

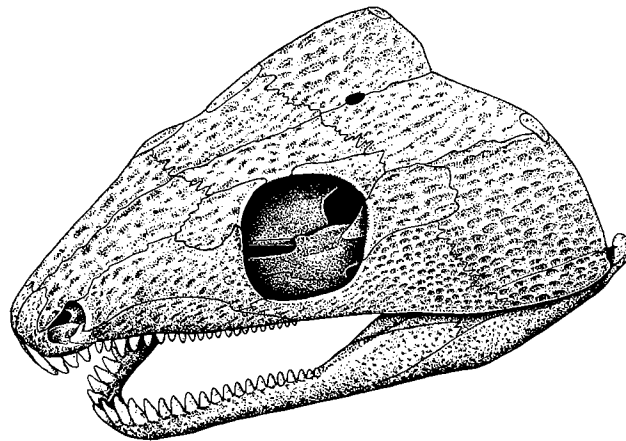


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**CRANIAL ANATOMY OF PRIMITIVE
CAPTORHINID REPTILES FROM THE LATE
PENNSYLVANIAN AND EARLY PERMIAN
OKLAHOMA AND TEXAS**

MALCOLM J. HEATON



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Title Page Illustration

Eocaptorhinus laticeps, n. gen. Isometric reconstruction of skull and mandibles. Ink drawing by the author.

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CRANIAL ANATOMY OF PRIMITIVE CAPTORHINID REPTILES FROM THE LATE PENNSYLVANIAN AND EARLY PERMIAN OKLAHOMA AND TEXAS

MALCOLM J. HEATON¹

Abstract—The primitive reptilian family Captorhinidae, which first appears in the Wolfcampian terrestrial deposits of central North America, is an early specialized development of the basic captorhinomorph structural pattern. A new genus of primitive captorhinid, based on Williston's type of *Pariotichus laticeps*, in the new combination *Eocaptorhinus laticeps*, n. gen., has been found in the upper Belle Plains Formation and the Clyde and Lueders Formations of north-central Texas and in the upper Wellington Formation of Oklahoma. It bears a superficial resemblance to the younger, well-known form *Captorhinus aguti* with which it has often been confused. It retains a primitive single-rowed marginal dentition in contrast to the distinctive multiple-rowed pattern of *Captorhinus* to which *Eocaptorhinus* gave rise. The sequence of *Romeria-Protocaptorhinus-Eocaptorhinus-Captorhinus* is interpreted as a single, continuous phylogenetic lineage of small captorhinids. *Romeria* and *Protocaptorhinus* are recognized as typical but primitive captorhinids.

Extremely well-preserved specimens of *Eocaptorhinus laticeps* from Oklahoma reveal all soft anatomy reflections on the bone. It is possible to identify the origins and insertions of the adductor, hyoid, and cervical musculature on the skull and mandibles as well as to trace most major, and many minor, arteries, veins, and nerves.

INTRODUCTION

The order Cotylosauria as defined by Romer (1956) is a diverse assemblage of primitive anapsid reptiles that contains (among other taxa) the diadectids, pareiasaurs, and captorhinomorphs. Of these, only the captorhinomorphs are recognized as being related to more modern reptilian lineages. This unique position at the base of reptilian phylogeny makes it essential that as much detailed information about this group is obtained as possible. Most of the more primitive captorhinomorphs have been described by R. L. Carroll (1964, 1969a, 1969b, 1969c, 1970), Carroll and Baird (1972), Carroll and Gaskill (1971), and Clark and Carroll (1973). For most of the species described, the material was scarce and fragmentary, so that only basic descriptions were possible.

One group of primitive reptiles, the Captorhinidae, while specialized in many ways, is close to the primitive structural pattern. The best known captorhinid is the type of the family, *Captorhinus aguti*, from the Arroyo Formation of the Leonardian of north-central Texas (table 1). The modern concept of the genus *Captorhinus* is basically that outlined by Case (1911) and developed by Romer (1933, 1945, 1956), Seltin (1959), and Fox and Bowman (1966), based on material from the type locality in Texas. It is a small reptile with an adult skull length of about 55 to 80 mm. The cheek region is noticeably swollen to produce the characteristic heart-shaped outline in dorsal view. Both the maxillae and dentaries bear multiple tooth rows. The teeth are short with round bases and with laterally and medially faceted, chisel-shaped tips. The teeth are arranged in three or four subparallel rows angled posteromedially across the jaws. The premaxilla is distinctly hooked.

Also from the Arroyo Formation of Texas is a much larger captorhinid, *Labido-*

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saurus hamatus. In its basic features, it appears to be more primitive than *Captorhinus*. The skull is more angular and relatively higher. There is only a single row of long, slightly recurved, laterally compressed teeth in the maxilla and dentary. The dental characters, as well as the larger size of *Labidosaurus*, allow immediate separation of these two taxa. As in *Captorhinus*,

the premaxilla is hooked. It is probable that both of these genera are the descendents of some genus that we would include within the family Captorhinidae. It would have been smaller than *Labidosaurus* and have possessed a single-rowed dentition and hooked premaxilla. Clark and Carroll (1973) described such an animal, *Protocaptorhinus pricei*, a small captorhinid from the Admiral

TABLE 1.—GENERALIZED CHRONOSTRATIGRAPHIC SECTION, TEXAS-OKLAHOMA

NORTH-CENTRAL TEXAS				SOUTHERN OKLAHOMA				NORTHERN OKLAHOMA															
PERMIAN	Wolfcampian	Wichita Group	Pueblo Fm.		PERMIAN	Leonardian	Hennessey Group			PERMIAN	Leonardian	Hennessey Group											
			Moran Fm.	• Cottonwood Creek				Summer Group	Garber Formation				Wellington Fm.	Lower	Upper	• Norman	Bean Farm	Wellington Fm.	Lower	Upper	• Navina		
			Putnam Fm.	• Archer City Bonebed												• N. Manitou					• E. Manitou	• Crescent	
			Admiral Fm.	• Rattlesnake Canyon												• W. Grandfield					• Dolese	• Hayward	• Pond Creek
			Belle Plains Fm.	• NW of Woodrum's												• Deep Red Run					• S. Grandfield	• Lucien 5	• Orlando
	Elm Creek sandstone		• Taylor	• Bean Farm		• Lucien 1-4	• Perry 1-6																
			Ryan Sandstone			Fallis Sandstone		Herington Limestone															

Solid circles denote approximate stratigraphic positions of vertebrate localities.

Editor's note: The correlations of this table are those recommended by the Oklahoma Geological Survey and do not necessarily reflect the author's views. The age assignments of the Oklahoma columns are based primarily on recent palynological determinations. (See Clendening, 1975; Olson, 1975; Simpson, 1973, 1974.)

Formation of Texas, as a "romeriid." It is now apparent that both *Protocaptorhinus pricei* and the two *Romeria* species, *R. texana* and *R. prima*,² are primitive, single-tooth-rowed captorhinids. This study was designed originally to find and describe forms intermediate between the common ancestor, *Protocaptorhinus pricei* and *Labidosaurus hamatus* on the one hand and *Captorhinus aguti* on the other. Although pre-*Labidosaurus* forms were found, the pre-*Captorhinus* specimens yielded such a wealth of information that the study has concentrated on these forms, with the pre-*Labidosaurus* specimens to be described subsequently.

Forms intermediate in age between *Protocaptorhinus pricei* and *Captorhinus aguti* but with all of the superficial characteristics of *Captorhinus* are well documented. Almost without exception these forms have been identified as *Captorhinus*, and usually as *C. aguti* (Case, 1911; Seltin, 1959; Fox and Bowman, 1966). In 1973, Clark and Carroll noted that one specimen from the Clyde Formation of Texas, Williston's (1909) type of "*Pariotichus*" *laticeps*, had a single-rowed marginal dentition and so was not *Captorhinus* as had so often been reported. Further investigation has revealed that no multiple-tooth-rowed captorhinids are known from sub-Arroyo (Wichita-age) deposits. A study of the Wichita captorhinids was begun, based on specimens from the Clyde Formation. Subsequently it was realized that a series of slightly older specimens from the Wellington Formation of Oklahoma, previously described by Seltin (1959) as *Labidosaurus oklahomensis*, were actually conspecific with the Clyde form (figs. 1, 2). The Oklahoma specimens consist of fully articulated skulls and skeletons preserved in a coarse, poorly cemented, red arkosic sandstone.

The separation of single-tooth-rowed and multiple-tooth-rowed forms along the Wichita-Clear Fork boundary is not as clear as one might wish. The Dolese Brothers quarry at Richards Spur, near Fort Sill, Oklahoma, contains pockets of residual clays of Early Permian age. From these fissure fillings come many fragmentary remains of

terrestrial tetrapods of which most are of small captorhinids. The Richards Spur deposits are generally considered to be equivalent to the Arroyo Formation of Texas and, therefore, of Clear Fork age (Fox and Bowman 1966; Olson 1967). This determination is based primarily on the presence of positively identified maxillae and dentaries belonging to *Captorhinus*. What has so often been ignored is that there are many maxillae and dentaries there identical in size and form with those of *Captorhinus*, except that the marginal dentition is single-rowed. Olson (1967) identified these variously as specimens of *Labidosaurus hamatus* or *Labidosaurus*, cf. *L. hamatus*. As Bolt and DeMar (1975) pointed out, this assignment is incorrect; they considered the jaws to belong to a small captorhinid that they believed to be a morphological variant of *Captorhinus aguti*, the most common small captorhinid in the Richards Spur deposits. It is here deemed inappropriate to change the diagnosis of a well-known, long-established genus (Case, 1911; Seltin, 1959; Fox and Bowman, 1966) by reference to a limited number of tooth-bearing elements from a unique deposit, within which there is no stratigraphic control and whose stratigraphic position has not been accurately established. The use of the Linnean system of classification has its limitations when applied to the continuum of organic evolution. Because it is impossible to determine whether the burial of the single-tooth-rowed forms antedated that of the multiple-tooth-rowed forms or to determine the degree of reworking and mixing of specimens that occurred during deposition and the subsequent mechanical removal of the residual clays from the Richards Spur fissures, within which the specimens are preserved, and its disposal in the general clay dump on the Dolese Brothers quarry floor, inferences such as those made by Bolt and DeMar (1975) with regard to the genetic character of the possible resident populations of small captorhinids seem to be inappropriate at this time. There is no proof that the high degree of variability in tooth-row morphology of the Richards Spur captorhinids was present in the living population at any time, since it is impossible to determine the length of time during which specimens were being entombed in the Richards Spur fissures. It is believed that the diagnosis of

²Emendation of original, published specific name in accordance with International Code of Zoological Nomenclature, Art. 30, 34 (b).

Captorhinus aguti as formulated by Case (1911) and strongly reinforced by Seltin (1959) and Fox and Bowman (1966) should not be altered on the basis of isolated tooth-bearing elements from a unique, isolated locality of dubious stratigraphic position and internal constitution. Rather, the morphological separation of single- and multiple-tooth-rowed forms, suggested by Clark and Carroll (1973) and accepted by Bolt and DeMar (1975) as a taxonomic convenience, seems most appropriate. Much additional work on the problems of the Richards Spur

captorhinids remains to be done, including evaluating the exact taxonomic status of these animals. The problem is too complex to be considered here, so that the Richards Spur single-tooth-rowed captorhinid is not discussed. The presence of these two forms may have handicapped the work of Fox and Bowman (1966), who were not able to distinguish between elements of *Captorhinus* and those of the single-tooth-rowed form except for the maxillae and dentaries. It may be that no such separation is possible, or that only a statistical analysis can separate the

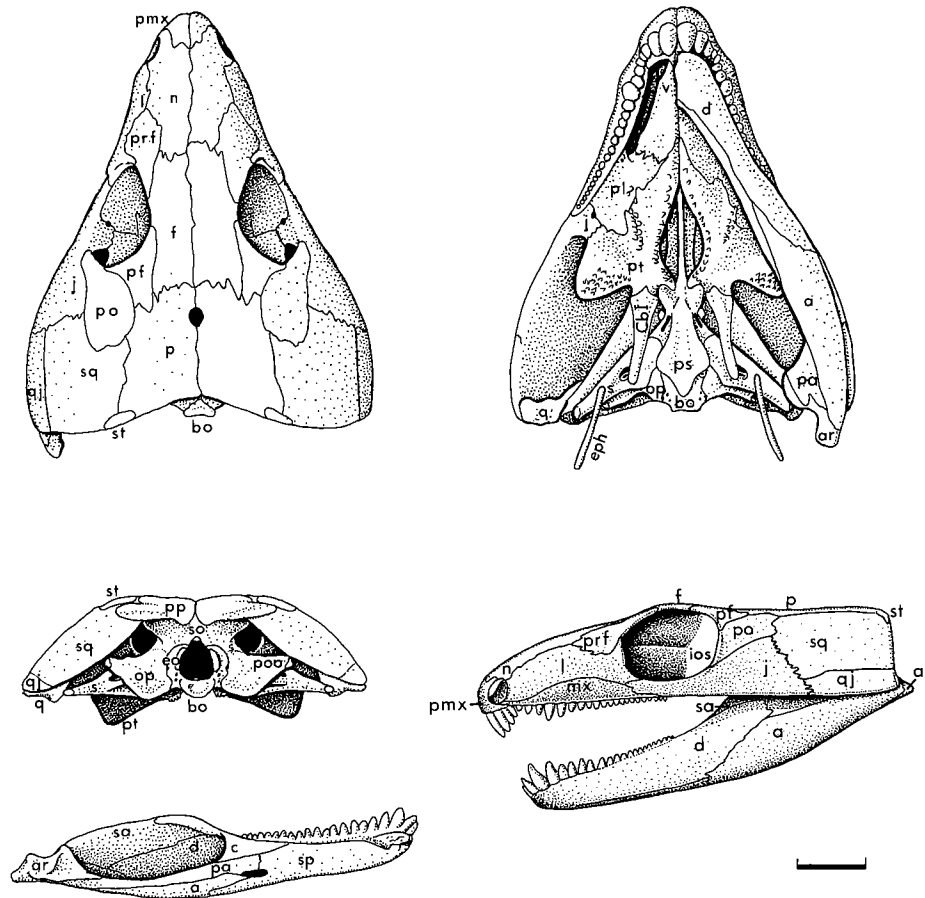


Figure 1. *Eocaptorhinus laticeps*. Outline guide to skull figures of primitive captorhinids. Abbreviations: a, angular; ar, articular; bo, basioccipital; bs, basisphenoid; c, coronoid; Cb l, cornua branchialia I; d, dentary; eo, exoccipital; eph, epihyale; ept, epipterygoid; f, frontal; ios, interorbital septum; j, jugal; l, lachrymal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pl, palatine; pmx, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sa, surangular; smx, septomaxilla; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; v, vomer. Lower-case letters identify individual bones. Upper-case letters identify regions of sutural attachment. Scale equals 1 cm.

genera on a basis other than tooth-bearing elements. No good suite of representative skulls of the Richards Spur captorhinids is available for comparative purposes.

Most of the specimens upon which this study has been based are those originally used by Seltin (1959) in his description of *Labidosaurus oklahomensis* from northern Oklahoma. They are so well preserved that the osteology can be determined in considerable detail. It has been possible to see all surfaces of all cranial elements in enough detail that foramina and muscle scars can be identified. For this reason, it was decided to limit this study only to the cranial osteology. In order to understand fully the structural and physiological advances that occurred during the great reptilian radiation of the late Paleozoic, the basic characteristics of both the hard and soft anatomy must be known for as many primitive reptiles as possible. The existence of numerous specimens of a relatively primitive captorhinomorph reptile, in which all osteological features can be seen in detail and used to reconstruct and interpret the soft anatomy, is extremely important. In this one species, *Eocaptorhinus laticeps*, can be found an anatomical pattern similar to that from which all other reptiles developed. It is the purpose of this study to produce, for the first time, a description of the cranial osteology of a primitive reptile with the characteristic reflections of the soft anatomy identified and illustrated. From this it will be possible to reconstruct the soft anatomy of the skull and apply this knowledge to a clearer interpretation of the skull mechanics of all primitive reptiles. It is hoped that this may lead to the development of a unified concept of the origin of the major reptilian groups.

It is the purpose of this study to attempt to identify and note the function of all foramina, fenestrae, tendon and muscle scars, and other reflections of the soft anatomy. Much of it is based on inference, drawn from a comparison of *Eocaptorhinus* with modern reptiles. The astonishing correlation of similar osteological characters between *Eocaptorhinus* and *Sphenodon* and primitive iguanid lizards has led to the use of these modern forms as the major source of information. Dissections of the lizard genera *Ctenosaura*, *Iguana*, *Gekko*, and *Tupinambus* have been used for comparative

purposes. An earlier attempt to use modern turtles for comparison, because of the apparently similar anapsid-skull roofing pattern, proved to be impractical because of the extreme modifications of the palate, braincase, and otic region in turtles and the considerable alterations in the soft anatomy that accompanied these changes. Likewise, crocodylian anatomy is viewed as having become too specialized for practical use in this study. It is felt that an attempt should be made to identify all details of the osteology, in the full knowledge that some of the designations may be overstated, in order to stimulate further discussion and research into the finer aspects of reptilian morphology. A number of papers have been of great use in determining anatomical homologies among modern reptiles that can be applied to *Eocaptorhinus* (Oelrich, 1956; Haas, 1960, 1973; Barghusen, 1968, 1973; Gaffney 1972; Schumacher, 1973).

Throughout the detailed description of the cranial elements, frequent reference is made to scars on the bone surfaces made by the tendinous or fleshy origins and insertions of the cranial musculature. In most cases these are tuberosities with distinct borders that are easily homologized with the origin or insertion scars of modern reptiles. The identifications are often confirmed by the location of easily identifiable foramina that, in modern reptiles, carry the nerves and blood vessels that typically are associated with these muscles.

I wish to express my thanks to Dr. Robert L. Carroll of McGill University, Montreal, for directing me into the study of Paleozoic reptiles. His emphasis on the determination of anatomical details of primitive reptiles as a basis for studying their early phylogenetic diversification has been a major factor in influencing the course of this study. His willingness to pass on his knowledge of primitive tetrapods is appreciated, as is his concise and constructive criticism of all aspects of the project. Many hours have been spent with Dr. Robert Reisz of Erindale College, University of Toronto, Philip J. Currie of the Alberta Provincial Museum, Edmonton, and Robert B. Holmes of McGill University, discussing the cranial anatomy of primitive reptiles and its bearing on the late Paleozoic reptilian radiation. Most of the specimens used are from the collections

of the Stovall Museum of Science and History of The University of Oklahoma. I am especially grateful to Dr. Jiri Zidek of that institution for his kind efforts in making all of this material available to me for study. I also wish to thank Drs. Rainer Zangerl and John Bolt of the Field Museum of Natural History, Chicago, for arranging for the loan of considerable captorhinid material, including the type specimen of *Eocaptorhinus laticeps*.

A 1-cm scale is provided in all figures.

The following are the abbreviations of the names of institutions from which specimens have been borrowed or latex casts obtained: AMNH, American Museum of Natural History, New York; CGH, National Museum of Czechoslovakia, Prague; FMNH UC or UR, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard University; OUSM, Stovall Museum of Science and History, The

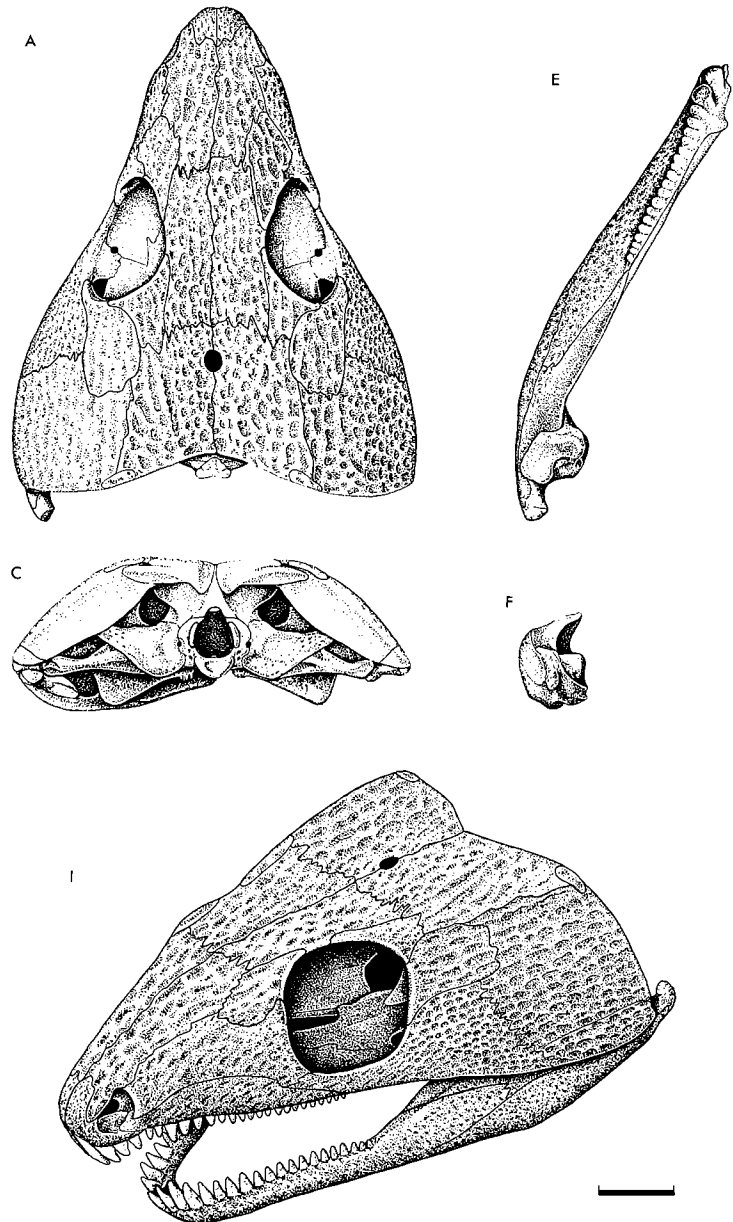


Figure 2. *Eocaptorhinus laticeps*. Reconstruction of skull and mandible. A, skull in dorsal view; B, skull in ventral view, right mandible removed; C, skull in occipital view; D, skull in left-lateral view; E, left mandible in dorsal view; F, left mandible in occipital view; G, left mandible in lateral view; H, left mandible in medial view; I, isometric reconstruction of skull and mandibles; J, palate in dorsal view. Scale equals 1 cm.

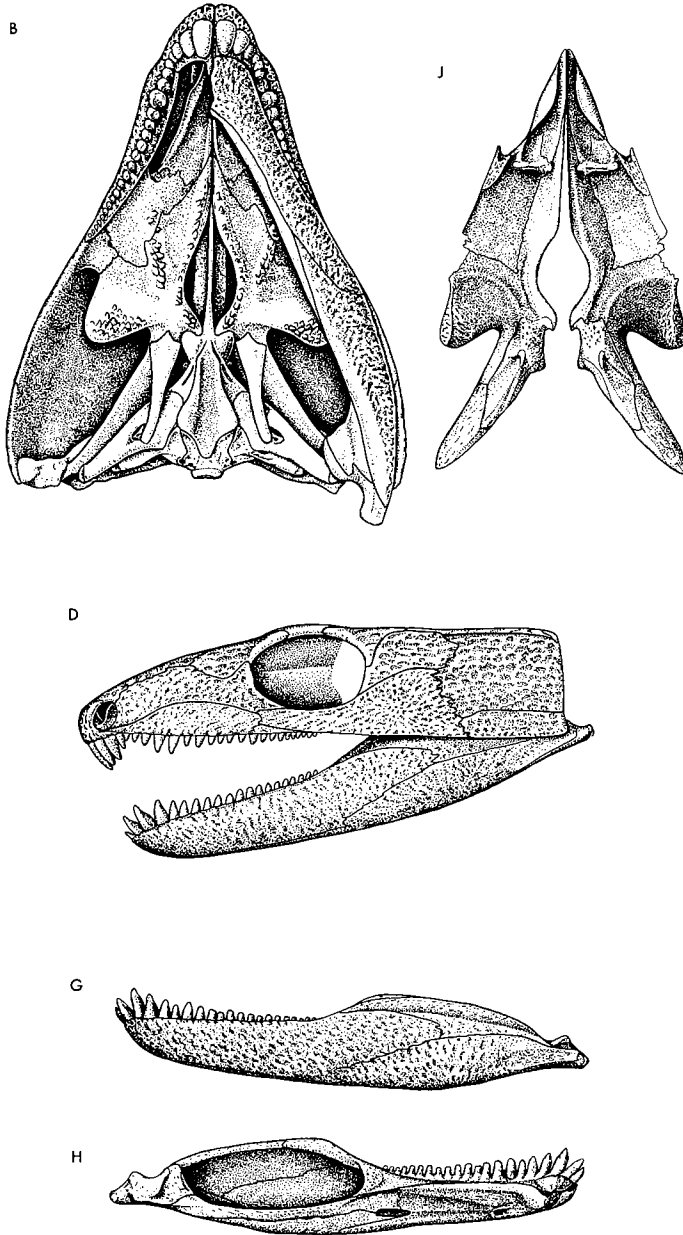
University of Oklahoma; and YPM, Peabody Museum of Natural History, Yale University.

TAXONOMIC REVIEW

The family Captorhinidae, as first established by Case in 1911, contained a number of specimens of extremely varied and confusing taxonomic background. So complex has been the history of this family

that an understanding of the changes that have taken place in the group is difficult without first examining the individual histories of each type or referred specimen. Table 2 illustrates the nomenclatural histories of all the genera and species of captorhinids from the Arroyo or older sedimentary rocks in North America, except at Richards Spur.

The specific name *Ectocynodon aguti* was first applied to a definitely identifiable



Williston (1916)	Williston (1917)	Price (1937)	Watson (1954)	Seltin (1959)	Fox and Bowman (1966)	Clark and Carroll (1973)	This paper
							<i>Pariotichus brachyops</i> (microsaur)
							<i>Nomen dubium</i>
				<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>
				<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>		<i>Captorhinus aguti</i>
	<i>Labidosaurus hamatus</i>			<i>Labidosaurus hamatus</i>	<i>Labidosaurus hamatus</i>	<i>Labidosaurus hamatus</i>	<i>Labidosaurus hamatus</i>
				<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>		<i>Captorhinus aguti</i>
					a romeriid (Eaton, 1964)		<i>Captorhinus aguti</i>
				<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>		<i>Captorhinus aguti</i>
	<i>Labidosaurus hamatus</i>			<i>Labidosaurus hamatus</i>	<i>Labidosaurus hamatus</i>		<i>Labidosaurus hamatus</i>
				<i>Captorhinus aguti</i>	<i>Captorhinus aguti</i>	" <i>Pariotichus</i> " [sic] <i>laticeps</i>	<i>Eocaptorhinus laticeps</i>
	<i>Puercosaurus obtusidens</i>						<i>Puercosaurus obtusidens?</i>
	<i>L. hamatus</i> or n. gen. & sp.			<i>Labidosaurus hamatus</i>	<i>Labidosaurus hamatus</i>		New genus and species?
							<i>Pleuristion brachycoelus</i>
		<i>Romeria texana</i>	<i>Romeria texana</i>		<i>Romeria texana</i>	<i>Romeria texana</i>	<i>Romeria texana</i>
			MCZ 1963			<i>Romeria primus</i>	<i>Romeria prima</i>
			MCZ 1478	<i>Captorhinus aguti</i>		<i>Protocaptorhinus pricei</i>	<i>Protocaptorhinus pricei</i>
			MCZ 1160	<i>Captorhinus aguti</i>		<i>Protocaptorhinus pricei</i>	<i>Protocaptorhinus cf. P. pricei</i>
			<i>Paracaptorhinus neglectus</i>				<i>Captorhinus aguti</i>
				<i>Labidosaurus oklahomensis</i>	<i>Labidosaurus oklahomensis</i>		<i>Eocaptorhinus laticeps</i>

captorhinid specimen (AMNH 4333) by Cope in 1882. He had based the genus *Ectocynodon* on a very poor specimen (AMNH 4342) to which he gave the specific name *E. ordinatus* (Cope, 1878). Cope later (1896b) placed the species *E. aguti* in the genus *Pariotichus*. *Pariotichus*, however, was a genus whose holotype, *P. brachyops* (AMNH 4328) (Cope, 1878), was subsequently shown to be a microsauro (Gregory and others, 1956).

Case (1911) was the first to recognize the generic distinction between the type of *Pariotichus*, *P. brachyops*, and that of the other assigned species, *P. aguti*. He believed that *P. aguti* was congeneric with *Ectocynodon ordinatus* but declined to state this formally because of the poor quality of the holotype of *E. ordinatus*. He was, in effect, declaring *Ectocynodon ordinatus* to be a *nomen dubium*. Case referred the type of Cope's *Pariotichus aguti* to another Cope genus, *Captorhinus*. The holotype, *Captorhinus angusticeps* (AMNH 4338) was, however, almost as poor a specimen as the *Ectocynodon ordinatus* holotype. It is probable that the holotype of *Captorhinus angusticeps* conforms to our current concept of *Captorhinus*. It is also possible, or even probable, that *Ectocynodon ordinatus* does also, but to consider this as a senior synonym of *Captorhinus* would be ill advised in light of the extensive usage of the name *Captorhinus* in the current literature. It seems most prudent to allow *Ectocynodon ordinatus* to continue as a *nomen dubium* and now also as a *nomen oblitum*, as it has had no real usage as a senior synonym since 1896. Regardless of the state of preservation of the holotype of *Captorhinus angusticeps*, the specimen was accepted as diagnostic by Case (1911), and the generic name was applied to all of Cope's remaining *Ectocynodon* and *Pariotichus* species except *P. incisivus* and *P. brachyops*. Case (1911) accepted the species *Captorhinus aguti*, *C. angusticeps*, *C. aduncus*, and *C. isolomus*.

In 1909 Williston described a new species of captorhinid, *Pariotichus laticeps*, from the Clyde Formation, Wichita Group, along Mitchell Creek in Baylor County, Texas. This specimen (FMNH UC 642) was markedly older than any previously known captorhinid; yet when Case reviewed the family in 1911, he synonymized *P. laticeps* with *Captorhinus isolomus*. Subsequent workers

(Seltin, 1959; Fox and Bowman, 1966) considered all of Case's *Captorhinus* species to be conspecific with *Captorhinus aguti*. "*Pariotichus*" *laticeps* thus became submerged in the literature until Clark and Carroll (1973) noted that this specimen (FMNH UC 642) (fig. 3) had but a single-rowed maxillary dentition. Since multiple-rowed marginal dentition is characteristic of the genus *Captorhinus*, the holotype of "*Pariotichus*" *laticeps* must represent a new

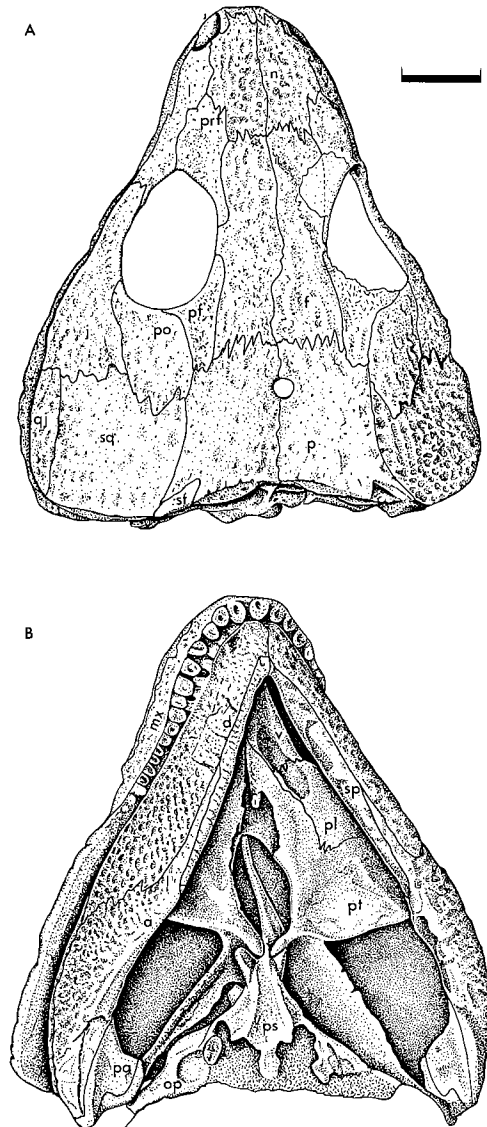


Figure 3. *Eocaptorhinus laticeps*. Holotype of *Pariotichus laticeps*. A, skull in dorsal view; B, skull in ventral view. FMNH UC 642. Scale equals 1 cm.

and as yet unnamed taxon worthy of careful study. Another complete skull with some postcranial material and a number of other specimens had also been found by Williston and Paul C. Miller along Mitchell Creek (FMNH UC 701). They all showed a single-rowed tooth pattern.

In 1959 Seltin described a new species of small, single-tooth-rowed captorhinid from northern Oklahoma as *Labidosaurus oklahomensis* (fig. 4). It is now apparent that this is conspecific with Williston's "*Pariotichus*" *laticeps*.

No question has been raised since Case's review as to the identification of any of the aforementioned forms as captorhinids. Such is not the case with some of the more primi-

tive forms. The most widely known of these is *Romeria texana*, described by Price (1937) from the Putnam Formation of Texas. Price based the family Romeriidae on one partial skull (MCZ 1480). In 1945 Romer considered *Romeria texana* to be a captorhinid, but later (1956, 1966) he resurrected Price's family designation. Clark and Carroll (1973) noted that *Romeria texana* was not a "typical" romeriid.

Clark and Carroll (1973) described *Protocaptorhinus pricei* from the Admiral Formation as a romeriid. Carroll (oral communication, 1977) now recognizes that *P. pricei* can be classified as a primitive captorhinid. *Romeria* is not typical of the modern concept of the family Romeriidae as established by Carroll (and coauthors) since 1964. *Romeria* does satisfy all of the criteria established for inclusion in the family Captorhinidae by Case (1911) and subsequent authors (Romer, 1956; Seltin, 1959). The boundary proposed by Clark and Carroll (1973) between the Romeriidae and the Captorhinidae was clearly an expedient based to a large extent on the desire to retain the family designation Romeriidae for primitive captorhinomorphs (Carroll, written communication, 1977).

The problems associated with the taxonomy of the earliest captorhinids are further complicated by the presence of a number of specimens assigned to two species, *Puercosaurus obtusidens* (Williston, 1916) and *Pleuristion brachycoelus* (Case, 1902; Olson, 1970). These specimens must be studied with great care, as it is quite possible that conspecificity exists between either or both of these and one of the other well-known, early captorhinids.

SYSTEMATIC DESCRIPTIONS

Class REPTILIA

Subclass ANAPSIDA

Order COTYLOSAURIA

Suborder CAPTORHINOMORPHA

Family CAPTORHINIDAE

Eocaptorhinus, new genus

Etymology.—Greek "eos"—"dawn"—plus *Captorhinus*, a well-known early Permian captorhinid. Indicates phylogenetic

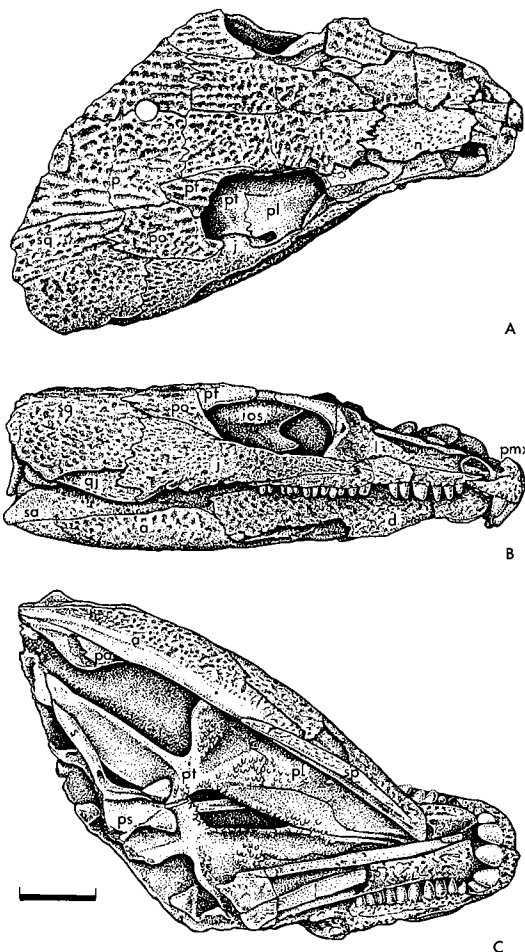


Figure 4. *Eocaptorhinus laticeps*. Holotype of *Labidosaurus oklahomensis*. A, skull in dorsal view; B, skull in right-lateral view; C, skull in ventral view. OUSM 15022 (3-1-S7). Scale equals 1 cm.

position between *Protocaptorhinus*, a primitive captorhinid, and *Captorhinus*.

