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The skull and the palaeoecological significance of *Labidosaurus hamatus*, a captorhinid reptile from the Lower Permian of Texas

SEAN P. MODESTO[1]*, DIANE M. SCOTT[2], DAVID S. BERMAN[1], JOHANNES MÜLLER[2] and ROBERT R. REISZ[2]

[1]*Section of Vertebrate Palaeontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213, USA*

[2]*Department of Biology, University of Toronto in Mississauga, Mississauga, Ontario L5L 1C6, Canada*

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The cranial skeleton of the large captorhinid reptile *Labidosaurus hamatus*, known only from the Lower Permian of Texas, is described on the basis of new, undescribed specimens. *Labidosaurus* is distinguished from other captorhinids by the more extreme sloping of the ventral (alveolar) margin of the premaxilla, a low dorsum sellae of the parabasisphenoid, a reduced prootic, a narrow stapes, and a relatively small foramen intermandibularis medius. Despite the presence of a single row of teeth in each jaw, the skull of *Labidosaurus* resembles most closely those of moradisaurines, the large multiple-tooth-rowed captorhinids of the latest Early and Middle Permian. A phylogenetic analysis confirms that the single-tooth-rowed *L. hamatus* is related most closely to moradisaurines within Captorhinidae, a relationship that supports the hypothesis of a diphyletic origin for multiple rows of marginal teeth in captorhinids (in the genus *Captorhinus* and in the clade Moradisaurinae). In view of the close relationship between *L. hamatus* and moradisaurines, which are regarded to have been herbivorous, *L. hamatus* is a critical taxon for studies of the evolution of herbivory in early tetrapods. *L. hamatus* shares several trademark features of herbivorous adaptation with moradisaurines, which suggest that this captorhinid species was omnivorous. As such, it represents a transitional taxon between faunivorous basal reptiles and the herbivorous moradisaurines.

ADDITIONAL KEYWORDS: Captorhinidae – herbivory – Reptilia.

INTRODUCTION

Captorhinids were the most conspicuous reptiles of the North American Early Permian. By the end of the Middle Permian (*sensu* Jin *et al*., 1997) these basal reptiles had spread across much of Pangaea, with representative taxa present in what is now Europe (Ivakhnenko, 1990), Asia (Kutty, 1972), and Africa (Gaffney & McKenna, 1979; de Ricqlès & Taquet, 1982; Jalil & Dutuit, 1996). Recent discoveries in Africa (Gow, 2000; Modesto & Smith, 2001) indicate that captorhinid evolution progressed without abatement thoughout the Middle Permian, when terrestrial vertebrate ecosystems underwent dramatic changes as therapsid synapsids succeeded their 'pelycosaurian' predecessors. Undescribed multiple-tooth-rowed jaw fragments from an uppermost Permian fissure-fill deposit in central Europe (Sues & Munk, 1996) may represent the youngest known captorhinid.

Captorhinids have been indispensable components of anatomical and phylogenetic studies of early amniotes, primarily because the skeletal anatomy of one particular captorhinid species, *Captorhinus aguti* from the Lower Permian of Texas and Oklahoma, is known in great detail (Fox & Bowman, 1966; Holmes, 1977, 2003; de Ricqlès & Bolt, 1983; Modesto, 1998). The clade Captorhinidae has been of interest from an evolutionary point of view not only because of its basal position within Reptilia, but also because it probably includes some of the oldest known herbivorous reptiles (Hotton, Olson & Beerbower, 1997; Reisz & Sues,

*Corresponding author. Current address: Cape Breton University, 1250 Grand Lake Road, Sydney, Nova Scotia, B1P 6L2, Canada. E-mail: sean_modesto@capebretonu.ca

2000). In association with the development of this hypothesized herbivorous lifestyle, a highly specialized dentition consisting of multiple rows of marginal teeth is present in many species. The first PAUP analysis of representative captorhinid taxa suggested strongly that multiple rows of teeth evolved twice within the group (Dodick & Modesto, 1995). It is now clear that the multiple-rowed dentition of *C. aguti* was acquired independently from that present in the larger multiple-tooth-rowed moradisaurines (Dodick & Modesto, 1995; Kissel, Dilkes & Reisz, 2002). The latter captorhinids were a speciose clade of relatively large herbivorous reptiles that appear to have originated in western Euramerica (what is now North America), and by the late Middle Permian had ranged as far as eastern Euramerica and northern Gondwana (Modesto & Rybczynski, 2000).

One of the most commonly mentioned captorhinids is *Labidosaurus hamatus*, from the Lower Permian Clear Fork Group of Texas. For instance, Lucas (2002) used the first appearance of this reptile to mark the onset of his 'faunachron D' in a biochronology based on Permian tetrapods. *L. hamatus* is a relatively large species with a maximum skull length of about 20 cm, which makes it the largest known single-tooth-rowed captorhinid. Whereas the postcranial skeleton of this captorhinid is now known in appreciable detail (Sumida, 1987, 1989, 1991), the skull has not been described since the work of Williston (1910) and Case (1911), apart from brief descriptions of the dentition (Heaton, 1979; Olson, 1984). This is unfortunate, because *L. hamatus* is also represented by several excellent skulls. A detailed understanding of the skull structure of *L. hamatus* is necessary in order to re-examine in a rigorous manner the hypothesis that this captorhinid is the closest relative of moradisaurines. Accordingly, we redescribe the structure of the skull and the mandible of *L. hamatus* in this paper.

SYSTEMATIC PALAEONTOLOGY

REPTILIA LAURENTI, 1768

CAPTORHINIDAE CASE, 1911

LABIDOSAURUS COPE, 1896

Type species: L. hamatus (Cope, 1895).

Diagnosis: Same as for *L. hamatus*, the only valid species.

Comment: Case (1911) erected *Labidosaurus broilii* for a specimen described by Broili (1904) and reposited in the Alte Akademie, Munich, and differentiated it from the type species on the basis of the subequal size of the first two premaxillary teeth. Seltin (1959) demonstrated that there is considerable variation in the relative size of these teeth in *C. aguti*, and concluded that *L. broilii* was an 'indeterminate' species, which we have interpreted to mean it is a junior synonym of *L. hamatus*. Seltin (1959) erected *Labidosaurus oklahomensis* for a small single-tooth-rowed captorhinid specimen from the McCann Quarry, Oklahoma, but this taxon is now recognized as a junior synonym of *Captorhinus laticeps* (Heaton, 1979: fig. 4).

LABIDOSAURUS HAMATUS COPE, 1895

Diagnosis: A single-tooth-rowed captorhinid distinguished by the following features: extreme angulation of the alveolar margin of the premaxilla, at roughly 45° to the long axis of the maxillary alveolar margin; a low dorsum sellae; an extensive, thin sagittal flange of the dorsum sellae that deeply invades the retractor pit and sella turcica; lateral exposure of prootic greatly reduced by the stapedial and opisthotic contacts and equal to about one-third of the entire lateral portion of the bone; slender stapes; and a small intermeckelian medius foramen that is bounded anteriorly by a small postsymphysial dorsal extension of the splenial.

Holotype: AMNH 4341 (American Museum of Natural History, New York, NY, USA), a complete skull.

Material examined: CM 73370 (Carnegie Museum of Natural History, Pittsburgh, PA, USA) (formerly 'UCLA VP 3167'; Vertebrate Palaeontology Collections, University of California, Los Angeles, CA, USA), greater part of an articulated skeleton that includes a complete, undistorted skull with tightly closed mandible; CM 73371 (formerly 'UCLA VP 3200'), greater part of an articulated skeleton that includes a complete, obliquely compressed skull, with partly detached left and fully detached right mandibular rami; CM 76876, a partial right mandibular ramus; FMNH UR 161 (Field Museum of Natural History, Chicago, IL, USA), a complete skull with detached braincase; MCZ 8727 (Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA), a nearly complete skull that has undergone extreme dorsoventral compression.

Horizon and geographical provenance: Lowermost strata (the 'Arroyo Formation' of early literature) of the Clear Fork Group, Texas; Leonardian (= Artinskian), Lower Permian. CM 73370, 73371, and 76876, and FMNH UR 161 were collected by E. C. Olson from his '*Labidosaurus* pocket' locality (Coffee Creek, Baylor County, TX, USA). Specific locality data is missing for MCZ 8727, which was collected by 'Chas. H. Sternberg during 1882 in NW Texas' (C. Schaff, pers. comm., 2005).

DESCRIPTION

Several complete skulls of *Labidosaurus* are available and allow a comprehensive cranial reconstruction in several views (Fig. 1; see the Appendix for a list of the anatomical abbreviations used in this and subsequent figures), which depict a typically captorhinid construction, retaining such features as the downturned premaxilla, the heart-shaped skull, and the characteristic sutural patterns that are readily evident in smaller captorhinids (e.g. species of the genus *Captorhinus*). On the other hand, *Labidosaurus* exhibits many characteristics that are shared with large multiple-rowed captorhinids (e.g. *Labidosaurikos*). These include the relatively narrow muzzle, modifications of the circumorbital elements associated with the achievement of a relatively large size, and the morphology of the braincase and its position relative to the skull roof.

Skull roof

The premaxilla (Figs 2, 3, 4) of *Labidosaurus* is distinguished from those of other single-rowed captorhinids by its relatively large size and conspicuous downward flexure. Its relatively large size is illustrated by the observation that the subnarial height of the premaxilla is almost one and a half times the height of the maxilla at its tallest point, whereas in *C. aguti* the two dimensions are roughly equal. The ventral margin of the premaxilla is angled at approximately 45° relative to the ventral margin of the maxilla, whereas this angle is about 35° in *C. aguti*. As a consequence of the extreme angulation of the alveolar margin, the anterior surface of the premaxilla projects approximately 1 cm beyond the first tooth. The premaxilla forms a deeply serrate suture with the nasal, resulting in the dorsal and alary processes being exceedingly slender. Four or five teeth are present, with the first being the largest and the series exhibiting a progressive and dramatic decrease in tooth size posteriorly. Except for their larger size, the teeth are essentially identical to those of *Captorhinus* (Heaton, 1979; de Ricqlès & Bolt, 1983).

