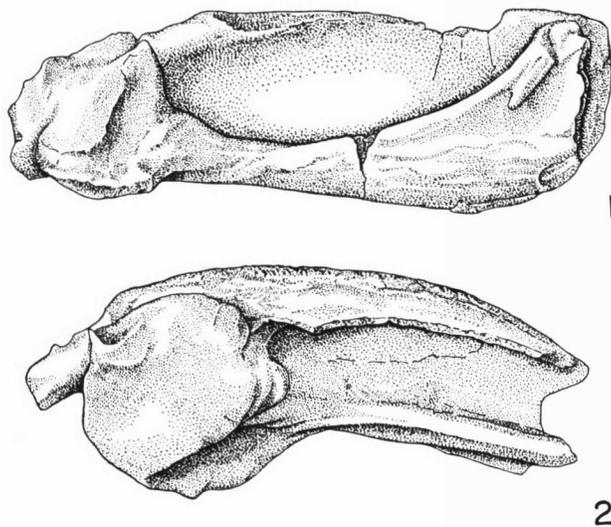


FIGURE 21. *Captorhinus aguti* (COPE). —1. Internal view, posterior part of left mandibular ramus, KU 14753. —2. Dorsal view, posterior part of left mandibular ramus, KU 14756. Both $\times 3$.

level of the "tusks," the lateral surface of the mandible bulges outward.

The dorsal edge of the dentary tilts slightly inward posteriorly; consequently, the posterior teeth slant obliquely inward in relation to the posture of the anterior teeth.

Both the dentary and the splenial contribute to the symphysis; the splenial enters the symphysis by means of a raised pad, oriented vertically in the mid-sagittal plane of the jaw. The dentary contribution extends upward from the splenial pad, which it partially surrounds, to the base of the most anterior tooth. The anterior-most part of the Meckelian canal pierces the symphysis, opening externally as a minor foramen in the symphyseal line. From the inner face of the mandible, between the pad of the splenial and the dentary above it, a second and larger foramen opens into the Meckelian canal. At the level of the most posterior teeth, the inner surface of the mandible is pierced by the major infra-Meckelian foramen, bordered by the splenial, angular and prearticular. This opening is well down on the inner face of the jaw and is perhaps four times as long as it is broad (Fig. 20).

The posterior half of the mandible possesses several features of interest; the coronoid process, articulation with the quadrate, retroarticular process, and adductor fossa. The coronoid process arises directly behind the tooth row; occasionally a few small teeth are found along its ascending edge, but these relate to the dentary and not to the coronoid. The anterior border of the process is made up of the dentary externally and the coronoid internally. The leading edges of both bones rise steeply from the tooth row to the dorsal edge of the process, then extend backward in an approximate horizontal plane, lending to the coronoid process an abruptly truncated appearance (Fig. 20). Posteriorly, the surangular replaces the coronoid and dentary along the edge of the process.

The glenoid fossa of the articular rests as a large pad that extends from the dorsal to the ventral margin of the jaw behind the adductor fossa. The glenoid faces dorso-medially, slanting obliquely across the plane of the tooth row; the quadrate-articular joint consequently cannot be said to lie above or below the level of the teeth. The orientation of the joint was such to suggest that when the jaw was depressed, the rami were forced apart by turning outward slightly. If this were to occur, the symphysis could not have been a firm articulation, but one which possessed some flexibility, with either ligaments or cartilage forming the actual connection between the rami. The nature of the articulating surfaces of the symphysis is also such to suggest that movement of the symphyseal joint was possible; although the apposing surfaces possess pits and grooves, these do not fit together into a firmly locked jaw. Consequently, the topographical features seem to be related to either ligaments or cartilage rather than to an immovable bony articulation.

The adductor fossa in *Captorhinus* extends from the ascending edge of the coronoid process to the glenoid fossa and opens solely on to the inner face of the mandible, for the coronoid process leans medially, roofing the fossa from above and preventing it from opening dorsally (Fig. 21).

The glenoid fossa and the part of the prearticular in which the posterior pterygoid muscles inserted (see below) ventrally overhang the main body of the jaw as a thin flange extending from the retroarticular process forward to the posteroventral lip of the adductor fossa. Within the groove formed by the back of the flange, the anterior pterygoid muscles found a part of their insertion.

The retroarticular process is described below.

The canal for the passage of the chorda tympani opens externally on the posteroventral edge of the jaw between the glenoid and the base of the retroarticular process; the internal opening is at the base of the rear wall of the adductor fossa, at the junction of surangular, angular, prearticular and articular bones.

In the extent of the tooth row and the dentary which supports it (roughly half the length of the lower jaw),

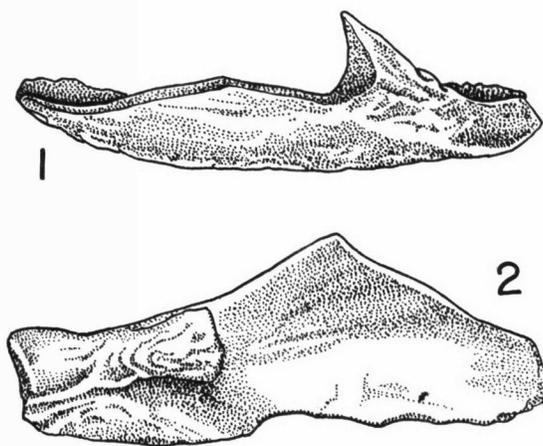


FIGURE 22. *Captorhinus aguti* (COPE). Incomplete surangular bone, uncatalogued specimen, Clarke collection, $\times 4$. —1. Dorsal view. —2. Medial view.

Captorhinus differs from both embolomeres and seymouriamorphs. In these more primitive tetrapods, the dentary commonly extends far posteriorly; even in the near-reptile (or reptile) *Seymouria*, the dentary is about three-quarters of the length of the jaw. As well as being proportionally shorter than this, the dentary of *Captorhinus* is proportionally deeper than in either seymouriamorphs or embolomeres, for in the captorhinid genus the dentary extends to the ventral edge of the mandible; consequently, the splenial of *Captorhinus* possesses none of the exposure on the outer face of the jaw that splenial and postsplenial do in both *Seymouria* and *Kotlassia*. The difference in the proportional length of the tooth row to that of the overall length of the jaw may be viewed as either a decrease in the length of the anterior part of the mandible or an increase in the length of the posterior part; the biological significance of either interpretation is not apparent. In any case, in *Captorhinus*, the anterior and posterior regions are about equal in length and carry with them a proportional adjustment in the size of their component bones. As one result, both the surangular and angular in *Captorhinus* are proportionally longer than in embolomeres and seymouriamorphs, although the increase in the length of the captorhinid surangular seems to be somewhat greater than that of the angular.

In *Captorhinus* the coronoid does not invade the outer face of the jaw; in *Seymouria* and *Kotlassia* the coronoid is conspicuous there.

The jaw of *Captorhinus* possesses but one coronoid and one splenial. The coronoid extends about as far anteriorly as do the multiple coronoids in the seymouriamorphs, but that of *Captorhinus* is narrower, particularly in comparison with the coronoids of *Kotlassia*. The single splenial ossification in *Captorhinus* occupies a similar extent on the inner face of the jaw in relation to the length of the tooth row as does the combination of splenial and postsplenial in *Seymouria*. In relation to the total length of the jaw, however, the splenial of *Captorhinus* is far shorter than that of *Seymouria*.

The prearticular in both *Seymouria* and *Kotlassia* extends forward of the level of the most posterior teeth; that of *Kotlassia* nearly reaches the symphysis. In *Captorhinus* the prearticular is proportionally shorter, extending no further anteriorly than the level of the most posterior teeth.

The proportions of the component bones of the jaw in *Limnoscelis* approach more nearly those of *Captorhinus*. The dentary is exposed widely on the outer face of the jaw, and surangular and angular possess, in relation to the dentary, proportions similar to those of *Captorhinus*. On the inner face, ROMER (1946) has shown two coronoids, a long infra-Meckelian fenestra, a prearticular that extends forward nearly to the symphysis, and a posterior process in the region of the articular and prearticular, presumably for the attachment of jaw adductors on the inner face of the jaw.

The jaw of *Romeria*, although known (PRICE, 1937), has not been described, as far as is known. Of *Hylonomus lyelli*, CARROLL (1964, p. 68) notes that the position of the dentary relative to the other bones of the jaw is similar to that of *Captorhinus*. CARROLL reports an apparent similarity in the extent of the splenial in *Hylonomus* to that of *Ophiacodon*, in which the splenial sheathes most of the

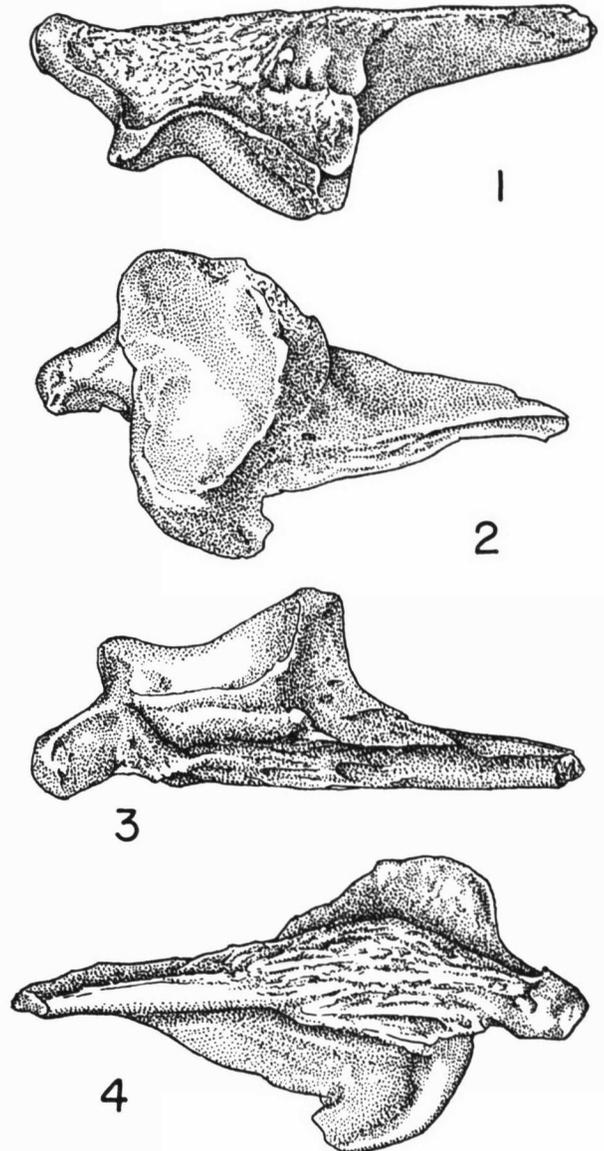


FIGURE 23. *Captorhinus aguti* (COPE). Articular bone, uncatalogued specimen, Clarke collection, $\times 4$. —1. Dorsal view. —2. Condylar view. —3. Ventral View. —4. Lateral view.

inner face of the anterior region of the jaw (ROMER & PRICE, 1940, p. 489, pl. 2). Angular, anterior coronoid, and articular are known in *Hylonomus*, although CARROLL has not compared them to *Captorhinus*. *Hylonomus* seems to have possessed a minimum of two coronoids; the anterior coronoid, at least, was covered with small teeth.

The jaw of *Cephalerpeton*, as restored by GREGORY (1948), possessed a rather foreshortened tooth-bearing region. The splenial appears to have extended far up the side of the inner face of the jaw. *Cephalerpeton* possessed a retroarticular process of distinctly reptilian form.

The mandible of *Paracaptorhinus* has been described by WATSON (1954), who notes a resemblance in it to the

jaw of *Captorhinus*. The mandible of *Labidosaurus* is extremely close to that of *Captorhinus*, with the paramount difference being in the dentition.

MANDIBULAR DENTITION

Peculiarities of the dentition of *Captorhinus* have long been known. Recently, EDMUND (1960) commented rather extensively on tooth replacement in the mandible of *Captorhinus*, revealing that the multiple rows of posterior teeth are ankylosed *Zahnreihen*, the growth of which has ceased. The smallest of the rows are the most posterior and labial, and were laid down when the animal was young; subsequent rows are parallel to the first rows and are anterior and lingual to them. All of the teeth of the posterior series are retained.

The mandibular dental series is divided into three regions: multiple posterior rows of laterally compressed teeth; an anterior marginal row of conical, sharply pointed teeth, compressed anteroposteriorly at their bases; and a short series of teeth intermediate in shape and position between the anterior and posterior series. The differences in shape and size between the teeth of the anterior series and the teeth posterior to it are maintained throughout the life of the individual. Even in the smallest of the jaw fragments examined, the anterior series is usually set off morphologically from the intermediate and always from the posterior dentition, and these from each other. The numbers of the multiple posterior rows are dependent upon the age of the individual (e.g., SELTIN, 1959; EDMUND, 1960). No fewer than two rows and no more than four have been found among those specimens from the Richard's Spur locality in The University of Kansas collections; these limits agree with those reported by SELTIN (1959, p. 477).

The anterior series characteristically consists of either four or five teeth. Infrequently six or seven teeth occur.

The anterior teeth are marginal in position and follow one another in a single row backward from the symphysis. The first of the teeth, by far the most slender and shortest of the series, juts obliquely forward beyond the anterior tip of the dentary. The teeth behind this become stouter and successively and evenly more upright in stance, much as the blades of a narrowly spread hand fan. There is no similar gradation in the height of these teeth, however, as the tips of the second and third teeth tower over the others of the series. Of this pair the second predominates, and the descent from its tip down to the plane of the tips of the teeth following is abrupt.

In sequence, posture and shape, individual teeth of the anterior series, whether they be three or seven, are readily distinguishable from individual teeth of the posterior series and are usually separable from the one or two intermediate teeth. Conversely, none of the teeth of the posterior series exhibits the characters that define either anterior or intermediate teeth. Regardless of the size of the jaws, these distinctions among the components of the dental battery seem to hold true. The integrity of the components suggests that the anterior and intermediate teeth are never incorporated into the advance of the posterior series as the jaw grows. The marginal anterior dentition usually remains without replacement, except within the limits dis-

cussed below. Unlike the posterior series, growth of the anterior teeth does not appear to cease when a certain height is achieved. The anterior teeth continue to increase both in height and in diameter long after they have been put into use. Very rarely does wear of these teeth occur, regardless of the age of the individual, so that growth of the anterior teeth throughout much if not all adult life can hardly be conceived of as an activity compensatory for the grinding down of crowns. Continued growth can more conveniently be thought of as a mechanism for the maintenance of the dimensions of the teeth in relation to the growing jaws, in the absence of continued replacement and of the supplementary addition of parallel rows of teeth present more posteriorly.

How are increments made to the dentition anterior of the multiple posterior rows of teeth? Apparently the timing of these additions is correlated with increase in the length of the jaw only in a general way. Examination of Table 1 discloses that exceedingly small jaws are commonly found with five teeth in the anterior series; conversely, many large jaws have but four anterior teeth. In theory it is impossible to dissociate the age factor (as revealed by size) completely from the number of teeth in the anterior series, as it is obvious that the smaller complement of these teeth must precede the time at which the fifth tooth appears.

The data show that in fact the mandibles of younger animals tend to have but four anterior teeth in contrast to the five teeth that are more characteristic of older animals. The data do not reveal any similar tendency for the stabilization at two for the number of intermediate teeth with increase in age. This suggests that increments to the anterior series are distinct from those to the intermediate series and that the teeth in each series are the products of distinct *Zahnreihen*.

In contrast to what the numerical counts indicate is the fact that anterior and intermediate teeth are characteristically arranged in a single unit line that curves posteriorly in a slight arc toward the mid-line. The arcuate arrangement suggests that anterior and intermediate teeth are the products of a single *Zahnreihe* parallel to but displaced forward from the posterior rows.

EDMUND's work on tooth replacement in *Captorhinus* was limited to the posterior rows. He observed no resorption pits at the bases of these teeth and correctly concluded that the teeth of the posterior rows were not replaced. But examination of seventy mandibles of *Captorhinus* from the Richard's Spur locality reveal the presence of resorption pits at the bases of either the second or the third teeth in the anterior series among four individuals. Each individual is small and presumably young.

The presence of these pits suggests that the anterior marginal row of teeth, including the anterior and intermediate series, is replaced in the manner characteristic of most reptiles, although the sample studied is too small to point to the sequence of the replacement. From this it may be concluded not that the anterior and intermediate series each represents a *Zahnreihe*, or that the entire marginal dentition represents a *Zahnreihe*, but that each of the anterior and intermediate teeth is the terminal member of a *Zahnreihe*. The number of *Zahnreihen* of the marginal teeth thus corresponds to the number of marginal teeth, in

TABLE 1. Measurements of Representative Mandibular Fragments of *Captorhinus* from Richard's Spur, Oklahoma.

Thickness of Dentary beneath Tooth 2 in mm.	Number of Anterior Teeth	Number of Intermediate Teeth
1.5	5	2
1.6	6	1
1.6	4	1?
1.6	4?	4?
1.6	4	2?
1.7	5	1?
1.7	5	2
1.8	4	2
1.9	4	2?
1.9	4	1
2.0	4	2
2.0	5	2
2.0	4	2
2.1	4	1?
2.1	4	2?
2.1	4	2
2.1	5?	1?
2.1	5	2
2.1	4	2
2.3	4	2?
2.3	4	2?
2.3	4	2
2.4	5	2
2.4	4	2
2.4	5	2
2.5	5	2
2.5	4	2
2.6	4	2
2.6	5	2
2.6	5	2
2.6	5?	2
2.7	4	2
2.7	4	1
2.7	5	2
2.8	5?	2
2.8	5	0
2.9	4	2
2.9	5	1
2.9	5	2
3.0	4	2
3.0	5	1
3.1	6	2
3.2	5?	3
3.3	4	1
3.4	5	2
3.4	4	1
3.5	4	1
3.5	5	1
3.5	5	1?
3.5	5	2
3.5	3	2
3.5	4	2?
3.5	4	2
3.5	4	2
3.7	6	3?
3.7	5	2
3.7	4	2
3.8	5	1
3.8	5	2
3.8	5	2
3.8	4?	2?
3.9	4	2
4.0	5	2
4.1	5	1?
4.1	4	2?
4.2	5	2

contrast to the posterior band of teeth in which the number of *Zahnreihen* corresponds to the number of rows of teeth.

This explanation is in keeping with what is known of the ancestry of *Captorhinus*. The romeriids possess a single row of marginal teeth on each jaw, and from such an arrangement the dentition of *Captorhinus* has to be derived. No evidence suggests the sequence of replacement of the teeth in romeriids, but one may judge that the teeth of romeriids are the terminal members of separate *Zahnreihen*. The dentition of *Captorhinus* has become specialized in the appearance and retention of all of the teeth in the posterior *Zahnreihen*; the anterior teeth presumably have retained their ancestral identity as terminal members of separate *Zahnreihen*.

Replacement of the anterior series does not appear to continue throughout life. Resorption pits among the sample studied were found in small individuals; they were absent among individuals larger than the mean value of the size index. Thus rearrangement of the marginal row appears to take place only among young animals and rarely, if at all, among moderately aged or old individuals. Part of the rearrangement of the anterior series appears from the data to be a function of increasing size (and age). But it is equally apparent that there is no single constant number of anterior and intermediate teeth characteristic of the species; individuals above the mean size may have four or even three anterior teeth and but one intermediate tooth.

Aside from replacement, the anterior teeth differ from the teeth of the posterior series in another regard. They continue to grow apparently after they become functional. That such is the case has not been revealed by histological studies but by the demonstrated rarity of resorption pits and by the absence of replacement gaps—both in the face of an increase in the height and diameter of the teeth proportionate to increase in the dimensions of the jaw.

SURANGULAR

In the mandible of *Captorhinus* the surangular (Fig. 22) is long and narrow, and lies along the posterior part of the opening of the adductor fossa dorsally and laterally. Anteriorly the surangular rests beneath the coronoid along the dorsal edge of the coronoid process, and is overlapped by the dentary along the lateral surface of the jaw and by the coronoid in the anterior part of the adductor fossa. Ventrally the surangular slips under the angular in a long dorsally curved suture. The surangular, with the angular, covers the lateral surface of the articular and sends a minor spur posteriorly over the base of the retroarticular process. The surangular sends a deep process inward from the main body of the bone partly across the articular in front of the glenoid fossa. This process, with contributions from the articular and prearticular below, forms the posterior wall of the adductor fossa.

The external surface of the surangular possesses a vertical or near vertical flange of unornamented bone that, with the dentary and coronoid more anteriorly, surmounts the coronoid process. The flange slipped up inside the cheek when the jaw was adducted, and is thought to have provided the area of insertion for the masseter muscle (Fox, 1964).

ANGULAR

The angular bone in *Captorhinus* is long, slender, and occupies the outer surface of the posteroventral region of the jaw. In its extension forward from the retroarticular process, the angular adjoins the surangular and dentary above, the splenial along the ventral edge, and the prearticular on the inner face of the mandible. A limited angular-splenial contact is found below the Meckelian foramen. The angular covers the lateral surface of the articular and possesses a short posterior spur that incompletely sheathes the ventrolateral surface of the retroarticular process. The angular terminates anteriorly at the Meckelian foramen and provides the posterior border of that opening.

The angular forms the lower part of the outer wall of the adductor fossa and, with the prearticular, the posterior part of its floor.

The anterior pterygoid muscle probably was inserted on the angular along the ventral edge and inner face of the jaw (Fox, 1964).

SPLENIAL

The single splenial in *Captorhinus* is mainly exposed along the anterior part of the inner face of the mandible, but it also wraps around the ventral edge of the anterior half of the jaw to contact the dentary and angular. The splenial is not exposed on the lateral face of the jaw. Contacts of the splenial on the inner face of the jaw include those with the coronoid, dentary, prearticular, and angular. The contact with the dentary is only partly surficial, expressed in a suture exposed below the anterior part of the tooth row. The major part of the articulation, however, is not exposed, since beneath the splenial-dentary suture, the splenial, in forming the medial wall of the Meckelian canal, covers the dentary above and below the canal.

The contact of splenial and coronoid is in a long suture that is the posterior continuation of that between the splenial and dentary. Below the coronoid and above the Meckelian foramen, the splenial abuts against the prearticular. The splenial rims the Meckelian foramen anteroventrally, then continues obliquely backward in a gently curving suture with the angular.

The splenial participates in the mandibular symphysis by means of a small, flattened plate that faces medially. The plate articulates with its twin on the opposite side of the symphysis, and is backed by the dentary.

CORONOID

The single, edentate coronoid bone of *Captorhinus* is a flat, three-pronged component of the lower jaw, with a central plate located on the inner face of the jaw at the anterior rim of the adductor fossa. A process of the coronoid extends anteriorly as a long, thin strip of bone that lies medial to the tooth row. A second process, short and stubby, is sent obliquely backward and downward to provide the most anterior part of the ventral rim of the adductor fossa. A third process ascends the coronoid process with the dentary and forms the dorsal rim and lateral wall of the anterior part of the adductor fossa. The three processes meet in the central plate on the inner surface of the jaw, directly in front of the adductor fossa, comprising its anterior rim.

The anterior process of the coronoid reaches forward to the level of the most posterior of the anterior set of teeth. The process lies on the inner side of the tooth row and rests on the dentary beneath. The ventral edge of the anterior process articulates with the splenial anteriorly and the prearticular posteriorly.

The ventral process of the coronoid extends backward beneath the opening of the adductor fossa and overlaps the prearticular.

The dorsal process bears a low knob at the junction of the ascending and dorsal edges of the coronoid process, which may have provided the insertion for a medial adductor muscle (Fox, 1964). The coronoid here articulates with the surangular, and with that bone, is thought to have provided the insertion for the masseter muscle (Fox, 1964).

ARTICULAR

The articular (Fig. 23) in *Captorhinus* is a blocky, irregularly shaped bone that is in contact with the surangular, angular, and prearticular. Three features dominate the descriptive morphology of the articular: a posteriorly directed retroarticular process, a central glenoid fossa, and an anteriorly directed finger-like projection extending forward in front of the fossa.

The glenoid fossa is roughly trapezoidal in outline, with the longer of the parallel sides the posterior one, the shorter side bounding the fossa anteriorly, and the oblique sides limiting the fossa medially and laterally. The posterior border is notched about midway in its length for the intrusion of a spur of finished, nonporous bone from the base of the retroarticular process. The remainder of the borders of the glenoid are entire and rounded at the corners of the glenoid surface. The glenoid fossa itself consists of porous, nonfinished bone that presumably in life was covered by cartilage.

The glenoid fossa is not at all flat; it consists of a medial and a lateral depression, separated by a broad, low, rounded ridge. The ridge is most broad anteriorly where it terminates at the edge of the invading spur. The antero-posterior orientation of the depressions and ridge suggests that the jaw was capable of sliding back and forth (Watson, 1954; Fox, 1964).

The retroarticular process is robust. Its orientation is primarily posteriorly, but it also bends slightly medially and ventrally. The process tapers but little through its length, possessing nearly the same cross-sectional dimensions distally as it does at its base. The retroarticular process is partially sheathed laterally by the angular and medially by a minor extension of the prearticular.

The anterior projection of the articular is lanceolate in outline, possessing a relatively acute tip in comparison to its base. An edge of this projection is exposed medial to the concavity of the prearticular and may have participated with the prearticular in providing the insertion for the posterior pterygoid muscle (Fox, 1964).

The articular, with the surangular above and the prearticular below, forms the posterior wall of the adductor fossa.

A ridge between the anterior projection and the retroarticular process is found in back of the glenoid fossa. The surangular and angular meet in a suture that covers this ridge.

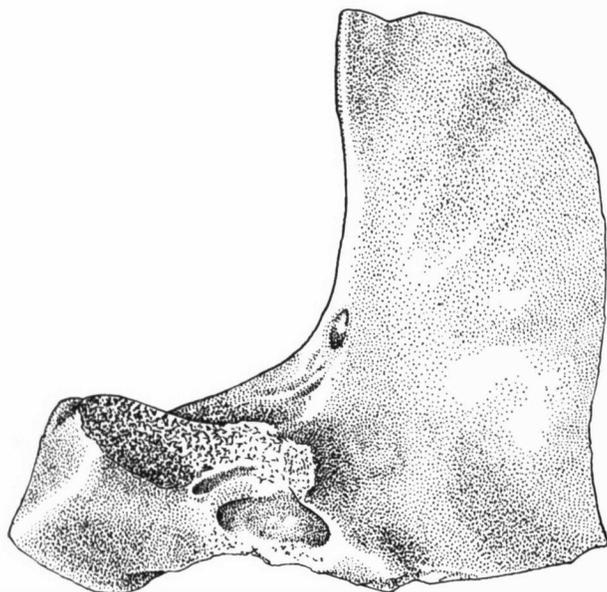


FIGURE 24. *Captorhinus aguti* (COPE). Lateral view of scapulocoracoid (KU 14757), $\times 3.3$.

The articular in *Captorhinus* is a bone of substantial size welded firmly in its contacts with its neighbors. There is no suggestion in the complexity of the surfaces that articulated medially with the prearticular or ventrally and laterally with the angular and surangular that the articular had entered into the series of events that culminated in the loosening of the bone in its setting seen in the advanced synapsids.

PECTORAL GIRDLE

The certain endochondral ossifications of the pectoral girdle of *Captorhinus* are a scapula, anterior coracoid and posterior coracoid; a cartilaginous suprascapula is presumed to have been present. The certain dermal ossifications are the clavicle and interclavicle. *Captorhinus* may have possessed a cleithrum, but the element has yet to be found. No sternum is known in *Captorhinus*, but ROMER (1956, p. 295) suggests that in cotylosaurs "it may have been present in cartilaginous form deep to the posterior end of the interclavicles and the anterior gastralia."

SCAPULOCORACOID

The scapulocoracoid (Fig. 24, 25) is a large plate consisting of three centers of ossification, an anterior and dorsal scapula, and two ventral coracoids that attach to the base of the scapula and extend backward from it. The plate is the dominant element of the anterior thoracic region; the bones that articulate with the plate are small and are placed at its periphery. Ventrally, along the mid-line, the interclavicle lay between the scapulocoracoids on either side and was partially overlapped by them. Anteriorly the clavicles abutted the scapulocoracoids and extended upward along their anterior borders. Dorsally a cartilaginous suprascapula capped each plate. The suprascapulae are not

PREARTICULAR

The prearticular in *Captorhinus* extends from its anterior articulation with the splenial backward to the retroarticular process of the articular along the inner face of the jaw. Throughout much of its length the prearticular furnishes the inner rim of the adductor fossa; with the articular and surangular above, the prearticular forms the posterior wall of the adductor fossa.

Anteriorly the prearticular expands into a broad plate limited by the coronoid dorsally and the Meckelian foramen ventrally. Here the prearticular is overlapped by the coronoid and comprises the dorsal and posterior rims of the Meckelian foramen. As it extends posteriorly the prearticular narrows beneath the adductor fossa and overlaps the angular ventrally. The inner lip of the fossa is formed by the prearticular; the bone also provides the uppermost part of the inner wall of the fossa. Posteriorly the prearticular overlaps the articular and extends beneath the glenoid fossa to terminate finally at the base of the retroarticular process. In front of the glenoid the surface of the prearticular is conspicuously hollowed, presumably for the insertion of the posterior pterygoid muscle (FOX, 1964).

On the ventral edge of the jaw the prearticular forms a groove that extends from the base of the retroarticular process forward, behind the glenoid fossa and the depression for the posterior pterygoid muscle. The groove has been thought by SHUTE (1956) to be associated with a submandibular sulcus or lateral extension of the buccal cavity. It is doubtful that the groove possessed this role in *Captorhinus*; the surface of the groove bears striations and pits characteristic of areas concerned with anchoring muscles. It is more probable that the groove participated in the insertion of the anterior pterygoid muscle.

preserved, but evidence indicating their presence is provided by a wide groove of unfinished porous bone present on the dorsal edge of the scapula. When in place, the scapulocoracoids and their associated elements formed a cradle for the anterior part of the trunk.

In outline the scapulocoracoids are essentially L-shaped. The scapular portion may be likened to the dorsal arm of the L, extending upward from the basal coracoids. Anterior and posterior borders of the scapula are parallel or nearly so through much of their length, but whereas the posterior border is straight or only slightly concave throughout, the anterior border curves backward to grade insensibly into the dorsal edge. The dorsal edge meets the posterior edge at a right angle.

The coracoids attached to the base of the scapula and are related to it spatially as the horizontal arm is to the vertical arm of the L. In outline the anterior coracoid is disc-shaped, with about half of the rim protruding in front of the anterior edge of the scapula and curving ventrally to extend beyond the ventral limit of the adjoining posterior coracoid. Posteriorly the junction of the anterior coracoid with the posterior coracoid is marked ventrally by a notch. The notch thus provides a useful landmark for delimiting the anterior and posterior ossifications from

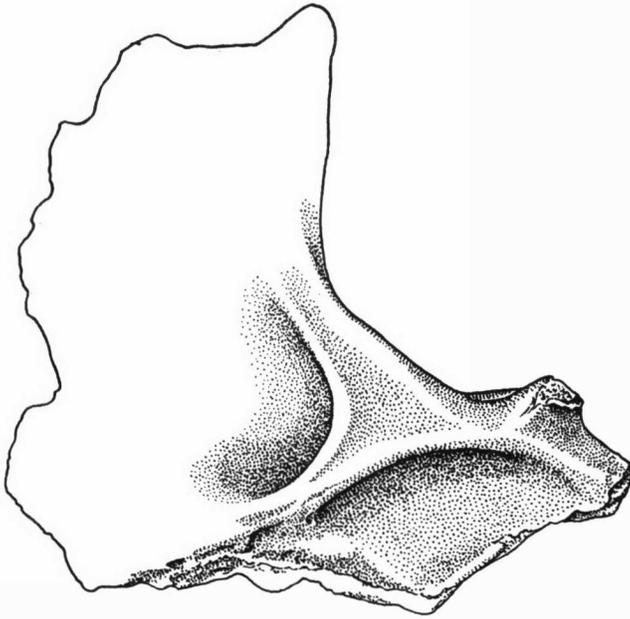


FIGURE 25. *Captorhinus aguti* (COPE). Internal view of right scapulocoracoid (KU 14749), $\times 3.3$.

each other. Behind the notch, the ventral border of the posterior coracoid continues to its termination at the posteroventral corner of the plate. The border is slightly convex throughout its length.

The remaining two edges of the posterior coracoid are the shortest of all the margins of the scapulocoracoid plate. The posterior edge, the longer of the two, is shallowly concave and slants slightly forward. The dorsal edge, only approximately two-thirds the length of the posterior edge, extends parallel to and behind the posterior part of the glenoid cavity. Here the edge meets the posterior part of the scapular blade.

Among the edges of the scapulocoracoid, only the posterior edge of the scapular blade and the posterior edge and dorsal edges of the posterior coracoid are of finished, nonporous bone. The other borders of the scapulocoracoid were presumably rimmed by cartilage; they were also the edges that are associated with the articulations of the scapulocoracoid with the subsidiary bones of the pectoral girdle.

The dominant surficial feature of the scapulocoracoid is the glenoid cavity. The surface of the cavity is of unfinished, porous bone, indicating that in life, the cavity was lined with cartilage for the reception of the head of the humerus. If this surface were to be stretched out, it would form a narrow ribbon, the ends of which were rounded and the sides of which were essentially parallel. If this ribbon then were to be twisted a quarter turn with the result that the posterior end faced dorsally and the anterior end faced laterally, and if the anterior end were then to be turned posteriorly, the shape of the glenoid fossa in *Captorhinus* would be duplicated in all of its essentials. The posterior-most third of the articular surface lies as a horizontal platform upon the posterior coracoid, supported from below by a broadening of the bone. The plane of the

anterior third is vertical and faces posteriorly. It is heavily buttressed from behind and extends outward from the base of the scapular blade.

The remaining surficial features are less conspicuous than the glenoid fossa. Above the anterior part of the fossa, the base of the posterior border of the scapular blade broadens into a triangular surface that is feebly depressed in its center. The depression is also triangular and marks the area of insertion of the subscapularis muscle. Immediately sideward from the apex of this scar is the supraglenoid foramen, which presumably carried blood vessels and nerves of the brachial plexus (ROMER, 1956, p. 307).

