THE CRANIAL ANATOMY OF THE CAPTORHINID REPTILE *LABIDOSAURIKOS MEACHAMI* FROM THE LOWER PERMIAN OF OKLAHOMA

by J. T. DODICK *and* S. P. MODESTO

ABSTRACT. Study of *Labidosaurikos meachami*, from the Lower Permian Hennessey Formation (Sumner Group) of north-central Oklahoma, reveals the presence of over thirty new cranial characters not present in single-tooth-rowed captorhinids and *Captorhinus aguti*. However, it is uncertain if these new characters represent autapomorphies of *L. meachami* because the skulls of all other large, multiple-rowed captorhinids are poorly known; many of these characters may instead diagnose subclades of multiple-tooth-rowed taxa within Captorhinidae. A suite of skeletal features, including the presence of tooth plates, prominent tooth wear, and the morphology of the skull roof, suggests strongly that *L. meachami* was herbivorous. Propaliny was probably a significant component of the feeding mechanism.

Phylogenetic analysis of the interrelationships of the well known North American captorhinids indicates that *Labidosaurikos meachami* is more closely related to the large, single-rowed *Labidosaurus hamatus* than it is to *Captorhinus aguti*. The sister-group relationship between *Labidosaurikos meachami* and *Labidosaurus hamatus* is supported by fifteen synapomorphies, and is the most robust clade within Captorhinidae. This relationship supports the hypothesis that multiple rows of teeth evolved independently at least twice among captorhinids. *Eocaptorhinus laticeps*, recently assigned to the genus *Captorhinus* as '*Captorhinus* sp.', is formally recognized as *Captorhinus laticeps* (new combination). The phylogenetic analysis indicates that *C. laticeps* and *C. aguti* form a clade, identified here as *Captorhinus*, that is the sister group of the *L. meachami–L. hamatus* clade.

THE Permian red-beds of North America are highly fossiliferous and document a diverse terrestrial biota. Members of the reptile family Captorhinidae are common in these deposits, and because of their distinctively hooked snouts, heavily sculptured skull bones, and 'swollen' neural arches, they are among the most distinctive of red-bed fossil taxa. These reptiles occupy a prominent role in discussions of early amniote phylogeny. Although they were once considered the closest fossil relatives of turtles (Clark and Carroll 1973; Gauthier *et al.* 1988; Gaffney 1990), recent work indicates that captorhinids were the first reptiles to have diverged from a lineage that led to the most taxonomically and ecologically diverse reptile group, the diapsids (Laurin and Reisz 1995).

Captorhinid anatomy and interrelationships are known almost exclusively from studies of the Lower Permian genera *Romeria*, *Protocaptorhinus*, *Rhiodenticulatus*, *Captorhinus* and *Labidosaurus*. All these taxa except the last are characterized by small size (skull length under 80 mm), and, except for *Captorhinus aguti*, possess a single row of teeth per jaw (described here as 'single-rowed'). A faunivorous diet has been attributed to these forms (Clark and Carroll 1973; Heaton 1979). Less well known members of the family from younger Permian deposits include the genera *Labidosaurikos*, *Rothianiscus*, *Captorhinikos*, *Gecatogomphius*, *Kahneria*, and *Moradisaurus*. All taxa except *Captorhinikos parvus* are large (skull length exceeding 100 mm) and feature 5–11 multiple rows of teeth on medially expanded maxillae and dentaries (henceforth termed 'multiple-rowed'). The dental batteries and the prominent tooth wear suggests strongly that these forms were herbivorous.

One of the best preserved specimens of a large, multiple-rowed captorhinid is the holotypic skull and mandible of *Labidosaurikos meachami*. This specimen, from the Lower Permian Hennessey Formation of Oklahoma, was described briefly by Stovall (1950). He was impressed by the close

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resemblance of this captorhinid to *Labidosaurus hamatus*, a large, single-rowed captorhinid from slightly older deposits in north-central Texas.

Several species of large, multiple-rowed captorhinids have been described since Stovall's (1950) work. Despite the apparent close resemblance between *Labidosaurikos* and *Labidosaurus*, recent cladistic studies (Gaffney and McKenna 1979; Ricqlès and Taquet 1982; Ricqlès 1984), have allied the large, multiple-rowed taxa with *Captorhinus aguti*. This postulated sister-group relationship was based solely on the basis of dental characters and suggests that multiple tooth-rows evolved once within Captorhinidae. However, it is unclear at present what significance a monophyletic origin for multiple tooth rows would hold, since the tooth rows in *Captorhinus aguti* are positioned obliquely with respect to the long axis of the jaw, whereas the teeth are aligned with the long axis of the jaw in the large, multiple-rowed taxa (Bolt and DeMar 1975; Ricqlès and Bolt 1983). Furthermore, the recent synonymy of *Eocaptorhinus* under *Captorhinus* (Gaffney 1990) suggests an independent origin for multiple tooth rows in the latter genus, since the former was erected to encompass single-rowed forms otherwise indistinguishable from *C. aguti* (Heaton 1979).

The re-examination of *Labidosaurikos meachami* provided here has three objectives. The first is to provide a thorough description of the cranial anatomy of a large, multiple-rowed captorhinid. All previous descriptions of the cranial anatomy of large captorhinids lack the attention to detail given to those of small captorhinids, and therefore are of limited use in phylogeny and life reconstruction. The second objective is to evaluate the interrelationships of the better known captorhinids using the new cranial information. The resultant phylogeny should help elucidate the origin of multiple tooth-rows in Captorhinidae. Lastly, a brief treatment of the hypothesis of herbivory, attributed to *Labidosaurikos* and other large multiple-rowed captorhinids by Olson (1955, 1971), is presented.

MATERIALS

The holotype, OMNH 04331 (formerly MU03-1-S2), is the only known specimen of *Labidosaurikos meachami*. The richly haematitic sediments in which the specimen was deposited are extremely hard and approach the consistency of ironstone. Portions of the skull were cleaned originally by Stovall (1950). Stovall (1950) also removed the lower jaw from the skull, resulting in significant damage to the articular. The braincase was separated from the rest of the skull sometime prior to our study, resulting in loss of bone from the postparietals and the pterygoids. The untouched areas of the specimen were prepared with pneumatic jackhammer, grinder, and pin vice.

The following are abbreviations of the names of the institutions from which specimens were borrowed or examined: FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard University; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; UCLA VP, Vertebrate Paleontology Collections, University of California, Los Angeles.

SYSTEMATIC PALAEONTOLOGY

REPTILIA Laurenti, 1768

EUREPTILIA Olson, 1947

Family CAPTORHINIDAE Case, 1911

Genus LABIDOSAURIKOS Stovall, 1950

Type species. Labidosaurikos meachami Stovall, 1950.

Revised diagnosis. The following description reveals numerous apomorphies that are present in *Labidosaurikos* but are absent in all single-rowed captorhinids and *Captorhinus aguti*. Since these characters cannot be determined faithfully in other large multiple-rowed taxa, they represent ambiguous autapomorphies for *Labidosaurikos meachami*: premaxillary posterodorsal processes short; maxilla dorso-ventrally low in lateral view; septomaxillary facial process present; jugal anterior process deep and transversely thick; jugal medial process bisected ventrally by the maxilla;

postfrontal broad posteriorly; postorbital greatly underlies postfrontal posterior process; squamosal occipital flange lateral portion directed anteroventrally and medial portion expanded slightly posteriorly; parietals domed; supratemporal with distinct dorsal and occipital portions; supratemporal-postparietal contact well developed; squamosal posterior margin notched ventrolaterally; quadratojugal dorso-ventrally tall; quadrate foramen absent; palatine anteromedial process overlies vomer posteriorly; denticles absent from anterior process of pterygoid; basicranial channel present on quadrate flange of pterygoid; epipterygoid with lateral pocket; epipterygoid dorsal process greatly thickened; parasphenoid plate expanded transversely; retractor pit shallow; supraoccipital tall and leans posterodorsally; supraoccipital lateral process feebly developed ventrally; supraoccipital-braincase ossification greatly reduced; paroccipital process compressed dorso-ventrally; paroccipital process sutured to stapedial columella; basioccipital transversely wide; stapedial footplate overlapped by parasphenoid; stapedial foramen relatively small; posttemporal fenestrae large; splenial forms most of jaw symphysis; anterior process of coronoid process short; posteroventral process of coronoid absent.

Labidosaurikos meachami Stovall, 1950

Text-figures 1–14

1950 *Labidosaurikos meachami*; Stovall, p. 50, pl. 1.
1959 *Labidosaurikos meachami*; Seltin, p. 487, fig. 200.
1984 *Labidosaurikos meachami*; Ricqlès, p. 13, fig. 3*a*.

Holotype. OMNH 04331, a skull with palate, braincase, and right mandible.

Diagnosis. Distinguished from *Labidosaurikos barkeri* Olson, 1954 by the possession of an additional tooth row in both the maxilla and dentary.

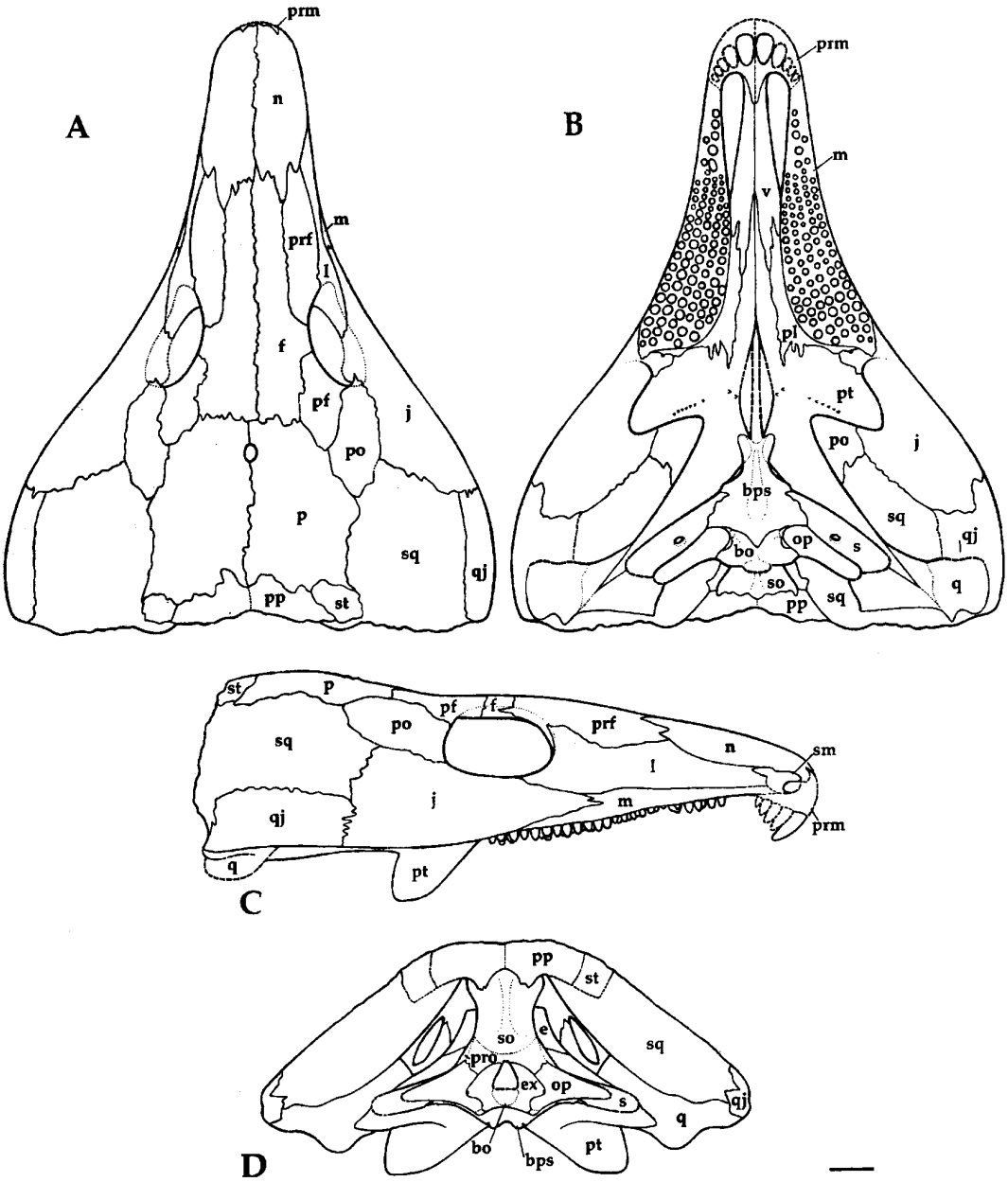
Horizon and locality. Collected by J. W. Stovall in 1939 from shales of the Hennessey Formation (Sumner Group), 2·7 km north-east of Crescent, Logan Country, Oklahoma; Leonardian, Lower Permian.