Apart from tooth morphology and organization, the maxilla (Figs 2, 3, 4) of *Labidosaurus* appears intermediate in morphology between those of *Captorhinus* and *Labidosaurikos*. For example, it is more elongate than the maxilla of the former genus, but it is not quite as elongate as the maxilla of the latter. Similarly, the dorsal lamella, which is relatively high in *Captorhinus* (with respect to the point where the suture with the lacrimal meets that with the jugal) and almost non-existent in *Labidosaurikos*, appears to be intermediate in relative height between these two conditions. The maxilla maintains contacts typical of other captorhinids with the surrounding elements of the skull roof and palate. Unlike the maxilla of *Captorhinus* and those of other small captorhinids, the maxilla of *Labidosaurus* exhibits no lateral flexure, but rather it is gently curved posteriorly in ventral view. The normal complement of teeth is 22, arranged in a single row from immediately posterior to the contact with the premaxilla to a point just anterior to the level of the suborbital foramen. The teeth are slightly compressed labiolingually and range in basic shape from conical pegs at the anterior end of the series, to stouter, more chisel-like structures posteriorly. There is no caniniform tooth or region, although the teeth exhibit a progressive serial decrease in size, both anteriorly and posteriorly, from subequal maximums exhibited by approximately the fourth through eighth teeth.

Heaton (1979) reconstructed the septomaxilla of *Captorhinus* (*Eocaptorhinus*) *laticeps* as a curved, sheet-like element, but his specimen drawings do not support this interpretation. Heaton (1979: 23) remarked that the septomaxillae of other early reptiles conformed to his description of this element, but the septomaxilla of *Labidosaurus* is an irregularly convoluted bone (Fig. 3). The floor of the external naris is sheathed by a ventral lamina, which has a peaked medial process. The latter gives rise to a dorsal bulbous expansion that lies within the posterodorsal corner of the external naris. There is no facial process of the dorsal bulbous portion, as seen in *Labidosaurikos* (Dodick & Modesto, 1995).

In keeping with the narrow snout, the nasal (Figs 2, 3, 4) is relatively slender compared with that of *Captorhinus* (Heaton, 1979; Modesto, 1998). The suture with the premaxilla is better developed than in that genus, with anterior processes of the nasal extending far anteroventrally over the external surface of the premaxilla. The pattern of sculpturing is almost identical to that seen in *Captorhinus*, ranging from a simple, roughened surface with a few small pits anteriorly to short, nearly parallel furrows posteriorly.

The lacrimal (Figs 2, 3, 4) is a distinctly elongate element and, apart from minor differences in the suture with the nasal, closely resembles that of *Labidosaurikos*. The elongation appears to be a product of the reduction in the total relative height of the snout, in combination with the reduction in the relative size of the orbit. The posteroventral process is well developed, although it does not reach as far ventrally as in *Captorhinus* (Heaton, 1979), and has a deep overlapping suture with the jugal.

A long and narrow prefrontal was one of the synapomorphies used by Dodick & Modesto (1995) to diagnose the sister-group relationship between *Labidosaurus* and *Labidosaurikos*. Their description of this bone in *Labidosaurus* (and in *Labidosaurikos* for that matter) is not entirely correct. The prefrontal (Figs 2, 3, 4) does not appear relatively long compared with that

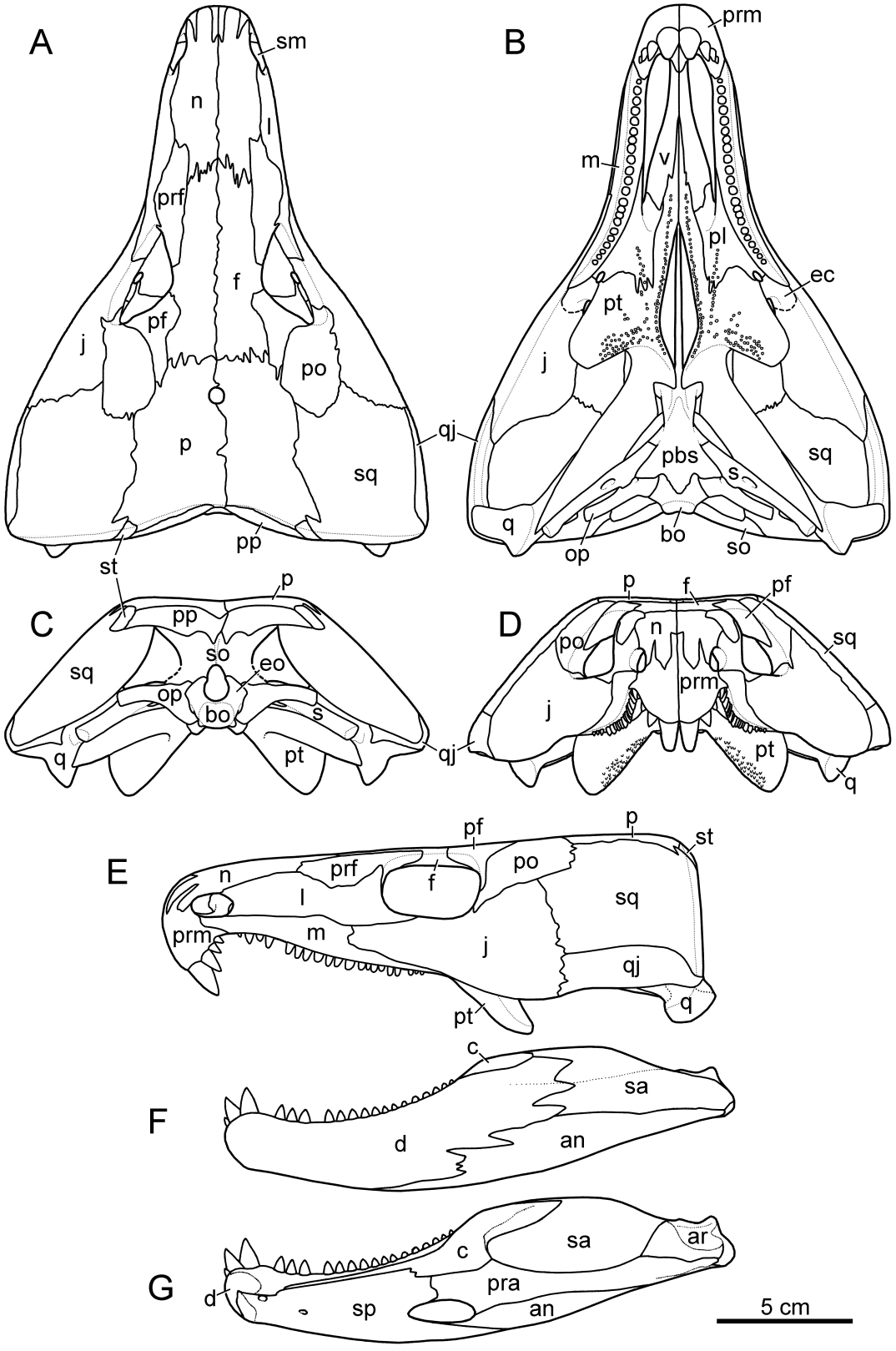

Figure 1. Reconstruction of the skull of *Labidosaurus hamatus* in dorsal (A), ventral (B), occipital (C), anterior (D), and lateral (E) views, and of the mandible in lateral (F) and medial (G) views.

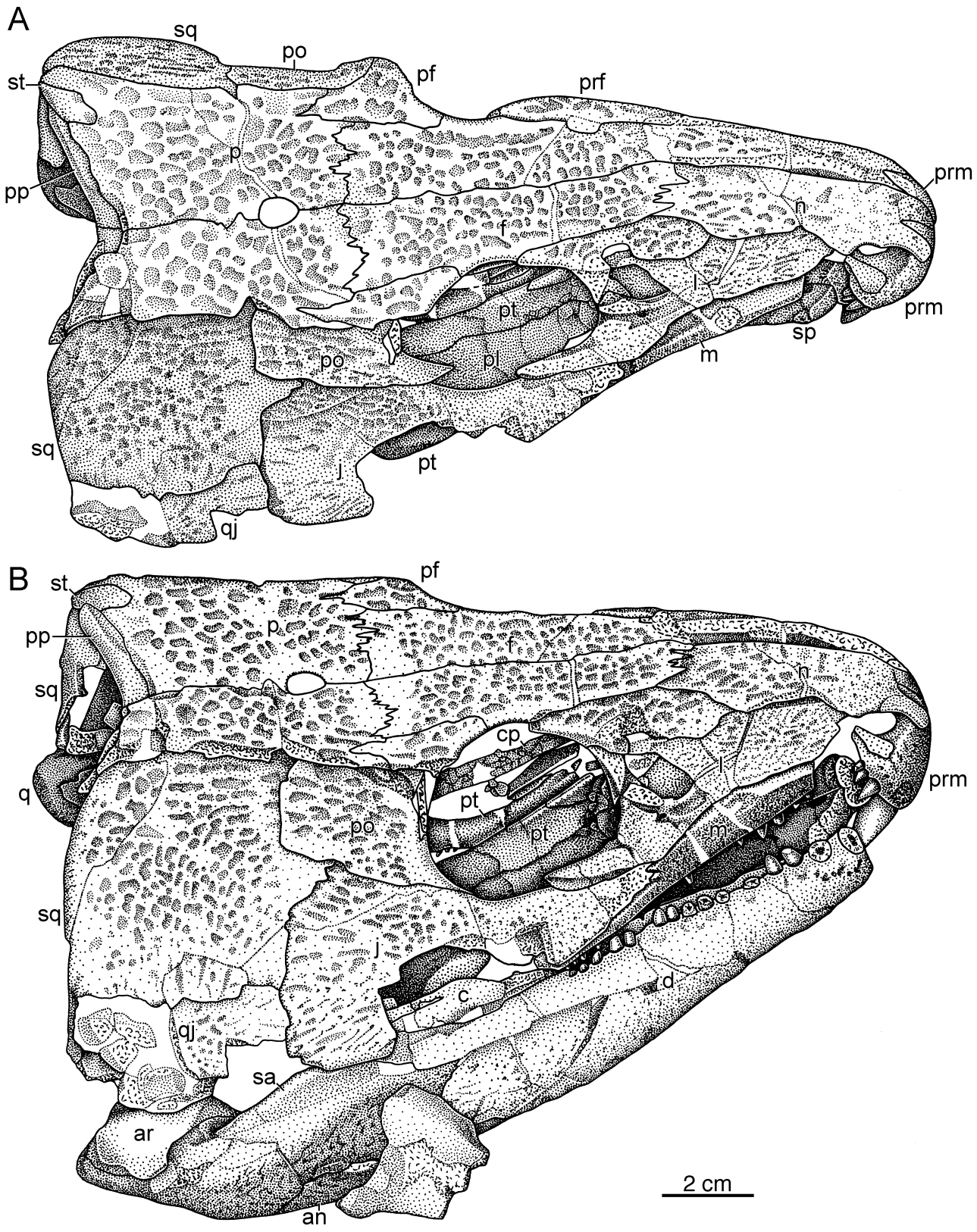

Figure 2. *Labidosaurus hamatus*, CM 73371. Skull in dorsal view (A) and skull with mandible in right lateral view (B).

