Reiszorhinus olsoni, a New Single-Tooth-Rowed Captorhinid Reptile from the Lower Permian of Texas

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REISZORHINUS OLSONI, A NEW SINGLE-TOOTH-ROWED CAPTORHINID REPTILE FROM THE LOWER PERMIAN OF TEXAS

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ABSTRACT—A new genus and species of captorhinid reptile from the Lower Permian Waggoner Ranch formation of north-central Texas, *Reiszorhinus olsoni*, is described on the basis of well-preserved cranial material. The holotypic specimen, consisting of a partial skull and mandible, was misidentified by S. W. Williston in 1917 as *Labidosaurus hamatus*. Autapomorphies of the new taxon include recurved teeth and the possession of an extremely large Meckelian foramen on the medial surface of the lower jaw. The new taxon retains the primitive condition of a single row of dentary and maxillary marginal teeth. It is distinguished from other single-tooth-rowed captorhinids, with the exception of *Labidosaurus hamatus*, by its large size, and it lacks the marked cheek expansion found in other large captorhinids. PAUP and Bayesian analyses suggest the new genus is the most basal of described captorhinid genera with the exceptions of *Romeria*, *Concordia*, and *Protocaptorhinus*. The description of a new, large, single-tooth-rowed form suggests that, in addition to multiple tooth rows, relatively larger size evolved more than once in the basal reptilian family Captorhinidae.

INTRODUCTION

Reptiles of the family Captorhinidae occupy an important position among basal amniotes, both phylogenetically and historically. The wide temporal and geographic distribution of the family (Berman et al., 1997), its generalized morphology (Dilkes and Reisz, 1986; Sumida, 1997), and alleged conservative nature (Dilkes and Reisz, 1986; Dodick and Modesto, 1995) have lead to captorhinids being regarded as model representatives of basal Reptilia.

Captorhinids are known primarily from Late Pennsylvanian through Middle Permian rocks of North America (Müller and Reisz, 2005). However, the family achieved a cosmopolitan distribution by the late Middle Permian, with representatives recorded from Russia, North America, Africa, India, and possibly even Tasmania (Romer, 1973) and Germany (Sues and Munk, 1996). Additionally, *Thuringothyris*, a small reptile from the Lower Permian of Germany (Boy and Martens, 1991; Müller et al., 2006), has been suggested as transitional between Captorhinidae and the basal (and almost certainly paraphyletic) group of reptiles referred to as "Protorothyrididae." Berman et al. (1997) have suggested that the distribution of captorhinids and their close relatives reflected the lack of significant geographic barriers to dispersal during the Late Paleozoic and the highly terrestrial nature of these reptiles.

As currently defined, Captorhinidae includes 15 genera, though work by Modesto (1996) suggests that incomplete materials may be indicative of a greater degree of taxonomic diversity within the family. Most of the features used to diagnose captorhinid genera have been dental characters and body proportions. Genera acknowledged to include more primitive members of the family are relatively small and usually possess single rows of marginal dentary and maxillary teeth. These include

the Late Pennsylvanian *Concordia* and numerous genera from the Early Permian, including *Romeria*, *Rhiodenticulatus*, *Protocaptorhinus*, and at least one unnamed taxon from Oklahoma (Modesto, 1996). Although *Labidosaurus* attained larger size, it retained single tooth rows. On the other hand, both *Captorhinus laticeps* and *C. magnus* possess single marginal tooth rows, whereas *C. aguti* possesses multiple tooth rows, and the species of *Captorhinus* retain a relatively smaller size than *Labidosaurus* or the form described here. All of the above-mentioned genera are known exclusively from Permo-Pennsylvanian rocks of North America except possibly *Protocaptorhinus* (but see Modesto, 1996). Zimbabwean specimens assigned to that genus, together with South African *Saurorictus* (Modesto and Smith, 2001), are from the Middle Permian of southern Africa (Reisz and Modesto, 2007). The only captorhinid known from the Indian subcontinent (Kutty, 1972) is a skull similar in size to *Protocaptorhinus*, but the specimen is being restudied (Müller et al., 2007) and its phylogenetic position remains unresolved at this time. Whereas the phylogenetic relationships of more primitive members of the family have been resolved with relatively little controversy (Berman and Reisz, 1986; Dodick and Modesto, 1995; Modesto et al., 2007), the relationships among the more derived members remain somewhat controversial. In a series of studies involving the more derived members of the family, Ricqlés (1984) and Ricqlés and Taquet (1982) advocated an essentially orthogenetic progression within the family. This hypothesis of relationships was based almost exclusively on dental features. A more complex scenario was proposed by Dodick and Modesto (1995) following an analysis that included 39 cranio-dental characters. Two multiple-tooth-rowed lineages were identified among the more derived captorhinids, one originating within the smaller captorhinids, and the other more closely related to the larger *Labidosaurus*.

More derived captorhinids are generally larger in size, typically possess multiple rows of maxillary and/or dentary teeth, and often include extensive batteries of palatal dentition as well.

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Labidosaurikos, *Kahneria*, and *Rothianiscus*, all from the Middle Permian of North America, possess three or more tooth rows in skulls that are larger in size than the entire body of most earlier, less derived taxa. The genus *Captorhinikos* is currently being restudied, but all specimens assigned to that genus have multiple tooth rows, regardless of size (Albright, 2002). Most of the captorhinids known from outside North America are examples of more derived lineages of the family. *Hecatogomphius*, from the Upper Permian of Russia (Vyushkov and Chudinov, 1957; Olson, 1962), and *Acrodonta*, from the Upper Permian of Morocco (Jalil and Dutuit, 1996), are both known only from cranial materials. *Moradisaurus* is known from cranial and postcranial materials from the Upper Permian of Niger (Ricqlés and Taquet, 1982; O'Keefe et al., 2005), and an unnamed moradisaurine from the Upper Permian of Morocco (Jalil and Dutuit, 1996; O'Keefe et al., 2005).

Despite the number of described captorhinid genera and species, most are characterized by a relatively small number of characters. Further, those characters continue to focus on skull and body proportions, as well as dental features. The limited pool of characters used to define captorhinid taxa points to the difficulty of defining taxa within any relatively generalized or primitive group of organisms. It would be most desirable to define each genus exclusively on the basis of synapomorphies and autapomorphies. However, the generalized nature of basal captorhinids requires that taxonomic definitions derive from a unique mosaic of derived and primitive features. The new taxon described here, based on FMNH UC183, is no exception. Williston (1917) utilized it in his reconstruction of the skull of *Labidosaurus*. Clark and Carroll (1973) acknowledged that it might be related to *Labidosaurus* but were not willing to assign it to that taxon with confidence, instead indicating that it probably represented a new taxon. Heaton (1979:fig. 6) appears to have used FMNH UC183 as the basis of his illustration of the teeth of *Labidosaurus*. Heaton and Reisz (1980), however, concurred with Clark and Carroll (1973) and suggested that it represented a new, large species of the genus *Protocaptorhinus*. The present study confirms that it does indeed represent a new taxon, and a phylogenetic analysis based on a data set derived in part from that of Dodick and Modesto (1995) and this study (Appendix 1) indicates that it is distinct at the generic level. This study includes the first report of CM 81785. It is less complete than FMNH UC183, but those elements that are preserved are virtually identical to those of FMNH UC183.