DESCRIPTION

OMNH 04331 represents the best preserved cranial material from a large, multiple-rowed captorhinid. Although it is free of distortion, it is missing a large segment of bone from its left half. The high degree of ossification, suggested by the strongly developed external sculpturing and the tightly interdigitating sutures, indicates that the holotype probably came from an adult individual.

The skull (Text-fig. 1) has an estimated total length of about 280 mm. Among captorhinids, only the skull of *Moradisaurus grandis*, with a skull length of 410 mm, is larger (Ricqlès and Taquet 1982). Relative to skull length, the slender snout of *Labidosaurikos* is roughly 25 per cent. longer than those of other captorhinids. Although only one large premaxillary tooth is preserved, the premaxilla of *Labidosaurikos meachami* is reconstructed here with five premaxillary teeth because those of all other captorhinids have four of five teeth that decrease in size posteriorly (with the exception of *Rhiodenticulatus heatoni*, in which the premaxillary teeth are isodont). A relatively long antorbital region has been restored also for *Rothianiscus multidonta* (Olson 1962), but this needs to be confirmed by restudy of the type and referred material. Posteriorly, the skull of *Labidosaurikos* exhibits the broadly flared posterior cheeks characteristic of *Labidosaurus*, *Captorhinus*, and all other multiple-rowed taxa.

In lateral view, the skull (Text-fig. 1C) exhibits the low, wedge-shaped profile of most captorhinids. The maximum height of the skull roof, measured from the top of the postparietals to the base of the quadrate, is approximately 35 per cent. of the length of the skull. In contrast, skulls of single-rowed forms are flat and relatively low; skull height in *Labidosaurus* and *Captorhinus* is roughly 25 per cent. of skull length. The increased height of the skull roof of *Labidosaurikos* contributes to its arched outline in posterior view and may have provided an enlarged internal space for jaw musculature. A high, domed skull roof has been interpreted for other captorhinids. The reconstruction of *Captorhinus aguti* by Fox and Bowman (1966) resembles slightly that of *Labidosaurikos* in posterior view (Text-fig. 1D). However, the skull roof of *Captorhinus* is low and broad



TEXT-FIG. 1. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; reconstruction of skull. A, dorsal view; B, ventral view; C, right lateral view; D, occipital view. Scale bar represents 20 mm.

as in more basal captorhinids (Heaton 1979). Similarly, Clark and Carroll (1973) reconstructed *Romeria prima* (taxonomic emendation of the improperly formed *Romeria primus*, after Heaton 1979) with a tall skull roof, but personal examination of the holotype of *Romeria prima*, MCZ 1963, shows that the skull roof has been elevated by transverse crushing and bending along the squamosal-parietal contact. Olson (1962) restored

Rothianiscus multidonta with a lateral profile similar to that given here for *Labidosaurikos*, but the skull table of the former captorhinid was probably not domed (S. Sumida, pers. comm.). Finally, as in other members of the family, the posterior edge of the skull of *Labidosaurikos* is nearly vertical in lateral view, but the braincase is recessed within the skull roof, as seen clearly in ventral view (Text-fig. 1B).

Skull roof

Although both premaxillae are very poorly preserved, it is clear that each was directed anteroventrally, as in other captorhinids, since the ventral border of the external naris lies at the same level as the ventral border of the maxilla. In contrast with the condition in other early reptiles, where the dorsal process of the premaxilla extends posterodorsally to the level of the external naris, that of *Labidosaurikos* fails to reach even to the level of the anterior narial margin (Text-figs 2–3, 6). Only a single large tooth was preserved in association with the premaxillae. Stovall (1950) restored this tooth immediately below the posterior extent of the external naris, but it was almost certainly the first premaxillary tooth, and, as in other captorhinids, it was succeeded presumably by smaller teeth.

The maxilla (Text-figs 4–6) is the most distinctive cranial element. As in *Rothianiscus* and *Moradisaurus*, the maxilla is greatly enlarged medially, constricting the palate and forming a tooth plate that accommodates six parallel rows of teeth, and is described in detail below. The maximum width of the tooth plate is approximately 25 per cent. of the total length of the bone. Slightly taller teeth, arranged in a single row anteriorly and two smaller rows posteriorly, precede the tooth plate dentition. The maxilla is relatively low in lateral view (Text-fig. 6). In contrast with its great medial expansion, the maxilla is reduced in height laterally, for it has a height-to-length ratio that is roughly one-half that of maxillae in single-rowed captorhinids. The lateral surface of the maxilla can be divided into two regions: anterior to the jugal the external surface is nearly vertical; caudal to this region the maxilla exhibits a lateral flexion of approximately 15–20°. Such flexion marks the beginning of the characteristic cheek swelling found in *Labidosaurus*, *Captorhinus*, and other multiple-rowed captorhinids.

The septomaxilla in most respects resembles closely those of other captorhinids (Text-fig. 6). However, it differs notably in that it has a short, sculptured posterodorsal process that extends onto the skull roof to insert between the lacrimal and the nasal.

The long, narrow lacrimal shares an extensive suture with the jugal that ends well anterior to the orbit (Text-figs 2, 6). The lacrimal and the nasal share a strong overlapping joint; ventrally, an anterodorsal flange of the lacrimal appears to underlie most of the nasal, falling 10 mm short of the internasal suture (Text-fig. 6).

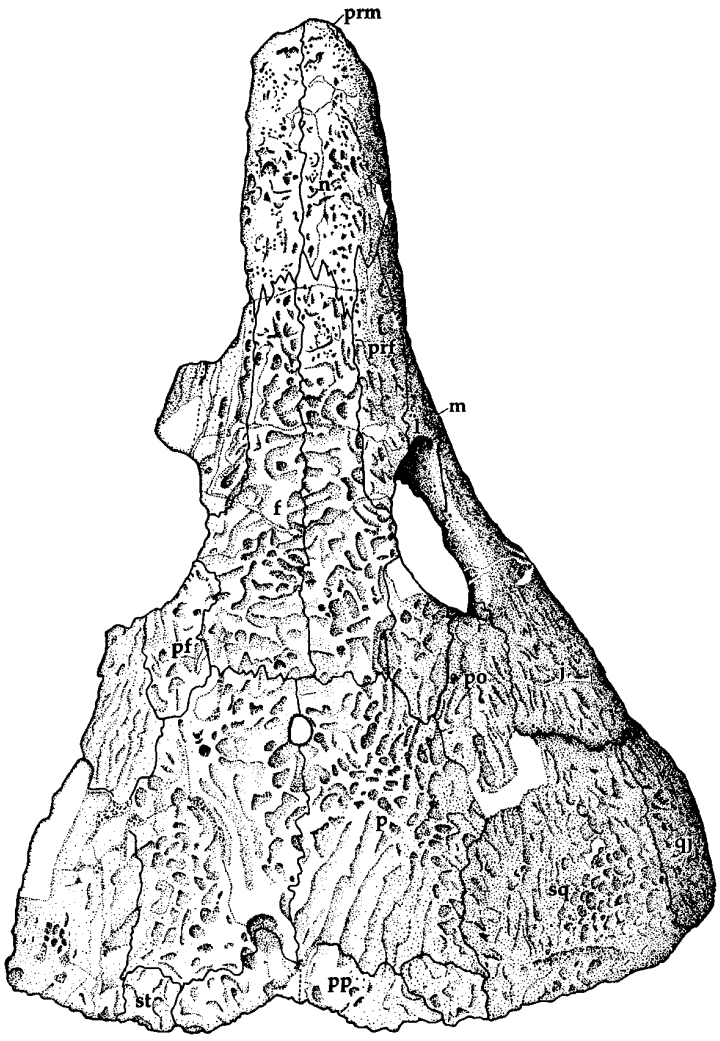
The nasal is slightly broader than those of other captorhinids, and extends ventrolaterally slightly more than half-way down the snout (Text-figs 2–3, 6). In contrast with Stovall's (1950) description, the posterior end of the nasal in both *Labidosaurikos* and *Labidosaurus* is positioned slightly further anterior to the orbits than in other captorhinids, and is undoubtedly related to the presence of a long narrow anterior frontal process in both taxa. Ventrally, the internasal suture is buttressed along a narrow, elevated ridge.

Among captorhinids, the prefrontal of *Labidosaurikos* resembles most closely that of *Labidosaurus* (Text-figs 2–3, 6). The posterodorsal process contributing to the orbital margin is much less acuminate than in other forms. The anterior process of the prefrontal is very long relative to its width and to neighbouring elements; it is approached in relative size only by that found in *Labidosaurus*. Along the anterior orbital margin, the prefrontal has a transversely expanded ventral process that formed an antorbital buttress with the lacrimal.

The frontal is roughly rectangular, and its anterior process is relatively longer and narrower than in all other captorhinids except *Labidosaurus* (Text-figs 2, 4, 6). The frontal lateral lappet, although normally developed dorsally, is overlapped extensively by the prefrontal and postfrontal in ventral view (Text-fig. 4).

Unlike the parietal of other captorhinids, that of *Labidosaurikos* (Text-figs 2–6) is arched in transverse section, such that the paired parietals give the skull roof a slightly domed appearance. Each parietal is also bowed parasagittally, a feature that is accentuated slightly by deformation at the suture shared with the frontal. The elliptical parietal foramen is positioned along the anterior quarter of the interparietal suture, and reflects the anterior displacement of the braincase. The parietal shares overlapping sutures with neighbouring roofing elements that are much more extensive than in earlier captorhinids. As noted by Stovall (1950), the parietal is excluded from the posterior margin of the skull table by the anterodorsal process of the postparietal, a condition found also in *Rothianiscus* (S. Sumida, pers. comm.). The dermal sculpturing most closely resembles that seen in *Labidosaurus*, with which it shares the presence of pits that exceed in size all other pits and grooves. These large pits are found near the parietal foramen and along the suture with the postparietal.