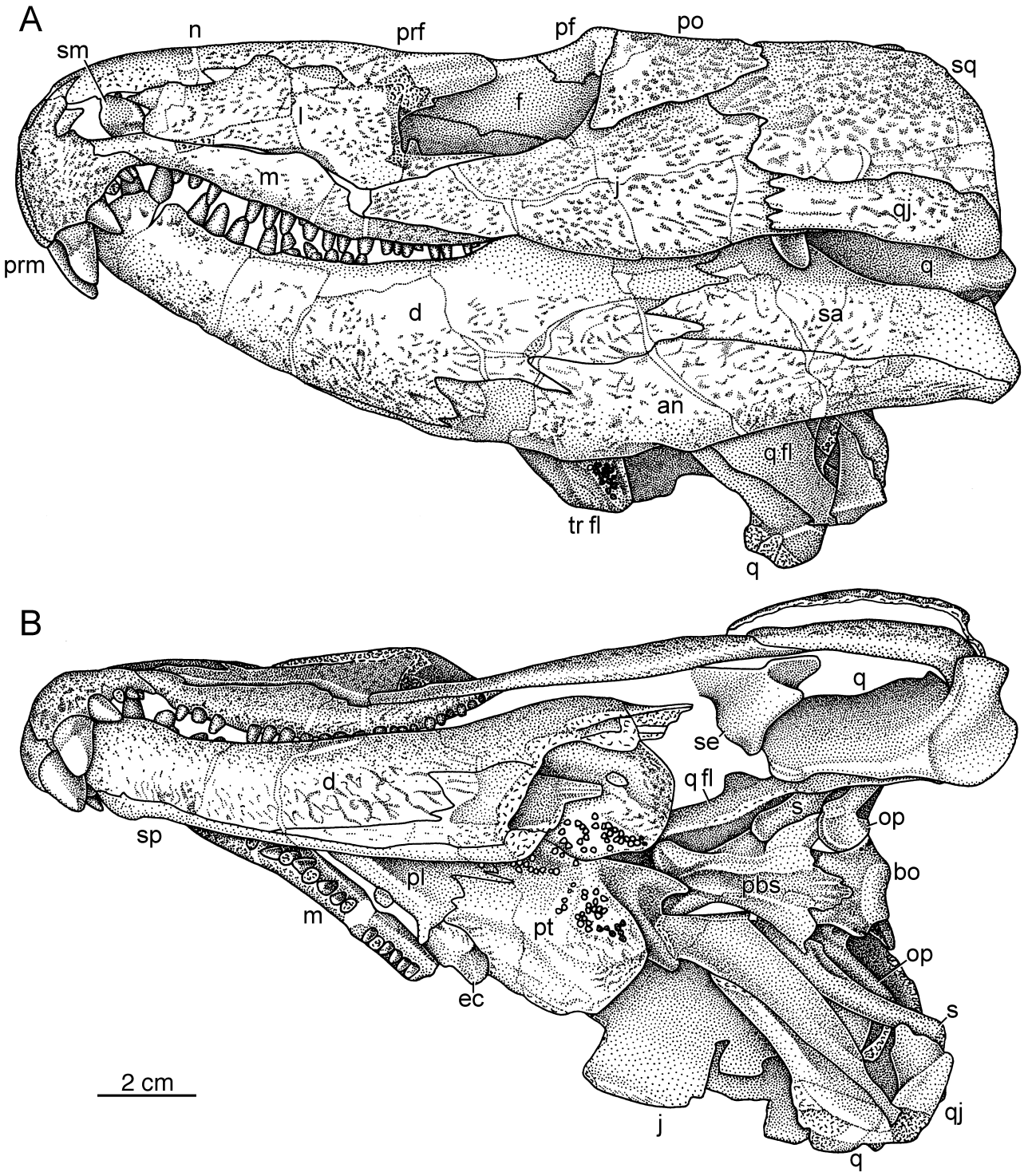

Figure 3. *Labidosaurus hamatus*, CM 73371. Skull and mandible in left lateral view (A) and skull and partial right mandibular ramus in ventral view (B); the left mandibular ramus and posterior portion of the right ramus have been removed to reveal the palate and the braincase.

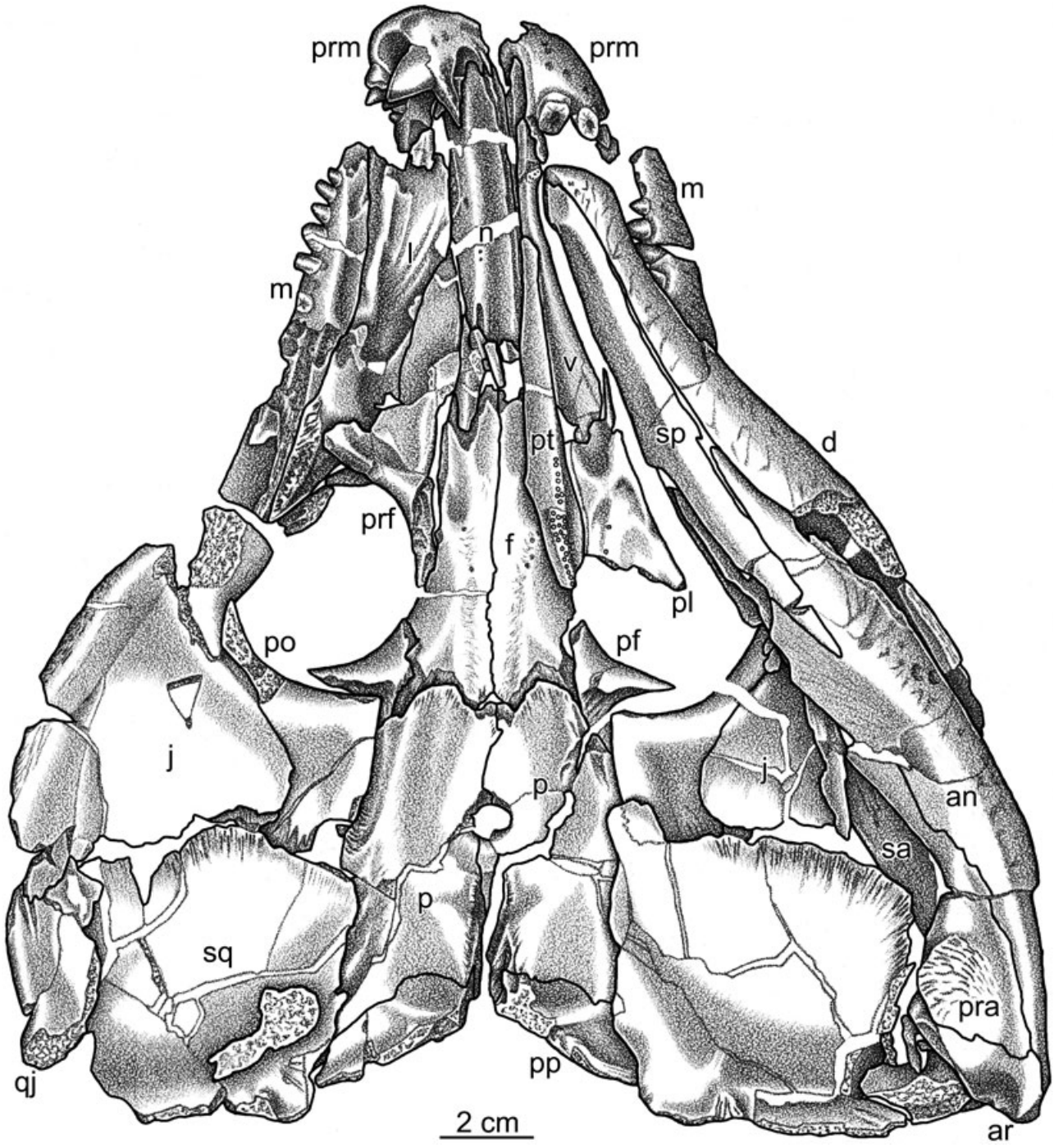

Figure 4. *Labidosaurus hamatus*, MCZ 8727. Skull roof and left mandibular ramus in ventral view.

of *Captorhinus* (and, by extension, those of other small captorhinids), because the prefrontal extends anteriorly approximately halfway along the dorsal margin of the lacrimal to the external naris in all three captorhinid genera. It appears that Dodick & Modesto (1995) were misled by Heaton's interpretation of the prefrontal in his erroneous reconstructions of the skull of *C.* (*Eocaptorhinus*) *laticeps* in both lateral and oblique (isometric) views [Heaton, 1979: fig. 2(D, I)]. Here, he shows an anteroposteriorly short prefrontal that does not agree with either the morphology shown in his reconstruction in dorsal view (Heaton, 1979: fig. 2A), or that seen in his specimen drawings. The prefrontal of *Labidosaurus* is slightly less broad (or deep)

than that of *Captorhinus*, and this is undoubtedly related to the relatively narrower snout of the former genus. The prefrontal of *Labidosaurus* ends posteroventrally with a truncated tip, as in *Labidosaurikos* and *Protocaptorhinus* (Clark & Carroll, 1973: fig. 14), which defines the anterior border of the lateral frontal lappet. The prefrontals of captorhinids such as *Captorhinus* (Heaton, 1979; Modesto, 1998) and *Sauroricus* (Modesto & Smith, 2001) feature more acuminate posterodorsal processes.

Relative to its length, the frontal of *Labidosaurus* (Figs 2, 3, 4), like that of *Labidosaurikos*, is conspicuously narrower than that of *Captorhinus* (Modesto, 1998). The frontal can be divided into three regions: a central portion that contributes to the orbital margin, and larger anterior and posterior portions. Relative to the midline length of the skull roof, the middle portion of the frontal is positioned slightly farther posterior than in *Captorhinus*, resulting in a relatively longer anterior process and shorter posterior process. Concomitant with the relatively smaller orbit in *Labidosaurus*, the contribution of the frontal to the orbital margin is roughly 8% of the midline length of the frontal, whereas the same measurement in *Captorhinus*, with its relatively larger orbit, is approximately 12%. The frontal of *Labidosaurus* also has a narrow lateral lappet, a feature that it shares with *Labidosaurikos*, *Romeria*, *Protocaptorhinus*, and large individuals of *Captorhinus* (Heaton, 1979: fig. 20). Despite being greater in absolute size, the frontal of *Labidosaurus* is slightly less densely sculptured with the characteristic pits and short furrows as are the frontals of the various species of *Captorhinus* (Heaton, 1979; Modesto, 1998; Kissel *et al*., 2002).