Institutional Abbreviations—CM, Carnegie Museum of Natural History, Pittsburgh; **FMNH**, Field Museum of Natural History, Chicago; **UCLA VP**, University of California Los Angeles, Vertebrate Paleontology collections.

Anatomical Abbreviations—a, angular; **ar**, articular; **c**, coronoid; **d**, dentary; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **pra**, prearticular; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **st**, supratemporal.

GEOLOGICAL CONTEXT

Both of the specimens described here were recovered from Lower Permian rocks in north-central Texas. Traditional methods of dividing the terrestrial Lower Permian deposits of this region were revised by Hentz (1988). The previous formational names, based primarily on the schemes of Plummer and Moore (1921) and Romer (1973) have nonetheless remained persistent in the literature. We have adopted the more recent nomenclature proposed by Hentz. Hook (1989) provided a useful key to formational equivalents between Hentz's (1988) work and earlier designations. Here the older terminology is retained paren-

thetically to aid in the identification of the specimens and facilitate comparison to the literature in which the specimens are referenced. FMNH UC183 was recovered by Paul C. Miller from the Mitchell Creek locality in Baylor County, Texas. Although recorded as from the Clyde Formation of the previous formational framework, Hook (1989) has pointed out that specimens recovered from the Mitchell Creek locality are now assignable to the Waggoner Ranch Formation (Leonardian). The late E. C. Olson collected CM 81785 (formerly UCLA VP 2597) from a locality near Mitchell Creek, but did not provide more detailed locality data. Its proximity to the locality yielding FMNH UC183 would suggest that it can also be considered to be from the Waggoner Ranch Formation.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768
CAPTORHINIDAE Case, 1911
REISZORHINUS OLSONI, gen. et sp. nov.
(Figs. 1–4)

Holotype—FMNH UC183, a nearly complete skull, lacking portions of palate and braincase and crushed slightly transversely.

Locality and Horizon—Mitchell Creek locality, Waggoner Ranch Formation (formerly Clyde Formation), Lower Permian, Baylor County, Texas.

Referred Specimen—CM 81785 a partial skull, including right lower jaw, caudal portion of right side of skull roof and cheek regions, and partial left lower jaw. From Mitchell Creek, Waggoner Ranch Formation, Lower Permian, Baylor County, Texas.

Diagnosis—Relatively large captorhinid reptile with single row of recurved, labiolingually compressed maxillary and dentary teeth, and extremely large meckelian foramen on the lingual surface of the lower jaw, and relatively large splenial (approximately two-thirds the length of the mandible). Further distinguished from *Romeria*, *Rhiodenticulatus*, *Protocaptorhinus*, and *Saurorictus* by significantly greater size, presence of a postparietal-supratemporal contact, and a horn-like process of the supratemporal. Further distinguished from *Saurorictus* by its more robust teeth, more extremely recurved teeth, and retention of supratemporal. Further distinguished from *Labidosaurus* by having a relatively narrower skull table and lack of 'heart-shaped outline' in dorsal aspect. Further distinguished from more derived captorhinds by its primitive retention of a single rows of maxillary and dentary teeth.

Etymology—The generic name is derived from *Reisz*, in honor of Robert R. Reisz and his extensive work on basal amniotes, and *rhinus* (Latinized Greek, meaning 'nose'), a common suffix for captorhinid taxa. The specific epithet honors Everett C. Olson, collector of one of the specimens described, and central figure in the development of Late Paleozoic vertebrate paleontology during the previous century.

DESCRIPTION

The type specimen (Figs. 1–3) demonstrates that *Reisz orhinus* is a moderately large-sized captorhinid with a single row of mandibular and maxillary teeth (hereafter referred to as 'single-rowed,' as opposed to those with multiple rows of maxillary and mandibular teeth, or 'multiple-rowed'). *Reisz orhinus* is larger than any other single-rowed captorhinid with the exception of *Labidosaurus*. It does not display the heart-shaped outline of the skull in dorsal view that typifies *Labidosaurus* or large, multi-rowed captorhinids. Although the holotype preserves most of the skull, it has been dorsolaterally crushed so that the skull table is visible in left lateral view. Most of the palate has been sandwiched between the left cheek and right lower jaw, and cannot be exposed without damaging the skull. Both lower jaws are visible in lateral view, and the crushing of the specimen allows inspection
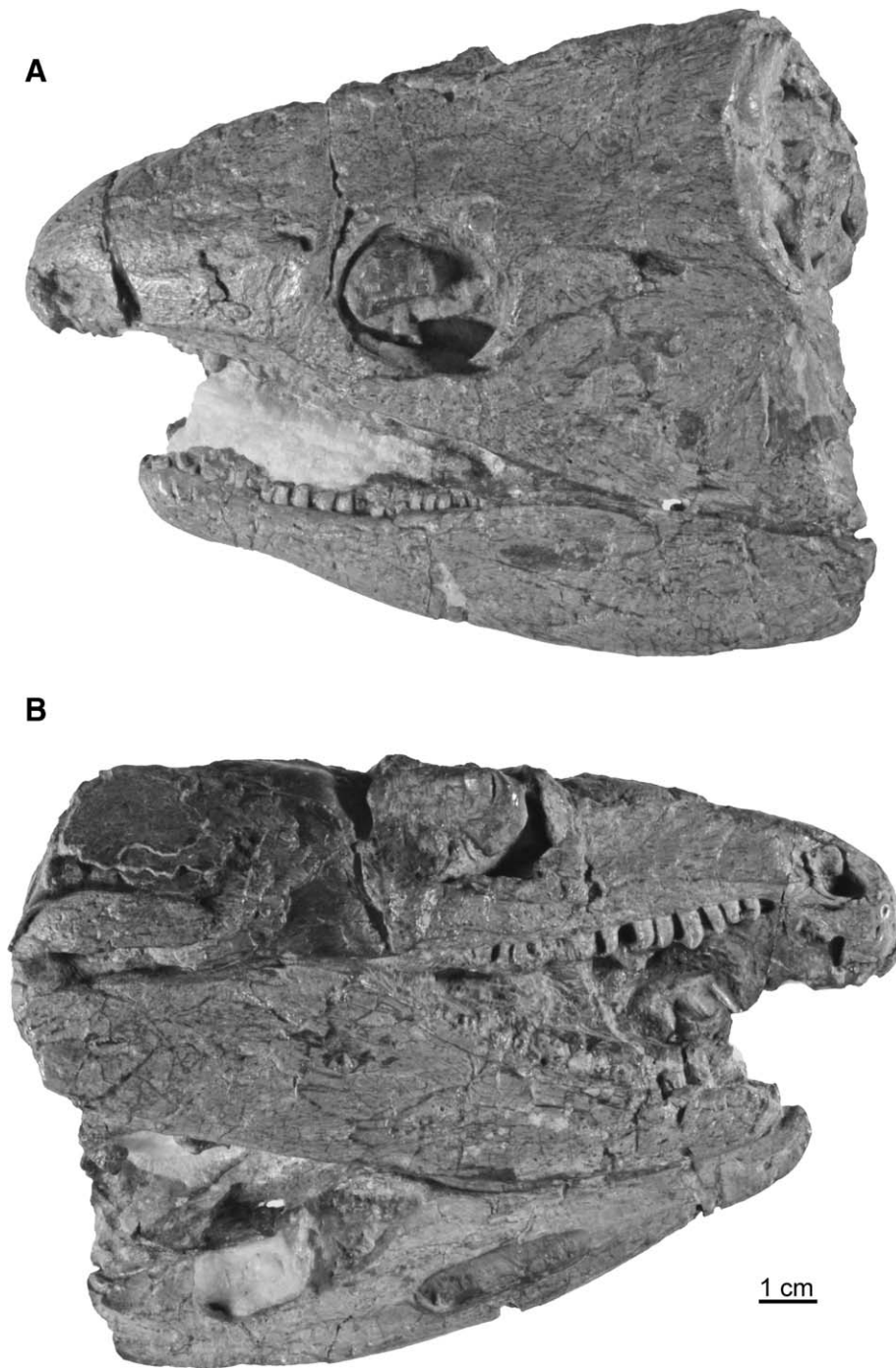
FIGURE 1. *Reiszorhinus olsoni*, gen. et sp. nov., FMNH UC183, holotype. Skull in **A**, left and **B**, right lateral views.