A second and larger foramen, the coracoid foramen, is present directly beneath the anterior lappet of the glenoid cavity. This passage pierces the bone, carrying the supra-coracoid nerve and its associated vessels (ROMER, 1956, p. 308).

The internal surface of the scapulocoracoid is interrupted by a system of ridge (Fig. 25). The first of these ridges extends along the posterior part of the posterior coracoid. The ridge is low and broad; dorsally it fans out even more broadly to back the glenoid fossa. Superimposed upon the expanded part of this ridge is a narrow ridge that extends horizontally behind the glenoid cavity; the ridge originates from the anteroventral region of the anterior coracoid. A third ridge extends down the posterior border of the scapular blade, broadens out in back of the glenoid cavity and joins with the ridges of the anterior and posterior coracoids. The scapular ridge and the ridge of the anterior coracoid are undercut at their junction to form a conspicuous hollow, the subscapular fossa. The coracoid foramen opens into the deepest part of the fossa; the supraglenoid foramen enters above the coracoid foramen.

The ridges can be viewed primarily as a triradial system of struts with two supportive functions. First, the expansion of the ridges at their common junction effectively braced the glenoid cavity against the stresses passed to it by the humerus. Second, the extension of the ridges towards the periphery of the scapular plate must have given considerable rigidity to the plate as a whole. The ridge backing the anterior coracoid seemingly would have been particularly important in this regard, for this component of the scapulocoracoid is thin and fragile in *Captorhinus*.

Muscle scars on the scapulocoracoid of *Captorhinus* are not conspicuous. But the use of what meager evidence is available and reference to ROMER's (1922) reconstruction of the muscles in *Labidosaurus* has permitted a reasonable assessment of the position and extent of most of the muscles that attached to the primary girdle of *Captorhinus*. The attachment of muscles to the upper part of the scapular blade is particularly difficult to resolve. The insertion of the serratus anterior superficialis on the lateral surface of the scapula was largely limited to the posterior edge of the blade. A roughened area along the upper third of this edge and encroaching very slightly out upon the lateral surface proper of the scapula marks the attachment of the muscle. The center portion of the lateral surface of the scapula presumably anchored the deltoideus scapularis, but there are no scars to suggest the extent of the area of

attachment. The levator scapulae superficialis occupied the anterodorsal corner of the blade, but once again scars to indicate the extent of the attachment are lacking.

The mid-portion of the external surface of the scapula was occupied by the scapulohumeralis anterior. The limits of the attachment are suggested by a slight depression that occupies the transverse width of the scapula from the glenoid to the anterior border of the blade. The supracoracoideus attached below this, on the external surface of the anterior coracoid. The separation of the supracoracoideus and the scapulohumeralis anterior followed a slight ridge that extends forward from the buttress of the glenoid cavity. The lateral surface of the posterior coracoid anchored the coracobrachialis and the biceps. The scars and cluster of small foramina that the area possesses do not reflect the division of the attaching muscle mass into the two component muscles.

The coracoid head of the triceps originated from a broad groove that rims the glenoid posteriorly. The scapular head of the triceps originated above and in front of the glenoid buttress, but no scars are determinable in the specimens examined. The subcoracoscapularis arose from the triangle that surrounds the supraglenoid foramen at the base of the scapular blade.

The uppermost part of the internal surface of the scapula was the area of attachment of the levator scapulae profundus and the serratus anterior profundus. Below these and bordering the latter the subcoracoscapularis extended on to the internal surface from the triangle enclosing the supraglenoid foramen. The lower limit of the attachment is formed by a ridge that extends obliquely up the internal surface of the scapular blade from the triangle enclosing the supraglenoid foramen.

The remainder of the muscles attaching to the internal surface of the primary girdle were anchored to the coracoids. The sternocoracoidei inserted below the ridge that backs the glenoid cavity. The costocoracoideus inserted on that ridge and the triceps head of the coracoid arose partly from a small knob at the posterodorsal corner of the posterior coracoid.

The scapulocoracoid of *Hylonomus* is known only from a fragment of the scapula, too incomplete to merit description (CARROLL, 1964). Of the element in *Archerpeton*, only the outline and glenoid are known. CARROLL reports that anteroposteriorly the scapulocoracoid is broad and the coracoid large, but without demonstrable division into anterior and posterior ossifications. Extension dorsally in cartilage of the short scapular blade seems probable. *Archerpeton* possesses the primitive screw-shaped glenoid, and is without the depression lying in front of the glenoid cavity that is found in microsaur.

The scapulocoracoid of *Protorothyris* is known (PRICE, 1937) but has not been described.

Cephalerpeton possesses a scapulocoracoid with prominent supra-glenoid buttress, separate coracoid ossifications and reptilian outline (GREGORY, 1948).

The scapulocoracoid of *Limnoscelis* is similar in shape to that of *Seymouria*, but the number of coracoids is unclear (e.g., VAUGHN, 1955, p. 451; ROMER, 1956, p. 493). The short scapular blade was probably continued dorsally in cartilage. The opening of the large supraglenoid foramen,

posteriorly and immediately above the glenoid, is an amphibian feature (ROMER, 1946, p. 179).

The scapulocoracoid of *Labidosaurus* duplicates that of *Captorhinus* in all of its essentials; the major difference lies in the robustness of the bone, with that of *Labidosaurus* being proportionally more heavy, as would be expected.

SCAPULOCORACOIDS OF GYMNARTHRIIDS AND CAPTORHINIDS

The gymnarthrid microsaur that have been recovered from the fissure deposits of the Richard's Spur locality include at least two genera, *Cardiocephalus* and *Euryodus*. The scapulocoracoids of these amphibians resemble in many features those of *Captorhinus*. An expanded dorsal blade that curves up and around the chest is common to all; the origin of the blade from a ventral and posterior coracoid region is likewise a common feature. The screw-shaped glenoid fossa is present in the microsaur, as well as in *Captorhinus*. The duplication is nearly precise in the detailed characters of the fossa, with the most obvious difference being that in the gymnarthrids the glenoid is shorter in relation to its width than in *Captorhinus*. In the gymnarthrid element the scar for the subscapularis muscle is triangular, as in *Captorhinus*, and bears a relationship to the glenoid similar to that in *Captorhinus*.

The coracoid region extends as an abbreviated posterior plate in both groups; in the gymnarthrids the coracoid region possesses the same smallness in comparison to the scapular blade that is exhibited in *Captorhinus*. The supraglenoid foramen in the gymnarthrids is quite large and slitlike, in contrast to the much smaller and circular passage in *Captorhinus*. The position of the foramen, however, is essentially the same in both groups. The coracoid foramen is proportionally smaller than in *Captorhinus*, but its relation to the glenoid closely resembles that in *Captorhinus*. The glenoid foramen of the gymnarthrids is absent in the reptilian genus.

These similarities in structure might be interpreted as indicative of some kind of special relationship between the gymnarthrids and *Captorhinus*. But the weight of these resemblances is overridden by a profound difference in the development of the scapulocoracoids in the two groups. The primary girdle in gymnarthrids has been reported to be a single ossification (GREGORY, PEABODY & PRICE, 1956, p. 33). This observation is accurate, for examination of approximately 20 scapulocoracoids of *Euryodus* and *Cardiocephalus* in The University of Kansas collections has failed to reveal the presence of sutures. In contrast to the gymnarthrid plate, the scapulocoracoid of *Captorhinus* consists of three centers of ossification, a dorsal scapula and two ventral coracoids.

Consequently, the resemblances in morphology of the endochondral girdle of gymnarthrids to the girdle in *Captorhinus* seem best accounted for by an explanation employing convergence. The occurrence of gymnarthrids with the remains of *Captorhinus* suggests that a similar habitat was utilized by both, one which at most was semi-aquatic and which demanded considerable time spent walking on land without buoyant support. The ossification of the endochondral girdles is extensive among adults; cartilage was limited to the margin of the plates, indi-

cating that rigid support for limb muscles was requisite for locomotion.

ANALYSIS OF SHOULDER JOINT MOVEMENT

ROMER (1922) has commented upon the shoulder joint in primitive tetrapods and has related its morphology to the movement of the humerus within the glenoid. Using *Dimetrodon* as an example, he pointed out that in that genus the humerus possesses a ridge on its articular surface that extends posteriorly and ventrally, effectively dividing the articular head into two surfaces. Of these surfaces "one commences broadly at the anterior dorsal edge and dwindles as it curves underneath to terminate at a distinct notch on the underside of the bone. The other commences behind the first and continues dorsal to it to the posterior end of the articular surface" (ROMER, 1922, p. 549). Unlike the humerus, however, the glenoid exhibits no such ridge. Instead, the ends of the glenoid are expanded and the mid-section is constricted in width. In ROMER's view the "change in width of the articular surface, found in all types, is difficult to explain on the theory of the unity of the surface, but fits perfectly with the idea of two distinct surfaces. The second expanded surface is the anterior termination of the second surface of the joint" (ROMER, 1922, p. 549).

The morphology of the apposing surfaces of the shoulder joint in *Captorhinus* agrees with that in *Dimetrodon* in most particulars; an articulated specimen in the Clarke collection augments our knowledge of the movement of the forelimb.

The first feature that should be noted is that the curve of the articular head of the humerus of *Captorhinus*, i.e., that portion of the proximal expansion of the humerus that is of porous, unfinished bone, is longer than the apposing surface of the glenoid cavity. Consequently, when the humerus is fitted into the glenoid, some part of either end of the articular head extends outward beyond the glenoid surface. For example, if the humerus is in a forward position, the anterior and middle parts of the articular head are in contact with the anterior and middle parts of the glenoid cavity. The posterior part of the articular head is free.

This bears on ROMER's (1922, p. 548) objection to WATSON's interpretation of the glenoid as a single screw-shaped surface. ROMER, in support of his view of the glenoid as two distinct surfaces, states that: "Any motion of more than about 20 degrees would cause the humerus to cut the muscular surfaces at the anterior and posterior edges of the joint. The joint capsule and ligaments would be greatly strained" if the surface were single. But in *Captorhinus* at least a quarter of the length of the articular head of the humerus is free of the glenoid regardless of the position of the humerus during locomotion. Seemingly, the comparative great extent of the articulating head beyond the glenoid would, in ROMER's view, greatly strain the joint capsule and ligaments in *Captorhinus*. In view of the fact that in *Captorhinus* some considerable part of the head *always* extends beyond the glenoid, ROMER's objection would not seem to apply in this genus.

The second factor of importance concerns the orientation of the articular head of the humerus within the

glenoid cavity. The humerus of *Captorhinus* resembles that of *Dimetrodon* in having a low, broad ridge extending obliquely across the articular head. Adjacent and anterior to this ridge is a shallow groove that also passes obliquely across the head and parallels the ridge. Furthermore, the surface of the glenoid cavity is divided into two parts: first, a wide upper and inner band and, second, a narrow recessed groove that rims the lower and outer two-thirds of the glenoid surface. The common border between the band and the groove depressed below the surface of the band acts as a ridge between the two areas. When the humerus is in articulation with the glenoid, the groove on the head of the humerus fits over the ridge of the glenoid. The ridge is essentially horizontal, but the groove of the humerus is oblique to the plane of the proximal expansion of the humerus. Consequently, when the ridge and groove are apposed in articulation, the plane of the proximal expansion of the humerus is slanted downward.

An analysis of the movement of the shoulder joint leads to results at variance with those of both ROMER and WATSON although elements of the analysis of each are upheld. Two factors dictate the movement of the humerus within the glenoid. First, it seems clear that the humerus moved in a manner such that its distal end described an ellipse during the complete cycle of one step. Second, the ridge of the glenoid and the articulating groove of the humerus were the major surfaces of articulation. The other surfaces guided the movement of the humerus by sliding against each other. In addition to the elliptical swing of the humerus upon the ridge of the glenoid, there was also a twisting of the limb bone along its long axis.

At the beginning of the power stroke, the humerus was in a forward and downward position distally. The dorsal lappet of the articular surface of the humerus abutted against the lower surface of the supraglenoid buttress. The glenoid ridge and articular groove were in contact throughout their length. The surfaces of the articular head of the humerus posterior to the groove were largely free of the glenoid cavity and only in contact with it adjacent to the groove. The uppermost extent of the glenoid was also free throughout its length. As the humerus was drawn back, its head rolled in the glenoid cavity on the pivot provided by the groove and ridge. In the initial stages of the movement there was little sliding of the groove of the humerus upon the glenoid ridge, but as the humerus was progressively pulled farther back in the power stroke, the groove of the humerus slid forward slightly on the glenoid ridge. The contact between the dorsal lappet of the articular head and the anterior and lower surface of the supraglenoid buttress pushed down on the head of the humerus causing it to become nearly vertical. Consequently, the distal expansion assumed a nearly horizontal orientation.

In the last stages of the power stroke, the ventral posterior parts of the articular head (facing down and inward) apposed the rear surface of the glenoid (facing upward and outward). As this occurred, the head pivoted on the ridge of the glenoid, and the rear part of the head rode up on to the rear part of the glenoid, a movement that continued with the upstroke. In so doing, the proximal expansion became more horizontal and the distal expansion came to slant down and backward. The humerus was then

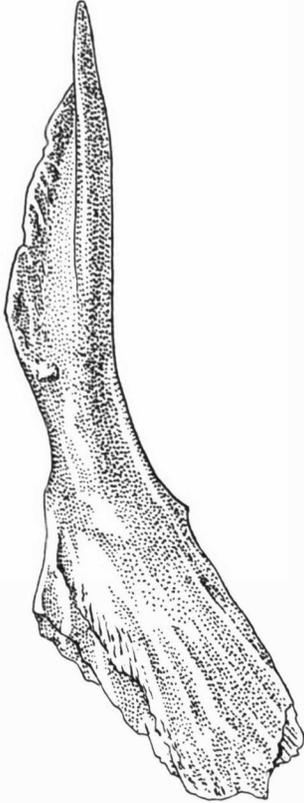


FIGURE 26. *Captorhinus aguti* (COPE). Internal view of left clavicle, uncatalogued specimen, Clarke collection, $\times 6$.

drawn forward on the recovery stroke, again rolling along the ridge of the glenoid. The articular head behind the groove was in contact with the glenoid surface above the ridge throughout the recovery stroke. This was accompanied by a slight sliding movement of the groove on the ridge, shifting the head backward within the glenoid as the distal humerus moved forward. At the top of the recovery stroke the dorsal lappet of the humerus regained contact with the buttress. The two surfaces, that of the glenoid buttress facing downward and outward and that of the lappet of the humerus facing upward and inward, slid against each other, forcing the anterior part of the head down. When the surface of the humerus anterior of the groove fitted into the groove of the glenoid beneath the ridge, the downstroke was completed and a new power stroke begun.

The complexity of the movement is more apparent than real. The major fulcrum of movement is at the glenoid ridge-articular groove contact, about which the humerus moves in an ellipse. Minor sliding movements, forward as the distal humerus is moved backward, and backward as the distal humerus moves forward, are involved. The anterior and posterior surfaces of the glenoid direct the anterior part of the articular head down on the downstroke and the initial parts of the power stroke, and posterior part of the articular head up in the last stages of the power stroke and the upstroke. The latter is not so much direction as supplying a plane on which the rear

part of the head rides. The band of the glenoid surface above the ridge acts as a single surface in the recovery stroke, with the head rolling along it and sliding slightly upon it. The ventral groove of the glenoid acts similarly with the head of the humerus anterior to its groove during the power stroke.

CLAVICLE

In *Captorhinus* the clavicle (Fig. 26) adheres to the primitive reptilian morphology in consisting of a slender dorsal stem applied to the anterior edge of the scapula, and a broad ventral foot that curves around the anterior coracoid and overlaps the interclavicle. The stem extends along the leading edge of the scapula through perhaps three-quarters of the latter's height; this contact was enhanced by a narrow flange on the stem that wrapped slightly around the lateral surface of the scapula. The flange presumably also anchored part of the deltoid musculature (ROMER, 1956, p. 300). Between the dorsal termination of the flange and the tip of the stem, the scapular surface of the stem bears a shallow depression; the depression probably marks the overlap of the cartilaginous supra-scapula by the clavicle.

The foot attaches to the stem at an angle slightly greater than 90 degrees. The foot consists of a thin plate notched posteriorly for the reception of the raised area of the head of the interclavicle. The foot is relatively thick anteriorly; posteriorly it thins to a featheredge. The external surface of the foot is modestly sculptured.

The clavicles probably did not meet in the mid-line. The adjacent edges of the clavicles at the mid-line consist of extremely thin bone that does not suggest abutment. CASE (1911a, p. 100, fig. 45) shows the clavicles articulating with one another along a straight contact at the mid-line; this edge in the specimens that were examined for this study is not straight, but extends obliquely posterolaterally in a manner at variance with CASE's presentation. Cartilaginous contact is not suggested either; the edges are of finished, nonporous bone.

INTERCLAVICLE

The interclavicle (Fig. 27) of *Captorhinus* is a T-shaped structure, the crossbar extending laterally on either side of the mid-line, and the stem extending posteriorly from the crossbar along the mid-line of the body.

The ventral or outer surface of the crossbar consists of two regions, a border of thin bone extending in front of the crossbar, and a central raised portion. The anterior extent of the border often cannot be determined with accuracy because of its frequent partial or complete loss. The border area is deepest along the midline and was overlapped by the clavicles.

Internal to the border the bone is raised and sculptured. The outline of the region parallels that of the border. The central area slopes gently on each side toward its lateral limits.

The ventral surface of the stem tapers posteriorly from its junction with the head. The surface is smooth, except for from two to four striations in the mid-line toward the caudal end.

The dorsal or internal surface of the stem is smooth

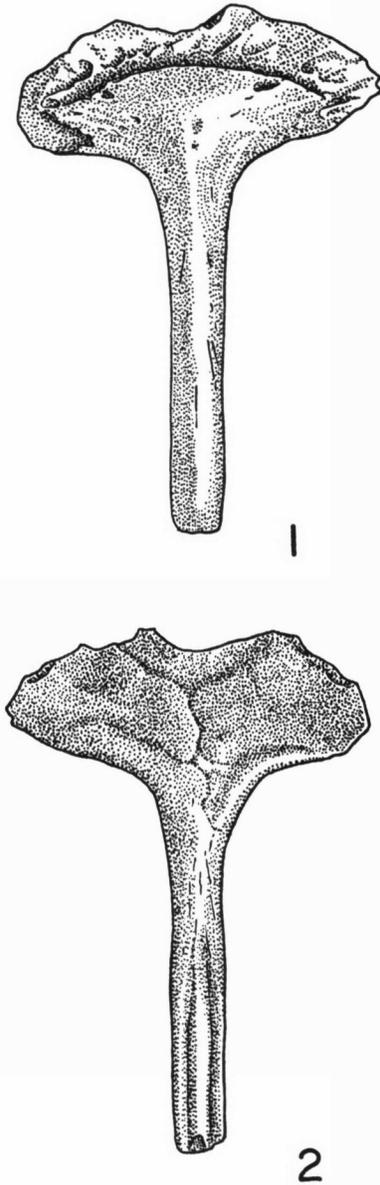


FIGURE 27. *Captorhinus aguti* (COPE). Interclavicle, uncatalogued specimen, Clarke collection, $\times 4$. —1. External view. —2. Internal view.

and unsculptured, and commonly is higher anteriorly than posteriorly. Posteriorly two broad and shallow grooves separated by a narrow ridge are present.

The interclavicle of *Captorhinus* differs considerably from that of the captorhinid *Labidosaurus*. WILLISTON

(1908a, p. 143, fig. 4) has pictured the pectoral girdle of *L. incisivus* in ventral view as restored by him. The head, although partly obscured in articulation by the clavicles, appears to be diamond-shaped. The head is wide in proportion to the short stem. The border area is restricted to the anterior portion of the ventral surface of the head. The caudal end of the stem is pointed, as is the anterior end of the head, the latter shown extending beyond the clavicles. CASE (1911a, p. 108, fig. 47c) has faithfully reproduced the WILLISTON restoration. CASE says of the interclavicle (p. 109): "The interclavicle is rhomboidal with a strong posterior projection." ROMER (1956, p. 300, fig. 143E) pictures the pectoral girdle of *Labidosaurus* in ventral view. His presentation is based on that of WILLISTON, but with some modification. The interclavicle no longer protrudes beyond the anterior limits of the clavicles. By implication, at least, a notch is shown in the border area of either side directed medially and slightly posteriorly into which fits a posterior prong of the clavicle. The stem is unchanged from WILLISTON'S and CASE'S illustrations. A specimen of the interclavicle of *Labidosaurus* in the American Museum of Natural History differs from those that have been described in the literature. This specimen (AMNH 4394a) is of rather heavy bone. The head resembles the shape of an isosceles trapezoid rather than a rhomboid. The anterior margin is deep, accounting for better than half of the anteroposterior length of the head. The anterior edge of the margin is slightly curved; in no way does it approach a point at the mid-line. The head is approximately three times as wide as the average width of the stem, not the four or five times that earlier restorations indicate. The stem is proportionally longer than those shown by WILLISTON, CASE, and ROMER. The head possesses two narrow and deep clefts for the reception of the prongs of the clavicles.

In comparison to the interclavicle of *Captorhinus* the head of the American Museum specimen is much narrower proportionally with little or no lateral flaring and trapezoidal rather than rhomboidal. The anterior margin and posterior clefts are essentially separate and discrete; they are not a continuous surface as in *Captorhinus*.

The interclavicle of *Captorhinus* is dissimilar to those of pelycosaurs. The interclavicles of sphenacodonts (ROMER & PRICE, 1940, p. 118, fig. 21) are characterized by diamond-shaped heads and prominent ridging oriented in a cross. The interclavicles of ophiacodonts, especially *Ophiacodon uniformis*, are more similar to *Captorhinus*, but the head is much smaller in proportion to the stem, and the surface ridges are proportionally higher in the pelycosaur.

The interclavicles of the gymnarthrid microsaur of the American Permian are unknown (GREGORY, PEABODY & PRICE, 1956, p. 52). In *Petrolacosaurus* the interclavicle closely resembles those of ophiacodont pelycosaurs.

ANTERIOR LIMB

The anterior limb was held in the sprawling position common to primitive reptiles, with the humerus extending from the body in an approximately horizontal plane and the epipodials hinged on the humerus in a nearly vertical plane.

The comparatively small body size of *Captorhinus* was probably a major factor in those departures from the presumed primitive condition that the anterior limb exhibits. *Petrolacosaurus* and *Araucoscelis*, also small reptiles, reflect in their elongated, slender limbs, not only body size, but

also the assumption by these animals of agility afoot usually associated with lizard-like habits (VAUGHN, 1955, p. 365; PEABODY, 1952, p. 34). *Captorhinus*, lacking these habits, may be suspected of showing modifications in its limb structure more strictly related to body size alone.

An articulated individual from the Clarke collection possesses a humerus measuring 45 mm. in length. The radius of this individual measures 25 mm. in length. CASE (1911a, p. 101) reports that in one specimen (AMNH 4424) the humerus measured 35.5 mm. and the radius 19.5 mm. The propodial would seem to be about 50 to 60 percent longer than the epipodial in *Captorhinus*, a ratio comparable to that in the more primitive and heavy bodied *Seymouria*, *Limnoscelis*, and *Diadectes* (ROMER, 1956, p. 348).

HUMERUS

The tetrahedral nature of the primitive reptilian humerus has been recognized by ROMER (1922, 1956). The humerus of *Captorhinus* (Fig. 28) retains the essentially triangular surfaces that characterize the primitive reptilian humerus, but departs from this early morphology in a number of other features.

In *Captorhinus* the proximal and distal expansions of the humerus broaden into flat surfaces that are twisted, as it were, on their connecting shaft to a position in which they are at approximately right angles to one another. The orientation of the expanded ends in articulation depended upon the progress of the humerus in its passage through the locomotory stroke. The whole of the humerus rotated from an anterior position in which the proximal and distal expansions were obliquely oriented to a posterior one where they more nearly approached horizontal and vertical positions respectively.

The surface of articulation of the humerus with the glenoid fossa curves across the entire rim of the proximal expansion as a strip of unfinished, porous bone. The strip is divided into distinct anterior and posterior segments, each narrow, roughly parallel, and partially overlapping near the center of the articular head. Both extend obliquely backward along the articulating end of the proximal expansion. The anterior segment terminates on the ventral face of the expansion; the posterior segment extends along the edge, curving away from the anterior segment, and terminates near the posterior apex of the proximal expansion. In cross section the anterior segment is a shallowly hollowed groove throughout all but the anterior-most part of its length. In contrast, the surface of the posterior segment in cross section exhibits a low convexity throughout all of its length. The relationship of the segments to the configuration of the glenoid has been analyzed more completely above.

Although for ease of description the proximal expansion may most profitably be viewed as a triangle, in actuality the shape of the expansion departs from that concept. The articular head, corresponding to the base of the triangle, is a convex rim, curving to fit loosely enough into the glenoid fossa to permit the rocking movement of the humerus that is a part of the action of the shoulder joint. The head and the expansion that it rims are not set equilaterally upon the shaft. If the axis of the shaft were to be continued through the expansion, most of the expansion

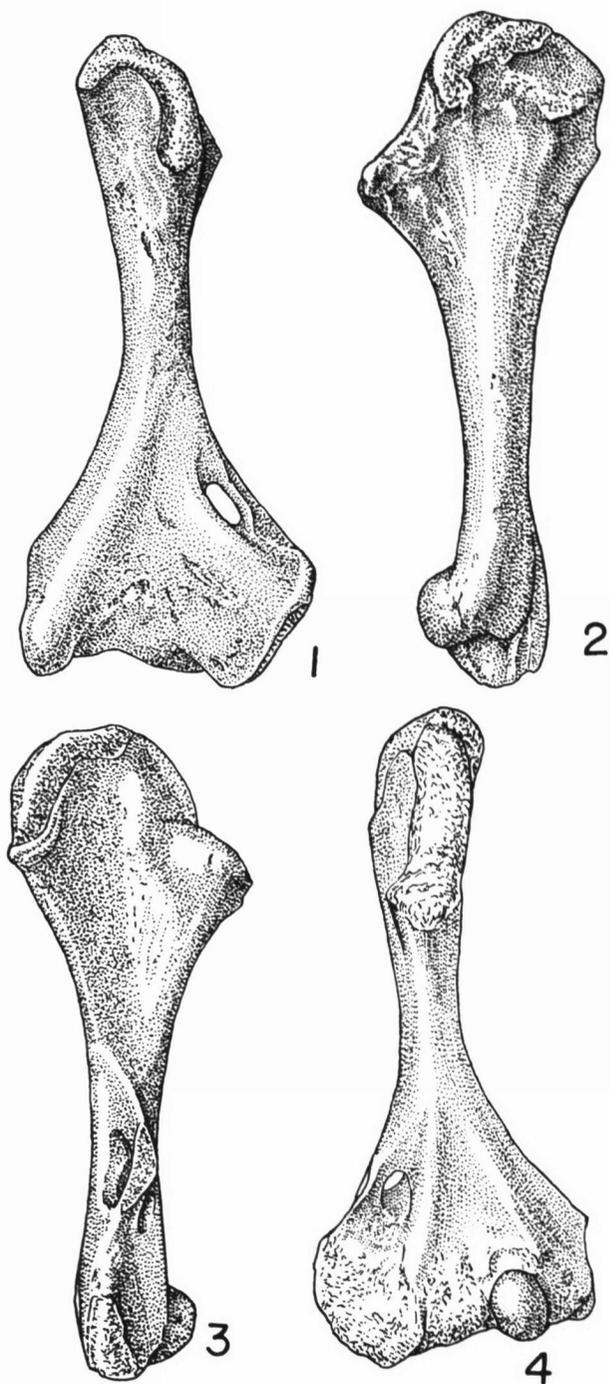


FIGURE 28. *Captorhinus aguti* (COPE). Left humerus (KU 14745), $\times 4.9$. —1. Dorsal view, distal end. —2. Dorsal view, proximal end. —3. Ventral view, proximal end. —4. Ventral view, distal end.

and its articulating rim would lie caudally of the axis. The asymmetry is at least partially balanced by the antero-ventral projection of the deltopectoral crest, even though the apex of the crest occurs more distally than does the opposite and posterior apex of the head proper.

The crest, therefore, bears much the same relationship to the head proper as an abbreviated thumb would bear to a stubby and mittened hand. The distal slope of the crest arises from the anteroventral border of the expansion near its origin from the shaft and then ascends rather gradually to the roughened, apical scar marking the attachment of the pectoralis muscle. The scar broadly caps the crest and extends down its slope to the reunion of the crest with the proximal expansion. Adjoining the base of this slope, on the ventral surface of the proximal expansion, is a conspicuous roughened area, commonly containing a small knob within its borders. It was to the whole of this scar that the supracoracoideus muscle attached.

The ventral surface, adjacent to the supracoracoideus and bordering the articular rim, was the site of attachment for additional muscles. Immediately next to the supracoracoideus, the coracobrachialis brevis inserted on a broad and irregular band of roughened bone set in a shallow depression. The insertion was partially by means of a tendon running to a knob that is just within the posterior border of the scar. The next and last of the series of scars in this region is that of the subcoracoscapularis muscle, which was inserted onto a ridge on the posteriormost part of the articular head.

The dorsal surface of the proximal expansion is also the site of numerous muscle scars. The scar of the deltoideus extends down the dorsal edge of the deltopectoral crest as a thin ridge running between the anteriormost part of the articular head and part of the scar of the pectoralis that caps the apex of the crest. At approximately the mid-point of the length of this ridge and slightly posterior to it on the dorsal surface is a small boss to which the brachialis muscle was attached.

Both of these scars are relatively minor features of the dorsal surface. Far more conspicuous is a posterior roughened area bordered by the entire extent of the articular head proximally. The ridge and grooves that define the area spread out over the dorsal surface to a level nearly equal to the deltopectoral crest anteriorly and to the shaft proper posteriorly. Within this area are three major topographical features. The first of these is a broad boss inset slightly on the dorsal surface from the posterior apex of the proximal expansion. A ridge runs obliquely backward from this knob toward the articular rim. The latissimus dorsi was attached in this area.

The knob may be used further as a reference point, for from its anterior side, extending obliquely forward and toward the articular rim is a second and longer ridge. Presumably the scapulohumeralis was attached here.

The third major topographical feature of the proximal dorsal surface is a ridge that extends from the posterior border of the expansion obliquely forward paralleling the ridge of the scapulohumeralis anterior. This ridge is the longest of those exhibited on the dorsal surface of the proximal expansion and limits the roughened area distally. No grooves extend beyond it toward the shaft. It was on this mark that the lateral head of the triceps was inserted.

At the anterior end of the latter ridge is a small depression squeezed between it and the dorsal lappet of the articular surface. This seems to have marked the insertion of the humeroradialis muscle. Finally, two scars are present on the posterior border of the expansion: the sub-

scapularis, adjacent to the articular rim, and the depressed insertion for the medial head of the triceps, bordering the subcoracoscapularis distally.

The shaft of the humerus of *Captorhinus* makes up less than one-third of the total length of the bone, and yet because of the extreme slenderness that the shaft exhibits in comparison to the breadth of the proximal and distal expansions, it is a distinct topographical entity. In its gross aspect the shaft is a smoothly rounded and contoured cylinder, subovate in cross section and lacking strong ridges or other marks.

Ridges are not entirely absent however. Dorsally a feeble line extends from the posterodistal quadrant of the proximal expansion that may have marked the division between the abductor and adductor musculature. Ventrally there are two stronger ridges that unite distally at the bridge of the entepicondylar foramen. The anterior ridge of the V arises from the deltopectoral crest; its more posterior partner extends to the bridge from the insertion of the medial head of the triceps. The surface of the shaft enclosed by the ridges appears to have been the area of insertion of the long head of the coracobrachialis.

Passing distally from the shaft the humerus broadens into a large, paddle-shaped and square-cut expansion that provided extensive surfaces for the origins of the lower leg muscles and strong articulations for the radius and ulna. The capitellum and trochlea are the dominant features of the ventral surface of the expansion, the former as an oval, smoothly rounded knob, and the latter as a subtriangular patch of porous bone adjacent to the capitellum and wrapping around the distal end of the expansion to extend for a short distance on to its dorsal surface.

Between the trochlea and capitellum on the one hand and the shaft on the other is a large depression, triangular in shape, the base of which borders on the trochlea and capitellum. This depression seems to have afforded an increase in freedom for the movement of the radius and ulna on the humerus. Part of the freedom is provided by the trochlea and capitellum in raising the ulna and the radius away from the surface of the distal expansion. The depression surrounding the raised areas acts to augment this effect.

The ventral and dorsal surfaces of the square-cut entepicondyle are covered by the grooves and ridges left by the origins of the flexor and extensor muscles of the lower leg. The attachment of these muscles appears to have been concentrated along the posterior edge of the entepicondyle, for here the ridges and grooves are especially strong. The muscle scars of the ectepicondyle are much more limited, being restricted mainly to its prong-like tip and the broad ridge extending proximally from it along the anterodorsal edge of the distal expansion. The ectepicondylar foramen and supinator process are lacking in *Captorhinus* (ROMER, 1956, p. 353).

The retention of expanded proximal and distal ends twisted in relation to each other upon the shaft of the humerus of *Captorhinus* is a primitive reptilian feature. The absence of a supinator process and ectepicondylar foramen in *Captorhinus* bears a strong resemblance to the condition shown by *Limnoscelis* (e.g., ROMER, 1956, p. 354, fig. 165A), in which the supinator process and ectepicondylar foramen are absent and the ectepicondyle is short proximo-

distally. To change the ectepicondyle of *Limnoscelis* to that of *Captorhinus* would seem only to require a lengthening or drawing out of the ectepicondyle along its proximal-distal axis. The retention of the elongate proximal articular surface is a primitive reptilian feature (ROMER, 1956, p. 353) exhibited by *Captorhinus*, as is its short shaft.

The major advance from the primitive reptilian condition exhibited by the humerus of *Captorhinus* is in the general loss of massive stoutness, with the extremely short shaft and high development of the major ridges and crests that accompany this stoutness. That the comparative slenderness of the humerus of *Captorhinus* is at least partly a function of absolute body size has been suggested by ROMER (1956, p. 353).