Both the postfrontal and the postorbital of *Labidosaurus* (Figs 2, 3, 4) appear to be more or less larger versions of these elements in the smaller captorhinids, such as *Captorhinus* (Heaton, 1979). The density of dermal sculpturing on the postfrontal, however, is slightly less than that in smaller captorhinids.

In most respects the jugal of *Labidosaurus* (Figs 2, 3, 4) is indistinguishable from that of *Labidosaurikos*. In both genera the jugal resembles that of smaller captorhinids in its general morphology, but features a relatively deeper subtemporal process, which forms approximately 40–45% of the height of the skull as measured through the orbital midpoint. Judging from MCZ 8727, in which this bone is nearly fully exposed, the morphology of the jugal of *Labidosaurus* departs from that of other captorhinids in its lack of a medial, alary process. In other captorhinids in which the jugal is known completely, the jugal bears an alary process that occupies the position of the absent ectopterygoid, contacts both the palatine and the pterygoid, and forms the posterior half of the suborbital foramen. In CM 73371, however, what appears to be an ectopterygoid is present (Fig. 3B), and it occupies the position of the alary process, and presumably contacted a rugose oval patch on the medial surface of the jugal, as seen in MCZ 8727 (Fig. 4). Thus, the jugal of *Labidosaurus* makes direct contact with the palate via its contacts with the palatine and the ectopterygoid (Fig. 2), rather than via contacts with the palatine and the pterygoid as in other captorhinids.

The parietal of *Labidosaurus* (Figs 2, 4) is essentially a larger version of the parietal of *Captorhinus* (e.g. Heaton, 1979). The most notable difference with the parietal of the latter genus is that the parietal of *Labidosaurus* is slightly narrower relative to its length. The pineal foramen is relatively small, occupying approximately 11% of the midline length of the parietal, which is matched by that in *Labidosaurikos* (Dodick & Modesto, 1995); the same measurement ranges between 15 and 20% in *Captorhinus* judging from the specimen drawings of Heaton (1979). As in those genera, the pineal foramen of *Labidosaurus* is positioned in the anterior third of the interparietal suture. Its position appears to be farther anteriorly than in *Captorhinus*, but this may be an illusion resulting from the relatively smaller size of the opening in *Labidosaurus*: in both genera, approximately 20% of the interparietal suture lies anterior to the pineal foramen. The same measurement in *Labidosaurikos* is 13%, which is consistent with the hypothesis of Dodick & Modesto (1995) that the slightly more anterior position of the pineal foramen they observed is related to the anterior displacement of the braincase in this moradisaurine. The posterolateral corner of the parietal has a shallow notch for the reception of the supratemporal and a small triangular process of the squamosal. The dermal sculpturing in *Labidosaurus* is consistent with that seen in most other captorhinids, except for the additional presence of a few pits in the parietal that are conspicuously larger than the usual ridge-and-pit excavations, a condition that is shared with *Labidosaurikos*.

As in all captorhininds, the postparietal (Figs 2, 4, 5) is transversely expanded, occupies the space where the tabular is present in other early reptiles, and contacts most of the posterior margin of the parietal. In posterior view the postparietal is wing-like, curving slightly throughout its length as it tapers laterally. The midline contact of the postparietals is slightly interposed ventrally by the supraoccipital, which underlies most of the length of the postparietal. This contact is more than a straightforward overlapping suture, however, because the ventral margin of each postparietal receives a short, tongue-like process just lateral to the midline, as observed in *Captorhinus* (Modesto, 1998: fig. 8A). The postparietal sends a thin flange anteriorly to underlie the posterior margin of the parietal (Fig. 4). Medially the postparietal is an

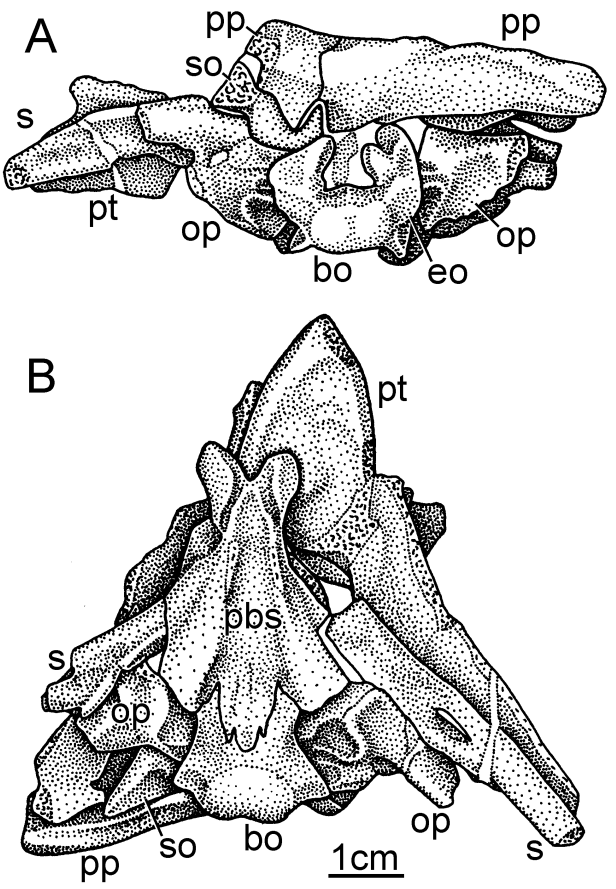

Figure 5. *Labidosaurus hamatus*, FMNH UR 161. Braincase in occipital (A) and palatal (B) views.

entirely occipital element, and the parietal forms the occipital rim, but midway along the contact with the latter bone the postparietal extends onto the skull table and forms part of the occipital rim (Fig. 2). The sculpturing on the parietal does not extend onto the postparietal, as seen in *Captorhinus* (Modesto, 1998: fig. 4B). The truncated lateral tip of the postparietal is bordered entirely by the supratemporal.

The supratemporal (Figs 2, 4) is a relatively small, spindle-shaped splint that lies obliquely in the posterolateral corner of the skull table. The anterior end of the bone is wedged into the parietal, whereas the remainder is cradled by the squamosal and, to a lesser extent, the postparietal medially. Judging from MCZ 8727, the squamosal probably underlies most of the supratemporal, and it is possible that part of the postparietal also underlies it, as observed in *Captorhinus* (Modesto, 1998). The supratemporal contributes to both the skull table and to the occiput, but the exact extent of each is subject to individual variation.

Squamosal morphology is conservative among captorhinids, and *Labidosaurus* is no exception. Despite its absolutely larger size, the squamosal of *Labidosaurus* (Figs 2, 3, 4, 6) differs only in minor respects from that of *Captorhinus* (Heaton, 1979; Modesto, 1998). For instance, the occipital flange is aligned almost entirely in the vertical plane, such that it has a very slender exposure in lateral and dorsal views; in *Captorhinus*, the occipital flange is angled more posteromedially (Modesto, 1998; *contra* Heaton, 1979). The pattern of dermal sculpturing on the temporal portion of the bone is similar to that seen on the same bone in *Captorhinus*, except for the pits and furrows being relatively smaller than those in the larger *Labidosaurus*.

The quadratojugal (Figs 2, 3, 4, 6) closely resembles those of *Captorhinus* and *Labidosaurikos*. It consists mainly of a rectangular temporal portion that posteriorly curves smoothly into a smaller occipital flange. The quadratojugal has deeply overlapping sutures with both the squamosal and the jugal; it overlies the latter bone in lateral view, and is overlain in turn by the former. It shares a simple abutment contact with the quadrate. It is unclear whether a quadrate foramen was present, although the concave margin of the medial end of the occipital flange is suggestive of the participation of the quadratojugal in the formation of such an opening.

Palate

In ventral aspect, the vomer (Fig. 4) is a narrow triangular bone that bridges the skull roof and the palate proper, and, as in all Permian captorhinids, is edentulous. The vomer has a narrow contact with the premaxilla anteriorly and more substantial contacts with the palatine and the pterygoid posteriorly. The suture with the pterygoid is unusually extensive, to the point that it runs for approximately two-thirds of the entire length of the vomer. As a result, the intervomerine suture is the shortest among all captorhinids where the palate is known, with the exception of *Romeria texana* (Clark & Carroll, 1973). The vomer appears greatly elongated, but it is the same relative length as that of *Captorhinus* when regarded as a proportion of the total length of the palate (measured from the anteriormost tip of the vomer to the posteriormost point of the transverse flange of the pterygoid).

The palatine is transversely narrow compared with that of *Captorhinus* (Modesto, 1998: fig. 2). The anterior process of *Captorhinus* is mainly flush with the rest of the palatal surface, with only the lateral portion contributing to the fossa bordering the choana raised, whereas all of the anterior process of the palatine of *Labidosaurus* is raised above the larger posterior portion of the bone as part of the choanal fossa (Figs 3, 4). The remainder of the palatine of *Labidosaurus* differs little from that of small captorhinids, except for its cluster of palatal teeth, which continues posteriorly onto the pterygoid, being narrower and slightly longer than that seen in *Captorhinus*.