of their lateral surfaces as well as the medial surface of the left lower jaw. The single referred specimen, CM 81785, is a partial skull that preserves not only the right side of the skull in a manner virtually identical to that of FMNH UC183 (Figs. 1B, 2B, 4), but also includes the lower portion of the circumorbital series and most of the lower jaw. This specimen also provides information regarding the degree of dermal sculpturing present.

The skull is approximately triangular in dorsal outline, resembling more closely *Romeria* and *Rhiodenticulatus* (Clark and Carroll, 1973; Berman and Reisz, 1986) than *Captorhinus* or *Labidosaurus* (Heaton, 1979; Sumida, 1990). The overall length of the holotypic skull is approximately 120 mm. CM 81785 is vir-

tually identical in measure for those elements that are preserved. Little may be made of the dermal sculpturing from the type, but CM 81785 indicates that it was very well developed (Fig. 4).

It is clear that the premaxillae in the holotype are directed anteroventrally in a manner characteristic of most captorhinids (*Concordia* being a possible exception). The dorsal process is short, but ends in a three-pronged interdigitation with the nasal bone. Each premaxilla held five teeth, two of which are preserved in the left premaxilla. Judging from the empty alveoli, the two mesial-most teeth appear to be the largest, with the remaining three decreasing in size distally. This pattern is characteristic of all the single-tooth-rowed captorhinids with the exception
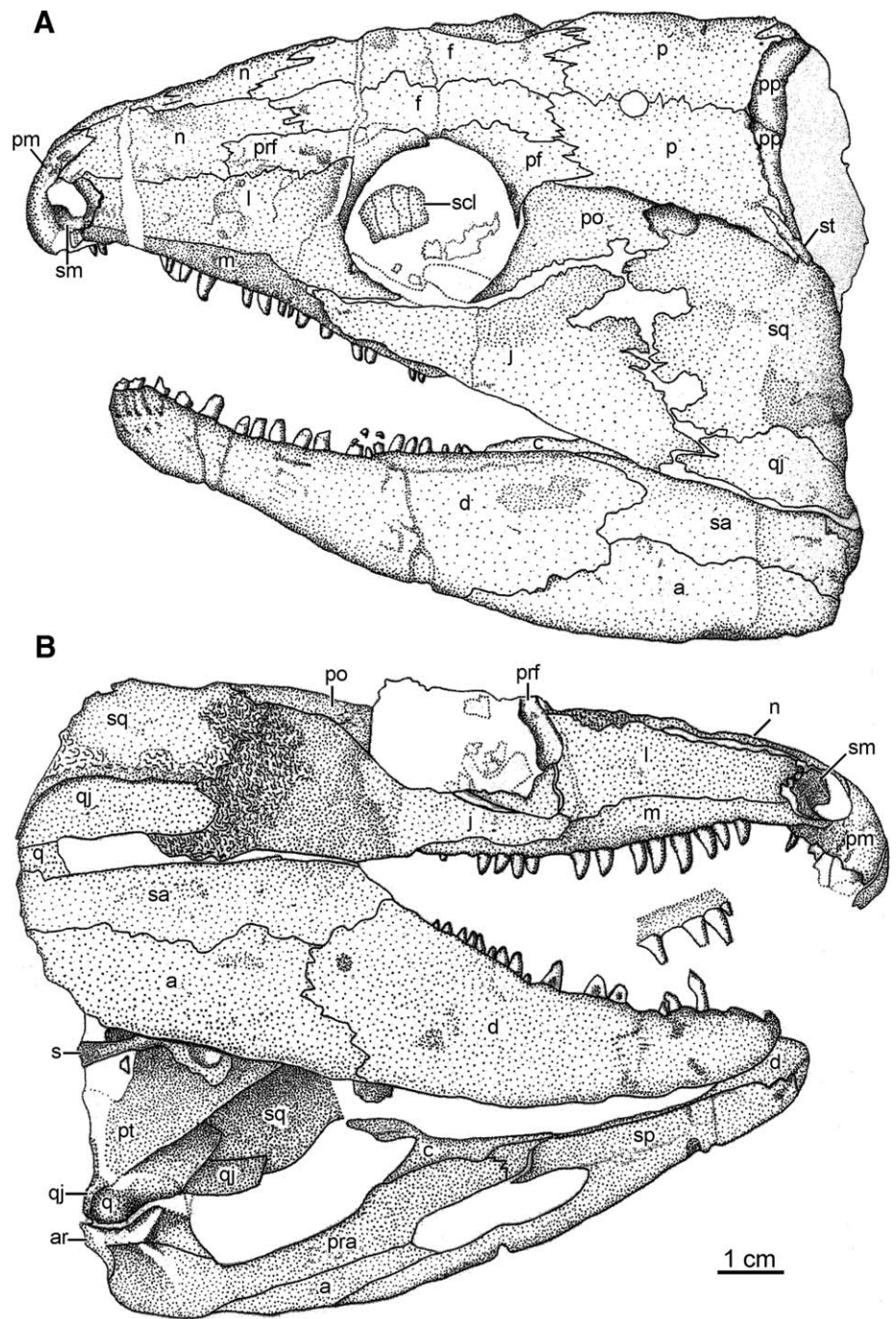
FIGURE 2. *Reiszorhinus olsoni*, gen. et sp. nov., FMNH UC183, holotype. Illustrations of skull in **A**, left and **B**, right lateral views.

of *Rhiodenticulatus*, in which the premaxillary teeth are approximately equal in size.

Although the maxillae of FMNH UC183 each carry a single row of 19 or 20 tooth positions, only 12 and 13 teeth are preserved in the right and left maxillae, respectively. The teeth are pointed and slightly recurved at the tip (Figs. 1, 2, 4), distinctly labiolingually compressed, and are very tightly spaced at their basal margins. Anterior to the level of the eighth maxillary tooth position, the maxillary-lacrimal suture is relatively straight and directed anterodorsally. Posterior to this position the maxilla decreases in height until the eleventh tooth position, where the bone then becomes a thin process overlain by the jugal. The fourth or

fifth tooth is the largest of the series, but the deepest portion of the maxilla does not correspond to its position. The right maxilla and overlying right lacrimal are fortuitously separated in CM 81785, affording a clear view of their complimentary articular surfaces. Their contact is not interdigitated, but overlaps enough to be characterized as a scarf joint. More posteriorly, the articulation with the jugal is shallowly slotted. The posteriormost tooth of the maxilla lies at the level of the midpoint of the orbit, a feature characteristic of most other derived captorhinid species.