Type species.—*Eocaptorhinus laticeps* (Williston), new combination.

Synonymy.—*Pariotichus laticeps* Williston, 1909; *Captorhinus isolomus* Case, 1911; [non] *Captorhinus aguti* Seltin, 1959; *Labidosaurus oklahomensis* Seltin, 1959; *Labidosaurus stovalli* Olson, 1962a, 1962b; *Labidosaurus oklahomaensis* Olson, 1967.

Generic diagnosis.—(Based only on skull; figs. 2A–J, 5, 6). Medium-sized single-tooth-rowed captorhinid. Differs from *Romeria* in its larger size, fewer maxillary and dentary teeth, proportionately wider skull, wider but shorter supratorpals, centrally embayed posterior border of parietals without nuchal swelling, heavy sculpturing (in adults), and long retroarticular process. Distinguished from *Protocaptorhinus* by its proportionately wider skull, shorter supratorpals, embayed rather than straight posterior margin of parietals, coarse heavy

sculpturing (in adults), and long retroarticular process. Separated from *Labidosaurus* by much smaller adult size; shorter, wider teeth; wider snout; and long retroarticular process. Distinguished from *Captorhinus* by single-rowed marginal dentition rather than dentition of overlapping teeth or multiple tooth-rows; toothless parasphenoid; and much coarser but equally well-delineated sculpturing.

Eocaptorhinus laticeps (Williston), 1909

Specific diagnosis.—Same as for genus.

Stratigraphic zone.—Clyde Formation, Wichita Group, Lower Permian. Mitchell Creek, Baylor County, Texas.

Holotype.—FMNH UC 642: complete skull and skeleton.

Referred specimens.—See Appendix.

Short description.—(Based only on skull; figs. 2, 3, 4). Medium-sized early captorhinid. Skull low, broad; moderately swollen cheeks.

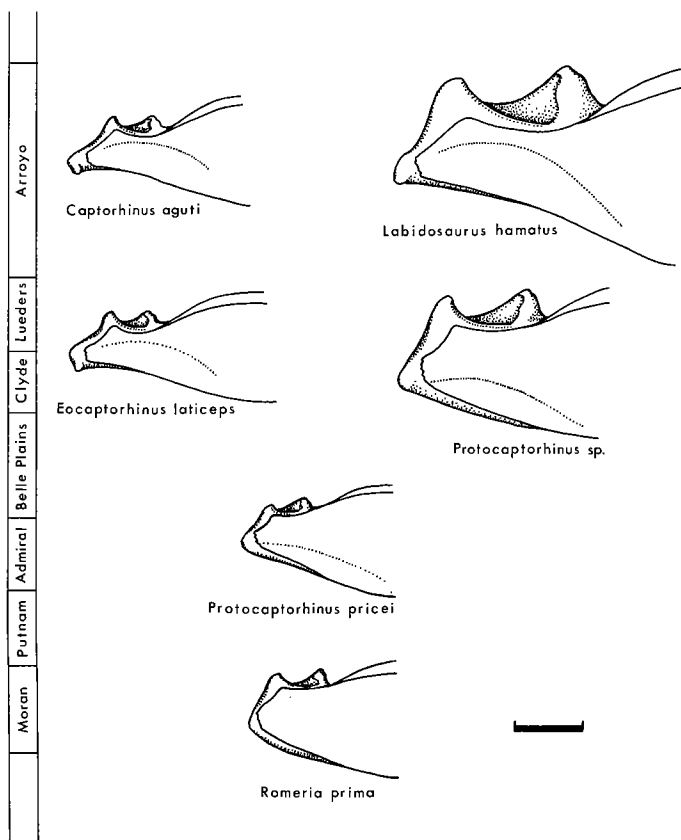


Figure 5. Posterior end of right mandibles of primitive captorhinids. Stratigraphic units shown at left. Scale equals 1 cm.

Four, occasionally five, premaxillary teeth; 17 to 22 maxillary teeth (age determinant); 20 to 27 dentary teeth (also age determinant). Maxillary and dentary teeth arranged in single row of successive groupings of four or five teeth; teeth ankylosed to jaw; teeth replaced very rapidly; replacement-related gaps in tooth row not observed; most posterior teeth of first maxillary tooth set (i.e., third, fourth and/or fifth maxillary teeth) caniniform. Jugal bears strong medial process that does not meet the maxilla; small inferior orbital foramen in anterior edge of medial process. Squamosal large, with prominent occipital flange; vertical posterior margin. Parietal wide, depressed along centerline; pineal foramen situated well forward; deep centerline excavation of posterior margin. Supratemporal small. No tabulars. Postparietals vertical, not seen in dorsal aspect. Quadrate and articular bear facets to prevent opening of jaws without mandibular retraction. Vomer bears prominent vertical alar projection laterally; deep depression for nasal capsule in dorsal surface. No ectopterygoid. Pterygoid not involved in

basicranial articulation. Parasphenoid toothless. Well-ossified interorbital septum. Large heavy stapes with large footplate; long columella. Large otoliths. Rod-like cornu branchiale I and epihyale.

Single splenial with foramen intermandibularis oralis but no foramen intermandibularis medius; latter replaced by small vertical foramina between splenial and dentary. Articular with prominent retroarticular process; condyle allows slight parasagittal motion.

SKULL

Williston (1908, 1909, 1917), Case (1899, 1911), and Broili (1904) provided the earliest illustrations of the skulls of the advanced captorhinids *Captorhinus aguti* and *Labidosaurus hamatus*. Much more detailed descriptions and illustrations of the skull of *Captorhinus aguti* were provided by Romer (1933, 1945, 1956, 1966) and by Fox and Bowman (1966). The primitive captorhinids were illustrated by Watson (1954) and by Clark and Carroll (1973).

In general, all captorhinids exhibit a similar "heart-shaped" skull with swollen cheeks and an acuminate muzzle. The more primitive, smaller forms have shorter muzzles and less swollen cheeks than do the larger, more advanced forms.

Eocaptorhinus laticeps (figs. 2, 3, 4) is a medium-sized captorhinid with an adult skull length of between about 65 and 80 mm. The skull is broad posteriorly with a width of approximately 85 percent of the skull length. Juvenile or subadult specimens with a skull length of about 58 mm typically have a much narrower skull with a width of only 50 percent of the skull length. The great width of the skull posteriorly in adults is accounted for by the inflated or swollen cheek region that accommodated the heavy adult adductor jaw musculature. In juveniles, where the adductor mass was not yet strongly developed, the skull was narrower and cheek swelling greatly reduced or nonexistent.

The posterior margin of the skull table is embayed medially as in *Captorhinus aguti*. There is no nuchal expansion of the parietals. The postparietals are oriented vertically. The occiput is vertical in typically captorhinid configuration. The occipital surface of

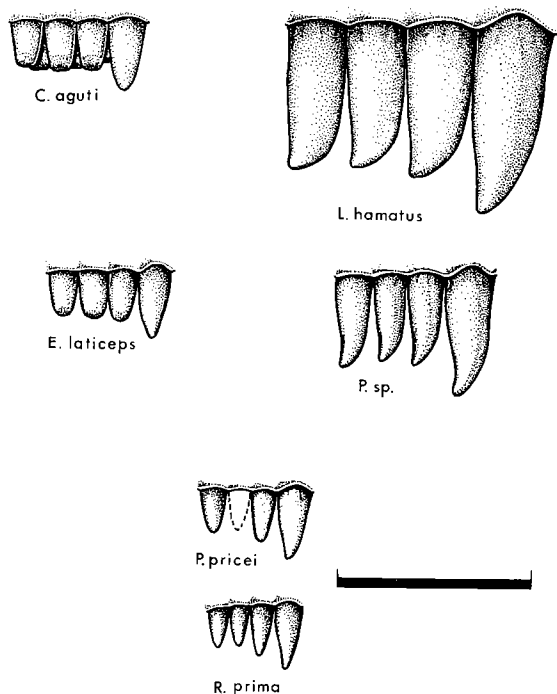


Figure 6. Right caniniform and three post-caniniform teeth of primitive captorhinids. Scale equals 1 cm.

the skull reveals large, interlocking medially oriented flanges on the squamosals, quadra-tojugals, and postparietals for the insertion of strong occipital musculature. There is no tabular.

The dorsal surface of the skull table is slightly depressed along the mid-line in contrast to the domed pattern illustrated by Fox and Bowman (1966) in *Captorhinus aguti* but is identical with that shown, also for *Captorhinus*, by Romer (1933, 1945, 1956, 1966). The parietals are long and relatively narrow, with a large, anteriorly situated pineal opening. The supratemporals are small and well separated from the postorbital. The entire external surface of the dermal skull roof is ornamented by a coarse, vermiculate, ridge-and-pit sculpture pattern (figs. 2, 5) that is less well developed in juveniles.

The skull is low in lateral view. Except for the typically hooked premaxilla, the ventral border of the skull is straight horizontally. The quadrate condyle is in line with the ventral maxillary border. The 17 to 22 sub-theodont, maxillary teeth are arranged in a single row without any overlap. The orbits are situated slightly anterior of mid-length. The lateral surface of the muzzle is vertical in both *Eocaptorhinus* and *Captorhinus*, not inclined as in many reconstructions of *Captorhinus* (Fox and Bowman, 1966) and primitive captorhinids (Clark and Carroll, 1973). The maxilla is never seen in a dorsal view, nor is most of the ventral portion of the lachrymal. There is no otic notch.

Premaxilla

The premaxilla is a triradiate structure typically supporting four or five teeth in mature animals. The first tooth is the largest in all specimens with the remaining teeth decreasing in height posteriorly. Wear facets are present on the lingual surfaces of all the teeth but are more noticeable on the most anterior (fig. 7A-F).

The axes of the nasal ramus and the first tooth coincide, thus transferring the primary vertical stresses on the premaxilla through the narrow nasal ramus to the rigid, box-like muzzle. The premaxilla-nasal suture is formed by a complex interdigitation of angled processes from both bones (fig. 7D).

Typically the nasal ramus bifurcates dorsally, with the median process being the longer and stouter of the two processes (fig. 7D). The median process of the nasal ramus is perforated through its length by a vascular canal that carried the rostral sinus and orbitonasal vein (fig. 7E).

The rostral body forms the massive, highly vascularized base for the anterior teeth. A large posterior premaxillary foramen (fig. 7E) is located in its concave posterior surface. This admitted the subnarial branch of the maxillary artery, which passed anterior to the internal naris, a short vein connecting the transverse palatine sinus and rostral sinus, and the medial branch of the medial ethmoidal nerve (V_1). The nerves and capillaries anastomosed through fine foramina to the skin of the snout. Venous blood was transferred through the hollow nasal ramus (fig. 7F) by way of the osseous tube, on the ventral surface of the nasal, to the orbital sinus.

Directly behind the teeth and below the posterior maxillary foramen is a smaller, vertical prepalatal foramen, passing from the dorsal to the ventral surface of the anterior border of the internal naris. It allowed passage of the terminal branch of the inferior nasal artery, which supplied the vomeronasal (Jacobson's) organ, vomerine raphe, and anterior palate, a short venous connection between the lateral palatine sinus and the transverse palatine sinus, and a ventral twig of the medial branch of the medial ethmoidal nerve, which innervated these structures in conjunction with the medial palatine nerve. The latter nerve also passed through the foramen.

The vomerine ramus is the shorter of the two ventral rami. It tapers both medially and dorsoventrally. A pronounced rectangular depression on the median surface (fig. 7B) received the anteroventral end of the rostrum of the basitrabecular process and the internarial septum. A small foramen is located at the anterior end of this depression on some specimens. Its exact purpose is unknown, although it presumably drained venous blood from the premaxilla into the medial palatine sinus. The dorsolateral surface of the vomerine ramus exhibits a small, triangular, concave, sutural facet where it received the ventral surface of the premaxillary process of the vomer.

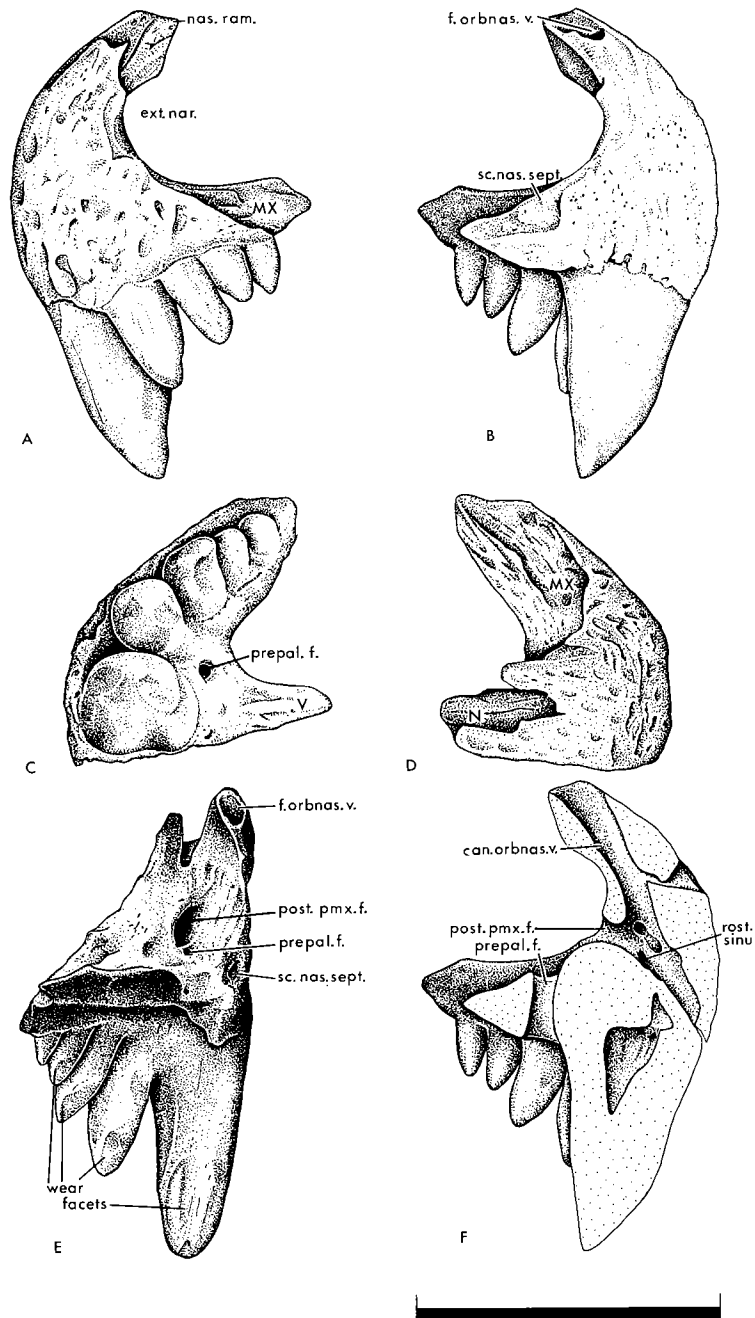


Figure 7. *Eocaptorhinus laticeps*. Left premaxilla. *A*, lateral view; *B*, medial view; *C*, ventral view; *D*, dorsal view; *E*, posterior view; *F*, sagittal section 2 mm lateral to skull midline. Abbreviations: *can. orbnas. v.*, canal for orbitonasal vein; *ext. nar.*, external naris; *f. orbnas. v.*, foramen for orbitonasal vein; *nas. ram.*, nasal ramus; *post. pmx. f.*, posterior premaxillary foramen; *prepal. f.*, prepalatal foramen; *rostr. sinu.*, rostral sinus; *sc. nas. sept.*, scar for insertion of nasal septum. OUSM 15021 (3-1-58). Scale equals 1 cm.

The maxillary ramus is a stout, posterolaterally projecting, tapered process supporting the posterior two or three premaxillary teeth. The anterolateral surface forms the anteroventral rim of the external naris. The external surface of the maxillary

process consists of a heavily scarred, dorsolaterally facing, elongate, sutural contact with the premaxillary process of the maxilla (fig. 7A).

The anterior surface of the rostral body is heavily sculptured with deep, irregular

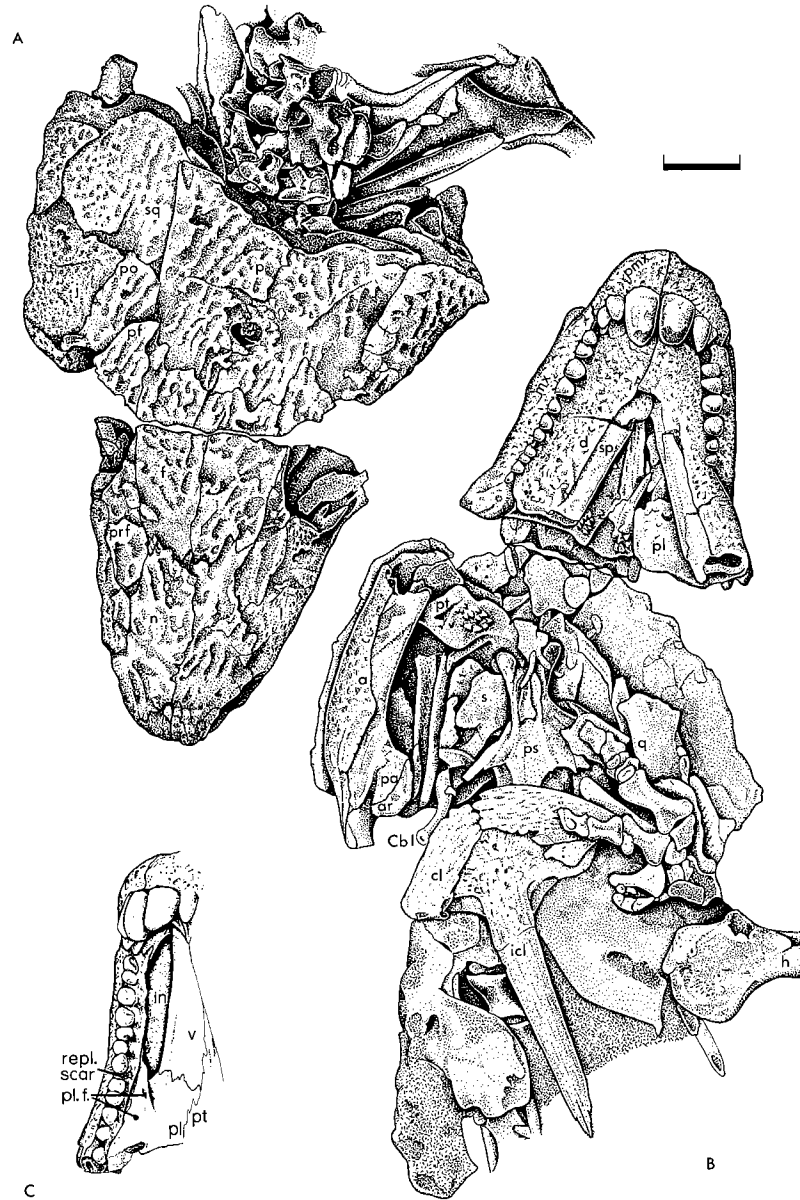


Figure 8. *Eocaptorhinus laticeps*. Paratype (in part) of *Labidosaurus oklahomensis*. A, skull in dorsal view; B, skull and pectoral girdle in ventral view; C, snout in ventral view with right mandible removed to show palate. Abbreviations: *cl*, clavicle; *icl*, interclavicle; *pl. f.*, palatine foramina; *repl. scar*, tooth-replacement scar. OUSM 15020A (3-1-S4) and 15020B (3-0-S5). Scale equals 1 cm.

pits that communicate with a system of fine internal canals. Through this complex ran the nerves and arteries that supplied the snout.

The premaxillae of *Romeria*, *Protocaptorhinus*, *Eocaptorhinus*, and *Captorhinus* are virtually identical in external view. *Eocaptorhinus* and *Captorhinus* are the only captorhinids in which the premaxilla is well known internally. No significant differences are noted.

Reconstructions of *Romeria prima*, *R. texana*, and *Protocaptorhinus pricei* by Clark and Carroll (1973) show broad butt joints between the premaxillae and vomers. This is unlikely, especially since the premaxilla of *Romeria texana* has a tapered vomerine process identical to that of *Eocaptorhinus* and *Captorhinus*.

Maxilla

As the chief tooth-bearing element in the skull, the maxilla had to be heavily

constructed and supported to oppose the loads applied to it during normal feeding processes. In *Eocaptorhinus laticeps*, where it is seen to best advantage in OUSM 15020A (figs. 8, 9) and OUSM 15102 (fig. 10), the maxilla is a long, low, narrow bone supporting a single row of 17 to 22 sub-thecodont teeth.

A long, thin, anteriorly directed premaxillary process extends forward to lie on the dorsolateral surface of the maxillary process of the premaxilla, with which it forms the ventral border of the external naris and the anterolateral border of the internal naris. At the base of the premaxillary process, a prominent notch (fig. 10B) appears on the medial surface. It is limited dorsally by a short septomaxillary tubercle where the medially directed portion of the septomaxilla is held in position by the maxilla. The notch is occupied by a ventral extension of the maxillary process of the premaxilla and is situated directly above the first and second maxillary teeth. To the rear of the septo-

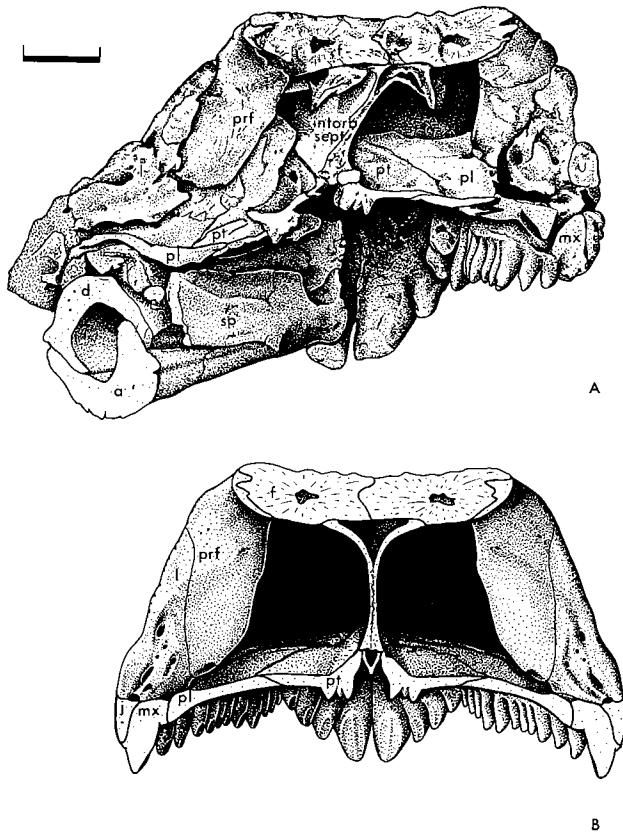


Figure 9. *Eocaptorhinus laticeps*. Preorbital region of skull. A, snout in posterior view, as preserved. B, snout in posterior view, reconstructed. Abbreviations: *interorb. sept.*, interorbital septum. OUSM 15020A (3-1-S4). Scale equals 1 cm.

maxillary tubercle, on the internal surface, is a small depression from which a prominent ridge curves posteriorly up onto the dorsal surface of the maxilla. This ridge supported the ventrolateral border of the lamina transversalis anterior, a principal nasal cartilage. The ridge extends posteriorly from the third maxillary tooth position. Within the groove formed dorsal to the ridge ran the subnarial branch of the maxillary artery as it passed anteriorly to the posterior premaxillary foramen. Between the fourth (caniniform) and fifth tooth positions, a ventral thickening of the ridge occurs and extends rearward to a position between the seventh and eighth teeth where the maxillo-palatine suture scar begins. The thickened region extends posterodorsally above the suture scar until it ends at the tenth tooth position. The ventral thickening of the ridge corresponds with the differentiation of the cartilaginous nasal capsule in the region bounding the posterior portion of the internal naris and the supporting maxillary process of the lachrymal ridge of the lamina transversalis anterior directly below the paranasal sac. The narrow region of the ridge bounded the anterior portion of the internal naris.

A long, narrow ridge that closely resem-

bles the thickened border of the internal naris and that is continuous with it stretches posteriorly to the end of the maxilla from a position between the seventh and eighth teeth. The medially convex posterior ridge has a smooth surface pierced by numerous very fine pits. This is the area of contact between the palatine and the maxilla.

The maxilla is pierced posterodorsally by a prominent foramen (fig. 11B) that continues forward as a canal above the tooth-row. These are the supramaxillary foramen and canal, through which passed the supramaxillary (inferior orbital) artery, the supramaxillary ramus of the infraorbital nerve, and the lateral palatine ramus of the facial nerve. The supramaxillary artery also sent cutaneous, labial branches to the skin through fine pores located in shallow sculpture pits on the lateral surface of the maxilla (fig. 11A). These pits were not as strongly developed as on the lachrymal or the skull table elements, nor were they as specialized as the superior labial foramina of lizards that they foreshadowed. These foramina also served as channels for the passage of fine sensory branches of the supramaxillary nerve to the skin.

Similar foramina perforate the internal

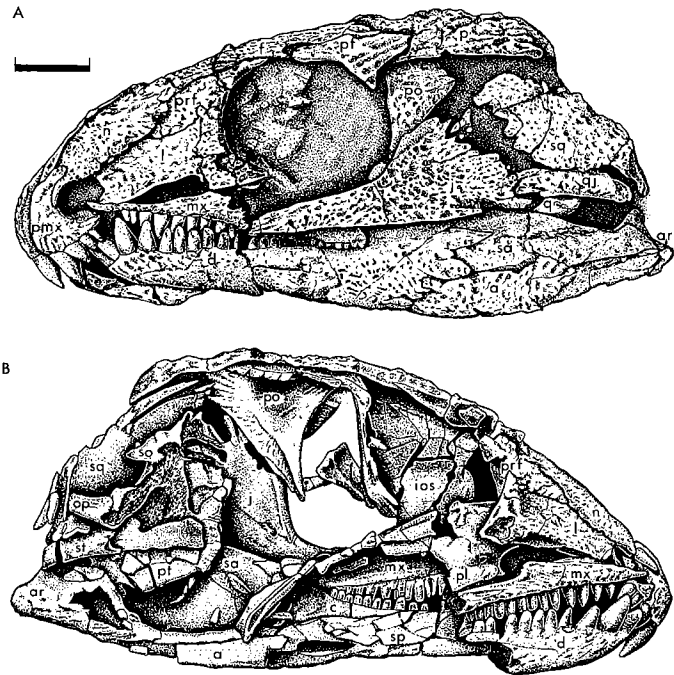


Figure 10. *Eocaptorhinus laticeps*. A, skull in left-lateral view; B, skull in right-lateral view. OUSM 15102 (3-1-S3). Scale equals 1 cm.

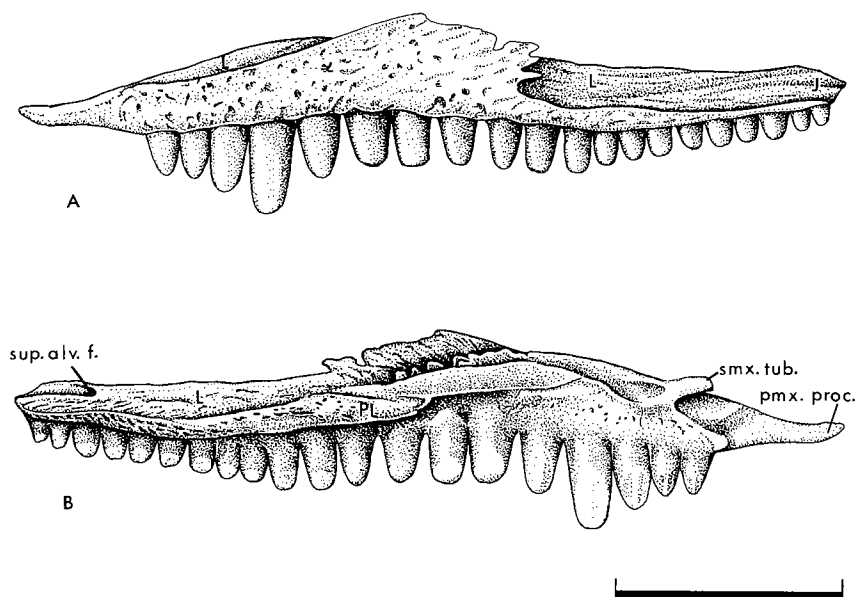


Figure 11. *Eocaptorhinus laticeps*. Left maxilla. A, lateral view; B, medial view. Abbreviations: *smx. tub.*, septomaxillary tubercle; *sup. alv. f.*, superior alveolar foramen. Reconstruction based on OUSM 15021 (3-1-S8) and 15102 (3-1-S3). Scale equals 1 cm.

surface of the maxilla and carried fine medial branches of the maxillary artery, the supramaxillary nerve, and lateral palatine ramus of the facial nerve to the lateral edge (lachrymal ridge) of the lamina transversalis anterior, the oral mucosa lining the lateral border of the internal naris, and the internal lips and their associated labial glands surrounding the maxillary teeth. Some of the foramina appear on the maxillo-palatine sutural surface, where they kept the region well supplied with blood and nerve endings. The superior maxillary artery passed medially, in a shallow groove, along the dorsal surface of the narrow medial palatal shelf of the maxilla internal to the maxillo-lachrymal suture. Both the postnarial and the subnarial arteries separated from the superior maxillary foramen just before it entered the maxilla through a small superior alveolar foramen, situated dorsomedial to the caniniform tooth.

The maxilla's ventral surface, in which the teeth are embedded, is so complex that it is difficult to determine accurately the type of tooth implantation that occurred. Forward of the seventh tooth position in

Eocaptorhinus, the ventral tooth-bearing surface of the maxilla is inclined dorsomedially at about 70° to the frontal plane. Posteriorly, this slope is reduced abruptly to about 20° or less. Laterally, a shallow (1-2-mm) lip is formed below the ventral surface, thus giving it a pleurodont-appearing supporting surface. This lateral rim is in sharp relief, thus making it a more appropriate reference line for measuring the degree of lateral maxillary deflection ("cheek swelling" of Clark and Carroll, 1973) than would be the highly variable tooth-row. In *Eocaptorhinus laticeps*, a lateral flexure of about 12° occurs at the eighth tooth position (OUSM 15020, 15101) (figs. 8, 12). This corresponds to the position of the posterior limit of the internal naris. Lateral flexion of the maxilla of 10° - 15° occurs at the 10th tooth position in *Protocaptorhinus pricei* (MCZ 1478) and of 5° - 10° at the 12th tooth position in *Romeria texana* (MCZ 1480). Juveniles generally have a less marked lateral maxillary deflection than do adults of the same species, as may be observed in FMNH UC 1698 (fig. 13A, B), a juvenile *Eocaptorhinus laticeps*, where the angle of

flexure is approximately 3° – 6° .

The number of maxillary tooth positions is quite variable, with younger, smaller individuals having fewer teeth than the older ones. Smaller, more primitive species generally have a slightly greater number of teeth. The variation in tooth number is also affected by individual variation, so that when it is combined with variations in maxillary deflection, differentiation of small primitive species from juveniles of more advanced forms becomes difficult. While it is possible to come to some conclusions based on the number of teeth, it is not really a satisfactory

method of taxonomic differentiation. In *Eocaptorhinus laticeps* from the Clyde Formation, an accurate tooth count is known only for the juvenile specimen (FMNH UC 1698) where there are 18 teeth. *Romeria prima* (MCZ 1963) and *R. texana* (MCZ 1478), which are almost identical in size (57–58 mm), have 23 and 22 tooth positions, respectively. *Protocaptorhinus pricei* (MCZ 1478), which is of similar size (52 mm), has 22. Although *Eocaptorhinus laticeps* is considerably larger, ranging in this sample from 66.6 to 81 mm in skull length, the number of maxillary teeth is almost constant at 22 and 23.

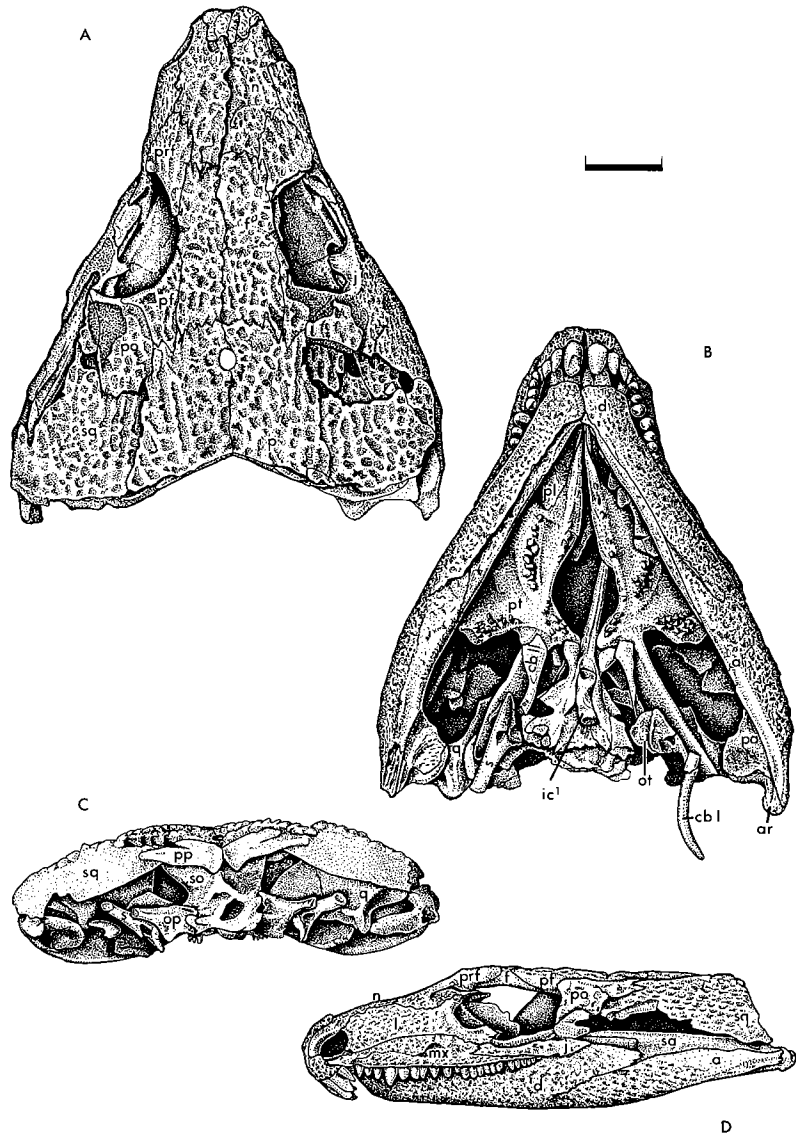


Figure 12. *Eocaptorhinus laticeps*. A, skull in dorsal view; B, skull in ventral view; C, skull in occipital view; D, skull in left-lateral view. Abbreviations: *ic'*, atlas intercentrum; *ot*, otolith. OUSM 15101 (3-0-54). Scale equals 1 cm.

Eocaptorhinus laticeps from the Clyde Formation appears to have fewer maxillary teeth (18 to 20) than the slightly older Oklahoma form, but this may be only the result of the difficult preparation caused by the extremely hard matrix. In general, there is a trend toward a reduction in the number of maxillary teeth in progressively larger, later forms.