Eleven humeri of *Captorhinus* measured by SELTIN (1959) average 24.5 mm. in total length and 8.5 mm. in proximal width. Ten of these specimens average 11.4 mm. in distal width. CASE (1911a, p. 101) reports the length of a single humerus (AMNH 4424) (part) as 34 mm. and its distal width as 25.5 mm. Of this specimen, he says (p. 99): "The humerus has the upper and lower ends expanded and turned almost at right angles to each other; the articular surfaces are well-formed. There is a prominent entepicondylar process and a good-sized entepicondylar foramen. The ectepicondylar process is extended as a distal hook." The latter statement appears to be a *lapsus*, as CASE's illustration (1911a, p. 98, fig. 43) shows no hook, nor is such a hook present in any of the specimens examined for this study.

GREGORY, PEABODY & PRICE (1956, p. 55) compared the humerus of the gymnarthrid microsauro *Cardiocephalus* with that of *Captorhinus* and illustrated a humerus (YPM 3854) (fig. 26). No measurements were taken.

The humerus of *Labidosaurus* appears to have all of the features, grossly at least, of that of *Captorhinus*, except for the coarsening of those features in *Labidosaurus* in keeping with its larger body size. CASE (1911a, p. 109-110) reports:

The humerus is relatively short, with wide proximal and distal ends turned at right angles to each other. There is a total lack of the strong processes and general heaviness found in the humerus of the Diadectidae. The condyles are not well-developed; the articular face on the proximal end is not distinct.

The shaft is slender and has a triangular section. There is a distinct entepicondylar process, an entepicondylar foramen, and a well-marked hemispherical articular process for the head of the radius, almost entirely on the anterior surface of the bone.

The humerus is not illustrated except in the reconstruction of the entire skeleton following BROILLI. Measurements reported by CASE (1911a, p. 111) (based on UC 641) are greatest length, 66 mm., distal width, 30 mm.

ROMER (1922, pl. 37) pictured the humerus of ?*Labidosaurus* in the plane of the distal dorsal surface but little can be made of this representation.

Three humeri of *Labidosaurus hamatus* were measured by SELTIN (1959, p. 504). They average 72.7 mm. in length, 48 mm. in distal width and two of the three average 31 mm. in proximal width. These were not illustrated.

ROMER (1956, p. 354, fig. 165E) has illustrated the humerus of *Labidosaurus* in the plane of the distal ventral surface. This representation shows little detail beyond the

coarsening of the features of the limb in *Labidosaurus* already commented upon.

The humerus of *Captorhinikos chozaensis* is known, and one specimen included by SELTIN (1959) measured 53.5 mm. in total length, 22.0 mm. in proximal width and 31.2 mm. in distal width. The humerus of *C. valensis* has not been reported upon in the literature. The humerus of *C. chozaensis* is illustrated by OLSON (1954b, p. 215, fig. 86C). The specimen (CNHM UR 100) has an extremely well-developed, square-cut entepicondyle, the shoulder of which appears to leave the shaft at approximately a right angle, in contrast to the obliquely sloping shoulder in *Captorhinus*. Little else can be determined from the illustration.

The humerus of *Labidosaurikos barkeri* is known (OLSON, 1954b, p. 213), but so far as is known has neither been described nor illustrated. The material of *L. meachami*, as originally described by SELTIN (1959), includes no known humerus. Similarly the humeri of *Captorhinoides* are unknown. Of the humerus of *Kahneria*, OLSON (1962a, p. 16) reports: "Two humeri, a radius, two partial femora and a tibia make up the identifiable limb elements. The humerus is a short stocky bone with a very short shaft." Of the humerus of *Rothia* OLSON (1962a, p. 20) says: "A problematical bone which may be the humerus is preserved in US 263. . . . All that can be said . . . is that the front limb was lightly built and small in proportion to the axial skeleton in comparison with other captorhinids of comparable size." The humerus of the Russian *Hecatotomphius* is unknown.

GREGORY, PEABODY & PRICE (1956, p. 55) compared the humerus of the advanced gymnarthrid *Cardiocephalus* to that of *Captorhinus*. The humeri of *Cardiocephalus* differ from those of *Captorhinus*

in smaller size, much more slender proportions, much less expanded proximal and distal ends, relatively more shaft, and in having no entepicondylar foramen. The proximal end is rather similar to that of *Captorhinus*, with spiral head area and the deltoid process rather distant from the head but in the same plane. The distal end differs from *Captorhinus* in lacking the wide and distally projecting entepicondyle. There is no trace of foramen and groove on either epicondyle.

Examination of specimens in the collections of The University of Kansas reveals that the above comments are essentially accurate, except that there seems to be no particular resemblance of the proximal articular surface in *Cardiocephalus* to that in *Captorhinus*. In *Cardiocephalus* the surface is broad in relation to its length and shows little if any tendency toward division into two overlapping segments; the surface does cross the rim obliquely and overlap onto the anterodorsal surface. The major part of the head is anterior to the axis of the shaft, rather than posterior, as in *Captorhinus*.

Of the humerus of *Petrolacosaurus*, PEABODY (1952, p. 26) says:

The humerus is primitively constructed; the proximal and distal ends are expanded plates, twisted approximately 90 degrees with respect to each other. Immature humeri are constructed simply and lack any pronounced processes or definitive articular surfaces. The head of the humerus has a narrow convex surface which was capped by cartilage; a lateral (deltoid) process is only slightly developed and is delineated from the convex surface by a slight convexity (fig. 6C). Distally, an elongate entepicondylar foramen

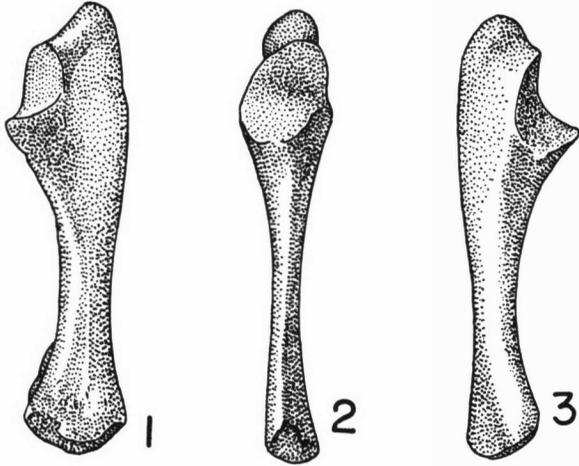


FIGURE 29. *Captorhinus aguti* (COPE). Left ulna (KU 14752), $\times 3$. —1. Anterior view. —2. Medial view. —3. Posterior view.

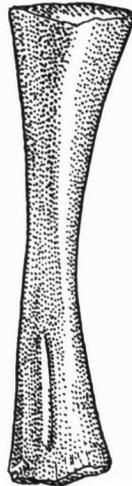


FIGURE 30. *Captorhinus aguti* (COPE). Left radius, anterior view, uncatalogued specimen, Clarke collection, $\times 6$.

pierces the entepicondyle, which is somewhat larger than the ectepicondyle. The distal articular surface is simple and lacks definitive radial and ulnar surfaces.

Thus the humerus of *Petrolacosaurus* would seem to bear little specific resemblance to that of *Captorhinus*.

CARROLL (1964, p. 71, 78) states of the humeri of *Hylonomus* and *Archerpeton* that they resemble generally those of other captorhinomorphs, although the entepicondylar foramen in *Hylonomus* is directed dorsally rather than posteriorly, as in *Captorhinus*. Of the humerus of *Archerpeton*, CARROLL (p. 78) says: "It resembles in a general way the humeri of *Captorhinus*, but the distal end is less expanded, and is set at less of an angle to the proximal end (the latter may be due to distortion)." Apparently, the humerus of *Cephalerpeton* (GREGORY, 1948) follows the pattern shown in other romeriids.

ULNA AND RADIUS

The ulna (Fig. 29) of *Captorhinus* possesses a proportionally large olecranon process for the attachment of the triceps muscle, a broad semilunar notch, and an expanded and flattened distal end for the articulation with the intermedium and ulnare. The facet for articulation with the ulnare is transverse to the long axis of the bone, while the facet in contact with the intermedium is proximally oblique. The ulna is stout, particularly in the region of the semilunar notch and the olecranon.

Surficial marks are few. The extensor or anterior surface of the proximal half of the bone is hollowed into a broad groove that backs the lip of the notch. Proximally the groove terminates at the scar for the triceps on the tip of the olecranon. Distally the groove extends nearly to the midpoint of the length of the bone.

The radius (Fig. 30) is quite unremarkable in *Captorhinus*. It is thin, with proximal and distal ends expanded. The articular heads are essentially three-sided in outline, and the connecting angles are rounded. The proximal articulation is only slightly hollowed for the reception of the radial condyle of the humerus. The distal surface of articulation, joining the radiale, is flat.

MANUS

The carpus (Fig. 31) of *Captorhinus* is almost completely known; the remainder of the manus is incompletely known. Radiale, intermedium, ulnare, proximal centrale and distal carpals 1-4 are known with certainty, as are metacarpals of digits I-IV, the first phalangeal segments of the second and third digits, and the second phalangeal segment of the second digit.

The radiale is substantial in all of its dimensions. The proximodistal length of the bone is approximately equal to its dorsoventral height; the width of the radiale exceeds the greatest of these dimensions by about a factor of two. The proximal edge of the radiale, in contact with the radius, is gently convex; the distal edge contacts the distal

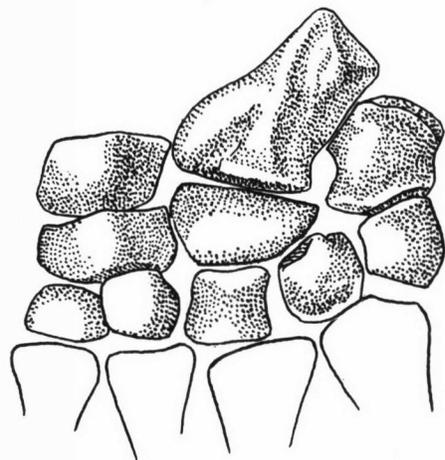


FIGURE 31. *Captorhinus aguti* (COPE). Left carpus, composite, about $\times 8$.

centrale broadly; contacts with the proximal centrale and intermedium are along the ulnar side of the radiale. Consequently, the outline of the radiale in dorsal view exhibits a comparatively wide central area, lying between more narrow tips on the radial (inner) and ulnar (outer) sides. The area of greatest width is displaced slightly toward the intermedium, making the inner tip more acuminate than the outer tip.

When viewed from either the proximal or distal surfaces of articulation the outline of the radiale resembles a tear drop, the acuminate end of which is free. The blunt end contacts the intermedium by means of a facet along its edge. The facet fails to join the proximal edge of the radiale; the intervening area is incised by a groove for the passage of blood vessels.

The dorsal surface of the radiale is highly convex; the underside is only slightly so.

In comparison with *Ophiacodon mirus* (WILLISTON, 1925, p. 160, fig. 131) the radiale of *Captorhinus* is not so long proximodistally, nor does it bear distinct facets for articulation with the intermedium and proximal centrale. In *Captorhinus* both of these bones presumably articulated with the radiale along its oblique inner edge. The radiale of *Petrolacosaurus* resembles that of *Ophiacodon mirus* and *Varanosaurus*, and consequently differs from *Captorhinus* in these features.

The intermedium of *Captorhinus* is a flat, slender bone, longer than wide, and in articulation with the radiale, proximal centrale and ulnare. The distal articulation, with the proximal centrale, is along a transverse edge that becomes progressively thicker toward the ulnare. The transverse edge joins a short, oblique surface that abuts against the radiale. Bordering on the articulation with the radiale is a groove that crosses this edge; the groove, with that of the radiale, permits the passage of vessels through the foot.

Beyond the groove, the edge of the intermedium extends obliquely towards the base of the ulna and becomes progressively thicker as it nears the ulnar articulation. The edge is free, as in pelycosaurs, and presumably served mainly for muscle attachment.

The ulnar articulation of the intermedium joins the free edge at about right angles; the articulating facet is ovate. The remaining edge of the intermedium, that which faces the ulnare, possesses two distinguishing features. The first is a facet in contact with the ulnare. The facet extends a little over half the length of the edge, faces down as well as toward the ulnare, and terminates distally in a sizeable notch. The notch, with an apposing notch in the edge of the ulnare, produces a comparatively large foramen that acts as the major portal for the passage of blood vessels through the foot.

The dorsal surface of the intermedium is shallowly concave. The ventral surface bears a broad and shallow groove extending from the foramen obliquely across toward the junction of the free edge and the facet that contacts the ulna.

The intermedium of *Captorhinus* is similar to that of *Ophiacodon*, both in shape and its size relative to that of the radiale and ulnare.

The ulnare is somewhat disc-shaped, vaguely resembling the calcaneum in outline. Proximally the ulnare

contacts the ulna, intermedium, and pisiform (which is not known), medially the intermedium and possibly the proximal centrale, and distally the fourth and fifth distal carpals. The outer edge of the ulnare is free. The contact with the intermedium is interrupted by the foramen referred to above. The proximal edge of the ulnare bears facets for articulation with the intermedium, the ulna and the pisiform. The facet for articulation with the pisiform is the longest of the three and faces obliquely away from that for articulation with the ulna. The distal edge of the ulnare also possesses three facets, for possible articulation with the proximal centrale and the fourth and fifth distal carpals. The facets facing the proximal centrale and the fifth distal carpal are oblique to that in contact with the fourth distal carpal.

The proximal and distal edges of the ulnare are raised slightly above the dorsal and ventral surfaces. The dorsal surface is convex in cross section; the ventral surface is concave.

In comparison with ophiacodont pelycosaurs, the ulnare of *Captorhinus* is shorter relatively, possessing nearly equal proximodistal and mediolateral dimensions. The ulnare of *Captorhinus* is unlike that of sphenacodonts in which the proximal portion, supporting intermedium, ulna and pisiform, is bulblike in outline and arises from a comparatively small distal foot that articulates with the proximal centrale and the fourth and fifth distal carpals.

The proximal centrale is a large flat element that broadly adjoins the intermedium by means of a long transverse proximal edge. A shorter inner edge, at approximately right angles to the contact with the intermedium, articulates possibly with the radiale and the distal centrale; extending distally from this, an oblique edge contacts the distal centrale. The distal edge meets both third and fourth distal carpals. The outer side of the proximal centrale may contact the ulnare.

The distal centrale resembles the radiale in shape. It touches the radiale proximally by a long transverse, slightly concave edge. The distal edge bears two concave facets for the first and second distal carpals and may join the third distal carpal along its oblique outer edge. Near the junction of the outer edge and the proximal edge the distal centrale narrowly touches the proximal centrale.

The distal centrale appears to resemble that of *Ophiacodon* closely. The proximal centrale is rather unlike the element in *Ophiacodon*, which is elongate proximodistally, with a central constriction between expanded proximal and distal ends. In *Captorhinus* the bone is five-sided, with its transverse edge directed proximally and apex directed distally.

The fourth is the best known of the distal carpals in *Captorhinus*. The bone is pentagonal in dorsal outline. The proximal facets, for articulation with the proximal centrale and ulnare, face obliquely away from each other. The medial and lateral facets extend as parallel sides and connect with the third and fifth distal carpals respectively. The sides meet the transverse distal facet, articulating with the metacarpal of the fourth digit, at right angles. The distal facet sends a broad, truncated flange ventrally, to underlie partially the proximal end of the metacarpal of the third digit.

The fourth distal carpal of *Captorhinus* possesses a

more equilateral pentagonal outline than does that of *Ophiacodon mirus*, pictured by WILLISTON (1925). However, the carpal of *Captorhinus* more closely resembles that of ophiacodonts than sphenacodonts, which, from ROMER & PRICE's (1940, p. 161, fig. 40) illustration, do not appear to be pentagonal in outline.

The first and second distal carpals are much alike in shape, possessing a distal facet that forms a slightly concave distal edge in the dorsal outline of the bone. The other boundaries appear to be uniformly curved, making a single rounded proximal edge in dorsal outline. The first distal carpal is slightly wider than long; the second slightly longer than wide.

The third distal carpal is pentagonal in dorsal outline. The inner side is essentially perpendicular to the distal facet and adjoins the second distal carpal. The outer side, which is very short, seems to join the fourth metacarpal. The proximal surfaces of articulation face obliquely away from each other. The inner of these may be against the distal centrale; the outer touches the fourth distal carpal.

The metacarpal and phalangeal elements that are

known resemble those of contemporary reptiles of similar size as *Captorhinus* in that the proximal and distal ends of the segments are expanded. Each segment is slightly more than half the length of its metacarpal.

WILLISTON (1909) described a distorted manus of *Captorhinus* in which a part of the intermedium and the nature of the proximal centrale were uncertain. CASE (1911a) included a verbatim account of WILLISTON's description and reproduced his illustration of the front foot. The probable phalangeal formula given by WILLISTON is 2,3,3,4(3),2.

The description in the present study is based on an incomplete front foot from the Richard's Spur locality in the collections of the Chicago Museum of Natural History (UC 392). In the specimen only the dorsal surfaces of the component bones are exposed.

From isolated elements taken from the Clarke collection, the features of the ventral surfaces of the radialis, intermedia, ulnaria, and fourth distal centralia have been secured. The foot as a whole in *Labidosaurus* appears broader in relation to its length than that of *Captorhinus*.

PELVIC GIRDLE

In immature individuals, the three centers of ossification of the pelvis are clearly distinguishable: a dorsal ilium, an anteroventral pubis, and a posteroventral ischium. The defining sutures of the ossifications become less distinct with increase in age. In the largest and presumably the oldest individuals the sutures are not visible. The suture between the ilium and pubis is the first to close, and that between the ilium and ischium the last (Fig. 32).

The major portion of the acetabulum is set into the base of the ilium. The depression is broadly but imperfectly ovate, more narrow anteriorly than posteriorly, vaguely screw-shaped and invaded in its posterodorsal corner by a lappet of nonporous bone, the supraacetabular notch. The pubis contributes to the acetabulum only by the width of its dorsal edge. The uppermost extent of the pubis joins the ilium along the anteroventral rim of the acetabulum.

The more posterior parts of the acetabulum are made up of the ilium dorsally and the ischium posteroventrally. The face of the ischial component curves outward and forms a broad, anterodorsally directed buttress in the posteroventral quadrant of the acetabulum. The articular surface of the buttress is slightly swollen and is heavily filled in with bone from behind. The buttress assisted in preventing the femoral head from slipping backward and downward out of the acetabulum.

Below the acetabulum the ischium and pubis expand into an oblique plate, slightly more dorsal laterally than medially, and causing the acetabulum to face laterally.

The pubis is perforated beneath the ventral rim of the acetabulum by a small obturator foramen for the passage of the obturator nerve. Extending from the anterior margin of the foramen, obliquely forward and down, is a ridge that reaches the margin of the pubis.

When viewed in lateral aspect, the dorsal border of the pubis extends horizontally a very short distance forward of the acetabulum. The border of the anterior edge meets

the dorsal border in almost a right angle at the pubic tubercle, and extends medially from this junction. The ventral border of the pubis meets the anterior border in a rounded corner and extends backward from this junction approximately horizontally. The posteroventral corner is rounded. Beyond the corner the free edge enters into the suture between pubis and ischium. The suture continues dorsally to the rim of the acetabulum.

The ischium is slightly longer and narrower than the pubis. In lateral aspect the margin of the ischium posterior to the acetabulum is thick, rounded, concave and extends posteriorly and slightly ventrally to its termination at the ischial tubercle. The posterior border of the free edge is gently convex in its entirety. Ventrally the border is nearly straight, except anteriorly, where it ascends to join with the pubis. The ventral border of the pelvis is therefore notched near its mid-point, where ischium and pubis curve dorsally united in the ischiopubic suture. The ischiopubis is slightly concave in the entirety of its ventrolateral face.

Above the acetabulum the ilium narrows, continues dorsally, and curves slightly caudally as a slender blade. The lateral face of the ilium is shallowly concave. The medial face is flat. Along the length of the blade a series of ridges appear which extend to the distal termination of the bone. The blade widens distally, but becomes thinner, particularly along the distal anterior edge.

The topography of the internal face of the pelvis is dominated by a massive, oblique ridge extending from the medial face of the ilium to the anteroventral expansion of the symphysis. Presumably the ridge supported the sacral articulation of the ilium, reinforced the rear wall of the acetabulum, and strengthened the pubic symphysis. Most importantly, perhaps, the ridge acted as a general structural backbone for the pelvic plate and provided the attachments of the pubo-ischio-femoralis internus muscle.

Immediately in back of the ridge is a large concavity, the posterior limits of which are marked by a low ridge.

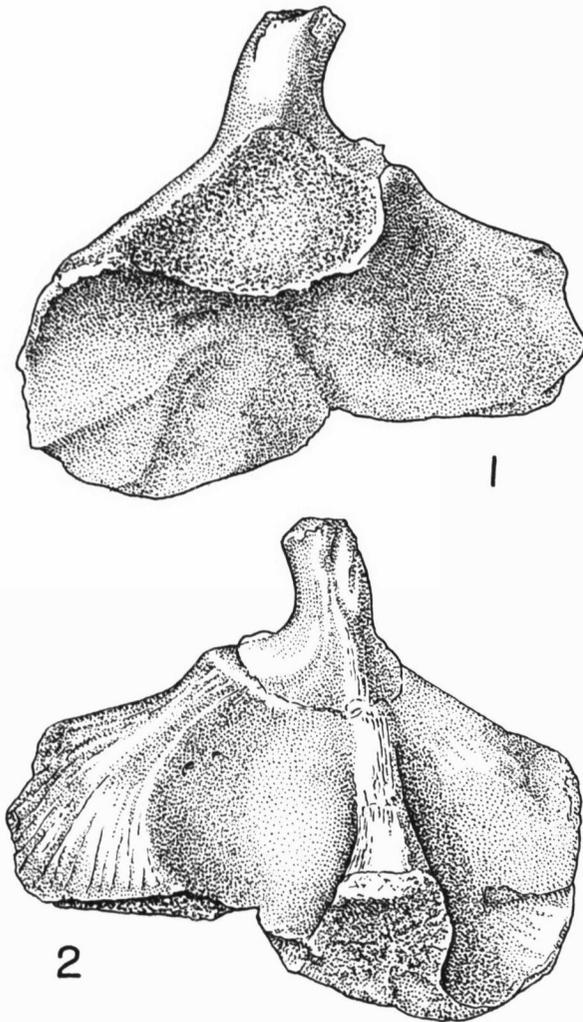


FIGURE 32. *Captorhinus aguti* (COPE). Left pelvis (KU 14748), $\times 4$. — 1. External view. — 2. Internal view.

At the base of the major ridge that crosses the medial face there is an expanded, oblique surface of porous unfinished bone, the symphyseal face. The surface is decidedly anterior of the midpoint of the ventral border of the plate, in keeping with the condition described by ROMER (1956, p. 310-319) among primitive reptiles in which the posterior portions of the pubis provide the major surface of the symphysis. The ventral posterior portions are thickened in *Captorhinus*, but the thickening is only slight. In front of the major ridge the medial surface of the pelvis is nearly flat, and except for the internal opening of the obturator foramen, is undistinguished by noteworthy features.

The rigidity of the pelvic plate is increased by the overlapping of the foot of the ilium on to the ischium and pubis. The surface expression of the suture between the ilium and the two ventral elements is more ventral on the internal surface of the plate than on its external surface.

ROMER (1956) has established a number of characters that are usually found in the primitive anapsid pelvis. Be-

low, in tabular form, these characters are contrasted with their counterparts in the pelvis of *Captorhinus*.

COMPARISON OF PRIMITIVE STRUCTURE OF ANAPSID PELVIS WITH THAT OF CAPTORHINUS

(modified from ROMER, 1956, p. 315-319)

PRIMITIVE ANAPSID	CAPTORHINUS
1. Ilium, pubis and ischium contribute to the acetabulum.	Pubis participates in the rim of the acetabulum, but contributes little to the concavity proper.
2. Oval acetabulum of large size but of no great depth.	Same
3. Greatest diameter of the acetabulum is along an axis running from the pubis backward and slightly upward to the iliopubic surface.	Greatest diameter runs horizontally from the anterior limit of the acetabulum to the peak of the ischial buttress.
4. The acetabulum possesses a distinct rim, although less so posteriorly.	The rim of the acetabulum is distinct, more so posteriorly, because of the buttress of the ischium.
5. Dorsally a primitively overhanging buttress under which the head of the femur thrusts.	Same, although because of the orientation of the plate, this buttress is merely the dorsal rim of the acetabulum.
6. The ilium contracts somewhat to a neck above the acetabulum, and then expands into the iliac blade.	Same
7. The iliac blade extends upward, but to no great height.	The blade is elongate and high.
8. There is little if any forward extension of the blade beyond the level of the acetabulum.	Same; the blade at its base is only slightly posterior to the midpoint of the acetabulum. The base of the blade is its most anterior part.
9. Posteriorly a long tapering extension of the blade terminates in a point.	The blade is entire and continues to taper distally.
10. The pubo-ischiadic plate primitively faced as much or more ventrally as laterally.	The plate faces more ventrally than laterally.
11. The anterior pubic portion of the plate was, in general, notably shorter than that formed by the ischium and faced rather more laterally.	Same in regard to length; both pubis and ischium faced in the same direction.
12. With a thick upper rim of the pubis extending forward, well outward and somewhat downward above this part of the plate.	Not to any extent, although this area is thickened somewhat. The extent of the pubis anterior to the acetabulum is slight.
13. The pubic plate commonly terminated anteriorly in a blunt tip (of cartilage) with an unfinished surface.	Same
14. Below this point the anterior margin of the pubis descended abruptly to the symphysis.	Same
15. The upper ischiadic rim was thinner than that of the pubis and generally somewhat curved.	Same

16. Primitively the ventral margin of the plate formed nearly a straight line. The pubis descends more ventrally than does the ischium; both are curved at the ends, and are straight in mid-portion. The ventral margin is marked by a notch at the ischio-pubic suture, which may have been filled by cartilage.
17. The pelvic symphysis extended the entire length of the pelvic plate. Same
18. The symphysis was strongest and thickest near the posterior end of the pubis. The pubic portion of the symphysis appears to have been a quite solid union of the two sides. . . . The more posterior, ischiadic, area of the symphysis is thinner, or, if of some depth, shows a series of striae, indicating a relatively loose, ligamentous union. Same, thin with no striae.

The above comparisons show that *Captorhinus* has departed little from the primitive architecture of the pelvis. What modifications have occurred are largely limited to the acetabulum and the iliac blade. The exclusion of the pubis from the acetabulum may have yielded greater rigidity to the articular surface in immature animals, before the sutures had fused, and may have been selectively advantageous on that account.

In the specimens available to us the region of articulation of the inner surface of the iliac blade and the sacral ribs is indicated by a slight depression, elongated in the direction of the long axis of the iliac blade. The depression is usually restricted to the part of the blade that is expanded, distad of the neck, although the depression extends onto the neck in some individuals. At its distal limits, the depressed surface bears a series of striae paralleling the long axis of the blade. The presence of the striae may indicate ligamentous support for the sacral joint. The striated surface seems not to be included in the contact between the pelvis and the sacral ribs, however.

There can be little doubt that the sacral joint was weak in *Captorhinus*. The inner surface of the iliac blade is unmarked but for the depression and striae alluded to above, which are dorsal to the sacral attachment. Heavy rugosities or porous unfinished bone that would point singly or in combination to a firm joint are lacking. In contrast, the pelvic symphysis gives every indication of strength of union and being welded into a single unit of bony architecture. It may well have been that the pelvis as a whole was capable of a limited amount of rocking movement around the sacral articulation.

Following ROMER (1922) an estimate of the areas of attachment of muscles to the pelvis can be made with reasonable certainty. The major part of the external surface of the iliac blade acted as the origin for the ilio-femoralis muscle. The mass arose from the plate-like surface of the blade; the ridge extending along the blade's posterior border served as the origin for the ilio-fibularis. The anterior border of the iliac blade anchored the ilio-pubic ligament, which extended from the junction of the dorsal and anterior borders of the blade to the pubic tu-

bercle. The dorsal border of the ilium anchored both the longissimus dorsi and the ilio-costalis. A ligament of the ilio-femoralis externus attached to the base of the iliac blade, above the acetabulum. The lateral caudal extensor originated at the posterodorsal corner of the ilium.

The ambiens and ilio-tibialis arose from a slightly raised scar immediately in front of the acetabulum.

The broad ischio-pubic plate beneath the acetabulum was the area of origin for the pubo-ischio-femoralis externus, the major femoral adductor. The medial limits of at least the anterior part of the origin are presumably marked by the strong ridge extending to the anterior border of the pubis from the obturator foramen. Medial to the border was the region from which the various lessor flexors originated; the absence of scars in this region prohibits the more precise delineation of the origins of these muscles that might be desired.

The ilial-ischial ligament extended between the posterior border of the iliac blade and the tubercle of the ischium.

The broad plate of the pubis that faces anteriorly was the origin of the fleshy pubo-ischio-femoralis internus. The muscle sent a ligament to the base of the lateral surface of the iliac blade. The posterior limits of the origin of the fleshy muscle are demarcated by the robust ridge extending across the medial face of the pubis from the base of the iliac blade to the symphysis. The deep concavities behind this ridge are largely free of muscle attachments; however, the posterior part of the concavities was the site of attachment for the ischio-trochanteris. Above this, along the posterior border of the ischium and ilium, the deep portion of the ilio-caudalis attached.

The anterior ventral musculature in the main probably attached, as in modern lizards, to the ilio-pubic ligament, although the rectus may have passed over the ligament to insert on the ischiadic symphysis. The ischiadic tubercle is thought to have served as the origin for the ischio-caudal muscle, the main component of the posterior ventral musculature in Permian forms (ROMER, 1922, p. 561).

The iliac blade of *Hylonomus*, as pictured by CARROLL (1964, p. 72, fig. 8; p. 73, fig. 9) resembles that of *Captorhinus* in shape; in its possession of a smooth external surface, except for a few ventral grooves; in the attachment of the sacral rib at the base of the blade; and in the absence of the dorsal groove, present in primitive pelycosaurs and *Limnoscelis* (ROMER, 1946, p. 180, fig. 10) for the axial musculature. Unfortunately, the ilia of *Eosaurus* (PEABODY, 1959) and *Cephalerpeton* (GREGORY, 1948) are unknown, and the ilia of the Texas romeriids, if known, still await description. The gaps between *Hylonomus* and *Captorhinus* do not allow any positive statement regarding the inversion of the iliac blade in the romeriid-captorhinid sequence. However, the apparent similarities in the iliac blade in *Hylonomus* and *Captorhinus* suggest that either the blade did not invert in this phylum or that the inversion was already completed at the appearance of *Hylonomus*. If the former alternative applies, the groove shown in the ilium of *Limnoscelis* may represent a terminal event rather than a step in the rebuilding of the iliac suggested by ROMER (1956, p. 317). The latter alternative, that the blade is already inverted in

Hylonomus, seems unlikely both because of the earliness of *Hylonomus* and the absence of the dorsal groove in the ilium of the contemporary primitive pelycosaur, *Protoclepsydrops* (CARROLL, 1964, p. 82). Seemingly, none of the eosuchians display a dorsal trough on the ilium, im-

plying, in the absence of inversion in the romeriid-captorhinid line, that the iliac blade in lizards has not been rebuilt, but retains the primitive relationship to the axial musculature, if indeed the eosuchian-lizard phylum can be related to captorhinomorphs.

POSTERIOR LIMB

The posterior limb, like the anterior, was held in the primitive sprawling position, with the femur extending in a near horizontal plane from the body, and the tibia and fibula nearly vertical to the femur. The fit of the femur into the acetabulum in an articulated individual from the Clarke collection suggests that the distal end of the femur may have been held slightly higher than the proximal head. Such an orientation would agree with the position of the femur in other primitive reptiles (e.g., PEABODY, 1952, p. 34, fig. 11 for *Petrolacosaurus*; VAUGHN, 1955, p. 397, fig. 15 for *Araeoscelis*) of comparable body size, and in Recent lizards, such as *Sceloporus* (personal observation).

The femur of the articulated individual from the Clarke collection is 50 mm. in length; the tibial length is 27 mm., roughly 50 percent of the length of the femur, indicating a relatively short epipodial. The humero-femoral ratio in this individual is 90/100, a difference usual among primitive reptiles generally (ROMER, 1956, p. 346).

FEMUR

The features of the femur (Fig. 33) are dominated by expanded proximal and distal ends tapering towards one another and joining in a comparative slender and straight shaft. Roughly one third of the length of the bone is devoted to the shaft and one third to each of the expanded ends.

The expansion of the proximal end is primarily due to the width of the articular head and the development of the internal trochanter. In end view these are set at approximately right angles to each other, with the trochanter arising as an extremely short, broad, thumblike projection from the anteroventral base of the articular head. The articular head and the internal trochanter thus partially face one another ventrally, forming a trough for the intertrochanteric fossa.

The distal expansion, normally rotated about 45 degrees from the plane of the articular head, is flat dorsally, but its surface is bifurcated by a deep intercondylar fossa separating the anterior and posterior condyles. These are dissimilar in shape; the anterior condyle is broad and flat and tapers to a narrow but rounded anterior edge; the posterior condyle, the longer of the two, is narrow laterally and deep dorsoventrally.

In articulation the long, narrow and gently convex articular surface was thrust into the acetabulum in an essentially horizontal plane. The articular surface is most broad at its anterior end and gradually tapers posteriorly to form a gentle crescent of porous bone. A lappet of this surface extends toward the internal trochanter but generally fails to meet its base. Consequently, the crotch between the base of the trochanter and the articular head is often

sharply ridged, and of finished, non-porous bone. The lappet is of variable shape; most commonly it is a rather bulbous expansion extending from the major articular surface, separated from it by a constricted neck. In other individuals this isthmus is absent, and the width of the lappet is constant throughout its length. A second but smaller tongue commonly extends from the articular crescent a short distance on to the dorsal surface.

The smooth contours of the dorsal surface of the articular head are uninterrupted except for a posterior swelling at a level opposite that of the internal trochanter. A tendon for the pubo-ischio-femoralis internus muscle attached here, with the fleshy insertion of the muscle spreading out over the neighboring surface. The limits of the attachment are usually determinable in all but the smallest (and presumably the youngest) specimens. The insertion extended as a band across the dorsal surface of the articular head, but the width of the band is quite variable among the specimens examined. In some, its distal limits are beyond the attachment of the tendon; in others they don't exceed it. The band pinches out anteriorly and curves toward the articular surface.

The insertion of the ilio-femoralis here bordered that of the pubo-ischio-femoralis internus and inserted on the femur along its posterior border leaving a small scar between the insertion of the tendon of the pubo-ischio-femoralis internus and the tapered posterior limit of the articular surface. Distally the insertion broadened and spread out on to the ventral surface of the shaft, up to the adductor ridge.