The septomaxilla is a somewhat crescent-shaped bone that lies along the posterior and ventral edges of the narial opening. The septomaxilla owes its crescent shape to a flattened plate of bone,
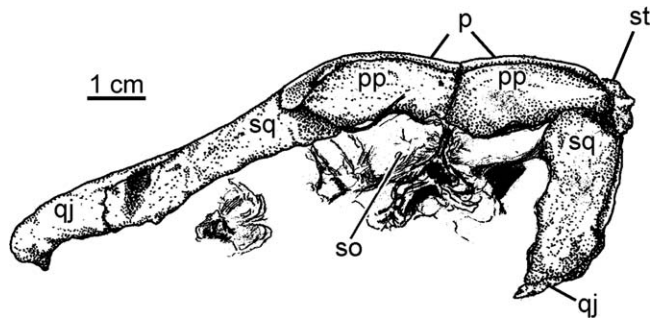
FIGURE 3. *Reiszorhinus olsoni*, gen. et sp. nov., FMNH UC183, holotype. Skull in occipital view.

just anterior to the lacrimal, that narrows into a thin lamina as it extends both ventrally and anteriorly along the maxillary border. Along the contact between the septomaxilla and the lacrimal are two foramina separated by a septomaxillary process. The dorsal foramen, positioned at the nasal-lacrimal contact, was interpreted by Romer and Price (1940) as having allowed the passage of branches of both the superior orbital artery and facial nerve to the nostril in the pelycosaurian-grade synapsid *Dimetrodon limbatus*. The ventral foramen, positioned at the lacrimal-maxilla contact, was suggested by Romer and Price (1940) as having transmitted either the distal end of the lacrimal duct or a separate air passage to the Jacobson's organ. The septomaxilla is rarely preserved in captorhinids, having been described only in *Captorhinus laticeps* (Heaton, 1979) and *Labidosaurus* (Modesto et al., 2007), the latter of whom disagreed with the former's characterization of this element as scroll-shaped. In *Reiszorhinus* the septomaxilla is a rectangular sheet of bone shaped as a conical

FIGURE 4. *Reiszorhinus olsoni*, gen. et sp. nov., CM 81785, paratype. **A**, photograph and **B**, outline drawing of partial skull in right lateral view.

funnel, distinctly different from the 'irregularly convoluted' element in *Labidosaurus* (Modesto et al., 2007:239). The distinction could be due to the size difference between *Reiszorhinus* and *Labidosaurus*; however, given the rarity with which the fragile septomaxilla is preserved in captorhinids, any broad comparisons of the element in this group remain speculative.

The lacrimal in *Reiszorhinus* is a subrectangular bone that extends from the antorbital process of the prefrontal and the anteroventral edge of the orbit to the posterior edge of the septomaxilla. The sutural contact separating the dorsal margin of the lacrimal from the nasal and the prefrontal becomes more serrated posteriorly. An acutely angular suborbital process of the lacrimal overlies the anterior end of the suborbital process of the jugal and creates part of the orbital margin. The pattern of dermal sculpturing on CM 81785 suggests that a well-developed center of ossification was located just rostral to the anteroventral margin of the orbit. The left lacrimal of FMNH UC183 reveals what is left of two foramina along its posterior edge that were most likely associated with the 'lacrimal canal' (Heaton, 1979:25). The presence of these foramina are confirmed on the orbital margin of the right lacrimal of CM 81785.

The left prefrontal is well preserved in FMNH UC183, but the right is somewhat damaged. A portion of the right prefrontal is also preserved in CM 81785. It is roughly divisible into two principal parts. A subrectangular plate extends from the nasal to the orbit, and it is overlain along its medial margin by the posterior extension of the nasal and the anterior half of the frontal. The anterior half of the plate fits tightly into a ventrolateral recess of the nasal. This creates a straight, continuous border formed by the ventrolateral margins of the nasal and the prefrontal, and underlain by the lacrimal. There is no such embayment in *Captorhinus laticeps* where the resulting rounded plate resides in a posterodorsal embayment of the lacrimal. An antorbital process of the prefrontal extends ventrally to form much of the anterior orbital rim. *Rhiodenticulatus* also possesses an extended ventral antorbital process (Berman and Reisz, 1986).

The main body of each nasal is a rectangular plate that is notched posterolaterally to receive the prefrontal. Whereas the medial articulation between the two nasals and the lateral suture with the lacrimals are relatively straight, the contacts with the premaxilla rostrally, the frontal caudally, and the prefrontal caudolaterally are highly interdigitated.

Both frontals are well preserved in FMNH UC183, and a small portion of what may be that bone's contribution to the right orbit is present in CM 81785. They are elongate, rectangular elements with highly interdigitated sutures along all margins. As in other captorhinids, a very small but distinct lateral portion of each frontal contributes to the dorsal margins of the orbital rims.

The parietals are also subrectangular in outline. In the holotype they have become disarticulated on both sides laterally, demonstrating clearly a smooth, straight suture with the postorbital and the squamosal ventrolaterally. Despite the slight postmortem distortion, it appears likely that the lateral margin of the parietals marks the approximate intersection between the skull table and the more nearly vertical cheek region. The parietals have interdigitating sutures with the frontals and the postfrontals, but overlap the postparietal, and underlie the anterior two-thirds of the small supratemporal. The occipital margin of the skull table is formed by the parietals entirely and is nearly straight, forming more of a single shallow embayment as opposed to the bilateral embayments exhibited by 'protorothyridids,' *Romeria* (Clark and Carroll, 1973), and *Protocaptorhinus* (Olson, 1984), or the deep, median embayment seen in *Labidosaurus* and *Captorhinus* (Heaton, 1979).

The narrowly rectangular, paired postparietals are vertically restricted to the occiput. Each is narrow, curved, and partially embedded into the concave posterior margin of the parietals by way of a short, straight suture. The postparietal surface is smooth
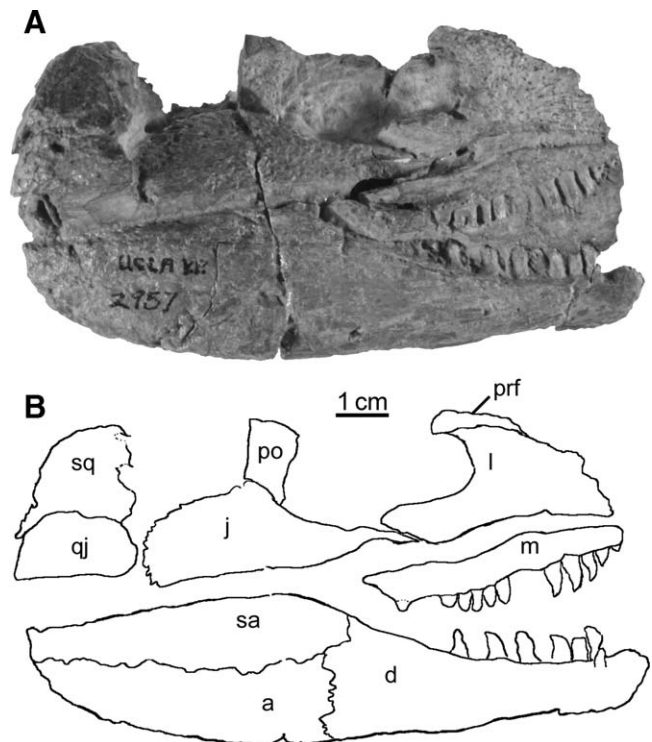
except for a groove that divides it into ventrolateral and dorsolateral processes. The slightly longer ventrolateral process contacts the posterior third of the medial margin of the supratemporal, before ending in a small indentation of the occipital flange of the squamosal. The greater medial portion of the dorsal edge of the postparietal underlies the posterior edge of the parietal, and is attached firmly to it. The ventral edge of the postparietal delineates the anterior edge of the supraoccipital, but it cannot be determined to what extent it was attached.