In the specimens of *Eocaptorhinus laticeps* from Oklahoma, the preservation is so good and the matrix so soft and easily prepared that all features of the maxillary tooth-row are visible. In fact, it is possible to see exactly how the teeth were implanted

in the jaw, how they are replaced, and how they are worn. When the maxillary tooth-row is seen in lateral view (fig. 11A), definite groupings of teeth according to height is noticeable. The teeth are separable into three or four sets, identified by Bolt and DeMar (1975) in their specimens as Zahnreihen, usually four or five teeth, that become progressively lower posteriorly except for the first set, in which this pattern is reversed. The first set of four (occasionally five) teeth culminates in the largest maxillary tooth, the caniniform, that is usually twice the height of the first tooth. The second set begins with a large tooth that occasionally

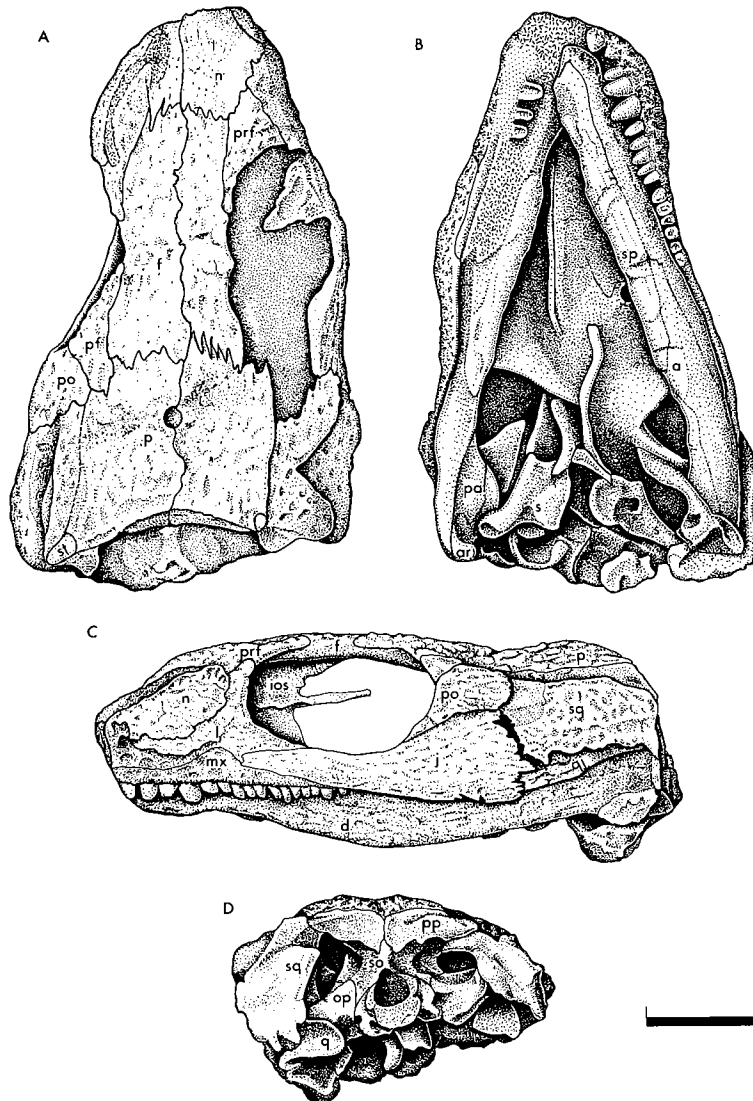


Figure 13. *Eocaptorhinus laticeps*. Juvenile. A, skull in dorsal view; B, skull in ventral view; C, skull in left-lateral view; D, skull in occipital view. FMNH UC 1698. Scale equals 1 cm.

rivals the caniniform in length (OUSM 15021, fig. 11A; 15101, fig. 12C; 15102, fig. 12B). The second set usually consists of five or six teeth progressively diminishing in height posteriorly to the 10th tooth position (OUSM 15101, 15102). The third set begins with the 11th tooth, which is fractionally larger than the 10th. The last tooth of the second set is usually offset medially about one-quarter tooth width. This is especially noticeable in OUSM 15101 and 15020 but is not so apparent in OUSM 15102.

A number of specimens of small captorhinid maxillae grouped under the number FMNH UC 404 [referred to as *Labidosaurus hamatus* and *Labidosaurus*, cf. *L. hamatus* (Olson, 1967)] and the numbers FMNH PR 916 and PR 944 have been recovered from the Richards Spur deposits. Their taxonomic position is confused, since they are from animals that are indistinguishable from the *Captorhinus* species (usually referred to as *C. aguti*) present there, save for the presence of a single-rowed marginal dentition. It might be acceptable to refer these specimens to the genus *Eocaptorhinus*, were it not for the fact that the Richards Spur deposits contain many patterns intermediate between *Eocaptorhinus* and *Captorhinus*. Bolt and Demar (1975) preferred to group them with *Captorhinus aguti*.

Occasional reference has been made to the problem of tooth replacement in captorhinids (Fox and Bowman, 1966; Bolt and Demar, 1975). Usually, it has been thought that captorhinids, or specifically *Captorhinus aguti*, had acrodont dentitions that were not, or could not be, replaced. It has been assumed that replacement waves of teeth erupted medially to the current tooth generation and displaced it laterally to leave a multiple-rowed pattern. While this may be true for the large parallel tooth-rowed forms like *Labidosaurikos* (Stovall, 1950) or *Moradiosaurus* (Taquet, 1969), it is only partially true for *Captorhinus*. In fact, tooth replacement is common although apparently very rapid. Replacement scars are often seen on *Captorhinus* maxillae from Richards Spur, as is one in *Eocaptorhinus laticeps* from the McCann Quarry (OUSM 15020, fig. 8C). Replacement gaps in the tooth-rows have not been observed in *Eocaptorhinus laticeps* (FMNH UC 642, 701; OUSM 15020, 15021, 15022, 15101, 15102) or *Romeria*

texana (MCZ 1480). Gaps have been observed in *Protocaptorhinus pricei* (MCZ 1478), a probable subadult, only one of which is a possible replacement gap, the rest being caused by breakage of the right maxilla in the region of the 10th to 13th tooth positions. The absence of the seventh maxillary tooth does not appear to be related to replacement, since there is neither an empty socket nor a juvenile tooth or tooth bud in this position. *Romeria prima* (MCZ 1963) shows a number of gaps in the maxillary tooth-row, many of which by nature of their unusual spacing are surely the result of postmortem loss either during preservation or preparation. Only three teeth are missing from the right maxilla, all apparently as a result of crushing rather than replacement. It appears that tooth replacement in adult captorhinids was rare or absent. Evidence that replacement of teeth occurred in younger individuals is seen in a few specimens. What replacement has occurred appears to have progressed rapidly with the resorption pits or gaps quickly being filled.

The teeth themselves reveal much additional information about the evolution of the Wichita captorhinids. Both species of *Romeria* possess a relatively large number of teeth (22 to 23) in a short maxilla, while *Eocaptorhinus laticeps* has the same number of teeth in a longer jaw. The absolute length of the teeth is not increased in the younger forms but is, in fact, occasionally decreased (OUSM 15101). This causes a proportionate increase in tooth diameter that has had a marked effect on tooth-wear patterns and probably on feeding behavior. The teeth of both *Romeria prima* and *R. texana* are the long form seen in the primitive captorhinomorphs *Hylonomus*, *Paleothyris*, and *Protothyris*. Little parasagittal shear developed between the maxillary and mandibular dentitions. Contact between maxillary and dentary teeth was limited, as simple vertical motion was the only interaction of consequence. The teeth of the upper jaws typically seated themselves in the intervals between the teeth of the lower jaws, thus causing a wear pattern typified by a slight vertical ridge on the medial surface of the maxillary teeth and on the lateral face of the dentary teeth. This pattern is difficult to see in small forms preserved in hard matrix, especially if the mandibles are in place. The faceting

of the occlusal surfaces of the teeth produces a marked lateral "pinching" of the tips. This is especially noticeable on the caniniform teeth where it is the major factor involved in keeping the tips sharp.

The pattern in *Protocaptorhinus pricei* (MCZ 1478) is identical, but the greater thickness of the teeth results in blunter tips. Only the caniniforms, which unfortunately have been ground down during preparation, possessed a sufficient length-to-thickness ratio to allow a sharp tip to develop. Only a nubbin of a retroarticular process had begun to develop in *P. pricei*.

The situation changed rapidly as the retroarticular process developed. In *Eocaptorhinus laticeps*, all post-caniniform teeth are bluntly rounded. The internal surfaces of the maxillary teeth have rounded the vertical medial ridge. Only the most anterior maxillary teeth have not been rounded. The medial face of the caniniform tooth has taken on a distinctly hollowed appearance. This pattern is developed to its fullest in the undescribed, small, single-tooth-rowed captorhinid from Richards Spur (UK FEP 60.G-1, FMNH UC 404), where the post-caniniform teeth have been worn to a flat-tipped, chisel-shaped pattern suited for shearing and chopping. The pronounced changes in dentitions and adductor mechanics that occurred during the evolutionary history of the Wolfcampian captorhinids appears to have been intimately involved with changes in the feeding habits of the group that may have allowed them to expand greatly both in numbers and diversity during Leonardian and Guadalupian times.

Septomaxilla

The septomaxilla (fig. 14) is a thin, rectangular sheet of bone that has been curved around a basic conical form. The result is a short, quickly tapering, medially directed funnel that is open along its antero-dorsal side. In lateral view, the septomaxilla appears as a C-shaped lamina lining the posterior border of the external naris. It lies on a dorsomedial facet of the premaxillary process of the maxilla and is supported posteroventrally by a small septomaxillary process of the maxilla. The medial opening of the septomaxillary funnel is located 1 to 2 mm above the anterior end of the vomer.

There is no evidence of a bony support of this end of the fragile septomaxilla. The cartilage of the nasal capsule and particularly of the vestibulum (cupola) constituted the main supports. The distance by which the medial end of the septomaxilla is separated from the floor of the vomer strongly suggests the presence of a small vomeronasal (Jacobson's) organ at the anterior end of the nasal capsule below the septomaxilla.

The septomaxillae of most primitive reptiles appear to be similar when they can be observed.

Lachrymal

The lachrymal of *Eocaptorhinus laticeps* is a long, thin bone extending from the anterior and anteroventral border of the orbit to the posterior rim of the external naris (fig. 15A, C). Posteriorly, the lateral surface is sculptured with deep pits and prominent ridges; anteriorly the sculpturing is less pronounced. Each pit is pierced by one or more fine pores confluent with an extensive inner vascular system.

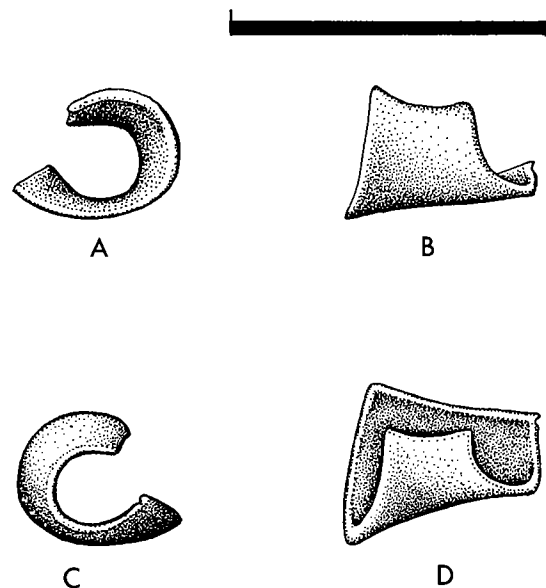


Figure 14. *Eocaptorhinus laticeps*. Left septomaxilla. A, lateral view; B, posterior view; C, medial view; D, dorsal view. Reconstruction based on OUSM 15020A (3-1-S4), 15101 (3-0-S4), and Richards Spur specimens. Scale equals 1 cm.

The ventral border of the lachrymal forms a wide, complex suture with the maxilla. Anteriorly the sutural plane is a smooth, ventrolaterally sloping surface, while it is roughly grooved and ridged ventromedially and forms a ventrally inclined surface in the central and posterior regions.

The lachrymal-nasal structure (fig. 15A) is a combination overlapping scarf joint and slightly interdigitating butt joint. Internally

a thin, flat shelf of bone extends dorsally for a short distance beneath the nasal. Externally a heavy irregular edge abuts a similarly thickened edge of the nasal.

The lachrymal-prefrontal suture (fig. 15A-C) is extremely complex. Dorsally the lachrymal overlaps the prefrontal along a long, shallow, undulating recess on the medial surface of the thin shelf that underlies the nasal. Thus, anteriorly nasal, lachrymal,

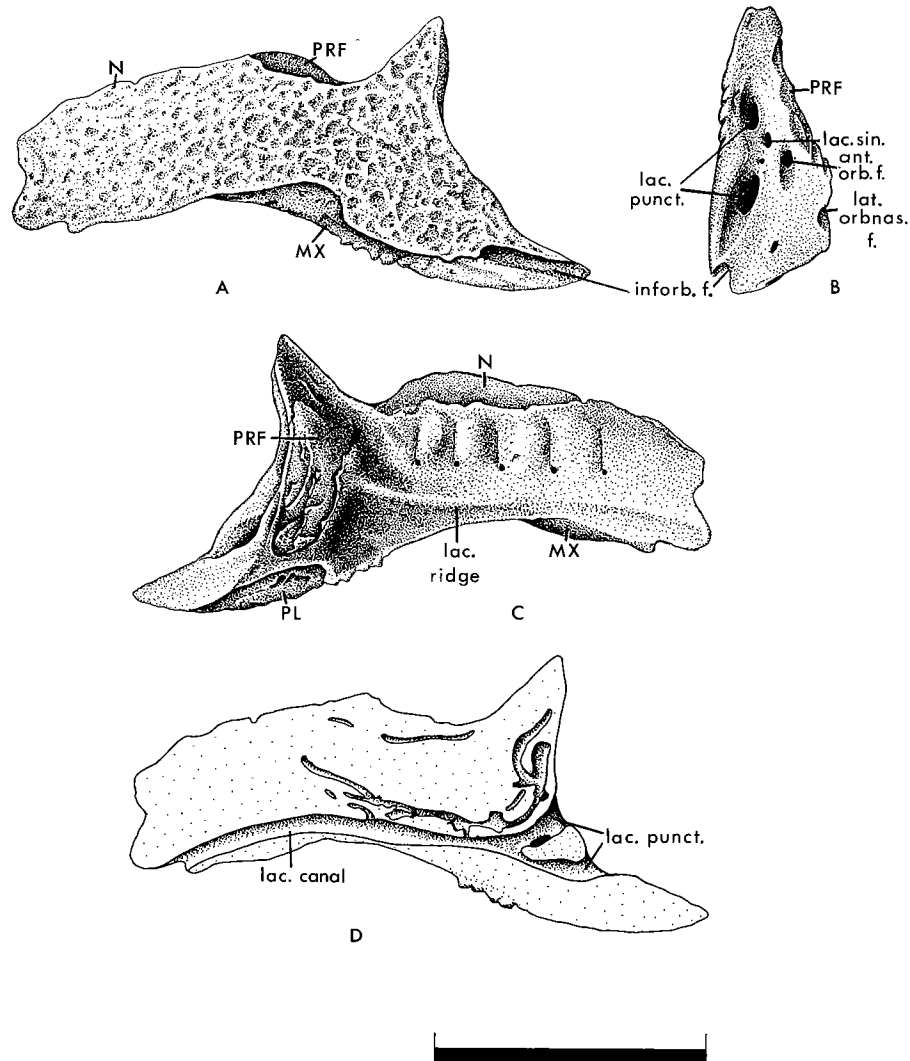


Figure 15. *Eocaptorhinus laticeps*. Left lachrymal. A, lateral view; B, posterior view; C, medial view; D, sagittal view 2 mm medial to external bone surface. Abbreviations: *ant. orb. f.*, anterior orbital foramen; *inforb. f.*, infraorbital foramen; *lac. canal*, lachrymal canal; *lac. punct.*, lachrymal punctum; *lac. ridge*, lachrymal ridge; *lac. sin.*, lachrymal sinus; *lat. orb. nas. f.*, lateral orbitonasal foramen. Reconstruction based on OUSM 15020A (3-1-S4), 15021 (3-1-S8), 15101 (3-0-S4), and Richards Spur specimens. Scale equals 1 cm.

and prefrontal sequentially overlap one another (fig. 15A–C). Posteriorly the lachrymal is thickened along the orbital margin. The medial surface of this thickened region is heavily scarred by sharp, bony ridges on the lachrymal-prefrontal sutural surface.

A small irregularly striated suture scar 1/2 to 1 mm below the prefrontal scar on the orbital rim marks the short sutural contact with the palatine.

Ventromedially along the maxillo-lachrymal sutural surface a thickened, medial, lachrymal ridge extends from the orbital margin to the narial rim. The internal surface of the thin dorsal blade of the lachrymal is marked by five shallow, vertical grooves, each pierced at its ventral extremity by a small foramen (fig. 15C). Into these foramina passed small branches of the lateral palatine nerve. The grooves mark the course of the arterial branches dorsolaterally over the zona annularis within the olfactochoanal membrane.

The lachrymal and prefrontal form the wide anterior rim of the orbit. When viewed in posterior aspect (fig. 15B), several foramina appear on the concave surface of the lachrymal as does a prominent groove at its posteroventrolateral extremity and another on the medial edge between the prefrontal and palatine sutural surfaces.

The lateral groove forms the upper border of the infraorbital foramen, which is also bounded by the jugal laterally and the maxilla ventrally. The infraorbital foramen is confluent with the supramaxillary foramen and canal penetrating the postero-dorsal sutural surface of the maxilla. This is the route taken by the inferior orbital (supramaxillary) artery, by the infraorbital (supramaxillary) nerve (V_2), and by the lateral palatine ramus of the facial nerve.

The groove on the ventromedial edge of the lachrymal directly below the broad sutural contact with the prefrontal forms the posterior border of the lateral nasal fenestra (Gaupp, 1900). The medial border of the foramen was formed by the fibrous orbitonasal septum that separated the nasal capsule and the orbit. The large lateral branch of the inferior nasal artery and a large communicating sinus between the lateral palatal sinus and the orbital sinus passed through the lateral orbitonasal foramen.

Of the numerous perforating foramina, the two largest, the lachrymal foramina, are situated in a deep, conjunctival groove near the lateral border of the lachrymal. As can be seen in figure 15D, both of the canaliculi from the dorsal and ventral lachrymal foramina join soon after entering the bone to form a common lachrymal canal that passes forward through the heavy, ventral lachrymal ridge to the external naris.

The anterior orbital artery passed through the anterior orbital foramen, which opens directly into the osseous canal, through which the lachrymal duct passed, at the junction of the two lachrymal canaliculi. Numerous small anastomosing canals within the bone are connected to this canal. They enclosed fine arterial branches that passed laterally through fine pores in the bases of the sculpture pits to supply the skin with blood from the anterior orbital artery.

Posteromedial to the ventral lachrymal foramen is a small foramen that extends anteriorly as a fine venous canal, here thought to be the inferior palpebral canal, running parallel to the lachrymal duct and ventrolaterally to it. This canal carried the inferior palpebral vein that drained the skin of the lateral surface of the snout through some of the many small pores in the bases of the surface sculpturing pits.

Several small foramina appear on the posterior surface of the lachrymal. Their positions vary considerably, although they tend to be concentrated within the triangular region delineated by the lachrymal foramina and the anterior orbital foramen. Their function is not definitely known, but it is to be expected that they contained fine branches of the anterior orbital artery.

There are no discernible differences between the lachrymal of *Eocaptorhinus* and that of any other primitive captorhinid. Lachrymals of primitive captorhinomorphs are poorly known. The bone described by Carroll (1964) as the lachrymal of *Hylonomus* is a right jugal, since the paired foramina enter the orbital rim not from the orbit but from the bone-ensheathed cheek. Complete lachrymals are absent in known specimens of *Anthracodromeus*, *Brouffia*, and *Coelostegus* (Carroll and Baird, 1972). In *Paleothyris* the lachrymal is poorly preserved (Carroll, 1969a). It extends anteriorly to the rim of the external naris. Only in

Protorothyris and *Cephalerpeton* is the lachrymal well known. That of *Protorothyris*, seen only in external aspect (Clark and Carroll, 1973), is similar to that of the primitive captorhinids and ophiacodontid pelycosaurs. *Cephalerpeton* (Carroll and Baird, 1972) has a much different lachrymal that is visible only medially. The lachrymal duct extends forward only to a point halfway between the orbit and the external naris. The maxilla appears to be quite high laterally. In general, the maxilla-lachrymal region of *Cephalerpeton* appears to be much more like that of *Haptodus* (Romer and Price, 1940; P. J. Currie, oral communication, 1977) than any other known primitive captorhinomorph or captorhinid, although this may only be a convergent development.

Nasal

The roughly rectangular-shaped nasal (fig. 16A, B) meets its fellow along a slightly undulating median suture. The lateral edges are moderately convex with the posterior half sutured to the prefrontal and the anterior half to the lachrymal. The nasal-prefrontal suture exhibits a more extensive

interdigitation at the surface than does the nasal-lachrymal suture. The prefrontal extends a thin flange forward beneath the nasal for some distance. The remaining two junctions, the nasal-premaxilla and the nasal-frontal, are both deeply interdigitated sutures oriented perpendicular to the center line. The anteroventral extremity of the nasal forms the dorsal rim of the external naris.

The ventral surface of the nasal (figs. 16B, 17) is smoothly concave. It is marked by a hollow, longitudinal ridge that opens posteriorly in a small foramen. This tube contained the orbitonasal vein that drained blood from the nasal sinus and rostral sinus

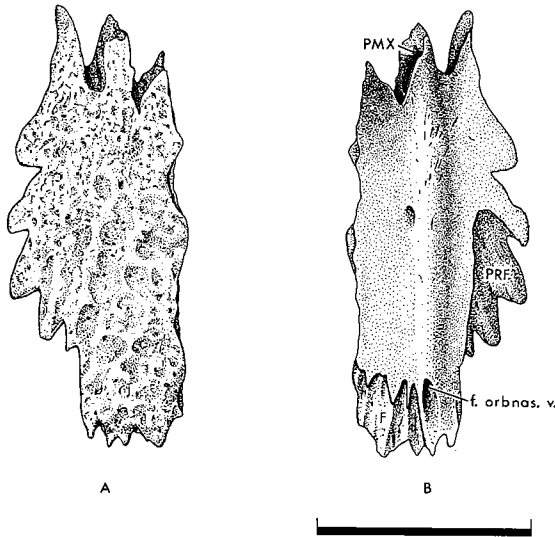


Figure 16. *Eocaptorhinus laticeps*. Left nasal. A, dorsal view; B, ventral view. Abbreviation: f. orbnas. v., foramen for orbitonasal vein. Reconstruction based on OUSM 15021 (3-1-58). Scale equals 1 cm.

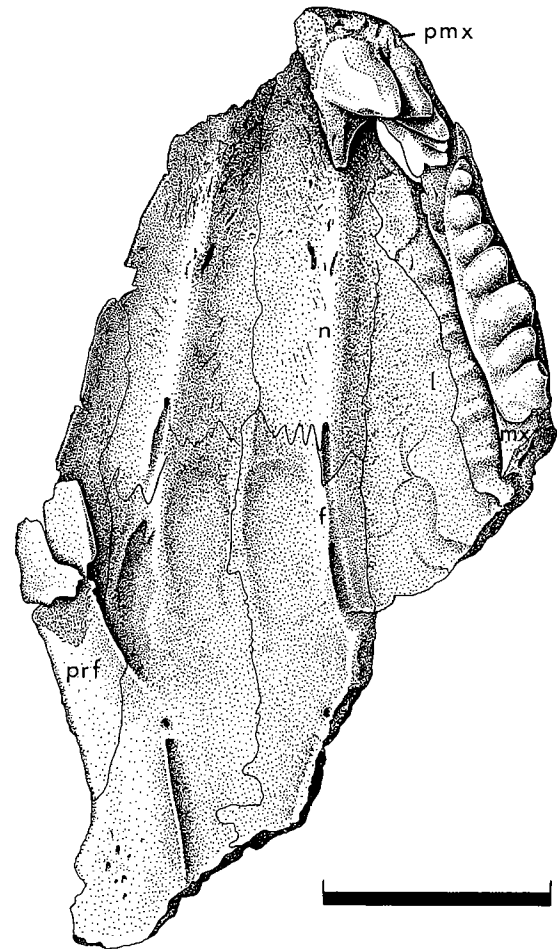


Figure 17. *Eocaptorhinus laticeps*. Preorbital region of snout in ventral view with palate removed. OUSM 15021 (3-1058). Scale equals 1 cm.

of the premaxilla to the orbital sinus. Numerous small venous foramina communicated with the tube from the ventral surface of the bone.

The nasals of the other small captorhinids are similar in general shape. As reconstructed by Clark and Carroll (1973), the nasals of *Romeria texana* appear to be much narrower than in the other forms. In fact, the nasal has been ground away during preparation so that the ventral, anterior flange of the prefrontal is exposed. Clark and Carroll's reconstruction shows the internal nasal-prefrontal suture line, not the external.

Prefrontal

The prefrontal of *Eocaptorhinus laticeps* (fig. 18A-C) consists of a thin, dorsolaterally convex anterior plate with a thickened, posterior border that forms the anterodorsal rim of the orbit. The front one-third of the anterior plate underlies the nasal in a broad, flat suture. Medially along its entire post-nasal length, the prefrontal forms a "tongue-and-groove" suture with the frontal. Along the lateral edge of the anterior plate the lachrymal overlaps the prefrontal along a narrow, undulating shelf. Posteriorly the nature of the suture changes entirely as the lachrymal becomes wedged under the posterior edge of the anterior plate. The thickened orbital rim portion of the lachrymal becomes

sutured medially to the lateral surface of the orbital-rim portion of the prefrontal (fig. 18A). This suture is strengthened by numerous deep grooves and corresponding ridges on the sutural surfaces of both the lachrymal and the prefrontal.

The posterior two-thirds of the lateral surface of the anterior plate (fig. 18) is heavily sculptured with deep pits each pierced by one or more small pores leading directly into the system of longitudinal venous and arterial canals within the bone. The major source of arterial blood was through fine branches of the superior nasal artery that pierced the posterior rim of the prefrontal through several very small foramina (fig. 18B). Presumably one or more of these foramina served as a passage for venous tributaries, including the superior palpebral vein, to the orbital sinus.

The heavy posterior thickening of the prefrontal forms the anterodorsal border of the orbit (fig. 18B). It extends ventromedially to form the vertical edge to which the fibrous, transverse, orbitonasal membrane was attached that separated the orbit from the nasal capsule. Near its ventromedial extremity, this edge is notched to form the dorsolateral border of the lateral nasal fenestra through which passed the prefrontal vein, the lateral ramus of the inferior nasal artery, the lateral palatine nerve, and the intermediate palatine nerve. Posterodorsally, the thickened orbital rim allows the

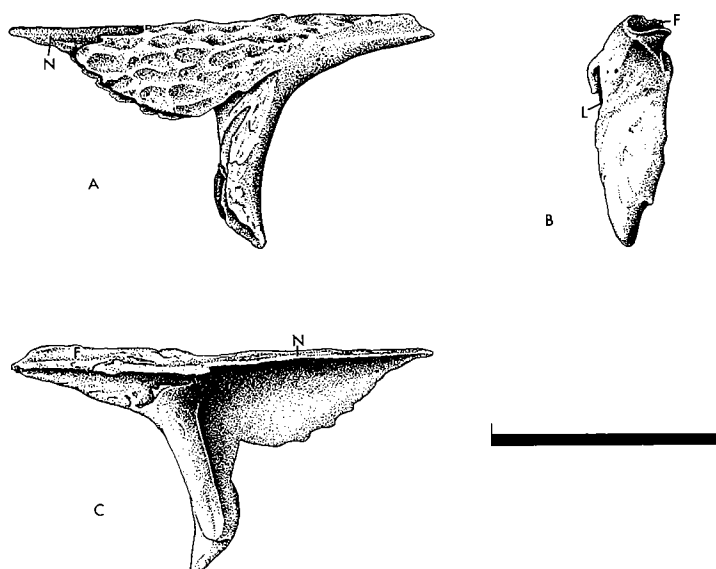


Figure 18. *Eocaptorhinus laticeps*. Left prefrontal. A, lateral view; B, posterior view; C, medial view. Reconstruction based on OUSM 15020A (3-1-S4). Scale equals 1 cm.

“tongue-and-groove” contact between the prefrontal and frontal to be expanded greatly ventrally (figs. 9A, B; 18).

The prefrontals are well preserved in all of the species of primitive captorhinids being considered. The prefrontals are best exposed in *Romeria prima* (MCZ 1968). In all respects they conform to the description as presented for *Eocaptorhinus laticeps*, although the anterior portions underlying the nasal are not visible. In *Romeria texana* (MCZ 1480) preparation has removed much of the bone surface so that the underlying anterior shelf has been exposed. As a result, the prefrontals appear to be abnormally long when, in fact, the true external surface view would have shown prefrontals no different from those seen in *R. prima*. No significant differences are noticeable in proportion or configuration of the prefrontals in *Protocaptorhinus pricei*, *Eocaptorhinus laticeps*, or *Captorhinus aguti*.

Frontal

The frontal is a long, narrow, rectangular bone joined to its fellow along a wavy, “tongue-and-groove” medial suture (figs. 1A, 2A, 10A). The posterior extremity forms an interdigitating suture with the parietal oriented at right angles to the midline. A similar suture unites the nasal and frontal anteriorly, although the frontal overlaps the nasal extensively in the region of the posterior end of the nasal ridge. Along the anterior third of its lateral border, the frontal consists of a straight suture with the prefrontal, while the central third of its border forms a short projection into the orbital rim. The remaining portion of the lateral border consists of a straight suture between the frontal and postfrontal similar to the frontal-prefrontal suture.

Externally the frontal is sculptured with the same pattern as the nasal. The internal surface is gently concave with a heavy lateral edge, particularly around the orbital rim. It is to this stout ridge that the prefrontals and postfrontals are strongly attached in order to brace the anterodorsal and posterodorsal corners of the orbit. Medially the ridge ends abruptly, thus forming a step against which the ossified solum suprasedale portion of the interorbital septum is buttressed (fig. 17). A slight anterior ridge forms a

continuation of the nasal ridge. A groove along its crest is continuous with the enclosed tube on the ventral surface of the nasal. The groove angles laterally before the ridge becomes part of the orbital-rim thickening. This would have directed the orbitonasal vein into the orbital sinus, lateral to the interorbital septum.

Just anterior to the posterior limit of the nasal-prefrontal suture is a slight medial swelling of the orbital rim that obliterates the sharp step formed by the contact of the solum suprasedale. A small foramen that conducted fine twigs of the frontal ramus of the ophthalmic nerve to the skin of the frontal is present in this swelling in line with the lateral edge of the solum suprasedale. This region marks the point at which the sphenethmoidal commissure diverged laterally from the solum suprasedale and formed the dorsal margin of the orbitonasal fissure through which the frontal artery, antorbital artery, and frontal ramus of the ophthalmic nerve entered the nasal capsule and the orbitonasal vein made its exit.

The shape and proportions of the frontal of all early captorhinids are nearly identical and are considerably wider than in *Protorothyris archeri* or *Paleothyris acadiana*.

In all early captorhinids, the prefrontal and postfrontal are deeply incised into the greatly thickened orbital-rim buttress of the frontal. As a result, both pre- and postfrontals extend onto the skull roof. The frontal extends a narrow flange laterally between these bones to the orbital rim. The smaller, lighter primitive captorhinomorphs do not show as great a thickening around the orbital rim, so that the prefrontals and postfrontals are not deeply incised into the frontals. While the frontal does contribute to the border of the orbit, it does not extend laterally to the orbit.

Parietal

The parietal is a subrectangular plate of bone bounded medially by its fellow and laterally by the squamosal and the postorbital (figs. 1A, 6A, 8A, 10A). Posteriorly it joins the postparietal and supraoccipital, and anteriorly, the frontal and postfrontal. The supratemporal occupies a deep notch in the posterolateral corner.

The interparietal suture is of the same

wavy, "tongue-and-groove" form as the interfrontal suture. A large pineal foramen is situated on the midline ahead of the center. The undulating lateral sutures are formed by the parietals overlapping the squamosals and postorbitals extensively. Both the ventral contact surfaces of the parietals and the dorsal contact surfaces of the squamosals and postorbitals have extensive, laterally directed ridge-and-groove scarring. This is a very solid suture line gusseted posteriorly by the supratemporal, squamosal, and quadrate, and anteriorly by the ventral process of the postfrontal.

The fronto-parietal union occurs along a deeply interdigitating suture in which the frontal extensively overlies the parietal. The postfrontal is deeply incised into a notch in the dorsal surface of the anterolateral corner of the parietal. The postparietals lie vertically at the back of the skull and are incised anteromedially at an angle of about 20° to the occipital plane. The postparietal fits close up under the posterior edge of the parietal.

The posterior border of the ventral surface of the parietal is heavily scarred along a deeply incised and heavily striated shelf that served as a sutural contact with the ascending process of the supraoccipital medially and the postparietals posteriorly (fig. 16).

The parietals are slightly depressed along the midline. Sculpturing is of the usual deep, pit-and-ridge type with perforating pores. There is a tendency for the pits to align themselves longitudinally except for a single, well-developed ring of pits around the pineal foramen.

The configuration of the internal surfaces of the parietal is extremely complex (fig. 19). Laterally a suture scar one-quarter of the width of the parietal extends the length of the bone. It consists of many narrow, shallow striae directed toward the parietal's growth center. Similar striae occur along the medial border but are not suture scars. Fox and Bowman (1966) referred to these as muscle scars, an unacceptable explanation because of their presence internal to the orbital-plate cartilages (*taenia marginalis*). Rather, they appear to represent scars marking the attachment of the orbital-plate cartilage itself and the meningeal membrane to the skull roof. The supraoccipital-suture scar extends forward along the

midline almost to the pineal and accounts for the heaviest scarring in the region of the midline. The region of the medial striae is slightly domed to accept the rounded optic lobes posterior to the pineal opening and the cerebrum anteriorly. The cerebellum lay ventral to the median ascending process of the supraoccipital.

The area of the parietal available for muscle attachment is surprisingly small. Three well-developed muscle origins are illustrated (fig. 19) lateral to the orbital-plate cartilages and braincase. A well-developed *M. adductor mandibulae externus superficialis* originated on a longitudinal lateral ridge extending from the postorbital posteriorly along the parietal parallel to the squamosal suture. An anterior division of the lateral slip of the *M. adductor mandibulae externus superficialis*, the *M. levator anguli oris* originated on the medial surface of the postorbital.

Medial to this ridge is a broad area of origin of the *M. adductor mandibulae externus medius* that is subdivided into two prominent scars. The most obvious of these is a deeply dished posterior parabolic depression perforated by a prominent anterolaterally situated temporoparietal foramen. It is believed that the temporal and temporoparietal arteries separated two segments of the pars media corresponding approximately to the *M. adductor mandibulae externus 2 c* (pars media C) medially and 2 a (pars media A) that Lakjer (1926) and Haas (1973) noted in *Sphenodon*. The presence of the foramen, through which the temporoparietal artery, a subdivision of the temporal artery, supplied the parietal and its overlying skin with blood, identifies the point of division. Anterior to the parabolic scar is a region of low posteromedially directed ridges with their anterolateral limits marked by a number of prominent tuberosities. This is interpreted as the origin scar of a more anterior slip of the pars media corresponding to the *M. adductor mandibulae externus 2 b* (pars media B) of *Sphenodon* (Lakjer, 1926; Haas, 1973). The close resemblance between the origins of the slips of the pars media in *Sphenodon* and the origin scars in *Eocaptorhinus* is astonishing.

This leaves a smoothly concave surface anterior to the *M. adductor mandibulae externus medius* and medial to the pars super-

ficialis that may have been occupied by lachrymal glands dorsally or by various muscles, especially those with origins on the braincase and epipterygoids. The epipterygoids apparently did not reach the parietals but were instead attached ligamentously to the taenia marginalis. In one specimen (OUSM 15022), the epipterygoids have been preserved in their natural position with only minor crushing of the skull roof down to touch the dorsal tips of the columella of the epipterygoid.

A long, deep, anteromedially directed groove in the ventral surface of the posterolateral corner of the parietal received a sharp crest from the dorsal flange of the squamosal that helped strengthen the parietal squamosal suture. The medial edge of the notch may have supported a tendon from

which one or more lateral slips of the *M. adductor mandibulae externus medius* probably attached, as in *Sphenodon* (Lakjer, 1926; Haas, 1973).

When viewed in dorsal aspect, the parietals of *Eocaptorhinus* appear to be quite different from those of *Romeria* or *Protocaptorhinus*. General proportions are similar, although the smaller forms with proportionately larger braincases are slightly wider. As far as can be determined, the smaller forms are less heavily sculptured, but this is difficult to ascertain with certainty because of the severe treatment several of these specimens have received during preparation. The single point of variance is related to the posterior border of the parietal that is deeply emarginated in *Romeria* and is less so in *Protocaptorhinus* and *Eocaptorhinus*.