The only other noteworthy feature of the antero-dorsal proximal surface concerns the internal trochanter and its origin. As noted above the internal trochanter is placed at right angles to the articular head. The forward edge of the articular head is thickened and falls sharply away from the dorsal surface. The trochanter is a ventral continuation of this edge, directed down and towards the midline. It is broad, flat, blunt and short, standing as an abbreviated thumb in relationship to the remainder of the bone. Among larger individuals the trochanter is directed less medially than ventrally, as the proportional depth of the crotch apparently decreases with increase in the size of the femur. The tip of the trochanter is capped by a broad scar that stands as evidence for the attachment of the pubo-ischio-femoralis externus. This muscle also was inserted on the inner surface of the trochanter and on the adjoining bowl-shaped intertrochanteric fossa.

The features of the ventral face of the proximal expansion complement those of the dorsal face, although the mirror replication is not exact. The convexity of the dorsal surface in both antero-posterior and proximodistal axes is reflected in the concavity of the ventral surface beneath, which lies along the same imaginary lines. Similarly, the

dorsal interruption for the attachment of the posterior tendon of the pubo-ischio-femoralis internus lies directly

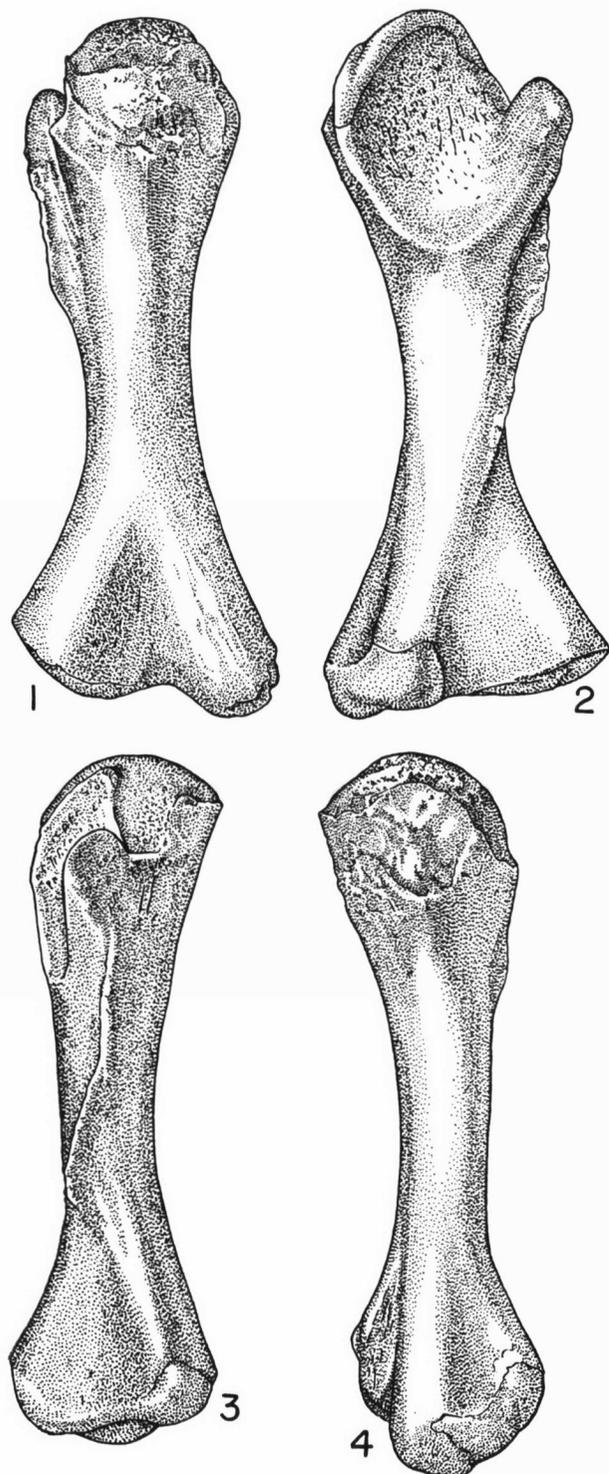


FIGURE 33. *Captorhinus aguti* (COPE). Left femur (KU 14747), $\times 3$. —1. Dorsal view. —2. Ventral view. —3. Anterior view. —4. Posterior view.

above the deepest part of the intertrochanteric fossa, and is recognizable as a discrete posterior depression. Less exactly, but still in keeping with the above, the genesis of the slope from the shaft to the summit of the proximal expansion occurs at about the level of the change in slope of the corresponding ventral surface leading into the intertrochanteric fossa. The general effect of these features is to turn the proximal end of the femur up in relation to the shaft, inclining the ventral surface more in apposition to the surface of the pelvis, for the reception of the pubo-ischio-femoralis externus. The dorsal surface is also raised, but in relation to the shaft only and not appreciably to the surface of articulation. The surface remains low in relation to the articulation with the pelvis, so that efficiency in raising and advancing the femur with contraction of the pubo-ischio-femoralis internus is retained.

The proximal and distal expansions of the femur taper gently toward one another and meet in the narrow shaft between. The shaft is a distinct topographical region between the expanded proximal and distal ends and recognizable on that basis as well as functionally. Dorsally the shaft is essentially featureless, even in the most mature of the specimens examined. No ridges or grooves cross it; neither do muscle scars nor fossa interrupt its smoothly moulded contours.

The ventral surface of the shaft is rather different. Bordering the intertrochanteric fossa distally is the ridge for the attachment of the ilio-femoralis. This scar extends in a shallow arc from the base of the internal trochanter to the posterior border of the femur as a subtle rise concentric with the heel of the intertrochanteric fossa and actually forming the distal boundary of the fossa. The ridge is slightly more conspicuous at its posterior end than it is anteriorly.

A more conspicuous feature of the ventral surface is the fourth trochanter. This appears as a thin flange extending from the base of the internal trochanter to the proximal limit of the adductor ridge. Its summit is roughened, elevated and occasionally expanded laterally as a narrow platform capping the ridge, the point for the insertion of the coccygeo-femoralis tendon, extending from the tail, beneath the ilio-femoralis, and to the femur (ROMER, 1922, p. 572). The trochanter protrudes ventrally, down and away from the ventral surface of the shaft, carrying the coccygeo-femoralis away from the ilio-femoralis crossing beneath.

Distally the fourth trochanter decreases in height and curves posteriorly, obliquely across the ventral surface of the shaft. Its extent in this direction is not at all great; by the midpoint of the shaft width the trochanter has become confluent with the adductor ridge and the latter has turned distally. The adductor ridge increases in height and continues along the mid-line of the shaft until it reaches the proximal limit of the popliteal fossa. It then turns for a short distance along the posterior rim of the popliteal fossa, becomes progressively lower, and disappears into the base of the posterior condyle. The adductor ridge separated the femoral adductors and femoro-tibialis on the posterodorsal surface, and presumably was also used for the attachment of these muscle masses.

The ventral ridge system is therefore the only conspicuous landmark in the whole of the femoral shaft. It

dominates the shaft ventrally; its development implies a disposition of relatively powerful muscle groups attaching to it.

The first appearance of the progressive increase in the width of the shaft that marks the beginning of the distal expansion is nearly coincident with the proximal limit of the ventral popliteal fossa. However, the depression of the ventral surface that forms the fossa falls entirely within the distal expansion and does not encroach upon the shaft proper. The shaft, then, is discrete from the distal expansion; the only landmark that overlaps from one region to the other is the ventral adductor ridge.

In viewing the distal expansion from either above or below, one is struck by its triangularity. But the resemblance to a triangle is not exact; the apex is buried in the shaft; the anterior edge is abruptly concave; the posterior edge leaves the shaft at a more gentle angle, is only mildly concave, and distally becomes the rounded external edge of the posterior condyle; and the base in outline consists of two unequal convexities (the condyles) separated by a wide groove (the intercondylar fossa). The posterior condyle is long, relatively narrow and deep dorsoventrally. The anterior condyle is the obverse in these regards: comparatively thin, flat and broad. The interrupting intercondylar fossa extends from the dorsal surface to the distal face, fading into the ridge that rims the popliteal fossa distally. Its broad dimensions accentuate the distinctiveness of the condyles from one another.

When the femoral head is placed in the acetabulum, the dorsal surface of the distal expansion faces both anteriorly and dorsally. The displacement of this surface from the horizontal is further emphasized by the leading edge of the anterior condyle that is beveled, much in the manner of the cutting edge of a chisel, in relationship to the dorsal surface. Thus, in end view the dorsal surface is oriented obliquely, slanting down and forward from the high posterior condyle, across the intercondylar fossa and on to the flat dorsal surface of the anterior condyle. The leading edge of the condyle falls abruptly away from this surface.

The opposite border in end view, that of the ventral surface, is asymmetrically concave. In outline it parallels anteriorly the dorsal outline of the anterior condyle in its gradual ascent, but curves away from the dorsal surface, abruptly downward, posteriorly along the posterior condyle. The anterior and posterior condyles, being at opposite ends of this crescent and descending ventrally at these ends, are the major points of articulation for the tibia.

The expansion of the distal end provides a broad table for the attachment of muscles and ligaments running to the lower leg. The medial ligament leaves the anterior condyle from a roughened eminence on the dorsal surface bordering the back of the beveled leading edge of the condyle. The posterior condyle, in turn, is the origin for the peroneus longus, an extensor running to the foot, and for the extensor communis digitorum, attaching to the toes. Ventrally the gastrocnemius arises from the popliteal fossa.

With the close relationship of *Captorhinus* to *Labidosaurus* one would expect that the femur of the latter genus would resemble that of *Captorhinus* closely. And so it does, although differences do exist.

The first of these differences is in size. CASE (1911a, p. 111) reports that a femur of *Labidosaurus* (AMNH 4883) measures 70 mm. in length and 35 mm. in distal width. SELTIN (1959, p. 504, table 8) lists an unnumbered femur of *L. hamatus* as 81 mm. in length, 26 mm. in proximal width and 37 mm. in distal width. Among 26 femora of *Captorhinus* measured by SELTIN the mean total length is 24.5 mm., with extremes of 32.0 mm. and 16.6 mm. The proximal widths of these average 6.0 mm. (4.0 mm.-9.1 mm.), the distal widths of 25 of the 26, 7.8 mm. (5.3 mm.-10.7 mm.). CASE (1911a) includes no measurements of the femur of *Captorhinus*. The femora measured for the present study averaged 27.3 mm.

Other features besides size are different. In the figure of a femur of *Labidosaurus* (AMNH 4883), (CASE, 1911a, p. 109, fig. 48c), there is a greater coarseness of the proximal and distal expansions of the internal and fourth trochanters and of the ventral system of ridges than in *Captorhinus*. The trochanters appear disproportionately large in comparison to *Captorhinus* and reflect the more powerful musculature necessary to propel the body of *Labidosaurus* forward as the femur is pulled backward.

The diagrammatic illustration of ROMER (1956, p. 363, fig. 171C) emphasizes even more the massiveness of the femur of *Labidosaurus*. Here the shaft is broad in relation to the distal and proximal ends and the landmarks associated with the ends are equally heavy.

The illustration of the femur of *Labidosaurus* in ROMER (1922, pl. 46), identified as ?*Labidosaurus*, resembles *Captorhinus* rather more closely than *Labidosaurus*, in that its slenderness is usually not found in the latter genus. It bears little resemblance to ROMER's 1956 presentation.

The information regarding the femora of other captorhinids is sketchy. SELTIN (1959, p. 504, table 8) reports the dimensions of an unnumbered femur of *Rothia* as 116.0 mm. in total length, 37.5 mm. in distal width. OLSON (1962a, p. 17, table 3) reports the length of a femur of *Rothia* (CNHM UR 263) as 106 mm.

The right femur is preserved but is strongly compressed dorsoventrally. The intertrochanteric fossa was deep and the ridge anterior to the fossa was strong and carried a well-developed internal trochanter. The fourth trochanter was located at the dorso-anterior margin of the fossa and the adductor ridge carried well down onto the shaft. The distal condyles were well expressed. The femur appears to have been very lightly built and extremely small as compared with the skull and axial skeleton (OLSON, 1962a, p. 20).

Of *Kahneria* only two partial femora are known. "The general morphology is typically captorhinid. The femora are very poorly preserved and show only that the element was small in proportion to the size of the animal as suggested by the skull and axial structures" (OLSON, 1962a, p. 17). No illustrations of the specimen are produced in the paper.

KONZHUKOVA (1953) reports on the presence of an Early Permian labidosaurian captorhinomorph in the Cis-Uralian region of the Soviet Union, but this publication has not been examined and the completeness of the material, which is described by OLSON (1962a, p. 160) as "scrappy and small" is not known to us.

The femur of *Captorhinoides* is unknown (OLSON, 1951, p. 97-104; SELTIN, 1959, p. 489-490), as is the femur of *Captorhinikos valensis* (OLSON, 1954b, p. 215-216). The

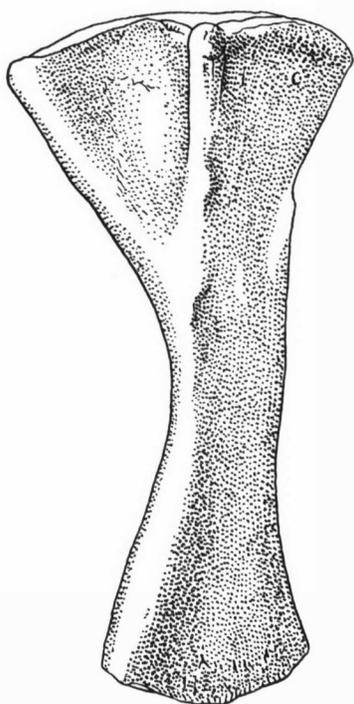


FIGURE 34. *Captorhinus aguti* (COPE). Right tibia, external view, uncatalogued specimen, Clarke collection, $\times 8$.

femur of *Captorhinkos chozaensis* is known (included in CNHM UR 99), but we are unaware of its description and illustration, if such has been published.

Knowledge of the femur of *Labidosaurikos barkeri* rests upon OLSON's original description. The head of a right femur is included in the materials of the type (CNHM 110) (OLSON, 1954b, p. 212, fig. 85B). The illustration suggests that the internal trochanter and the articular head were joined in a continuous articular surface so that the trochanter did not have an existence separate from that of the head. This condition differs from that in both *Captorhinus* and *Labidosaurus*. SELTIN (1959) has synonymized *Labidosaurikos barkeri* with *L. meachami*. The latter, originally described by STOVALL, contains no postcranial material (SELTIN, 1959, p. 495).

The femur of *Captorhinus* is similar to that of the primitive *Petrolacosaurus kansensis*, as PEABODY (1952, p. 29) has already pointed out, and his illustration of the type (KU 1424) supports his textual thesis. However, examination of two crushed femora (KU 9951), one exposed dorsally and one ventrally, suggest that in *Petrolacosaurus* the posterior condyle is considerably longer than the anterior condyle, the shaft occupies more than approximately one third the length of the bone, and proximal and distal expansions are relatively narrow. The summation of these characters point to a slender femur, similar perhaps to those of young individuals of *Captorhinus*, but bearing no especial resemblance to individuals in maturity other than that which might be expected because of the respective primitiveness of the two genera. Additionally, and as shown by PEABODY, the internal trochanter is not a thumblike projection from the articular head, but is rather

a rounded flange. This quality of the trochanter is also present in KU 9951.

The femora of *Cardiocephalus*, a gymnarthrid micro-saur common in the Richard's Spur deposits, and *Captorhinus* were compared by GREGORY, PEABODY & PRICE (1956, p. 59).

Cardiocephalus femora differ from those of the associated *Captorhinus* (fig. 29) in greater slenderness and more delicate build, smaller size, and less expansion of the distal end. The adductor ridge is straight and extends far distally whereas in *Captorhinus* it is irregular, terminates well above the distal end, and may have some development of a fourth trochanter for the caudifemoralis muscle.

TIBIA AND FIBULA

The tibia (Fig. 34) of *Captorhinus* is a stout element, the proximal and distal ends of which are expanded in width to a degree that, in comparison to the slim mid-section, is reminiscent of the shape of an hourglass. The proximal end is the more massive of the two; its outer surface is incised by a deep groove. The groove is bordered

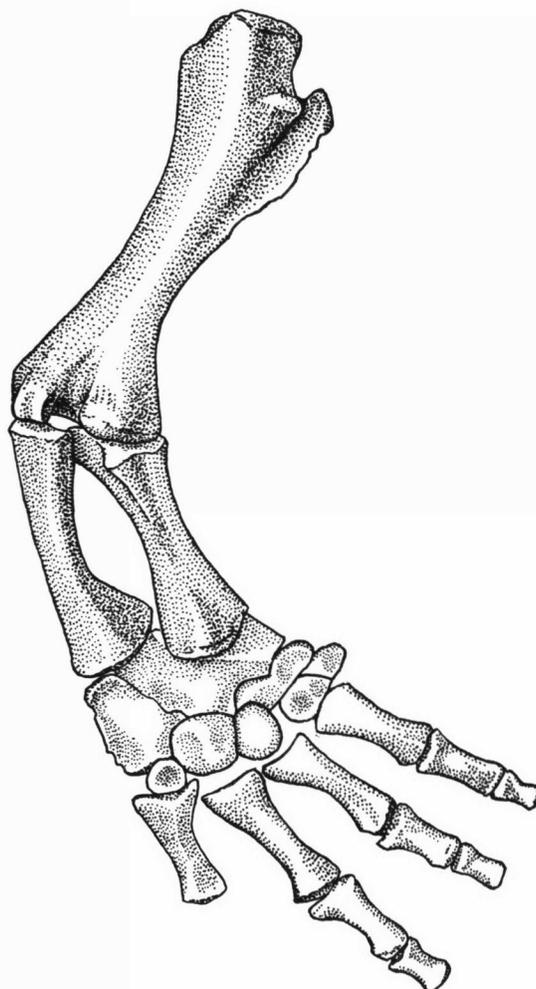


FIGURE 35. *Captorhinus aguti* (COPE). Mounted right posterior limb and incomplete foot, uncatalogued specimen, Clarke collection, about $\times 2.5$.

anteriorly by a prominent cnemial crest to which the *triceps femoris* attached. The head of the tibia is partially divided into two articular surfaces that contact the femoral condyles. The distal end of the shaft is turned forward slightly in the primitive fashion. The shaft is bowed away from the fibula; at its waist it is subcircular in the outline of its cross section.

The fibula (Fig. 35) is compressed dorsoventrally, causing its extensor and flexor surfaces to be flat. It bows outward away from the tibia to such a degree that its inner edge is distinctly concave and its outer edge convex. Both proximal and distal ends are expanded, but unlike the tibia, the distal end of the fibula is the broader of the two. The distal end is turned forward in relation to the head. The proximal surface of articulation is a uniformly gentle convexity; the distal surface is angled sharply to enable the bone to articulate with both astragalus and calcaneum.

PES

The pes (Fig. 35) of *Captorhinus* is well known, particularly from the work of PEABODY (1951). A well-formed astragalus and calcaneum dominate the pes, articulating by means of broad facets with the tibia and fibula. Distally the astragalus abuts against a dumbbell-shaped navicular and the fourth distal tarsale. The distal articulations of the calcaneum are with the fourth and fifth distal tarsalia. The navicular is in contact with the first, second and third distal tarsalia.

Reassembly of a complete pes from the Richard's Spur locality reveals that the tarsal elements articulated with each other in such a manner that the tarsus in life was gently bowed downward toward the ground surface. The major joint was the articulation of the tibia and fibula with the tarsus. The calcaneal and particularly the astragalar facets are broad here. No specific mesotarsal joint was developed; movement of the tarsal elements upon one another was primarily a uniform bending through the tarsus in which no elements or combination of elements predominated. A second major joint was between the tarsals and metatarsals. The metatarsal facets of the distal tarsalia are broad, as are the adjoining surfaces of articulation of the metatarsals. Both are somewhat convex dorsoventrally, permitting a rather free rocking movement of the tarsus upon the metatarsals.

Metatarsals and phalanges articulate with one another in such a manner that they bow gently upward; the digits did not lie flat upon the substrate, but were weakly flexed. Both metatarsal and phalangeal elements are flattened. Each digit terminates in a laterally compressed claw.

One is impressed by two aspects of the pes of *Captor-*

hinus. The first is the emphasis on width that the pes exhibits. The tarsus is wide (although not as wide proportionally as that of *Labidosaurus*, e.g., PEABODY, 1951, p. 343), the digits are flattened and decidedly spread when in articulation with the distal tarsalia. Secondly, the pes exhibits a gently sigmoid curve in articulation; the tarsus bends downward, the digits upward, giving the whole structure an impression of springiness and resiliency that seems to belie the usual picture of a shuffling gait that is supposed to be characteristic of such primitive tetrapods as *Captorhinus*. This is not to imply that *Captorhinus* was a fleet pursuer of its prey, but the structure of the pes does not suggest slow, laborious movement, performed with little efficiency and comparatively great effort.

SCHAEFFER (1941) and PEABODY (1951, 1959) have amply discussed the evolution of the tarsus among primitive reptiles; nothing additional to their conclusions has been revealed by the present study, except to emphasize the primitiveness among reptiles of the *Captorhinus*-like tripartite astragalus. As PEABODY (1959) has reported, the structure occurs in the early and primitive *Eosauravus* and CARROLL (1964) noted the occurrence of an astragalus in the earlier *Hylonomus lyelli*. Both of these primitive kinds of reptiles antedate the known occurrence of the seymouriamorphs and the primitive *Limnoscelis*. In these latter genera the intermedium, tibiale, and fourth centrale are separate and unfused. Of the primitive nature among reptiles of the tarsus of *Eosauravus* there can be no doubt, since it possesses separate median and lateral centralia and the postminimus. PEABODY (1959: 11) states: "Only early pelycosaurians have separate centralia—they are fused in *Captorhinus* and *Limnoscelis*. No reptiles presently known have a postminimus."

SCHAEFFER (1941, p. 430) believed that in *Labidosaurus*

there is no indication, however, that the ankle joint was crurotarsal . . . as in the pelycosaurians. The tibial facet being essentially a plane surface, although directed dorsomedially as well as proximally, it allowed very little movement between the tibia and astragalus. Hence there is reason to believe that the functional ankle-joint was still in its old location between the tarsalia and the metatarsals.

In *Captorhinus* the tibial facet of the astragalus certainly suggests a major joint. The facet is convex, providing a rounded surface for articulation of the tibia. The astragalar and calcaneal facets for the fibula, although by no means as extensive as the tibial facet, also permit free bending of the tarsus on the fibula. There can be no doubt of a moveable crurotarsal joint in *Captorhinus*, as VAUGHN (1955, p. 423) surmised from the illustration of PEABODY (1951).

AXIAL SKELETON

VERTEBRAE

The vertebral structure in *Captorhinus* is that commonly possessed by primitive reptiles; the centra are amphicoelous and notochordal, and the neural arches are swollen and appear massive in relation to the centra beneath.

The differentiation of the column into broad vertebral

regions is most profitably viewed as being three-fold: presacral, sacral, and postsacral or caudal. In *Captorhinus* it does not appear to be particularly useful to discriminate subregions of the presacral series. "Cervicals" and "dorsals" grade insensibly into one another without a sharp break; the usage of "dorsals" here is equivalent to "presacrals."

In number the vertebrae seem to fall well within the limits usual among cotylosaurs, but in so far as is known, the exact number of presacral and postsacral vertebrae has yet to be determined for *Captorhinus*. Two specimens are present in existing museum collections that bear directly on this problem. The first and most important of these is a skull and incomplete postcranial skeleton of *Captorhinus* in the possession of the American Museum of Natural History (AMNH 4332). The initial count of the vertebrae of this specimen indicated that there are 22 visible vertebrae between the skull and the first of the sacra. However, preservation in the anterior part of the column is poor; later inspection suggested that an additional vertebra is present, raising the partial presacral count to 23. This number, added to the atlas and axis, which are not preserved (in AMNH 4332) indicates a total of 25 presacrals, the sum adhered to in the reconstruction presented in this paper.

The second significant specimen belongs to the Chicago Museum of Natural History (CMNH 4421). This is a composite specimen from the Richard's Spur, Oklahoma locality. The count taken from this specimen numbers 23 presacrals plus a plaster-filled break between the 22nd and 23rd vertebrae. The relative certainty of the count in AMNH 4332 (24 or 25) suggests that the composite Chicago specimen lacks at least one of the presacral series.

In contrast to the number of presacral vertebrae no doubt arises as to the number of vertebrae involved in the sacral connection. Both AMNH 4332 and CMNH 4421 clearly show that two vertebrae make up the sacral joint. This number has been reported previously by CASE (1911a, p. 98, fig. 43c).

The number of caudal vertebrae is uncertain. CMNH 4421 possesses 22 caudal vertebrae, which is probably too few. ROMER (1956, p. 268-269) reports that *Seymouria* possessed about 40 caudals, but that other seymouriamorphs may well have had a higher number. The tail of *Limnoscelis* has from 50 to 60 segments, and that of *Labidosaurus* around 40 (our observation). All of these primitive reptiles are larger in body size than *Captorhinus*, and the long stout tail characteristic of them may well be correlated, as ROMER (1956, p. 267) has suggested, with the development of powerful caudifemoralis muscles. *Captorhinus* has been restored for this study with 36 caudals, a number that is not thought to be exact, but one which is in keeping with the order of magnitude of the number of caudal segments in closely related captorhinomorphs and in other primitive reptiles that are essentially unrelated to *Captorhinus*.

In morphology the presacral series exhibits a gradual and continuous change from front to back along the column. The anteriormost of the series are characterized by short centra, short, wide, upright neural arches, and a limited projection of the postzygapophyses beyond the posterior faces of the centra. Progression posteriorly yields an increase in length of the centra and neural arches, an increase in the posterior projection of the postzygapophyses, and a decrease in the width of the neural arches. The leading edges of the neural arches become more oblique as the arches increase in length.

The initial dorsals possess prominent transverse processes that extend relatively far out from the centra and

that are oriented nearly vertically. At about the 14th dorsal the processes extend but slightly beyond the sides of the centra; in the five or six vertebrae immediately preceding the sacrum, the processes are oblique linear scars, retaining little or no lateral projection. Accompanying these changes is one in height of the processes. In the first dorsals the transverse processes arise from the wall of the neural arches. At about the fifth or sixth dorsal, the processes become higher so that they arise both from the walls of the neural arches and the uppermost parts of the sides of the centra beneath. From about the fifth or sixth dorsal to the 18th or 19th there is little change in this feature except for a slightly greater extent of the processes down on sides of the centra. At the 18th or 19th dorsal the processes descend abruptly, leaving the neural arch entirely and being limited to small scars at the junctions of the sides and the anterior faces of the centra.

Presumably the progressive lengthening of the neural arches goes hand in hand with the increase in length of the centra, permitting the continuation of close zygapophyseal contact throughout the column. Less obvious in meaning is a change in the surface topography of the centra. The sides of the anterior centra are excavated, leaving a central keel ventrally. The fifth or sixth dorsal lacks this feature as do all posterior to it. The significance for this is not readily apparent, other than the possibility that the feature is correlated with the greater differentiation of the subvertebral musculature in the anterior part of the column.

All of the presacral series are characterized by slightly divergent pre- and postzygapophyses, which are also tilted moderately toward the mid-line. The dorsal surfaces of the prezygapophyses are concave; the apposing postzygapophyseal surfaces are convex.

Each segment of the presacral series possesses a neural spine. The dorsal extent of the spines is indeterminable; all have been broken off near their bases in the many specimens examined in this study. The base tapers into the spine gradually from the dorsal surface of the neural arch; the spine does not arise abruptly.

In the region of the sacrum there is a departure from the anteroposterior trend hitherto seen in the attachment of the ribs to the centra. The last of the presacral series bears a stout rib on either side that extends laterally from a broad, round base. This rib does not touch the pelvis. The first of the sacral ribs arises from an even more broad base on the entire lateral face of the centrum and the side of the neural arch. It is compressed laterally, and is not at all rounded like the rib of the adjacent anterior vertebra. The first sacral rib narrows into a comparatively slender neck, which in turn extends horizontally to adjoin the pelvis in a distal expansion that is spatulate in outline and distinctly concave dorsally. The rib is secured to the pelvis at the base of the iliac blade by ligaments.

The second sacral rib arises from the side of the centrum in the same manner as does the last of the presacrals. The rib narrows to a slender neck midway in its length, although the comparative narrowness here is not nearly so great in relation to the expanded proximal and distal ends of the rib as in the first sacral rib. The second sacral rib turns forward to abut distally against the posteroventral edge of the first sacral rib and, behind this, against the



FIGURE 36. *Captorhinus aguti* (COPE). Lateral view of axis-atlas complex, uncatalogued specimen, Clarke collection, $\times 6$.

pelvis at the base of the iliac blade. In lieu of any marks suggesting a bony articulation, ligaments presumably connected the end of the second sacral rib to the inner face of the pelvic plate.

The neural spines of the sacral vertebrae are somewhat more compressed from side to side than those of the presacral series. It seems also that the spines are slightly higher here than anteriorly, although this cannot be stated with any degree of certainty because these, too, have always been broken in the specimens examined. However, it is true that the remnant of the spines is usually somewhat higher than in the presacral series.

A more accurate appraisal can be made of the neural arches of the sacral vertebrae. These narrow conspicuously in transverse interzygapophyseal width from the last of the presacrals to the first of the caudals. The change is greatest between the last sacral and first caudal.

The initial caudal vertebrae are narrow from side to side and bear high neural spines that become increasingly shorter and more obliquely oriented toward the termination of the tail. The last of the caudal segments are little more than centra, as the neural arches are very small.

The first four or five caudals bear ribs that are fused to the centra and extend for a short distance laterally from the centra. These curve distally to extend parallel to the tail. The entire rib is oriented in the horizontal plane, and the distal part of each is compressed dorsoventrally. None of the caudals posterior to these initial segments bear ribs, and it is only the segments posterior to these that are associated with intercentra that bear haemal arches.

CASE (1911a) reports that AMNH 4424 has 25 presacrals. A break between the 20th and the 21st is present

and part of the anterior part of the 21st is lost. WILLISTON'S (1909) count of 23 or 24 in UC 642 is uncertain because the anterior dorsals are obscured by the skull and a break occurs near the sacrum (CASE, 1911a). WILLISTON estimated that *Captorhinus* had 25 caudal vertebrae, but this seems too few in view of the 40 or so in *Labidosaurus*.

ATLAS-AXIS COMPLEX

(Fig. 36)

PEABODY (1952, p. 32, fig. 10A) briefly described the atlantal arch and illustrated both it and what he believed to be the atlantal centrum.

The latter body is a subtriangular disc, with the apex directed ventrally. The bone is pierced centrally by the notochordal canal, and possesses a posterolaterally directed tubercle on either side adjacent to the centrum of the axis and relatively far from the known articulation of the atlantal rib at the foot of the atlantal arch. The tubercles assisted in the support of the rib of the axis and suggest that what PEABODY thought was the atlantal centrum is actually this bone fused to the intercentrum of the axis. Seemingly no suture marks the line of fusion between the atlantal centrum and the axial intercentrum such as appears in *Ophiacodon retroversus* (ROMER & PRICE, 1940, p. 224, fig. 44), for example, but the region of the bone from the tubercles to the ventral keel resembles that of an intercentrum in that the articular faces are beveled to form a wedge-shaped profile. The fusion of atlantal centrum and axial intercentrum is further indicated by the absence of a gap between the atlantal body and the axis for the reception of an independent intercentrum of the axis.

The atlantal arch in *Captorhinus*, as PEABODY has noted, possesses a short neural plate, and relatively large foot process separated from the neural plate by a constricted neck. The atlantal rib articulates with a lateroventral tubercle on the ventrolateral tip of the foot.

The atlantal intercentrum is not known. The ventral part of the anterior face of the atlantal centrum and fused axial intercentrum is beveled obliquely backward, suggesting, as discussed above, the nature of the atlantal central body. The atlantal intercentrum, if present, articulated with this face posteriorly, and with the condyle anteriorly.

The proatlas has been tentatively identified in collections taken from Richard's Spur, Oklahoma. The specimens consist of a basal plate that possesses a delicate posteriorly directed spine on its dorsal surface. Posteriorly, a broad edge contacted the atlantal arch. Anteriorly, the halves of the proatlas adjoined paired facets of the exocci-

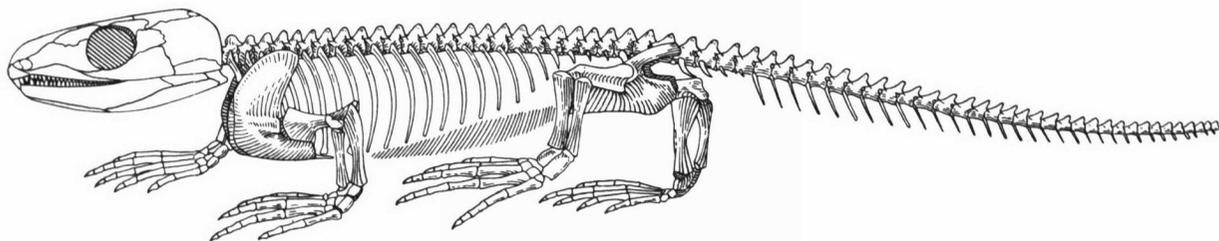


FIGURE 37. *Captorhinus aguti* (COPE). Restoration of skeleton, about $\times 0.5$.

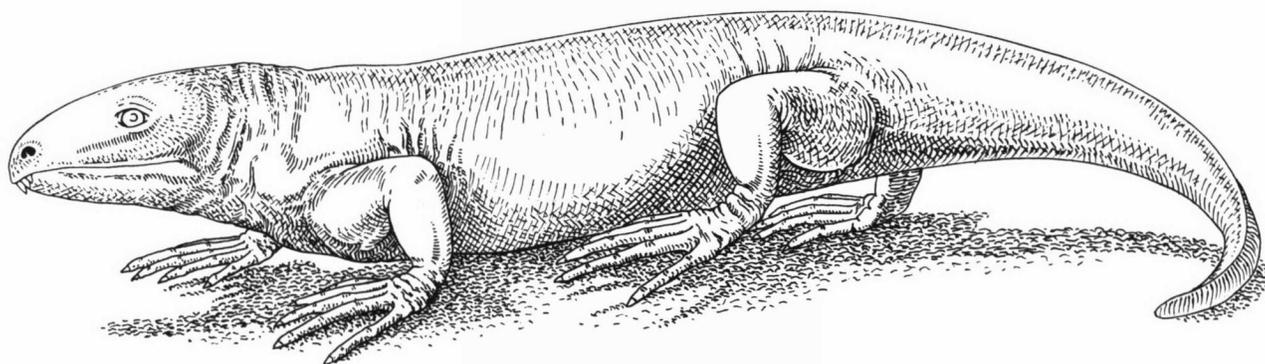


FIGURE 38. *Captorhinus aguti* (COPE). Restoration as in life, about $\times 0.5$.

pital bordering the foramen magnum (PRICE, 1935, pl. 8A).