The supratemporal is an extremely small, slender element with a posterolaterally oblique orientation in the skull roof. Anteriorly it inserts tightly into a posterolateral notch of the parietal, whereas posteriorly it lies in a small indentation of the squamosal. Two-thirds of its ventromedial edge contacts the end of the ventrolateral process of the postparietal, whereas the ventrolateral edge contacts the squamosal. Despite the small size of the element, a distinct, horn-like process may be seen extending posterolaterally from its trailing corner (Fig. 3).

The postfrontal is subtriangular in outline. A thickening of its anterodorsal orbital rim is extended ventrally as a small process that continues to the posterior border of the orbit. The postorbital is a flat bone. Its ventral margin extends ventrally as an anteriorly directed process dorsal to the jugal. Its thickened free margin forms the anterodorsal margin of the orbit. Only the left postorbital of FMNH UC183 is well preserved, whereas a small portion of this bone is present on the left side of CM 81785. In the former specimen, the posterodorsal corner appears to be partially bound by a large foramen, but close examination indicates that the upper corner of the squamosal has actually collapsed here and inspection of the opposite side confirms that no foramen is present posterior to the postorbital. The anterodorsal corner of the postorbital is distinctly rounded due to the ventral projection of the postfrontal. Anteroventrally, the postorbital projects forward dorsal to the jugal in a gently sigmoid process. This results in a significant contribution to the posterior and posteroventral margins of the orbit. The contribution of the postorbital to the margin of the orbit is greater than that seen in *Romeria*, *Protocaptorhinus*, *Rhiodenticulatus*, and *Captorhinus*.

The left jugal in the holotype is complete and well exposed, whereas the right is partially preserved in both the holotype and CM 81785. Although only partially preserved in the latter, its surface demonstrates clearly a pattern of elongate grooves radiating from the posteroventral margin of the orbit. The sutures on the left side of the holotypic skull are widely separated, whereas on the right side only partial separation has occurred. In lateral view the anterior process of the jugal is acuminate and curves slightly upward as it wedges between the suborbital process of the lacrimal and the distal end of the maxilla, to end just anterior to the orbit. The jugal becomes very broad posteriorly. The suture with the maxilla is smooth and straight. The suture with the postorbital is very smooth, terminating at a level at the midpoint of the orbit. Posteriorly, the suture between the squamosal and the quadratojugal is continuous with that between the jugal and the quadratojugal. The suture between the jugal and the squamosal appears to be more deeply interdigitated than that between the jugal and the quadratojugal. In right lateral view the posterodorsal region of the jugal curves upward along the suture with the quadratojugal.

The posterior cheek region is dominated by the large subrectangular squamosal. An interdigitated suture slopes posteroventrally between the squamosal with the jugal. The jugal underlies some of the squamosal in this region. Most of the squamosal overlies the quadratojugal along a straight suture that slopes posteroventrally. Both the holotype and CM 81785 indicate that the occipital exposure of the squamosal was devoid of sculpturing, and in the latter specimen the occipital surface appears to be slightly depressed. Ventrally, it overlaps the quadratojugal significantly.

The quadratojugal forms the posteroventral corner of the vertically oriented cheek region. The left quadratojugal of the holotype and the right in CM 81785 are well preserved, but that on the right side of the holotype is damaged. The dorsal margin of the quadratojugal is somewhat rounded. It is slightly disarticulated from the squamosal in the holotype. However, in CM 81785 the quadratojugal butts up against the ventral margin of that element in a stout suture laterally.

Due to the transverse crushing of the holotype, very little of the palate is visible. The small portion of the quadrate flange of the pterygoid that is visible exhibits no significant differences from that of other captorhinids. A small portion of the lateral corner of the transverse flange is also visible, and although it appears to be edentulous, this is likely due to overpreparation. The only palatal element preserved well enough to warrant detailed description is the quadrate. What can be seen of its dorsal lamina articulates with the pterygoid, as in all captorhinids. The quadrate condyle is subdivided into two ventrally directed crests, and it appears to be slightly broader transversely and narrower anteroposteriorly than in *Captorhinus* and *Labidosaurikos* (Heaton, 1979; Dodick and Modesto, 1995). However, crushing prevents an accurate quantitative interpretation of its proportions and orientation. No palatal elements are clearly visible in CM 81785.

Due to crushing in both specimens, very few braincase elements can be confidently interpreted. FMNH UC 183 affords a partial view of the occipital surface of the braincase (Fig. 3) and the only occipital element that can be described is the supraoccipital. The width of the supraoccipital at the level of the dorsal margin of the foramen magnum is approximately 19 mm. More dorsally the width decreases to a minimum of 11.2 mm before increasing to a maximum width of approximately 25.8 mm at the ventral contact with the postparietals. A low, but discernable sagittal crest of the supraoccipital terminates at an unusual depression on the dorsal margin of the foramen magnum. The depression is subcircular in occipital view, has a diameter of 3.2 mm, and its rim is concave in dorsal view.

Exposure of the braincase of CM 81785 is limited to a ventral view. The only element of the braincase that can be confidently recognized is a portion of the parasphenoid. It exhibits a characteristic 'diamond-shaped' outline with paired anterior basipterygoid tubera. Between the two cristae ventrolaterales there is a distinct midventral, depressed groove. The base of the cultriform process is visible, but the greater part of the anterior portion has been lost.

Within the left orbit of the holotype, a short series of four rectangular dermal elements appear to be part of a sclerotic ring. Although sclerotic elements are not uncommon in fossil tetrapods, they have been reported only rarely in captorhinid reptiles. Fox and Bowman (1966) noted them in *Captorhinus*, and pointed out that Romer (1956) noted them in *Labidosaurus*. It is likely that the latter reference was actually to FMNH UC 183.

Both lower jaws are well preserved in the holotype, but only the left is exposed in medial as well as lateral view. CM 81785 preserves the greater portion of the right mandibular ramus, visible in lateral view, as well as the posterior half of the left ramus. In both specimens, the lower jaw is rounded anteriorly, but flattened considerably posteriorly. In transverse cross-section, the lower jaw is fairly deep in overall proportions. At its greatest depth, the height of the mandible is approximately 25% the length of the jaw. Dermal sculpturing on the holotype is faint, but it is clear and well developed in CM 81785 (Figs. 1, 3). The most striking feature of the lower jaw is an extremely large, expanded Meckelian foramen, which extends along approximately 25% of the lower jaw. A moderately large opening is found in *Labidosaurus* and *Captorhinus* (Ricqlés and Bolt, 1983), but they are both proportionally much smaller than that in *Reiszorhinus*.