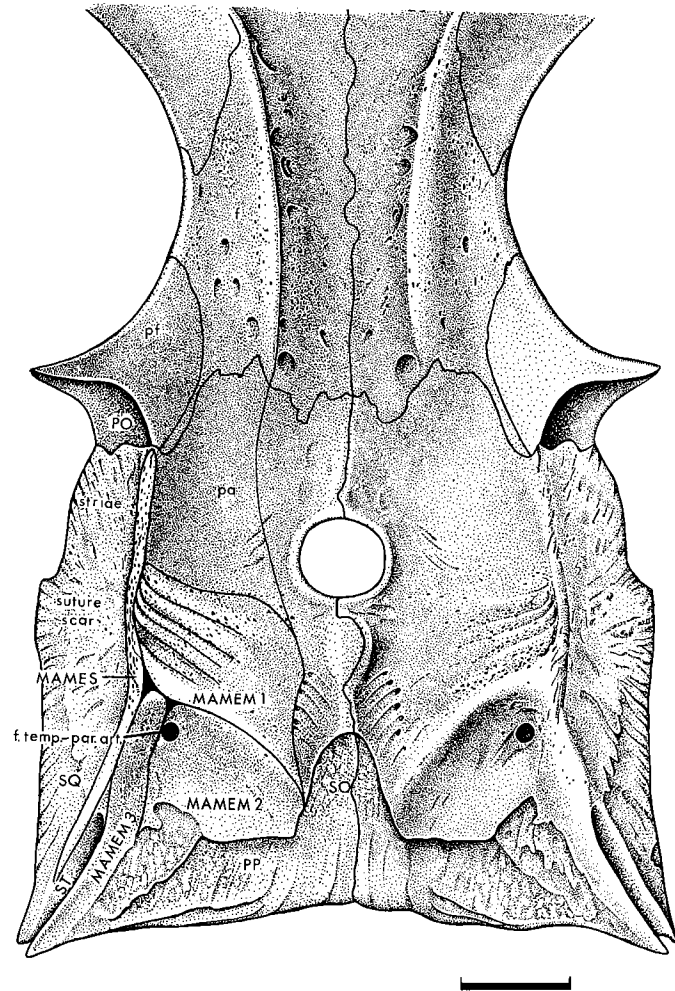


Figure 19. *Eocaptorhinus laticeps*. Skull table in ventral view. Abbreviation: *f. temp. par. art.*, temporoparietal artery foramen. Areas of attachment of *MAMEM*, *M. adductor mandibulae externus medius*; *MAMES*, *M. adductor mandibulae externus superficialis*. Reconstruction based on OUSM 15020B (3-0-S5), 15022 (3-1-S7), and Richards Spur captorhinid specimens. Scale equals 1 cm.

An examination of the internal surface of the parietal of *Eocaptorhinus* shows that the embayment, for the attachment of the underlying postparietals, is still quite prominent. Two factors, both size dependant, affect this feature. Apparently *Eocaptorhinus*, a much larger form than *Romeria*, with consequently thicker bone, was able to extend a sheet of bone of mechanically useful thickness further posteriorly over the postparietal. More important is the decrease in possible lateral movement of the head and neck related to the increased width of the head that did not require as long a resting fiber length of the *M. spinalis capitis*. A shorter, wider, more powerful *M. spinalis capitis* was distinctly advantageous if the lateral flexibility of the neck was limited by external factors, thus the continuing trend to reduce the lateral embayment of the parietals. It is also probable that grinding of the type specimen of *Romeria texana* has accentuated the embayment by revealing the internal boundary of the suture much as it has the prefrontal-frontal and frontal-parietal junctions. The type specimen of *Romeria prima* does reveal a noticeable embayment that has not been accentuated by preparation.

Postparietal

The postparietals of *Eocaptorhinus laticeps* (figs. 2B, 12C, 13D) lie vertically on the embayed posterior margin of the parietals. They are paired elements separated ventromedially by a vertical ridge on the posterior surface of the medial-ascending process of the supraoccipital. Laterally they extend onto the occipital flange of the squamosal. The longer ventrolateral process just reaches the posteroventral extension of the supratemporal. A deep groove separates the ventrolateral process from the dorsolateral process. The whole dorsal edge (parietal flange) of the postparietal curves forward to underlie the posterior edge of the parietal to which it is strongly attached. In some cases, the external surface of the parietal continues smoothly above the suture line (OUSM 15101; fig. 12C), while in others the parietals extend posteriorly as a strong rim on the occipital surface along the upper edge of the postparietals (OUSM 15020B). The dorsolateral process extends laterally to the

parietal-supratemporal suture where its slightly swollen crest is continued along the lateral rim of the occiput by the supra-temporal and then the raised lateral edge of the occipital flange of the squamosal. The dorsal surface of the anteriorly projecting parietal flange of the postparietal is covered by a heavy suture scar. The rest of the external surface is smooth with very light muscle scarring.

The dorsolateral process and its ventrolateral extension served as the insertion region for the *M. spinalis capitis*. The *M. rectus capitis posterior superficialis* inserted onto the slightly hollowed posteromedial region of the postparietal. The *M. longissimus capitis dorsalis* had the largest region of insertion on the ventrolateral process of the postparietal and the posteromedial surface of the occipital flange of the squamosal. The deep groove that extends medially from the lateral notch separating the dorsolateral and ventrolateral processes of the postparietal carried the occipital artery, which passed laterally from below the ventromedial edge of the postparietal.

Protocaptorhinus pricei (MCZ 1478) has postparietals that are nearly identical with those of *Eocaptorhinus laticeps*. Slight crushing of the skull has caused the supraoccipital to push the ventral edge of the postparietals rearward, thus exposing them in dorsal view. As seen in FMNH UC 1119, the postparietals lie vertically on the occipital surface but do not exhibit the characteristic embayment of *E. laticeps*. This raises a serious question as to the identity of the specimen from the contemporaneous Wellington Formation at Orlando, Oklahoma, attributed to *Pleuristion brachycoelus* (FMNH UR 678) by Olson (1967, 1970), since it, too, is of the same size and proportions, has vertical postparietals, and seems otherwise identical.

Since the postparietals of *Romeria texana* (MCZ 1480) are unknown, all reference to the postparietals of the older genus must be based on *Romeria prima*. The supraoccipital has been raised slightly, thus pushing the postparietals rearward as in MCZ 1478. This distortion is not great enough to account for the oblique position of the postparietals that must, therefore, have been present in the living animal. The flexure between the occipital surface and the dorsal sutural sur-

faces was slightly greater than as preserved. The thinner bone of the parietals of the smaller animals, particularly *Romeria*, prevented a heavy supporting layer from building up over the anterodorsal extension of the postparietal. It also appears that some of the surface bone has been removed during the grinding that occurred during initial preparation, thus accentuating the emargination of the parietals in both *Romeria prima* and *R. texana*. This is especially important in *R. texana*. Some of the surface detail, including the lateral tips of the postparietals, has been lost to the grinding. The lateral notch separating the dorsolateral and ventrolateral processes has been destroyed, but its position can be established accurately. A faint representation of the groove that extends medially from the notch is still visible. The area dorsal to the groove is larger than that ventral to it, while they are the same size in *Protocaptorhinus* and *Eocaptorhinus*.

Supratemporal

The supratemporals of *Eocaptorhinus laticeps* (FMNH UC 642, fig. 5A; UC 701, fig. 20A; OUSM 15101, fig. 12A) are small elliptical skull-roof elements 4 to 5 mm in length and 2 mm in width that occupy a deep notch in the posterolateral corner of the parietals. The medial surface of the notch is overlain by a thin wedge of bone from the dorsal flange of the squamosal that extends upward almost to the surface of the skull roof. The supratemporal rests upon this squamosal wedge and is thus separated from the parietal ventromedially. The parietal does contact the supratemporal anterolaterally. The supratemporal sits on the squamosal, so that the only exposure of the supratemporal in occipital view is as part of the thin, raised occipital rim. The ventral process of the postparietal extends laterally across the occipital flange of the squamosal. It is in very close proximity to the ventral edge of the supratemporal but does not seem actually to touch it in *Eocaptorhinus laticeps* (OUSM 15101, fig. 12A). In *Eocaptorhinus laticeps* (UC 642, fig. 5A; UC 701, fig. 20A) tenuous contact between the ventral process of the postparietal and the supratemporal is made as it is in *Captorhinus aguti* (Fox and Bowman, 1966). In primitive captorhin-

ids like *Romeria prima* (MCZ 1963) and *Protocaptorhinus pricei* (MCZ 1478) a posteromedial projection of the parietal separated the supratemporal from the postparietal. The primitive captorhinomorphs had the separation increased by the interposition of the tabular, which is not present in captorhinids. The trend toward development of a postparietal-supratemporal contact is continued in advanced captorhinids where a secondarily enlarged supratemporal is solidly fused to a dorsally situated postparietal in *Labidosaurikos meachami*.

The posterior edge of the supratemporal in *Eocaptorhinus* appears to have functioned as the primary origin of the M. depressor mandibulae.

Postfrontal

The postfrontal of *Eocaptorhinus laticeps* (fig. 21A, B) looks very much like a reversed, although somewhat smaller, copy of the prefrontal. There is a thin, lateral, posterior plate and an anterodorsal orbital rim thickening with both an anterior ramus and a ventral ramus. Isolated postfrontals are easily confused with prefrontals unless care is taken to note that there is no posterior shelf underlying the postorbital or parietal (as the prefrontal underlies the nasal) and that the ventral ramus on the orbital rim lies external to the postorbital and is thus complete laterally whereas the prefrontal is deeply embayed to accept the lachrymal.

The postfrontal, like the prefrontal, acts as a gusset strengthening the skull in the region where the flexure between the skull roof and cheek (or lateral surface of the snout in the case of the prefrontal) intersects the orbit. The postfrontal is sharply convex dorsolaterally, with most of the posterior plate occupying a dorsal position on the skull roof, while the ventral process extends down on the cheek in the orbital rim. It meets the frontal medially in a "tongue-and-groove" suture. On the posterior plate of the postfrontal behind the thickened orbital rim (fig. 21B) is a lightly scarred region marking the area of sutural contact with a wide, thin, dorsal flange of the postorbital, which it overlies. Posteriorly the postfrontal overlaps a shallow notch in the anterolateral corner of the parietal.

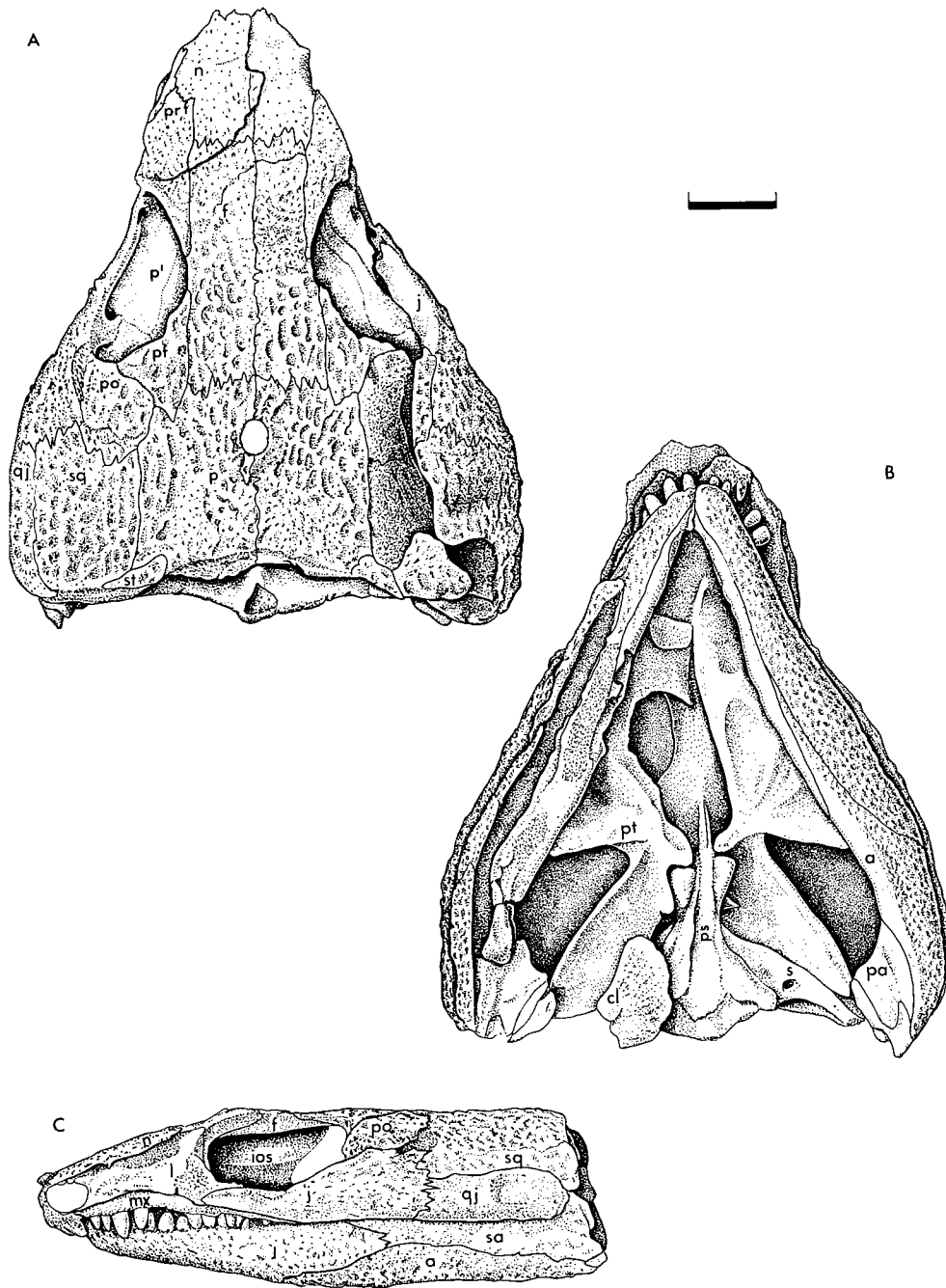


Figure 20. *Eocaptorhinus laticeps*. A, skull in dorsal view; B, skull in ventral view; C, skull in left-lateral view. FMNH UC 701. Scale equals 1 cm.

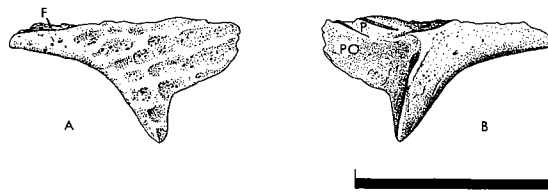


Figure 21. *Eocaptorhinus laticeps*. Left postfrontal. A, lateral view; B, medial view. OUSM 15102 (3-1-S3). Scale equals 1 cm.

The entire external surface of the postfrontal (fig. 21A) is heavily sculptured with deep pits and irregular intervening ridges. On the posterior plate a distinct pattern of three or four longitudinal rows of pits is present.

The postfrontals of *Romeria prima*, *R. texana*, *Protocaptorhinus pricei*, *Eocaptorhinus laticeps*, and *Captorhinus aguti* show no significant differences. The seemingly large postfrontal of *Romeria prima* as reconstructed by Clark and Carroll (1973; figs. 10A, 11) is a preservational artifact. The dorsolateral flexure of the postfrontal has been destroyed by crushing, so that both dorsal and lateral surfaces appear in the same plane. No effort has been made to compensate for this problem, hence the excessively wide appearance of the postfrontal in their dorsal reconstruction. Much the same is true for the left postfrontal in Clark and Carroll's reconstruction of *R. texana* (MCZ 1480) (1973, fig. 15), although the right postfrontal is essentially correct. The postfrontals of *Protocaptorhinus pricei* (MCZ 1478) are indistinguishable from those of *Eocaptorhinus* or *Captorhinus* except on the basis of size.

Postorbital

The postorbital of *Eocaptorhinus laticeps* (fig. 22A, B) is a roughly trapezoidal bone forming the posterior border of the orbit and sutured dorsally to the prefrontal and parietal, posteriorly to the squamosal and ventrally to the jugal. It is basically a laterally convex plate with a thickened anterior border that strengthens the orbital rim. The lateral surface, except for a triangular, dorsal shelf of bone that underlies the postfrontal, is heavily sculptured with the typical pitted pattern. The more dorsally located pits tend to become aligned longitudinally like those of the postfrontal and the parietal. Ventrally the pits are scattered. As with the other dermal skull bones, the pits are pierced by small pores that carried the arterial and venous tributaries and nerve filaments to the skin surface. Access to the internal vascular systems of the postorbital by branches of the mandibular artery was made through several large foramina situated on the posteromedial surface of the ridge that forms the orbital rim.

The postorbital-postfrontal sutural surface consists of an elongate, triangular shelf on the dorsal edge of the postorbital that underlies the postfrontal behind the orbital ridge, and a shallow, oblique groove on the upper half of the anterior edge. The tapered ventral process of the orbital ridge of the postfrontal lies in the oblique groove. The lower medial surface of the postorbital is heavily scarred in the region where it overlies a dorsal tongue of the jugal. The ventromedial sutural area slightly undercuts the anterior orbital ridge in such a way that a shallow groove is produced into which fits

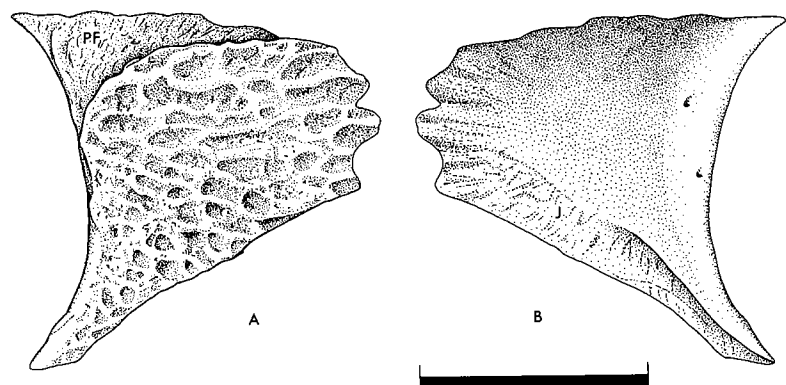


Figure 22. *Eocaptorhinus laticeps*. Left postorbital. A, lateral view; B, medial view. OUSM 15102 (3-1-S3). Scale equals 1 cm.

the anterior edge of the dorsal tongue of the jugal. The same sutural surface extends over the posterior edge of the postorbital where it overlaps the squamosal.

No essential differences between the postorbitals of *Romeria prima*, *R. texana*, or *Protocaptorhinus pricei* and *Eocaptorhinus laticeps* are noted. The reconstruction of *Romeria prima* by Clark and Carroll (1973) shows a narrow postorbital with a straight ventral margin extending to the parietal. Examination of the left postorbital of the type specimen (MCZ 1963) indicates that the posteroventral corner of the postorbital is a blunt, overlapped suture just as in *Eocaptorhinus*. In the type of *Romeria texana* (MCZ 1480), the posterior angle of the postorbital also is truncated, as may be seen by examining the left postorbital. Clark and Carroll (1973) stated that the postorbital extends very slightly onto the skull roof, but this appears to be unlikely. The specimen has been chipped and damaged during preparation, so that it gives this impression. The parietal margin was straight as in other captorhinids. The postorbital of *R. texana* is identical to that of *Eocaptorhinus* except in size.

Clark and Carroll (1973) indicated in their diagnosis of *Protocaptorhinus pricei* that the postorbitals extend onto the skull roof. Examination of the type specimen (MCZ 1478) shows that the postorbitals of *P. pricei* are identical to those of *Eocaptorhinus* except in size and are confined only to the cheek region.

Jugal

The jugal is formed of a laterally bowed posterior plate and an acuminate anterior process (fig. 23A, B). The free ventral margin is straight with only slight thickening. Some light scarring from ligament attachment is noticeable directly to the rear of the prominent maxillary scar on the lower internal surface of the anterior process. Posteriorly the jugal-squamosal and jugal-quadratojugal junction is a continuous, deeply interdigitating, immovable suture in which the squamosal and quadratojugal overlap the jugal. Dorsally the postorbital overlaps a prominent dorsal flange of the jugal in a straight, smooth suture. Anteriorly, the suture curves ventrally with the edge of the postorbital lying in a channel in the dorsal

surface of the orbital rim of the jugal.

The anterior process of the jugal borders the lower rim of the orbit. It is not thickened in this area as are the other circumorbital bones. Anteromedially (fig. 23B) this process meets the lachrymal dorsally and the maxilla ventrally at positions marked by heavy suture scars. Between these scars, a smooth, flat surface marks the area of jugal-palatine contact, there being no rough scarring of this sutural surface.

The external surface of the posterior plate (fig. 23A) is sculptured with deep pits, all perforated by small pores. The anterior process is marked by many small, shallow, vermiculate pits much like those of the maxilla. Communicating pores are less common in this region.

The internal surface of the jugal, which formed the lateral margin of the coronoid recess, is smoothly curved, with the orbital rim accentuating the concavity of the posterior plate (fig. 23B). Along the posterior surface of the ridge, three prominent foramina enter the bone. Identification of specific arteries, veins, or nerves entering or leaving these foramina is not possible.

From the midpoint of the internal surface of the jugal, a prominent process is directed medially to contact the palatine and the pterygoid, thus replacing the ectopterygoid of more primitive forms and forming the anterior border of the coronoid recess (fig. 23B). The medial surface of the internal process is heavily scarred where it forms a deep, interdigitating suture with the pterygoid. The pterygoid contact is restricted to the head of the process. Anteriorly, an even more deeply interfingered contact unites the palatine with the internal process. Midway along the length of the process, there exists a small anterodorsally directed sub-orbital fenestra entirely surrounded by the palatine and jugal. Through this opening passed the lateral palatal ramus of the facial nerve, and possibly a branch of the inferior orbital artery (lateral palatine artery). The fenestra was too small to accommodate a pterygoid vein as in *Sphenodon* and lizards (Bruner, 1907; O'Donoghue, 1921). The palatine is in contact for a short distance with the internal surface of the anterior process of the jugal forward of the medial process. This contact bears no heavy sutural scarring.

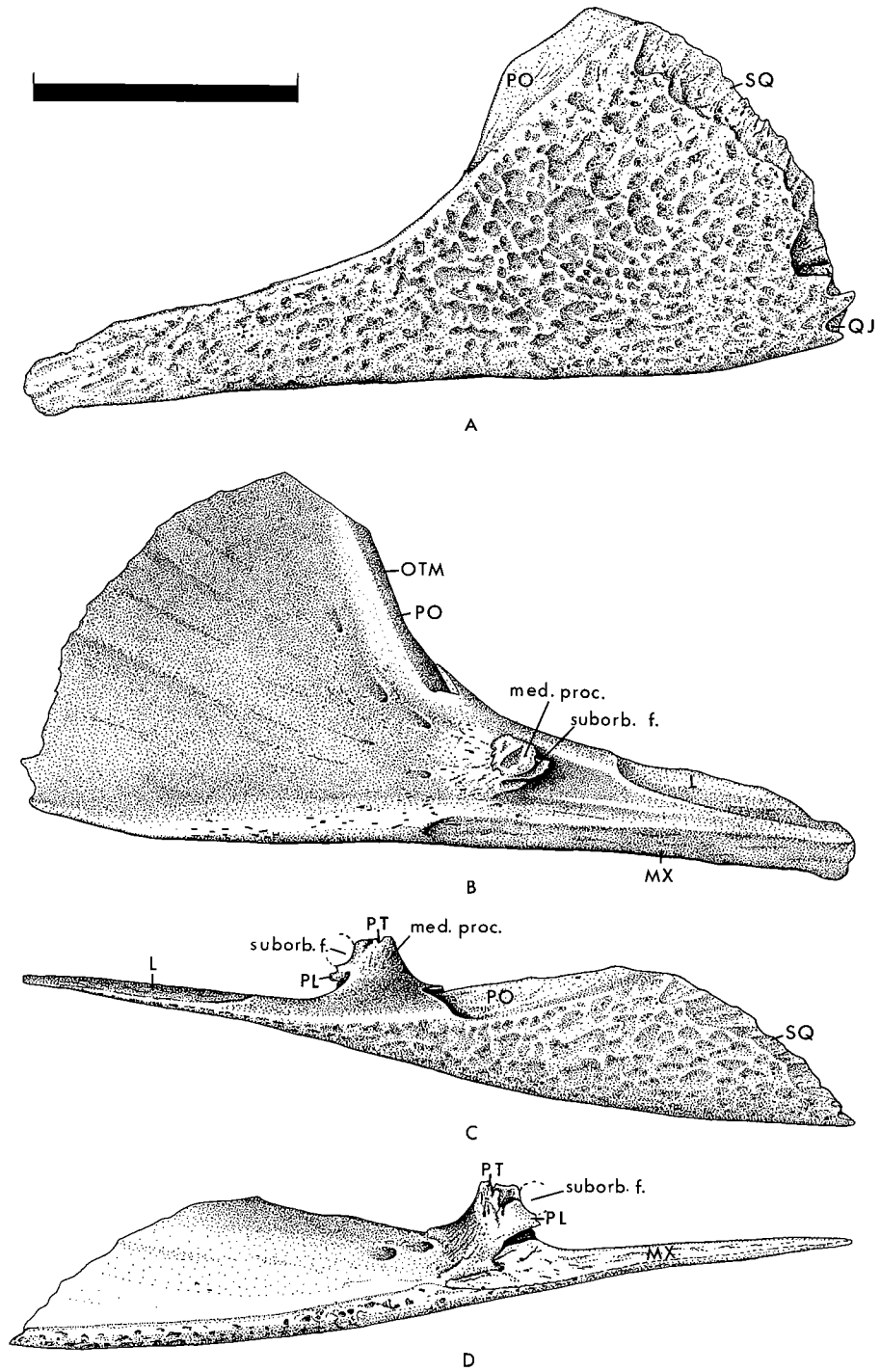


Figure 23. *Eocaptorhinus laticeps*. Left jugal. *A*, lateral view; *B*, medial view; *C*, dorsal view; *D*, ventral view. Abbreviations: *med. proc.*, medial process; *suborb. f.*, suborbital foramen; *OTM*, attachment of orbitotemporal membrane. OUSM 15021 (3-1-S8). Scale equals 1 cm.

In general shape and proportion, the jugals of all early captorhinids are similar. The older forms are smaller and have less pronounced flexure of the jugals. Detailed preparation of the orbital region of *Protocaptorhinus pricei* (MCZ 1478) has revealed the presence of an internal jugal process. This is best seen in a ventral view of the right jugal in the region where the anterior process has been sprung away from the maxilla by the partial collapse of the cheek. Moderate crushing of the palate by the coronoid region of the left mandible has disrupted the jugal-palatine-pterygoid junction. The process is visible but poorly preserved and has been slightly damaged in preparation. The condition seen in *P. pricei* with respect to the internal structure of the jugal is identical to that seen in *Eocaptorhinus* and *Captorhinus*.

The type specimen of *Romeria texana* (MCZ 1480) as preserved has neither ectopterygoids nor internal jugal processes.

Additional preparation of the holotype of *R. prima* (MCZ 1963) has revealed what may be an internal jugal process. The mandibles have been crushed upward against the lower cheek margin, distorting it into an unnatural upward curve and pulling the jugals upward, away from the palate. Lateral crushing of the skull has crumpled the palate, and slight telescoping of the postorbital region of the skull forward over the snout has also occurred. Thus, the right internal jugal process has been raised by the vertical crushing, then sheared off and moved rearward during the telescoping action. The left internal jugal process has suffered more from the original crushing but has not been greatly displaced by the longitudinal shear forces. As with *Protocaptorhinus pricei*, *Romeria prima* appears to have an internal jugal process extending medially to the palatine and pterygoid and replacing the ectopterygoid in the typical captorhinid fashion.

Squamosal

Most of the posterior cheek region is roofed by the large subrectangular squamosal (figs. 5A, 6B, 12D, 13C, D, 20C). Anterodorsally, it is overlain by the postorbital. More ventrally, the squamosal joins the

jugal in a long, interdigitating, posteroventrally sloping suture. The jugal overlies marginally the squamosal in this area. Along its ventral border, the squamosal underlies the quadratojugal along a narrow, straight suture line. Posteriorly, the squamosal contributes a prominent, medially directed flange to the occipital surface. Dorsally, this flange is overlain by a lateral extension of the postparietals in the position occupied by the tabulars in primitive captorhinomorphs and pelycosaurs. Internally, the quadrate is attached firmly to the anterior surface of the occipital flange. The squamosal extends a long, horizontal, dorsal flange medially parallel to the longitudinal axis of the skull. This flange is heavily striated dorsally where it is strongly sutured to the ventrolateral margin of the parietal.

The dorsal and occipital flanges meet in the posterodorsal corner of the squamosal where a short narrow ridge forms as a dorsal continuation of the lateral edge of the occipital flange. It crosses the dorsal flange anteromedially to the inner edge. The ridge is inclined medially to a slight degree where it lies within the prominent notch in the posterolateral corner of the parietal. The ridge lies upon the dorsal surface of the medial margin of the notch. Thus the supratemporal, when in place within the parietal notch, is in contact with the squamosal ventromedially.

The internal surface of the squamosal shows no apparent muscle scars. There may, however, have been a narrow region of attachment of the *M. adductor mandibulae externus superficialis* along the medial edge of the dorsal flange. No prominent foramina for nerves or blood vessels have been noted. The external surface of the squamosal is heavily sculptured in the usual manner.

The squamosals of the different primitive captorhinids show a slight but noticeable amount of variation. The older species *Romeria prima* and *R. texana* appear to have marginally shorter squamosals than do *Protocaptorhinus pricei* or *Eocaptorhinus laticeps*.

Quadratojugal

The quadratojugal forms the posterolateral cheek margin (figs. 5A, 6B, 12D, 13C, D, 20C). Dorsally, it overlies narrowly the

straight ventral border of the squamosal on both the cheek and the occipital plate. Anteriorly it extends a short tongue forward into a groove on the external surface of the posterior edge of the jugal. The ventral rim is continuous with that of the jugal and is similar in form. Posteriorly a stout, medially directed projection forms a strong suture with the posterodorsolateral surface of the lateral process of the quadrate condyle. The anteromedial end of this projection forms the lateral border of the quadrate foramen.

The quadratojugals of other primitive captorhinids have been illustrated by Clark and Carroll (1973). Unlike the quadratojugal of *Eocaptorhinus laticeps*, the quadratojugals of *Romeria* and *Protocaptorhinus* tend to be somewhat convex upward rather than straight. Clark and Carroll (1973) illustrated *Romeria prima* as having a very high quadratojugal with a prominent emargination of the lower edge of the squamosal. In fact, the dorsal edge of the quadratojugal in *R. prima* is not significantly different from that of *R. texana*. The *R. prima* skull (MCZ 1963) has been crushed laterally, so that a prominent crack appears on the lower right cheek along what was assumed to have been the quadratojugal-squamosal suture. In fact, the suture can be seen as a thin, smooth line running horizontally below the crack, thus reducing the height of the quadratojugal to half that illustrated and aligning it with the quadratojugal-squamosal suture as revealed on the occipital flange. All of the primitive captorhinids thus conform to the same pattern. This condition is similar to that seen among some primitive captorhinomorphs, most notably *Hylonomus* (RM 12016a), *Paleothyris* (Carroll, 1969a), and *Brouffia* (Carroll and Baird, 1972). Other primitive captorhinomorphs have lower cheek margins more reminiscent of primitive pelycosaurs, particularly ophiacodonts, in the form of a minimal or nonexistent quadratojugal-jugal junction. A number of these forms, *Cephalerpeton* and *Coelostegus* (Carroll and Baird, 1972), and *Protorothyris* (Clark and Carroll, 1973) show other pelycosaurian features in their dental patterns and skull proportions.

PALATE

The palate is of a generalized reptilian

pattern similar to that seen in many primitive pelycosaurs and diapsids but with some specializations. It is slightly domed, with the highest point opposite the anterior end of the orbit. The interpterygoid vacuities are broadly lanceolate in outline. The suborbital fenestra ("ectopterygoid foramen"), which is absent in pelycosaurs and rather large in diapsids, is present as a small foramen 1 mm in diameter, between the palatine and the medial process of the jugal. This process replaces the ectopterygoid that has been lost in captorhinids. The ventral surface of the palate bears three prominent ridges covered with rows of small sharp teeth.

Vomer

The vomers of most primitive reptiles are poorly known either because the specimens are badly crushed or because the mandibles are still in place. Fortunately, complete vomers of *Eocaptorhinus laticeps* (OUSM 15021) have been preserved separately. The right mandible of OUSM 15020A was removed to show the vomer (fig. 8C) in ventral and lateral aspect. Comparison has shown that the vomers of *E. laticeps* and *Captorhinus aguti* (OUSM 15007) from Richards Spur are identical (fig. 24A, B).

In ventral aspect, the vomer appears as a roughly triangular element sutured to the premaxilla anteriorly and the palatine posteriorly. The entire lateral border forms the medial rim of the internal naris. The medial margin of the vomer is free along the anterior half where it lies in contact with the opposing vomer along the midline. The anteromedial process of the pterygoid is sutured to the posterior half of the medial edge of the vomer.

The ventral surface of the vomer is smoothly concave anteroposteriorly. A prominent lateral ventral ridge appears to act as a flange reinforcement of the medial border of the internal naris. The actual thickness of the bone in this region is not increased. Anteriorly on this ridge is developed a low but sharp crest that passes medially to join the equally prominent but crestless median ridge in a heavy, rounded, premaxillary process. The ventral surface of the vomer is identical in basic form with that of some lizards (iguanids).

The premaxillary process of the vomer

bears a long, narrow suture scar on its ventral surface. The surface is lightly marked, bearing only one prominent lateral longitudinal ridge.

While the appearance of the ventral surface of the vomer is remarkably similar to that of an iguanid, the dorsal surface is strikingly different (fig. 24A). The two major components of the vomer—the transverse ventral plate and the lateral vertical alar projection—are easily distinguished. The ventral plate has been described in ventral

view. It is formed as a thin dermal sheath below the cartilaginous nasal capsule. Dorsomedially it is strengthened by the heavy anteromedial process of the pterygoid. There is no significant increase in thickness of the vomer medially. The apparent concavity of the dorsal surface of the palate in the region of the vomer is a result of the extensive dorsal development of the anteromedial process of the pterygoid.

The alar projection is a thin dermal sheath that forms the medial border of the

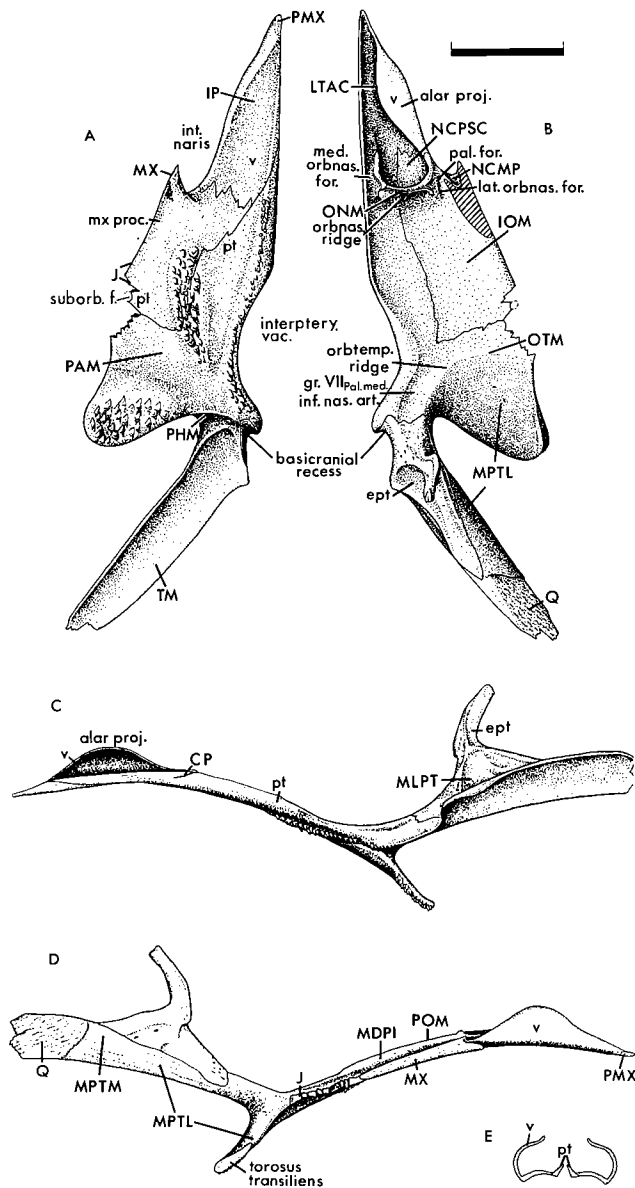


Figure 24. *Eocaptorhinus laticeps*. Right palate. A, ventral view; B, dorsal view; C, medial view; D, lateral view; E, cross section through alar projection of vomer. Abbreviations: *alar proj.*, alar projection of vomer; *gr. VII_{Pal. med.} inf. nas. art.*, groove for median palatal ramus of facial nerve and inferior nasal artery; *int. naris*, internal naris; *interptery. vac.*, interpterygoid vacuity; *lat. orbnas. for.*, lateral orbitonasal foramen; *med. orbnas. for.*, medial orbitonasal foramen; *mx. proc.*, maxillary process; *orbnas. ridge*, orbitonasal ridge; *orbtemp. ridge*, orbitotemporal ridge; *pal. for.*, palatal foramen; *suborb. f.*, suborbital fenestra. Attachment of: *IOM*, inferior orbital membrane; *IP*, incisive pas; *LTAC*, lamina transversalis anterior cartilage; *MDPI*, M. depressor palpebrae inferioris; *MLPT*, M. levator pterygoidei homologue; *MPTL*, M. pterygoideus lateralis; *MPTM*, M. pterygoideus medius; *NCMP*, maxillary process of nasal cartilage; *NCPSC*, paraseptal cartilage of nasal capsule; *ONM*, orbitonasal membrane; *OTM*, orbitotemporal membrane; *PAM*, palatal membrane; *PHM*, pharyngeal membrane; *POM*, periorbital membrane; *TM*, tympanic membrane. Reconstruction based on OUSM 15020A (3-1-S4), 15021 (3-1-S8), 15022 (3-1-S7), 15024 (3-1-S6), 15101 (3-0-S4), 15102 (3-1-S3), and Richards Spur captorhinid specimens. Scale equals 1 cm.

internal naris. It is a continuation of the transverse ventral plate dorsally from the lateral ridge. Contrary to Fox and Bowman's (1966) description of the vomer of *Captorhinus*, there is no thickening of the bone at the lateral ridge (or at the medial ridge) in either *Captorhinus* or *Eocaptorhinus*. The alar projection has a basic parabolic outline in lateral aspect. There is little vertical development above the premaxillary processes of the vomers. The high point of the alar projection occurs at the midpoint of the internal naris opposite the caniform tooth. The maximum height is about 5 mm. The alar projection tapers abruptly posteriorly to the vomeropalatine junction. In cross section the alar projection is seen to be strongly curved dorsomedially with a very narrow reflex curvature at the dorsal extremity. The vomer thus forms a thin-walled tubular structure, the Stammteil (Parsons, 1973), which was floored by the paraseptal cartilage. The paraseptal cartilage extended posteriorly into a prominent depression where it overlapped dorsally onto the vomer. The paraseptal cartilage does not appear to have extended medially as far as the internarial septum, being separated from it by the dorsal projection of the anteromedial process of the pterygoid. At a point just anterior to the orbitonasal membrane, a depression in the dorsomedial surface of the palatine identifies the route by which the paraseptal cartilage was connected to the trabecula communis and the internarial septum. The extent to which the paraseptal cartilage extended up the medial surface of the alar projection is unknown. In OUSM 15021, this projection is so weak that the matrix had to be left in place as an internal support. The lateral surface of the alar projection was sheathed with oral mucosa. The reflexed dorsal rim is believed to have supported, at its highest point, the lamina transversalis anterior of the concha. Posteriorly, the concha was situated in a typically lacertilian position above the vomer. Anteriorly, the concha remained in contact with the lateral border of the vomer as it extended anteroventrally beneath the septomaxilla, where it was continuous with the cartilage of the vomeronasal organ. At no time is the septomaxilla in contact with the vomer.