The axis in *Captorhinus* bears a neural spine of impressive proportions that rests on the neural arch as a tall vertical plate extending the full length of the arch. The prezygapophyses face outward at an angle approximately thirty degrees from the horizontal; the postzygapophyses face inward at an angle perhaps half of that. The neural canal is relatively large, and the centrum possesses a strong ventral keel. The posterior face of the centrum slants forward, allowing the reception of the intercentrum between the axis and the first of the dorsal vertebrae. The parapophyses of the axis are elongate, extending forward and downward along the side of the neural arch and the most dorsal part of the side of the centrum.

Movement between the axis and atlas appears to have been extremely limited. As noted above, the apposing surfaces of the atlantal and axial centra fit tightly together. Movement of the atlantal elements on each other and on the condyle of the skull may have been more permissive, because the apposing surfaces possess enough convexity to prevent a tight fit. Even so, the character of these surfaces is nowhere such as to suggest that movement of the atlantal-axial region was extensive.

RIBS

Each vertebra from the atlas to the fourth or fifth caudal presumably bore ribs. The doubt concerning the distribution of the ribs is focussed on the posterior presacral vertebrae, which possess, as noted above, short transverse processes at the junction of the sides and anterior faces of the centra. No specimens are known that show ribs articulated here; WILLISTON'S (1925, p. 156, fig. 128) figure of a skeleton of *Captorhinus* in ventral view shows at least two of the last three presacrals without ribs; a third vertebra may be obscured by the pelvic plate. If this is so, the obscured vertebra is the last of the presacrals and bears a stout rib that extends laterally toward the pelvis, although it fails to touch it (Fig. 37).

CASE (1911a, p. 100-101) states that the axis possesses a small rib, and the atlas probably, also, although the atlantal rib is still not known. The rib of the first dorsal is abruptly larger than the rib of the axis. Capitulum and tuberculum are joined by a web of bone and the distal end of the rib is broadly spatulate. The ribs of the first four dorsals are en-

larged distally in this manner; those more posterior are slender distally. CASE (1911a, p. 100, fig. 45) has restored *Captorhinus* in ventral view and shows ribs articulated to all vertebrae except the last two of the visible presacrals. In his text, however, he states (p. 101): "On the fourth vertebra anterior to the sacrum there is no face for a rib, so the last articulated rib probably occurred on the twenty-first." His restoration shows the last rib free of vertebral contact.

In a vertebral column reconstructed from the Clarke collection and taken from the Richard's Spur locality, the transverse processes of dorsal vertebrae 4 to 17 possess surfaces of articulation that appear to be restricted to the neural arches and centra. The ventral termination of the articulating surfaces borders on the anterior edges of the centra, but at a level that appears to be above the tips of the intercentra, thereby suggesting an absence of intercentral contact for these ribs. Behind these segments, the ends of the scars are open anteroventrally and at a level that seemingly would permit the head to abut against the intercentrum. PEABODY (1952, p. 18), in discussing the articulations of the ribs in *Petrolacosaurus*, states that in that reptile the ribs of the mid-dorsal vertebrae abutted against the intercentrum, in a manner like that seen in captorhinids, but that in the mid-dorsals of a *Captorhinus* individual at hand, the capitulum and intercentrum do not meet. Seemingly, the inferences made from the Clarke specimen concerning this part of the column are in accord with PEABODY'S observation (Fig. 38).

The detailed configuration of the surfaces of articulation for the ribs is of help in deciding the extent of the articulation of the ribs. The surface in the axis possesses a comparatively broad exposure for contact with the tuberculum that is confluent with a narrow anteroventral contact that stops just short of the face of the centrum. The constricted area was in contact with the bony web between the tuberculum and capitulum. The first dorsal has a tubercular contact as extensive as that of the axis; the isthmus is longer but not noticeably more broad than that of the axis. As noted above, the surface that is thought to be in contact with the isthmus is above the gap for the reception of the intercentrum; presumably the capitulum, lacking contact with the centrum, articulated with the intercentrum. From the fourth dorsal to about the 17th dorsal, the scar for the rib articulation on the vertebrae is clearly

made up of a swollen posterodorsal tubercular contact and a swollen anteroventral capitular contact connected by the isthmus. The third dorsal shows an incomplete capitular contact suggesting that the rib abutted against the intercentrum.

The vertebrae between the 17th and the last presacral have progressively diminishing articular surfaces for the ribs. The ribs in this region may have abutted against the intercentra, for the reasons noted above.

CASE (1911a, p. 98, fig. 43A) has illustrated the axis and the first four dorsal vertebrae in articulation. The axial rib is incomplete distally, and the proximal articulation seems limited to the axial centrum. The rib of the first dorsal clearly has an intercentral contact, and the rib of the second dorsal may have one also, although the pertinent area is obscured by the first dorsal rib. The rib of the third dorsal also probably at least abutted against the intercentrum, from CASE's illustration. The rib of the fourth dorsal seems limited to the centrum. With the exception of the axis, the articulation of these ribs appears to be in accord with the reconstructed column from the Clarke collection.

If the ribs of the posterior dorsals in *Captorhinus* abutted against the intercentrum, a departure from the usual picture in primitive reptiles is represented and is suspect on that account. For example, ROMER (1946, p. 177) states in regard to *Limnoscelis*: "As in primitive reptiles generally (emphasis mine, RCF) the articular area of the rib contracts in width in the more posterior part of the trunk, the capitular articulation shifting upward and backward from the intercentrum toward and to a point on the centrum below the transverse process." *Captorhinus* displays a shifting downward and forward of the contact.

No notches are evident in the proximal ends of the ribs examined for passage of the vertebral artery: the tubercular and capitular areas are connected by a bony web. ROMER (1946, p. 177) has suggested that in *Limnoscelis* a

cartilaginous proximal tip may have been notched for the passage of the artery; the same conditions may have obtained in *Captorhinus*.

The descriptions of the sacral and caudal ribs, fused to the vertebrae, are included in the description of the vertebrae.

GASTRALIA

WILLISTON (1909) reported the presence of gastralia just anterior to the pelvis. CASE (1911a) suggested that they extended over the abdominal region.

INTERCENTRA

In *Captorhinus* the intercentra are small wedge-shaped crescents with little dorsal extent and presumably comparable in relative size to those of *Hylonomus*, *Cephalerpeton*, and *Eosauravus*. The intercentra are highest anteriorly, but the decrease in height posteriorly is slight. In either dorsal or ventral view the intercentra are somewhat wheat-shaped, being thicker in the middle than laterally. The curvatures of the dorsal and ventral surfaces in anterior or posterior view are not parallel: the arc inscribed by the ventral surface is broader and more open than that inscribed by the dorsal surface. The ventral surface is of finished bone; the remaining surfaces are porous, implying a covering of cartilage. Presumably the dorsal extent of the intercentrum was only slightly augmented by cartilage as the intercentra in examined specimens nearly fills the available gap between centra.

The anterior centra possess a faint keel on their ventral surface; the keel is lost by about the fifth postaxial vertebra.

Slender hemal arches are found posterior to the rib-bearing postsacral vertebrae and presumably are found between successive segments nearly to the tip of the tail. Their actual posterior extent is not known.

On none of the intercentra examined are there facets indicating contact with ribs.

SCLEROTIC PLATES

A specimen in the collections of The University of Kansas (KU 9780) bears a short and disturbed series of plates impressed into a block of clay taken from the Richard's Spur locality. The specimen originally included a part of the dermal roof of the skull. The bones of the skull have been removed and preserved separately. What remains on the clay is the impression of their external surface partially surrounding an area that does not bear the imprint of sculpturing. Presumably this was the orbit and

it is in this area that the plates are present. Most of the plates are fragmented to a degree that nothing can be made of them. One plate extends inward from the rim of the orbit toward the center of the opening; the plate is rectangular. A second plate is attached to the end of this; its base is broad, its distal half more narrow and truncated distally. Sclerotic plates have been reported previously in *Labidosaurus* (e.g., ROMER, 1956, p. 438).

POSITION OF CAPTORHINUS AMONG REPTILES

As has been shown, the osteology of *Captorhinus* is rather completely known; in determining the position of the genus among reptiles, we may discuss on the basis of the osteology;

- (1) Speciation in *Captorhinus*.
- (2) Relationship of *Captorhinus* to other genera of captorhinomorphs.
- (3) Position of the tympanum in *Captorhinus*.

- (4) Evidence provided by the middle ear to show the position of *Captorhinus* in relation to diapsid reptiles and to mammals.
- (5) Relationship of *Captorhinus* to microsaurian amphibians.
- (6) Relationship of *Captorhinus* to seymouriamorphs, by examining:
 - (a) Primitive characters common to captorhinomorphs, seymouriamorphs and embolomeres.
 - (b) Whether captorhinomorphs converge toward the seymouriamorphs backward in time.
 - (c) Postcranial skeleton of *Limnoscelis*.
 - (d) Relationship of time.
 - (e) Phylogenetic and ecologic position of the captorhinomorphs.

A number of modern workers have actively concerned themselves with the origin and early phylogeny of reptiles. The orthodox approach has viewed seymouriamorphs as intermediate between embolomeres and captorhinomorphs. This scheme would unite diadectomorphs, captorhinomorphs, and variously seymouriamorphs, into an order Cotylosauria, and the scheme stems from CASE's conception of a primitive reptilian group without temporal openings.

OLSON (1947) questioned the validity of the Cotylosauria, suggesting that the features of the braincase and middle ear in diadectids and seymouriamorphs were incompatible with those of captorhinomorphs; the last common ancestors that the seymouriamorphs and captorhinomorphs possessed were embolomereous amphibians. In more recent years OLSON (e.g., 1962b) has emphasized the apparent "terrestrialness" of captorhinomorphs in comparison to seymouriamorphs as an added factor in support of his eureptilian-parareptilian division.

GOODRICH (1916, 1930), WATSON (1954), and VAUGHN (1955) have suggested phylogenies which resemble one another in that a basic sauropsid-therapsid dichotomy is advocated in which a captorhinomorph-synapsid line gave rise to mammals and a seymouriamorph-diadectid line to living reptiles and birds. To WATSON, the seymouriamorphs and captorhinomorphs had independent origins from the embolomeres; VAUGHN (1955, p. 453) would maintain the Cotylosauria.

WESTOLL (1942a) sought the ancestry of the captorhinomorphs among microsaurian amphibians, a view that has been articulately attacked by ROMER (1950).

SPECIATION IN CAPTORHINUS

Captorhinus is known from the Admiral, Belle Plains, Clyde, Arroyo, Vale, and possibly the Choza Formations, Lower Permian, of Texas (OLSON, 1962a, p. 172). The genus is known also from the Lower Permian fissure deposits at Richard's Spur, Oklahoma, possibly equivalent in age to the Arroyo, and from the Cutler Formation, Rio Arriba County, New Mexico (UC 735), of probable late Wolfcampian age (LANGSTON, 1953, p. 410).

OLSON (1962a, p. 172) states:

Captorhinus was an extremely successful and morphologically stable genus. . . . Throughout (its) range in time and over its geographic range in Texas and Oklahoma, specimens show no striking differences in the skull, dentition or postcranium. From a morphological point of view all may be placed in a single species, *Captorhinus aguti* (OLSON, 1954b). Several species have been named (e.g., CASE, 1911a), but there seems to be no very sound basis for their differentiation.

SELTIN's (1959) review of the captorhinids arrived at the same conclusion by means of statistical tests for significant differences of the characters that CASE and before him COPE had used in the assignment of four species to the genus. Among the characters that SELTIN investigated were: (1) the position of the large maxillary tooth; (2) the abrupt difference in size of the median premaxillary teeth; and (3) the angle of the premaxillary alveolar border with that of the maxillary.

Case also used the size and shape of the skull, the sculpture, the proportions of the bones and the size of the orbits. In addition, in

my preliminary examination of this genus I felt that actual number of rows of maxillary and dentary teeth and actual number of premaxillary teeth would be of importance.

There appear to be a great number of characters used in the separation of the species of *Captorhinus*. Even using these characters, however, one cannot accept without question the division of the genus made by Case in 1911. Case himself said that ". . . each specimen might be considered as distinct and numerous species formed with characters given; or, with a little more freedom, all might be placed in a single species" (SELTIN, 1959, p. 470).

SELTIN's conclusions, as OLSON's after him, were that the continued retention of CASE's four species is incompatible with the evidence. "In this sample there is no evidence of the existence of more than one species of *Captorhinus-C. aguti* (Cope), originally described as *Ectocynodon aguti* Cope (1882), but removed from that genus and assigned to *Captorhinus* by Case in 1911" (SELTIN, 1959, p. 477-478).

It is nearly inconceivable that *Captorhinus aguti* should have continued as the sole species of the genus throughout most of the Early Permian. Among contemporary but shorter-lived captorhinid genera, *Labidosaurus* contains two species, as do both *Labidosaurikos* and *Captorhinkos*. Among pelycosaur, for example, *Casea*, extending from the Lower Vale to the Middle Choza, contains three species, and the long-columned dimetrodons belonging to series B of ROMER & PRICE (1940) include five species from the Wichita to the Arroyo (see below, however). The Arroyo Formation contains two species of *Diplocaulus* (OLSON, 1952a); from Admiral to Choza times three species of *Trimerorachis*, a comparatively stable genus, evolved (OLSON, 1955). Of the great number of early tetrapod genera known from North America OLSON (1955, p. 273) states:

Eryops, and possibly *Lysorophus*, show a somewhat similar (to *Trimerorachis*) persistence of species. The only non-aquatic genera that have a comparable continuity of form, and low rate of speciation, are *Dimetrodon*, a terrestrial carnivore in which the species are not markedly different from one another, and *Captorhinus*. One species of *Dimetrodon*, *D. gigashomogenes*, persisted from the lower Arroyo, or perhaps from the Clyde, through the middle Choza without change. *Captorhinus aguti* ranges from the Admiral through the Vale and probably into the Choza.

Environmental conditions were not constant during the time represented by *Captorhinus*. OLSON (1952b, p. 184, fig. 2) suggests an increase in seasonality in the geographical area represented by the Texas deposits with an uplifting of source areas and an increase in local relief from the base of the Arroyo to the base of the Choza. In regard to the persistence of species, OLSON (1952b, p. 188) states:

Dimetrodon gigashomogenes and *Captorhinus aguti*, both of the upland subzone, illustrate this pattern (fig. 4). They both persisted from the beginning of the Arroyo into the Choza without detectable morphological change. During this time, topography, rainfall, both in amount and seasonal distribution, and the associated animals of the subzone changed. The two species appear to have lived outside the delta during the Arroyo-Vale transition. In spite of these events, the two species persisted and their success is attested to by the relative abundance, particularly in the case of *Dimetrodon gigashomogenes*, in rocks deposited throughout much of the period of time involved.

Thus it is clear that on the basis of the reported evidence only a single species of *Captorhinus* can be defined. Examination of the collected specimens of *Captorhinus* re-

veals that owing to the quality of the preserved material species differentiation is impossible on a morphological basis. The specimens taken from the Texas deposits consist mainly of skulls, the vast majority of which are markedly incomplete. Spalling, fragmentation, and overzealous preparation obscure many of the features that might be useful in species definition, if in fact more than one species of *Captorhinus* occurred in Early Permian times. In material from Richard's Spur, the surfaces of the bone are often faithfully preserved; however, most of the preserved remains are disarticulated and fragmented. Complete individual bones are comparatively rare and articulated specimens are quite uncommon. Comparisons between the Texas and the Oklahoma materials are therefore extremely difficult. The limits of the variation that material from known sites exhibits are seemingly impossible to incorporate into any system of taxonomic recognition at the species level, even though it seems unlikely that only one species of *Captorhinus* was represented in Texas, Oklahoma and New Mexico during the Early Permian.

POSITION OF CAPTORHINUS AMONG CAPTORHINOMORPHS

Captorhinus has long been recognized as possessing numerous specializations that bar it from an ancestral position within the Captorhinomorpha and that were recognized as departures from the presumed primitive condition even when immediate forerunners of the genus were not known. Recent work by WATSON (1954), however, has thrown into clear light the position of the genus in regard to possible ancestral forms and recent work by OLSON (1962a) has discussed *Captorhinus* in relation to the later, more advanced members of the Captorhinomorpha.

The genus most similar to *Captorhinus* is *Labidosaurus*. As OLSON (1962a, p. 173, fig. 63) has indicated, neither genus can be derived from the other; SELTIN's (1959, p. 496) derivation of *L. oklahomensis* from *Captorhinus* is incompatible with the specializations of the dentition of *Captorhinus* known from its earliest appearance. *Captorhinus* appears in the record by early Wichita time; consequently it is somewhat older than *Labidosaurus*, which is reported to be first known from the Clyde Formation (SELTIN, 1959, p. 505), variously assigned to the Wichita and Clear Fork Groups (e.g., ROMER, 1935; ROMER & PRICE, 1940; OLSON, 1955). However, OLSON (1962a, p. 172) restricts *Labidosaurus* to the Arroyo Formation and its presumed equivalents.

There are great structural resemblances between the two genera. The comparisons that have been made between *Captorhinus* and *Labidosaurus* in the descriptive portions of this study have attempted to recount these resemblances, but it should be borne in mind that the differences that are present are of sufficient magnitude seemingly to warrant the assignment of generic rank to both.

There is characteristically a difference in size between *Captorhinus* and *Labidosaurus* (although see SELTIN, 1959, p. 482). The skull of *Labidosaurus* is normally more acuminate anteriorly than that of *Captorhinus*: the cheeks are more greatly inflated and the rostrum seems to be drawn out to a greater length proportionally. Differences in skull proportions are greatly affected by post-mortem

disturbances and are less than certain on that account; more important than such differences, *Labidosaurus* possesses but a single row of marginal teeth in each jaw, while multiple batteries of posterior teeth are characteristic of *Captorhinus*. The socket for the basal articulation of the braincase is located more posteriorly on the quadrate wing of the pterygoid in *Labidosaurus* than in *Captorhinus*. According to SCHAEFFER (1941) the functional ankle joint in *Labidosaurus* is tarso-metatarsal; that of *Captorhinus* is crurotarsal (VAUGHN, 1955, p. 452). These are the most obvious differences; reference to specific sections of this paper should be made for the other differences between the two genera that are known. Two identifiable species are known in *Labidosaurus*; one species of *Captorhinus* is known.

Captorhinus and *Labidosaurus* may be viewed as morphological equivalents. Both, as OLSON (1962a: 173, Fig. 63) has shown, are descendants of an unknown ancestor. *Labidosaurus* is not known to have given rise to any descendant forms, but OLSON (1962a, p. 172), who derives several kinds of captorhinomorphs from *Captorhinus*, states:

The multiple row pattern of cheek teeth is characteristic of all known post-Arroyo captorhinids. *Labidosaurus*, on the other hand, does not show this feature. Presumably it is from the *Captorhinus* type of dentition that the post-Arroyo captorhinids arose, but no precise transition from the somewhat irregular arrangement in *Captorhinus* to the regular rows of later genera and species has yet been found.

OLSON has suggested that *Captorhinoides* and a common *Labidosauriikos-Captorhiniikos* stock each may be traced back to *Captorhinus*. After diverging in early Clear Fork times, *Labidosauriikos* gave rise to *Rothia* and *Captorhiniikos* to *Kahneria* and *Hecatogomphius*. No evidence is seen to contradict OLSON's phylogeny of the derivative genera of *Captorhinus*.

WATSON (1954) discussed a group of primitive captorhinomorphs that in his opinion could be placed in a morphological series leading to *Captorhinus*. The series consists of *Protorothyris*, *Romeria*, and two undescribed specimens, all of which are in the collections of the Museum of Comparative Zoology at Harvard University. *Protorothyris* and MCZ 1963 are from the Moran Formation, *Romeria* from the Putnam Formation, and MCZ 1478 from the Admiral Formation, Wichita Group, of Texas. Arranged in this order, the skulls exhibit a progressive flattening, reduction of the supratemporal bone, reduction and loss of the tabular bone, and straightening of the posterior edge of the dorsal skull roof, tending, as it were, toward the features of *Captorhinus*. The similarities between MCZ 1478 and *Captorhinus* are so great that Watson has suggested that the former may have been the actual ancestor of *Captorhinus*. SELTIN (1959, p. 478) believes that MCZ 1478 is in fact referable to *Captorhinus aguti*. Since then, no other study has been made of these specimens; consequently, reliance must be placed upon the estimates of WATSON and SELTIN of the position of these animals in relation to *Captorhinus*.

More specifically, the features in which the skull and lower jaw of *Captorhinus* appear to depart from at least one of the primitive romeriids (*Hylonomus*, *Archerpeton*,

Cephalerpeton, *Eosauravus*, and *Protorothyris*, as reported in the literature) are listed below:

- (1) Low rounded skull and consequent raised jaw articulation.
- (2) Elongate parietal.
- (3) Reduced supratemporal.
- (4) Absent tabular.
- (5) Supratemporal far removed from postorbital.
- (6) Dorsal margin of occiput not emarginate.
- (7) Sutural attachment of cheek and skull roof.
- (8) Development of beaklike premaxillary bearing enlarged incisors.
- (9) Enlarged squamosal lappet extending on to occiput.
- (10) Paroccipital process in direct contact with quadrate.
- (11) Narrow supraoccipital.
- (12) Large post-temporal fenestrae.
- (13) Basispterygoid joint at or slightly posterior to level of pterygoid flanges.
- (14) Edentate vomer.
- (15) Absent ectopterygoid.
- (16) Palatal teeth arranged in discrete patterns on palatines, pterygoids and, variably, parasphenoid.
- (17) Parasphenoid relatively narrow posteriorly.
- (18) Sliding mechanism of jaw articulation.
- (19) Multiple posterior rows of dentary and maxillary teeth.
- (20) Single edentate coronoid.

Some features are not known to be present or absent in the romeriids; consequently, their appearance in *Captorhinus* may or may not have been a departure from the romeriid morphology. Among these are:

- (1) Apparent hinge-like mechanism of palatal halves.
- (2) Fusion of exoccipitals and basioccipital.

The important features in which the postcranial skeleton appears in *Captorhinus* to have departed from the romeriid condition are:

- (1) Neural arches swollen.
- (2) Apparent fusion of axis intercentrum and centrum, and of atlantal intercentrum and centrum.
- (3) Capitulum and tuberculum of ribs connected by bony web.
- (4) Atlantal centrum a complete disc, not open ventrally.
- (5) Scapular ossification extensive dorsally.
- (6) Two coracoid ossifications.
- (7) Cleithrum presumed to be present, but reduced.

The sum of these features does not override the many resemblances between *Captorhinus* and the romeriids; the latter appear to be firmly established in the ancestry of *Captorhinus* on the basis of these resemblances, and to a seemingly much more sound degree than *Limnoscelis*. In CARROLL'S (1964, p. 82) opinion *Limnoscelis* is not closely related to the romeriids of the Joggins deposits; the ancestry of these "can presumably be sought somewhere within the anthracosaurs."

POSITION OF TYMPANUM IN CAPTORHINUS

WATSON (1951) expressed the view that *Captorhinus* was without a tympanum and received sound vibrations through the bones of the head. He based his opinion on (1) an apparent co-ossification of the stapes with the quadrate in a specimen of *Captorhinus* belonging to his private collection; (2) a belief, not otherwise elucidated, that (p. 144) "the shapes of all the structures concerned make it improbable that *Captorhinus* had a tympanic membrane"; (3) an inability to understand how a stapedia-tympanic contact could be made to a membrane curving from the supratemporal to the retroarticular process of the lower

jaw; (4) an inability to see where a tympanum could have been placed in the primitive *Limnoscelis*.

The articulated skull from the Clarke collection and the numerous disarticulated stapes and quadrates from the Richard's Spur locality show that stapes and quadrate were not co-ossified in *Captorhinus*; the nature of the articulation, as noted above, and the nature of the articulation of the foot plate with the braincase, as observed by PRICE (1935), suggest that perhaps some small movement of the stapes was possible. In this connection, HOTTON (1959) has shown experimentally that gross movement is not necessary for transmission by bone of sounds received from a membrane.

In *Captorhinus* the stapedia recess of the quadrate is exposed in occipital view; the terminal parts of the recess, which support the stapes, are nearly parallel to the plane of the occiput. The ventral lip of the recess (located on the dorsal surface of the foot of the quadrate) forms a shelf that extends backward from the plane of the occiput, so that the distal end of the stapes and the tympanic process, if one were present, were posterior to the occiput and free of bony tissue posteriorly and dorsally.

The part of the groove of the stapedia recess that is exposed occipitally opens laterally, facing the posterior edge of the cheek. The groove continues laterally, although much constricted, as a faint impression on the length of the posterior or occipital edge of the quadrate lappet of the quadratojugal, to open onto the posteroventral corner of the cheek. The groove on the quadratojugal seems to be the anterior wall of the external auditory meatus.

From the shapes of the bones it seems probable that the tympanum was placed a short distance from the terminal end of the osseous stapes, medial to the quadrate foramen, and was supported by the lower part of the occipital flange of the squamosal and by the quadrate in front, by the dorsal side of the foot of the quadrate below, and by connective tissue above and behind. The tympanum in this position agrees essentially with the position of the membrane pictured by HOTTON (1960, p. 198, fig. 2C) and suggested earlier by WESTOLL (1943) and PARRINGTON (1955). Under such circumstances the cartilaginous tympanic process was short.

PRIMITIVE CAPTORHINOMORPHS, SYNAPSIDS AND THE MIDDLE EAR

In recent years considerable attention has been focused on the morphology of the middle ear in primitive reptiles as a guide to their origin and subsequent differentiation. The most recent significant contribution has been made by HOTTON (1960) who used the path of the chorda tympani division of the facial nerve and its relation to the stapes to show that:

The middle ear appears to have gone through four main stages in its evolution. The first stage is that of the labyrinthodont, which is characterized by an otic notch and a tympanic cavity homologous with the spiracular cleft; chorda tympani is post-tympanic in position. The second stage is found in large and primitive pelycosaur and the most primitive captorhinomorphs, and is characterized by loss of the otic notch, an obliquely oriented stapes, and attachment of a large part of the tympanum to the internal process; chorda tympani does not yet lie in the pre-tympanic position. The third stage is that shown by small pelycosaur and advanced captorhinomorphs, and is characterized by a horizontally oriented stapes

with tympanum lying terminal to it and a neomorphic process; chorda tympani has finally come into a pretympanic position. Two divergent fourth stages are shown by the lines leading to diapsid reptiles and to mammals, respectively. Both are characterized by modifications for improved detection of air-borne sound; they differ in origin only because of fortuitous differences in the relationship between the new tympanic process and chorda tympani, and they diverge because of a continuation of jaw changes that affected the middle ear in the line leading to mammals (HOTTON, 1960, p. 207-208).

Consequently, three elements of interest are incorporated in HOTTON's explanation of the events that transpired during the amphibian-reptilian transition and the early evolution of reptiles: (1) the position of the tympanum; (2) the homologies of the stapes and its processes; (3) the path of the chorda tympani. The discussion below will consider these serially.

(1) In suggesting that the old labyrinthodont tympanic process was lost in the transition to primitive amniotes and that the quadrate process, by cradling the tympanum, functionally became the new tympanic process in primitive reptiles, HOTTON believes that when primitive reptiles lost the dorsal labyrinthodont otic notch, they also lost the terminal tympanum. Evidence now known contradicts this belief.

LANGSTON (1965) has recently described an extremely primitive reptile, *Oedaleops campi*, an eothyridid pelycosaur of Early Permian age, in which the pattern of skull bones resembles that of the contemporary *Limnoscelis* (LANGSTON, 1965, p. 34). *Oedaleops* possesses a synapsid opening in the temporal region; it also possesses a peculiar pit and a projection of the supratemporal beyond the limits of the posterior edge of the skull. LANGSTON (1965, p. 23) believes it certain "that the structure was somehow related to an ancestral otic notch." Although the occiput is as yet unknown and the position of the stapes consequently indeterminate, it does not seem unreasonable to associate the projection of the supratemporal in *Oedaleops* with dorsal support for the tympanum. If so, the membrane was surficial or very nearly so, and terminal to the stapes. *Eothyris parkeyi*, which LANGSTON believes is similar to *Oedaleops* possesses, according to WATSON (1954), a similar projection on the tabular bone. LANGSTON tentatively concurs in WATSON's identification of the bone, but leaves open the possibility that it might be the supratemporal. Regardless of the identity of the bone, its projection behind the posterior edge of the skull resembles that in *Oedaleops* and the bone in *Eothyris* also may have functioned in tympanic support.

Pelycosaurs more advanced than *Oedaleops* possibly offer evidence in support of a tympanum terminal to the stapes. Various individuals of *Dimetrodon* show a notch, particularly evident in MCZ 2779, *D. limbatus* (EATON, 1963, personal communication), along the posterior edge of the cheek. The notch is bordered by the squamosal, the supratemporal and the distal end of the paroccipital process (BAIRD, 1965, personal communication). BAIRD interprets the notch as the opening to the external auditory meatus and, on the basis of the limiting bones, would homologize it with the primitive otic notch. An opening for the external auditory meatus in this position has already been suggested by PARRINGTON (1955, p. 34, fig. 14B), and the presence of a notch here supports PARRING-

TON's suggestion. If the notch is indeed the opening of the external auditory meatus, then the tympanum in *Dimetrodon* occupied a deep position, either terminal to the stapes, as advocated by ROMER & PRICE (1940) and PARRINGTON (1955), or cradled by the stapes, as suggested by HOTTON (1959, 1960).

But regardless of whether the tympanum was terminal to the stapes or was cradled by it in *Dimetrodon* (the latter position of the membrane would be unique among vertebrates), it seems reasonable to suggest that the tympanum in the pelycosaur ancestors of *Dimetrodon* was terminal to the stapes in the otic notch, which has been retained in *Dimetrodon* as the opening for the external auditory meatus.

(2) Evidence also suggests that the quadrate process is retained as a functional quadrate process in pelycosaurs and one that is fully homologous with that of labyrinthodonts.

ROMER & PRICE (1940, p. 88) report that the stapes of *Dimetrodon* bears an elongate area on its anterior or outer surface that may have afforded attachment for a ligament extending from the otostapes to a pit present on the medial face of the quadrate; in their opinion such a ligament would be the homolog of the quadrate process. Little else in the way of concrete evidence is available to verify the presence of a quadrate process homologous to the labyrinthodont quadrate process, but the suggested presence of a tympanum terminal to the stapes in the primitive *Oedaleops* and the ancestors of *Dimetrodon* partially relieves the necessity of suggesting the loss of the labyrinthodont process in primitive reptiles in HOTTON's sense.

HOTTON believes (p. 201, *et seq.*) that large-bodied early pelycosaurs, such as *Ophiacodon* and *Clepsydrops* are primitive in the structure of the middle ear, with the stapes slanting obliquely down. And yet to get to that position, the stapes had to descend from the dorsal position it occupied in the labyrinthodonts; *Oedaleops* may show, when better known, an intermediate step in this descent. *Oedaleops* is not large; the skull as preserved is but 76 mm. long (LANGSTON, 1965, p. 7); the apparent pelycosaur described by CARROLL (1964), *Protoclepsydrops*, on the basis of comparing the figures of postcranial elements of *Protoclepsydrops* and *Oedaleops*, is even smaller, suggesting that "smallness" in pelycosaurs (or in captorhinomorphs, for that matter) is not a secondary adaptation.

If the captorhinomorphs are examined in the matter of support of the tympanum and the position of the tympanum, differences between them and the early pelycosaurs are apparent. In *Limnoscelis* the stapes is not known (e.g., WATSON, 1954) but its orientation may be reasonably assessed from the location of the fenestra ovalis and the paroccipital process of the opisthotic. These suggest that the stapes extended laterally and slightly ventrally from the fenestra ovalis toward the quadrate bone.

The position of the remnant of the otic notch is shown dorsally on the posterior border of the skull by a spur of the supratemporal that juts slightly beyond the plane of the occiput. ROMER (1956, p. 69) states: "... its position is also marked, it would seem, by a line of weakness at the point at which the notch was formerly present." The remnant of the otic notch is dorsal, suggesting to ROMER (1946) that it was squeezed posteriorly by the ingrowth of

its limiting bones. Although *Limnoscelis*, in the light of the Joggins reptiles, may not be ancestral to later captorhinomorphs, it nevertheless is an extremely primitive member of that group, and presumably shows in the character of the loss of the otic notch in the manner in which the notch was lost among those captorhinomorphs that were closer to the main root of the group. If this is true, the modifications of the otic notch in captorhinomorphs and pelycosaurs may have proceeded along divergent lines.

In keeping with the evidence that has been presented thus far, it seems clear that captorhinomorphs and pelycosaurs are united by a primitive, but as yet, undiscovered reptilian stock, in which the tympanum was located at the posterodorsal corner of the skull and in which the stapes extended dorsolaterally to its tympanic contact. Very early in the history of the one group the otic notch, retaining its posterodorsal position, was squeezed backwards by the pinching together of its limiting bones in the manner suggested by ROMER (1946). *Limnoscelis* is a member of this group as are the romeriids and captorhinids.

In the second group the otic notch was not entirely lost, but descended, with the descent of the tympanum and stapes, down the posterior edge of the cheek until a posteroventral position was achieved. This group consisted of the primitive pelycosaurs, as demonstrated by *Oedaleops* and *Dimetrodon*.

(3) If the descent of the tympanum-stapedial complex was as a unit with no radical modifications of its components, how are the supposed discrepancies among tetrapods of the position of the chorda tympani in its relation to the stapes to be explained? It should be recalled at this point that in labyrinthodonts the chorda tympani is post-tympanic, as shown by the work of ROMER (1941) in which the hyomandibula of *Ectosteorachis* was homologized with the stapes of primitive tetrapods; in living birds and reptiles the chorda tympani is pretympanic (VAUGHN, 1955, p. 400); in mammals the picture is complicated by the interposition of malleus and incus between the stapes and tympanum, "but the nerve does not pass below the tympanic cavity as in the frog" (HOTTON, 1960, p. 195).