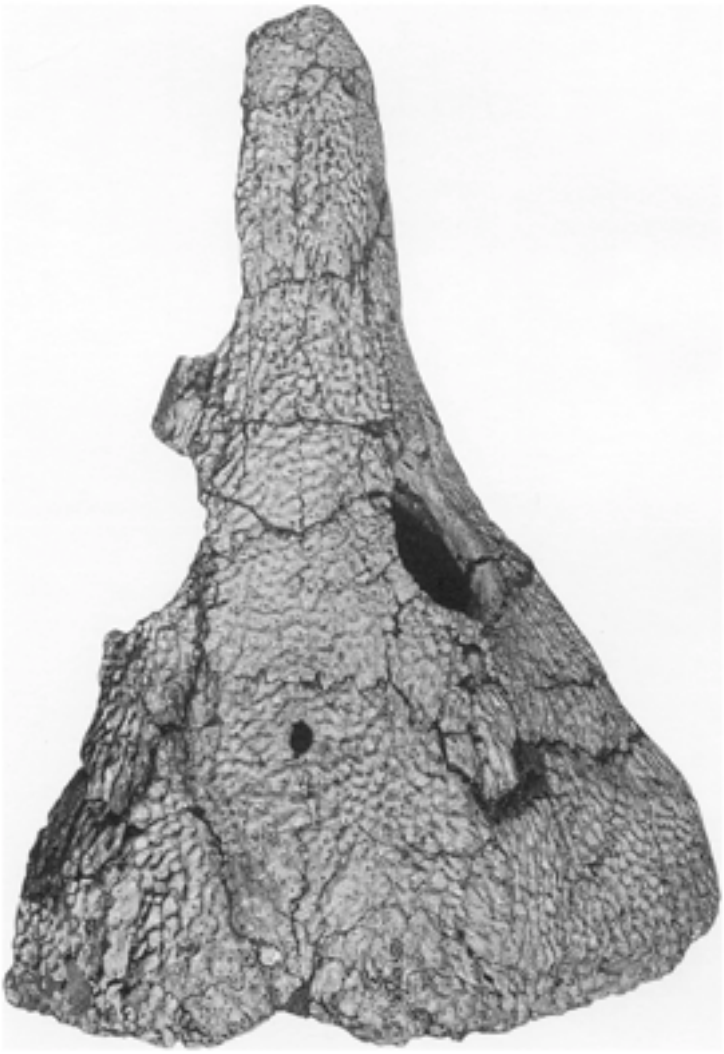
The postparietal (Text-figs 2–4, 7) is unusual in that only the anterior half of the dorsal portion is overlain



TEXT-FIG. 2. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull roof in dorsal view. Scale bar represents 10 mm.

by the parietal, whereas the posterior half is exposed dorsally and is as strongly pitted as the other roofing bones. Accordingly, the postparietals form the median embayment along the occipital margin of the skull roof, as in *Rothianiscus* (S. Sumida, pers. comm.). In contrast, the embayment is formed by the parietals in both *Labidosaurus* and *Captorhinus*. Posteriorly, the postparietal is a flat, lightly scarred plate that is inclined marginally posteroventrally. The anteroventral surface of the postparietal is complex: anterolaterally the postparietal forms a thin flat lamina that underlies the parietal, whereas posteromedially it forms with its mate a stout T-shaped platform that contacted the supraoccipital and the parietal. Unfortunately, when the braincase was removed from the skull, the posterolateral extensions of this platform were damaged. However, enough of the ventral tips of these flanges are preserved in full articulation with the supraoccipital (Text-fig. 7) and demonstrate that they served to strengthen the contact between the skull roof and the occiput.

In most basal eureptiles, the supratemporal is a narrow sliver of bone. In strong contrast, the supratemporal of *Labidosaurikos* (Text-figs 2, 6–7) consists of two plates, joined at roughly 90°. The dorsal portion of the

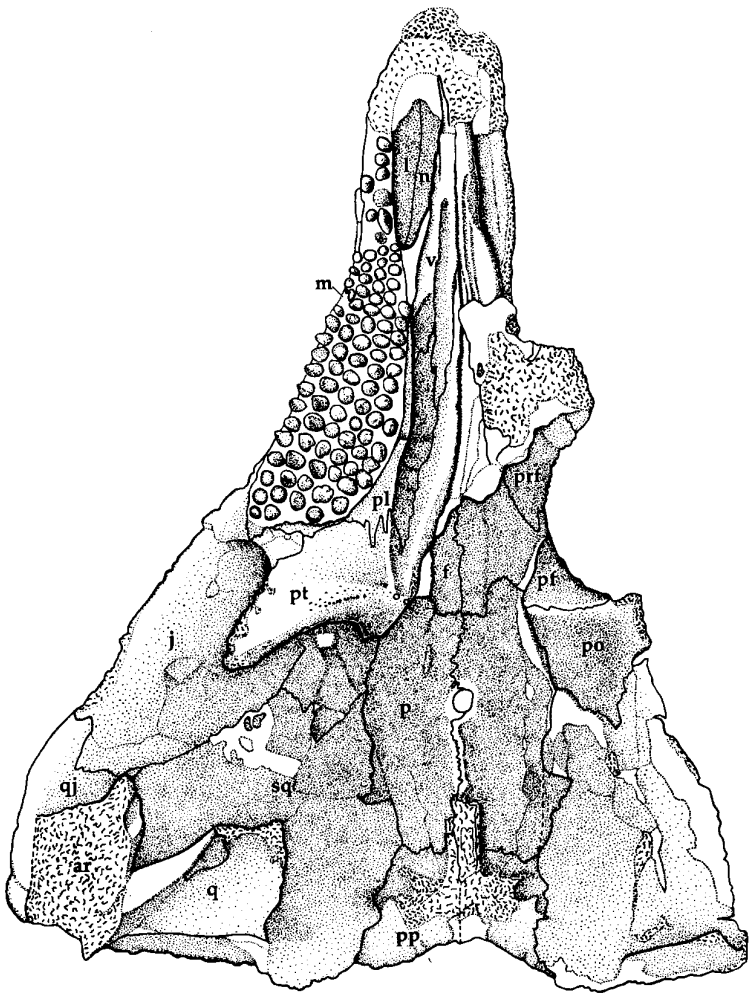


TEXT-FIG. 3. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull in dorsal view; for interpretation and scale, see Text-figure 2.

supratemporal does not overlie the posterolateral corner of the parietal as in other reptiles, but instead it overlies the posterodorsal corner of the squamosal. Medially, the supratemporal is sutured firmly to the postparietal.

The postfrontal (Text-figs 2–6) is unique among captorhinids in that the posterior process is relatively broad, plate-like, and more heavily sculptured. Sutures with neighbouring elements in dorsal view are more irregular than in other captorhinids. They are clearly influenced by the pattern of the sculpted pits and furrows, since the sutures occur as gentle curves in ventral view. The free ventral surface of the postfrontal rises slightly posteriorly to form a weak, buttressing ridge along the suture with the postorbital.

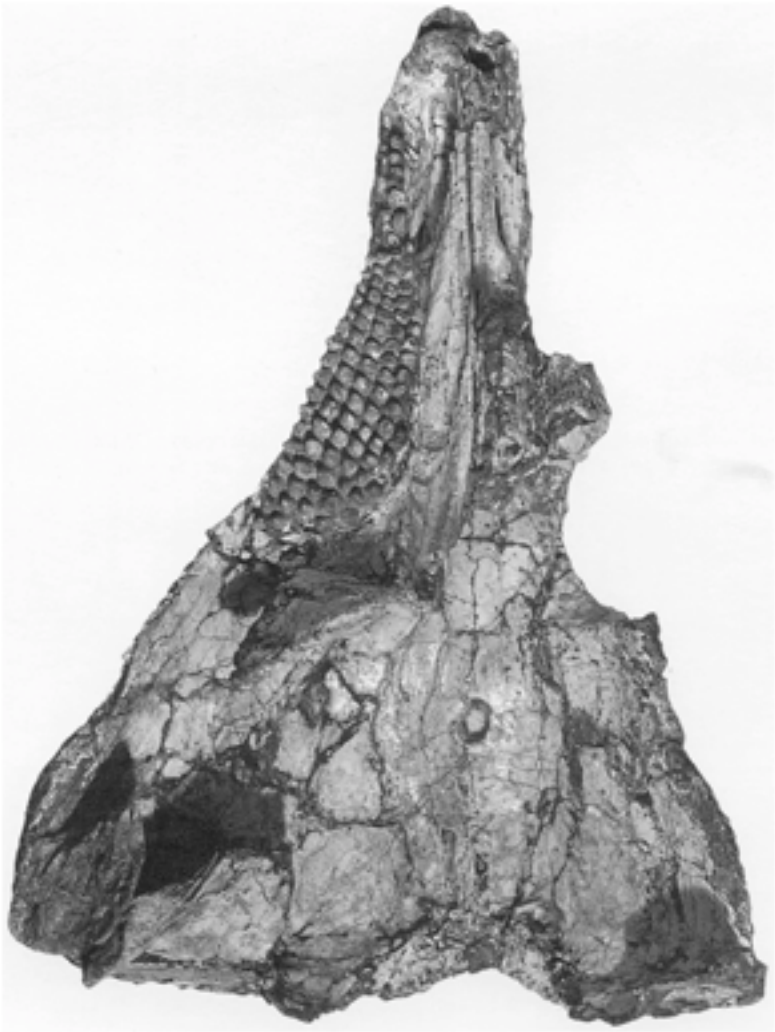
The postorbital (Text-figs 2–6) of *Labidosaurikos* differs little from those of other members of the family, except that a medial triangular flange underlies the posterior process of the postfrontal, and the overlapping suture with the squamosal is strongly developed.



TEXT-FIG. 4. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull roof in ventral view. Scale bar represents 10 mm.

The suborbital ramus of the jugal is extremely tall in lateral view, occupying 40–50 per cent. of the height of the skull in the region of the orbit (Text-fig. 6). Accordingly, the orbital margin is almost straight ventrally instead of concave as in the basal captorhinids. The suborbital process is also very thick transversely, and ends anteriorly with an acuminate tip well forward of the orbit (Text-figs 2, 6). The medial process differs from those of other captorhinids in that it is bisected deeply in ventral view by the posterior tip of the maxilla (Text-fig. 4). The suborbital foramen is relatively tiny. The temporal portion of the jugal is well developed, but does not extend as far posteriorly as in other captorhinids (although it is not as abbreviated as described by Stovall 1950). The dorsal and posterior margins of the temporal portion are deeply overlain by the postorbital and the squamosal and quadratojugal, respectively. The suture with the squamosal is reduced laterally, owing to the slight increase in the height of the quadratojugal. The free ventral margin of the jugal is slightly convex, in contrast with the straight or slightly concave ventral margins of other captorhinid taxa.