The vomers are visible in ventral view

in *Romeria texana* (MCZ 1480). Except for their smaller size, they are identical to the vomers of *Eocaptorhinus laticeps*. Clark and Carroll's (1973) reconstruction of the palate shows a slightly undulating butt join between the premaxilla and the vomers. This is incorrect, as the premaxillary processes of the vomers clearly are sutured to the dorsal surface of the vomerine processes of the premaxillae.

In primitive captorhinomorphs, the vomer is visible only in one specimen of *Protorothyris archeri* (MCZ 1532). It is similar to that of *Eocaptorhinus* in ventral outline. Unlike the vomer of *Eocaptorhinus*, that of *Protorothyris* bears several rows of denticles along the medial edge, the rim of the internal nares, and anterolaterally across the posterior half of the bone.

Palatine

The palatine is a strongly arched element bounded along its entire medial and posterior margin by the pterygoid. Anteriorly it meets the vomer (fig. 24B). The lateral margin is formed by the internal naris anteriorly, the maxilla and lachrymal centrally, and the jugal posteriorly. Medially the palatine underlies the pterygoid along a wide plane (fig. 9A, B). The scarring of the sutural surface appears to be poorly developed, thus indicating that either the contact was slightly flexible or, more likely, that the palate was seldom heavily stressed in this region. In both OUSM 15102 and 15020 (fig. 9A) lateral compression of the skull has caused slippage along this plane. Anteriorly the palatine overlies the vomer as a wedge-shaped sheet situated laterally toward the rim of the internal naris. The sutural surface is much more heavily scarred and thus more heavily bonded than is the palatine-ptyerygoid contact. The heavy maxillary process of the palatine forms the posterior boundary of the internal naris as well as the contact with the maxilla. The palatine-maxilla suture is a strong tongue-and-groove suture that offered little opportunity for any flexibility or mobility. The lateral surface of the maxillary process forms a long, narrow, longitudinal ridge internally. This fitted against the convex, lightly grooved sutural surface of the maxilla (fig. 10B). Posteriorly, the maxillary process thins slightly where

it abuts the internal surface of the anterior process of the jugal. This suture appears to have been relatively weak. It is strengthened posteriorly by the strongly interdigitating suture between the palatine and the internal process of the jugal posteriorly. This region of the suture is discontinuous where the inferior orbital foramen perforates the palate.

The palatine varies considerably in thickness. The region of greatest thickness is the transverse, orbitonasal ridge that separates the nasal capsule from the orbital region. The axis of greatest palatal flexure parallels this ridge (fig. 24B). A small pocket is formed in the anterior surface of the ridge at the posterior end of the internal naris, in which sat the maxillary process of the paranasal cartilage of the nasal capsule. The ridge bears a heavy scar laterally, directly above the posterior end of the internal naris. This is the lachrymal scar that descends posteriorly from the ridge along the lateral margin of the maxillary process for a distance of about 5 to 7 mm. An equally prominent scar marks the posterior edge of the orbitonasal ridge. It consists of a horizontal groove bounded posteriorly by a low sharp crest. The crest does not extend as far laterally as the lachrymal scar from which it is separated by a distance of 2 mm. The crest extends medially as far as the pterygoid, at which point it ends as a small dorsomedially directed process 1 mm in height. The crest served as the ventral point of attachment of the orbitonasal membrane, which was attached to the medial edge of the prefrontal laterally, the interorbital septum medially, and the frontal dorsally. The groove that lies along the anterior edge of the crest served as a channel carrying the main branch of the inferior nasal artery and the anterior communicating branch of the palatine plexus of the facial nerve medially into the nasal capsule. The space separating the crest from the lachrymal scar is the bottom of the lateral nasal fenestra. Medially, the crest is bounded by the medial orbitonasal foramen, the nasal ramus of the trigeminal nerve, the small superior nasal artery, and the larger medial ramus of the inferior nasal artery.

Anterior to the ridge, the palatine extends a triangular wedge forward over the dorsolateral surface of the vomer. A deep

anteriorly opening excavation in the dorsal surface forms the posterior extremity of the trough that runs the length of the vomer. As previously mentioned, this trough was lined with the paraseptal cartilage that formed the ventral section of the cartilaginous nasal capsule. This depression is not, as Fox and Bowman (1966) suggested, a "recess for [the] olfactory bulb of the brain," for there is no reason to believe that the olfactory bulbs were not located dorsally against the internal surface of the frontals as they are in modern reptiles.

The region of the palatine posterior to the ridge slopes away steeply posteriorly. The dorsal surface is smooth and possessed of no apparent muscle or tendon scars. It was presumably sheathed in a thick fibrous sheet of connective tissue, the inferior orbital membrane.

In ventral view (figs. 8C, 24A) the palatine appears to be gently arched dorsally, the great thickness of the transverse ridge having reduced the apparent amount of flexure relative to the dorsal surface. The heavy diagonal toothed ridge of the pterygoid extends marginally onto the medial edge of the central region of the palatine. There does not appear to be a significant reduction in the height of the teeth compared with those of the pterygoid. The average height is about 1 mm. The tips are very sharp, with no evidence of wear. The whole of the ventral surface of the palatine was sheathed in oral mucosa posterior to the incisive pad of the vomer.

The ventral surface of the anterior end of the maxillary process is pierced by two prominent foramina, the more anterior of which actually lies within the posterior rim of the internal naris. In only one specimen of *Eocaptorhinus laticeps* (OUSM 15102, fig. 10B) is it possible to find any connecting foramen on the dorsal surface of the palatine. Here, one large foramen exists within a short channel that borders the lachrymal scar at the entrance to the lateral fenestra. In all other specimens of *Eocaptorhinus* and *Captorhinus*, the lachrymal shields most of the channel, thus making observation difficult, especially if any crushing of the skull has occurred. There is only the single dorsal palatine foramen, which bifurcates within the maxillary process. The palatine foramen transmitted the lateral branch of the inferior

nasal artery and the intermediate palatine branch of the facial nerve. Whether each exited the palatine through its own separate foramen or whether the nerve and (or) the artery divided to send branches out of both is unknown.

Among primitive captorhinids, the palatines are visible only in *Romeria texana* (MCZ 1480), in which case they are poorly preserved. The palatine foramina are in the same position relative to the internal naris in *R. texana* as in *Eocaptorhinus laticeps*. The posterior end of the palatine is proportionately considerably narrower in *Romeria texana*. This appears to be related to the loss of the ectopterygoid and the presence of a short internal jugal process.

The palatines are known in only two primitive captorhinomorphs. In *Paleothyris acadiana* (MCZ 3485) a separate anterior fragment of the left palatine exhibits a structure similar to that of *Eocaptorhinus*. It is not known posteriorly, although Carroll (1969a) believed that an ectopterygoid was present. In *Protorothyris archeri* (MCZ 1532) the palatine is well exposed ventrally. The anterior portion is somewhat broader than in *Paleothyris*. In this feature it more closely resembles *Eocaptorhinus*. The median toothed ridge of *Paleothyris* bears a large number of denticles. In *Protorothyris*, the number of teeth is reduced to a single row of about 18 small teeth. Posteriorly, there is a major difference in development. A large ectopterygoid separates the pterygoid from the jugal and is sutured strongly to the palatine. *Protorothyris archeri* was reconstructed by Clark and Carroll (1973) without a suborbital (ectopterygoid) fenestra.

Pterygoid

The pterygoid is the largest and most complicated of the dermal elements of the palate (figs. 24, 12B). It is composed of three main regions: the anteromedial palatine ramus; the posterior quadrate ramus; and the lateral transverse flange. The palatine ramus forms the entire lateral border of the interpterygoid vacuity. Anteriorly it is sutured to the posteromedial edge of the vomer, and the entire dorsomedial edge of the palatine (fig. 8C). The transverse flange abuts the medial end of the internal process of the jugal and forms the anterior margin of

the subtemporal fossa and the medial margin of the coronoid recess. The quadrate ramus extends posteriorly from the medially directed epipterygoid notch as a thin, near-vertical sheet of bone. There is no contact between the pterygoid and the basipterygoid tubercle. The notch is lined medially by a thin ventral projection of the anteroventral end of the epipterygoid, which is sutured broadly to the dorsal edge of the quadrate process. The pterygoid is overlapped broadly by the medial surface of the pterygoid lamella of the quadrate.

The palatine ramus extends forward from the neck of the pterygoid where the quadrate ramus joins the anterior portions. The medial margin forms a thin, smoothly rounded lateral border to the posterior half of the interpterygoid vacuity. Forward of this region, which lies directly medial to the suborbital fenestra, a prominent vertical ridge is formed that extends forward to the anterior end of the pterygoid, where it is then continued as the medial ridge of the vomer. The ridge extends 2 mm above the dorsal surface of the palate over most of its length. The palatine ramus is directed anterodorsally toward the transverse orbitonasal ridge of the palatine. The palatine, which underlies the lateral edge of the pterygoid, impinges upon the pterygoid anteromedially, causing the pterygoid to taper rapidly. The anteromedial corner of the palatine is developed into a prominent dorsally directed boss at the medial end of the orbitonasal ridge that served as the lateral edge of the medial orbitonasal foramen through which passed the medial palatal ramus of the facial nerve, the nasal ramus of the ophthalmic division of the trigeminal nerve, the small superior nasal artery, and the medial ramus of the inferior nasal artery. A prominent longitudinal channel for the medial palatine ramus of the facial nerve, the medial palatine artery, and the inferior nasal artery is excavated in the dorsal surface of the palatine ramus directly lateral to the medial ridge. The bone underlying the channel is quite thick, since it forms a prominent ventral extension of the medial ridge as already seen in dorsal aspect. The medial surface of this area is up to 4 mm wide and slopes dorsomedially until it contacts the narrow trabecula communis directly anterior to the end of the cultriform

process. A faint elongate depression on this beveled surface near its posterior end accommodated the anterior end of the cultriform process. There is no indication that this was a sutural contact of any sort.

The rest of the medial surface bears numerous fine, longitudinal scars that appear to have been the origin of ligaments holding the oral mucosa and heavy incisive pad to the roof of the palate, as well as the median palatine sinus. The ventral edge of the medial ridge bears a small number of prominent and exceedingly sharp teeth. The lateral surface of the vertical projection of the medial ridge is lightly scarred by the anterior origin of the *M. depressor palpebrae inferioris* (*M. levator bulbi dorsalis*) and the attachment of the periorbital membrane.

There is a second thickened tooth base on the ventral surface of the palatine process directed anteromedially at about 15° to the skull centerline and converging on the neck. This ridge continues onto the palatine. About 12 small, sharp teeth occur on the pterygoid section of the ridge, and up to six on the palatine.

The palatine ramus is separated from the transverse flange by a distinct semilunate ridge that bisects the neck onto which it runs from the processus sellaris of the crista sellaris and the processus clinoides of the basisphenoid medial to the epipterygoid. This is the orbitotemporal ridge to which the ventral edge of the orbitotemporal membrane was attached. The ridge arcs anterolaterally across the neck and the dorsal surface of the pterygoid until it meets the posterior edge of the internal process of the jugal. The membrane separated the orbit from the subtemporal fossa. The dorsal surface of the pterygoid anterior to the ridge was sheathed in a fibrous inferior orbital membrane.

The transverse flange of the pterygoid slips steeply posteroventrally at an angle of about 60° to the frontal plane. The flange is roughly parabolic in outline, with the lateral margin paralleling the cheek margin as the medial border of the coronoid recess. The lateral edge is characterized by a heavy, scarred tuberosity—the torus transiliens (OUSM 15024)—that functioned much as it does in crocodiles and turtles (Schumacher, 1973). It presumably supported a cartilaginous pad that guided the mandible during

adduction. *Romeria texana* (MCZ 1480) has been preserved without mandibles so that it can be determined that a small torus transiliens was present.

The dorsal surface of the transverse flange bears a prominent scar that is most strongly developed laterally, adjacent to the torus transiliens. This was the origin of the *M. pterygoideus posterior*. The scar covers most of the area of the transverse flange. There is no suggestion of the former presence of an *M. pterygoideus atypicus*, as in *Sphenodon* (Haas, 1973), medial to the main mass.

The ventral surface of the transverse flange bears a cluster of about two dozen small, sharp teeth. A prominent ridge extends medially from the posterolateral edge of the transverse flange onto the basicranial process of the pterygoid. To this ridge was attached the anterior end of the pharyngeal membrane, which was a posterior continuation of the thin fibrous palatal membrane that covered the ventral surface of the transverse flange. Posterior to this ridge is the scar marking the origin of the *M. pterygoideus anterior*.

The quadrate ramus of the pterygoid is a thin, anteromedially sloping sheet of bone extending posteriorly from the constricted neck to its broad attachment to the medial surface of the pterygoid lamella of the quadrate. The ventral edge forms the straight medial margin of the subtemporal fossa. There is no thickening of the ventral rim as there is in *Sphenodon* or lizards. The thickness of the quadrate ramus is a near constant 0.5 mm posterior to the epipterygoid notch. Dorsally this sheet curves medially until it forms an almost horizontal platform on the dorsal surface on which is located the epipterygoid recess. Into this recess is sutured the broad base of the epipterygoid. The epipterygoid recess occupies most of the medial edge of the quadrate ramus of the pterygoid between the epipterygoid notch and the quadrate suture. Midway along this section of the edge a thin rim of the pterygoid, about 5 to 6 mm in length and 1 mm in width, is exposed dorsally. This is the insertion point of the *M. levator pterygoidei*. Near the anterior end of this exposure is a small ventromedially directed expansion of the pterygoid directly lateral to the crista sellaris. The anteromedial edge is strongly

depressed ventrally so that it lies in the same plane as the processus clinoides of the basisphenoid to which it was connected by the posterior extension of the orbitotemporal membrane. The special arrangement of the dorsomedial edge of the pterygoid and the braincase is such that there is no room for an *M. protractor pterygoidei*. This is not an unexpected observation, since the akinetic nature of the skull would not allow for any palatal protraction. The *M. levator pterygoidei*, or its homologue, not only is present but also appears to have been well developed as is outlined in the description of the epipterygoid. The condition here is analogous to that found in *Sphenodon* by Ostrom (1962), although the *M. levator pterygoidei* was apparently larger in *Eocaptorhinus laticeps*.

The entire concave ventral surface of the quadrate ramus was sheathed by a thin mucous epithelium that lined the entire middle ear cavity. The pterygoid was thus connected to the processus clinoides of the basisphenoid by this epithelial layer that continued posteroventrally over the lateral surface of the braincase.

The lateral surface of the quadrate ramus is heavily scarred by the pinnate origins of the *M. pterygoideus posterior*. In two specimens of *Eocaptorhinus laticeps* (OUSM 15020 and 15024), two distinct scars are visible. The lower scar is a constant 4 to 5 mm in height and extends along the ventral edge of the quadrate ramus from the neck of the pterygoid posteriorly to the pterygoid lamella of the quadrate. This is the scar marking the origin of a lateral slip of the *M. pterygoideus posterior*. The upper scar is smaller, tapering from a maximum width of 6 mm at the pterygoid lamella to a point, ventral to the center of the epipterygoid. This is the scar of the origin of a medial slip of the *M. pterygoideus posterior*.

The lateral surface of the posterior end of the quadrate ramus forms a rough sutural contact with the pterygoid lamella of the quadrate.

Among the primitive captorhinids, only *Romeria texana* (MCZ 1480) has a readily accessible pterygoid. As with so many other skull elements, no major differences are noted between the pterygoids of *Romeria* and *Eocaptorhinus* except size. As in *Eocaptorhinus*, the epipterygoid notch is deep and completely lined by the basicranial recess

of the epipterygoid. There was no possibility of a basisphenoid-pterygoid contact developing. As in *Eocaptorhinus*, the epipterygoid notch is located posteriorly, level with the posterior limit of the transverse flanges of the pterygoids. There are no palatal teeth evident in *Romeria texana*, but this is surely a result of the preparation methods needed for such hard matrix as that in which the specimen (MCZ 1480) was preserved.

Hylonomus lyelli (Carroll, 1964) has a well-preserved pterygoid (RM 12016a) that differs markedly from that of a typical primitive captorhinid. Rather than having three narrow bands of distinct palatal teeth, the entire palate, and the pterygoid especially, is covered by a shagreen of small denticles that extend posteriorly behind the epipterygoid notch. The notch is located well forward of the transverse flange. In *Paleothyris acadiana* (Carroll, 1969a) true palatal teeth are arranged in three, anteriorly divergent rows as in *Eocaptorhinus*. The epipterygoid notch is still located anteriorly as in *Hylonomus*.

The pterygoids of *Protorothyris archeri* are quite distinct in form from either early captorhinids or other primitive captorhinomorphs. The triradiate pattern of ridges that bear palatal teeth is retained in modified form. Each ridge has but a single row of sharp teeth. The row bordering the ventral edge of the transverse process is composed of a single row of six or seven large teeth. This pattern is identical to that seen in *Ophiacodon* (Romer and Price, 1940). There is no evidence of a suborbital fenestra in either *Ophiacodon* or *Protorothyris*.

Epipterygoid

The epipterygoid is a high, dorsolaterally directed pillar with a long triangular base (fig. 25A, B) that is sutured into the epipterygoid recess on the dorsal surface of the quadrate ramus of the pterygoid. Its only direct sutural contact with another osseous element is with the pterygoid. It completely lines the epipterygoid notch of the pterygoid and forms a synovial joint with the basisphenoid.

In lateral aspect, there are three major regions of the epipterygoid: the dorsal columella; the broad, triangular base; and the hooked, basicranial recess. The high point is slightly posterior to the midpoint. The

maximum width of the base occurs just posterior to the basicranial recess. The base tapers to a point posteriorly (fig. 25C). The lateral surface is smooth and unscarred. The anterior continuation of this surface curves anteromedially around the anterior end of the base. Here, especially in the ventromedial region above the basicranial recess, the surface becomes heavily scarred by the ori-

gin of the *M. pseudotemporalis profundus*, which slides over the smooth lateral surface during mandibular depression and adduction. Several small grooves on the lateral surface indicate the posteroventral orientation of this muscle.

The medial surface of the base (fig. 22A) bears a deep, triangular depression over most of its area. An *M. levator pterygoidei* pre-

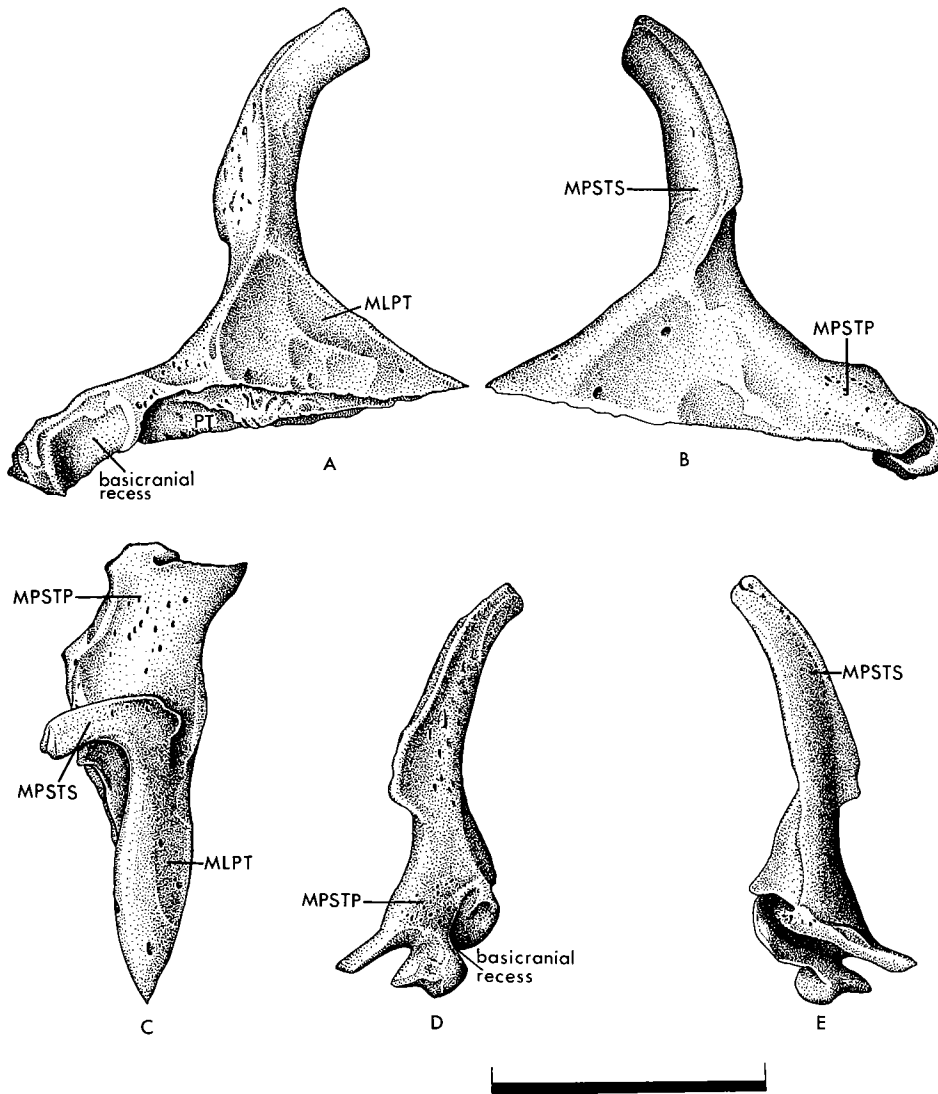


Figure 25. *Eocaptorhinus laticeps*. Left epipterygoid. A, medial view; B, lateral view; C, dorsal view; D, anterior view; E, posterior view. Attachments of: *MLPT*, *M. levator pterygoidei* homologue; *MPSTP*, *M. pseudotemporalis profundus*; *MPSTS*, *M. pseudotemporalis superficialis*. Reconstruction based on OUSM 15020B (3-0-S5), 15022 (3-1-S7), 15024 (3-1-S6), 15101 (3-0-S4), and Richards Spur captorhinid specimens. Scale equals 1 cm.

sumably inserted along the thin, dorsomedial edge of the pterygoid as it is exposed at the base of the depression. The *M. levator pterygoidei* does not typically insert onto the ventromedial surface of the epipterygoid in lizards because of the absence of a large base. In *Sphenodon*, the broad base of the epipterygoid allows for more extensive insertion. In *Eocaptorhinus laticeps* the insertion of the *M. levator pterygoidei* was massive, covering virtually all of the medial surface of the base. Its chief function appears to have been as antagonist of the *M. pseudotemporalis*, to restrict or prevent rotation of the quadrate ramus of the pterygoid.

The anterior edge of the depression for the *M. levator pterygoidei* forms a small ridge on whose anterior surface ventral fibers of the *M. pseudotemporalis profundus* originated.

The columella is a high, curved, near-vertical blade that is heavily scarred on its anteromedial surface by the origin of the dorsal slip of the *M. pseudotemporalis profundus*. The lateral surface is composed entirely of a roughened scar marking the origin of the *M. pseudotemporalis superficialis*. It is apparent that two distinct regions of muscle origin on the lateral and anteromedial surfaces of the epipterygoid exist that are identified here as the *partes superficialis* and *profunda*, respectively, of the *M. pseudotemporalis* and are believed to be homologous to the same muscle parts seen in *Sphenodon* and lizards. This is in contrast to the view expressed by Barghusen (1973) with respect to the development of this muscle in the sphenacodont pelycosaur *Dimetrodon*. He stated that the differentiation of this muscle appeared to be a specialization of diapsid reptiles "initially developed as an invasion of musculature into the superior temporal fenestra." It is apparent that, in contrast to *Dimetrodon*, *Eocaptorhinus* and possibly other captorhinomorphs did possess a subdivided *M. pseudotemporalis*, as do many amphibians (Luther, 1914; Säve-Söderbergh, 1945), that was elaborated upon by diapsid forms. The anterior border of the blade of the columella is formed by a curved, ventrolaterally projecting ridge to which a strong tendon and associated intermuscular fascia was attached that separated the origins of the two divisions of the *M. pseudotemporalis*.

The basicranial recess is a small J-shaped notch surrounded by a sharp ventral ridge that projects about 1.5 mm below the ventral surface of the anterior end of the base (fig. 25D). It lines completely the medial surface of the anterior end of the epipterygoid notch of the pterygoid. A short, thin flange of the pterygoid is insinuated dorsal to the anterior end of the ridge between the ridge and the ventral surface of the base, thus firmly locking the two elements together. The medial surface of the recess bears the typical frosted scar that marks the former presence of an interstitial cartilage typical of a synovial joint, in this case between the epipterygoid and the basiptyergoid tubercle of the basisphenoid. The pterygoid does not enter into the joint.

The epipterygoids of primitive captorhinomorphs are present (Carroll, 1969a) but poorly known. Of the primitive captorhinids, only *Romeria texana* (MCZ 1480) shows any of the epipterygoid—in this case, the basicranial recess. It is identical to that of *Eocaptorhinus laticeps* and forms the entire basicranial articulation with the basisphenoid.

Quadrate

Well-preserved quadrates are present in OUSM 15020 and 15101. The quadrate is a complex bone made up of a triangular dorsal pterygoid lamella that is sutured medially to the posterolateral end of the pterygoid and posteriorly to the occipital flange of the squamosal, and a heavy basal condylar surface that is sutured posteriorly to the quadratojugal (fig. 26).

The pterygoid lamella is twice as high (12 to 13 mm) as it is long (6 to 7 mm). The posterior edge is expanded into a caudally facing, dorsomedially inclined sutural facet 2 to 3 mm wide and 10 mm long. The surface is heavily scarred from its attachment to the occipital flange of the squamosal. Ventrally the scar is bounded by a prominent groove that forms the anterior margin of the quadrate foramen through which passed the mandibular nerve and muscular artery. The dorsal edge of the pterygoid lamella is a smoothly rounded, anteroventrally sloping crest. As Fox and Bowman (1966) indicated in *Captorhinus*, the dorsal edge of the pterygoid lamella was free and did not contact

the dorsal flange of the squamosal. The same feature is especially well shown in the antecedent form, *Protocaptorhinus pricei* (FMNH 1119). This is a primitive arrangement that is present in captorhinomorphs and pelycosaurs generally and is quite different from the living sauropsid pattern.

Medially the pterygoid lamella bears a prominent scar formed by the articulation with the quadrate ramus of the pterygoid where its anterodorsal striations indicate a rigid union. Directly posterior to the pterygoid scar is a smooth region representing the contact with the stapes ventrally and the articulation with the opisthotic dorsally.

The columellar recess is a deep, parabolic excavation, emarginated posteroventrally by the quadrate foramen, in which the bulbous distal end of the stapes sat. The quadrate and stapes seem only to have been separated by a thin, intervening layer of the periosteum and mucous epithelium. The columellar recess is crossed vertically by a small ridge whose position conforms with that of the distal end of the stapes. Posteroventral to this small ridge is another similar

ridge. The intervening length (2 mm) of the columellar recess apparently served as a region for the attachment of a very short intercalary cartilage. There is no evidence that this was in any way similar in shape or function to the extracolumella of most sauropsids, although they may be homologous. The stapes does not appear to be isolated acoustically from the quadrate.

Immediately dorsal to the columellar recess is a shallow depression 1 to 2 mm wide. Posterodorsal to this is a lightly frosted boss on the medial surface of the expanded posterior squamosal flange that formed the articulation with the intercalary cartilage separating the distal end of the paroccipital process from the quadrate. There is a small free area dorsal to the columellar recess and anterior to the opisthotic articulation that was sheathed by the tympanic membrane.

Posterior to the pterygoid scar and dorsal to the columellar recess is a shallow groove through which passed a sub-branch of the mandibular branch of the stapedia artery, the posterior condylar artery.

The lateral surface of the pterygoid

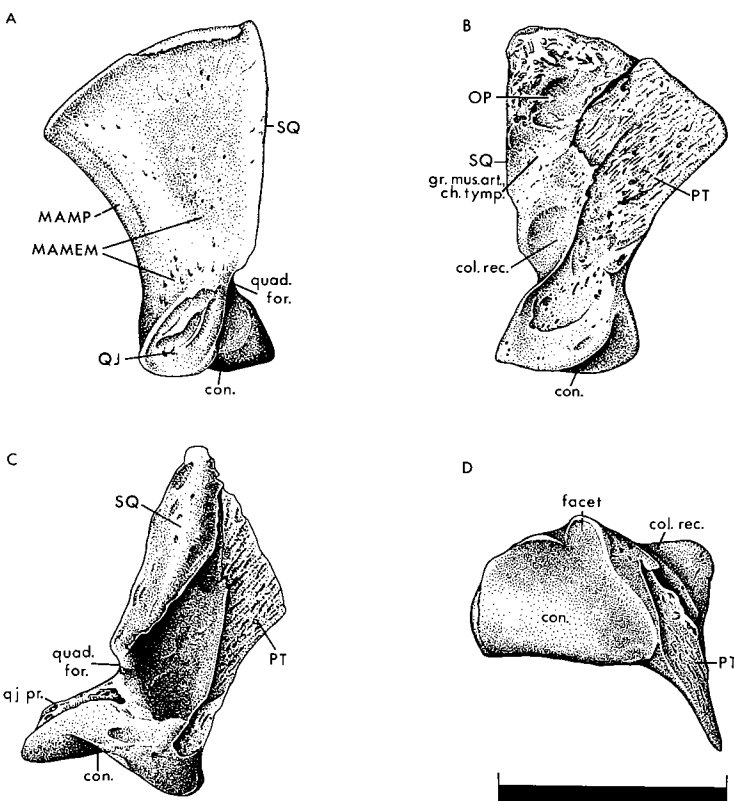


Figure 26. *Eocaptorhinus laticeps*. Left quadrate. A, lateral view; B, medial view; C, occipital view; D, ventral view. Abbreviations: col. rec., columellar recess; con., condyle; gr. mus. art., ch. tymp., groove for muscular ramus of mandibular artery and chorda tympani nerve; qj. proc., quadratojugal process; quad. for., quadrate foramen. Muscle attachments: MAMEM, M. adductor mandibulae medius; MAMP, M. adductor mandibulae posterior. Reconstruction based on OUSM 15020B (3-0-S5), 15101 (3-0-S4), and Richards Spur captorhinid specimens. Scale equals 1 cm.

lamella is smoothly concave. It bears only light scarring anteriorly from the origin of the *M. adductor mandibulae posterior*. Posteriorly, a more heavily scarred region on the anterior surface of the squamosal flange and the quadratojugal process formed the origin of the *M. adductor mandibulae externus medius*.

The quadrate condyle is formed by the ventral extension of the pterygoid lamella and a ventrolaterally projecting quadratojugal process. These form two roughly sagittally oriented ventral crests that straddle the anteromedial and posterolateral bosses of the articular. The curved profile of these condylar projections allows them to slide freely in the hollow between the two aforementioned bosses of the articular in such a manner as to introduce a small amount of parasagittal motion to the mandible. The articular surface of the condyle of the quadrate is frosted in the manner of a typical synovial joint except for a very small, smooth region about 1 mm in diameter that articulates with a similar small facet on the articular when the jaws are shut. The compression of the two facets against one another produced a weak couple that prevented rotation of the quadrate-articular until the articular had been retracted about 1 mm and the facets disengaged.

The lateral process of the quadrate condyle bears a heavily grooved scar on its posterodorsal surface where it is sutured to the occipital process of the quadratojugal.

BRAINCASE

The captorhinid braincase was described in detail by Price (1935). It is a solid structural entity united with the skull roof through a strong junction between the parietals and the postparietals and the supraoccipital. The well-ossified paroccipital processes reinforce the rigid positioning of the braincase.

The stapes, while not of the same embryonic origin as the braincase, is most easily included here. It is a relatively large element with a heavy footplate and a long, slender columella that is perforated by a large stapedia foramen. The footplate sits in a cup-shaped recess formed by the basioccipital, opisthotic, and prootic on the lateral surface of the braincase. The distal end of

the stapes was held firmly within the columellar recess of the quadrate.

Parasphenoid

The parasphenoid is solidly fused to the ventral surface of the basisphenoid so that no parasphenoid-basisphenoid suture is discernible (fig. 27A, C). Posteriorly it sheathes the ventral surface of the basioccipital, while laterally it forms the ventral margin of the foramen ovale.

In ventral view, the base of the parasphenoid is roughly diamond shaped in outline, with the posterior, basioccipital projection one-third the length of the anterior, basisphenoid lamella. The anterior tip projects forward as an elongate cultriform process (parasphenoid rostrum) that arcs anterodorsally above the palate before descending to meet the medial edge of the pterygoid at the anterior end of the interpterygoid vacuity. The cultriform process is a V-shaped trough (fig. 27B) in which lay the fused trabecular cartilages that extended forward from their origins on the cristae trabeculares of the basisphenoid. The ossified portion of the interorbital septum included the ossified trabecular cartilage anterior to the optic foramen and was thus seated within the anterior portion of the trough. The anterior tip of the cultriform process lies directly ventromedial to the orbitonasal ridge of the palatine (fig. 2B, J), thus corresponding with the position of the sphenethmoidal commissure and the junction between the interorbital and internarial septa.

The parasphenoid expands slightly between the basipterygoid tubercles of the basisphenoid. It is bounded laterally by a prominent groove that deepens posterolaterally as the lateral edges of the parasphenoid continue to expand ventrolaterally as the crista ventrolateralis (fig. 27A). This groove is the vidian sulcus and was lined by the carotid fold of mucous epithelium. Through this sulcus passed the vidian nerve (palatal ramus of the facial nerve), the medial cranial sympathetic trunk nerve, and the palatal artery (a branch of the internal carotid artery). The crista ventrolateralis continues to expand laterally until it reaches its greatest width at the ventral extremity of the fenestra ovalis. Posterior to this point, the parasphenoid abruptly tapers to a point between the basioccipital tubera.