On the basis of evidence provided by Recent tetrapods HOTTON's opinion concerning the course of the chorda tympani among primitive tetrapods is questioned. HOTTON (1960: 197-199) supposed that the chorda tympani passed below the tympanic process of the stapes and above the quadrate process in anthracosaur amphibians, in consequence of the nerve being pushed ahead of the hyomandibula as it swung out into its new position as the stapes of tetrapods. It has been noted above that these changes resulted in a post-tympanic position of the chorda tympani in reptilian ancestors, and there seemingly can be little room for doubt in suggesting that the nerve passed below the tympanic process in these animals. But the path of the chorda tympani in Recent tetrapods in relation to the quadrate process suggests that primitively the nerve passed below the quadrate process as well as below the tympanic process. In *Lacerta* the nerve crosses the posterior face of the quadrate below the quadrate process of the stapes (GOODRICH, 1930, p. 454, fig. 478; DEBEER, 1937, p. 226). A similar relationship of nerve to process also apparently obtains in *Ctenosaura* (OELRICH, 1956, p. 65), in *Gecko*

(DEBEER, 1937, pl. 141), in *Holbrookia* (EARLE, 1961, p. 70, fig. 1) and in *Varanus monitor* (BAHL, 1937, p. 159, fig. 13). The consistency of the passage of the nerve external to the quadrate-stapedial contact may be further substantiated by the incus-stapedial contact in mammals. If, as WESTOLL (1944) has suggested, the point of contact between stapes and incus in mammals is homologous with the connection between stapes and quadrate via the quadrate process in reptiles, then the nerve in *Trichosurus*, *Didelphys*, *Hyrax*, and *Felis* occupies the same position as in the genera of reptiles referred to above: the nerve passes external to the contact (DEBEER, 1937, pl. 141).

The evidence provided by the hyomandibula of crossopterygians is not necessarily in conflict with the passage of the nerve ventral to both the tympanic and quadrate processes in anthracosaurs. As the hyomandibula swung out from the braincase to become the tetrapod stapes, the hyoid branch of the facial nerve, which arises from a common root with the chorda tympani, was left posterior to the stapes. No known evidence suggests that the chorda tympani could not also have been left behind the stapes to pass under the quadrate process. The seeming widespread occurrence of such a relationship among living tetrapods suggests that primitively such was the case.

The discussion concerning the positions of the chorda tympani probably cannot be resolved by considering only the phylogeny of adult structures; at least a partial answer may lie in the possible ontogenetic relationships both in time and in space that exist between the chorda tympani and the tympanic diverticulum of the first (spiracular) gill cleft. During embryonic development physical barriers in the middle ear (such as the stapes) may not have been completely formed at the time that the tympanic diverticulum and the chorda tympani were assuming their relationship to one another.

According to GOODRICH (1930, p. 471):

This (tympanic membrane) is not the original closing membrane of the spiracular slit, but a new formation, developed in essentially the same manner and position in all Amniotes. The expanding tympanic cavity tends to surround the skeletal structures. As the cavity enlarges behind the quadrate in reptiles the columella appears to sink into it from above and behind; while in mammals, not only does the stapes sink in from above and behind, but the incus and malleus from above and in front.

GOODRICH (1930, p. 469, fig. 494a) also indicates that the general sequence among amniotes is (1) appearance of the spiracular cleft in the first pharyngeal pouch; (2) appearance of the chorda tympani; (3) appearance of the tympanic diverticulum; and (4) appearance of the stapedial (otostapes) blastema moving down (relatively, at least) into the tympanic diverticulum. Lateral growth of the stapes must await the assumption of the definitive position of the stapes to the chorda tympani; otherwise, in its migration into the tympanic diverticulum, the stapes would catch on to the chorda tympani during the transition from the post-tympanic to the pretympanic passage.

In the embryos of the labyrinthodont stock that gave rise to primitive captorhinomorphs the tympanic diverticulum, fully homologous to the spiracular cleft of fish, was presumably directed dorsolaterally toward the otic notch. The stapes had a similar orientation within the tympanic diverticulum. The fenestra ovalis was probably located at

an intermediate height on the side of the braincase, similar to its position in *Paleogyrinus*. The chorda tympani was post-tympanic in position, passing down behind the tympanic diverticulum. The change from the labyrinthodont to the captorhinomorph condition involved a descent of the fenestra ovalis down the side of the braincase to a ventral position, a descent of the stapes extending from the fenestra ovalis, and a descent of the tympanum down the posterior edge of the cheek. Presumably the embryonic primordia of these structures shifted in position also, perhaps not to the same degree as the adult structures, but at least to the degree that they departed from the more dorsal position they held in labyrinthodonts. The new amniotic tympanic diverticulum came to assume a more ventral position and to extend laterally rather than dorsolaterally; it then occupied the area through which the chorda tympani had previously passed, below the diverticulum in anthracosaur embryos. The amniotic diverticulum, arising from an area below the spiracular cleft, effectively blocked the chorda tympani from its path forward. Freedom for passage of the nerve was found dorsal to the diverticulum, resulting in a pretympanic position for the nerve.

In the anthracosaurs the quadrate process was presumably outside of the tympanic diverticulum, as HORTON (1960, p. 199) has already suggested. The chorda tympani in these animals presumably passed down the back wall, crossed beneath the tympanic process and emerged from the diverticulum anteroventrally; from here the nerve continued down, forward and laterally until it crossed the posterior edge of the quadrate beneath the quadrate process of the stapes. The ventral position of the nerve in relation to the quadrate process was unaffected by the descent of the diverticulum and the stapes, because that part of the nerve lay outside of the diverticulum. It was only after the pretympanic position of the nerve had been achieved that the tympanic diverticulum expanded to an extent sufficient to include the quadrate process within it.

In advanced captorhinomorphs such as *Captorhinus*, the stapes, through raising of the quadrate, extends nearly horizontally to its quadrate articulation. In the more primitive *Protorothyris* the stapes slanted markedly downward distally, presumably representing the terminal stage in the descent of the tympanum during the early evolution of the captorhinomorphs from anthracosaurs. In *Captorhinus* the distal end of the stapes rests in the stapedia recess of the quadrate; the presumed position of the tympanum is but a short distance from the terminal end of the stapes, implying that the tympanic process was short. There is no evidence, either on the stapes or in the available areas of the quadrate, for a typical quadrate process. The assumption has to be made that the articulation between the stapes and the stapedia recess of the quadrate is homologous to the more usual cartilagenous or ligamentous connection between stapes and quadrate that is found in reptiles possessing a functional tympanum and stapes. If so, in *Captorhinus* the chorda tympani passed over the tympanic process of the stapes, then traveled downward and backward slightly to descend to the lower jaw. The posterior edge of the quadrate bears a notch at the end of the central groove of the articular face of the condyle; the notch lies directly above the foramen between the articular and the angular at the base of the retroarticular process for the en-

trance of the chorda tympani into the mandible. The notch may be interpreted as marking the location of the exit of the chorda tympani from the skull prior to its descent to the lower jaw. Although the quadrate process in *Captorhinus* has been reduced to merely the articulation between the bony stapes and the quadrate, the path of the nerve in relation to the processes of the stapes is essentially that found in diapsids. The diapsid relationship between the chorda tympani and the processes of the stapes presumably is derived from a captorhinomorph less advanced than *Captorhinus*, one in which the quadrate process was present as a process; alternatively, the quadrate process of diapsids could be a neomorph, but this seems unnecessary.

While the events that occurred in the evolution of the middle ear in the captorhinomorph-diapsid line appear to be relatively straightforward, the changes that occurred in the synapsid-mammalian line seem far more complex. The initial modifications among early synapsids paralleled those in early captorhinomorphs. Except for the continued possession of the remnant of a functional otic notch in pelycosaurs, the descent of the tympanum and the stapes appears to have duplicated that in captorhinomorphs. When the stapes of pelycosaurs had achieved a ventral position the chorda tympani crossed above the tympanic process and below the quadrate process. It is from this point that complications appear.

Two points of view regarding the changes that took place in the middle ear of the reptilian ancestors of mammals are evident. The overwhelming preponderance of authors writing on evolution of the middle ear judge that the mammalian tympanic membrane is not fully homologous with the membrane of living reptiles. For example, WESTOLL (1943, 1945) thought that the mammalian tympanum was a neomorph: Schrapnell's membrane (*pars flaccida*) is equivalent to the old labyrinthodont membrane, and its hyostapedial connection was maintained in therapsids and in mammalian embryos. The homology between *pars flaccida* and the reptilian tympanum is based upon the mutual lack of a middle, mesodermal (*membrana propria*) layer of tissue (VAUGHN, 1955, p. 402; HORTON, 1960, p. 205). *Pars tensa*, the mammalian neomorph, makes up most of the mammalian tympanum and is the result of a ventral diverticulum (*recessus mandibularis*) of the tympanic cavity.

The malleolar folds (*Chordafalten* of BONDY) "represent compressed tissues which separated the dorsal (labyrinthodont) tympanic diverticulum of the therapsids from the mandibular recess of the tympanic cavity" (VAUGHN, 1955, p. 402). Earlier workers (e.g., GAUPP, 1898; VERSLUYS, 1899; GREGORY, 1910) had previously questioned the full homology of the sauropsid and mammalian membranes; VAUGHN questions it also.

WATSON (1951, 1953) thought that pelycosaurs had no tympanic membrane and that captorhinomorphs also probably lacked it. In his view the mammalian tympanum was an entirely new development that had already appeared in cynodonts.

HORTON (1960, p. 205) has presented an alternative approach:

The theory that the mammalian middle ear chamber originated as an evagination of the reptilian cavity consists mainly of a description of the sequence of events in mammalian ontogeny fitted

into a phylogenetic frame of reference. The selective forces that would induce such an evagination are obscure. I suggest that there was never more than one membrane, and that it arrived at the mammalian infra-mandibular position simply because it got larger at the same time the quadrate was getting smaller. Increase in tympanum size was the result of selection toward more effective middle ear apparatus as it was in the protodiapsids, while reduction of the quadrate was related to changes in jaw structure.

Some evidence suggests that HORTON may be correct in contending that the mammalian and reptilian tympanic membranes are fully homologous. This appears if GREGORY (1910), who is cited by some authors in support of the view that only part of the mammalian tympanum is homologous to that of living diapsids, is quoted fully (p. 127):

From the considerations that follow it appears likely that the tympanic membrane of mammals may be considered homologous, at least in part, with the tympanum of reptiles. The tympanic membrane in man (Cunningham, 1902, pp. 706-707) consists of three layers: (1) stratum cutaneum, continuous with the external meatus; (2) the membrana propria, consisting of two sets of fibers, radial and circular, which center around the handle of the malleus; (3) the stratum mucosum, continuous with the general mucous lining of the tympanic cavity. In the tympanum of reptiles the stratum cutaneum is said to be lacking (Denker, 1901, p. 658). Versluys, however (1899, p. 359), in describing the tympanum of lizards, speaks of a middle layer of connective tissue provided with elastic fibers (and apparently homologous with the membrana propria) as sometimes occurring (ours). It is generally vestigial, he says, and in this case the lizard tympanum would be structurally comparable only to the dorsal segment of the mammalian tympanum, the "pars flaccida," where also the membrana propria is lacking.

Dr. JAMES HOPSON (1965, personal communication) has informed us that CORD (1908) reports that *Lacerta agilis* possesses a tympanum of three layers.

Parenthetically, it should be pointed out that a middle layer is by no means universally absent from the pars flaccida of mammals. For example, HENSEN (1961, p. 159), in his study of the middle ear of bats and insectivores, says of the pars flaccida:

A layer of stratified squamous epithelium, continuous with that of the external auditory meatus, forms an outer layer, the *stratum cutaneum*. An inner layer, the *stratum mucosum*, is continuous with the mucosal lining of the tympanic cavity, and a middle layer, the *substantia propria*, when distinguishable, is composed of loosely organized connective tissue.

Among insectivores, HENSEN noted the presence of the substantia propria in *Erinaceus europaeus* and *Cryptotis parva*; the layer was absent in *Scalopus aquaticus*. Among chiropterans the layer was present in *Glossophaga soricina*, *Rhinolophus ferrum-equinum*, *Natalus mexicanus*, *Eptesicus fuscus*, *Myotis velifer*, *Plecotus townsendii* and *Tadarida brasiliensis*. The presence or absence of the layer is not noted for *Eumops perotis*.

Observations by VERSLUYS, CORD, and HENSEN demonstrate that the three layers of the mammalian pars tensa are not unique to that structure, but are known also in the mammalian pars flaccida and the lacertilian tympanum. The character of the fibers in the substantia propria differs from that of the fibers of the stratum fibrosum; in the one the fibers are loosely organized and collagenic, while in the other they are oriented and elastic. In lieu of any evidence to the contrary, however, the fibers of both the substantia propria and the stratum fibrosum may be considered

mesodermal in origin because of their connective tissue nature. Since the reported absence of this middle layer in the mammalian pars flaccida and reptilian tympanum has contributed to the belief that only these membranes are homologous and, by extension, the pars tensa is a mammalian neomorph, the demonstrated presence of the middle layer in the tympanum of some lizards and the pars flaccida of some mammals weakens such a belief.

It should be noted too that the ontogenetic morphology of the tympanic diverticulum apparently has failed to reveal any indication of dual phylogenetic contributions to the mammalian tympanum. VAUGHN (1955, p. 405) states: "It may be that future work will distinguish between two diverticulae of the hyomandibular pouch, one dorsal to the chorda tympani and one ventral to it." SHUTE (1956, p. 263) comments:

Ontogeny, of course, is not obliged to repeat the stages of phylogeny, but an *ad hoc* postulate of this sort would gain in plausibility if some indication of its occurrence could be seen during embryonic development. One might, for instance, expect to find in mammalian development the tubotympanic recess first growing out around the primordium of the stapes, since it is the oldest ear ossicle; and later a pouch being thrown out towards the ectotympanic which would envelop the handle of the malleus. In fact, however, no such pouch is formed, and the tubotympanic recess meets the manubrium mallei first of all (Fig. 1), reaching the stapes and the otic region of the middle ear only at a relatively late state (Fig. 5A). This is a constant finding in eutherian mammals, and is in accordance with McClain's observations (1939) in the marsupial *Didelphys*.

WESTOLL's (1943) suggestion that a recessus mandibularis functioned as a resonating chamber before its capture of the angular and transformation into a neomorphic receptor of sound is weakened by PARRINGTON's (1955, p. 25) and SHUTE's (1956, p. 264) recognition that vocal resonating chambers among tetrapods are not known to be developed from the diverticulum of the middle ear. In the absence of this or some related function it is difficult to account for the selective advantage of a recess mandibularis prior to its incorporation into the sound receiving mechanism of the middle ear. The absence of any indication of two tympanic diverticulae in embryonic mammals and the lack of a *raison d'être* for the (hypothetical) recessus mandibularis in early synapsids makes the schemes of middle ear evolution based on these arguments less than certain. The pars tensa may be a mammalian neomorph, but substantiation for this view at present apparently must be derived from sources other than the histological structure of the tympanum in mammals and lizards or the ontogeny of the tympanic diverticulum during mammalian development.

An attempt to do this has been made by the examination of the association of the accessory bones of the lower jaw with the pars tensa. The association is taken to mean that the pars tensa originated at a more ventral level than did the original reptilian diverticulum (HORTON, 1960, p. 205). It does seem, however, that the primitive synapsid lower jaw is invariably located below the level of the middle ear; consequently, when these bones were included in the mechanism of the middle ear, any clues as to their ancestral position vis-a-vis the tympanum would almost have to point to a more ventral level regardless of the phylogenetic origins of the components of the mammalian

tympanum. These bones testify to their own history, but do not tell us anything as to whether the tympanum in mammals is fully homologous, partially homologous or not homologous at all to the reptilian ear drum. Descent of the tympanum and ascent of the accessory bones of the reptilian lower jaw and their inclusion in the mammalian middle ear mechanism are well documented, but seemingly we must seek evidence of a different nature to begin to arrive at a conclusion regarding the make-up of the mammalian tympanic membrane.

In this connection it should be noted that in later therapsids the relationship of the accessory bones of the jaw and the cavity of the middle ear is such to suggest that these bones did not ascend into the cavity of the middle ear but rather moved backward across the jaw joint to become part of the middle ear mechanism. For example, in *Thrinaxodon* most of the squamosal contribution to the zygomatic arch in ventral view lies behind the level of the quadrate (ROMER, 1956, p. 192, fig. 104B). In *Thrinaxodon*, *Leavachia*, *Cynognathus*, *Oligokyphus* (CROMPTON, 1964, p. 77, figs. 9-14) and *Diarthrognathus*, (CROMPTON, 1958, p. 201, fig. 7A) the zygomatic bar terminates behind the jaw articulation and the posterior surface of the skull extended backward behind this. The quadrate-articular joint was then located in front of the tympanic cavity and not beneath it as it was in such primitive reptiles as *Captorhinus* and *Dimetrodon* and in many Recent lizards.

Evidence to support this thesis is also available from the development of the region in Recent mammals. In mammalian embryos the posteroventral part of the chondrocranium curves down and around, behind the region of the developing ear. The exoccipital in the 45 mm. stage of *Lepus* is ventral to the malleus and tympanic bones, and, by implication, to stapes and incus, although these are not pictured (DEBEER, 1937, pl. 112). The oblique posterior border of the developing dentary abuts up against the tympanic bone, but again at a level that is dorsal to the inflated posterior portion of the chondrocranium. The 25-mm. stage of chondrocranial development of *Microtus* agrees with the picture in *Lepus*; a similar relationship is presented by such widely divergent mammals as *Talpa*, *Erinaceus*, *Perameles*, *Felis*, *Canis*, *Poecilophoca*, *Sus*, *Equus*, *Bos*, and *Homo* (DEBEER, 1937, pls. 108-134). However, in *Lacerta*, *Sphenodon*, *Tropidonotus*, *Chrysemys*, *Emys*, and *Crocodylus* the embryonic articulation of the lower jaw to the skull is not bounded by an inflated posterior part of the chondrocranium. The articulation is at or close to the posterior termination of the skull and at or close to the most ventral portion of the skull at this level.

SHUTE (1956, p. 269, fig. 4B) recognizes this relationship in his diagram of a hypothetical intermediate between the condition in lizards and that in mammals, in which he shows a tympanic ring, as yet incomplete and still attached to the lower jaw, beginning to assume its definitive position in relation to the malleus and the tympanum, but in front of this region rather than below it.

In summary to this point, the available evidence leads to the judgment that HOTTON (1960) is correct in his suggestion that the mammalian tympanum is homologous with that of reptiles, for (1) a single tympanic diverticulum forms the mammalian tympanic cavity (although the attic region lags somewhat in its pneumatization) (VAUGHN,

1955); (2) the tympanic membrane in at least some lizards and the pars flaccida in at least some mammals is three-layered, as is the pars tensa of mammals; (3) although the accessory bones of the lower jaw were primitively ventral to the cavity of the middle ear (in pelycosaurs), the tympanic diverticulum that is associated with these bones in mammals need not have been a ventral neomorph; in advanced synapsids these bones were in front of the jaw joint, and during the reptilian-mammalian transition they moved backward across the joint, not upward from beneath it.

If the mammalian tympanum is fully homologous with that of living diapsids how does it happen (1) that the pars flaccida and pars tensa show differences in structure, and (2) what is to be made of the mammalian epitympanic recess or attic region? VAN DER KLAUW (1931) reports that *Ornithorhynchus* does not possess an epitympanic recess; it does possess a pars flaccida (HOPSON, 1965, personal communication). Also HOPSON seems to think that tritylodonts lacked an attic region; CROMPTON's figures (1964, p. 77, figs. 13, 14) also suggest this for *Oligokyphus*. In the cynodonts, *Leavachia* and *Cynognathus* no evidence of an epitympanic recess is seen (CROMPTON, 1964, p. 77, figs. 9-12); CROMPTON's figures appear to show that the region from the fenestra ovalis to the presumed position of the tympanum at the proximal end of the external auditory meatus is essentially open, being partially and most conspicuously walled from behind by the posterior process of the paroccipital.

In this connection SHUTE (1956) has suggested that the pars flaccida is a mammalian neomorph, and that the pars tensa is homologous to the reptilian tympanum. The association of the attic region, a structure unknown in reptiles, with the pars flaccida, the lateral limiting membrane of the attic, suggests that the appearance of the one entailed the appearance of the other. However, the lack of an attic region and the presence of a pars flaccida in *Ornithorhynchus* may be taken to mean that the two structures were not related initially among mammals, or at very least the condition shown by *Ornithorhynchus* admits this possibility. In any case, the pars flaccida is not the invariable correlate of the epitympanic recess, an apparent mammalian neomorph.

The tympanic bone is present in all Recent mammals; it varies in shape from a broadly opened horseshoe to a closed ring (VAN DER KLAUW, 1931). Usual homologies equate the tympanic ring with the reptilian angular (see, however, HOTTON, 1960, p. 207). The tympanic ring supports the pars tensa; the pars flaccida, lying above the pars tensa, is

limited on the ventral side by the arcus terminalis (a band of connective tissue lying between the pars tensa and the pars flaccida) and sometimes also by the dorsal margin of the two legs of the tympanic ring; on the dorsal side by the skeletal element that closes the "Tympanicumdefekt" and also by the tympanic ring. If the tympanic ring is closed all around, both "Tympanicumschenkeln" above limit the membrana Schrapnelli dorsally. Finally, in all cases where the lateral wall of the recessus epitympanicus is not bony but membranous, as in *Echidna*, *Erinaceus*, *Sorex* and *Chiroptera*, a sharp limit cannot be defined (VAN DER KLAUW, 1931, p. 74).

VAN DER KLAUW states (p. 77) that in most mammals the tympanic ring is incomplete; in these instances the

"*Tympanicumdefekt*" is usually closed by the squamosal which, as a rule, provides the dorsal limit of the pars flaccida.

If the structure and relations of the attic, tympanic ring, pars tensa and pars flaccida are viewed in light of the therapsid ancestry of mammals, an explanation for the differentiation of the pars flaccida and pars tensa suggests itself. The angular bone in advanced therapsids foreshadows the embryological shape and position of the tympanic bone in mammals (e.g., GOODRICH, 1930, p. 475-477); both possess two posteriorly directed limbs which, in the tympanic bone of adult mammals, support the tympanum. As far as is known the angular of the most advanced therapsids still retains a gap between its posteriorly directed limbs. Possibly when the angular moved into the skull and first enclosed the tympanum, the gap between the tips of the limbs, now curved towards each other, still existed.

The bony support provided for the tympanum by the quadrate of therapsids was supplanted and amplified by the angular when the quadrate was reduced and incorporated into the mechanism of the middle ear. The tympanum, judging from the position of the proximal end of the external auditory meatus in, for example, *Cynognathus* and *Oligokyphus*, was supported dorsally by the squamosal, or, at least, was exceedingly close to the squamosal dorsally. When the angular-tympanic assumed support of the tympanum, the tympanic incisure or gap between the limbs, limited on either side that part of the tympanum that attached dorsally; the therapsid dorsal attachment was still available, unlike the quadrate support, and was retained. Only secondarily, it would seem, was a complete annulus developed, and the dorsal attachment of the tympanum to the squamosal supplanted by that of the tympanic ring.

It may have been that that part of the tympanum between the limbs of the annulus and upward to the dorsal attachment was initially less effective in the reception and transmission of sound vibrations because of its position outside of the inner borders of the tympanic ring; presumably selection did not lead to intense refinement of its receiving qualities and it became the relatively limp membrane, pars flaccida. The differentiation of the pars flaccida from the pars tensa may have been assured by the growth of the arcus terminalis, a band of connective tissue, across the tympanic incisure to provide support for the tympanum at the incisure equal to that provided by the bony annulus. The appearance of the band presumably meant an end to the exchange of vibrations from the membrane enclosed by the annulus and arcus terminalis, and the pars flaccida.

The pars flaccida presumably was retained primarily as the limiting wall laterally for the epitympanic recess. The membrane is variably sized and may be perforate in man (Goss, 1959, p. 1132).

The position of the chorda tympani in mammals can be adequately accounted for in a manner that is in keeping with the preceding scheme of middle ear evolution. It may be recalled that in primitive captorhinomorphs and pelycosaurs the stapes had already achieved a ventral position and that the descent of the stapes is thought to have resulted in a pretympanic position of the chorda tympani

in both groups. The reptilian tympanic and quadrate processes were homologous with those of the amphibian ancestors. During the evolution of the therapsids the stapes and its processes became smaller; the tympanic process became particularly reduced (HORTON, 1960). Consequently, the dorsal process was brought into close proximity to the tympanum. The chorda tympani, still passing over the stapes between the dorsal process and the tympanum, was also brought closer to the membrane. The distal position of the dorsal process on the shaft of the stapes is already seen, for example, in *Thrinaxodon* (ESTES, 1961, p. 177), *Kingoria* (Cox, 1959, p. 332) and the American dicynodont *Placerias* (CAMP & WELLES, 1956, p. 276). As the lateral distance between the dorsal process and the membrane became less, the chorda tympani was trapped in the tympanum. Movement of quadrate and articular posteriorly into the tympanic cavity and assumption of their definitive roles in the middle ear mechanism was the single remaining modification required to bring the chorda tympani to its mammalian relationships.

The quadrate-stapedial contact was in front of and medial to the chorda tympani, and the quadrate-articular contact was in front of and lateral to the nerve as it passed down into the lower jaw. In effect, then, the quadrate passed over the chorda tympani, external to its path.

During the migration of the quadrate and articular backward into the tympanic cavity, a tympanum-articular contact was established and the tympanum-stapedial contact was lost. The exact sequence of this is not known, but presumably the tympanum-stapedial contact was maintained until at least the quadrate was in a position to enable it to participate in the amplification of the vibrations of the tympanum. The articular followed the quadrate into the middle ear mechanism, and retained essentially the relation to the chorda tympani that it possessed while still a member of the lower jaw. In *Trichosurus*, for example, the chorda tympani passes downward internal to Meckel's cartilage; the nerve passes close to the future articulation between malleus and incus (GOODRICH, 1930, p. 463, fig. 488). In adult mammals the nerve passes lateral to the long crus of the incus and across the medial face of the manubrium of the malleus; the bones form a bridge over the path of the nerve, and are still external to it. The interposition of the manubrium of the malleus between the chorda tympani and the tympanum seemingly is the result of the maintenance of the primitive relation of the articular to the path of the nerve and in consequence of the expansion of the malleolar contact with the tympanum for the refinement of reception and transmission of sound waves.

MICROSAURS AND CAPTORHINOMORPHS

In recent years various workers have periodically suggested the possibilities of affinities between the microsaurian amphibians and the captorhinomorph reptiles. WESTOLL (1942a, 1942b) presented a scheme of descent in which the microsaurians arose from the ichtyostegid amphibians and, in their turn, gave rise to the captorhinomorphs. ROMER (1950) attacked this view, and, in so doing, showed that a number of genera hitherto thought to be microsaurians (*Petrobates*, *Cephalerpeton*, *Hylonomus*, *Fritschia*, *Leiocephalikön*, *Eusauropleura*) were actually

true reptiles. ROMER pointed out that some of those workers (e.g., DAWSON, 1863; BAUR, 1897; GREGORY, 1948) who had argued for a microsaurian-reptilian relationship had based their conclusions on various genera listed above. The assessment of the reptilian nature of these genera was correct since they are true reptiles. The microsaurian-reptilian affinities based upon these genera were invalid, because these animals, in being true reptiles, were not microsaurians.

The matter has not rested here, however. VAUGHN (1962a) returned to the question and, primarily by an examination of ROMER's (1950) arguments, suggests that the possibilities of a microsaur-captorhinomorph relationship should not be dismissed. A significant element of VAUGHN's argument is the view of WILLIAMS (1959) that the lepospondylous centrum can be equated with the amniotic pleurocentrum and the pleurocentrum of labyrinthodonts. Confidence in the conclusions of WILLIAMS removes a major barrier to microsaur-reptilian relationships.

If the construction of the centrum in the two groups were the only significant difference, WILLIAMS's work would have resolved the controversy. However, other features have been used in assessing the position of microsaurians and captorhinomorphs, and it is these that VAUGHN examines carefully.

VAUGHN is not certain whether the line of weakness between skull table and cheek in captorhinomorphs represents an ancestral otic notch, and, as an alternative, suggests that the line of weakness was adaptive in captorhinomorphs. However, the region of the ancestral otic notch is shown clearly in *Limnoscelis*; for want of a more satisfactory explanation of the loss of the notch and the appearance of the region in *Limnoscelis*, ROMER's (1946) explanation stands unmodified. That the line of weakness continues into the region of the ancestral otic notch in captorhinomorphs is beyond doubt; that selection was responsible for the posterior extension of the line of weakness is in accord with accepted evolutionary theory. Consequently, it seems probable that the "alternatives" are not that at all, and that the line of weakness has invaded the region of the ancestral otic notch by the process of selection, and that the remnant of the notch was preserved in its new function as an extension of the line of weakness.

VAUGHN's doubts about the nature of the line of weakness lead him to the broader question of whether captorhinomorphs were descended from labyrinthodonts. He cites the work of OLSON (1947), WATSON (1954), and VAUGHN (1955) that emphasized the distinctness of the captorhinomorphs and the diadectomorphs. That the members of the two groups are distinct is now generally accepted, but that the features of neither group bar it from an ultimate embolomerous origin seems in accord with presently available evidence. An overwhelming preponderance of similarities between primitive reptiles and embolomeres far outweigh the difficulties (e.g., PARRINGTON, 1958; HOTTON, 1960) mitigating against such a lineage.

VAUGHN devotes considerable attention to the size and position of the supratemporal bone in microsaurians. He notes that it is large in "typical" microsaurians, such as *Euryodus* and *Cardiocephalus*, and touches the postorbital and postfrontal bones broadly. In contrast to this pattern, Vaughn states that in the Mississippian genera *Dolichopareias* and *Adelogyrinus* the postorbital is interposed between the

postfrontal anteriorly and the supratemporal posteriorly. In his view, such a peculiar pattern may be correlated with the extremely long skull possessed by these genera. In the microbrachid genera *Hylopleision* and *Microbrachis*

the supratemporal has only limited contact with the postorbital and does not come anywhere near the postfrontal, being separated from that bone by a lateral lappet of the parietal. The sutural pattern in the recently described captorhinomorph reptile *Paracaptorhinus* (WATSON, 1954) is remarkably similar to that of microbrachids (VAUGHN, 1962a, p. 81).

However, in spite of the implication that if the supratemporal is large in "typical" microsaurians, it is of some other size in microsaurians that are not "typical," it has yet to be shown that the supratemporal in *any* microsaurian is small. An effort is made in this direction by Vaughn's noting that in primitive captorhinomorphs, such as *Limnoscelis* and "some romeriids," the supratemporal is larger than in more advanced genera, such as *Captorhinus*. The reduction of the supratemporal during the advance of the captorhinomorphs is well established. What is not established, but what is implied, is that the supratemporal in primitive captorhinomorphs occupies an area of the skull equivalent to that occupied by the bone in such microsaurians as *Microbrachis*. For example, in *Limnoscelis* the length of the supratemporal appears to be roughly one-fifth the length of the skull (ROMER, 1956, p. 69, fig. 35A); the width of the bone is a little less than one-fifth of the width of the dorsal skull table. In the most primitive romeriid of WATSON's (1954) morphological series, *Protorothyris*, the total length of the supratemporal can be included in the length of the skull some five-and-a-half times. The width of the supratemporal in *Protorothyris* can be included in the width of the skull table approximately eight times. The bone in other members of the series is comparable in size to that of *Protorothyris* or is smaller. In VAUGHN's figure of *Microbrachis*, on the other hand, the length of the supratemporal is included in the length of the skull slightly less than four-and-a-half times; the width of the skull roof is between two-and-a-half and three times the width of the supratemporal. In *Hylopleision* (ROMER, 1950, p. 635, fig. 2A) the length of the supratemporal is comparable to that of *Microbrachis*; the width is somewhat less than in that genus, being about one-fourth that of the skull table and, consequently, more like that in primitive captorhinomorphs. But in *Hylopleision* the supratemporal bears a posteriorly directed process strongly resembling that found in the Mississippian genus *Adelogyrinus*, but resembling nothing found in captorhinomorphs or pelycosaurians.

Turning to primitive pelycosaurians, VAUGHN states that in these, too, the supratemporal is large. In the eothyridid *Eothyris parkeyi* the length of the supratemporal is included in the length of the skull about seven times; the width is included in the width of the skull about six times (WATSON, 1954, fig. 10). VAUGHN's assessment of the size of the supratemporal in another eothyridid, *Colobomycter*, is inferential, as that element is not present in the specimen, the only skull of *Colobomycter* known, upon which his description was based. "There is a broad, rabbeted posterolateral edge, over which must have lain the anterior end of a rather large supratemporal, unusual among pelycosaurians" (VAUGHN, 1958b, p. 982). It should also be noted

that VAUGHN, in attempting to determine the affinities of *Colobomycter* and in spite of his estimate of the size of the supratemporal in that genus, states:

There is no possibility of any connection with microsaur. The pattern of parting of the sutures of the dermal roof under crushing pressure indicates the presence of a persistent line of weakness in the position of the ancestral otic notch (VAUGHN, 1958b, p. 985).

The above comparisons of the length and breadth of the supratemporal *relative to the dimensions of the skull* in microbrachids, captorhinomorphs, and eothyridids, supply ground for categorical disagreement with VAUGHN's contention (1962a, p. 81) that "It may be seen that the size of the supratemporal is not a safe criterion for distinction between microsaur and captorhinomorphs."