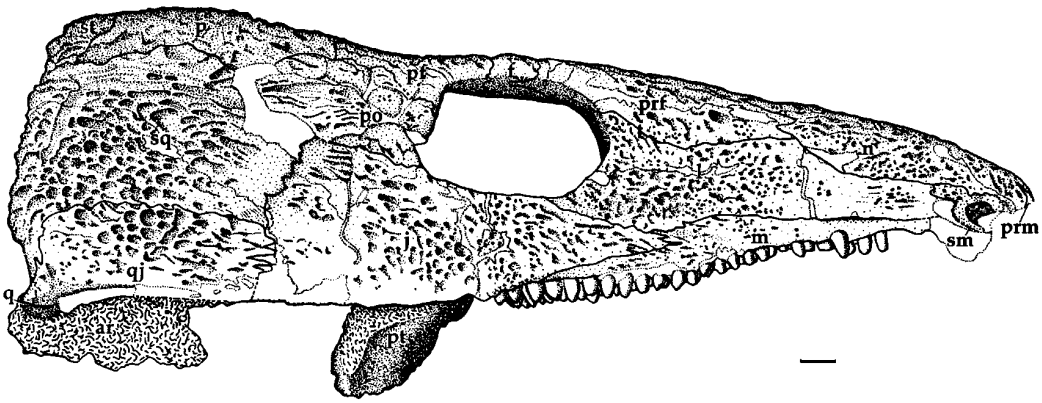
In lateral view, the squamosal (Text-figs 2, 4, 6–7) differs little from those of other captorhinid taxa, except that the occipital margin is roughened, and the small posteroventral process extends almost to the ventral



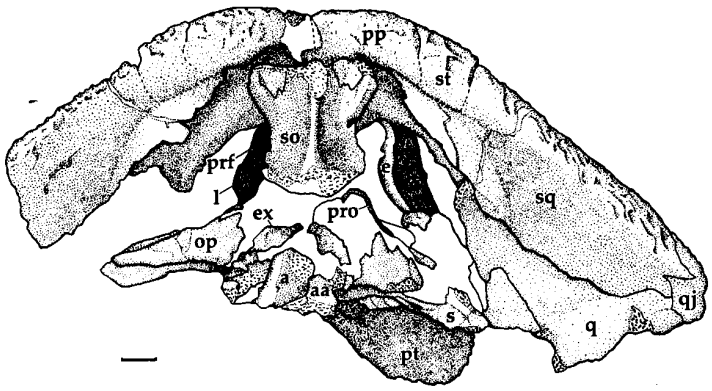
TEXT-FIG. 5. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull without braincase in ventral view; for interpretation and scale, see Text-figure 4.

margin of the skull. The occipital margin of this process is slightly concave posteriorly (Text-fig. 6). The occipital flange is not overlain by the postparietal to the extent seen in the single-rowed captorhinids, and its free edge in posterior view (Text-fig. 7) is slightly less convex in occipital view than in other captorhinids. The flange is also slightly more complex than in other captorhinids: the ventrolateral portion is distinctly plate-like and inclined slightly anteroventrally, whereas the dorsomedial portion is fan-shaped, gently curved, and extends posteriorly beyond the occiput. Laterally, the squamosal overlies the quadratojugal and the jugal to a greater extent than seen in all single-rowed captorhinids except *Labidosaurus*.

The quadratojugal (Text-figs 2, 4, 6–7) resembles those of *Labidosaurus* and *Captorhinus* most closely among captorhinids, except that it has a large, rounded boss that buttresses the lateral condyle of the quadrate, and the quadrate foramen is absent.



TEXT-FIG. 6. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull roof in right lateral view. Scale bar represents 10 mm.



TEXT-FIG. 7. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull roof and braincase in posterior view. Scale bar represents 10 mm.

Palate

The palate (Text-fig. 1B) resembles the general captorhinid pattern as described by Heaton (1979), but features several specializations associated with the presence of multiple rows of teeth. These include a transverse constriction of the palate between the medially expanded tooth laminae of the maxillae, the loss of teeth from the palatine and the anterior process of the pterygoid, and a finer interdigitation of the palatal sutures. As in other captorhinids in which the palate is adequately known, the ectopterygoid is replaced by the medial process of the jugal. Stovall (1950) did not describe the palate.

The edentulous vomer (Text-fig. 4) is remarkably long and slender. The ventral surface is smoothly convex anteriorly, but, posteriorly, the vomer is incised by a narrow groove which becomes deeper and broader posteriorly than in other captorhinids. The vomer is bifurcated ventrally by an anteromedial process of the palatine. An elongate vomer is present also in *Moradisaurus grandis* (Ricqlès and Taquet 1982).

The palatine (Text-figs 4, 8) is a long, dorsally bowed element, with a lateral portion that buttresses the maxillary tooth plate, and a raised medial portion that forms part of the dorsal trough that runs sagittally down the palate. Like the vomer, the palatine is edentulous, a condition shared with *Moradisaurus*. Anteriorly, the palatine forms the posterior end of the internal naris between the maxilla and the vomer, although this is not

visible in the figures. Despite the great medial expansion of the maxillary tooth plate, the palatine maintains its posterior contact with the medial process of the jugal.

The pterygoid (Text-figs 2, 6, 8) retains the triradiate organization characteristic of all early amniotes, but is edentulous except for a narrow band of tiny denticles and small teeth that are aligned along the posterior margin of the transverse flange. The palatine ramus of the pterygoid of *Labidosaurikos* is slender as in *Labidosaurus*, but differs from those of all single-rowed captorhinids in that it is raised slightly above the transverse flange. The transverse flange resembles most closely that of *Labidosaurus* in that its base is relatively narrow, but it is inclined slightly more to the frontal plane, at approximately 70°. The quadrate ramus does not differ from that of *Labidosaurus* or *Captorhinus*, except in size and in the region surrounding the basicranial recess. Here, the pterygoid supports the basicranial portion of the epipterygoid with broad anterior and narrow posterior ridges, and a deep groove runs anteroventrally between the two ridges from the recess.

The epipterygoid (Text-figs 7, 10–11) differs in a number of features from those of single-rowed captorhinids. The columella is a relatively large, transversely flattened pillar that arches slightly posterodorsally. On the lateral surface, a prominent ridge runs down from the base of the columella to the anteroventral corner of the epipterygoid proper. A well defined pocket, of uncertain function, lies immediately posterior to this ridge near the base of the columella. The basicranial recess is inclined posterodorsally, and is slightly more elongate than in other captorhinids.

Among captorhinids, the quadrate (Text-figs 4, 7–8) of *Labidosaurikos* resembles most closely those of *Labidosaurus* and *Captorhinus* in orientation and general proportions. There is no shallow pit on the medial surface of the dorsal lamella to receive the paroccipital process. The condyles cannot be described, because of the *in situ* preservation of the articular.

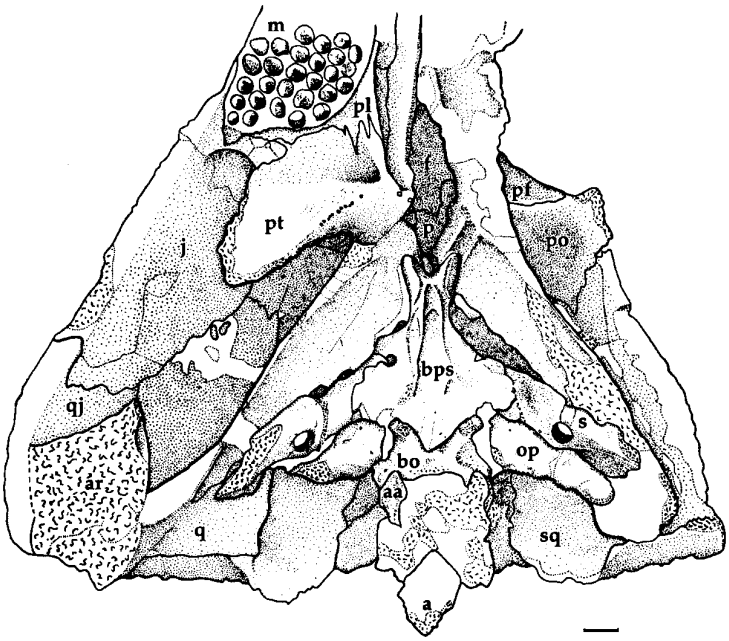
Braincase

The braincase of the holotype represents the only known material for *Labidosaurikos meachami*. Surprisingly, Stovall (1950) ignored it in his description. A second braincase, assigned originally to *Labidosaurikos* by Olson (1967) and described by MacLean (1970), was later attributed to *Seymouria* (Olson 1979). Of the three major units of the skull, the braincase appears to be the most highly modified from the basic reptilian pattern among captorhinids. In all parts of the skull there is a tendency towards increased ossification and structural reinforcement. However, the braincase of *Labidosaurikos* is unusual in that the sutures between the occipital elements and the rest of the braincase may have been replaced by cartilage; there appears to have been little or no osseous contact between the supraoccipital and the opisthotics and exoccipitals. As reconstructed, the post-temporal fenestra (Text-fig. 1D) is larger and relatively taller than in single-rowed captorhinids, a feature that may be attributed to the increased height of the skull.

Since the parasphenoid and the basisphenoid are fused indistinguishably, the resultant complex is referred to here as the basiparasphenoid. In ventral view, the basiparasphenoid (Text-figs 8–9, 11) is organized in the same manner as in *Labidosaurus* and *Captorhinus*, except that it is considerably wider and distinctly more diamond-shaped. Furthermore, the trough between the cristae ventrolaterales is shallower posteriorly than in those taxa. The basiparasphenoid appears to overlap the stapedial footplate more deeply than in other captorhinids. As in *Labidosaurus* and *Moradisaurus*, the cultriform process projects anterodorsally from between the basipterygoid processes at roughly 60° to the horizontal plane. Only the base of the process is present, but in relative dimensions this is almost twice as thick transversely and taller anteroposteriorly than those of other captorhinids. The bifaceted basipterygoid processes are slightly more slender in lateral view than are those of other captorhinids. In ventral aspect, the processes appear parabolic and project slightly laterally. In contrast, those of other taxa appear truncated anteriorly and do not project as far anterolaterally. In lateral view, the sella turcica is greatly constricted between the cultriform process anteriorly and the dorsum sella posteriorly. The clinoideus process is poorly developed, such that the retractor pit is much shallower than in other captorhinids. The dorsum sella resembles that of *Captorhinus* (Price 1935), but it is much thicker anteroposteriorly. Its apex is unfinished and was probably topped with cartilage.

Except for its larger size, and the observation that its sutures with neighbouring elements are more serrate, the proötic (Text-fig. 11) differs little from that of *Captorhinus* (Price 1935). Since the supraoccipital was preserved slightly above the remainder of the braincase with an intervening layer of matrix, the nature of the contact between it and the proötic is not clear; the two elements may have been connected via cartilage.