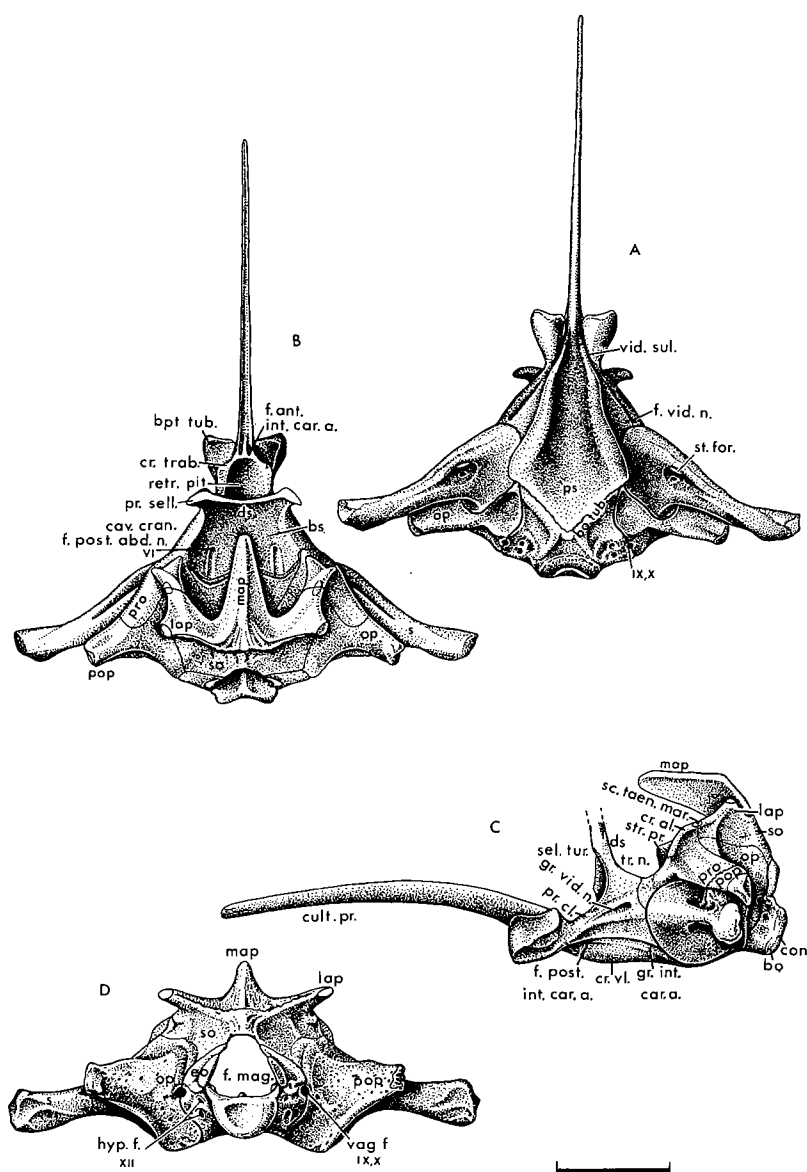


Figure 27. *Eocaptorhinus laticeps*. Braincase. A, ventral view; B, dorsal view; C, left-lateral view; D, occipital view. Abbreviations: *bo. tub.*, basioccipital tubercle; *bpt. tub.*, basipterygoid tubercle; *cav. cran.*, cavum cranii; *con.*, occipital condyle; *cr. al.*, crista alaris; *cr. trab.*, crista trabecularis; *cr. vl.*, crista ventrolateralis; *cult. pr.*, cultriform process; *ds.*, dorsum sella; *f. ant. int. car. a.*, foramen anterior of internal carotid artery canal; *f. mag.*, foramen magnum; *f. post. abd. n. VI*, foramen posterior of abducens (VI) nerve canal; *f. post. int. car. a.*, foramen posterior of internal carotid artery canal; *f. vid. n.*, foramen for vidian (VII) nerve; *gr. int. car. a.*, groove for internal carotid artery; *gr. vid. n.*, groove for vidian (VII) nerve; *hyp. f. XII*, hypoglossal (XII) nerve foramina; *lap*, lateral ascending process of supraoccipital; *map*, median ascending process; *pr. cl.*, processus clinoides; *pr. sell.*, processus sellaris; *retr. pit.*, retractor pit; *sc. taen. mar.*, scar for attachment of taenia marginalis; *sel. tur.*, sella turcica; *st. for.*, stapedial foramen; *str. pr.*, supratrigeminal process; *tr. n.*, trigeminal notch; *vag. f. IX, X*, vagus foramen (IX, X); *vid. sul.*, vidian sulcus. Reconstruction based on OUSM 15020B (3-0-S5), 15022 (3-1-S7), 15024 (3-1-S6), 15101 (3-0-S4), and Richards Spur captorhinid specimens. Scale equals 1 cm.

The ventral surface of the parasphenoid between the cristae ventrolaterales is a deep U-shaped trough that was lined by the pharyngeal membrane. In larger animals (OUSM 15024) the trough is quite deep (3 mm) and narrow (3.5 mm), while in smaller forms (OUSM 15022) the depth is much less (1 mm) but the width only slightly reduced (2.5 mm). In no case have teeth or denticles been found on the parasphenoid of *Eocaptorhinus laticeps*. The same obtains for both *Romeria* and *Protocaptorhinus*.

The parasphenoid of *Romeria prima* (MCZ 1963) is obscured by lateral crushing. Sufficient information is available to show that it is probably identical to that of *Eocaptorhinus laticeps* except in size. It is not preserved in *Romeria texana* (MCZ 1480). An excellent parasphenoid has been preserved in *Protocaptorhinus pricei* (FMNH UC 1119). It is identical, except for its smaller size, to that of *E. laticeps*.

The parasphenoid of primitive captorhinomorphs differs from captorhinids in a number of details. The basipterygoid articulation is situated more anteriorly and more dorsally than in captorhinids. In *Hylonomus lyelli* (Carroll, 1964), *Paleothyris acadiana* (Carroll, 1969a), and *Brouffia orientalis* (Carroll and Baird, 1972), the parasphenoid is narrow with small basipterygoid processes. The region between the processes is not deeply excavated. Large cristae ventrolaterales are not well developed. The level surface thus produced is covered by a shagreen of small denticles. The vidian sulci are narrow and shallow.

Basisphenoid

The basisphenoid is fused ventrally to the ensheathing parasphenoid. Posteroventrally, contact is made with the basioccipital (fig. 27B, C). This is a weak union in most of these animals, possibly as a result of an intervening cartilaginous pad, as Price (1935) illustrated in *Captorhinus*. Posterolaterally, the basisphenoid is sutured by a simple butt joint to the anterior edge of each of the pair of prootics. This is not a strong junction and has, in fact, been broken in all specimens at hand. This had usually occurred during crushing when the stapes were dislocated slightly and removed from the fenestra ovalis. The segment of the

basisphenoid between its contact with the prootic dorsally and the basioccipital and parasphenoid ventrally makes up the concave anterior rim of the fenestra ovalis.

The short rostral process of the basisphenoid is sheathed ventrally by the cultriform process. The trabecular cartilages lay in a short medial groove on its dorsal surface. A very low medial ridge separates two short, shallow, narrow pits in which are located a number of small foramina (fig. 24B). Price (1935) illustrated an anterior pair and a posterior pair of foramina. He referred to the posterior pair as the foramina for the internal carotid artery and the anterior pair as common foramina for the ophthalmic and cerebral arteries. The number of foramina present actually appears to be quite variable with some anterior and posterior foramina coalescing into a common duct. These foramina carried cranial and caudal branches of the cerebral artery as do similar foramina in a variety of living reptiles (O'Donoghue, 1921). These branches supplied the diencephalon and pituitary body.

The region posterior to the rostral process of the basisphenoid is known as the sella turcica. It has become popular to refer to the depression at the base of this region as the sella turcica itself (Price, 1935; Romer, 1956; Romer and Price, 1940; Fox and Bowman, 1966). This is not entirely correct, for the sella turcica in living reptiles is the space in which the pituitary body sits above the floor of the depression. It is floored ventrolaterally by the metoptic membrane, which fuses to its fellow ventrally to form a medial raphe that is attached to a low ridge between the anterior internal carotid foramina and the medial crest of the dorsum sellae. The membranous structure thus formed is the pituitary sac.

The large pit is the retractor pit in which the *M. retractor bulbi* had its origin. The lateral margin of the pit is formed by the processus clinoides and its posterior wall by the dorsum sellae. The processus clinoides is low and thick with a smooth, rounded dorsal border. The dorsal surface bears no scars, having been free from the orbitonasal membrane through which the *M. retractor bulbi*, *M. rectus posterior*, and *M. bursalis* extended forward. Just anterior to the dorsum sellae, the abducens canal opens through the anterior abducens foramen on

the midline of the dorsal surface of the processus clinoides.

The dorsum sellae is usually characterized as a single transverse sheet of bone in captorhinids (Price, 1935; Romer, 1956; Fox and Bowman, 1966). It is actually a rather complicated structure that separates the sella turcica from the cavum cranii and is composed of several identifiable parts. The ventral portion of the dorsum sellae that is bounded laterally by the processus clinoides is homologous with the dorsum sellae of lizards. A high anterodorsal projection arises from the posterodorsal edge of the processus clinoides directly posterior to the anterior abducens foramen. Price (1935) described this pillar as the prootic process, an unfortunate assignment in captorhinids where the dorsum sellae is derived from the basisphenoid but acceptable in pelycosaurs (sphenacodontids) where it is a prootic derivative (Romer and Price, 1940). This process where present in lizards has been referred to as the alar process (Oelrich, 1956). Since the thin, transverse sheet of bone connecting these processes is usually termed the crista sellaris, it is, perhaps, best to refer to these processes as the processi sellares, at least when discussing captorhinids. They are ossifications of the ventral portion of the pila antotica, not the whole structure as Romer's (1956) drawing and labeling in *Captorhinus* might suggest. The structure of the dorsum sellae of *Eocaptorhinus laticeps* is sufficiently primitive that it can be said to be representative of all captorhinomorphs. The reduced height of the processi sellares and the crista sellaris in lizards is a derived condition. The processi sellares are replaced by the cartilaginous ventral processes of the pila antotica, and the crista sellaris, by the posteroventral end of the metoptic membrane. An intermediate stage of development with a moderately high dorsum sellae is seen in the braincase of *Sphenodon*. A median crest extends down the anterior face of the lower half of the dorsum sellae and onto the posterior floor of the retractor pit of the sella turcica. This served as the posterior anchor of the median raphe of the fused lower section of the metoptic membrane. On either side of the median crest is a long, narrow, scarred depression that is bounded laterally by a low anterior ridge of the processus sellaris. This

served as the posterodorsal extension of the origin of the *M. retractor bulbi*. Lateral to the ridge on the processus sellaris is another scarred depression that marks the origin of the *M. bursalis*.

The posterior surface of the dorsum sellae is gently concave posterolaterally. The caudal surface is covered by many subdued crenulations formed by the differential growth of the endochondral bone impinging on the meningeal membrane (dura) of the lower rhombencephalon. This surface is raised slightly medially to form a vertical, low-relief ridge that conformed to the shallow ventral median sulcus of the hindbrain. On either side of this ridge at the bottom of the cavum cranii is the prominent posterior abducens foramen that gives access to the anterodorsally directed abducens canal. The canal is continued posteriorly over the base of the cavum cranii as a shallow groove, thus indicating that the origin of the abducens nerve was on the ventral surface of the medulla directly below the origin of the facial nerve and thus in the typical reptilian position.

The posterior limit of the dorsal surface of the basisphenoid is formed by the unfinished sinuous boundary with the cartilage that separates it from the basioccipital.

The lateral surface of the basisphenoid posterior to the basipterygoid tubercle is tapered both dorsoventrally and laterally to a narrow neck anterolateral to the retractor pit. The dorsal border is formed by the processus clinoides, the ventral, by the crista ventrolateralis of the parasphenoid to which it is fused. Three prominent longitudinal grooves cross this region (fig. 27C). The first of these runs from a large anteroventrally directed foramen in the posterodorsal corner of the basisphenoid, posteroventral to the base of the processus sellaris. This is the foramen for the palatal ramus of the facial nerve (vidian nerve). None of the specimens of *Eocaptorhinus laticeps*, nor of the Richards Spur captorhinids, shows a complete posterior bar separating the foramen from the fenestra ovalis because of minor dislocation and breakage in the area. The dorsal and ventral margins of the foramen reveal rough broken surfaces that confirm the presence, in undisturbed specimens, of a posterior bar. The nerve passed down the groove where it intercepted the internal

carotid artery, posterior to the posterior internal carotid foramen, and continued anteriorly with its major branch, the palatal artery, through the vidian sulcus. Below the posterior half of this groove is another similar groove extending forward from the posteroventral corner of the basisphenoid, that carried the internal carotid artery and medial cranial sympathetic trunk nerve. The two grooves join as outlined above. Just anterior to this junction, a small posterior internal carotid foramen opens into the internal carotid canal that, after branching, exits through the anterior internal carotid foramina. This canal is so small that it could not have given passage to as prominent an artery as the palatine artery, as Price (1935) suggested. Price believed that there was an additional small foramen within the vidian sulcus through which the palatine artery made its exit from the basisphenoid after bifurcation of the internal carotid artery within the bone. None of the specimens of *Eocaptorhinus laticeps*, nor of the Richards Spur captorhinids, shows more than a single, minute posterior internal carotid foramen piercing the lateral or ventral surfaces of the anterior portion of either the basisphenoid or parasphenoid. An arrangement such as Price suggested does not appear likely on the basis of dissection of modern reptiles.

The groove for the vidian nerve is bounded dorsally by a prominent narrow ridge to which the orbital fascia and orbitotemporal membrane were attached dorsally. Ventral to the ridge, the lateral surface of the basisphenoid was sheathed by the carotid fold of the mucous epithelium. A faint groove borders the dorsal edge of the ridge dorsal to the groove for the vidian nerve. It carried the vena capitis lateralis from the medial surface of the crista trabecularis posterior to its junction with the vena capitis medialis. The vein was supported by the orbitotemporal membrane medially and the tympanic membrane laterally. Further dorsal to the groove for the vena capitis lateralis is a slight depression in the lateral surface of the base of the processus sellaris over which passed the mandibular and maxillary divisions of the trigeminal nerve as they left the trigeminal notch (incisura prootica).

The basiptyergoid tubercles extend anterolaterally as extensions of the processus clinoides. They are thin, triangular plates

of about 1 to 1.5 mm in thickness (fig. 27A). The plane of the tubera is inclined ventrolaterally at an angle of 50° to the horizontal. The anterior edge is normal to the long axis of the skull. All of the dorsal surface is scarred by attachment of the thin cartilaginous lamella that lined the synovial joint between the basisphenoid and the epiptyergoid. Apparently a limited amount of rotational motion of the pterygoid and epiptyergoid could take place at this joint. A prominent crista trabecularis is situated at the posteromedial corner of the dorsal articulation scar.

Prootic

The prootic is the only known cranial element that has not been observed adequately in any specimen of *Eocaptorhinus* because of the inaccessibility of this region of the braincase. None of the other braincase elements shows any divergence in form from that illustrated by Price (1935) for *Captorhinus* sp. It seems reasonable to conclude that the same will hold true for the prootic. For the purposes of completeness, a description of the prootic of a small captorhinid is included here, based on Price's (1935) study of the braincase of *Captorhinus*.

The prootic is a small posterolaterally directed projection of the braincase dorsal to the fenestra ovalis (fig. 27B, C). Anteriorly it forms a short suture with the posterodorsal corner of the basisphenoid. Dorsally it has a free margin. Posteriorly it is bounded by the supraoccipital dorsally and the opishotic ventrolaterally. The ventral edge forms the dorsal margin of the fenestra ovalis.

The free dorsal margin slopes steeply posterodorsally and somewhat medially. The low anterior margin forms the posteroventral rim of the trigeminal notch (incisura prootica). The elevated posterior edge is formed by the crista alaris that supported the ventral extremity of the prootic membrane. At its posterior end, a small roughened area was described by Price (1935) as the attachment point of the orbitosphenoid cartilage. It is possible to homologize this area with the marginal process of the prootic of iguanids wherein it supports the ventral end of the taenia marginalis, the posterior cartilage supporting the prootic membrane (Oelrich, 1956). Price (1935) described a

“buttressed shelf in a slightly medial position” to the crista alaris. This is the supra-trigeminal process to which the pila antotica was attached. It is separated from the crista alaris by a deep, anteroventrally directed notch that formed the lower rim of the vena capitis medialis foramen and through which passed the vena capitis medialis.

The prootic extends a short distance posterolaterally along the anterior edge of the paroccipital process. It forms part of the shelf that overlies the stapes. This is the crista prootica to the ventral surface of which the dorsal process of the stapes was attached. The ventrolateral surface of the prootic, below the crista prootica, medial to the attachment of the dorsal process of the stapes bears a shallow groove formed by the passage of the vena capitis lateralis. Between the groove and the crista prootica is a small foramen through which passed the hyoman-dibular branch of the facial nerve.

The medial surface of the prootic forms the lateral wall of the cavum cranii. Posteriorly, the prootic is excavated for the shallow subarcuate fossa. Enclosed within the body of the prootic, dorsal to the fenestra ovalis, are the anterior and horizontal ampullar recesses and the anterior half of the horizontal semicircular canals of the osseous labyrinth of the inner ear that housed the corresponding elements of the membranous labyrinth.

Supraoccipital

The supraoccipital of *Eocaptorhinus laticeps* is exposed in posterior view in OUSM 15101 (fig. 12C) and FMNH UC 642. No other exposure has been observed. In OUSM 15022, a small fragment of the median ascending process is visible.

In general appearance the supraoccipital appears to differ only slightly from that of *Captorhinus* as illustrated by Price (1935). The only noticeable difference is the apparently broader base of each lateral ascending process in *Eocaptorhinus*. There is a pronounced posterior medial crest on the ascending process that extends vertically from the dorsal border of the foramen magnum. The foramen magnum forms the medial section of the ventral edge of the supraoccipital (fig. 27D). Lateral to the foramen magnum, the supraoccipital abuts the dorso-

medial edge of the opisthotic. The ventral edge of the supraoccipital is not as deeply incised by the margin of the foramen magnum as Price (1935) showed for *Captorhinus*. Fox and Bowman (1966) made the same observation in their study of *Captorhinus*. Price (1935) indicated that there is a fusion of the exoccipitals and supraoccipital in *Captorhinus*. Breakage and slight displacement of this region in OUSM 15101 have made it impossible to determine whether this same condition exists in *Eocaptorhinus*.

The supraoccipital is sutured to the prootic anterolaterally. The scar for the attachment of the taenia marginalis (marginal process) extends from the posterior end of the prootic portion of the crista alaris onto the anterodorsolateral end of the supraoccipital. The crista alaris is extended posteriorly by the supraoccipital to a termination in the posterodorsolaterally inclined lateral ascending process. The distal end of this process is braced posterodorsally against the internal surface of the postparietal on the flexure between the vertical posterior plate and the horizontal dorsal flange that underlies the ventral edge of the parietal. Laterally, the ascending process extends as far as the extreme posterodorsomedial corner of the pterygoid lamella of the quadrate. The posterior surface of the supraoccipital, lateral to the midline and ventral to the lateral ascending processes, bears scars marking the insertion area of the *M. rectus capitis posterior profundus*.

The supraoccipital is known in each of two species of primitive captorhinids. In *Protocaptorhinus pricei* (MCZ 1478, FMNH UC 1119), it is identical in proportions to that of *Eocaptorhinus laticeps* except in size, where it is only about 80 percent of the size of the *E. laticeps* supraoccipital. The lateral ascending processes are well developed and positioned as in *E. laticeps*. The *M. rectus capitis posterior profundus* insertion region is relatively as large as in *E. laticeps*. As in *E. laticeps*, the medial crest of the posterior surface is nearly vertical.

In *Romeria prima* (MCZ 1963), the lateral ascending processes appear to be well developed. The posterior surface is inclined anterodorsally more than in *P. pricei* as a result of the parietal emargination typical of this area. This has allowed an increase in the exposed posterior surface area of the

supraoccipital and a larger region for insertion of the *M. rectus capitis posterior profundus*.

The supraoccipitals of a number of primitive captorhinomorphs have been described and illustrated. Because of the poor state of preservation of many of these specimens, the reconstructions of the supraoccipitals are not entirely consistent. Only in *Paleothyris acadiana* (MCZ 3484; Carroll, 1969a) and *Protorothyris archeri* (MCZ 1532, 2148; Clark and Carroll, 1973) are the supraoccipitals well preserved. Both appear to have well-developed lateral ascending processes. The supraoccipitals of these two species are identical in basic form to those of primitive captorhinids.

Exoccipital

The exoccipital is a small element, roughly triangular in horizontal section, that arises dorsally from the posterolateral corner of the basioccipital. The internal surface of the triangular section has a sagittal orientation. It flares medially and anteromedially at its base. The thin anteromedial expansion has a smooth dorsal surface. It terminates posteriorly in a sharp transverse ridge. Directly anterior to this ridge is a small anterior ventral hypoglossal foramen, which is contained entirely within the exoccipital. It passes posterolaterally and somewhat ventrally to exit through the posterior ventral hypoglossal foramen on the occipital surface. Posterior to the transverse ridge is a larger anterior dorsal hypoglossal foramen, which passes laterally into the main body about 1 mm before turning posteriorly to appear on the occipital surface as the posterior dorsal hypoglossal foramen. Directly above the anterior dorsal hypoglossal foramen is a small dorsomedially directed hemispherical process the end of which is lightly frosted in the manner of a muscle or ligament origin scar. It has no known homologue in any living reptilian group, thus making an interpretation of its function difficult. There is a strong resemblance to the basis tuberculi basalis of turtles (Gaffney, 1972). This small protuberance may form the origin of a short ligamentous connection between the exoccipital and the meningeal membrane enclosing the medulla.

The posterior edge of the exoccipital

forms the lateral border of the foramen magnum (fig. 27D). Along this edge is developed a narrow crescentic condyle for articulation with the proatlas. A gap of 1 mm separates the proatlas condyle from the occipital condyle. Through this gap passed the ventral ramus of the first spinal nerve.

The anterolateral surface of the exoccipital forms a broad, anteriorly concave opisthotic recess about 2 mm in width. It has the lightly frosted appearance of most movable articulating surfaces. The vertical plane of the surface of the opisthotic recess is crossed by a posteroventrally directed vagus (jugular) canal through which passed branches of the vagus and vagus accessory nerves and the vena cerebialis posterior.

Basioccipital

None of the available specimens of *Eocaptorhinus* has a fully preserved basioccipital, although enough material is available from several specimens to allow a complete reconstruction. No significant difference has been noted between the *Eocaptorhinus* braincase and that of *Captorhinus* sp. (Price, 1935). Numerous apparently identical disarticulated basioccipitals are available from collections of small captorhinid material from the Dolese Brothers' quarry at Richards Spur, Oklahoma. Many details that are obscured on the *Eocaptorhinus* basioccipitals have been verified by reference to the specimens from Richards Spur.

Price (1935) indicated that the basioccipital is fused to the exoccipitals in *Captorhinus*. This is also true of *Eocaptorhinus*. It is possible to see what appears to be a very faint fused-up suture between the exoccipitals and basioccipital in some Richards Spur specimens, indicating that these bones developed from separate centers of ossification. The suture is best seen on the internal surface of the basioccipital, where it passes directly medial to the internal openings of both hypoglossal foramina. The exoccipitals do not meet along the midline but are separated from a 0.5-mm-wide medial ridge by about 1 mm. A broad opisthotic recess is composed of basioccipital anteriorly and exoccipital posteriorly. The suture is faintly visible in most Richards Spur specimens, descending vertically down the surface of the lower region of the recess. The suture enters the ventral surface of the braincase

posterior to the basioccipital tubera. In almost all cases, a small notch in the ventral margin of the opisthotic recess occurs to mark the suture. In some cases, the suture proceeds directly posteriorly along the ventral edge of the opisthotic recess in which it incises a narrow groove. The suture continues posteriorly until it reaches the occipital condyle, where all evidence of it is lost. It has not been possible to determine whether the occipital condyle is a unitary structure composed only of basioccipital as in *Araeoscelis* (Vaughn, 1955) or if it is tripartite as in most sauropsids. If the terminations of the ventral traces of the basioccipital-exoccipital sutures are taken into account, the tripartite form made up of both a basioccipital and paired exoccipitals is to be expected.

The dorsal surface of the basioccipital medial and anterior to the exoccipital sutures is slightly concave. Along its centerline is a medial crest to which presumably was attached the bifid ligament of the medulla (Kesteven, 1910; Gaffney, 1972). A number of minute foramina enter the dorsal surface of the basioccipital anterior to the exoccipital sutures. These appear to have served as nutrient canals.

Ventrally, the basioccipital can be divided into two regions (fig. 27A): the posterior occipital condyle and the anterior parasphenoid sutural surface. The basioccipital is thickened posteriorly in the region of its union with the exoccipitals. The condyle in occipital aspect (fig. 27D) is roughly oval in shape with a slight flattening of the foramen magnum. The condyle bears a deep, central, notochordal pit. The condyle is distinctly crescentic when viewed ventrally. Anteriorly, a sharp, narrow ridge separates the articulating surface of the condyle from the lightly scarred, laterally convex portion that formed the insertion region of the *M. rectus capitis anterior*. Anterolaterally, the *M. longissimus capitis transversalis cervicis* inserted along the basioccipital tubera. Directly anterior to the basioccipital tubera, the basioccipital thins abruptly anteriorly along the midline. There is no lateral thinning, thus producing a centrally concave depression bearing a slight median ridge and the light longitudinal grooves of a suture scar. It is onto this surface that a thin posterior extension of the parasphenoid is attached.

Laterally, the posterior half of the basioccipital is hidden by the exoccipital. Anterior to this the opisthotic recess continues for 1 to 2 mm. Most of the opisthotic recess is made up of exoccipital. Anterior to the opisthotic recess is a small (1 mm in diameter) dorsolaterally facing lagenar recess. The thin ventral edge of the lagenar recess formed the ventral border of the fenestra ovalis.

Price's (1935) assumption that a cartilaginous region separated the thin anterior edge of the basioccipital from the basisphenoid appears to be valid. The suture between the basisphenoid and the basioccipital was quite loose and may have had a thin separating layer of cartilage, although not as large as Price had indicated. Had a larger area of cartilage been present, postdepositional deformation would have collapsed the thin ensheathing parasphenoid in some of the more badly crushed specimens. This has not happened in any of the available specimens of *Eocaptorhinus*, although horizontal cracking of the parasphenoid is common (OUSM 15101, 15020, 15024).

Except for the obvious character of size, the exoccipitals of *Protocaptorhinus pricei* (MCZ 1478, FMNH UC 1119) and *Romeria prima* (MCZ 1963) are identical to *Eocaptorhinus laticeps*.

Opisthotic

The opisthotic of *Eocaptorhinus laticeps* is a short, posterolaterally directed, subconical element that forms the posterior segment and lateral extension of the paroccipital process (figs. 27, 28). It consists of a large base enclosing the posterior segment of the membranous labyrinth of the inner ear and the tapering shaft of the paroccipital process. It is bordered posteromedially by the basioccipital-exoccipital unit. Ventrally, contact is made with the footplate of the stapes. Dorsally, the opisthotic is sutured to the prootic anteriorly and the supraoccipital medially. These two sutures are strongly fused, although the bones are thin, so that simple disarticulation along these planes seldom occurs. Rough breaks through these relations are typical.

The opisthotic recess of the exoccipital is a smoothly concave surface in which the posteromedial edge of the opisthotic sat. The

two bones were separated by a thin, intervening layer of connective tissue. A single prominent channel extends posteroventrally across this surface. It forms the anterolateral wall of the vagus canal. The internal surface of the groove is perforated by many small foramina.

Ventrally the opisthotic recess continues in the lateral surface of the basioccipital. No grooves or foramina mark the rim of the opisthotic along its contact with the basioccipital. This contact also incorporated an intervening connective tissue layer. Dorsally the opisthotic is solidly sutured to the prootic and the supraoccipital.

The posterior surface of the opisthotic (fig. 28A) is marked by a number of prominent muscle-insertion scars. Ventromedially a large concave scar marks the point of insertion of the *M. longissimus capitis transversalis cervicus* and the *M. iliocostalis capitis*. It is not possible to separate the insertions of these two muscles. The *M. longissimus capitis transversalis cervicus* also inserted onto the lateral margin of the basioccipital. Another large scar extends laterally along the posterior surface of the paroccipital process and marks the origin

of the *M. obliquus capitis magnus*. A narrow vertical ridge occurs at the extreme lateral end of the paroccipital process. It appears to represent the medial edge of the insertion area of the *M. longissimus capitis transversalis capitis*.

The lateral tip of the paroccipital process is a small, rough, triangular projection that bore a small, intercalary cartilage joining the opisthotic to the occipital flange of the squamosal.

The ventral surface of the paroccipital process lateral to the stapedia recess bears a broad, shallow, longitudinal groove that marks the course of the vena capitis lateralis and the hyoid ramus of the facial nerve.

The stapedia recess (fig. 28B) is a lunate, medial excavation of the anteroventral surface of the opisthotic in which the large footplate of the stapes sits. The posteroventral margin of the recess has excavated the body of the opisthotic sufficiently to constrict the ventral border into a sharp crest that is homologous with the crista interfenestralis of lizards, even though no fenestra rotunda is present in *Eocaptorhinus*. The stapedia recess forms the posterodorsal rim of the large fenestra ovalis. Additionally, it forms

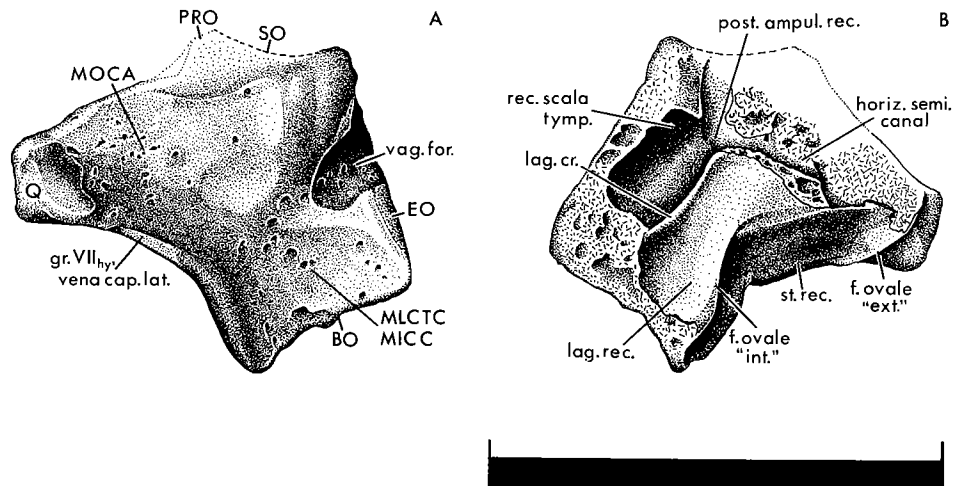


Figure 28. *Eocaptorhinus laticeps*. Left opisthotic. A, posterior view; B, anterior view. Abbreviations: *f. ovale "ext,"* foramen ovale "externus"; *f. ovale "int,"* foramen ovale "internus"; *gr. VII_{hy}*, *vena cap lat.*, groove for hyoid ramus of facial (VII) nerve and vena capitis lateralis; *horiz. semi. canal*, horizontal semicircular canal; *lag. cr.*, lagenar crest; *lag. rec.*, lagenar recess; *post. ampul. rec.*, posterior ampullary recess; *rec. scala tymp.*, recessus scala tympani; *st. rec.*, stapedia recess. Attachment of: *MICC*, *M. iliocostalis capitis*; *MLCTC*, *M. longissimus capitis transversalis cervicus*; *MOCA*, *M. obliquus capitis anterior*. Reconstruction based on OUSM 15101 (3-0-S4) and Richards Spur captorhinid specimens. Scale equals 1 cm.

a solid internal articulating surface against which the swollen medial surface of the stapedial footplate rests. The interior of the stapedial recess is identical in construction to the opisthotic recess of the basioccipital and exoccipital, and it, too, appears to have been lined with a connective tissue lamina. The rim of the stapedial recess might best be considered as being the border of the fenestra ovalis "externus." The articulating surface of the stapedial recess is bounded internally by a sharp, curved crest that constitutes the opisthotic section of the rim of a fenestra ovalis "internus." The fenestra ovalis "internus" is the homologue of the diapsid and turtle fenestra ovalis.

Dorsomedial to the fenestra ovalis "internus" is the lagenar recess. It is separated from the more medially situated recessus scala tympani by a prominent lagenar crest. The recessus scala tympani is the smaller ventral portion of the recessus vestibulae that held the posterior utricular sinus and the posterior ampulla. The most prominent part of the recessus scala tympani is the posterior ampullary recess that enclosed the caudal end of the membranous labyrinth. A narrow channel that bore the external or horizontal semicircular canal extends laterally. A similar narrow vertical channel formerly carried the posterior semicircular canal.

The medial wall of the osseous labyrinth was formed by a thin, vertical, internal lamina of the opisthotic. Price (1935) figured the internal surface of the posterior portion of this lamina without perforations. He showed a large area of the lateral wall of the cavum cranii as having been unossified, much in the manner of the hiatus acousticus of turtles. There is no posterior auditory foramen within the lateral surface of the internal lamina of the opisthotic. Neither is there a discrete perilymphatic foramen.

The opisthotics of primitive captorhinids are not well known. One specimen of *Protocaptorhinus pricei* (FMNH UC 1119) has the opisthotics preserved in place. They are identical in shape and proportions to the opisthotics of *Eocaptorhinus laticeps* but are of smaller size. Clark and Carroll (1973) reconstructed the type specimen of *P. pricei* (MCZ 1478) with an opisthotic with an unossified paroccipital process. Careful reexamination of this specimen has revealed that

the paroccipital processes were broken during preservation when the braincase was displaced laterally and the right opisthotic (the only one visible) twisted slightly. The crushed tip of the paroccipital process appears to have been lost during earlier preparation. Several small, unidentified bone scraps in the region of the opisthotic of MCZ 1478 may be fragments of paroccipital process, in which case MCZ 1478 and FMNH UC 1119 are identical in form and proportion, both to each other and to *E. laticeps*.

The braincase is missing from the type of *Romeria texana* (MCZ 1480), so that the opisthotics are unknown. The opisthotics of an immature specimen of *R. texana* (UT 40001-4) illustrated by Clark and Carroll (1973) are unossified. The type specimen of *Romeria prima* (MCZ 1963) is crushed laterally so that the paroccipital processes are not visible. The base of the opisthotic is well ossified as in *P. pricei* and *E. laticeps* and is, in fact, identical to them in form and proportion. The opisthotic of *R. prima* is the same size as that of *P. pricei* (MCZ 1478, FMNH UC 1119) but only about 80 percent of the size of an average *E. laticeps* specimen. It appears likely that the paroccipital processes of *Romeria* extended laterally to the quadrate as they do in *Protocaptorhinus* and *Eocaptorhinus*.

The opisthotics of primitive captorhinomorphs are very poorly known. The current literature (Carroll, 1969a, 1969b, 1969c, 1970; Carroll and Gaskill, 1971; Carroll and Baird, 1972; Clark and Carroll, 1973) indicates that an unossified paroccipital process is a uniform characteristic of the members of this group, either because of their primitive nature or their small size.

Interorbital Septum

The interorbital septum is a Y-shaped medial sheet of endochondral bone that arises vertically from the trough of the cultriform process to its bifurcation into the paired solum suprasedale (fig. 9A, B). It extends anteriorly to the orbitonasal membrane and posteriorly to a point medial to the inferior orbital foramen. The ventral margin is a heavy wedge that lies within the trough of the cultriform process. This appears to be the ossified trabecula com-

munis. The bifurcation of the septum occurs slightly dorsal to mid-height. The axis of separation is horizontal anteroposteriorly. The dorsal borders of the sola suprasedales are thickened slightly where they abut the ventromedial edge of the orbital rim thickening of the prefrontals, frontals, and postfrontals.

The septum is preserved in all of the complete skulls of *Eocaptorhinus laticeps* (OUSM 15020, 15022, 15101, 15102; FMNH UR 701). It is not known in any of the smaller captorhinids or primitive captorhinomorphs. It is present in *Captorhinus* sp. (OUSM 15007) from Richards Spur. In all cases, the septum has been badly crushed, making identification of muscle scars for the origins of some of the orbital musculature impossible. There are no perforations to be seen in the preserved portion of the septum.

In OUSM 15020A, the septum appears to continue anteriorly as a much thinner internarial septum. This specimen is larger, and presumably more mature than the others, which may account for the presence of what is, apparently, an ossified internarial septum in this specimen only.

Stapes

The stapes of *Eocaptorhinus laticeps* (fig. 29A, B, C, D) is a massive bone identical in all respects with that of *Captorhinus aguti* as described by Fox and Bowman (1966). It is of heavy construction, consisting of a massive footplate and tapering columellar process.

The footplate is a broad, oblate disk lying within the foramen ovale at an angle of about 20° to the longitudinal axis of the skull. The disk is formed of a thick pad of cancellous bone with a deep central excavation of parabolic cross section directly medial to the proximal end of the columella. The disk thins abruptly around its border. The posteromedial surface of the footplate sits within the broad, smooth stapedia recess of the opisthotic and basioccipital from which it was separated by a thin, fibroelastic, connective tissue lamina. Anteriorly the stapes formed an edge-to-edge contact with the basisphenoid and prootic. There was no room for an annular ligament to suspend the footplate within the fenestra ovalis. Anteriorly, the stapes appears to be lightly

sutured to the basisphenoid and prootic. This is an unusual arrangement that also occurs among more advanced captorhinids. In *Labidosaurus hamatus* (FMNH UR 161) the suture is well developed but still relatively weak. In *Labidosaurikos meachami* (OUSM acc'n no. 3-1-S2), however, a strong interdigitating suture has arisen. There is no latitude for any type of stapedia movement of sufficient amplitude to have transmitted airborne vibrations to the inner ear of *Eocaptorhinus*.