Where VAUGHN sees similarities in the sutural patterns of *Microbrachis* and *Paracaptorhinus*, we see dissimilarities. In the microsaur the supratemporal is broad and reaches medially to contact the postparietal. In *Paracaptorhinus* a moderately wide posteriorly directed lappet of the parietal intervenes between the supratemporal and the postparietal. In *Microbrachis* the lateral lappet of the parietal is quite weak, and the medial suture of the postorbital is dorsally convex. In *Microbrachis* the lateral border of the parietal extends beyond the lateral border of the postfrontal; in *Paracaptorhinus* it does not. In *Microbrachis* the anteriormost extent of the parietal falls rather short of the rim of the orbit; in *Paracaptorhinus* it reaches the level of the rim of the orbit. In *Microbrachis* the supratemporal is broader than long; in *Paracaptorhinus* the supratemporal is far longer than broad. In *Microbrachis* the postparietals are quite small; in *Paracaptorhinus* the postparietals are over twice as large as in *Microbrachis*.

The major resemblance in the sutural pattern of the two genera is in the narrow contact between the postorbital and the supratemporal. If this means that relationship between microsaur and captorhinomorphs is to be based on this single feature of the sutural pattern, what, for example, is to be said of the relationship of *Diadectes*, also the possessor of a narrow contact between postorbital and supratemporal, to the captorhinomorphs? Recent opinion holds that the diadectids and captorhinomorphs are related distantly, at best.

VAUGHN is uncertain of the orthodox belief that

microsaur is distinct in their relatively long postorbital region of the skull. This may be true for "typical" microsaur, but in the primitive *Hylopleosion* (ROMER, 1950, fig. 2A) the centers of the orbits lie as far back in the length of the skull as they do in the captorhinomorph *Paracaptorhinus* and in an unnamed captorhinomorph from the lower Permian (WATSON, 1954, fig. 7D).

The statement is accurate in regard to the latter genus, but is not so in regard to the former, as simple measurement of the figures concerned shows. The unnamed romeriid is too firmly fixed in the sequence of evolving captorhinomorphs for the resemblance in this feature to a single genus of microsaur to be significant. Among the genera pictured by ROMER (1950, p. 634, 635; figs. 1, 2), *Euryodus*, *Dolichopareias*, *Adelogyrinus*, *Pantylus*, *Ostodolepis*, and *Microbrachis* are all markedly short-faced forms. Mississippian, Pennsylvanian, and Permian times are represented by these genera. Even in *Hylopleosion* the orbits are located anterior of the mid-point of the skull

length. Consequently, the phenomenon is not one in which the microsaurian genera have shortened the facial region, but rather one in which a single captorhinomorph genus has lengthened the postorbital region and has converged toward the microsaurian condition that is characteristic of the vast majority of microsaur throughout their range in time. The single character of "short-facedness" perhaps would not be useful in distinguishing the genera that VAUGHN has selected for its application. But the character apparently is as deep-rooted in the microsaur as is its opposite among the captorhinomorphs. As such, it is useful in making judgments about the possible affinities of the two groups.

VAUGHN (1962a, p. 82) states that:

The structure of the palate offers no bar to a connection between microsaur and captorhinomorphs. The palate in certain advanced, early Permian microsaur as *Cardiocephalus* may be specialized in such features as broadening of the parasphenoid, but that in earlier microsaur is of a primitive pattern, with a narrow anterior process of the parasphenoid and movable articulation between braincase and palate.

In lieu of VAUGHN's lack of specification of the primitive microsaur to which he is referring, if we examine the illustrations of the palate in *Microbrachis* and *Hylopleosion* (two genera categorized as primitive by VAUGHN) we find in both genera wide interpalatal vacuities and a parasphenoid widened posteriorly (PIVETEAU, 1955, p. 293, fig. 22; p. 298, fig. 29). ROMER (1950, p. 636) is in agreement with VAUGHN's criteria of the palate as an aid to defining microsaur, but feels no need to call upon a broadened parasphenoid to do so. Nor does ROMER judge that the microsaurian palate characterized in part by a long parasphenoidal rostrum and movable basal articulation shows any specific resemblance to that of reptiles.

In the remainder of the features commented upon by VAUGHN—the apparent one-part construction of the vertebral centrum, the lack of swollen neural arches, the 3-toed manus and the radiate scales of microsaur (see, however, PEABODY, 1959)—little comment is called for. VAUGHN, however, states in regard to the large number of presacral vertebrae found in microsaur

about forty in *Microbrachis* as against twenty-five in cotylosaur— is probably a specialization without great significance in regard to the external connections of the group. There is, to choose an example from another group of tetrapods, no doubt of the relationship of snakes to lizards.

Although the count for *Microbrachis* is more than usual among microsaur (ROMER, 1950, p. 632), a slender body about four times the length of the skull appears to be the usual proportion. If this represents a specialization, it was one that was acquired early in the history of the group, and one which is not seen among captorhinomorphs. The analogy used by VAUGHN in regard to the origin of snakes from lizards is not exactly appropriate, since the increase in the number of vertebrae was exhibited in the descendant group rather than a decrease. An increase in the number of vertebrae is a common correlate to limb reduction or loss; this may be the case in the weak-limbed microsaur.

The captorhinomorphs do not appear to converge toward the microsaur backward in time. Some of the similarities that are present may reasonably be viewed as

adaptations to a mode of life in microsaurians that was similar to the mode of life of captorhinomorphs. Other features of the microsaurians that have been put forth as resemblances to features of captorhinomorphs are mainly limited to one microsaurian genus and one captorhinomorph genus. Both are rather far removed from the primitive morphology of their respective groups and are considerably younger than the earliest members of each group. Other features that are superficially quite similar in microsaurians and captorhinomorphs are fundamentally quite different, as has been shown above. The establishment of affinities between the microsaurians and the captorhinomorphs on the basis of these characters is, in our opinion, untenable.

An additional feature of at least some microsaurians has never been offered in the controversy concerning micro-saurian-reptilian relationships, as far as is known. At least among the gymnarthrid microsaurians the occipital-atlantal articulation resembles nothing that is known from among the reptiles, but bears a strong resemblance to the structure in urodeles. An "odontoid" knob of the atlas fits into a basioccipital depression (GREGORY, PEABODY & PRICE, 1956, p. 43). This feature among microsaurians that superficially resemble contemporaneous captorhinomorphs rather strongly is an additional barrier to affinities between the two groups.

PRIMITIVE CHARACTERS COMMON TO CAPTORHINOMORPHS, SEYMOURIAMORPHS AND EMBOLOMERES

The establishment of affinities between the seymouriamorphs and the captorhinomorphs depends in part on a determination of the features that are common to the two groups because of their special relationship to each other. Characters common to both captorhinomorphs and seymouriamorphs that are also found in embolomeres are not useful in establishing an ancestral-descendant relationship between seymouriamorphs and captorhinomorphs, given the time range of the two groups that is discussed below. These characters do not eliminate the possibility of such a relationship, but they do nothing to support it positively, as the characters may be used with equal effectiveness to support a direct origin of the captorhinomorphs from the embolomeres.

ROMER (1947, p. 301) lists six characters that are held commonly by embolomeres and seymouriamorphs but that are not characteristic of temnospondylous amphibians. These features thus unite the pre-reptilian line into a natural group and differentiate it from the divergent assemblage of temnospondylous amphibians and their descendants. In both embolomeres and seymouriamorphs a large tabular bone articulates with the parietal; the internal nares are relatively close together; the vomers are narrow; there is a large gap in the lateral walls of the braincase between sphenethmoid and otic regions; the carotid artery passes medial to the basiptyergoid processes; and the vertebrae are characterized by a complete ring-shaped true vertebral centrum. Of these features only the first is modified in captorhinomorphs: the tabular is usually reduced, sometimes assumes at least a partially occipital aspect, and is altogether lost in such advanced genera as *Captorhinus*.

ROMER also lists seven characters common to embolomeres and seymouriamorphs that are not held by temno-

spondyls and that, because of structural conservatism of the characters, indicate the existence of a special relationship between embolomeres and seymouriamorphs. These are retention of an intertemporal bone, small interptyergoid vacuities, movable basal articulation, single occipital condyle, entepicondylar foramen in the humerus, posterior elongation of the ilium, and retention of multiple coronoid bones in the lower jaw.

Of these seven characters all but the first are known in the captorhinomorphs. In them the intertemporal bone is lacking; a lateral lappet of the parietal occupies its former position. Although the captorhinomorphs do not commonly possess multiple coronoid bones. *Hylonomus* has at least two (CARROLL, 1964, p. 68).

As ROMER (1947) has remarked, diagnostic differences between embolomeres and seymouriamorphs are few; the differences that are present are not so much a matter of distinct features as a matter of different development or emphasis of the same features. The features that he includes in this category are a rounded otic notch and a cheek region solidly united to the skull roof in seymouriamorphs (except *Gephyrostegus*), versus a more narrow otic notch and a cheek region loosely united to the skull roof in embolomeres; the absence of a tabular horn in seymouriamorphs as opposed to its presence in embolomeres; the increased expansion of the gap in the lateral wall of the braincase in seymouriamorphs; and reduced jaw fenestrae among seymouriamorphs. The captorhinomorphs are more similar to the seymouriamorphs than to the embolomeres in these characters; the captorhinomorphs differ from the seymouriamorphs in their loss of the otic notch and retention of a weak connection between dorsal roof and cheek in primitive genera.

DO CAPTORHINOMORPHS CONVERGE TOWARD SEYMOURIAMORPHS BACKWARD IN TIME?

If two groups are related and their late members show little similarity to each other, tracing of their features backward in time should reveal greater and greater resemblance, even if no satisfactory intermediates are known.

The earliest reptiles known, from the Middle Pennsylvanian of Joggins, Nova Scotia, have recently been reviewed by CARROLL (1964). Two genera of romeriid captorhinomorphs, *Hylonomus lyelli* and *Archerpeton anthracos*, are described. *Hylonomus* is thought by CARROLL to be a captorhinomorph, "close to the ancestry of the Permian romeriids." *Archerpeton*, more poorly known than *Hylonomus*, nevertheless can be categorized as a primitive captorhinomorph. It is CARROLL's estimate that in the pattern of the skull roof, the palate, braincase, and postcranial skeleton, in so far as each and any of these are known, both *Hylonomus* and *Archerpeton* resemble captorhinomorphs. "On the basis of vertebral construction, their ancestry can presumably be sought somewhere within the anthracosaurs, but nothing more definite can be determined at present" (CARROLL, 1964, p. 82). Similarly, the fragmentary remains of the primitive pelycosaur from the Joggins that CARROLL has described, *Protoclepsydraps*, show no evidence of seymouriamorph affinities, although nothing known of the genus casts doubt on the widely

held view that pelycosaurs and captorhinomorphs are derivatives of a common stock.

The early reptiles from Joggins and those that are slightly later in time but still are among the earliest of the reptiles known, *Eosaurus* and *Cephalerpeton*, possess many characters to support the estimate that the captorhinomorphs, at their first appearance in the record, have progressed morphologically to a fully reptilian condition and show none of the mixture of amphibian and reptilian features that are possessed by the seymouriamorphs.

The skull roof, where known, of the early captorhinomorphs lacks the otic notch and the intertemporal bone. The supratemporal is small and extends to the posterior border of the skull roof; the tabular is small and adjacent to the supratemporal. The squamosal is large, an expansion of the bone beyond its size among anthracosaurs, and one that has been made largely at the expense of the quadratojugal. Even of *Limnoscelis*, far later than the early romeriids, but in some respects more primitive than they, ROMER (1947: 304) states:

I have recently (ROMER, 1946) discussed the structure of *Limnoscelis*, an archaic reptile which I believe to lie close to the base of that class. This form exhibits a pattern of the skull table which seems diagnostically reptilian, and is not found in known seymouriamorphs. In this pattern the intertemporal has been lost, and parietal and postorbital (much as in ichthyostegids) meet anterior to the supratemporal; the latter element remains wedged anteriorly into the lateral expansion of the parietal and runs back along the erstwhile margin of the vanished otic notch between tabular and squamosal to the posterior margin of the skull.

GREGORY (1950, p. 863, fig. 11) has reconstructed the skull of *Cephalerpeton* with postfrontal and squamosal meeting behind the postorbital, with the result that the postorbital and parietal fail to come into contact with each other. The pattern of these bones in *Cephalerpeton* seems to be a specialization in light of the more frequent captorhinomorph pattern seen in the early *Hylonomus* and the primitive *Limnoscelis*. The romeriids from Texas conform to this latter pattern, also.

The parasphenoid of *Hylonomus* is similar to that of *Captorhinus*, although the cultriform process is longer and wider in *Hylonomus*. The parasphenoid of *Archerpeton*, according to CARROLL,

is much more primitive than in any other reptile. The posterior plate is very broad and flat with little tendency to curve upward around the base of the braincase. The parasphenoid diminishes only gradually in width anterior to the basicranial articulation. The cultriform process is less differentiated from the plate than in any other Paleozoic reptile. The central portion of the plate and process is covered with denticles. The basiptyergoid processes extend ventrolaterally from the plate and only slightly anteriorly (p. 76).

The shape of the parasphenoid in *Archerpeton* suggests to CARROLL that the interptyergoid vacuities were larger in that genus than in any other reptile of comparable age, in contrast to the seymouriamorphs in which the interptyergoid vacuities are small at best (ROMER, 1956, p. 479). In *Protoclepsydrops*, the parasphenoid is intermediate in shape between those of *Hylonomus* and *Archerpeton*, and shows no specific resemblance to the parasphenoid in seymouriamorphs. Nor do the ventrolaterally and anteriorly directed basiptyergoid processes of any of the Joggins reptiles resemble the stout laterally directed processes seen in *Seymouria* and its relatives.

The pterygoid of *Hylonomus* is similar to that of *Captorhinus*, except, as CARROLL notes (p. 66), the socket for articulation of the pterygoid with the braincase lies in front of the lateral flange of the pterygoid, as in *Petrolacosaurus* and *Youngoides* (PEABODY, 1952, p. 12), and not behind it, as in *Captorhinus*. PEABODY suggests that this character may be primitive in reptiles; in *Limnoscelis*, however, the socket is comparatively far back of the level of the flange (WILLISTON, 1925, p. 38, fig. 24). In *Seymouria* the processes appear to be at the level of the flanges; in the presumably more specialized *Kotlassia*, however, the processes are in front of the flange (ROMER, 1956). The pterygoid of *Archerpeton* appears to bear its socket in front of the flange (CARROLL, 1964, p. 78, fig. 12) although no remark in the text is made of this feature other than it is crushed, making interpretation of the nature of the joint impossible. The element may not be of *Archerpeton*, but may be referable to *Protoclepsydrops* (CARROLL, 1964, p. 80). Regardless of the genus to which it pertains, it lacks seymouriamorph features.

The intercentra of *Hylonomus*, *Cephalerpeton*, and *Eosaurus* (the intercentra of *Archerpeton* and *Protoclepsydrops* are not known) do not extend far dorsally. CARROLL, in regard to *Hylonomus*, states (p. 69): In the few places where the vertebrae are in articulation, it is evident that the intercentra must have been small, as are those of *Cephalerpeton* and *Petrolacosaurus*. PEABODY (1959, p. 5, fig. 1) has represented the intercentra of *Eosaurus* as small ventral wedges. In the large-bodied *Limnoscelis*, ROMER (1946, p. 177) reports that the "intercentra are well developed, but reduced from the condition seen in *Seymouria*."

According to ROMER (1947) in the earliest and most primitive of known seymouriamorphs, *Gephyrostegus*, the intercentra are nearly complete rings, as in the Early Permian *Discosauriscus*; it is only in the more advanced *Seymouria* and *Kotlassia* that the intercentra become reduced, although they still retain an apparent dorsal continuation in cartilage of considerable extent.

The iliac blade of the pelvic girdle appears to be comparable in *Hylonomus* and *Captorhinus*; the blade in these genera also resembles that of *Protoclepsydrops* (CARROLL, 1964, p. 82). In these genera the ilium progresses posterodorsally as a thin extension from the ventral expansion. The blade in *Protoclepsydrops* lacks the dorsal trough for the axial musculature that is found in other early pelycosaurs and so appears to be primitive. Neither the romeriids nor *Protoclepsydrops* retain the bifurcate condition of the blade found in embolomeres nor the partial bifurcation found in seymouriamorphs.

Neither *Hylonomus* nor *Eosaurus* possesses a tarsus that resembles that of seymouriamorphs. CARROLL (1964, p. 75) notes that a *Captorhinus*-like astragalus is known in *Hylonomus*; PEABODY (1959, p. 8) reports the same structure in *Eosaurus*. The tarsus of *Hylonomus* is fully known, and, in CARROLL's estimate (p. 75) "agrees essentially with that of *Captorhinus*." With the exception of the retention of the sixth distal tarsal or postminimus, the tarsus of *Eosaurus* is fully compatible with later captorhinomorphs, although in these, median and lateral centralia are usually fused.

In summation, then, there seems to be no convergence

in these characters toward seymouriamorphs (or even embolomeres) backward in time. The seymouriamorphs do share characters with the captorhinomorphs, however. These are listed below, following ROMER (1947, p. 302):

Common Characters of Seymouriamorphs and Captorhinomorphs

1. Presence of a lacrimal duct.
2. A manus of five digits.
3. Phalangeal formula (in *Seymouria*) of 2.3.4.5.3 or 4.
4. A wide gap in the lateral wall of the braincase.
5. A supraoccipital bone.
6. A stemmed interclavicle.
7. A separate coracoid ossification.
8. Expanded iliac blade.
9. Combination of crescentic intercentra with "complete" true centra beneath the neural arch.

In so far as known the captorhinomorphs possess each of these features. It is the combination of these features with a long catalog of characters of embolomeres nature that is possessed by the seymouriamorphs. It is the combination of these same nine features with an equally long catalog of features modified from the embolomeres and, by extension, from the seymouriamorph condition, that defines the captorhinomorphs. And, as will be seen below, not all of these features are restricted to the captorhinomorphs and seymouriamorphs. In the shape of the skull, the pattern of the dermal roof, the nature of the palate, the character of the articulation of the palate and braincase, and the morphology of the postcranium, the early romeriids have already departed from the embolomeres and the seymouriamorphs; the seymouriamorphs that are pertinent in this regard are not *Seymouria* or *Kotlassia*; these are far too advanced and appear too late in time to be of significance in any discussion of the origins of the captorhinomorphs. The pertinent seymouriamorphs, if there are any, are much more primitive, earlier and less well known than these "typical" genera, but it is to these primitive genera that reference must be made in the discussion of the seymouriamorph origin of the captorhinomorphs.

POSTCRANIAL SKELETON OF LIMNOSCELIS

Limnoscelis is the most primitive of the known captorhinomorphs. If difficulties exist in appraising its features, these center about the proper evaluation of the resemblances that *Limnoscelis* bears to the seymouriamorphs. Are the similarities due to derivation of *Limnoscelis* from seymouriamorphs, or are they the result of the retention of characters from embolomeres? If the characters that have been used to support a seymouriamorph derivation for *Limnoscelis*, or, more exactly, for a *Limnoscelis*-like animal properly placed in geologic time, can be shown to exist in embolomeres, difficulties in logically attempting to derive A (captorhinomorphs) from B (seymouriamorphs) on the basis of characters found also in the ancestral C (embolomeres) are encountered.

ROMER (1946) and WATSON (1954) have devoted considerable attention to the features of the skull in *Limnoscelis*. To ROMER, the morphology of the skull is compatible with a seymouriamorph ancestry; to WATSON, it is not. No further analysis of the skull will be undertaken here; the postcranial skeleton has received less complete

attention, however, and yet does bear on the matter of the affinities of *Limnoscelis*.

One of the features of the postcranial skeleton that has been taken as suggestive of a seymouriamorph-*Limnoscelis* relationship has been the character of the neural arches. In both *Seymouria* and *Limnoscelis* these are swollen, implying that these and other primitive reptiles possessing swollen neural arches constitute a related assemblage. VAUGHN (1962a) points out that swollen neural arches appear to have arisen independently in several lines: the primitive *Gephyrostegus* and *Hylonomus* lack them although they are found in more advanced seymouriamorphs and captorhinomorphs, and they occur in various genera of microsaurus. VAUGHN suggests that swollen neural arches may well have been an early experiment in the solution of problems of support in an environment of air. *Limnoscelis* was a large animal, nearly 90 inches in length (WILLISTON, 1925, p. 219, fig. 164), and of bulky proportions. Swollen neural arches might reasonably be expected in a primitive reptile of such size.

Similarities in the pes of *Limnoscelis* and *Seymouria* are sometimes cited to advance the relationship between the two genera. SCHAEFFER (1941, p. 429) states, for example:

The tarsus of *Limnoscelis* (WILLISTON, 1911a) is almost identical with that of *Seymouria*, in that there are three separate proximal elements. The fibulare and intermedium are, incidentally, the only ossified elements. As in *Seymouria*, the intermedium articulates about equally with the tibia and fibula, the latter two bones being of the same length. With the tibia extensively articulating with the intermedium, it was in a position to support a large share of the body weight directly, thus removing the necessity of a weight transference from the tibia to the fibula as in *Trematops*.

However, in the tarsus of *Seymouria* only the tibiale, intermedium and fibulare are known with certainty; the number of centralia is unclear (ROMER, 1956, p. 391-392). In *Limnoscelis* only the fibulare and the intermedium are known (WILLISTON, 1911a). In both of these genera the tarsal elements appear to be rather characterless, roughly triangular blocks, and poorly ossified at least in *Seymouria*.

SCHAEFFER implies relationships between the seymouriamorphs and *Limnoscelis* by their mutual possession of a dual proximal articulation of the intermedium, both with the fibula and with the tibia, in contrast to the presumed primitive condition in the rachitome *Trematops*, in which the tibia is supported only by the tibiale and the fibula by the intermedium and fibulare. Yet this feature is already known in the embolomere *Archeria*, of presumed aquatic habits. ROMER (1957b, p. 147, fig. 15) has restored the tarsus of *Archeria*, and shows the distal end of the tibia articulating both with the tibiale and a medially directed facet of the intermedium. The distal articulation of the fibula is with both the fibulare and the intermedium. This primitive reptilian feature had been achieved already in embolomeres.

The character of the femur may be thought of as indicating a derivation of limnoscelids from seymouriamorphs; ROMER (1956, p. 362) states: "*Limnoscelis* has a femur quite similar to that of the seymouriamorphs," and again, in his diagnosis of limnoscelids (p. 493): "Limbs massively built, comparable in many ways to *Seymouria*, notably in general construction of humerus and femur." Pre-

sumably, however, those similarities in the femora of *Limnoscelis* and *Seymouria* are due to the primitive nature of these animals among reptiles. ROMER (1922), after describing the femur of *Eryops* as representative of the primitive tetrapod femur, states (p. 582):

In the most primitive cotylosaurs (*Seymouria*, *Diadectes*, *Limnoscelis*) there is essentially the same plan on the under side; dorsally, the only change is that the median portion is expanded, apparently because of the intrusion of the femoro-tibialis, giving the bone a more rounded form, in general, than in the Amphibia and thus reducing the apparent size of the ventral ridge system, which is still prominent.

The general plan of the femur among primitive reptiles is one readily comparable to that of the unrelated temnospondylous amphibians. Departures from this plan among primitive reptiles are possessed commonly by *Diadectes* and *Limnoscelis*, which current opinion holds are not closely related. The mutual possession by divergent primitive reptiles of a similar femur that differs from that of an ancestral "type" suggests that the origin of the similarity may be found among members of the group ancestral to reptiles. Again, turning to *Archeria*, ROMER (1957b, p. 130, fig. 8) has shown the femur of *Archeria* to be so captorhinid-like in dorsal and ventral views that the resemblance could be categorized as startling without running the risk of overstatement. Significant departures from the captorhinid femur appear to be in the weak development of the internal trochanter and the relatively proximal position of the fourth trochanter. Seemingly, according to ROMER's (1922) criteria, the reptilian advance beyond the plan in *Eryops* has been achieved already in *Archeria*.

The humeri of *Seymouria* and *Limnoscelis* are similar and the resemblances may be due to relationship. But it is also probable, if we consider the humerus alone without reference to other criteria, and more reasonable, if we take into account the late appearance of seymouriamorphs in the record, that the resemblances are derived from the primitive nature of the limbs and not from close affinity. In support of this thesis, ROMER (1956, p. 353) states:

In *Seymouria*, the diadectids and the large and primitive captorhinomorph *Limnoscelis*, the humerus is of a diagrammatic primitive nature, very heavily built and essentially a shaftless tetrahedron, with an entepicondylar foramen but otherwise very similar to that of such a contemporary amphibian as *Eryops*.

The humerus of *Archeria*, although compatible with the basic primitive type

is unusual in a number of features, most notably in the great expansion of the entepicondylar region, the relatively low degree of "twisting" of the ends of the bone, and the prominent lateral keel; it is further unusual, for an amphibian, in the presence of an entepicondylar foramen (ROMER, 1957b, p. 118).

The humerus of *Archeria*, in Romer's (p. 122) view, can be readily derived by simplification from that of *Ichthyostega*, among amphibians of aquatic habits. However,

the more "typical" tetrahedral type seen in such forms as *Eryops* and *Diadectes* was presumably developed in parallel fashion by forms which tended more toward a terrestrial existence (ROMER, 1957b, p. 122).

If seymouriamorphs and limnoscelids were derived separately from embolomeres, then the similarities that are present in the descendant groups can be explained reason-

ably on the same basis as those resemblances in the humerus of the unrelated *Eryops* and *Diadectes*.

The carpi of *Seymouria* and *Limnoscelis* are poorly known. In *Seymouria* the three proximal elements, radiale, intermedium and ulnare are present, as is the proximal centrale (ROMER, 1956, p. 381). The intermedium articulates about equally with the radius and ulna. However, the proximal centrale is no longer in contact with the radius; the primitive condition shown, for example, in *Eryops* has been lost. In *Limnoscelis* the same arrangement of the carpals as in *Seymouria* is found. The intermedium articulates with both radius and ulna; the second centrale and the third and fourth distal carpals are known (WILLISTON, 1925, p. 165, fig. 133). In *Limnoscelis*, however, the intermedium is equivalent in size to the other two proximal elements; in *Seymouria*, the intermedium is the smallest of the proximal series.

It appears that these primitive reptilian genera exhibit a carpus that departs from the arrangement of the carpals in more primitive tetrapods; the departure may coincide with the amphibian-reptilian transition. If this is true, the similarities in the carpus could be pointed to in evidence for a seymouriamorph-limnoscelid relationship. But WILLISTON (1910b) has shown that the manus of the rachitonomous labyrinthodont *Cacops* possessed three proximal elements arranged in the manner that those elements are arranged in *Seymouria* and *Limnoscelis*.

Any positive statement that takes us further in comparisons of the primitive reptilian carpus to the carpus of labyrinthodonts is very nearly impossible of attainment at present. The carpus among both temnospondyls and embolomeres is at best poorly known. ROMER (1947, p. 79) states:

The structure of the manus and pes should be extremely significant in evolutionary studies. But, as might be expected, this is known in very few cases and, even when found in articulated condition, much or all of the carpus and tarsus is often seen to have remained unossified (ROMER, 1957b, p. 126).

Knowledge of the carpus of *Archeria* is no exception to these limitations. The radiale is known, as are three of the other carpals. But the condition of the preserved material is especially unsatisfactory to do other than suggest a protoreptilian condition, rather than that known in temnospondyls and considered to be of normal amphibian type.

The pelvic girdle of *Limnoscelis* is, in most of its features, comparable to that of *Seymouria*. In the morphology of the iliac blade, *Limnoscelis* has advanced beyond the seymouriamorph condition and has departed even more radically from *Archeria*. ROMER (1957b, p. 112-118) has described in detail the morphology of the pelvis of *Archeria*. The ilium contributes to the acetabulum, then narrows to a relatively slender neck. Above this, the iliac blade bifurcates into a rather flat, dorsally directed anterior process, and a long, slender posteriorly directed posterior process. In *Seymouria* (ROMER, 1956, p. 316, fig. 150B) the iliac blade is nearly completely "filled in," as it were, in the area between the anterior and posterior processes, so that the blade is essentially a single, entire, subtriangular structure. Both in the pelvis of *Seymouria* and that of *Archeria* the dorsal axial musculature is thought to have overlapped on to the outside of the iliac blade (e.g., Ro-

MER, 1956, p. 317, fig. 151). Subsequent modifications in the external surface of the iliac blade resulted in the formation of a trough inset into the dorsal edge of the blade. The trough marked the lateral limit of the dorsal axial muscles; a correlative change involved the dorsal migration of the origins of the limb muscles up the external surface of the ilium. The iliac blade of *Limnoscelis* (ROMER, 1956, p. 317, fig. 151) exhibits a groove for the lateral restraint of the dorsal axial musculature; the external edge of the groove marks the intermediate height of the migration of the limb muscles on the external surface of the ilium. Seemingly, then, the iliac blade permits the derivation of *Limnoscelis* from seymouriamorphs.

Similarities exist in the shape of the endochondral pectoral girdle of *Seymouria* and *Limnoscelis*; ROMER (1947, p. 76) reports that the girdle is "almost identically constructed in both early reptiles and early amphibians." *Seymouria* possesses but one coracoid; the number in *Limnoscelis* is apparently still uncertain (e.g., VAUGHN, 1955, p. 451; ROMER, 1956, p. 493). Both the endochondral girdle and the dermal girdle offer little in the way of positive evidence to support a limnoscelid-seymouriamorph relationship. The number of coracoids is clouded, not only in *Limnoscelis*, but in many amphibians, as well, with indications that multiple coracoids may have arisen independently (ROMER, 1947, p. 76). Unfortunately, equal limitations apply to the dermal girdle; a stemmed interclavicle is not limited to seymouriamorphs and captorhinomorphs, but is found in other groups as well. According to ROMER (1947, p. 301), too, ". . . we have as yet little proof of its general absence among embolomeres." Significantly, a stemmed interclavicle occurs in such temnospondylous labyrinthodonts as *Cacops*, *Dvinosaurus*, and *Mastodonsaurus*; the interclavicle in these animals is comparable to that of the seymouriamorphs *Phaiherpeton*, *Kotlassia*, and *Discosauriscus* (ROMER, 1947, p. 74-75, figs. 13, 14). There seems little doubt that a stemmed interclavicle, like swollen neural arches, arose as an adaptation to increased terrestriality. A convergent interpretation is supported by the possession by microsaurids of an "interclavicle with a very broad but short fan-shaped head and short slender stem. . . . the interclavicle is however, a unique type" (ROMER, 1950, p. 633).

RELATIONSHIP IN TIME

Not only must related groups exhibit similar morphological features, but they must also have a relationship in time that is, at best, fully compatible with, or at worst, at least partially compatible with any conclusions drawn from morphological similarities.

In the discussion of the possibility of the captorhinomorphs and the seymouriamorphs bearing a descendant-ancestral relationship, six genera are particularly important. The first of these, *Gephyrostegus*, is the earliest and most primitive of known seymouriamorphs. The genus is in part characterized by normal, nonswollen neural arches, a parasphenoid that is of normal proportions, an otic notch that is more narrow than that of *Seymouria*, and skull contours that resemble those of primitive reptiles (ROMER, 1956). The nature of these and additional features place the animal close to embolomeres. There is no specific re-

semblance to captorhinomorphs other than in those features that are due to the primitive nature of the animal; such features presumably are retentions from embolomeres.

Gephyrostegus is from the Nýřany Gaskohle of Bohemia. The horizon lies at the top of the Upper Westphalian or the base of the Lower Stephanian.

Two genera from the United States are pertinent. The younger of these, *Eosauravus*, is from the upper Freeport coal of Linton, Ohio, at the top of the Allegheny Series. The horizon is perhaps equivalent to that of the Nýřany locality (ROMER, 1947). The other genus, *Cephalerpeton*, was taken from the Mazon Creek nodule beds, in the shales overlying the Morris or No. 2 coal, at the base of the Carbondale Formation, Middle Allegheny Series. This horizon is equivalent to the Westphalian C of Europe (GREGORY, 1948), and is consequently somewhat older than the Nýřany and Linton horizons.

The earliest of reptiles known are those from the Middle Pennsylvanian of Joggins, Nova Scotia. CARROLL (1964) suggests that *Hylonomus*, *Archerpeton*, and *Protoclepsydrops* are from a level equivalent to that of the Westphalian B of Europe or the Upper Pottsville of the United States.

Consequently, on the basis of the presently accepted evidence, *Cephalerpeton*, *Hylonomus*, *Archerpeton*, and *Protoclepsydrops* all antedate *Gephyrostegus*. Each of these North American reptiles has achieved a level of phyletic development sufficient to enable them to be assigned with reasonable security to groups of undoubted reptilian grade; one of the reptiles, *Protoclepsydrops*, appears to have diverged already from the captorhinomorph phylum, and, in CARROLL's estimate, is referable to the pelycosaurs; all of these events appear to have occurred at a time that preceded the appearance of the first known seymouriamorph, which itself is so primitive that the choice between an embolomere or seymouriamorph assignation is made with difficulty (e.g., ROMER, 1947, 1956; PIVETEAU, 1955).

PHYLOGENETIC AND ECOLOGIC POSITION OF CAPTORHINOMORPHS

The evidence that has been presented leads to the conclusion that the captorhinomorphs do not converge toward the seymouriamorphs backward in time; that the characters in common either are not known primitively and presumably have arisen in response to similar adaptive demands, or were possessed also by the ultimately ancestral embolomeres and logically cannot be used to support the derivation of captorhinomorphs from seymouriamorphs under the limitations imposed by the known range in time of each; and that the microsaurids have nothing whatever to do with the origin and relationship of captorhinomorphs.

At a less precise level of discussion, but one that is nevertheless pertinent, is the divergence in the adaptive nature of the captorhinomorphs and the seymouriamorphs. The latter, as well known, possess an intriguing combination of amphibian and reptilian characters that has resulted in the group at various times being assigned to the amphibians and at other times to the reptiles. The characters that have provided such a difficult moulange to assess satisfactorily to all concerned workers are the unique products of the selective forces that affected the seymouria-

morphs. The retention of embolomeric characters of a primitive nature in this group is a result of that selection, and the same can be said of the appearance of the new, "reptilian" characters. The peculiar combination of reptilian and amphibian features is not limited to the "typical" well-known genera, such as *Seymouria*, but is found to greater or less extent in all members of the seymouriamorphs. The characters of *Gephyrostegus*, the most primitive and the earliest of the known seymouriamorphs, include many that cause that genus to be placed close to the origin of the seymouriamorphs from the embolomeres. Nevertheless, *Gephyrostegus* is presently recognized as a seymouriamorph; it is not an embolomere nor a captorhinomorph, for *Gephyrostegus* seems to exhibit enough of the features that define seymouriamorphs to enable a reasonable judgment to be made that this animal was a part of the limited radiation characteristic of this peculiar amphibian-reptilian group.