In single-rowed captorhinids, the medial end of the opisthotic resides largely within a concave recess of the exoccipital. There is no indication that an ossified recess exists for the opisthotic of *Labidosaurikos* (Text-figs 7–9, 11) and contact with the other occipital elements was probably completed by cartilage. Ventrally, however, the basioccipital recess is present, but the bones are separated by a distinct gap which suggests that an



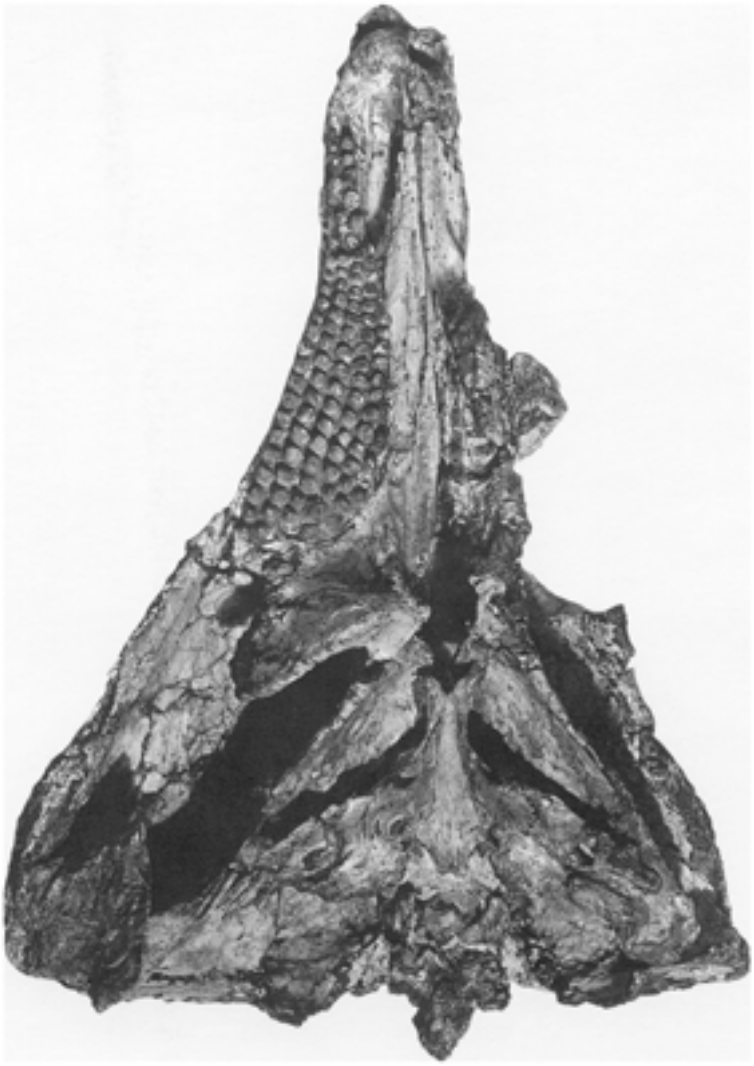
TEXT-FIG. 8. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; braincase and partial palate in ventral view. Scale bar represents 10 mm.

intervening layer of cartilage was present. The paroccipital process is dorso-ventrally flattened and rod-like, with a slightly rounded tip, which probably reflects damage; those of single-rowed captorhinids are circular in cross section, and possess truncated tips. The paroccipital process differs further from those of other captorhinids in that it is sutured to the stapedial columella. Based on their reconstructed dimensions, it is likely that the distal tips of both structures were finished with cartilage that extended posterolaterally to contact the medial surface of the quadrate.

The supraoccipital (Text-figs 7, 11) is greatly modified over the pattern exemplified by *Captorhinus* (Price 1935). Most striking is the absence of a true osseous connection with the rest of the neurocranium. When the skull was collected, the supraoccipital was suspended above the braincase by a bridge of matrix in the position it probably assumed in life. The surrounding elements form a clean, symmetrical margin around the base of the supraoccipital, but there is no apparent bony contact. In most captorhinids, the supraoccipital serves as the major support for the braincase; therefore, it is unusual that portions may have been replaced by cartilage, especially so for *Labidosaurikos*, one of the largest captorhinids. This development suggests that the basicranial articulation and the stapedial-opisthotic complex provided a greater degree of support than in the single-rowed forms. The supraoccipital is distinguished further among captorhinids by its greater height and strong posteroventral lean (Text-fig. 11B). The anterior ascending process and the posterior median ridge of the supraoccipital are better developed than in the single-rowed captorhinids. The lateral ascending process is well developed dorsally, but ventrally it is feebly developed. This is in strong contrast with the condition in *Captorhinus* in which the reverse is true. The lateral ascending process of the supraoccipital features a large opening, of uncertain function, on its dorsolateral edge. No such opening has been reported in other captorhinids.

The exoccipitals (Text-fig. 7) are poorly exposed. Apart from their larger size, they do not differ markedly from those of other captorhinids. The anterodorsal surface of the exoccipital appears to be covered in spongy bone; attachment to the supraoccipital was probably accomplished via cartilage rather than through a sutural contact. As in other early reptiles, the exoccipital was probably fused ventrally to the basioccipital.

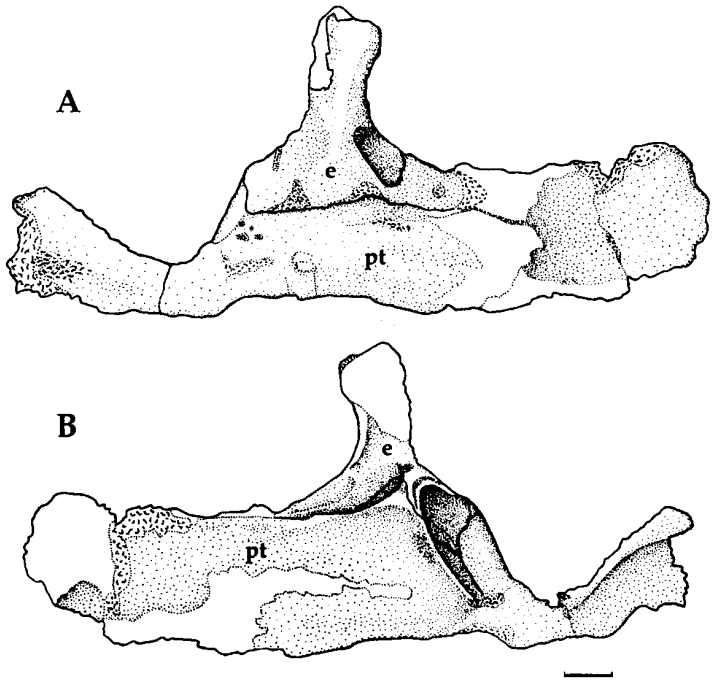
Ventrally, the basioccipital (Text-fig. 8) is much wider with respect to the rest of the braincase than in single-rowed taxa. As in *Labidosaurus*, there is a small, open space between the ventrolateral tuber of the basioccipital and the anteromedial corner of the opisthotic; this space is located immediately ventral to the lagenar recess



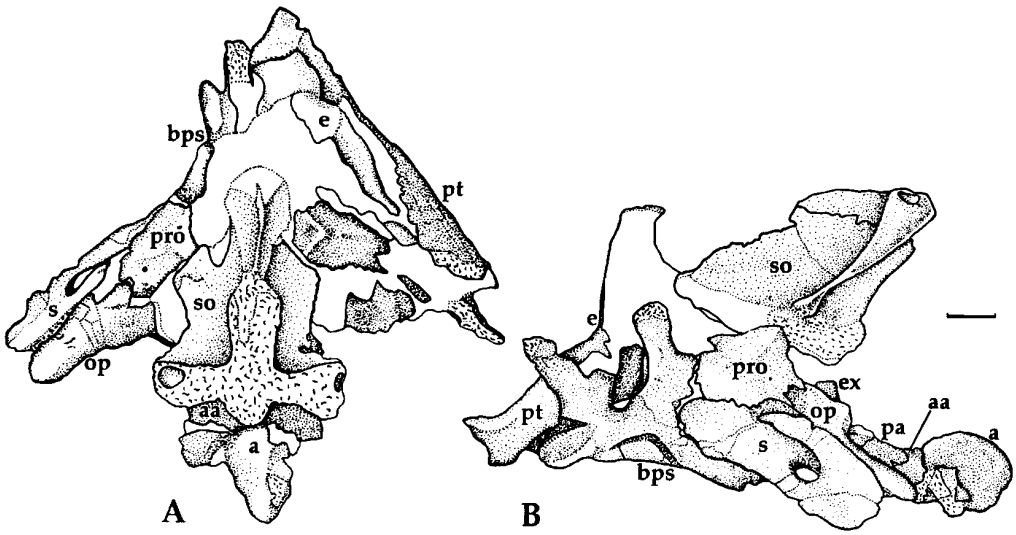
TEXT-FIG. 9. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull with braincase in ventral view; for interpretation and scale, see Text-figures 4 and 8.

of the opisthotic in *Captorhinus* (Price 1935). Posterior to the tuber, the basioccipital abuts firmly against the opisthotic. The condyle is absent, and the posterior margin of the basioccipital forms a thin, sharp edge. The absence of the condyle is problematical, since fragments of the atlas-axis complex are preserved in association with the occiput. Remnants of the condyle may have been displaced dorsally and obscured by the surrounding vertebral fragments.

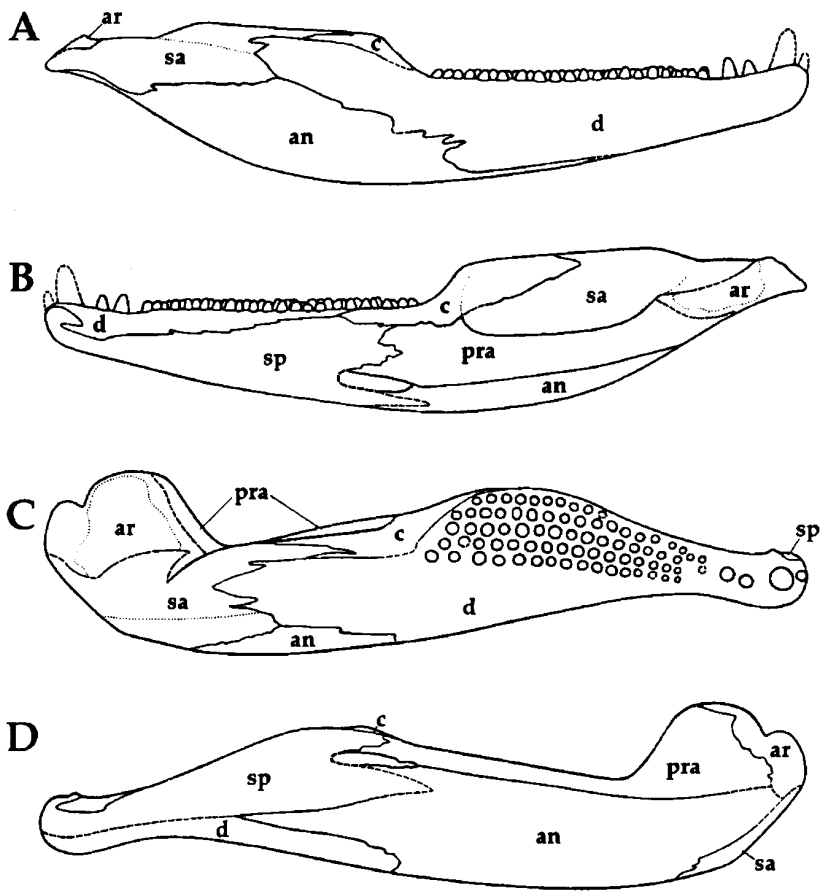
Both stapes are preserved in perfect contact with the braincase (Text-figs 7–9, 11). As in other captorhinids, the stapes is massively constructed, but its footplate is relatively much narrower in lateral view and its columella is deeper antero-ventrally. As in *Labidosaurus*, the stapedial footplate is covered slightly in ventral aspect by the posterolateral wing of the parasphenoid. In *Captorhinus* and most early reptiles, the footplate simply abuts the braincase. The stapedial foramen pierces the columella near the midpoint of the stapes, as opposed to the condition in other captorhinids, where it is positioned immediately distal to the footplate. In



TEXT-FIG. 10. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; epipterygoid and quadrate flange of pterygoid. A, lateral view; B, medial view. Scale bar represents 10 mm.



TEXT-FIG. 11. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; braincase. A, dorsal view. B, left lateral view. Scale bar represents 10 mm.