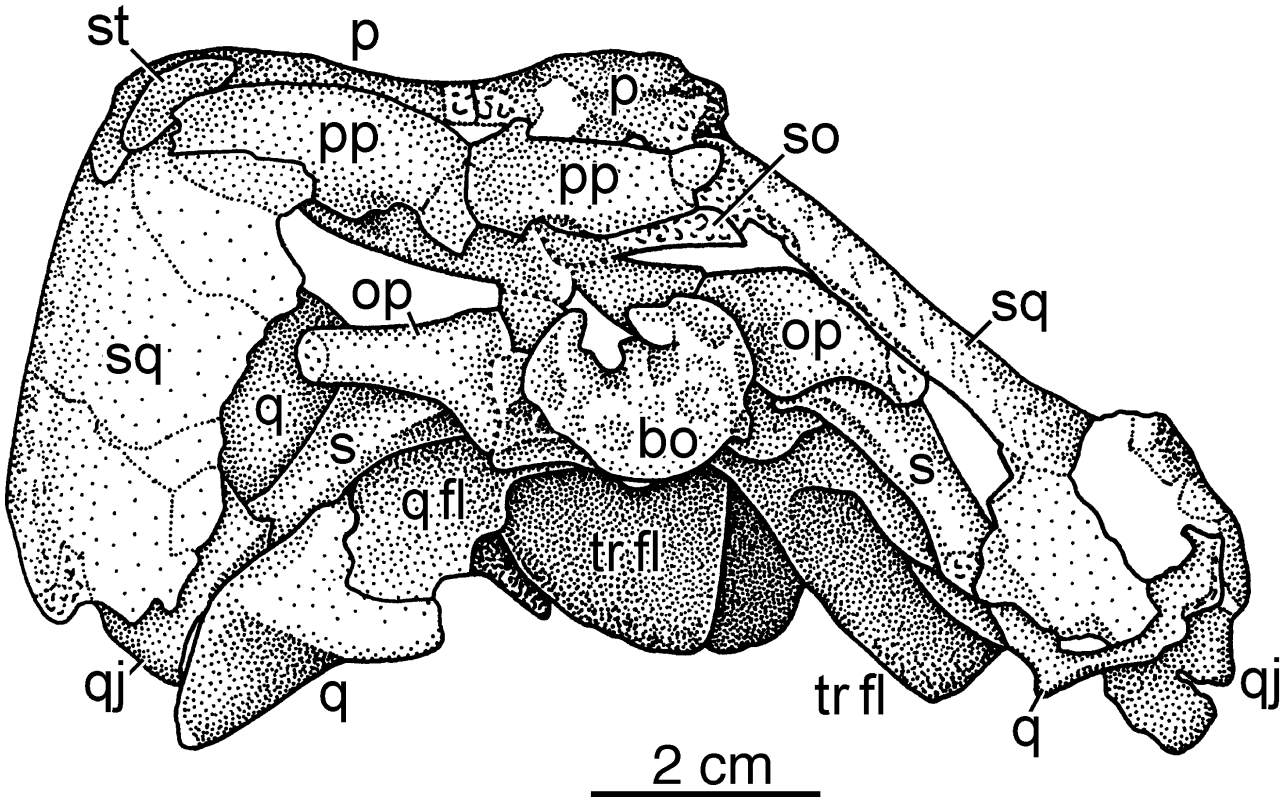

Figure 6. *Labidosaurus hamatus*, CM 73371. Skull in occipital view.

The morphology of the pterygoid follows the general construction of this element in other early reptiles. In its basic proportions, the pterygoid (Figs 3, 4) most closely resembles that of *Labidosaurikos* in being (like the vomer and the palatine) transversely narrow compared with the pterygoid of small captorhinids. For example, the palate in *Captorhinus* is about 15% broader with respect to its length (exclusive of the quadrate flange) than that of *Labidosaurus*. As mentioned in the description of the vomer, the pterygoid extends farther anteriorly than in any other captorhinid in which the palate is known, except for *R. texana*. Measured as a proportion of the length of the palate, the pterygoid of *Labidosaurus* occupies almost 90% of the distance from the anteriormost tip of the vomer to the posteriormost edge of the pterygoid flange, as compared with just under 75% in small captorhinids such as *Captorhinus*. The transverse flange of *Labidosaurus* is narrow, with the lateral and posterior margins forming an angle that is much more acute than that seen in the small captorhinids. This feature is shared only with *Labidosaurikos* among the captorhinids in which the palate is known. In *Labidosaurus* the anterolateral portion of the palatal surface bears a shallow laterally concave fossa, one that is similar to that evident, but not described, in *Captorhinus* (Modesto, 1998: fig. 2). A roughened surface on the lateral face of the transverse flange, the torosus transiliens, makes a small ventral incursion between the anterolateral fossa and the palatal surface proper. Except for its much larger size, the quadrate flange of the pterygoid of *Labidosaurus* is identical to that of *Captorhinus*.

The ectopterygoid is almost never discussed in the context of captorhinid cranial osteology. Interestingly, CM 73371 (Figure 3B) appears to possess a distinct ectopterygoid, which occupies the position of the jugal alary process that is generally present in captorhinids (see the description of the jugal above), in the same position that the ectopterygoid occupies in other basal reptiles. The ectopterygoid contacts the jugal laterally, the palatine and the maxilla anteriorly, and the pterygoid medially. As in other basal reptiles it forms, along with the palatine and the pterygoid, the suborbital foramen. The presence of a distinct ectopterygoid cannot be confirmed in other specimens of *Labidosaurus*, and we are uncertain as to whether the presence of an ectopterygoid is typical for *Labidosaurus*, or if this captorhinid is polymorphic with respect to either the presence or the absence of an ectopterygoid.

The deep position of the epipterygoid in the available *Labidosaurus* skulls precludes a detailed description of this element. What is visible suggests that the epipterygoid does not differ in either position or morphology

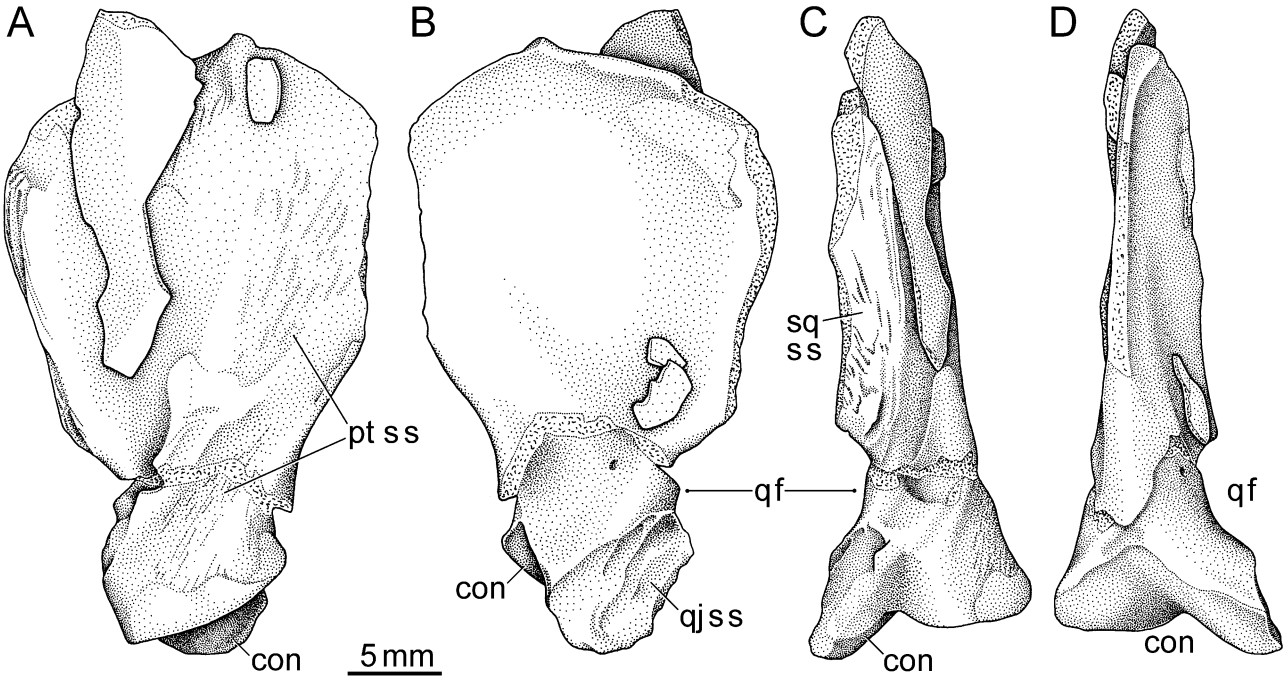

Figure 7. *Labidosaurus hamatus*, MCZ 8727. Left-hand quadrate in medial (A), lateral (B), posterior (C), and anterior (D) views.

from that of *Captorhinus*, except that it is much greater in size and that there are possibly small proportional differences of the major regions of the bone (Heaton, 1979). Only the distal tip (and thus the length) of the dorsal columella is unknown, either because it is missing (e.g. CM 73370) or because it is inaccessible without damage to the skull (e.g. CM 73371).

A complete picture of the quadrate is provided by the left element of MCZ 8727 (Fig. 7), which has been disarticulated from the skull. Four views of this element reveal only minor differences from the quadrate of *Captorhinus* (Heaton, 1979: fig. 26). The columellar recess, which received the distal end of the stapes on the posteromedial surface in life, is relatively deeper and exhibits a conspicuous lip or ridge on its medial margin that presumably served to strengthen the contact between the two bones. The sutural surface for the quadrate flange of the pterygoid, marked by faint lipping ventrally and a pattern of shallow irregular furrows elsewhere on the medial surface, is not as roughly developed as in *Captorhinus*. Lastly, the condylar facet can be divided into medial and lateral portions, in contrast to the single large articulating surface of the condylar facet of *Captorhinus*. The medial facet of *Labidosaurus* is slightly convex, broadly crescent-shaped in ventral aspect, and longer anteroposteriorly than the lateral facet; whereas the lateral facet is more convex than the medial facet, roughly quadrangular in ventral aspect, and its transverse breadth is greater than its anteroposterior length. The two facets meet parasagittally at an obtuse angle (approximately 110°), forming a peaked groove between them that receives a complementary ridge on the articulating facet of the articular.

Braincase

The length of the braincase (as measured from the level of the anterior margins of the basipterygoid processes to the posterior margin of the occipital condyle) is slightly shorter than those of small captorhinids, such as *Captorhinus*, relative to the ventral midline length of the skull. As a consequence the braincase of *Labidosaurus* appears partially recessed under the skull roof, so that only the occipital condyle is visible in dorsal aspect. In contrast the braincase of small captorhinids projects posteriorly well beyond the skull roof, so that the foramen magnum and surrounding elements are visible in dorsal aspect.