The columella extends posterolaterally from the center of the footplate at an angle of 50° to the plane of the disk or 70° to the longitudinal axis of the skull. It is roughly triangular in cross section with a vertical posterior surface and dorsal, ventral, and anterior ridges. The dorsal ridge extends from the distal tip of the columella laterally for three-quarters of the length of the stapes before extending dorsomedially along the dorsal process. The dorsal process is a stout,

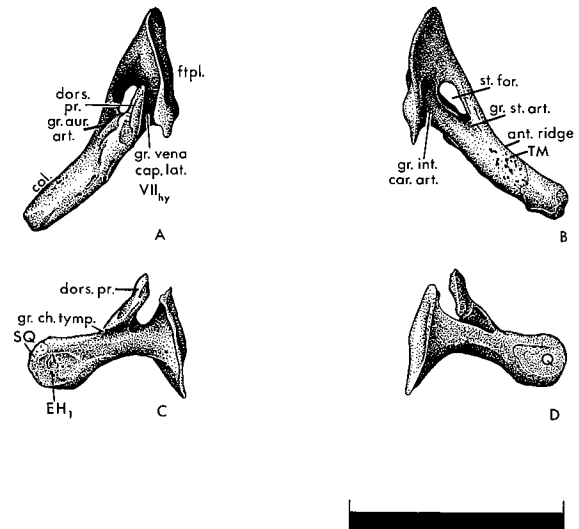


Figure 29. *Eocaptorhinus laticeps*. Left stapes. A, dorsal view; B, ventral view; C, occipital view; D, anterior view. Abbreviations: ant. ridge, anterior ridge; col., columella; dors. pr., dorsal process; ftpl., footplate; gr. art., groove for auricular artery; gr. ch. tymp., groove for chorda tympani nerve; gr. int. car. art., groove for internal carotid artery; gr. st. art., groove for stapedia artery; gr. vena cap. lat., VII_{hy}, groove for vena capitis lateralis and hyoid ramus of facial (VII) nerve; st. for., stapedia foramen. Attachment of: EH_v, epihyale I; TM, tympanic membrane. Reconstruction based on OUSM 15020B (3-0-S5), 15101 (3-0-S4), and Richards Spur captorhinid specimens. Scale equals 1 cm.

tapering extension of the columella to the ventral surface of the prootic, posterior to the crista prootica at the margin of the foramen ovale. Ventromedial to the dorsal process and dorsal to the columella is a smooth channel that marks the route of the vena capitis lateralis and the hyoid ramus of the facial nerve. The dorsal ridge itself was developed as an insertion region for the columellar fold of the tympanic mucous epithelium. The chorda tympani groove indicates passage of that nerve ventral to the columellar fold.

The anterior ridge extends from the ventrolateral tip of the distal end of the columella, where it is confluent with the ventral ridge for a short distance, to the anterior end of the footplate. Proximally, the ridge broadens and loses much of its sharp relief. As the ridge curves anteriorly it is pierced by a prominent, near-vertical foramen that allowed passage of the stapedia artery (fig. 29A). A short, deep groove extends laterally from the stapedia foramen along the dorsal edge of the anterior ridge. It carried the auricular artery, a small branch of the stapedia artery, into close proximity with the chorda tympani nerve. A similar, but shallower, groove on the ventral surface of the anterior ridge formed to accommodate the stapedia artery as it passed anterodorsally into the stapedia foramen. The columella is pierced by a small, posteriorly directed foramen within the posterior wall of the stapedia foramen. It appears to have carried a fine branch of the stapedia artery into the stapes, as Price (1935) suggested.

The distal end of the stapes is slightly flattened anteroposteriorly and expanded dorsoventrally. The anterior surface of this region between the dorsal and anterior ridge bears an elliptical scar that extends onto the ventral surface, formed by the attachment of an intercalary cartilage that held the tip within the deep, tightly fitting columellar recess on the medial surface of the quadrate.

The unfinished distal tip of the columella (fig. 29C) bore a thin cartilaginous pad that connected the stapes to the posteromedial corner of the occipital flange of the squamosal.

The ventral ridge is rounded and less prominent than either the anterior or the

dorsal ridge. Distally it is confluent with the slightly displaced anterior ridge. The ventral surface of the columella bears a long, narrow scar formed by the attachment of a fold of the tympanic mucous epithelium, similar to the processus internus fold of lizards (Oelrich, 1956). The posterior surface of the distal end of the columella bears a large rectangular scar that marks the attachment to the stapes of a cartilaginous epiphyse as in *Sphenodon*.

The stapes are known in both *Romeria prima* (MCZ 1963) and *Protocaptorhinus pricei* (MCZ 1478). Both have large footplates with a marked medial, annular swelling as in *Eocaptorhinus*. The columella of *R. prima* is long, stretching posteroventrolaterally to terminate in a columellar recess on the internal surface of the quadrate. In *Protocaptorhinus pricei* (FMNH UC 1119) an identical pattern has developed. Only in gross size do the stapes of *Romeria*, *Protocaptorhinus*, and *Eocaptorhinus* differ.

A certain degree of confusion exists over the structure of the stapes of primitive captorhinomorphs. It has long been thought that the captorhinid stapes is typical of the structure of all primitive reptiles. This is definitely not the case. In all primitive captorhinomorphs, where the stapes is well known, it is a short element with a relatively large footplate. In *Hylonomus lyelli* (Carroll, 1964) the stapes is well known. The footplate is long and relatively narrow and lacks the heavy, medial annular thickening. There was apparently a rather long, light, cartilaginous extracolumella. *Paleothyris acadiana* (Carroll, 1969a) is virtually identical to *Hylonomus* in the structure of the stapes. There appears also to have been a long, cartilaginous extracolumella as Carroll (1969a) showed. In a later publication (Carroll and Baird, 1972) having a reconstruction of the occiput of *Paleothyris*, the stapes was drawn with a long, ossified columella, although no new evidence was presented. In *Coelostegus prothales* (Carroll and Baird, 1972) the element described as a stapes is believed to be the opisthotic, although the stapes may be crushed beneath it. Only in *Protorothyris archeri* (Clark and Carroll, 1973) does the stapes approach the massiveness of the captorhinid stapes. The footplate is large and heavy. There is no evidence that there was a long ossified columella. The much larger

size of *Protorothyris* compared to earlier captorhinomorphs does not preclude this possibility.

Otoliths

In one specimen of *Eocaptorhinus laticeps* (OUSM 15101; fig. 12B) both stapes have been displaced to reveal the cavum vestibulae. During preparation of this recess, a soft, chalky, white mineral of noncrystalline or microcrystalline structure was encountered. It occurred as an irregular mass about 4 mm in length, 3 mm in diameter, and 2 mm thick in both vestibulae. The mineral involved could not be identified. It was unaffected by acetic acid. Since these structures have appeared only within the vestibulae of the inner ear and are of comparable size in both left and right ears, it seems probable that these are otoliths that developed within the sacculus.

MANDIBLE

The heavily built mandibular ramus is laterally convex posteriorly. The dentary tooth-row extends horizontally along the anterior 45 percent of the mandible in the same plane as the articular condyle. There are 20 to 27 sub-theodont teeth arranged in a single row along the crista dentalis. A modest coronoid-surangular crest is developed but not a prominent coronoid process. There is a well-developed retroarticular process and angular process on the articular. The lateral surface of the mandible is sculptured extensively by shallow, vermiculate pits. The unsculptured surface bears numerous prominent muscle-insertion scars. There are two prominent foramina: an anteriorly situated foramen intermandibularis oralis and a posterior foramen intermandibularis caudalis (meckelian foramen, infra-meckelian foramen). There is no large foramen intermandibularis medius as in many modern reptiles. The adductor fossa is long (about 35 percent of the mandibular length) and deep.

Dentary

The external surface of the dentary of *Eocaptorhinus laticeps* is well exposed in most of the specimens available (figs. 5B; 6B,

C; 10A, B; 12B, D; 13B, C; 20B, C) and is easily reconstructed (figs. 2E, G, F; 30A). The tooth-row is visible in FMNH UC 701 (fig. 20C), OUSM 15102 (fig. 10A, B), and OUSM 15021 (fig. 31A). The internal view of the dentary was examined during the removal of the anterior portion of the right mandible of OUSM 15020A when the palate was exposed in ventral view.

The dentary forms a roughly C-shaped sheath of thin bone around the dorsal and lateral surfaces of the Meckelian cartilage (fig. 30B, C, D). As the Meckelian canal tapers anteriorly, the wall thickness increases until the canal becomes a restricted channel 1 to 2 mm in width. The medial surface of the canal is formed by the splenial anteriorly and the coronoid posteriorly. The splenial forms a wide, firm suture with the lower edge of the dentary below the canal as far posteriorly as the foramen intermandibularis caudalis, at which point the angular assumes the function of flooring the Meckelian canal. Dorsally, the dentary forms an overlapping suture with the splenial as far posteriorly as the 10th or 11th mandibular tooth position, at which point the coronoid becomes the medial sheathing element. There is a considerable difference between the dorsal and ventral suture planes. The ventral plane bears a small number of deep longitudinal grooves into which fit corresponding tongues on the ventrolateral surface of the splenial. The dorsal suture is displaced 1 to 2 mm medial to the plane of the ventral suture. It is slightly convex medially in contrast to the deeply grooved ventral suture plane. The suture is quite complex, consisting of one or two low longitudinal ridges over which is superimposed a light chevron pattern of scars with posteriorly directed apices. Two fine, polished channels, conforming to the size and shape of these chevrons communicate between the Meckelian canal and the lingual margin of the tooth row. The more anterior of the two occurs at the anterior end of the coronoid-dentary union, the second about four tooth positions posteriorly. These foramina served as passages for the mucosal and lingual rami of the intermandibularis medius ramus of the mandibular nerve and the chorda tympani, and for lingual arterioles of the internal mandibular artery. These foramina were the functional precursors of

the foramen intermandibularis medius of modern reptiles (lizards, crocodiles, turtles). Anterior to the dorsal splenial suture

(ahead of the fourth mandibular tooth) the dentary forms a heavy symphyssial buttress above the restricted Meckelian canal. The

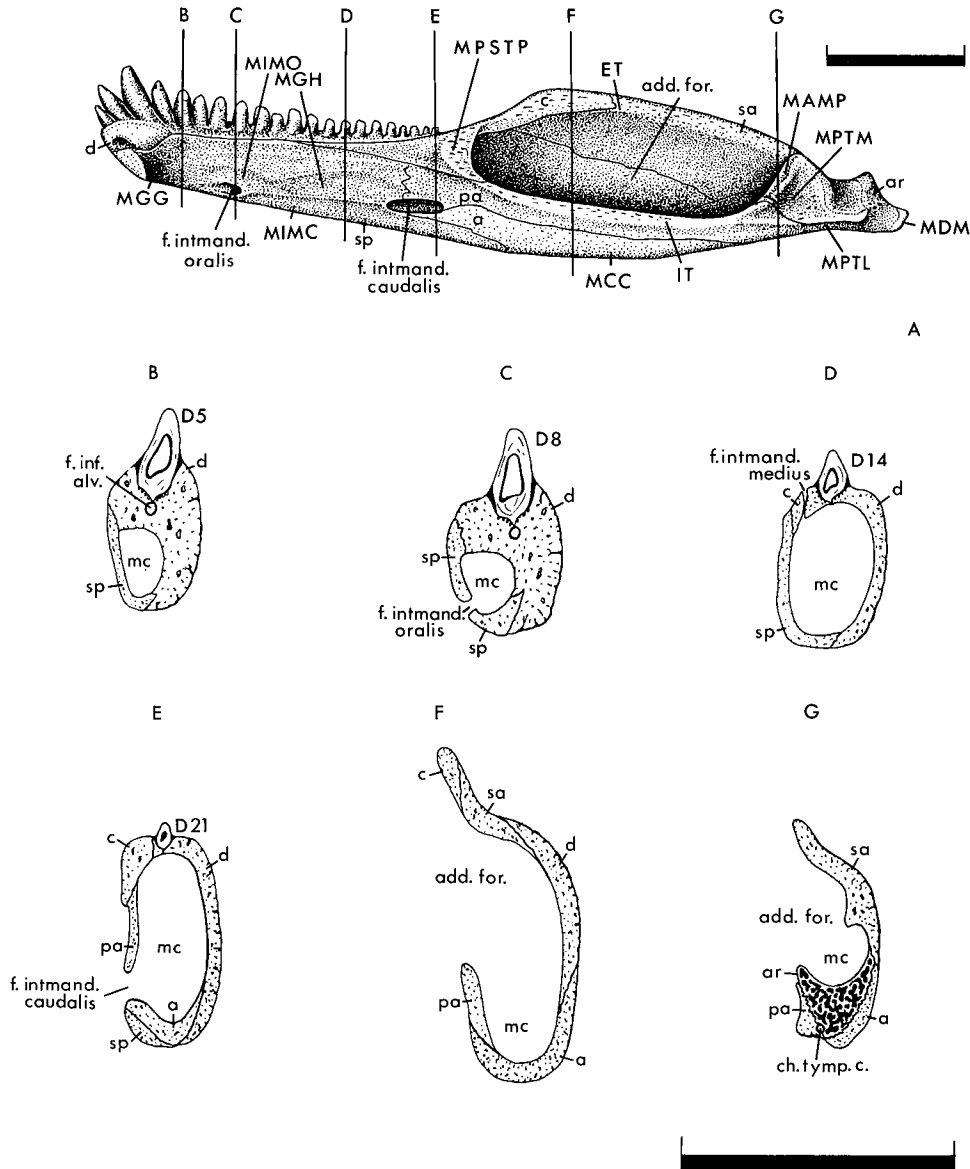


Figure 30. *Eocaptorhinus laticeps*. Right mandible. A, medial view. Sections of mandible at: B, dentary tooth 5; C, dentary tooth 8; D, dentary tooth 14; E, dentary tooth 21; F, maximum height of coronoid; G, posterior end of adductor foramen. Abbreviations: *add. for.*, adductor foramen; *ch. tymp. c.*, chorda tympani canal; *f. inf. alv.*, inferior alveolar foramen; *f. intmand. caudalis*, foramen intermandibularis caudalis; *f. intmand. medius*, foramen intermandibularis medius; *f. intmand.*, foramen intermandibularis oralis; *mc.*, Meckelian canal; *ms.*, Meckelian sulcus. Attachments of: *ET*, external tendon; *IT*, internal tendon; *MAMP*, M. adductor mandibulae posterior; *MCC*, M. constrictor colli; *MDM*, M. depressor mandibulae; *MGG*, M. genioglossus; *MGH*, M. geniohyoideus; *MIMC*, M. intermandibularis caudalis; *MIMO*, M. intermandibularis oralis; *MPSTP*, pseudo-temporalis profundus; *MPTL*, M. pterygoideus lateralis; *MPTM*, M. pterygoideus medius. Reconstruction based on OUSM 15021 (3-1-58). Scale equals 1 cm.

anterior half of the buttress forms an oval facet in the medial sagittal plane where it is sutured to its fellow medially. Directly below the Meckelian canal, anterior to the prominent splenial symphyseal buttress, is another oval sutural facet. The symphyseal surface is only lightly scarred by a radiating groove pattern. The great dorsoventral depth and somewhat sinuous surface of the symphyseal plane would have resisted torsional and shear loads adequately and prevented any movement. The Meckelian canal extends the full length of the symphysis.

The Meckelian cartilage extended forward to a position below the seventh or eighth mandibular tooth position directly lateral to the foramen intermandibularis oralis. Anterior to this, the heavy dental platform impinges upon the ventral border, thus restricting the Meckelian canal. The posterior surface of this thickened area that abutted the end of the Meckelian cartilage is pierced by a foramen and canal through which passed the internal mandibular artery which anastomosed within the bone to supply the skin of the "chin" through the sculpture pits and pores. The internal surface of the Meckelian canal is pierced by hundreds of minute foramina, all of which penetrate anterolaterally into the bone. These carried fine branches of the internal mandibular artery system into the vesicular bone of the dentary and thence to the skin through pores in the sculpture pits and to the dental lamina. The floor of the Meckelian canal is

heavily frosted by its contact with the Meckelian cartilage and its fibrous attachment to the dentary. A small-diameter canal extends forward from the end of the Meckelian canal between the dorsal and ventral symphyseal buttresses to the tip of the jaw. It carried the symphyseal ramus of the inferior alveolar nerve which innervated both the anterior and the posterior parts of the symphysis through small labial twigs, as in some turtles (e.g., *Pseudemys scripta* and *Batrachemys nasuta*; Schumacher, 1973).

The lateral surface of the dentary is heavily sculptured by many vermiculate pits, all perforated by fine pores communicating with the internal vascular system. Posteriorly the dentary overlies broadly the ventral surface of the surangular and is itself overlain even more extensively by the angular.

The tooth-row rests upon a heavy alveolar base that is perforated throughout its length by the inferior alveolar canal, which carried the inferior alveolar nerve. The medial edge forms the dentary's sutural contact with the splenial anteriorly and the coronoid posteriorly. Complete tooth-rows are visible in only two specimens of *Eocaptorhinus laticeps*: OUSM 15102, which has 22 dentary teeth, and OUSM 15021, which has 26. The teeth of OUSM 15021, which is the same size as 15102, appear to be much more cramped. This has resulted in numerous slight offsets of overcrowded teeth in 15201.

In OUSM 15021 (fig. 31A, B), the teeth are grouped into sets in which they progressively decrease in height rearward both within individual sets and as a whole.

Jaw sections as well as the few visible replacement pits show that the tooth implantation was basically sub-theodont. Unerupted juvenile teeth have not been observed in either the maxilla or the dentary. Replacement was infrequent, although when it did occur it apparently proceeded rapidly, with the result that spaces in the tooth-row caused by the loss of a tooth were filled quickly and so do not appear in any known specimens. In OUSM 15021 (fig. 31), tooth no. 7 is a young tooth that has completely replaced the most anterior (oldest) tooth of the posteriorly adjacent tooth set or Zahnreihe and almost completely occupied the replacement pit. Only a single tooth has been replaced in this specimen. This pattern

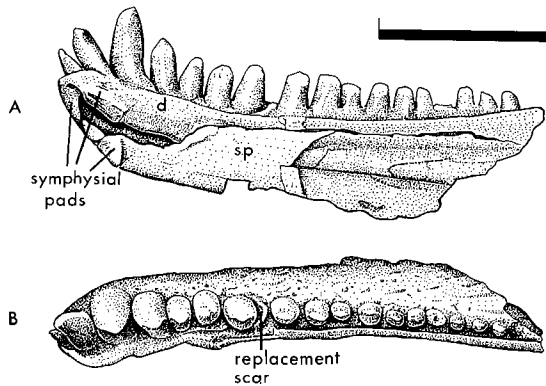


Figure 31. *Eocaptorhinus laticeps*. Right dentary and splenial. A, medial view; B, dorsal view. OUSM 15021 (3-1-58). Scale equals 1 cm.

is similar to that described by Bolt and DeMar (1975) for the small captorhinids from Richards Spur.

The only other primitive captorhinid in which the dentary is preserved in its entirety and is completely revealed for examination is *Romeria prima* (MCZ 1963). The pattern exhibited by the left dentary, which contains 23 teeth, is identical to that of *Eocaptorhinus*. There are no gaps in the tooth row. The tooth spacing appears to be similar, if not identical, to that of OUSM 15102. Some replacement appears to have occurred at tooth-row positions 5, 10, and 15. This pattern is different from that observed in primitive captorhinomorphs. The mandibular dentition of *Protorothyris archeri* (Clark and Carroll, 1973) shows none of the captorhinid characteristics. Teeth are all of approximately equal height with no specific tooth sets readily identifiable. Numerous replacement gaps are to be seen in the tooth row. Mandibular dentitions are known in *Cephalerpeton ventriarmatum* (YPM 796), *Brouffia orientalis* (CGH III B.21.C.587), *Coelostegus prothales* (CGH 3027), and *Paleothyris acadiana* (MCZ 3481, 3482, 3483) (Carroll, 1969a; Carroll and Baird, 1972). All show a homogeneous dentition with numerous replacement gaps in the tooth row. This pattern is typical of the smaller, primitive pelycosaur such as *Haptodus* and some as yet undescribed forms that may be either small pelycosaur or captorhinomorphs.

Splénial

The splénial is a thin dermal bone that forms the lingual surface of the anterior half of the mandible (fig. 31A). Dorsally it forms a wide overlapping suture with the dentary anteriorly and the coronoid posteriorly. This upper edge, composed of both splénial and coronoid, forms a narrow shelf, the crista dentalis, lingual to the tooth row. Ventrally a similar but less extensive, overlapping suture is made with the dentary along the lower edge of the mandible. The last quarter of this suture extends rearward over the angular. The external surface of the splénial is predominantly exposed on the vertical lingual plane, while a much narrower ventral surface is separated from it by a sharp flexure of about 90°.

Anteriorly, the Meckelian sulcus pro-

duces a short, concave emargination of the dorsal edge of the splénial, causing the bone to taper rapidly. At the narrow anterior end, an oval protuberance or pad (Fox and Bowman, 1966) extends lingually to the midline of the skull. The pad, easily seen in OUSM 15020A, 15023, 15101, 15102, and 15021 (*Eocaptorhinus laticeps*), is one of three pads, two ventral and one dorsal to the Meckelian sulcus, which forms the intermandibular symphysis. The other two are both processes of the dentary. The alignment of these pads is such that no symphyseal surface is exactly aligned with the medial sagittal plane. This produces a slightly undulating sutural surface that would have strengthened the symphysis. The pad itself is twice as deep as it is wide and twice the depth of the splénial directly to it. It is inclined anterodorsally at about a 60° angle.

About 10 to 12 mm posterior to the symphyseal pad, near the ventral border of the splénial, is a small, anteriorly directed foramen intermandibularis oralis through which passed the ramus intermandibularis oralis of the mandibular branch of the trigeminal nerve (mandibular nerve). Also passing through this foramen was the intermandibularis oralis branch of the internal mandibular artery. Anterior to the foramen intermandibularis oralis is a broad, smooth region extending onto the caudal surface of the symphyseal pad. This region is scar-free, apparently having been covered only by oral mucosa. The ventrolateral margin of this area is marked by a shallow lateral indentation of the ventral surface of the mandible. A narrow band, 1 to 2 mm wide, bounds this laterally; it is the origin scar produced by the *M. genioglossus*. Fibers of this muscle passed dorsally over the smooth inner face of the splénial to pass rearward above the *M. geniohyoideus* to an insertion on the medial processus entoglossus of the hyoid apparatus and the interhyal (cornu hyale). Although there is no concrete evidence to establish definitely the existence of the interhyal, the well-developed ossified epihyale and ceratobranchiale I make its presence and that of the corpus cartilaginis hyoidis all but assured.

A short (1- to 2-mm) gap of very lightly scarred bone separates the *M. genioglossus* origin scar from a heavily scarred region of the ventral surface of the splénial. This

scar begins about 3 mm anterior to the foramen intermandibularis oralis and extends rearward to the posterior end of the splenial beneath the foramen intermandibularis caudalis (inframeckelian foramen of authors; Meckel's foramen, Romer, 1956). This scar, 1 to 2 mm in width and possibly extending onto the ventral margin of the dentary, marks the origin of the *M. intermandibularis caudalis*. The ramus intermandibularis caudalis of the mandibular branch of the trigeminal nerve, and the intermandibularis caudalis branch of the internal mandibular artery, exited through the foramen intermandibularis caudalis.

On the medial surface of the splenial, directly posterior to the smooth region over which the *M. genioglossus* passed, and predominantly dorsal to the foramen intermandibularis oralis, is a slightly hollowed region perforated by numerous very small pits. This area appears to have been the origin of the *M. intermandibularis oralis*, the transverse muscle flooring the mouth, below and anterior to the tongue.

Posterior to the foramen intermandibularis oralis, dorsal to the origin scar of the *M. intermandibularis caudalis*, is an indistinct, slightly roughened area that may represent the origin of the *M. geniohyoideus*.

No other scarring is visible on the splenial. Its posterior border is divided into a short, wide dorsal process and a long, narrow ventral process by the foramen intermandibularis caudalis. The dorsal process forms a short, overlapping suture with the prearticular except along its dorsal edge, where it overlies narrowly the intervening coronoid. The ventral process is excluded from the foramen intermandibularis caudalis, which forms the ventral border of the dorsal process, by a thin, anterodorsal extension of the angular, which underlies its whole depth. A foramen intermandibularis medius has not been found in any specimen of *Eocaptorhinus*, its expected location being obscured by the transverse flange of the pterygoid in most cases (OUSM 15101, 15102, 15022).

Coronoid

The coronoid is a thin, triradiate bone whose anterior process forms the posterior segment of the crista dentalis where it forms

a wide, overlapping sutural contact with the dentary (fig. 30). The entire lateral surface of the coronoid is underlain by a dorsal wing of the prearticular. Anteriorly the short dorsal process of the splenial overlies the ventral edge of the coronoid. Posteriorly the coronoid forms the anterior margin of the adductor foramen. The coronoid has a long, narrow posterodorsal process that sheathes the internal surface of the surangular along the dorsal rim of the anterior half of the adductor foramen. The coronoid is exposed in external view as a thin rim above the surangular. There is no prominent coronoid process. The coronoid forms the dorsal surface only of the posterior portion of the Meckelian canal, the external, ventral, and internal surfaces being formed by the prearticular, angular, and surangular, respectively.

Individual muscle-insertion scars have not been defined on the dorsal rim of the coronoid. A large, smooth region of the lateral surface of the mandible appears to have been the principal insertion of a broad, diffuse muscle or tendon. The distance separating the mandible from the cheek in this region is quite small, making the presence of a tendon the more likely alternative. This external tendon was attached along the medial surface of the upper margin of the adductor foramen, predominantly to the coronoid and the surangular. The *M. adductor mandibulae externus superficialis* inserted onto the lateral surface and dorsal edge of the external tendon and down onto the lateral surface of the surangular. The *M. adductor mandibulae externus medius* inserted on the dorsal portion of the medial surface of the external tendon, and the *M. adductor mandibulae externus profundus*, to the ventral portion within the adductor foramen below the coronoid. The *M. pseudotemporalis superficialis* inserted onto a tendon that extended deep into the adductor foramen, presumably to the Meckelian cartilage. That this course was followed is revealed by the configuration of the anterodorsal corner of the adductor foramen (posterodorsal process of the coronoid). In this way, a deep, smooth-surfaced groove was formed on the posteroventral surface of the coronoid to accommodate the tendon. It is also probable that the *M. pseudotemporalis profundus* inserted onto the medial surface

of the internal tendon. Most of the internal-tendon scar occurs on the prearticular. It does run up onto a small triangular area on the lingual surface of the main body of the coronoid. Other muscle insertions into the adductor foramen and onto either of the tendon systems are unrelated to the coronoid.

No information is available regarding the configuration of the coronoid in other primitive captorhinids. Clark and Carroll (1973) figured the medial view of the left mandible of *Protorothyris archeri* based upon MCZ 1532 and MCZ 2149. The size and shape of the coronoid is much different than that of *Eocaptorhinus laticeps* in that it has been restricted along its ventral border by a dorsal movement of the prearticular out of contact with the splenial or the foramen intermandibular caudalis (inframeckelian foramen = submeckelian foramen).

Prearticular

The prearticular is a long, narrow bone that forms most of the dorsal margin of the foramen intermandibularis caudalis and the ventromedial rim of the adductor fossa (fig. 30). The prearticular underlies the coronoid for most of the latter's height in a solid suture designed to resist heavy shear loads between the dentary-coronoid biting contact and the resisting prearticular to which the heavy internal adductor musculature was attached through an insertion onto the internal tendon. The suture line between the coronoid and prearticular runs along the edge of a marked ridge that has offset the coronoid 0.5 to 1 mm medial to the prearticular (fig. 30A, E). This depression of the prearticular below the level of the coronoid is not a preservational artifact but appears simply to be a region to which no muscles or tendons were attached. This depression is terminated posterodorsally by a prominent medially directed ridge along the margin of the adductor fossa. This ridge abruptly dissipates posteriorly into the lightly scarred medial surface of the prearticular. The dorsal surface of this more posterior region is formed by the smooth curve of the rim of the adductor fossa.

Anteriorly, the prearticular underlies the short posterodorsal process of the splenial and forms the dorsal margin of the foramen intermandibularis caudalis. More

posteriorly, the prearticular underlies the angular along a narrow, horizontal suture. The articular makes a long, narrow sutural contact with the lateral surface of the tapering posterior end of the prearticular. The articular bears a large, horizontal, medially directed wing for the attachment of the pterygoideus musculature. The ventral surface bears a small lunate excavation anteriorly into which the posterior end of the prearticular fits. Most of the medial surface of the prearticular posterior to the front of the adductor foramen bears the slightly roughened insertion scar caused by the attachment of the internal tendon. The ventral margin of the insertion scar is marked by a slightly raised undulating ridge approximately coinciding with the prearticular-angular suture.

The prearticulars are unknown in primitive captorhinids. *Paleothyris acadiana* (MCZ 23481) and *Cephalerpeton ventriarmatum* (YPM 796) are preserved so as to reveal the prearticulars. The condition of these specimens is poor, so that little detail is available. Clark and Carroll (1973) reconstructed the prearticular of *Protorothyris archeri* based on MCZ 2149. The arrangement illustrated, with the splenial solely forming the dorsal border of the foramen intermandibularis caudalis, rather than the prearticular, is unique to this animal and much different from the captorhinid pattern.

Surangular

The surangular is a thin bone forming most of the lateral surface of the mandible posterior to the dentary and dorsal to the angular. It is anteroposteriorly concave laterally except along its dorsal border, where it forms a dorsomedially sloping, blade-like ridge along the upper margin of the adductor foramen (fig. 30A, F, G). Anteromedially, the surangular forms a wide, overlapping contact with the posterodorsal process of the coronoid. Anteroventrally, the surangular makes a 2- to 3-mm-wide, overlapping contact with the dentary. The dentary continues ventrally, medial to the angular, to the point where it reaches the bottom of the Meckelian canal.

The medial surface of the surangular is smooth and seemingly free of muscle or tendon insertion except along its dorsal edge. Here, light frosting of the medial surface

shows that the insertion of the external tendon extended posteriorly from the posterodorsal process of the coronoid. The internal surface of the adductor fossa was apparently lined with a fascia separating the bone from the Meckelian cartilage.

The lateral surface of the surangular is unsculptured except in its most ventrally exposed region. Most of the dorsolateral border is a concave, scarred region that served as the insertion of the external tendon along its dorsal ridge and as the insertion of the *M. adductor mandibulae externus superficialis*. Fox (1964) realized that this region in *Captorhinus* served as the insertion of a branch of the *M. adductor mandibulae externus* that he called the masseter muscle. The name masseter muscle should be restricted to discussions of mammalian anatomy. The origins of the muscle shown by Fox would have required a muscle of insufficient fiber length to allow the lower jaws to be opened to their largest gape, of about 45° (Barghusen, 1968; Gans, 1966). Furthermore, there is no evidence that any muscle attached to the internal surface of either the squamosal, the jugal, or the quadratojugal, as no scars of any type exist, as Fox (1964) noted.

The internal surface of the surangular shows no markings or perforations. There is no evidence indicating the presence of any surangular foramina, which are typical of lizards. The surangular, although thin, is quite porous, being extensively perforated by small canaliculi communicating with small pores at the bases of the sculpture pits on its ventrolateral surface. A thin anastomosing network of nerve twigs from the ramus auriculotemporalis presumably infiltrated this vascular system in accompaniment with the venous and arterial capillaries.

The surangular is known only in external aspect in the primitive captorhinids where no apparent difference except size is noted between either *Romeria* or *Protocaptorhinus* and *Eocaptorhinus*. The surangular of primitive captorhinomorphs, where known, appears to be identical to *Eocaptorhinus* except in size and, possibly, sculpturing.

Angular

The angular is the principal dermal

element of the posterior half of the mandible where it forms the ventrolateral walls of the Meckelian canal (figs. 2B, G; 30). The angular extends anteriorly, ventral to the dentary which it overlaps broadly, to the point where it meets the splenial. The angular, which overlies the dentary, is itself overlain by the splenial. All three bones form a sequence below the foramen intermandibularis caudalis. Medially the dentary is absent; laterally the splenial is absent. On the medial surface, an anterodorsal process of the angular extends to the foramen intermandibularis caudalis of which it forms the ventral border. The anterodorsal process thins abruptly along its dorsal edge where it overlaps the prearticular medially on a narrow, vertical sutural plane. Laterally, posterior to its overlap of the dentary, the angular overlies the surangular on a broad, vertical surface. Posteriorly, the angular tapers abruptly to become a superficial sheet extending over the lateral and anteroventral surfaces of the articular.

Most of the lateral surface of the angular is sculptured by deep pits radiating from an apparent growth center located near the midpoint of the ventral edge of the bone (fig. 2G). A long, narrow, slightly hollowed area on the lateral surface of the most posterior projection of the angular bears no sculpturing but is marked by numerous, fine anteroposterior ridges that served as the insertion of the end of the *M. pterygoideus*.

All of the ventral and medial surface of the angular is sculpture-free. The anterior half of the ventral surface bears light scarring for the attachment of the *M. intermandibularis caudalis*. Anteriorly, the angle between the ventral and medial surfaces of the angular remains as sharp as it is on the splenial. Posteriorly, the tendinous insertion of the *M. pterygoideus* has been displaced more laterally, and the ventromedial edge of the angular rounded more broadly. A sharp flexure occurs between the angular and prearticular where the latter extends onto the ventral surface of the mandible and the angular process of the articular.

The internal surface of the angular is unscarred. It presumably was sheathed by a fascia that separated it from the sagittally directed lateral slip of the *M. pterygoideus* that passed over its surface. The ventral

margin of the internal tendon that inserted onto the prearticular may occasionally have migrated onto the dorsal edge of the angular in some specimens, although this is not common.

No foramina, save those associated with the sculpturing pits and internal vascular system, have been noted in the angular.

Protocaptorhinus pricei (MCZ 1478), except for its size, has an angular identical to *Eocaptorhinus laticeps*. *Romeria prima* (MCZ 1963) is damaged in this area, preventing comparison.

As illustrated by Clark and Carroll (1973), the angular of *Protorothyris archeri* is vastly different from that of any known captorhinid. Whereas the captorhinid angular extends forward to the point where it meets the splenial posteroventral to the foramen intermandibularis caudalis, to which it sends an ascending process dorsally to the splenial, in *Protorothyris* the angular assumes much of the function of the splenial as the floor of the Meckelian canal where it passes far forward ventral to the splenial. Other primitive captorhinomorphs such as *Brouffia orientalis* (CGH 111B.21.C.587) and *Paleothyris acadiana* (MCZ 3481, 3482, 3483) (Carroll, 1969a; Carroll and Baird, 1972) show a pattern similar to that of *Protorothyris archeri*.

Articular

No single specimen of *Eocaptorhinus* reveals the articular in all views. Enough material is available, however, to allow a complete reconstruction to be made (fig. 32). The articular is the heavy ossification of the posterior end of the Meckelian cartilage. It is composed of a robust curved basal shaft upon which is located a broad, trapezoidal articulating condyle.

When viewed laterally, the basal shaft is seen to have a long, straight ventral edge and an arching dorsal border that reaches its maximum height at its midpoint beneath the condyle. Two distinct regions of the basal shaft are visible: an acuminate anterior process and a posterior retroarticular process. The retroarticular process extends posteriorly and slightly medially, while the anterior process projects anteriorly and strongly medially. A marked inflection is noted, in ventral aspect (fig. 32D), between

the anterior process and the retroarticular process. The anterior process tapers abruptly to become a thin wedge forming the ventromedial floor of the posterior half of the adductor fossa. The ventromedial surface of the articular is sutured broadly to the prearticular, which continues posteriorly to sheath the ventral surface of the angular process of the articular. Posteroventrally the anterior process bears many long, deep, groove-and-ridge suture scars that mark the contact with the prearticular. Similar scars mark the ventromedial surface except at its anterior tip. The canal for the chorda tympani and posterior condylar artery passes forward as a groove in the ventral surface of the angular process, thence along the ventromedial surface of the anterior process. The anterior process forms the lateral margin of the anterior chorda tympani foramen, hence its smooth surface. A low, longitudinal ridge on this surface appears to have separated the nerve and the artery.