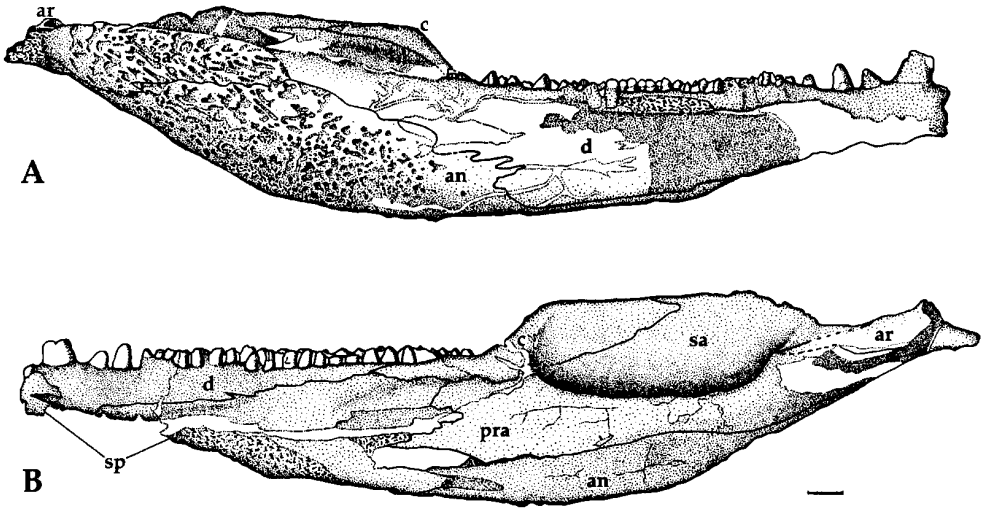
TEXT-FIG. 12. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; reconstruction of right mandible. A, lateral view; B, medial view; C, dorsal view; D, ventral view. Scale bar represents 20 mm.

addition, the stapedial foramen is rounder and relatively smaller than in other taxa. The dorsal process resembles closely that of *Labidosaurus*.

Lower jaw

The mandible of *Labidosaurikos* (Text-fig. 12) is remarkably broad for most of its length, and most closely resembles those of *Rothianiscus* and *Moradisaurus* among captorhinids. The maximum jaw width is roughly 14 per cent. of the total length of the jaw, whereas in *Captorhinus* this figure is not more than 9 per cent. The increase in mandibular breadth in *Labidosaurikos* is most apparent when the lower jaw is articulated with the dermal skull roof: its convex labial margin projects as much as 35 mm beyond the lateral edge of the skull, whereas the lower jaws of single-rowed captorhinids are flush with the lateral skull margin. In contrast with its width, the relative height of the mandible is similar to that of other members of the family. In dorsal and ventral views, the mandible has a distinctly sigmoidal outline. A relatively large posterior meckelian foramen (= foramen intermandibularis caudalis of some authors) occupies the lingual surface of the jaw; all single-rowed captorhinids except *Labidosaurus* and an unnamed taxon (FMNH UC 183) feature a small meckelian foramen. Since Stovall (1950) did not describe the mandible, beyond mention of the number of tooth rows present in the dentary, the mandible is described here in detail.

Like the maxilla, the alveolar ridge of the dentary (Text-figs 13–14) is greatly expanded transversely to



TEXT-FIG. 13. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; right mandible. A, lateral view; B, medial view. Scale bar represents 10 mm.

accommodate multiple rows of teeth. Five rows of teeth, aligned along the longitudinal axis of the jaw and curved slightly lingually, interdigitate perfectly with the opposing tooth plate of the maxilla. Four larger teeth precede the tooth plate, among which the second tooth is clearly the largest. Surprisingly, the dentary forms little of the actual sutural surface of the jaw symphysis; this region is overlain almost entirely by the splenial. The posterolateral end of the dentary extends further posteriorly than in single-rowed captorhinids, almost as far as the articulating facet for the jaw suspension. It forms with the surangular a wide lateral shelf at the base of the coronoid process.

In contrast with the condition seen in other captorhinids, where the jaw symphysis is formed equally between the splenial and the dentary, the splenial of *Labidosaurikos* (Text-figs 13B, 14A) forms most of the sutural surface of the symphysial pad. The symphysial pad of *Labidosaurikos* is relatively smaller than that of *Labidosaurus* and other single-rowed forms, another characteristic that is shared with *Moradisaurus* (Ricqlès and Taquet 1982). Immediately posterior to the symphysial pad, the splenial narrows abruptly to a slender neck, but then increases greatly in height and width posteriorly. In ventral view, the splenial dominates the anterior half of the jaw.

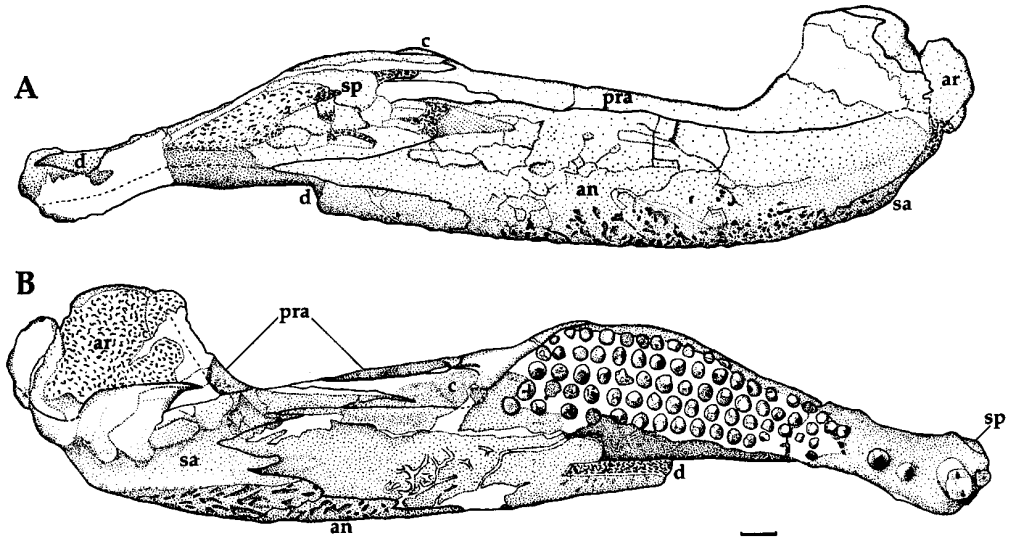
The coronoid (Text-figs 13–14) is modified distinctly over the form seen in most single-rowed captorhinids. The anterior process is short in contrast with the elongate anterior process present in *Labidosaurus* and *Captorhinus*. The posteroventral ramus is completely absent. The posterodorsal process is very deep dorsoventrally, and forms the dorsal ridge of the coronoid process in both medial and lateral views. The posterodorsal process is bifurcated deeply by the surangular in dorsal view.

Dorsally, the surangular (Text-figs 13–14) contributes a sharp ridge to the coronoid process. A broad, lateral shelf projects nearly perpendicularly from the base of the coronoid portion. Posteriorly, this shelf curves medially to form a flat rugose platform for the articular. Ventral to this shelf, the surangular is strongly convex laterally and has a deep overlapping suture with the dentary anteriorly and the angular ventrally.

The angular (Text-figs 13–14) is a large, broadly convex bone that comprises most of the posteroventral corner of the mandible. It is relatively long, approximately equal to the dentary in length. The posterior end, broadly tongue-shaped in ventral aspect, is narrowly acuminate in lateral view, owing to the dorso-ventral flattening of the posterior end of the jaw.

The prearticular (Text-figs 13B, 14) resembles those of other captorhinids, except that the anterior end, contacting the coronoid and splenial, is relatively deeper dorso-ventrally.

The articular (Text-figs 13–14) is compressed dorso-ventrally, a condition shared with *Moradisaurus*. The articulating facet for the quadrate is damaged and there is little surface detail, such that no more than its basic outline is visible. The posterolateral boss of the articular is reasonably preserved and delimits the posterior extent of the facet. The short, broad retroarticular process is similar to that seen in *Labidosaurus*.



TEXT-FIG. 14. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; right mandible. A, ventral view; B, dorsal view. Scale bar represents 10 mm.

Dentition

Only one premaxillary tooth (not illustrated) is preserved; it is the largest tooth and probably represents the first premaxillary tooth. Stovall (1950) reconstructed it erroneously below the posterior end of the external naris. As in most other captorhinids, this tooth is massive, with an estimated antero-posterior basal diameter of 19 mm and a transverse diameter of 9 mm. It differs from the corresponding tooth in other taxa in that it is slightly recurved.

For descriptive purposes, the maxillary and dentary dentitions of multiple-rowed captorhinids can be subdivided into two areas, multiple (MR) and single row (SR) regions (Bolt and DeMar 1975; Ricqlès and Bolt 1983). Interestingly, there are two short rows in the posterior SR region of the maxilla of *Labidosaurikos* (Text-fig. 4); these teeth do not appear to be part of the tooth plate proper. Otherwise, the teeth here resemble closely those of *Labidosaurus*. As in that genus, there is a weakly developed maxillary caniniform region, but there is no tooth that can be described as a caniniform. The anterior two dentary teeth have been damaged since the original description, but the photographs figured by Stovall (1950) indicate that they projected vertically as in *Labidosaurus*.

As in all large, multiple-rowed captorhinids, the tooth rows of *Labidosaurikos meachami* are nearly parallel to the lateral margins of the maxillary and dentary (Text-figs 4, 14B). Damage to the dentary tooth plate (Text-fig. 13A) reveals that implantation was protothecodont. Apart from the teeth, the tooth plates are covered by recalcitrant matrix, such that there is no direct evidence of MR tooth replacement in *Labidosaurikos*. However, the MR region of *Gecatogomphius kavejevi* features a few resorption pits (R. Reisz, pers. comm.), and is the best evidence for MR tooth replacement in the large, multiple-rowed captorhinids.

The four labial rows of the maxillary tooth plate consist of 17–18 teeth each, whereas the two lingual rows have 14 and four teeth (Text-fig. 4). The MR teeth are isodont pegs. There is a gradual decrease in tooth diameter anteriorly in the four labial rows, but tooth height is fairly consistent. Wear facets are present on most teeth in the MR region. In the outermost maxillary row, wear is confined largely to the lingual surface of each tooth. However, wear is found principally on the labial surface of the innermost maxillary teeth; all intervening maxillary teeth possess wear facets on both lingual and labial surfaces. The small anterior MR teeth are the most severely worn, whereas only a few posterolingual teeth on the edge of the dental platform have escaped wear. There is considerably more wear on MR teeth than on SR teeth, which suggests that they were used for grinding, whereas the SR teeth were probably responsible for simple shearing.

DISCUSSION

Phylogenetic relationships

There have been several phylogenetic analyses of captorhinid interrelationships published recently (Gaffney and McKenna 1979; Ricqlès and Taquet 1982; Ricqlès 1984; Berman and Reisz 1986). All have allied the large, multiple-rowed captorhinids with *Captorhinus aguti* on the basis of dentition alone. However, the above description reveals several non-dental characters shared by *Labidosaurikos* and the large, single-rowed captorhinid *Labidosaurus hamatus* that are not present in *C. aguti*. It is therefore necessary to re-evaluate the interrelationships of *Labidosaurikos*, *Labidosaurus* and *Captorhinus*.