The parasphenoid and the basisphenoid are fused indistinguishably in all available specimens (Figs 2, 5, 8). The component element, the parabasisphenoid, differs only in its greater size and in a few minor details from that of *Captorhinus*. A dorsoventrally low cultriform process projects anteriorly from the rostrum of the parabasisphenoid, at least as far as the anteriormost point of the interpterygoid vacuity. In *Labidosaurus* the ventral surface of the basipterygoid process bears a furrow that runs anterolaterally from the vidian sulcus to the margin of the articulating facet. The

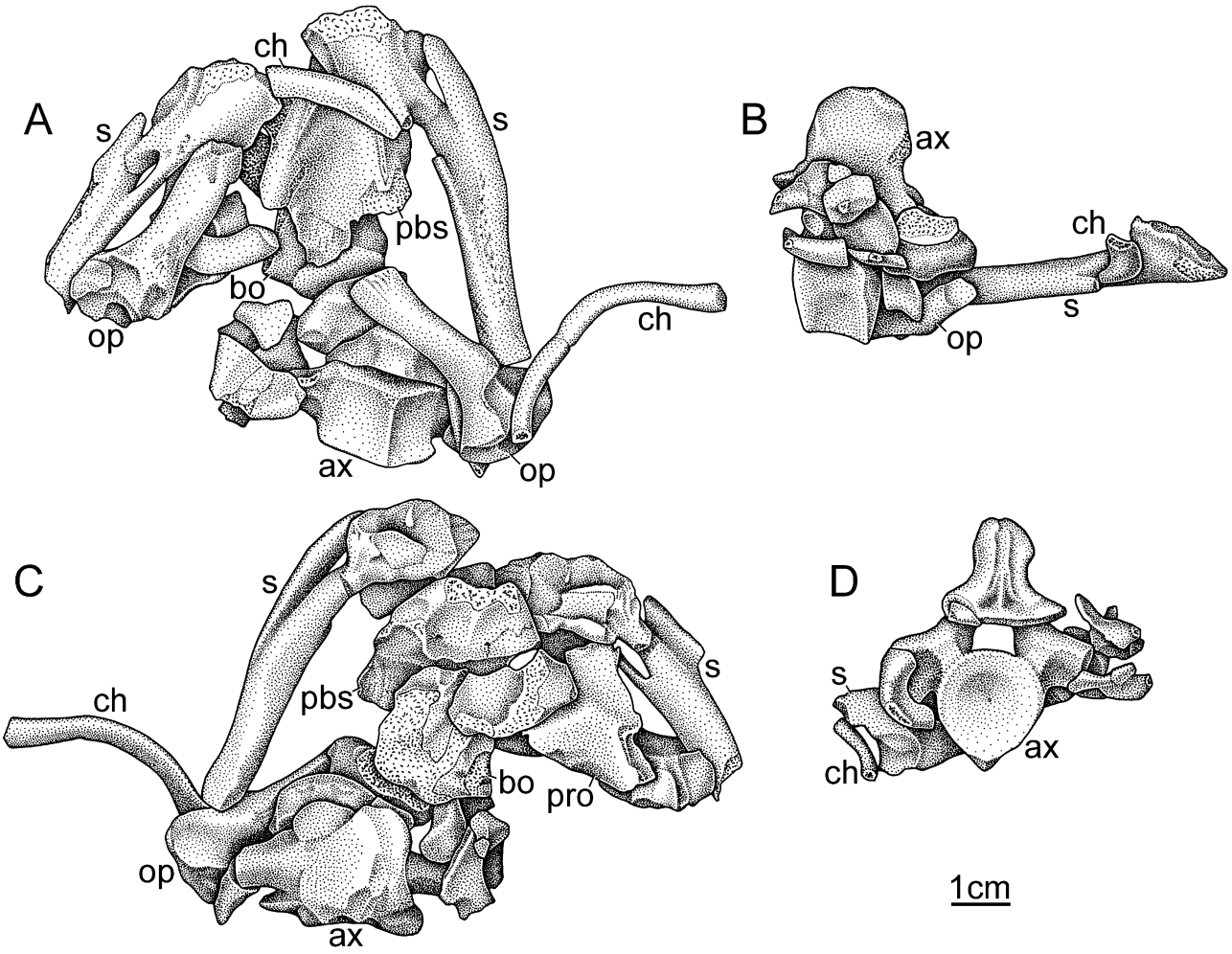

Figure 8. *Labidosaurus hamatus*, CM 73370. Braincase and associated elements in ventral (A) and dorsal (C) views. Left stapes is mainly in dorsal view and the axis is in right lateral view (B), and the same in distal and posterior views (D).

basipterygoid side of the sulcus is more steeply inclined than the parasphenoid side, such that a distinctly triangular boss forms the ventrolateral face of the basipterygoid process. This boss also appears to be present in *Labidosaurikos* (Dodick & Modesto, 1995: fig. 8). In addition to their larger size, the basipterygoid processes differ from those of *Captorhinus* (Modesto, 1998: figs 2, 6) in being conical and positioned relatively closer to the midline. *Labidosaurus* shares with *Captorhinus* and *Labidosaurikos* elongate sharply ridged cristae ventrolaterales, although those of CM 73370 and 73371 exhibit a marked difference in their anteroposterior lengths. The breadth of the median channel formed between the paired basitubera appears narrow in CM 73371, but this is probably attributable to the oblique compression that has affected the entire skull. The dorsum sellae (Fig. 8) is conspicuously shorter dorsoventrally than in *Captorhinus* and *Labidosaurikos*, extending no higher than the posterior suture with the prootic. The foramen for cranial nerve VI (abducens nerve) emerges at the base of the processus alaris in *Captorhinus*, whereas in *Labidosaurus* it opens on the medial side of the process, with the result that the foramen opens into the posterior wall of the retractor pit. The sagittal ridge that divides the posterior wall of the retractor pit in *Captorhinus* (Modesto, 1998: fig. 5C) is a moderately deep flange in *Labidosaurus*, one that extends 3–4 mm into the retractor pit and the sella turcica (the space dorsal to the pit) and almost divides the retractor pit into halves. The vidian groove for cranial nerve VII (facial nerve) is open laterally indicating that the prootic formed the lateral boundary for the foramen, as it does in other early amniotes. This is in contrast to the condition in *Captorhinus*, in which the opening is formed entirely by the parabasisphenoid (Price, 1935).

The left prootic of CM 73370 (Fig. 8) is disarticulated but still closely associated with the basisphenoid portion of the parabasisphenoid complex. It tapers anteriorly, and a shallow angular notch that forms the

anterior margin probably represents the posterolateral margin of the foramen for cranial nerve VII (facial nerve). The preserved dorsal margin of the bone forms a sharp ridge that rises gradually dorsally and curves slightly medially toward its posterior margin. The anterior third of the lateral surface of the prootic is slightly convex and smoothly finished, whereas the remaining lateral surface comprises the stapedial recess (for the reception of the stapedial footplate). Ventrally, the surface contacting the stapedial footplate is recessed by approximately 5 mm, narrowing dorsally to at least 3 mm. Most of the rim bounding the stapedial recess is slightly weathered, but it is clear that the portion of the rim that marks the posterior boundary of the lateral surface proper slightly overhangs the stapedial recess. At approximately the midpoint of the rim, the free lateral margin of the prootic ends and the remainder of the rim continues posteriorly (and perhaps slightly dorsally) as the dorsal part of the contact with the opisthotic. Accordingly, the prootic of *Labidosaurus* has the least lateral exposure among known captorhinid prootics (Price, 1935; Heaton, 1979; Dodick & Modesto, 1995; Modesto, 1998).

The supraoccipital is visible only in posterior aspect in CM 73371 (Fig. 6), whereas the supraoccipital of CM 73370 is missing. Examination of the former reveals an element that is a greatly enlarged version of supraoccipital of *C. aguti* (Modesto, 1998: fig. 8), but with a few exaggerated features. There is a sharp midline ridge, or 'nuchal crest', and its ventral end overhangs the dorsal margin of the foramen magnum. A relatively deep midventral embayment of the supraoccipital comprises at least the upper third of the foramen magnum. The supraoccipital of *Labidosaurus* is notably more waisted and the dorsolateral processes are relatively larger than in *Captorhinus*. In the former the processes form approximately two-thirds the height of the supraoccipital, whereas they comprise approximately a third in the latter. Despite both the absolutely and relatively larger size of the dorsolateral process in *Labidosaurus*, the contact with the postparietal closely resembles the contact in *Captorhinus* (Modesto, 1998: fig. 8A).

The exoccipitals are almost completely exposed in CM 73371 (Fig. 6). They are fused almost indistinguishably to one another ventrally and to the basioccipital. The contact between the two exoccipitals is apparently represented by a low flat ridge (presumably the attachment surface for the bifid ligament of the medulla: Heaton, 1979: 55) that extends midventrally across the floor of the foramen magnum, and in CM 73371 is divided posteriorly by a distinct seam, presumably the vestige of the midline suture of the exoccipitals, which ends at the rim of the notochordal pit. Two slight swellings that are superimposed onto the reniform occipital condyle, on either side of the notochordal pit, appear to represent the separate contributions of the exoccipitals to the condyle. There is no trace, however, of a sutural contact between the exoccipitals and the basioccipital on either the posterior or the lateral surfaces of the condyle (Figs 5, 6). The dorsal portion of the exoccipital is identical to that in *Captorhinus*, including the following features: the morphology of the strap-shaped articulating facet for the proatlas; the suture with the supraoccipital (dorsolaterally) and the opisthotic (laterally); the notch forming the medial margin of the foramen metoticum (the 'vagus foramen' of Heaton, 1979); and the paired openings for cranial nerve XII (hypoglossal nerve).

Except for its greater size, the basioccipital of *Labidosaurus* (Figs 3, 5, 6, 8) is almost indistinguishable from that of *Captorhinus*. Differences include the marginally more prominent, sharper, basioccipital tubera, and a slightly more extensive overlapping contact with the parabasisphenoid, in which the parasphenoidal sheath extends posteriorly to within 2 mm of the condyle (as evidenced by scarring on the ventral surface of the basioccipital of CM 73371). Heaton (1979: 54) described the basioccipital of *Captorhinus* as forming a narrow midline ridge that served to separate the exoccipitals. As described above, however, the ridge in *Labidosaurus* appears to be formed by the partially fused exoccipitals, and the basioccipital is excluded from the floor of the foramen magnum. The part of the basioccipital anterior to the sutures for the opisthotics (and presumably anterior to the midline suture of the exoccipitals, although this is not fully exposed in the available material) appears to form the floor of the cavum cranii. Occipital condyle morphology is the same as in *Captorhinus* apart from the relatively smaller size of the notochordal pit, which is positioned more dorsally in *Labidosaurus* than in *Captorhinus*.