On the other hand, at their first known appearance, before that of the known seymouriamorphs, the captorhinomorphs are clearly and definitely reptilian. No features in genera of known captorhinomorphs suggest that these animals occupied the amphibian-reptilian niche of seymouriamorphs. No known features or complexes of features suggest that at any time during their phyletic history the captorhinomorphs paralleled the seymouriamorphs in possessing a striking and persistent combination of amphibian and reptilian characters or that a combination of amphibian and reptilian features were useful to the survival of the group or any of its members. The origin and subsequent differentiation of the captorhinomorphs seems to have been a rapid change and to have been succeeded by an impressive radiation of new kinds of captorhinomorphs, all in keeping with a mode of life that appears to have been distinctly reptilian in all of its phases.

These differences suggest that different ancestral gene

pools were involved in the origin of each group from the embolomeres; not only were there differences in niches and evolutionary rates, but there was also a difference in the genetic putty among the embolomeres that separately gave rise to the seymouriamorphs and the captorhinomorphs. The long passage of time since the Early Pennsylvanian has left as its legacy much to obscure the early evolution of reptiles, but the fallibility of the record seems not great enough to explain the disparities in time, in niche, and in structure that must be taken into account if the captorhinomorphs are to be derived from the seymouriamorphs. If the entire aggregation of known seymouriamorphs are relicts, they must have arisen from seymouriamorphs that were rightly placed on the geologic calendar to give rise to their relict descendants and to the divergent captorhinomorph-pelycosaur stock, and that have remained quite unknown themselves. It is improbable that the record is so incomplete.

Time must be pushed back further to allow for the origin and development, to the degree known, of the observed captorhinomorphs. At their appearance, the genera are fully recognizable as captorhinomorphs. If these events are to be accounted for, the captorhinomorphs must have possessed a prehistory of some unknown length embracing the time of their origin from the embolomeres to the Middle Westphalian, the time of their first appearance in the record, and their history must be pushed back even further into this unknown time span to find suitable intermediates. In meeting these demands, the appearance of the first known seymouriamorph is further removed in time and if captorhinomorphs are to be derived from the seymouriamorphs, the first seymouriamorph must be placed even further back in time. It may be that future exploration and discovery will make the history of the seymouriamorphs compatible with the ancestry of the captorhinomorphs. That such will be the case is improbable.

DESCRIPTION OF SPECIMENS EXAMINED

The more important specimens examined in this study are listed below; most of them are skulls or partial skulls, or articulated postcranial material. Not included are hundreds of isolated elements, mostly uncatalogued, from the Richard's Spur locality, both in the collections of The University of Kansas and in the material loaned to Dr. THEODORE H. EATON, Jr. by Mrs. ANNA PEABODY.

The descriptions are reported both for the value they possess in themselves and for the purpose of providing an index and control for the features of *Captorhinus* and other genera that are discussed in this paper.

CAPTORHINUS AGUTI

ABO FORMATION

UR 735. Poleo Creek, Rio Arriba Co., New Mexico.

The specimen consists of numerous rock fragments containing: (1) eight articulated vertebrae exposed in ventral and left lateral view; (2) a single vertebra exposed in ventral view; (3) many unidentifiable fragments and a part of a front foot; (4) three vertebrae exposed ventrally; (5) four vertebrae exposed ventrally; (6) the head of a right humerus; (7) the head of a right femur; (8) the head of an ulna; (9) small unidentifiable scraps.

BELLE PLAINS FORMATION

MCZ 1483. Texas. The specimen is very poor. The skull has been smashed, and presumably consists only of the left half. Left parietal, squamosal, quadratojugal, jugal, postfrontal, postorbital, frontal and prefrontal can be identified, although all are badly cracked. The left maxilla is badly shattered as is the snout. A left femur adheres to the matrix. In spite of the poor condition of the skull, it does seem to show a small notch at the base of the squamosal and quadratojugal on the occiput.

UC 1119. Near Vernon Crossing, Wichita River, Baylor County, Texas. The entry consists of 14 fragments, all but one of which, a partial occiput, are essentially worthless. The occiput shows the stapes directed toward the position of the external auditory meatus. Although the stapes has been pushed back behind the stapedial recess, its normal position is clear. The extent of the occipital flange of the squamosal shows very well.

CLYDE FORMATION

UC 185. Mitchell Creek, near Wichita River, Baylor County, Texas. A flattened skull roof in poor condition. The right side is nearly completely missing. A partial scapulocoracoid(?) and a partial right mandibular ramus are also included in this entry.

UC 196. Mitchell Creek, Baylor County, Texas. Numerous fragments of rock containing vertebrae, limb bones, and disarticulated jaw and skull elements. The whole is very poor.

UC 1043. Mitchell Creek, below Maybelle, Baylor County, Texas. A

badly spalled, distorted, incomplete skull, in which much of the skull roof is represented by a cast only. Parts of the lower jaws are present.

UC 1698. Mitchell Creek, Baylor County, Texas. A small skull, crushed dorsoventrally and to the left. The occiput is partially preserved, showing the postparietals, the dorsal part of the supraoccipital and the occipital lappet of the squamosal. The external auditory meatus is not preserved, and the palate is not exposed.

¿ARROYO FORMATION

Locality 6 miles N Fort Sill, sec. 31, T 4 N, R 11 W, Comanche Co., Oklahoma, (Richard's Spur Locality).

MCZ 2146. The skull is an excellent one. The snout, part of the right orbit, the left cheek and left part of the occiput are missing. The rear parts of the parietals are also absent. The contact between the supraoccipital and the postparietals clearly shows that the postparietals fit firmly into the groove that traverses the occipital face of the supraoccipital. Right opisthotic and stapes are present although their shafts are displaced posteriorly. In palatal view the specimen shows that the left half of the palate has been displaced slightly forward; the right half, incomplete anteriorly, occupies a more dorsal position than normal. The basiptyergoid joint is open; no epiptyergoid appears. No parasphenoid rostrum is visible. The stapes nestles into the apposing concavity of the quadrate wing of the pterygoid, but only because of the displacement of the stapes.

UR 338. A tip of a dentary bearing teeth in long section.

UC 339. Single dentary.

UR 383. The specimen is a well-preserved skull and jaws. The snout and much of the posterior part of the skull roof are missing. The occiput and palate are the most valuable features of the specimen. The palate is in an essentially undisturbed position and shows that the palatal halves do not articulate by bony suture. In palatal view, the rostrum of the parasphenoid extends anteriorly to a level that falls slightly short of the total length of the medial row of pterygoid teeth. The rostrum shows as a thin bony strip embedded in crystalline calcite.

The pterygoquadrate articulation is visible on the left side. The quadrate is erect and its posterior flange clearly contacts the occipital lappet of the squamosal. Matrix intervenes in the pterygoquadrate articulation, moving the pterygoid slightly away from the quadrate and suggesting a loose joint.

UR 384. Badly crushed skull of moderate size that shows external features only and these poorly.

UR 385. Badly crushed skull, showing no features other than the dorsal skull roof and a partial view of the dorsal surface of the right half of the palate.

UR 386. Crushed skull that has been broken into two major pieces and compressed dorsoventrally. The region of the auditory channel has been obliterated. The palate is partially exposed. Basioccipital, basisphenoid, and parasphenoid are partially present; the right half of the complex is missing. Distortion has curved the ventral surface of these bones to resemble the normal recessed area of the braincase; consequently, the initial (but incorrect) impression is that of a braincase more slender than normal in *Captorhinus*.

UR 387. Small and incomplete skull, broken away between the orbits and across the snout.

UR 388. Partial skull, present anterior of the orbits, and a right mandible.

UR 389. This specimen is a block of clay containing numerous skeletal elements, including a scapulocoracoid exposed internally, and a humerus.

UR 390. The specimen consists of a block of clay containing a humerus and a femur.

UR 391. Nine articulated vertebrae, exposed in ventral view and without apparent intercentra.

UR 392. Front foot, embedded in matrix and but partially exposed.

UR 393. Isolated frontal bones.

UR 395. Isolated parietal bones.

UR 396. Isolated nasal bones.

UR 397. Isolated caudal vertebrae.

UR 398. The entry consists of three stapes, two of which are small and resemble *Captorhinus*. The third is about three times as large as the other two. It is incomplete; the anterior and lateral parts of the footplate are missing and the shaft is broken off within the posterior extent of the dorsal process. The dorsal process, which is comparatively massive, is broken off anteriorly, so that it no longer

retains its presumably characteristic hook. The shaft extends from the footplate at an angle more acute than is usual in *Captorhinus*; this quality and its size are the significant departures from the stapes of *Captorhinus*.

UR 401. This entry consists of approximately 45 partial lower jaws, none of which exhibit resorption pits at the bases of their teeth.

UR 402. Isolated fragmentary mandibles.

UR 425. Isolated premaxillary bones.

UR 594. Large stapes bearing an incomplete footplate and shaft.

UR 595. Moderately-sized stapes bearing an incomplete footplate and shaft.

UR 596. Small stapes with an incomplete footplate that is covered internally by matrix, and with a complete shaft.

UC 1699. The specimen consists of 14 isolated vertebrae, a palatal fragment that does not appear to be that of a captorhinid, and a tibia.

UC unnumbered. Isolated supraoccipitals.

UC unnumbered. Vial containing two dentaries. The fourth tooth of one has a resorption pit at its base. A pit is also present on the first tooth of the most anterior row and the fourth tooth of the second row of three teeth of this specimen.

UC unnumbered. Collection of seven basi-parasphenoidal fragments. The anterior portions only are present. In comparing these specimens with the ventral aspect of the braincase of UR 383, we can find no way in which they depart from it in characters that might be of taxonomic significance (see, for example, Olson, 1951: 101, fig. 45). The presence, absence and position of the teeth is variable among these specimens. In the bones in which the appropriate areas are present and which are otherwise referable to *Captorhinus aguti*, two have no teeth, one has four teeth restricted to the parasphenoid rostrum, one bears one tooth posterior to the rostrum, and one has at least six teeth, found both on the rostrum and posterior to the rostrum. These exhibit the same wide variation in this character as do the like specimens in the collections of The University of Kansas.

UMMP 50985. The entry includes five basi-parasphenoidal fragments.

The best of these include a nearly complete dorsum sellae. The specimen also shows the vertical mid-sagittal wall on the anterior face of the dorsum sellae extending to the floor of the sella turcica.

KU 9978. A fine skull, the right half of which is retained in matrix.

The skull outlines are little disturbed; the left jugal anteriorly is displaced slightly in relation to the maxillary below. The most posterior part of the left mandibular ramus is absent; most of the occiput is absent. The supraoccipital has been pushed forward, and the left opisthotic and stapes downward. The external auditory meatus shows clearly. The palate is exposed to the tips of the vomers anteriorly to where they meet the premaxillae, although the nature of this contact is not exposed. The palatal halves are free of the basiptyergoid processes and meet or nearly meet in the midline; part of the region is concealed by pyrite. The relation of the pterygoid flanges to the adductor fossae shows clearly, with the flanges crossing the anterior part of the openings and then extending to the ventral edge of the mandible. The jugal-palatine articulation is exposed. The relationship between the coronoid process and the cheek is unobscured by matrix. Most of the pterygoquadrate region is covered by calcite and pyrite and unavailable for study. The braincase is partially crushed, particularly posteriorly, and is only exposed ventrally. A partial septomaxilla is present on the left side, and suggests that the bone was crescentic in shape and closed the posterior half of the nares. The relationship between the stapedial recess of the quadrate, the plane of the occiput, the quadrate foramen and the external auditory meatus is apparent; the occipital lappet of the squamosal remains in place above this region. It is primarily on this specimen that the estimate of the tympanum in *Captorhinus* was first based.

KU 8962. The entry includes numerous isolated fragments, few of which are complete: premaxillary (89); maxillary (74); nasal (136); lacrimal (35); frontal (46); prefrontal (104); parietal (67); postorbital (119); postfrontal (57); jugal (123); squamosal (106); quadratojugal (50); postparietal (15); vomer (3); palatine (67); pterygoid (53); quadrate (70); dentary (many); surangular (82); angular (40); splenial (28); prearticular (30); coronoid (61); articular (48); stapes (7); basi-parasphenoid (13); opisthotic (2); basioccipital (17); supraoccipital (1); scapulocoracoid (22); clavicle (138); interclavicle (81); pelvis (56); radius (15); ulna (12); tibia (9); fibula (5).

KU 8963. This entry, too, consists mostly of isolated, fragmented ele-

- ments: Premaxillary (13); maxillary (28); nasal (5); lacrimal (23); frontal (21); prefrontal (6); parietal (75); postorbital (5); postfrontal (5); jugal (32); squamosal (14); quadratojugal (4); postparietal (1); vomer (1); quadrate (29); dentary (45); surangular (13); angular (37); splenial (3); prearticular (2); coronoid (1); articular (18); opisthotic (1); basioccipital (3); exoccipital (1); supraoccipital (13); epipterygoid (3); scapulocoracoid (13); clavicle (23); interclavicle (6); pelvis (51); humerus (64); radius (5); ulna (16); femur (69); tibia (17); fibula (5); proatlas (1); atlas (1); axis (1).
- KU 8964. Incomplete pes with associated tibia and femur, pictured by Peabody (1952: 32, Fig. 10C).
- KU 8965. Incomplete pes, showing astragalus, calcaneum, distal tarsals, metatarsals. The phalanges are absent from the first and fifth digits, but are complete in the second. The ungual phalange is absent from the third digit; the first phalange only is present in the fourth. Navicular and distal tarsals are partially obscured by pyrite. An associated tibia is present.
- KU 9780. Matched, but disarticulated, jugal, prefrontal, frontal, postorbital, parietal, squamosal, quadratojugal, and postparietal. Associated are sclerotic plates.
- KU 9924. Crushed right half of skull, showing frontals (right complete, left incomplete), partial right parietal, right prefrontal, postfrontal and postorbital, partial right jugal, partial right palatine, and nearly complete right mandibular ramus, all exposed internally.
- Clarke Collection, unnumbered. Elements of a skull, including vomers, palatines, pterygoids, stapes, quadrates, and dermal roof. The lower jaw is present, the right ramus more nearly complete than the left. Partial scapulocoracoids, clavicles and interclavicle, partial left manus and pes, sacrum, left femur, tibia and fibula, humerus, ulna and radius, all presumably from a single individual, are present. Other isolated elements are included from different individuals. An associated second sacrum and first four caudal vertebrae are represented. The whole is excellently preserved.
- #### ARROYO FORMATION
- MCZ 1202. Valley of *Diplocaulus* Hill between Indian and Coffee Creeks, J.S. Self Survey Sec. 2, A-1530, NW of Lake Kemp, Baylor County, Texas. A poor skull that shows the outline well enough, but not much else. The roofing bones that can be seen are the left squamosal, the posterior part of the left jugal, the frontals, the anterior part of the parietals, the left postorbital, the left postfrontal, the right lacrimal and the nasals. The latter bones (lacrimal and nasals) are in poor condition, as is the right cheek. No features of the occiput and palate show.
- UC 242. Indian Creek, near Wichita River, Baylor County, Texas. This specimen is a poor skull, consisting of the dorsal roof, the braincase in ventral exposure, and part of the palate. The stapes, poorly preserved, is directed toward the posteroventral corner of the skull, at the inner side of the junction between the quadrate and the lowest extent of the occipital lappet of the squamosal. Consequently, the stapes is in its normal position. A channel seems to extend from the distal end of the stapes to the external surface of the skull, but the features in this specimen may have been enhanced by preparation.
- UR 274. West Coffee Creek, Baylor County, Texas. The specimen is a poor and extremely weathered skull.
- UR 275. Mid-Coffee Creek, *Labidosaurus* pocket, Baylor County, Texas. The entry consists only of a fragmentary skull in poor condition.
- UR 292. Baylor County, Texas. A small and badly crushed skull with most of the roof missing.
- UR 351. East Coffee Creek, *Broiliellus* pocket, Baylor County, Texas. A small skull that has been crushed dorsoventrally. Only the roof and jaws are to be seen, and the roof is absent posterior of the orbits.
- UR 372. East Coffee Creek, Baylor County, Texas. A spalled skull, crushed slightly to the right and flattened. The palate is exposed, but exhibits its features poorly. Of the ventral surface of the braincase, only the anterior part is visible. Nothing can be made of the occiput.
- UC 642. Near Lucas Ranch, 2 miles S Big Wichita River, Baylor County, Texas. The specimen is a skeleton that is exposed in ventral view. Skull, shoulder girdle, left humerus, radius and partial foot, 11 vertebrae, pelvic girdle, both hind limbs and eight post-sacral vertebrae are present. An additional fragment contains portions of a limb, hind foot, and ten ribs. The detail of preservation is not exceptional, but the specimen gives an excellent general picture of the spatial relationships of skull, vertebrae, girdles and limbs. Type of *Pariotichus laticeps*.
- UC 651. Near Kennedy's Ranch, Coffee Creek, Baylor County, Texas. An incomplete, small skull, exhibiting the anterior part of the palate, the anterior upper dentition, the skull table anterior to the orbits and partially back between the orbits. What can be seen of the vomerine-premaxillary contact is indistinct. The internarial width and the dorsal ascending spines of the premaxillaries appear broader than usual, although no measurements were taken.
- UC 686. Vernon Road, near Cohan's Ranch, Willbarger County, Texas. A very poor skull and a vertebral column containing approximately 11 vertebrae, including sacrals.
- UC 687. X Pasture, 5 miles NW Maybelle, Baylor County, Texas. A skull and partial skeleton that are exposed in ventral view. The skull is also exposed dorsally. The postcranial material includes about twelve vertebrae, the interclavicle, a pubic spine and various components of the four limbs.
- UC 700. Hog Creek, near Wichita River, Baylor County, Texas. A skull that has been sectioned along its mid-sagittal axis, but which exhibits nothing of significance.
- UC 951. Indian Creek, near Big Wichita River, Baylor County, Texas. The specimens that are included within this entry are two mandibular rami, a humerus, five articulated vertebrae, a partial front foot showing the metacarpals, and a partial skull.
- UC 1206. Near Seymour, Baylor County, Texas. The specimen includes four very poor fragments.
- UC 1315. Craddock Ranch, Bushy Creek, Baylor County, Texas. The specimen is a left femur that has been broken into two pieces.
- UC 1702. East Coffee Creek, Baylor County, Texas. This skull is excellently preserved, even in comparison to the material from the Richard's Spur, Oklahoma locality. The skull has been slightly crushed from above; in consequence, for example, the two halves of the palate are spread out slightly from each other at the midline, more especially so posteriorly. The basis cranii is visible; the basioccipital is slightly disarticulated. The opisthotics and stapes of both sides are present. The left stapes is not displaced and is directed toward the stapedia recess of the quadrate. The end of the stapedia shaft rests in the recess, adjacent to the narrow notch that passes posterior to the neck of the quadrate. The parasphenoid rostrum is present, and extends about one-half the length of the palate. Most of the external surface of the skull is spalled.
- AMNH 4332. Indian Creek, Baylor County, Texas. The type of *Captothinus aduncus*. The specimen consists of a skull, vertebral column, pectoral girdle, left and right humeri, right radius, sacrum, pelvic girdle, right femur, right hind foot, and first three post-sacral vertebrae. The proximal part of the right femur has been glued to the distal end of the left humerus, which is in place. The atlas and axis are unrecognizable. Twenty-three visible presacral vertebrae are present. The palate shows clearly the interdigitation of pterygoids and palatines; the palatal teeth have been ground away. The flanges of the pterygoids clearly pass down and back across the front part of the adductor fossae of the lower jaws. The palatine-maxillary articulation shows well; the vomerine-premaxillary contact is obscured to a great extent, but what does show is in accord with the Richard's Spur material. The apparent extent of the maxillary into the rim of the naris varies bilaterally. There is a limited exposure of the postparietals on the dorsal skull roof. Two sacral vertebrae send ribs to the pelvis; the last presacral bears an incomplete stout rib on the left side.
- AMNH 4333. Coffee Creek, Baylor County, Texas. A poorly prepared skull that has been crushed laterally and twisted to the left. Of the features of the skull roof, the frontal-nasal suture is indistinct, the parietals are nearly completely missing, and the frontal-parietal sutures are unclear. The lateral limits of the postfrontals are impossible to determine. The right squamosal is absent; the left squamosal is present except dorsally. Both quadratojugals remain, but their limits are indistinct. The right postorbital is absent except for that portion which forms the orbital rim. The left postorbital and the jugals are present, differing in no way from Richard's Spur specimens. Of the prefrontals the left is absent; the right is present but its limits are indeterminate. The limits of maxillaries, premaxillaries, and lacrimals are indeterminate. Palatal features are indistinct, as are those of the ventral exposure of the braincase. The basiptyergoid joint shows, but is in poor condition; no deviation from Richard's Spur skulls can be seen in this

feature. The pterygoid flanges point rather sharply distally, but this is an artifact of preservation and preparation. The remainder of the palate is indistinct, as is the occiput. The type of *Captorhinus aguti*.

- AMNH 4334. West Coffee Creek, Baylor County, Texas. The specimen consists of skull, jaws, anterior vertebrae and shoulder girdle. The pterygoid flanges descend nearly to the ventral edge of the mandible, and cross the adductor fossae in such a way to leave part of the anteriormost portion of the opening exposed in front of the flanges. The subtemporal fossae are triangular in shape (as in AMNH 4332) and possess no anterior extension. In front of the pterygoid flanges the palate is largely obscured; the anterior part of the pterygoids at the midline is exposed, and reveals a slender, heart-shaped interpterygoid vacuity. The pterygoids meet in the midline at the basipterygoid joint; this may be in part a crushing or other postmortem effect, moving the palate upward in relation to the braincase. The stapes is directed toward the posteroventral corner of the skull sloping backward at an angle of about 45 degrees and downward at about an angle of 30 degrees. The postparietals are exposed dorsally, and meet at the midline of the occiput above the supraoccipital. The septomaxillaries are at least partially present and appear to close the posterior half or a little more than the posterior half of the external nares. Postcranially, little is good. Essentially nothing can be determined in dorsal view of the postcranium; in ventral view the clavicles and interclavicles are exposed. The stem of the interclavicle is broken off posteriorly; the left clavicle is represented only by its expanded foot, while the right is complete or nearly so. The clavicles overlap on to the adjacent edges of the interclavicle, but not, apparently, on to each other. Nothing can be determined of the scapulocoracoids that is of particular value.
- AMNH 4338. Coffee Creek, Baylor County, Texas. The type of *Captorhinus isolomus*. A fine skull. The preservation of the surface of the skull is reasonable. The palate is arched. The pterygoid flanges extend to the bottom of the mandible. The occiput is poor, although the approximate outline of the posttemporal fenestrae is indicated. The parasphenoid rostrum shows nicely, and extends most of the way through the interpterygoid vacuity.
- AMNH 4340. Baylor County, Texas. A large skull in which the dorsal roof is complete except for the snout. The left squamosal, quadratojugal and jugal are present. The right side of the skull is missing. The posterior part of the left mandibular ramus is present. The palate, particularly the vomers, is well-preserved, and the arch of the palate is consequently in evidence. The pterygoid flanges extend to the bottom of the mandible. The dorsal and lateral portions of the posttemporal fenestrae are present, as is the occipital lappet of the left squamosal. The entry also includes three mandibular fragments.
- AMNH 4410. Head of East Coffee Creek, Baylor County, Texas. The specimen is a skull, laterally compressed and twisted. The palate is in a fair state of preservation, and shows the characteristic dorsal arching. The pterygoid flanges are incomplete.
- AMNH 4438. Coffee Creek, Baylor County, Texas. A very poor skull. The only bone consists of fragments around the right orbit and part of the left jugal; some of the tooth-bearing elements remain. The teeth have been ground down in preparation. This specimen is the type of *Captorhinus angusticeps*, an assignation, in view of the condition of the specimen, that defies belief.
- AMNH 4443. Baylor County, Texas. The entry consists of four spalled fragments of a skull roof.
- AMNH 4444. "Boneyard", West Coffee Creek, Baylor County, Texas. A poor skull contained in matrix. The orbits and ventral depression marking the position of the palate are the only visible features.
- AMNH 4445. ?Coffee Creek, Baylor County, Texas. The entry includes only a partial mandibular ramus.
- AMNH 4458. West Coffee Creek, Baylor County, Texas. A badly crushed skull with only the right surface showing.
- AMNH 4877. Gray Shale, North side Big Wichita River, Baylor County, Texas. A skull with badly spalled surfaces. The pterygoid flanges reach nearly to the bottom of the mandible.
- AMNH 6791. Baylor County, Texas. A skull badly crushed dorsoventrally and to the left. The surfaces are badly spalled.
- USNM 17048. Baylor County, Texas. A partial skull in poor condition in which orbits and frontals are present; the remainder of the skull roof is mostly missing, but for a few fragments that adhere to the matrix.

VALE FORMATION

- UR 118. Locality KC, South wall of valley of Wichita River, Knox County, Texas. The specimen consists of 10 articulated vertebrae and many small fragments, all of which are in poor condition.
- UR 119. Locality KA, Knox County, Texas. The specimen consists of a minute fragment bearing six broken teeth, two of which are in an adlateral position.
- UR 220. East end of Sharner Breaks, Baylor County, Texas. The specimen consists of the impression of the rear portion of the parietals and the supraoccipital. At their posterolateral corners the parietals exhibit characteristic grooving for the reception of the supratemporals. The impression of the upper part of the left squamosal also is present. Associated with these remains are several jaw fragments bearing the multiple rows of teeth characteristic of *Captorhinus*. Assignment to *Captorhinus aguti* seems justifiable on the basis of these features.
- UR 219. East end of Sharner Breaks, Baylor County, Texas. Numerous fragments of small limbs, vertebrae, etc.

CLEAR FORK GROUP

- MMP 8921. Texas. A badly crushed skull.
- MCZ 1059. Coffee Creek, Baylor County, Texas. Part of the entry consists of a skull, distorted and crushed to the left. Part of the mandible, frontals and parietals have been restored. The palate is fairly good. The basisphenoid, parasphenoid (with two teeth?), quadrate wings of the pterygoid, pterygoid flanges and the posterior part of the palatines all show. The lower jaws have been little distorted, although they have been pushed together slightly anteriorly. The specimen generally seems to exhibit the exaggerated heart-shaped outline of many of the specimens in the American Museum of Natural History. The occiput is largely absent. The bones that remain include the basioccipital, exoccipitals, a partial left opisthotic, and a partial supraoccipital. The latter is more complete on the left than the right. Part of the occipital lappet of the right squamosal remains; the lappet of the left squamosal is present but in poor condition. A bone that may be the end of the stapedial shaft protrudes the occipital lappet of the squamosal on the left. Also included in the entry are two jaw fragments, eight fragments of rock that contain various numbers of vertebrae, and the distal part of a humerus. The fragmentary material is in poor condition.

LABIDOSAURUS HAMATUS

ARROYO FORMATION

- UR 161. Mid-Coffee Creek, *Labidosaurus* pocket, Baylor County, Texas. The specimen consists of a skull and associated fragments. The skull shows quite well the posterior position of the basipterygoid joint on the pterygoid. The basal part of the parasphenoid rostrum is visible as a flat, vertically oriented plate. The snout is more drawn out, more "beaked" terminally, and the cheeks wider than in *Captorhinus* proportionally. The femoral trochanter is very strong; it is a powerful anteroventrally directed, thumb-like projection. The condyle of the humerus is disproportionately developed in comparison to *Captorhinus*. The distal end of the femur departs little from the morphology of the femur in *Captorhinus*, except for an increase in the emphasis of the features that are present.
- UC 176. Indian Creek, Baylor County, Texas. The skull of the specimen is on exhibit. The remainder of the material includes an interclavicle and partial left scapulocoracoid exposed externally.
- UC 182. Whiskey Creek, Wilbarger County, Texas. A fragmentary skull showing part of the palate, the basis cranii and stapedial and opisthotic shafts. The specimen clearly shows the posterior position of the basipterygoid joint. The stapes is directed toward the posteroventral corner of the skull.
- UC 634. Near Seymour, Baylor County, Texas. The specimen exhibits a dual row of teeth on the medial border of the pterygoid. The skull is flattened. The pterygoid socket for the reception of the basipterygoid processes is set far back. The stapedial recess on the left quadrate possesses a clear receptacle for the stapedial shaft.
- UC 726. Near Kennedy's Ranch, Coffee Creek, Baylor County, Texas. The entry consists of articulated vertebrae (4, 4, 14, 7, 6, 1, 1), a partial interclavicle, an incomplete humerus, four isolated vertebrae, the posterior part of a pelvic plate, and a fragmentary scapulocoracoid.

P 12758. Coffee Creek, Baylor County, Texas. The specimen consists of four fragments. The first of these possesses a basioccipital, supraoccipital, exoccipital, opisthotics, right stapes, rear portion of pterygoids, the anterior part of the dorsal plate of the right quadrate, and the foot of the right epipterygoid. The basipterygoid joint is placed posteriorly on the quadrate wing of the pterygoid. The quadrate and pterygoid are separated by intervening matrix, suggesting that the joint was weak. The stapedial shaft is directed downward and backward. The basioccipital is small; the parasphenoid rostrum is lacking.

The second fragment consists of an interclavicle with two associated coracoid regions from which the scapular blades have been removed. The stem of the interclavicle possesses a slender neck, which shortly broadens, only to narrow again to its termination. The head bears a strong transverse ridge on its ventral surface. The coracoids resemble those of *Captorhinus* closely, being little more than enlarged versions of the coracoids in that genus.

The third fragment is a large partial scapulocoracoid, with only the region around the glenoid cavity preserved.

The fourth fragment consists of three vertebrae.

AMNH 4427. A skull, badly spalled and of little note, except that it does show the presence of the supratemporals wedged into the posterolateral corners of the parietals.

CAPTORHINIKOS CHOZAENSIS

HENNESSY FORMATION

Section 29, T9N, R2W, Cleveland Co., Oklahoma

UR 857. The specimen is made up of a skeleton in two pieces. The first consists of a skull and pectoral girdle exposed ventrally, a right humerus and lower limb segments. The remainder of the skeleton is exposed dorsally, including the sacrum. The whole is very poorly preserved and does not lend itself to a detailed comparison to *Captorhinus*.

UR 858. The specimen consists of a very poor spinal column and a right front limb.

CHOZA FORMATION

Locality FA, Foard County, Texas

UR 99. The entry includes a poor humerus in which the capitellum and trochlea are absent. The entepicondylar foramen is present. The entepicondyle is rather prominently paddle-shaped; its edge tapers toward the axis of the shaft distally.

INDETERMINATE CAPTORHINID

ADMIRAL FORMATION

MCZ 2794. One mile W Geraldine, American Tribune New Colony Subdivision, Section 97, Archer County, Texas. The specimen consists of two articulated but incomplete vertebrae. They are moderately large and possess swollen neural arches. It is impossible to designate these generically; presumably they are captorhinid.

CLYDE FORMATION

MCZ 2804. One mile S Electra, HT and B RR Survey A-137, about middle of N section line, Wichita County, Texas. The specimen consists of jaw and partial braincase. The teeth appear to be single-rowed. Parasphenoid, supraoccipital, exoccipital, basioccipital, left opisthotic and left stapes show. Both stapes and opisthotic seem large in comparison to *Captorhinus*. Associated with the skull are vertebral fragments that possess swollen neural arches. It is impossible to make a generic designation; the specimen is presumably captorhinid.

CLEAR FORK GROUP

UMMP 11653. Near Comanche, Stephens County, Oklahoma. A skull in which the right side of the occiput to a distance in front of the orbit is present; most of the remainder of the skull roof is absent. The foot of the right quadrate is exposed, as is the head of the interclavicle. A pencilled notation on the label by Case, dated 12 January 1936, says "not *Captorhinus*." The teeth that are exposed appear to be in a single row, bearing out Case's estimate. Grinding of the area would make certain whether the specimen is *Captorhinus* or not.

INDETERMINATE ROMERIID

ARROYO FORMATION

AMNH 4335. Baylor County, Texas. The specimen consists of two skulls, one swallowing the other, first pointed out by Case (1911a). Stratigraphic and geographic locality follows Seltin (1959), who placed the specimen in *Captorhinus*; familial assignment follows Eaton (1964).

ARCHERIA CRASSIDISCA

ADMIRAL FORMATION

BRIER CREEK, ARCHER CO., TEXAS

- UMMP 3001. Dorsal roof of skull.
- UMMP 3008. Six intercentra.
- UMMP 3029. Right lower jaw in four pieces.
- UMMP 3044. Right and left ulnae.
- UMMP 3045. Anterior half mandibular ramus.
- UMMP 3246. Two right humeri.
- UMMP 3247. One left and two right pubes.
- UMMP 3340. Centrum and intercentrum.
- UMMP 3341. Two caudal vertebrae.
- UMMP 3342. Two dorsal vertebrae.
- UMMP 3343. Centrum and intercentrum.
- UMMP 3355. Two tibiae.
- UMMP 3358. Crushed femur, ?*Archeria*.
- UMMP 3362. Left femur.
- UMMP 3363. Right femur.
- UMMP 3418. Jaw fragment.
- UMMP 3421. Scapulocoracoid.
- UMMP 3422. Scapulocoracoid.
- UMMP 3423. Left ulna.
- UMMP 3424. Radius.
- UMMP 3426. Two fibulae.
- UMMP 3427. Right femur.
- UMMP 9681. Sacral centrum and intercentrum.
- UMMP 9682. Small sacral centrum and intercentrum.
- UMMP 9683. Two dorsal vertebrae and one fragmented arch.
- UMMP 9684. One centrum.
- UMMP 9685. Two ischia.
- UMMP 9686. Intercentra.
- UMMP 9687. Two caudal intercentra with chevrons.
- UMMP 9688. One vertebra.
- UMMP 9727. Three angulars and articulars.
- UMMP 9728. Angular and articular.
- UMMP 9729. Dorsal roof of skull.
- UMMP 17298. Co-ossified centrum and intercentrum.
- UMMP 22218. Four femora.
- UMMP 38516. Left ilium.
- UMMP 38537. Vertebrae.
- UMMP 38538. Five vertebrae.
- UMMP 38539. Two vertebrae.
- UMMP 38540. One sacral vertebra.
- UMMP 38541. One dorsal vertebra.
- UMMP 38542. Ischium.
- UMMP 38543. Ilium.
- UMMP 38544. Pubis.

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