The dentary forms the lateral two-thirds of the outer mandibular surface. Posteriorly it articulates with the angular and the

surangular. Five small labial foramina trace a path close to and parallel with the dorsal edge of the lateral surface of the dentary from the level of tooth positions 1–4. From each foramen a shallow groove extends to the dorsal edge of the dentary. These may have carried fine branches of the mandibular artery. The dentary forms a large symphysial pad mesially. The medial suture with the splenial is marked by what may be a remnant of the Meckelian sulcus, a small groove that extends to the tip of the mandible. Whereas there appears to have been space for 20 or 21 dentary teeth, 18 are present on the left dentary of the holotype and only 14 teeth on the right. The right dentary of CM 81785 is not complete enough to confidently estimate the number of tooth spaces, but the general spacing of teeth and empty sockets is consistent with the estimates for the holotype. As in the holotype, the teeth are moderately recurved, though this condition is significantly reduced in the most distal of them.

The splenial forms the anterior half of the medial surface of the mandible. It is a relatively long element, extending along approximately two-thirds the length of the mandible. Rostrally, extensive preparation makes it difficult to determine exactly how much of the symphysis was formed by the splenial, but it is clear that this bone made some contribution to the symphysis. Posteriorly, the splenial diverges dorsally and ventrally into two distinct processes that bound the enlarged Meckelian foramen (Figure 2B). The posterodorsal splenial process contacts the coronoid and the prearticular, whereas the posteroventral process contacts the angular. The splenial has no lateral exposure along the ventral surface of the mandible. This condition is similar to that in *Romeria* (SSS, pers. observ.) and *Rhiodenticulatus* (Berman and Reisz, 1986), but is in contrast to the condition in *Captorhinus* (Heaton, 1979; Ricqlés and Bolt, 1983) in which the splenial has a low lateral exposure.

Visible only in left lateral view of the holotype is a thin splint of the coronoid that overlaps the dorsal surface of the dentary (Fig. 2A). The splint-like process is only partially separated from the dorsal edge of the lateral surface of the dentary by a narrow anterior projection of the surangular in *Reiszorhinus*, whereas it is separated completely by the surangular in *Captorhinus* (Heaton, 1979). On the medial surface of the lower jaw (Fig. 2B) the coronoid displays three small but distinct regions: a short (less than 25% of its length), narrow anterior process that overlaps the dentary and the splenial, a central body of the coronoid that overlaps the anterodorsal surface of the prearticular, and a posterodorsally directed process that forms the anterodorsal edge of the adductor fossa.

From its exposure on the posteroventral corner of the medial surface of the mandible, the strap-like prearticular extends anteriorly from the articular region to contact the angular ventrally and the coronoid dorsally, and forms an interdigitating suture with the splenial anteriorly. It forms the ventral margin of the adductor fossa and most of the upper margin of the Meckelian foramen. Its ventral edge parallels the internal exposure of the angular and with that element completes the posterior margin of the foramen. This condition is similar to that in other captorhinids except for the significantly larger size of the foramen. The posteroventral end of the prearticular flares widely to provide a supporting buttress for the overlying articular.

The main body of the surangular is narrowly quadrangular in outline, articulating with the angular ventrally and the articular posteriorly. As in *Captorhinus* (Heaton, 1979), a delicate anterior projection of the surangular extends a short distance along the dorsal margin of the dentary. Together with the coronoid, it contributes to a low but distinct coronoid eminence.

In a manner similar to that of the surangular, the angular is nearly quadrangular in outline in lateral view, although its posterior region tapers slightly towards the end of the mandible. Anteriorly, its ventral margin is extended as a broad, bluntly rounded process that embraces the dentary from below. In doing so, the angular ultimately accounts for approximately 40% of the inferior margin of the lower jaw. Although surface sculpturing has been prepared away in the holotype, the angular and other laterally exposed elements of the mandible in CM 81785 demonstrate it clearly. Significantly, the sculpturing extends onto the medial surface of the angular in this specimen as well. Only a narrowly rectangular strip of the angular is visible in medial view of the mandible (Fig. 2B), where it contributes narrowly to the posteroventral margin of the enlarged Meckelian foramen.

The articular (Fig. 2B) consists of a stocky basal shaft that is surmounted by a large facet for reception of the quadrate condyle. Anteriorly the basal shaft forms the posterodorsal edge of the adductor fossa. The concave surface of the facet is delineated by two interconnected rims of bone, one sloping anterodorsally and the other posterodorsally. A third ridge extends anteroventrally and forms with the anterodorsal rim a well-defined depression. This depression was likely the area of insertion of the medial head of the pterygoid muscle. The suture with the underlying prearticular is complex. Rising from the posteroventral edge of the adductor foramen, it extends over the posterodorsal rim of the articulating condyle and cuts sharply in a ventral direction to meet the posterior edge of the mandible. As in *Romeria* and *Protocaptorhinus*, there is no distinct retroarticular process.

Given the unique nature of the teeth in *Reiszorhinus*, particular attention needs to be given to the structure of tooth cusps. Recent studies have focused increased attention on the details of the apical structure in captorhinid teeth. Whereas earlier studies have characterized the teeth as simply conical in shape, more recent studies (e.g., Modesto, 1996; Müller and Reisz, 2005, 2006) have noted two distinct apical morphologies: a bluntly conical tooth that is characteristic of most teeth in *Labidosaurus* (Modesto et al., 2007), or a sharp, chisel-shaped crown with the long axis of the edge arranged in a mesial-distal orientation (also known as 'ogival') as is characteristic of more distal teeth in *Captorhinus aguti* (Modesto, 1998) and *C. magnus* (Kissel et al., 2002). Significantly, *Reiszorhinus* posseses a unique apical morphology wherein the teeth are slightly elongate and recurved. As *Reiszorhinus* is the only captorhinid taxon known to possess this condition, its polarity as a character cannot be determined with any confidence. In an effort to avoid the addition of unnecessary new characters, it is coded as a second derived character state relative to the primitive conical condition in the phylogenetic analysis that accompanies the description here.

PHYLOGENETIC ANALYSIS AND DISCUSSION

Reiszorhinus is confidently assigned to the basal reptilian family Captorhinidae on the basis of its characteristically downturned premaxilla and absence of the tabular bone. It is a moderately large, single-tooth-rowed captorhinid that can be distinguished from all other members of the family by its unique possession of an extremely large Meckelian foramen on the medial surface of the lower jaw and its closely spaced, recurved teeth. The phylogenetic position of *Reiszorhinus* within the Captorhinidae was evaluated relative to 11 other basal reptilian taxa. Taxa included nine other taxa commonly assigned to Captorhinidae: *Concordia*, *Romeria*, *Protocaptorhinus*, *Rhiodenticulatus*, *Saurorictus*, *Captorhinus laticeps* and *C. aguti*, *Labidosaurus*, and *Labidosaurikos*. The captorhinid taxa used in this analysis do not represent the entirety of this family. Although two species of the genus *Captorhinus* are represented, the recently described *Captorhinus magnus* (Kissel *et al*., 2002) was not, because it is based on only fragmentary specimens. Similarly, the Oklahoma genus *Baeotherates* (May and Cifelli, 1998) is based only on jaw fragments. Certain specimens assigned to the genus *Captorhinikos* are currently being restudied by one of us (G.M.A.), and because that genus requires revision, it was not included at this time. *Kahneria* and *Rothianiscus* are currently being restudied, and inclusion

of characters derived from those taxa would be premature. Although *Hectagomphius*, *Acrodonta*, and *Moradisaurus* are generally considered amongst the more derived of captorhinid taxa, we were not able to examine specimens assigned to those genera, and thus they are not included in this analysis. In addition to the captorhinid taxa examined, two other closely related genera were included in the analysis. The Early Permian *Thuringothyris* from central Germany was described as intermediate between 'protorothyridids' and captorhinids by Boy and Martens (1991), whereas Müller et al. (2006) and Müller and Reisz (2006) suggested that it was more properly characterized as the sister genus to the traditionally defined Captorhinidae and that the Protorothyrididae is actually a paraphyletic grouping. Amongst the 'protorothyridid' reptiles, *Protorothyris* is fairly well known and was thus included as a taxon generally considered more basal than the other taxa included in this study.