Several opisthotics are represented in the available material and together allow a complete description of the element (Figs 3, 6, 8, 9). The most distinguishing feature is the elongate paroccipital process, which comprises between half and two-thirds of the transverse length of the element, a condition that is shared with *Labidosaurikos* (Dodick & Modesto, 1995). In contrast this figure is approximately one-third in *Captorhinus*, judging from the opisthotic figured by Modesto (1998: fig. 7). The paroccipital process is an anteroposteriorly compressed rod-like structure; in MCZ 8727, the process is arched slightly dorsally. In all the specimens the distal tip of the process is lunate/teardrop-shaped in end view, slightly concave, and in life probably contacted the occipital flange of the squamosal via a cartilaginous extension (Heaton, 1979: 56). The proximal portion consists of the same components described for the opisthotic of *Captorhinus* by Heaton (1979), except for slight differences attributable to its absolutely larger size in *Labidosau-*

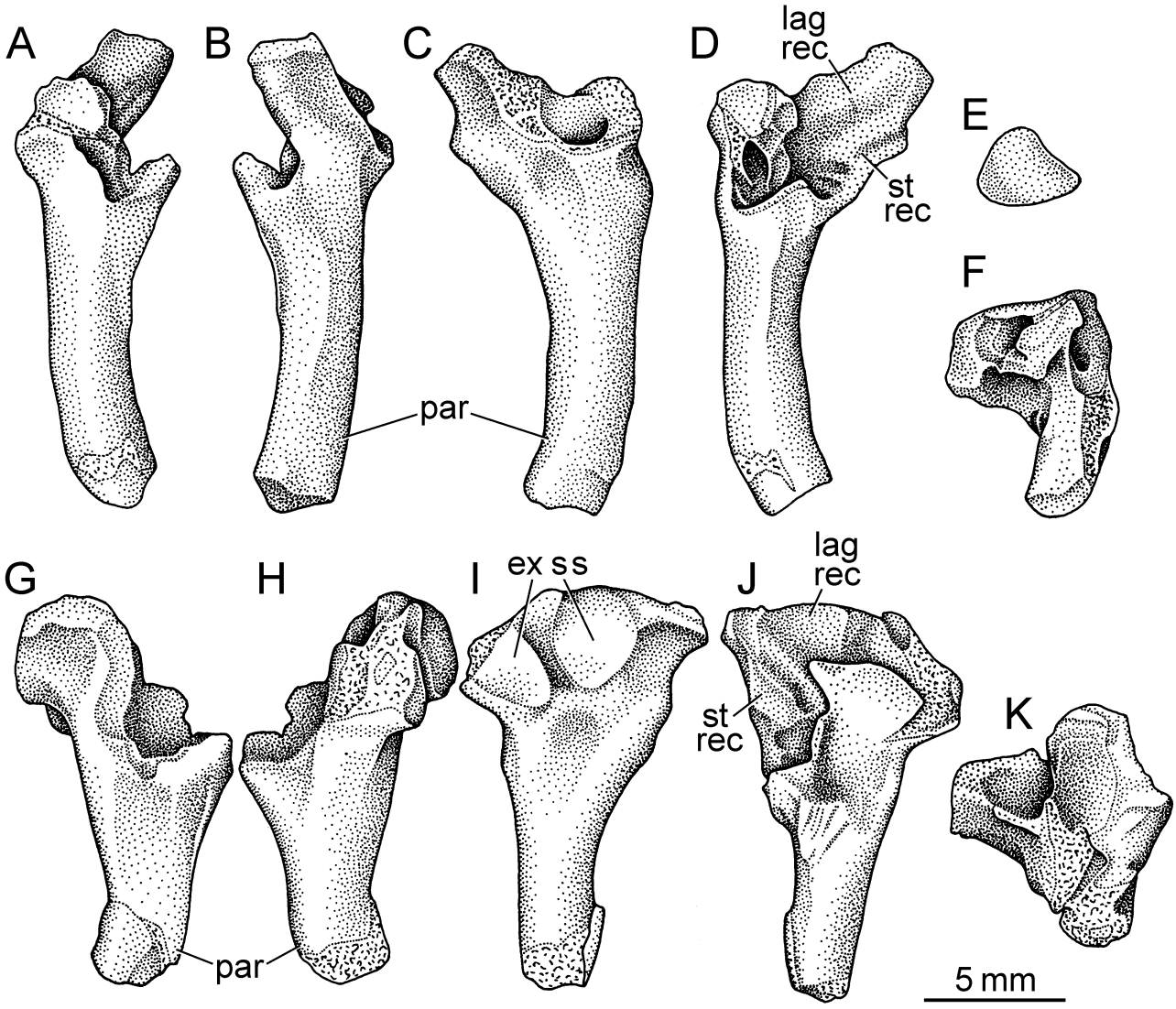

Figure 9. *Labidosaurus hamatus* opisthotics. Right opisthotic of MCZ 8727 in dorsal (A), ventral (B), posterior (C), anterior (D), distal (E), and proximal (F) views. Left opisthotic of CM 73370 in dorsal (G), ventral (H), posterior (I), anterior (J), and proximal (K) views.

rus. For example, the channel that bisects the sutural surface for the exoccipital and forms the anterolateral wall of the foramen metoticum is relatively narrow compared with that in *Captorhinus* (Modesto, 1998: fig. 7A) (Fig. 9I). The anteromedial surface of the proximal portion features the same organization of the stapedial, lagenar, and scalae tympani recesses (as these cavities were attributed to *Captorhinus* by Heaton, 1979), and the excavation for the horizontal semicircular canal. The stapedial recess is relatively larger in *Labidosaurus* compared with the stapedial recess in *Captorhinus* (Modesto, 1998), apparently at the expense of the lagenar recess which is slightly smaller. The cavity identified by Heaton (1979) as the 'recessus scalae tympani' is relatively small. This vacuity, however, is not homologous with the recessus scalae tympani of some extant reptiles (e.g. lepidosaurs; Rieppel, 1985) because *Labidosaurus* and other captorhinds feature an undivided metotic fissure; the 'recessus scalae tympani' identified by Heaton (1979) is merely an extension of the recessus vestibulae.

The stapes (Figs 3, 5, 6, 8, 10) is a conspicuously slender element. This is a result of the narrow build of the columellar portion and the low inclination of the dorsal process. The latter feature arises as a continuation of a low dorsal ridge that extends along the central third of the stapes. The process extends medially as a tongue-like blade that is either parallel to the main axis (CM 73370) or curves slightly dorsally (MCZ 8727). The process is separated ventrally from

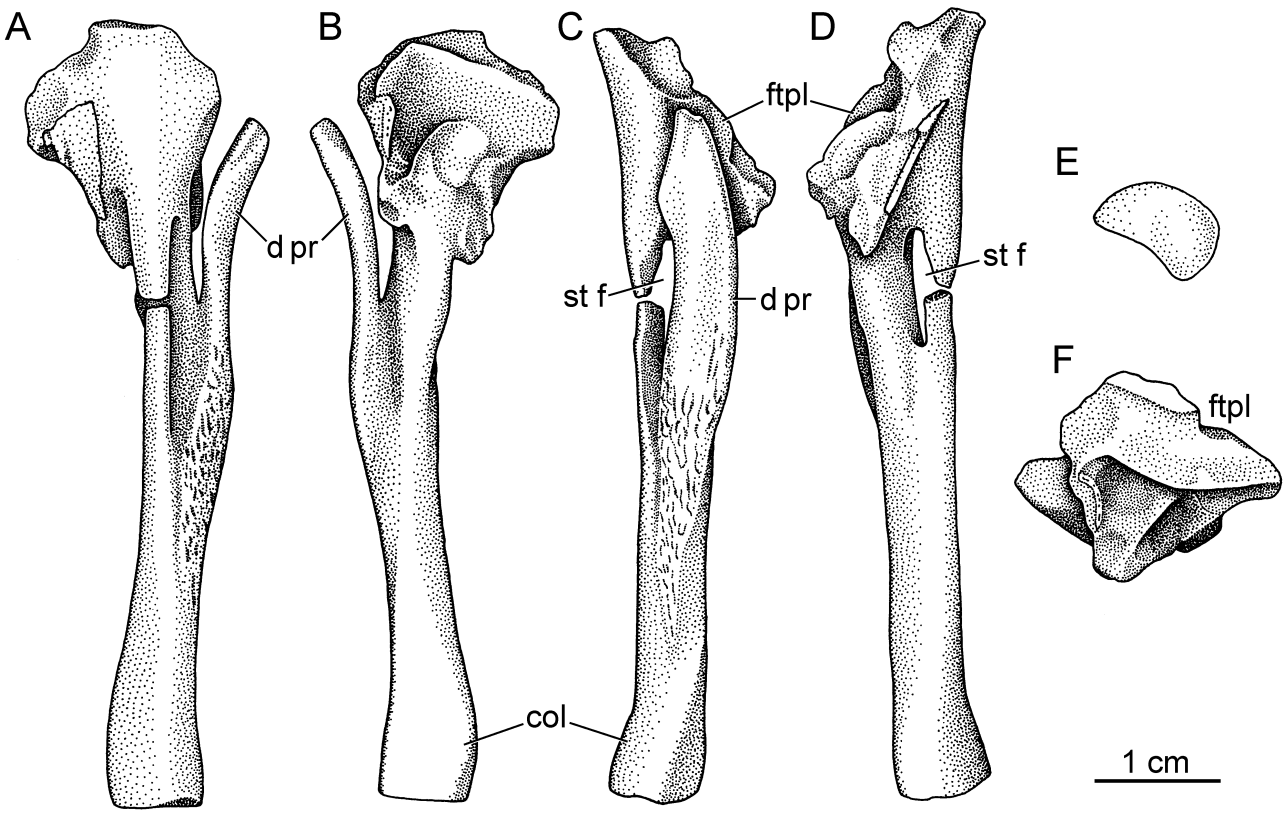

Figure 10. *Labidosaurus hamatus*, MCZ 8727. Left stapes in anterior (A), posterior (B), dorsal (C), ventral (D), distal (E), and proximal (F) views.

the main axis by a narrow slit and from the footplate by a slightly broader channel for the vena capitis lateralis and hyoid ramus of the cranial nerve VII (facial nerve). The alignment of the proximal surface of the stapedial footplate is at the same approximate angle as in *Captorhinus*. The ventral rim of the footplate has a quadrangular excavation that would have been overlain by a posterolateral extension of the parasphenoidal basitubera, as seen in *Labidosaurikos* (Dodick & Modesto, 1995) and as interpreted for *Captorhinus* (Modesto, 1998: 30). The elliptical stapedial foramen is positioned just anterolateral to the base of the dorsal process. In end view the slightly expanded tip of the columella is broadly lunate in outline with a slightly concave unfinished surface. Presumably the stapes continued distally as extra-columellar cartilage and inserted into the stapedial pocket of the quadrate.

The sphenethmoid is present only in CM 73371, where it has been displaced from its median interorbital position and now lies in the left subtemporal opening (Fig. 3). In frontal aspect, it is a Y-shaped element of a sagittally aligned trough mounted onto a median blade. Judging from the sphenethmoid drawn for *Captorhinus* in deBraga & Rieppel (1997: fig. 3A), the sphenethmoid of CM 73371 is preserved with its posterior end projecting slightly out of the subtemporal opening. The dorsal trough has a slightly ogival cross-section at its posterior end, and a more rounded one at its anterior end. There is a modest decrease in the depth of the trough from anterior to posterior. Thus, the V-shaped cross-section ascribed to the posterior ends of sphenethmoids in various reptiles by deBraga & Rieppel (1997: 315–316) is not evident in the sphenethmoid of *Labidosaurus*. The anteroposterior length of the ventral median keel is slightly less than that of the dorsal trough where the two portions make contact. The keel decreases dramatically in its anteroposterior length ventrally up to the point where the bone is obscured by matrix; this decrease is accomplished by the posterior margin sloping anteroventrally at about 45°, whereas the anterior margin appears to maintain a more-or-less vertical alignment. There is no evidence of openings for cranial nerves II–IV, which is consonant with their reported absence in *Captorhinus* (Heaton, 1979; deBraga & Rieppel, 1997).