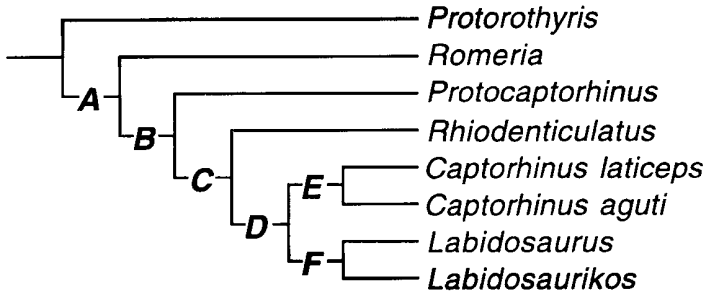
The following taxa form the ingroup: *Captorhinus aguti*, '*Eocaptorhinus*' *laticeps*, *Labidosaurus hamatus* and *Labidosaurikos meachami*. *Captorhinus aguti* is perhaps the best known captorhinid (Price 1935; Fox and Bowman 1966; Ricqlès and Bolt 1983). We also had access to excellent, articulated and disarticulated cranial material referable to this captorhinid that was collected recently from the Fort Sill fissure-fill locality. The genus *Eocaptorhinus* was recently made a junior synonym of *Captorhinus* by Gaffney (1990). Since Gaffney (1990) identified what was formerly '*E. laticeps*' only as '*Captorhinus* sp.,' we recognize this single-tooth rowed form as a valid taxon for the purposes of phylogenetic investigation, regardless of its generic identity. The large single-rowed taxon *L. hamatus* has been linked closely with both *Captorhinus* and *Labidosaurikos*. Since the most recent study of the cranial anatomy of this large captorhinid was by Williston (1917), information on this form is taken from MCZ 8727, UCLA VP 3167, and UCLA VP 3200.

The following taxa serve as outgroups: *Rhiodenticulatus heatoni*, *Romeria texana*, *Protocaptorhinus pricei*, and *Protorothyris archeri*. The captorhinid *Rhiodenticulatus heatoni* was described recently on the basis of two skeletons from New Mexico (Berman and Reisz 1986) that were also available to us for examination. The basal captorhinids *Romeria texana* and *Protocaptorhinus pricei* were illustrated and described briefly by Clark and Carroll (1973). The protorothyridid *Protorothyris archeri* (Clark and Carroll 1973) serves as a non-captorhinid outgroup.

Although *Labidosaurikos* appears to share several apomorphies with other large multiple-rowed captorhinids (noted in the description), these forms are omitted from the analysis because they are less adequately known than other captorhinid taxa. These problematic taxa include *Gecatogomphius kavejevi*, a Russian form known only from fragmentary tooth-bearing bones (Olson 1962); *Moradisaurus grandis*, a large African taxon represented by a complete skull, although sutural patterns are unknown (Ricqlès and Taquet 1982); *Rothianiscus multidonta*, distinguished by its rows of massive, occlusally flattened teeth (Olson and Beerbower 1953; Olson and Barghusen 1962), and its congener *R. robusta* (Olson 1965). Similarly, the available literature on the cranial anatomy of *Captorhinikos chozaensis*, *C. valensis*, *C. parvus* and *Kahneria seltina* is inadequate by recent standards. Lastly, *Labidosaurikos barkeri*, represented by fragmentary cranial and postcranial materials (Olson 1954), probably represents a junior synonym of *Labidosaurikos meachami* (Seltin 1959). All these taxa need to be restudied, since they are distinguished from one another largely by their dentition or by size (Olson 1954; Seltin 1959; Olson and Barghusen 1962).

Thirty-nine characters were used in the analysis. Several are from previous studies (Gaffney and McKenna 1979; Berman and Reisz 1986), but many are new. No postcranial characters were used, since *Labidosaurikos* is known only from cranial material, and the postcranial skeleton is known adequately only in *Labidosaurus*, *Captorhinus* and *Rhiodenticulatus*. The analysis was run on a Macintosh Quadra 800 computer using the branch-and-bound algorithm of PAUP 3.1, which is guaranteed to find the most parsimonious trees. All characters were optimized using delayed transformation (DELTRAN) and run unordered.

One parsimonious tree was found (Text-fig. 15). It has a tree length of 49 steps and a consistency index of 0·918 excluding uninformative characters. *Labidosaurikos* is most closely related to *Labidosaurus* among the taxa considered here. This relationship is very robust, as 13 more steps are



TEXT-FIG. 15. Hypothesis of relationships for *Labidosaurikos meachami*. Interior branches are defined by the following unambiguous characters: *A* (diagnosing Captorhinidae), premaxillary ventral margin aligned antero-ventrally ('premaxilla hooked' of earlier literature); maxilla posterior end flexed laterally; tabular absent and postparietal transversely elongate; caniniform region present anteriorly on dentary; pineal foramen positioned anterior to midpoint of interparietal suture; maxillary dentition reduced to 25 or fewer teeth. *B*, postparietals partially separated ventrally by supraoccipital; skull table posterior margin straight; retroarticular process present. *C*, quadratojugal square-tipped anteriorly. *D*, maxillary dentition ends posteriorly at level of orbital midpoint; postorbital region expanded laterally; skull table posterior margin with single median embayment; pterygoid transverse flange narrow and tongue-like; parasphenoid with deep groove present between cristae ventrolaterales; mandibular posterior end acuminate; marginal 'cheek' teeth chisel-shaped. *E* (diagnosing *Captorhinus*), jugal medial process positioned dorsally on anterior process; retroarticular process elongate; anterior dentary teeth procumbent. *F*, snout narrow; frontal anterior process long and narrow; supratemporal-postparietal contact well-developed; pterygoid transverse flange narrow; supraoccipital posterodorsal processes tall; occipital condyle positioned anterior to jaw symphysis; large pits present on posterior skull table; mandibular ramus sigmoidal in ventral view; mandibular ramus broad in ventral view; adductor shelf present ventrolateral to coronoid process; meckelian foramen large; coronoid posterodorsal process expanded dorso-ventrally; maxillary caniniform teeth absent; caniniform tooth present anteriorly on dentary with caniniform region absent.

required to break it and unite *Labidosaurikos* with *Captorhinus*. The sister-group relationship between *Labidosaurikos* and *Labidosaurus* is supported by the presence of 15 synapomorphies, listed below. The number of the character is enclosed by parentheses, and derived states other than '1' are enclosed by square brackets. Minus signs indicate reversals, and ambiguous characters are denoted by asterisks:

1. Snout narrow (5).
2. Prefrontal anterior process long (*6).
3. Frontal anterior process long (−7).
4. Supratemporal-postparietal contact well developed (12).
5. Cultriform process projects anterodorsally at more than 45° to the basal plane (*20 [2]).
6. Supraoccipital lateral ascending processes tall (22).
7. Occipital condyle anterior to level of jaw suspension (23).
8. Large sculpture pits present on posterior skull table (25).
9. Mandible sigmoidal (26).
10. Mandible broad (27).
11. Lateral shelf present below coronoid process (29).
12. Meckelian foramen large (31).
13. Coronoid posterodorsal process expanded dorso-ventrally (32).
14. Maxillary caniniform teeth absent (35).
15. Dentary caniniform tooth present (38 [2]).

The cladistic analysis supports the hypotheses of Ricqlès and Taquet (1982) and Berman and Reisz (1986) concerning the positions of the basal captorhinids within Captorhinidae. However, our tree differs notably from those of previous phylogenetic studies (Gaffney and McKenna 1979;

Ricqlès and Taquet 1982; Ricqlès 1984) in that *Labidosaurikos* is more closely related to the single-tooth rowed *Labidosaurus* than *Captorhinus*. The close relationship of *Labidosaurikos* and *Labidosaurus* is the most robust proposed for any two captorhinid taxa.

A corollary of our phylogeny is that the origin of multiple-tooth-rows in Captorhinidae is diphyletic. This is not unusual, given that serial repetition of tooth-rows evolved independently in rhynchosaurs. Bolt and DeMar (1975) remarked that their explanation for the development of multiple-tooth-rows in *C. aguti*, reiterated by Ricqlès and Bolt (1983), might require modification if it were to be applied to the *Labidosaurikos* and other large, multiple-rowed captorhinids. Our results suggest that this would indeed be the case, but a detailed examination of tooth-row development and tooth replacement in *L. meachami* is beyond the scope of the present study.

Captorhinus aguti and '*Eocaptorhinus*' *laticeps* are recognized officially here as sister taxa. This sister-group relationship is relatively robust, since three additional steps are required to break it. It supports Gaffney's (1990) recent synonymy of *Eocaptorhinus* under *Captorhinus*. Since Gaffney (1990) abstained from identifying the single-rowed form as anything other than '*Captorhinus* sp.', we therefore recognize formally the new combination *Captorhinus laticeps*. This species of *Captorhinus* appears to be separable from *C. aguti* only by the presence of single rows of marginal teeth, although it is possible that a thorough re-examination of skulls and tooth-bearing elements assigned by Heaton (1979) to '*Eocaptorhinus*' *laticeps* may determine apomorphies distinguishing the former species from the latter. We rediagnose *Captorhinus aguti* by the presence of multiple rows of teeth that are aligned divergently across dental laminae. The sister-group relationship between these two taxa also provides the opportunity to rediagnose the genus itself. *Captorhinus* was diagnosed heretofore by the presence of multiple rows of teeth (Seltin 1959; Fox and Bowman 1966; Clark and Carroll 1973; Heaton 1979), which we interpret instead as an autapomorphy of *C. aguti*. We redefine the genus *Captorhinus* on the basis of the following apomorphies:

1. Alary process of jugal positioned dorsally on medial surface and flush with orbital margin (8).
2. Retroarticular process longer antero-posteriorly than broad (33).
3. Anteriormost dentary tooth strongly procumbent (39).

Despite the presence of relatively strong relationships between some captorhinid taxa, we have not been able to improve upon certain aspects of captorhinid phylogeny. The weakest part of the tree is the position of *Rhiodenticulatus*, as node C is diagnosed by a single apomorphy. Interestingly, it takes only one more step for *Rhiodenticulatus* to either exchange positions with *Protocaptorhinus*, or for these two taxa to form a clade. Since the anatomy of *Rhiodenticulatus* is reasonably well known, it is entirely possible that future studies on basal captorhinids will alter the position of *Rhiodenticulatus* within Captorhinidae. Furthermore, the status of two characters recognized traditionally as captorhinid apomorphies, the absence of the ectopterygoid and the presence of a medial process of the jugal, is regarded here as ambiguous. Neither character can be determined faithfully in any of the specimens assigned to *Romeria*, whereas only the latter was detected by Heaton (1979) in *Protocaptorhinus*. Re-examination of these two taxa should resolve the uncertainty regarding such problematical characters.

Lastly, we note in the description that *Labidosaurikos* shares several apomorphies with *Gecatogomphius*, *Moradisaurus*, *Rothianiscus*, *Captorhinikos* and *Kahneria*, implying that they form a clade (the 'Moradisaurinae' of Ricqlès and Taquet 1982). However, despite an unprecedented high number of new cranial apomorphies revealed by our redescription, the available literature on other large, multiple-rowed captorhinids is so poor that we could not identify a single unambiguous autapomorphy for *Labidosaurikos meachami*. These multiple-rowed forms need to be restudied in order to identify unambiguous autapomorphies for *Labidosaurikos meachami* and to determine the exact relationships of these taxa to *Labidosaurikos* and *Labidosaurus*. Additional work on multiple-rowed captorhinids may result in modifications to the phylogeny presented here, or at least change the distribution of the character states. Furthermore, it is quite possible that future studies may determine that some of the more problematical captorhinid species (those represented by partial, fragmentary remains) may be recognized as junior synonyms of better known taxa.

Diet

Stovall (1950) refrained from speculating upon the probable diet of *Labidosaurikos*. Indeed, no one has cared to discuss the diet of the large, multiple-rowed captorhinids except Olson (1955, 1971), who regarded them as herbivores. The morphology of the tooth plates and other aspects of the skull support the hypothesis that *Labidosaurikos* was herbivorous.