Forty-eight characters (Appendices 1, 2) were scored for the 12 taxa, including the new taxon described here. Thirty-four of the characters were modified from the work of Dodick and Modesto (1995), with additional characters derived from this study, Berman and Reisz (1986), and Ricqlés (1984). Two methods for phylogeny construction were employed. Maximum parsimony was performed in PAUP*4.0b10 (Swofford, 2002) using a branch-and-bound search with the following character treatments. Forty-four of the 48 characters were parsimony informative, multistate taxa were considered as polymorphic, and undetermined characters states were treated as missing data. All characters were unordered with equal weight. A bootstrap analysis to estimate clade support was also performed, with the same character treatment, using a branch-and-bound search with 1000 replicates.

In order to provide an alternate phylogenetic analysis of the data, a Bayesian analysis of the data set was performed using Mr-Bayes 3.1XX (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003; see Müller and Reisz, 2006). The standard discrete morphology model was employed with the following parameters (priors). State frequencies were allowed to vary under a symmetric Dirichlet distribution. All topologies were equally probable, and branch lengths were unconstrained. One million generations were performed, and sampled every 100 generations. Clade support was determined from a consensus of the remaining 7500 sampled trees, after the first 2500 samples were conservatively discarded to ensure stabilization. Two trees were produced using PAUP* 4.0b10 (Swofford, 2002), one with branch lengths corresponding to number of changes and the second with the a posteriori clade support values for the ingroup taxa. The values from the two analyses are presented in a single tree (Fig. 5).

As expected, the majority of the results do not contradict the phylogenetic positions suggested for previously described taxa in the studies of Dodick and Modesto (1995), Müller and Reisz (2005, 2006), or Modesto et al. (2007). *Concordia* sorts as the most primitive member of Captorhinidae, whereas *Thuringothyris* and *Protorothyris* represent successive outgroups to the captorhinids. Also as expected, the two members of the genus *Captorhinus* considered here grouped together, *Labidosaurus* and *Labidosaurikos* grouped together, and these two groups formed a larger monophyletic group. The analysis here agrees with that of Modesto et al. (2007), which places *Rhiodenticulatus* between *Protocaptorhinus* and *Saurorictus*, whereas the analysis of Müller and Reisz (2005) places *Rhiodenticulatus* in a relatively more basal position between *Romeria* and *Protocaptorhinus*. This has some significance, because our analysis places *Reiszorhinus* in a relatively basal position within the Captorhinidae between *Romeria* and *Protocaptorhinus*, whereas *Rhiodenticulatus* is placed in a relatively more derived position than *Protocaptorhinus*. Müller and Reisz (2006) also obtained a relatively higher placement for *Rhiodenticulatus*, but only in their Bayesian runs and not in the parsimony analysis. Signif-
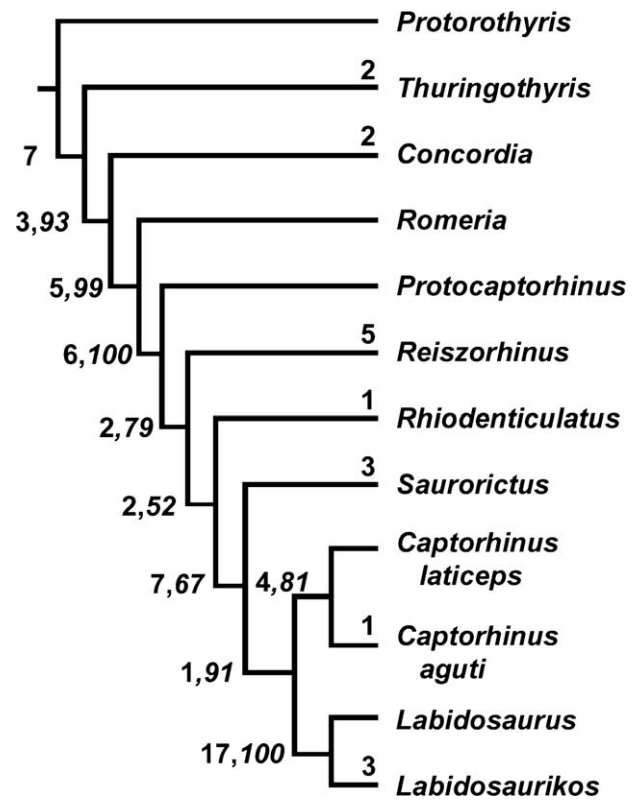

FIGURE 5. Phylogenetic tree indicating hypothesis of relationships of captorhinid reptiles. Non-italicized numbers indicate branch lengths corresponding to number of changes, and italicized numbers indicate bootstrap support values for the ingroup taxa.

icantly, *Reiszorhinus* did not sort to a position close to either *Labidosaurus* or *Protocaptorhinus*, taxa to which FMNH UC183 had been speculatively assigned in earlier reviews (Clark and Carroll, 1973; Heaton, 1979; Heaton and Reisz, 1980). This topology was stable and highly resistant to change. Subsequent to the initial analysis, a variation of analysis search parameters was applied, including branch and bound as well as exhaustive maximum parsimony. Additionally, the reliability of internal branching was tested with 100 bootstrap replications (Felsenstein, 1985) with and without re-weighting of characters. In all cases, the same basic tree was generated. These results conflict with those of some studies, including Ricqlés (1984), Ricqlés and Taquet (1982), and Gaffney and McKenna (1979), but are consonant with the more recent studies.

The designation of a new captorhinid reptile of the size of *Reiszorhinus* has certain implications for the interpretation of basal reptiles. The family Captorhinidae has frequently been characterized as morphologically conservative (Seltin, 1959; Gaffney and McKenna, 1979; Olson, 1984; Ricqlés and Taquet, 1982; Ricqlés, 1984). The low number of defining characteristics for genera and species in the family could be a reflection of that conservatism. However, the types of characters that diagnose each taxon are of note. In the case of *Reiszorhinus*, the autapomorphic features of the jaw and teeth diagnose it firmly. However, given its basal position in the family, its moderately large size may be significant, as this must have developed in parallel with that in the ancestor of *Labidosaurus* and *Labidosaurikos*, and other more derived taxa. Large size in captorhinids must have developed at least twice, and possibly more than that; however, confirmation of such awaits description of other new taxa currently under study. Clearly, some

degree of homoplasy is demonstrated by the captorhinid taxa assessed here, and a strict characterization of the family as morphologically conservative may be an oversimplification.

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APPENDIX 1. Description of characters used in phylogenetic analysis of captorhinid reptiles. '0' indicates primitive character state. '1' and '2' indicate derived characters states, but with no ordering implied. Characters from Dodick and Modesto (1995) unless indicated otherwise.

Skull Shape

(1) Skull length: small, less than 5 cm anteroposteriorly in mature specimens (0); large, greater than 5 cm anteroposteriorly in mature specimens (1). This study.

(2) Snout width: broad, equal to or greater than 35% of skull length (0); narrow, equal to or less than 25% of skull length (1).