The lateral surface of the anterior process (fig. 32A) forms the smooth concave channel which lay alongside the medial surface of the Meckelian cartilage. Along the dorsal edge, directly anterior to the highest point of the condyle, is an anteroventrally trending ridge to which the M. adductor mandibulae posterior was attached. It is continuous with the ventral rim of the adductor foramen. Medial to this ridge, dorsal to the anterior portion of the angular process, and anterior to the condyle, is a heavily scarred, triangular depression into which the medial slip of the M. pterygoideus posterior inserted. The medial slip of the M. pterygoideus posterior was innervated by a twig of the M. pterygoideus ramus of the mandibular branch of the trigeminal nerve that entered its lateral surface near the base, through a notch in the dorsal ridge that formed the insertion of the M. adductor mandibulae posterior.

OUSM 15020 has a perfectly preserved retroarticular process. The retroarticular processes of OUSM 15101 and 15102 are also excellently preserved. The detailed information available from these specimens and from identical disarticulated articulars from Richards Spur is of primary importance in understanding the development and the origin of the reptilian external and middle ear. The retroarticular process, which is

about 4 mm in length, is the earliest to develop in the Captorhinidae. It is oval in cross section proximally and tapers slightly posteroventrally from a maximum thickness of 3 to 3.5 mm to 2 to 2.5 mm at its distal end. The retroarticular process has its base lateral to the centerline of the condylar facet from which it extends posteromedially.

The lateral surface of the retroarticular process is lightly scarred by the attachment of the angular, which wraps around beneath the condyle and extends over the most posterior region of the lateral surface of the anterior process. There is a distinct rim or

ridge on the articular against which the edges of the surangular abut. This rim is developed especially strongly on the retroarticular process. Directly below the surangular sutural surface is the heavily scarred prearticular suture.

The dorsal and medial surfaces (fig. 32B, C) of the retroarticular process are lightly pitted by the M. depressor mandibulae or M. cervico mandibularis origin. The medial surface bears two prominent foramina directly posterior to the angular process. They are positioned one above the other. Two small arteries, the auricular artery and the articu-

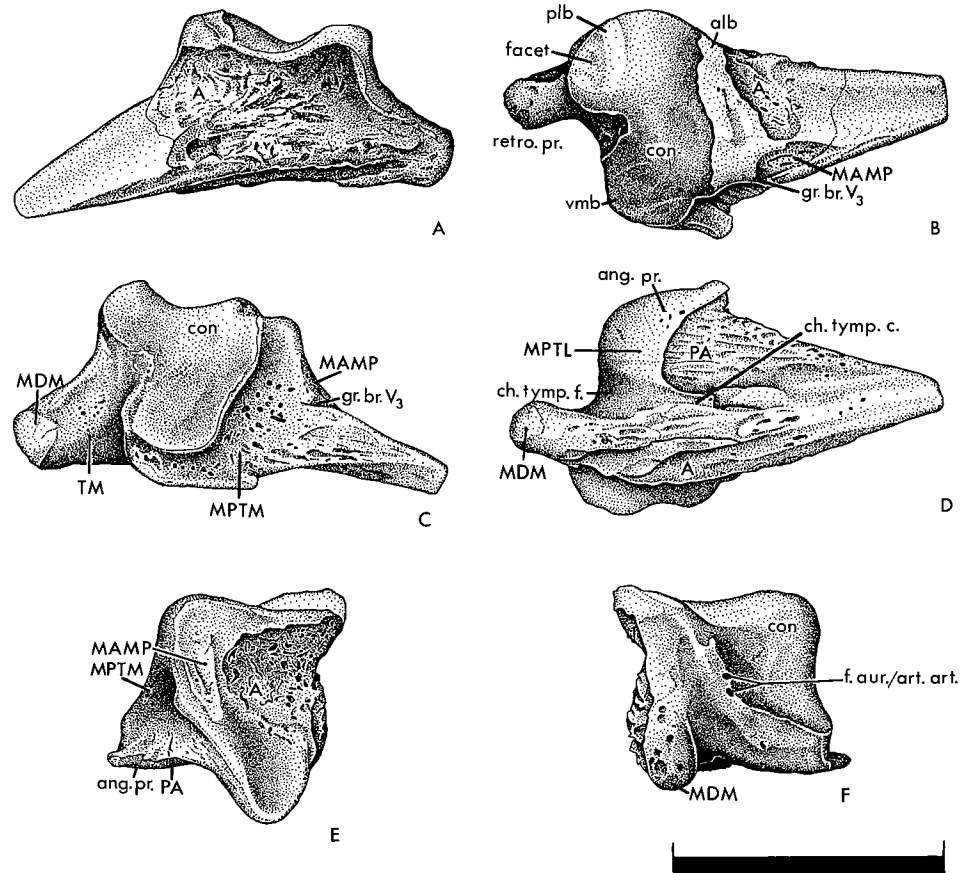


Figure 32. *Eocaptorhinus laticeps*. Left articular. A, lateral view; B, dorsal view; C, medial view; D, ventral view; E, anterior view; F, posterior view. Abbreviations; *alb.*, anterolateral boss; *ang. pr.*, angular process; *ch. tym. c.*, chorda tympani canal; *con.*, condyle; *f. aur./art.*, foramina for auricular and articular arteries; *gr. br. V₃*, groove for MAMP branch of mandibular ramus of trigeminal (V_3) nerve; *plb.*, posterolateral boss; *retro. pr.*, retroarticular process. Attachments of: *MAMP*, M. adductor mandibulae posterior; *MDM*, depressor mandibulae; *MPTL*, M. pterygoideus lateralis; *MPTM*, M. pterygoideus medius; *TM*, tympanic membrane. Reconstruction based on OUSM 15020B (3-0-S5), 15021 (3-1-S8), 15101 (3-0-S4), and Richards Spur captorhinid specimens. Scale equals 1 cm.

lar artery, passed into these foramina, although into which is unknown. One of the Richards Spur specimens was sectioned to reveal that, as in lizards, the arteries anastomose into the cancellous bone of the articular. Anteroventral to these foramina is another larger foramen bounded dorsally by the articular and ventrally by the prearticular. This is the foramen posterior chorda tympani through which passed the chorda tympani nerve and the posterior condylar artery (fig. 32D).

The medial surface was covered by an extensive mucous epithelium, which extended onto the lower surface of the retroarticular process.

The condylar facet is roughly trapezoidal in dorsal aspect (fig. 32B). Three of the apices form prominent bosses above the posterodorsal and medially sloping facet surface. The larger anteromedial apex forms the posterior border of the adductor foramen along its anterior edge. A low, broad ridge connects it with the prominent posterolateral boss. The top of this posterior boss shows a slightly different articular surface pattern. It appears that a small facet on this boss served to prevent mandibular depression without retraction by locking the articular against an opposing facet on the posteroventral border of the quadrate at the base of the anteroventral ridge that forms the lower margin of the stapedial recess. The quadrate condyle straddles the edge connecting the anteromedial and posterolateral bosses. The ridge has a saddle-shaped depression in its dorsal surface. Deeper depressions are present on the condylar facet both laterally and medially to the ridge. A small posteromedial boss is located on the posterior edge of the medial depression which separates it from the anteromedial boss. The anterolateral apex is low, being a posterior continuation from the dorsolateral margin of the surangular. The articular surface is long anteroposteriorly, being twice as long as that of the quadrate. During depression of the mandible, the articular had not only to rotate but also to retract. This is the result of the construction of the posterolateral boss. This retraction of the mandible was necessary in order to allow the anterior dentary teeth to clear the large premaxillary teeth during adduction and depression.

The ventral surface of the posteromedial

boss of the condyle forms the angular process of the articular. It is a horizontal, semicircular, medial projection with a coarsely scarred ventral surface on the prearticular sutural plane. It is traversed ventrally by a longitudinal chorda tympani canal, which transmitted that nerve and the posterior condylar artery. All of the ventral surface is sheathed by the prearticular except for the indented posterior border and medial edge. The chorda tympani foramen lies at the apex of the indentation. The lateral margins bear many deep grooves, scars of the insertion of the lateral slip of the *M. pterygoideus*.

The articulars of both *Romeria prima* (MCZ 1963) and *Protocaptorhinus pricei* (MCZ 1478) are preserved and separated from the quadrates sufficiently to allow examination. They are typically captorhinid in form, possessing the trapezoidal condyle with the prominent bosses and depressions. The angular process is a well-developed semicircular, medial extension below the posteromedial apex in both genera. The angular process is much more strongly developed than in *Protorothyris archeri* (MCZ 1532, 2148, 2149). There is no retroarticular process, nor is there one in *Romeria prima*. *Protocaptorhinus pricei* has only an abbreviated boss on the posterior surface of the articular. A comparison of the area of the articular condylar surface and that of the quadrate surface indicates that some jaw retraction may have occurred. The absence of a retroarticular process or the possession of one of greatly reduced size would have made the existence of a typical sauropsid quadrate-supported tympanum unlikely if not impossible. There is neither evidence of any type of tympanic support nor room for such a structure in a region that would have been covered by the *M. depressor mandibulae* or *M. cervicomandibularis*.

The articulars of primitive captorhinomorphs are poorly known. In no case has a retroarticular process been observed.

Hyoid Apparatus

Several specimens of *Eocaptorhinus laticeps* (OUSM 15020, 15024, 15101) contain ossified hyoid elements. Only in OUSM 15101 are they preserved in position with a minimum of crushing (figs. 2B, 13B). The

elements preserved are the epihyale and the ceratobranchiale I.

The epihyale is a long, slender, curved bony rod that extends posterodorsolaterally lateral to the crista ventrolateralis of the braincase and ventral to the stapes. It is well preserved in OUSM 15101. There are no identifiable muscle scars, presumably because of the small size.

The ceratobranchiale I is the larger, more anterior of the two cornua. It is well exposed in OUSM 15101 but is badly damaged in two other specimens (OUSM 15020, 15024). It is a heavily ossified, slightly curved rod with a wide, flattened anterior end. The anterior extremity is positioned lateral to the basiptyergoid tubercle and medial to the ventral edge of the quadrate ramus of the pterygoid. A low crest runs posteriorly down the ventral surface of the spatulate anterior end. Laterally there is an elongate insertion scar of the *M. hyoglossus*, *M. branchiomandibularis*, and *M. geniohyoideus*. Medially there is a similar scar that extends posteriorly over most of the ventral surface of the shaft that indicates the region of *M. coracohyoideus* and *M. omohyoideus* insertion. The posterior end of the shaft bears a slight ventrolateral facet that may indicate that a short, cartilaginous extension (epibranchiale I) was present.

DISCUSSION

Differentiation of *Captorhinus* and *Eocaptorhinus*

A review of the literature pertaining to small captorhinids reveals an almost universal tendency to identify all captorhinids from the Wichita Group, except Price's type of *Romeria texana*, as *Captorhinus* or its earlier presumed synonym *Pariotichus* (Williston, 1909; Case, 1911; Olson, 1952, 1954, 1962a; Seltin, 1959; Fox and Bowman, 1966). Only Watson (1954) and Clark and Carroll (1973) recognized that all of the specimens from the Wichita Group possess single-rowed marginal dentitions and, thus, were not *Captorhinus*. It should be recognized now that *Captorhinus* is a genus of rather short stratigraphic range, being limited to the Arroyo and, possibly, the lower Vale Formations of the Clear Fork Group of the Texas stratigraphic section. The general abun-

dance of *Captorhinus* material in the terrestrial sediments of the southern Midcontinent region of North America makes it useful as a zone fossil for the purposes of stratigraphic correlation.

Captorhinus aguti from the Arroyo Formation of Texas was described by Case (1911), Romer (1933, 1945, 1956, 1966), Seltin (1959), Fox and Bowman (1966), and Clark and Carroll (1973). *Captorhinus aguti* has a maxillary and mandibular dentition consisting of three, and in some specimens four, subparallel, posteromedially directed rows of short, chisel-shaped teeth. Even in very young specimens with skull lengths of about 15 mm (many Richards Spur jaws), three short rows of teeth are present. The misidentification of Wichita captorhinids has stemmed largely from the failure of previous researchers to prepare tooth-rows adequately so that the single-rowed nature of the dentition could be observed. Before Clark and Carroll (1973) described the single-rowed dentitions of these animals only a few previous papers had referred to single-tooth-rowed Wichita captorhinids. Williston (1917) mentioned a possible specimen of *Labidosaurus hamatus* from the Clyde Formation. Watson (1954) described briefly a series of small captorhinids from the Wichita Group of Texas that were re-described in greater detail later by Clark and Carroll (1973). Watson was careful to state that only *Captorhinus* had multiple tooth-rows, a point that was missed by Seltin (1959), who identified two of these forms (MCZ 1478, 1160) as *Captorhinus aguti*. Seltin did have a number of excellent specimens that possessed single tooth-rows. He failed to recognize their close relationship to *Captorhinus* and, instead, referred the specimens to the genus *Labidosaurus*, to which they are related only distantly.

Two previously described forms, Williston's (1909) *Pariotichus laticeps* and Seltin's (1959) *Labidosaurus oklahomensis*, appear superficially to be identical to *Captorhinus aguti*. Both, however, have single-rowed dentitions and so, by definition, do not belong to the genus *Captorhinus*. The new generic name *Eocaptorhinus* is used here in the new combination *Eocaptorhinus laticeps* (Williston) to include all Wichita captorhinids that are identical to *Captorhinus aguti* except for the single tooth-row.

Three genera of Wichita captorhinids—*Romeria*, *Protocaptorhinus*, and *Eocaptorhinus*—form a continuous phylogenetic sequence that gave rise to *Captorhinus* in the lower Clear Fork (Group). On the basis of the Texas sequence, an orderly evolutionary scheme can be developed. The lack of intermediate forms between *Eocaptorhinus* and *Captorhinus* in Texas is perplexing, suggesting rapid replacement of *Eocaptorhinus* by *Captorhinus* from a region outside of north-central Texas. Alternatively, a hiatus may exist in the sedimentological record at the time intermediate forms were present.

The fissure-fill deposits of the Dolese Brothers quarry at Richards Spur, Oklahoma, have produced thousands of fragmentary specimens of Early Permian reptiles and amphibians. Most of the reptiles (at least 90 percent, according to Peabody, 1961) are identifiable as being the remains of small captorhinids. Of the cranial elements, only the maxillae and dentaries indicate that more than one taxon is present. Most bear multiple rows of teeth in a pattern identical to that of *Captorhinus aguti* from Texas, the species to which they are usually assigned. About 1 in 20 tooth-bearing elements has only a single row of teeth. Olson (1967) identified these as *Labidosaurus*, cf. *L. hamatus*. As Bolt and DeMar (1975) noted, this is not the case. The number, shape, and wear patterns of the teeth, as well as their very much smaller size, preclude this identification. *Labidosaurus hamatus*, a contemporary of *Captorhinus aguti*, is often found with specimens of *Captorhinus* in the lowland, deltaic, and pond deposits of north-central Texas. *L. hamatus* has not been identified positively from the dry, upland, karst deposits of the Wichita Mountains at the Dolese quarry, Richards Spur, Oklahoma.

A full analysis of speciation among the captorhinids from the Dolese quarry is beyond the scope of this paper, although a few comments should be made. To date, only Peabody (1961) discussed the actual geologic occurrence of the Richards Spur specimens. Some have come from fissures (Peabody's localities FEP 60/A and FEP 60/B), while others are from isolated clay pockets that may represent sections of true cave systems (localities FEP 60/C, FEP 60/D, FEP 60/E, and FEP 60/F). Many specimens have been collected on a general dump of noncommer-

cial clay piled on the quarry floor. It is from this locality, referred to as FEP 60/G (Peabody, 1961) that the most complete skull of *Eocaptorhinus laticeps* (Peabody field no. FEP 60/G-1) was collected.

No stratigraphic control exists over any of the separate occurrences at the Dolese quarry. The lower part of the Hennessey Group surrounds the area for several miles. It is believed that the initial deposits were of coarse, arkosic sandstone, similar to that of contemporaneous sediments in the immediate vicinity of the Wichita Mountains. The coarseness of the sand is indicative of active transportation by fast-moving, probably intermittent, streams in a well-developed karst region. The large quantity of broken and scattered bone that commonly occurs as a bone breccia suggests frequent reworking and redeposition of these sediments. Alteration of the arkosic sandstones to undisturbed kaolinite occurred *in situ* through the action of percolating ground water (Ada Swineford, oral communication, *in* Peabody, 1961).

Numerous specimens of small captorhinids appear at the Dolese quarry with tooth-row patterns that are intermediate in form between the definitive forms of *Eocaptorhinus laticeps* and *Captorhinus aguti*. The lack of stratigraphic control makes it impossible to tell whether the captorhinids at the Dolese quarry comprise one extremely variable species with interbreeding single-rowed or multiple-rowed phenotypes or whether they constitute a single lineage, evolving through time from a single to a multiple-rowed condition, that has become badly mixed by frequent reworking of the sediments. In the absence of stratigraphic or genetic control, it appears to be most reasonable to retain the usual paleomorphospecies concept wherein the tooth-rows are deemed to be of primary importance as the morphological indicator separating the species, and in this case also the genera. By this reasoning, all specimens with single tooth-rows are referred to as *Eocaptorhinus laticeps*, while multiple-tooth-rowed forms are referred to as *Captorhinus aguti*. Some intermediate forms will, of course, require a rather subjective separation into one or the other of these genera. This is simply a taxonomic expedient that prevents unwarranted alteration of a long-established generic diagnosis; see Case (1911), Seltin

(1959), and Fox and Bowman (1966).

It is apparent that the taxonomic and phylogenetic problems of the Richards Spur captorhinids are extremely complex and open to a variety of interpretations. The solution suggested here is a speculative, interim one meant only to suffice until more information on the structure and development of all the Richards Spur captorhinids and, in particular, the evolution of their dental patterns can be accumulated.

Speciation within Early Captorhinids

Watson (1954) recognized that a nearly complete phylogenetic lineage leading to *Captorhinus aguti* was visible in a sequence of specimens collected from the lower Wichita Group (Wolfcampian) deposits of north-central Texas. Clark and Carroll (1973) produced a detailed redescription of the members of this sequence. The sequence provides an excellent example of gradual change through time. Differentiation between genera and species is difficult on strictly morphological grounds. To a large extent, it has become customary to regard the Wolfcampian captorhinids as successional species, with each readily identifiable time boundary (usually a formation boundary) serving to limit temporally the range of any species. The two species of *Romeria* are separated on the basis of "the difference in age and dentition" (Clark and Carroll, 1973). As has been noted, *R. texana* has four, not five, premaxillary teeth, as has *R. prima*, and 21 rather than 20 maxillary teeth, thus increasing the apparent similarity between the species. The material used in developing the descriptions of these species is incomplete, thus preventing any definite conclusions from being reached relating to the differentiation of the species on morphological grounds. At the present time, it seems reasonable to retain the two species—*Romeria prima* from the Moran Formation and *Romeria texana* from the Putnam Formation—as successional or temporal species. The applicability of the species names in regions outside of the type area in north-central Texas is extremely limited because of the difficulty experienced in correlating the Texas deposits with those of other North American Wolfcampian localities.

Clark and Carroll (1973) described a small captorhinid from the upper Admiral Formation as the new species *Protocaptorhinus pricei*. It is distinguishable from the species of *Romeria* only in the reduction of the slight nuchal crest characteristic of *Romeria*. The sedimentological record indicates that the difference in age between the appearance of *R. prima* and that of *R. texana* was somewhat less than that between *R. texana* and *Protocaptorhinus pricei*. The differences exhibited between *Romeria texana* and *Protocaptorhinus pricei* are sufficiently small that as strong a case can be made for retaining the latter species within the genus *Romeria* as for assigning it to a different genus. It too is a successional or temporal species, but it was judged by Clark and Carroll (1973) to have sufficient differences in structure that it also might be considered to be a new, morphological genus. A specimen, probably referable to *Protocaptorhinus pricei*, is known as late as the lower Belle Plains Formation (FMNH UC 1119).

In this study all forms resembling *Captorhinus aguti* in skull structure, except for the presence of a single row of maxillary and dentary teeth, have been included in the morphospecies *Eocaptorhinus laticeps*. Considerable individual variability is accepted as normal; thus, gross size, number of teeth, and degree of "cheek swelling" are considered to be of little taxonomic significance. The species has a wider stratigraphic and, thus, temporal range than does any one of the more primitive species. The earliest specimen of *E. laticeps* (MCZ 1483) is from the upper Belle Plains Formation of Texas. Numerous identical specimens have been collected from the contemporaneous upper Wellington Formation (McCann quarry) of Oklahoma. Other specimens are known from throughout the Clyde Formation of Texas (Appendix), including the type specimen (FMNH UC 642). Because the species *E. laticeps* is defined more broadly than are the species *Romeria prima*, *R. texana*, or *Protocaptorhinus pricei*, it is possible to observe numerous progressive changes, particularly in development of tooth-wear patterns, that are at least as prominent as those that occur between the appearance of *Romeria prima* and *Protocaptorhinus pricei*. Since these changes occurred progressively and gradually, subdivision of this taxon into

successional species would be artificial and confining.

The differentiation between *Protocaptorhinus pricei* and *Eocaptorhinus laticeps* was based less on a desire for scientific accuracy than on a desire to retain as much of the existing taxonomic scheme as possible. Thus, all specimens believed to have evolved from forms identified as *Protocaptorhinus pricei* by Clark and Carroll (1973) and being in the direct lineage of *Captorhinus aguti* are referred to the species *Eocaptorhinus laticeps*. This form is present from the upper Belle Plains Formation to the Lueders Formation in Texas. A small time gap separates the earliest specimen of *Eocaptorhinus laticeps* (MCZ 1483) from the youngest specimen of *Protocaptorhinus pricei* (MCZ 1160). MCZ 1160 shows a number of features, most notably larger size, incipient development of the retroarticular process, and fewer, heavier teeth, that make it an excellent intermediate between the definitive *Protocaptorhinus pricei* (MCZ 1478) and the earliest *Eocaptorhinus laticeps*. *Eocaptorhinus laticeps* typically has a larger overall size, more strongly developed retroarticular processes, and more strongly swollen cheeks than does *Protocaptorhinus pricei*.

Variation within Species *Eocaptorhinus laticeps*

Two forms of variability must here be taken into consideration: individual variability within any single population (fixed time) and variability through time. The degree of individual variability may be judged by reference to the numerous specimens from the McCann quarry. Specimens of apparently adult animals exhibit skull lengths of between 81 mm (OUSM 15102) and 66.6 mm (OUSM 15101). This difference in skull lengths may be attributable to any of a number of reasons of which slight sexual dimorphism and relative individual ages are the most likely. The number of maxillary teeth in adults is remarkably constant at 22 or 23, regardless of size.

The variability through time is significant to an understanding of the stages through which *Eocaptorhinus laticeps* developed before giving rise to *Captorhinus aguti*. An estimated mean skull length for adult specimens of *E. laticeps* of about 68 mm is

typical of both the older Oklahoma specimens and the younger Texas specimens. The earlier forms appear to have a greater average skull size of 71.8 mm, as opposed to only 64.0 mm for the later forms. While the number of specimens is small and, thus, of doubtful statistical significance, it does seem to indicate that there was a tendency for juvenile and subadult animals to become buried in the Texas deltaic deposits with much greater frequency than in the upland stream deposits of Oklahoma. The implication is that environmental constraints rather than genetic programming are responsible for the high degree of variability in average skull size in preserved and collected specimens of *E. laticeps*.

All of the uncrushed specimens of *Eocaptorhinus laticeps* from the McCann quarry show a markedly angular cheek-skull table junction (fig. 2C) similar to that seen in *Captorhinus* (Romer, 1956). Some cold-flow deformation of the type specimen of *Eocaptorhinus laticeps* (FMNH UC 642) has occurred, thus giving this specimen a completely rounded dorsal, occipital margin.

Lateral deflection of the maxillae is a feature common to all captorhinids. In *Romeria* and *Protocaptorhinus* the deflection is not great, so that cheek swelling, although definitely present, is not highly developed. Cheek swelling is, in large part, a natural consequence of greater size related to the second-power multiplication of the cross-sectional area of the adductor musculature. Thus, juveniles can be expected to have less pronounced cheek swelling or even none at all, while adults may exhibit considerable swelling. This is especially apparent when a juvenile specimen of *Eocaptorhinus laticeps* (FMNH UC 1698) (fig. 13A) is compared with an adult (FMNH UC 642, 701) (fig. 3A, 20A). There is a minor degree of variation in the amount of cheek swelling between early and later forms of *Eocaptorhinus laticeps*. The slightly older *E. laticeps* specimens appear to show a slightly less pronounced degree of cheek swelling that is surely closely correlated with the more angular cheek-skull table union (fig. 33, 34).

A more pronounced change in dental-wear patterns occurred during the evolution of the Wichita captorhinids. It is beyond the scope of this paper to enter into a detailed discussion of the evolution of the captorhinid

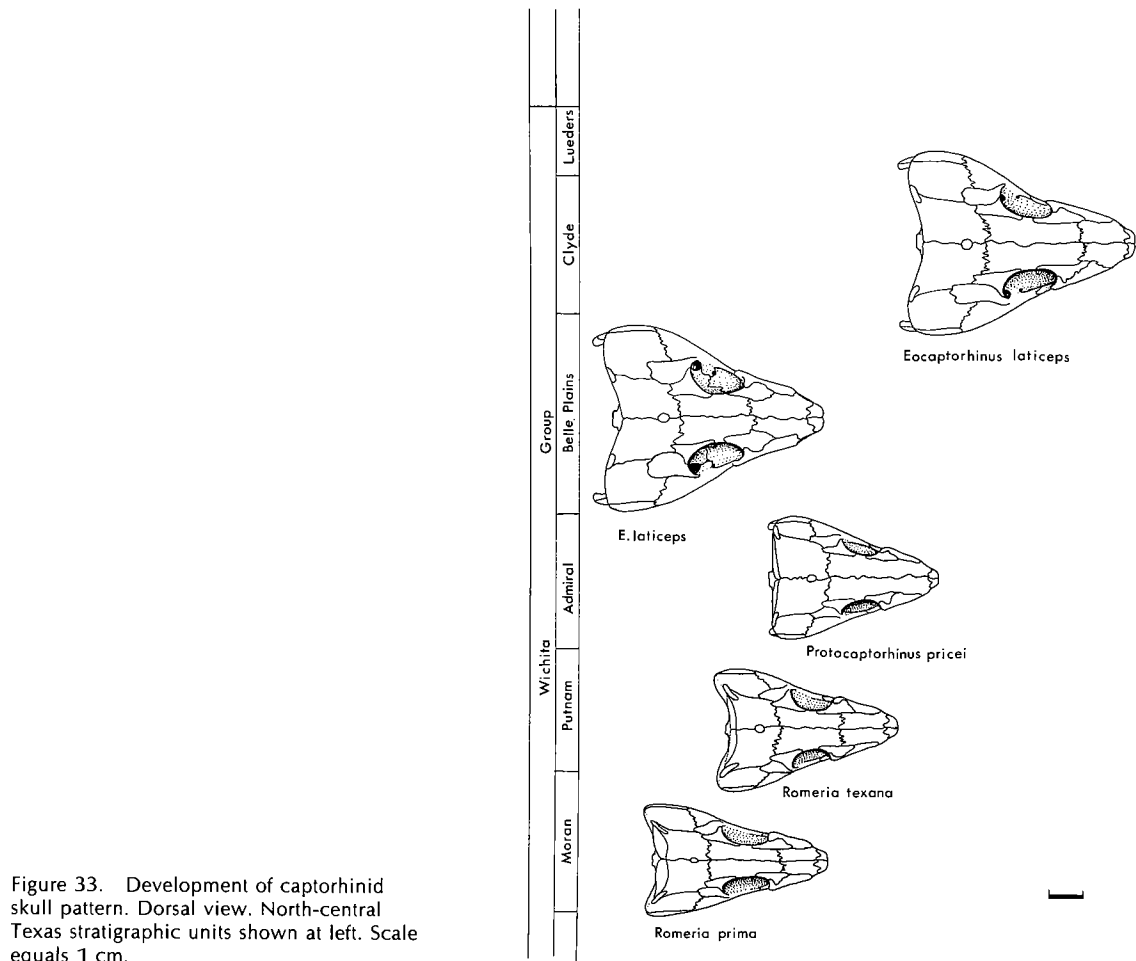


Figure 33. Development of captorhinid skull pattern. Dorsal view. North-central Texas stratigraphic units shown at left. Scale equals 1 cm.

jaw mechanisms and its bearing on the development of the specific tooth-wear patterns and tooth-row structures. The lack of any appreciable parasagittal motion has helped to maintain the primitive, sharp, conical tooth pattern in *Romeria* and *Protocaptorhinus*. Early specimens of *Eocaptorhinus laticeps* had developed moderate parasagittal motion that, combined with the increased cheek swelling, led to slight facetting (often casually referred to as "lateral compression") of the lingual surface of maxillary teeth and labial surfaces of dentary teeth posterior to the point of maxillary deflection. Thus, in specimens of *E. laticeps* (OUSM 15022, 15101, 15102), the teeth in the posterior half of the jaws features low, rounded tips. Anteriorly the teeth remain sharp. This pattern is typical of all the *E.*

laticeps specimens from the McCann quarry in northern Oklahoma. One other specimen of *E. laticeps* (MCZ 1483) from the "Trematops Locality," upper Belle Plains Formation in Baylor County, Texas, shows this pattern. MCZ 1483 is the oldest definitely identified specimen of *Eocaptorhinus laticeps* from the Texas section. In Texas, the best *E. laticeps* specimens come from the younger upper Clyde Formation. The Clyde *E. laticeps* (FMNH UC 642, 701), in consequence of its slightly greater cheek swelling and parasagittal jaw motion, has an increased degree of wear on the post-caniniform teeth. The more posterior teeth are heavily worn with straight chisel-shaped tips. Berman (1970) described a number of captorhinid dentaries that he originally believed belonged to gymnarthrid microsaur. In fact, these specimens

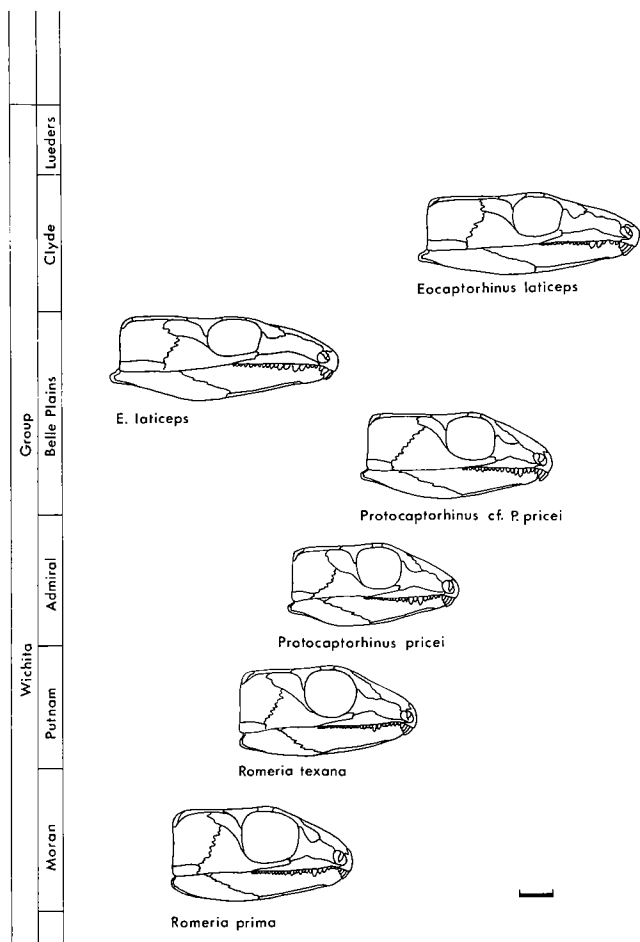


Figure 34. Development of captorhinid skull pattern. Lateral view. Scale equals 1 cm.

(UCLA VP 1973, 1974, 1975, 1976) are advanced forms of *Eocaptorhinus* sp. identical to the single-tooth-rowed form from Richards Spur. A significant amount of crushing or grinding action has also been introduced into the occlusal motion, thereby producing flat-topped, chisel-shaped teeth with a wear pattern virtually indistinguishable from that of *Captorhinus aguti*.

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APPENDIX

Specimens Examined

Clyde Formation

Eocaptorhinus laticeps

- FMNH UC 196: Mitchell Creek, near Wichita River, Baylor County, Texas. Very poor fragmented skull, pieces of parietal and snout.
- FMNH UC 228: Mitchell Creek, Baylor County, Texas. Mandibular fragments; mold of single tooth-row.
- FMNH UC 642: Holotype of *Pariotichus laticeps* Williston; Mitchell Creek, Baylor County, Texas. Complete skull and skeleton in claystone nodule.
- FMNH UC 701: Mitchell Creek, Baylor County, Texas. Uncrushed skull with some postcranial material in claystone nodule.
- FMNH UC 1043: Mitchell Creek, below Mabelle, Baylor County, Texas. Crushed partial skull; most bone spalled off; cast of internal surface of skull; single maxillary tooth-row.
- FMNH UC 1045: Mitchell Creek, Baylor County, Texas. Fragment of posterior portion of left mandible.
- FMNH UC 1698: Mitchell Creek, Baylor County, Texas. Complete juvenile skull; some dorsoventral crushing.
- MCZ 1740: Weiss locality, Red pasture line house, Wilbarger County, Texas. Complete skull in very hard clay matrix; bone replaced by silica(?); some crushing of back of skull.
- MCZ 2804: 1 mile south of Electra, HT&B RR. Survey A-137, about middle of north section line, Wichita County, Texas. Fragmentary skull, including both maxillae and both mandibles; single maxillary tooth-row; some vertical fragments.

Belle Plains Formation

Eocaptorhinus laticeps

- MCZ 1483: *Trematops* locality, west of Williams Ranch, J. Gibbs Survey A-5666, southeast of Fulda, Baylor County, Texas. Badly crushed and fragmented skull, including most of right side; single tooth-row; much of bone surface destroyed by acid etching.

Protocaptorhinus, cf. *P. pricei*

- FMNH UC 1119: Wichita River, near Vernon crossing, Baylor County, Texas. A complete occiput indistinguishable from type of *Protocaptorhinus pricei*.
- MCZ 1160: 1.5 miles northwest of Woodrum house, Archer County, Texas. A badly crushed, complete skull; dorsoventrally flattened; single maxillary tooth-row.

Admiral Formation

Protocaptorhinus pricei

- MCZ 1478: Rattlesnake Canyon, Archer County, Texas. Skull and associated elements of anterior postcranial skeleton.

Putnam Formation

Romeria texana

- MCZ 1480: Archer City Bonebed, Archer County, Texas. Skull lacking braincase, postparietals, and mandibles.
- UT 40001-3: Zott pasture, SW $\frac{1}{4}$ sec 55, block 3, Clark and Plumb Survey, 3 miles north of Windthorst, Archer County, Texas.

Moran Formation

Romeria prima

- MCZ 1963: Cottonwood Creek, Archer County, Texas. Skull with associated fragmentary postcranial skeleton.

Wellington Formation

Eocaptorhinus laticeps

- OUSM 15020A, 15020B (3-1-S4, 3-0-S5): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Also termed Eddy site and Nardin site. OUSM 15020 consists of two blocks originally given different museum numbers (3-1-S4 and 3-0-S5). 15020A (3-1-S4) was the paratype of Seltin's (1959) *Labidosaurus oklahomensis*. 15020B (3-0-S5) was not described.
- OUSM 15020A: Complete snout forward of center of orbits; right mandible has been removed to reveal single maxillary tooth-row; right mandible was completely destroyed during this procedure.
- OUSM 15020B: Partial skull rearward of center of orbits; first 21 presacral vertebrae; fragmentary shoulder girdle; right forelimb.
- OUSM 15021 (3-1-S8): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Partial snout; five premaxillary teeth; single-row maxillary dentition; complete right mandible with single-row dentition; left jugal; both vomers.
- OUSM 15022 (3-1-S7): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Holotype of *Labidosaurus oklahomensis* Seltin (1959). Partially crushed skull; left-rear portion with braincase missing.
- OUSM 15023 (3-4-S6): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Scattered skull fragments.
- OUSM 15024 (3-1-S6): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Braincase and excellent palate in partially crushed skull; good cultriform process; some sclerotic plates; well-preserved manus; considerable postcranial skeleton with tail, pes.

- OUSM 15025 (3-34-S3): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Scattered fragments of skull, limbs, vertebrae.
- OUSM 15027 (3-0-S3): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Assorted fragments.
- OUSM 15101 (3-0-S4): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Complete skeleton and skull; slight crushing of skull; vertebral column twisted through 180° ; has suffered some damage through poor preparation.
- OUSM 15102 (3-1-S3): McCann rock quarry, 2 miles northeast of Eddy, Kay County, Oklahoma. Left half of skull; crushed laterally; excellent preservation and disarticulation.

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