In general, the tooth plate teeth are relatively small, isodont, and bear prominent wear facets. When the jaws were adducted, the mandibular tooth rows would have rested between maxillary tooth rows. Comprised of relatively small, serially repeated teeth, the tooth plates of *Labidosaurikos* present multiple contact points that could pass one another in a single motion, a feature necessary for shredding fibrous plant material (Throckmorton *et al.* 1981). For shredding to occur, propalinal jaw movement must be possible. Not surprisingly, propaliny has been identified in several early herbivorous tetrapod lineages (Throckmorton *et al.* 1981; King *et al.* 1989; Olson *et al.* 1991). Striation patterns on wear facets have been used to determine the direction of mandibular motion in both reptiles and mammals (Greaves 1973; Weishampel 1983). Unfortunately, no striations are visible on the teeth of *Labidosaurikos* under light microscopy. Evidence for propalinal jaw movement in this reptile instead must be determined from non-dental evidence.

In their investigation of herbivory in dicynodont therapsids, King *et al.* (1989) established the ability of the quadrate to slide antero-posteriorly over the articular as the most important evidence for propaliny. Unfortunately, the articulating surfaces of the quadrate and articular are damaged in the holotype of *Labidosaurikos*, and it is uncertain to what extent propaliny may have been present. Fore-and-aft movement of the lower jaw has been proposed for two other captorhinids. The morphology of the suspensorium in *Moradisaurus* suggests strongly that the lower jaw of that genus was capable of fore-and-aft translation (Ricqlès and Taquet 1982). Similarly, Heaton (1979) suggested that propaliny was also present in *Captorhinus*. However, examination of quadrates and articulars from the Fort Sill locality that are referable to *Captorhinus* suggests that this is not the case. The observation that the articular of *Labidosaurikos* resembles more closely that of *Moradisaurus* than those of more basal captorhinids suggests that the suspensorium of the former genus also may have fostered propaliny. Regardless, determination of whether the jaw articulation of *Labidosaurikos* was osteologically capable of propaliny must await better preserved material.

There is additional osteological evidence that may suggest the presence of propaliny in *Labidosaurikos*. Apart from the jaw articulation morphology, King *et al.* (1989) noted that the adductor musculature must have been arranged appropriately in dicynodonts to effect relative movement of the lower jaw. The antero-posteriorly elongate temporal fenestrae of dicynodonts was interpreted by King *et al.* (1989) to suggest that the jaw adductor muscles originating in the temporal region were angled sufficiently to draw the lower jaw posteriorly. Although the anapsid condition of captorhinids precludes comparison with the synapsid condition of dicynodonts, the temporal region of the skull roof of *Labidosaurikos* does differ from those of *Labidosaurus*, *Captorhinus* and the more basal captorhinids in that it is notably vaulted. This doming, formed mainly by the paired parietals, but expressed also in the unusual posterior expansion of the occipital flange of the squamosal, suggests that the majority of muscle fibres of the adductor mandibulae muscles arising from this region would have inserted onto the coronoid process at an angle of approximately 45° to the horizontal. If this interpretation is correct, this arrangement of the jaw adducting musculature would have served adequately to draw the lower jaw posteriorly in what was presumably the power stroke of propalinal jaw action. The fibres arising from the skull roof were presumably better positioned for effecting and controlling relative movement of the lower jaw than those arising from the palate, which probably served to draw the mandible forwards in recovery. The slightly greater ventral incline of the pterygoid transverse flange of *Labidosaurikos* with respect to the orientation observed for those of *C. aguti* and single-rowed captorhinids supports the latter hypothesis. A more extreme anterior positioning of this flange in dicynodonts was thought by King *et al.* (1989) to be associated directly with propaliny in these synapsids.

The hypothesis of herbivory attributed here to *Labidosaurikos* can be extended to other large,

multiple-rowed captorhinids. The tooth plates of *Captorhinikos*, *Rothianiscus*, *Moradisaurus* and *Gecatogomphius*, although differing from one another and those of *Labidosaurikos* in terms of tooth size, number of tooth-rows and relative size, share a fundamental organization that suggests they were used for the same purpose: the mechanical breakdown of fibrous plant matter. However, additional research on these forms is needed to confirm this hypothesis. Future work on these long-neglected taxa should elucidate further the hypothesis of herbivory attributed to these early reptiles.

Labidosaurikos meachami and its multiple-rowed relatives represent the culmination of a series of morphological changes in the family Captorhinidae that resulted ultimately in a worldwide radiation as herbivores. Heaton and Reisz (1981) and Dilkes and Reisz (1986) have commented upon the lack of variation in captorhinid postcranial anatomy with respect to that seen in other early amniote groups. It is quite possible that this conservative nature, associated with an adaptation to herbivory, may have been responsible for the success of the captorhinids during the Permian.

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J. T. DODICK[1]

S. P. MODESTO

Department of Zoology
Erindale College
University of Toronto
Mississauga
Ontario, Canada L5L 1C6

[1] Present Address:
The Weizmann Institute of Science
P.O.B. 26
Rehovot 76100, Israel

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ABBREVIATIONS USED IN THE TEXT-FIGURES

a	axis	f	frontal	pf	postfrontal	s	stapes
aa	axis neural arch	j	jugal	pl	palatine	sa	surangular
an	angular	l	lacrimal	prm	premaxilla	sm	septomaxilla
ar	articular	m	maxilla	po	postorbital	so	supraoccipital
bo	basioccipital	n	nasal	pp	postparietal	sp	splenial
bps	basiparasphenoid	op	opisthotic	prf	prefontal	sq	squamosal
c	coronoid	p	parietal	pro	proötic	st	supratemporal
d	dentary	pa	proatlas	pt	pterygoid	v	vomer
e	epipterygoid	pra	prearticular	q	quadrate		
ex	exoccipital			qj	quadratojugal		

APPENDIX 1

Description of characters used in the phylogenetic analysis: primitive character states are denoted by 0, and derived states are indicated by 1 or 2.

1. Premaxilla: ventral margin aligned antero-posteriorly (0) or antero-ventrally (1) in lateral view.
2. Maxilla: relatively straight (0) or posterior end flexed laterally (0).
3. Maxilla: posteriormost tooth positioned at level of posterior margin of (0) or positioned at level of midpoint of (1) orbit.
4. Lacrimal: suture with jugal small (0) or well developed (1).
5. Snout: broad, equal to or greater than 35 per cent. of skull length (0) or narrow, equal to or less than 25 per cent. of skull length (1).
6. Prefrontal: anterior process short and tall, approximately equal to the posterodorsal process in antero-posterior length (0) or long and narrow, approximately twice the antero-posterior length of the posterodorsal process (1).
7. Frontal: anterior process short, less than 40 per cent. of the frontal sagittal length (0) or long, approximately 55 per cent. of the frontal sagittal length (1).
8. Jugal: alary process absent (0), present and positioned no higher than the midpoint of the suborbital process of the jugal and distinct from orbital margin (1), or positioned dorsally on the medial surface of the jugal and flush with orbital margin (2).
9. Quadratojugal: antero-posteriorly elongate (0) or short, not extending anteriorly beyond midpoint of postorbital region (1).
10. Quadratojugal: acuminate (0) or square-tipped (1) anteriorly.
11. Postorbital cheek: relatively straight (0) or expanded laterally (1).
12. Supratemporal: contact with postparietal tenuous (0) or well developed (1).
13. Pineal foramen: positioned at (0) or anterior to (1) midpoint of interparietal suture.
14. Postparietal: contacts mate fully along height (0) or dorsally only, postparietals separated slightly ventrally by supraoccipital (1).
15. Postparietal: transversely short with tabular present (0) or transversely elongate with tabular absent (1).
16. Skull table occipital margin: embayed bilaterally (0), straight (1), or with single median embayment (2).
17. Ectopterygoid: present (0) or absent (1).
18. Pterygoid: transverse flange broad-based and distinctly angular (0) or narrow and tongue-like (1) in ventral view.
19. Parasphenoid: deep ventral groove absent (0) or present (1) between cristae ventrolateralis.
20. Cultriform process: extends anteriorly (0), extends slightly dorsally at roughly 15° to the basal plane (1), or extends anterodorsally at more than 45° to the basal plane (2).
21. Supraoccipital: slopes anterodorsally (0), or vertically (1), or is angled posterodorsally (2).
22. Supraoccipital: lateral ascending processes account for half or less (0) or two-thirds or more (1) of the height of the bone.
23. Occipital condyle: at level of (0) or immediately anterior to (1) quadrate condyles.
24. Paroccipital process: short (0) or rod-like (1).
25. Sculpturing: consists of small honeycombing pits and grooves (0) or of pits and grooves with notably larger, randomly positioned pits on posterior skull table (1).

26. Mandibular ramus: relatively straight (0) or sigmoidal (1) in ventral view.
27. Mandibular ramus: narrow, 8 per cent. or less of total jaw length (0) or broad, no less than 14 per cent. of total jaw length (1).
28. Mandibular ramus: posterior end rectilinear (0) or acuminate (1) in lateral view.
29. Mandibular ramus: lateral shelf absent (0) or present (1) below coronoid process.
30. Coronoid: anterior process short (0) or elongate (1).
31. Meckelian foramen: small, antero-posterior length roughly 9 per cent. or less of total jaw length (0) or large, antero-posterior length greater than or equal to 14 per cent. of total jaw length (1).
32. Coronoid posterodorsal process: slender, forms dorsalmost quarter of lateral wall of adductor fossa (0) or deep, forms dorsalmost third of lateral wall of adductor fossa (1).
33. Retroarticular process: absent (0), present and broader transversely than long (1), or present and longer antero-posteriorly than broad (2).
34. Maxillary dentition: tooth stations number 30 teeth or more (0) or 25 or less (1); for multiple-rowed taxa, only those teeth with unobstructed profiles when viewed laterally are considered.
35. Maxillary caniniform teeth: present (0) or absent (1).
36. Multiple tooth rows: absent (0) or present (1).
37. Marginal dentition: 'cheek' teeth conical (0) or chisel-shaped (1).
38. Dentary: teeth isodont (0), caniniform region present anteriorly (1), or caniniform tooth present anteriorly with caniniform region absent (2).
39. Dentary: first tooth oriented mainly vertically (0) or leans strongly anteriorly (1).

APPENDIX 2

Distribution of character states among the seven captorhinids examined in the analysis. The numbers in the top column (1–39) refer to the characters described in Appendix 1. A question mark indicates that the character state could not be determined because of missing data.

Character number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taxon:																				
Protorothyris	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
Romeria	1	1	0	0	0	0	0	?	1	0	0	0	1	0	1	0	?	0	0	0
Protocaptorhinus	1	1	0	?	0	0	0	1	1	0	0	0	1	1	1	1	?	0	0	0
Rhiodenticulatus	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0	0	0
C. laticeps	1	1	1	1	0	0	0	2	0	1	1	0	1	1	1	2	1	1	1	1
C. aguti	1	1	1	1	0	0	0	2	0	1	1	0	1	1	1	2	1	1	1	1
Labidosaurus	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	2	1	1	1	2
Labidosaurikos	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	2	1	1	1	2

Character number:	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Taxon:																			
Protorothyris	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Romeria	0	?	0	?	?	0	0	0	0	?	?	?	0	1	0	0	0	1	0
Protocaptorhinus	0	0	0	1	0	0	0	0	0	?	?	?	1	1	0	0	0	?	0
Rhiodenticulatus	?	0	0	?	?	0	0	0	0	1	?	?	?	1	0	0	0	1	0
C. laticeps	0	0	0	1	0	0	0	1	0	1	0	0	2	1	0	0	1	1	1
C. aguti	0	0	0	1	0	0	0	1	0	1	0	0	2	1	0	1	1	1	1
Labidosaurus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	2	0
Labidosaurikos	2	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	2	0