Dermal Skull Roof

(3) Premaxilla; ventral margin straight (0); ventral margin flexed and aligned anteroventrally in lateral view (1). From Berman and Reisz (1986).

(4) Premaxilla: alary process on posterodorsal process absent (0); present (1). From Modesto et al. (2007).

(5) Maxilla: relatively straight (0); posterior end flexed laterally (1).

(6) Maxilla: posteriormost tooth positioned at level of posterior margin of orbit (0); positioned at level at level of orbital midpoint (1).

(7) Lacrimal: suture with jugal small (0); suture with jugal well developed (1).

(8) Prefrontal: anterior process short and broad, approximately equal to posterodorsal process in anteroposterior length (0); long and narrow, approximately twice the anteroposterior length of the posterodorsal process (1).

(9) Frontal: anterior process short, less than 55% of the total frontal sagittal length (0); long anterior process, approximately 60% of the total frontal sagittal length (1).

(10) Jugal: alary process (= 'median process' of Berman and Reisz, 1986) is absent (0); alary process is present, positioned no higher than the midpoint of the suborbital process of the jugal and is distinct from the orbital margin (1); alary process is present and positioned dorsally on the medial surface of the jugal flush with the orbital margin (2).

(11) Jugal: subtemporal process dorsoventrally low (≤25% of skull height through orbital midpoint) (0); subtemporal process dorsoventrally deep (≥40% of skull height through orbital midpoint) (1). From Modesto et al. (2007).

(12) Quadratojugal: anteroposteriorly elongate, subrectangular in shape (0); relatively shorter, almost square in shape (1). Reworded from Dodick and Modesto (1995).

(13) Quadratojugal: acuminate/convex upward (0); square tipped anteriorly (1).

(14) Postorbital cheek: Mostly straight/little lateral convexity/sculptured (0); convex/expanded laterally (1).

(15) Supratemporal: separation from the postparietal (0); solid fusion with the postparietal (1).

(16) Parietal foramen: positioned at midpoint of interparietal suture (0); positioned anterior to midpoint of interparietal suture (1).

(17) Postparietal: contacts mate fully along dorsal-ventral thickness (0); contacts mate dorsally only, postparietals separated slightly on ventral side by dorsal aspect of supraoccipital (1). Reworded from Dodick and Modesto (1995).

(18) Postparietal: flat in parasagittal section (0); concave in parasagittal section (1). This study.

(19) Postparietal: majority of postparietal on occipital surface and unsculptured (0); majority of postparietal on dorsal skull surface and sculptured (1). This study.

(20) Supratemporal: no contact with postparietal (0); contact with postparietal (1); absent (2). This study.

(21) Occipital margin of skull table: embayed bilaterally (0); straight (1); single medial embayment (2).

(22) Tabular: present, resulting in transversely short postparietal (0); absent, resulting in transversely elongate postparietals (1). Reworded from Dodick and Modesto (1995).

(23) Supratemporal horn: absent (0); present (1). This study.

Palate

(24) Ectopterygoid: present (0); absent (1).

(25) Vomer: denticulate (0); edentulous (1). From Modesto et al. (2007).

(26) Vomer/pterygoid contact: extensive (≥50% median border of vomer) (0); short (≤33% median border of vomer) (1). From Modesto et al. (2007).

(27) Pterygoid: transverse flange broad-based and distinctly angular in ventral view (0); narrow and tongue-like in ventral view (1).

(28) Parasphenoid: deep ventral groove absent between cristae ventrolateralis (0); deep ventral groove between cristae ventrolateralis (1).

Braincase and Occiput

(29) Cultriform process: extends anteriorly (0); extends anterodorsally at an angle of approximately 15° to basal (horizontal) plane (1); extends anterodorsally at an angle greater than 45° to basal plane (2).

(30) Supraoccipital: in lateral view slopes anterodorsally (0); vertical (1); angled posterodorsally (2).

(31) Supraoccipital, lateral ascending process: accounts for one-half or less of height of supraoccipital (0); accounts for two-thirds or more of height of supraoccipital (1).

(32) Occipital condyle: at level of quadrate condyles in ventral view (0); immediately anterior to quadrate condyles in ventral view (1).

(33) Paroccipital process: short (less than one-half the length of the stapedial columella) (0); long and 'rod-like' (more than one-half the length of the stapedial columella) (1).

Lower Jaw

(34) Mandibular ramus shape: ventral view, relatively straight (0); ventral view, sigmoidal shape (1).

(35) Mandibular ramus size: ≤8% of total jaw length (0); ≥14% of total jaw length (1).

(36) Posterior mandibular ramus: rectilinear (broadly expanded) (0); acuminate (pointed) (1).

(37) Lateral shelf: absent below coronoid process (0); present below coronoid process (1).

(38) Coronoid anterior process: short (0); long (1). Reworded from Dodick and Modesto (1995).

(39) Meckelian foramen (= posterior foramen intermandibularis caudalis): small foramen that is less than 9% of lower jaw (0); large, anteroposterior length that is greater to or equal to 14% of lower jaw (1).

(40) Coronoid process, posterodorsal process: slender and does not form wall of adductor fossa (0); deep and forms dorsal most third of lateral wall of adductor fossa (1).

(41) Retroarticular process: absent (0); present and slender (1); present and broader transversely than long (and short) (2).

Dentition

(42) Premaxillary dentition: first tooth relatively small compared with maxillary caniniform (0); first tooth largest marginal tooth present or subequal to maxillary caniniform in length (1). Reworded from Modesto et al. (2007).

(43) Maxillary dentition: tooth stations number 30 teeth or more (0); 25 or less (1). From Berman and Reisz (1986).

(44) Maxillary caniniform teeth: present (0); absent (1).

(45) Number tooth rows: single (0); multiple (1). Modified from Ricqlès (1984).

(46) Marginal dentition: cheek teeth conical (0); cheek teeth chisel-shaped (1); recurved (2). Modified from Dodick and Modesto (1995); this study.

(47) Dentary: teeth isodont (0); caniniform region present anteriorly (1); caniniform tooth present mesially with caniniform region absent (2). Reworded from Dodick and Modesto (1995).

(48) Dentary: first tooth oriented mainly vertically (0); first tooth leans strongly rostrally (1). Reworded from Dodick and Modesto (1995).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis of relationships of captorhinid reptiles. Characters listed in Appendix 1.

	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	44444444 12345678
Protorothyris	0000000000	0000000000	0000000000	?000000000	00000000
Thuringothyris	0000000000	0110010000	0000100?00	0000000000	00000000
Concordia	0000110100	0?00010000	0101??0000	0000000???	01100000
Romeria	001110000?	1000100000	010?100000	?0?0000???	01100010
Protocaptorhinus	001110?001	0100011100	110???0000	0010000???	11100010
Reiszorhinus	101110100?	0000011101	1111??0??0	00?010?11?	01100210
Rhiodenticulatus	0011101001	001101110?	11?1?1000?	00?000001??	?0100010
Saurorictus	00?111100?	0010001 1?2	?10??????0	???0??????	?1100010
Captorhinus aguti	0011111002	0011011111	2101111110	0010010100	21101111
C. laticeps	001111?002	0011011111	2101111110	0010010100	21100111
Labidosaurus	1111111111	1011111111	2111111121	1111111111	11110120
Labidosaurikos	1111111111	1011111211	2111111122	1111111011	11111120