MANDIBLE

Apart from a few minor details and its greater size, the mandible of *Labidosaurus* resembles the mandibles of smaller captorhinids, such as *Captorhinus*, very closely. The anterior two-thirds of each ramus is

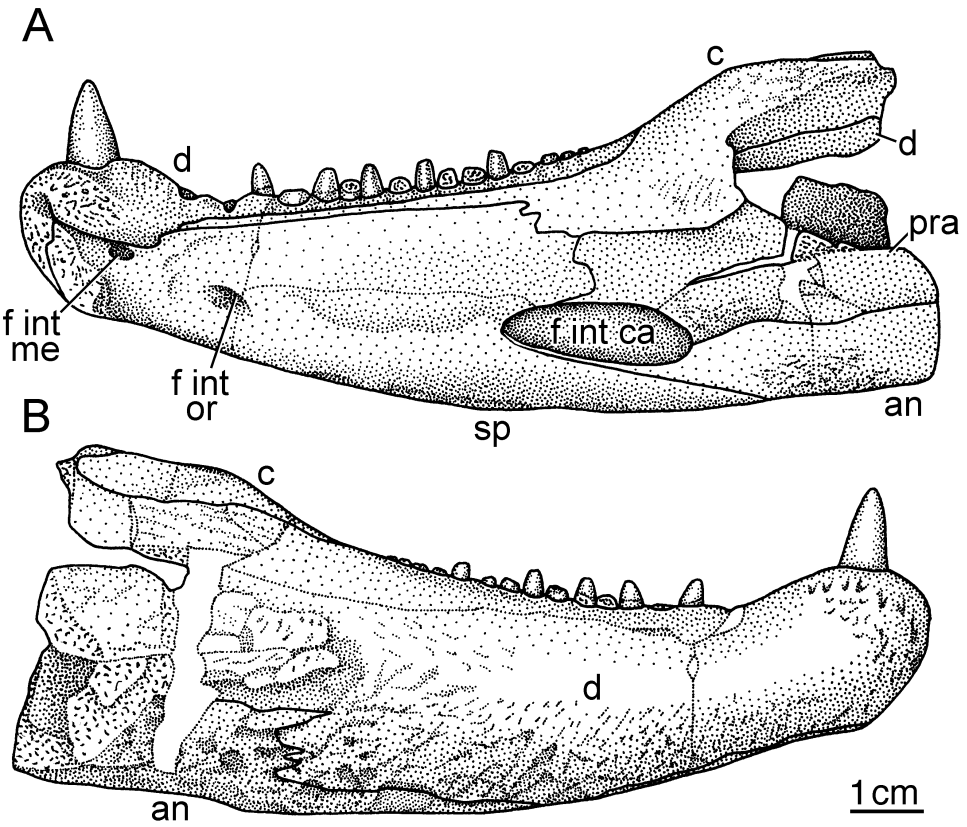

Figure 11. *Labidosaurus hamatus*, CM 76876. Partial right mandibular ramus in medial (A) and lateral (B) views.

very slightly concave medially through its longitudinal axis, becoming conspicuously convex laterally at its posterior end. Dentition occupies approximately 40% of the upper margin, which is slightly less than the figure of 45% found for *Captorhinus* (Heaton, 1979). Extending between the posterior end of the dentition and the glenoid region is a low but well-developed coronoid eminence. The base of the eminence is emphasized by a lateral shelf, a feature that *Labidosaurus* shares with the moradisaurine *Labidosaurikos* (Dodick & Modesto, 1995).

With the exception of the dentition (discussed below), little separates the dentary of *Labidosaurus* from that of *Captorhinus* (Fox & Bowman, 1966; Heaton, 1979; Modesto, 1998) with the exception of the following details. The dentary (Figs 2, 3, 4, 11) has a relatively smaller medial exposure in *Labidosaurus* than in *Captorhinus*, with only the symphysial area and the adjacent area posterior to the level of the fifth tooth broadly visible. Most of the symphysis is formed by the dentary, via a rounded triangular pad that is not invaded posteriorly by the foramen intermandibularis medius, as it is in *Captorhinus* (Modesto, 1998: fig. 9B). The dentaries of *Labidosaurus* and *Captorhinus* are similar in forming the dorsal margin of the foramen intermandibularis medius, but in the latter the dentary has a relatively short contribution that is bounded both anteriorly and posteriorly by the splenial. Laterally the dentary of *Labidosaurus* exhibits the same general morphology and relationships with neighbouring elements as it does in *Captorhinus*. Almost the entire lateral surface is sculptured by fine pits, and a line of distinctly larger pits, the infralabial foramina, parallels the dentition; their sizes reflect the sizes of the teeth. Close to the sutures with the splenial and the angular, the pits give rise to oblique slightly anastomizing furrows. On the right mandibular ramus of CM 73371 a relatively large oval pit is superimposed onto the system of furrows, which may represent the anteriormost extent of an irregular pattern of sculpturing that is largely borne by the angular. Twenty one tooth positions are present and arranged in a single row.

The morphology of the splenial (Figs 3, 4, 11) conforms to the general pattern seen in other captorhinids. Anteriorly the splenial produces a relatively small teardrop-shaped symphysial pad. The suture with the dentary curves around the top of the splenial pad and continues posteriorly for a few millimeters before ending at the foramen intermandibularis medius, a slot-like opening that is roughly 3-mm long. The foramen differs from that in *Captorhinus*, where it invades the

symphysial region and is effectively confluent with that of the other ramus (Modesto, 1998). That part of the splenial forming the posterior border of foramen intermandibularis medius continues posterodorsally to a level just below the alveolar shelf. From here the splenial continues posteriorly to cover the entire medial surface of the dentary and much of the anterior process of the coronoid. A relatively small foramen intermandibularis oralis is positioned at a level between the fourth and fifth dentary teeth, almost half way up the lingual surface of the bone. The posterior end of the splenial is deeply bifurcated, the upper ramus of which is a tongue-like process that extends posteriorly only as far as the level of the penultimate dentary tooth and overlaps the anterior end of the prearticular. The ventral ramus, on the other hand, is distinctly acuminate and a little over three times the length of the upper ramus. The anterior portion of its dorsal edge forms the anteroventral border of the foramen intermandibularis caudalis, and the entire ramus appears to be underlain by the angular. The splenial wraps around the ventral margin of the mandible, but is only narrowly exposed, if at all, in lateral view. The laterally exposed portion of the splenial is set off at a distinct angle to its lingual surface and exhibits a less prominent version of the system of fine pits that marks the external surface of the dentary. The sculpturing becomes a little more accentuated posteriorly, but does match the sculpturing seen on the dentary and the angular.

The coronoid (Figs 2, 11) is almost indistinguishable from that of *Captorhinus*, except for its larger size, and, as in all captorhinids in which the mandible is exposed in lingual aspect (with the notable exception of the large multiple-rowed *Labidosaurikos*), exhibits a long splint-like anterior process that extends to a level just anterior to the foramen intermandibularis oralis. The partial loss of the splenial of CM 73371 reveals that it sheathes the medial surface of the anterior process of the coronoid, leaving only its dorsal surface exposed between the splenial and the dentary. Posteriorly the coronoid becomes deeper in medial aspect and overlies the prearticular anterodorsally. The posterodorsal process of the coronoid curves around the anterior end of the adductor fossa to form the anterior portion of the coronoid eminence. The sutural relationships with the dentary and the surangular are exactly the same as the sutural relationships seen in the mandible of *Captorhinus*. This includes the characteristic interfingering section of the coronoid-dentary suture at the anterior base of the coronoid process and the posterior bifurcation of the distal end of the posterodorsal process of the coronoid, which receives an anterodorsal process of the surangular.

The prearticular of *Labidosaurus* (Figs 4, 11), like that of *Labidosaurikos*, has a slightly greater anterior extent than the prearticular of *Captorhinus*, with approximately 30% of the prearticular length extending beyond the adductor fossa compared with just under 20% in *Captorhinus*. Anteriorly the prearticular forms the dorsal margin of the foramen intermandibularis caudalis, and posteriorly its ventral margin is overlain slightly by the angular. Most of its dorsal margin of the prearticular forms the medial border of the adductor fossa. Close to the posterior end of the fossa the prearticular expands in height as it sheathes the ventromedial surface of the articular. There is a shallow subcircular pocket on the anteromedial surface of the articular that continues onto the prearticular, which Heaton (1979) identified in *Captorhinus* as the insertion area for the M. pterygoideus medius. In *Captorhinus* the medial end of the pocket is well defined by a curved ridge of bone formed entirely by the articular, but in *Labidosaurus* the ridge is conspicuously taller and formed mostly by the prearticular. As observed in *Captorhinus* (Modesto, 1998), the prearticular ends posteriorly at a level just beyond the glenoid facet.

The morphology of the surangular of *Labidosaurus* (Figs 2, 3, 11) is intermediate between those of *Captorhinus* and *Labidosaurikos*, although the outline of this bone in lateral aspect closely approximates that of *Captorhinus* (e.g. Heaton, 1979: fig. 10A). In *Labidosaurus*, however, the portion contributing to the coronoid eminence is separated from the more ventral sculptured portion by a distinct step that divides the bone ventral to the coronoid eminence into a narrow, smoothly finished, dorsal ledge and a more extensive sculptured lateral region. In dorsolateral view the lateral margin of the surangular can be seen to have a preglenoid region that is set off from the posterior region at an obtuse angle. Both the stepped lateral surface and the lateral angulation of the surangular are seen also in *Labidosaurikos*, but the ledge below the coronoid eminence is relatively larger and the angulation occurs much farther posteriorly in *Labidosaurikos*. The surangular sheathes the lateral surface of the articular and, as in *Labidosaurikos*, the posterior end of the adductor fossa invades this part of the surangular relatively deeply. The surangular extends posteriorly to the tip of the retroarticular process, where it wraps around the process to sheathe part of its dorsal surface. Apart from the contribution from the posterodorsal process of the coronoid and a small portion of the angular (hidden by the medial wall of the adductor fossa), the surangular forms the lateral wall of the adductor fossa in medial aspect.

Apart from its larger size and minor details of the dermal sculpturing, the angular of *Labidosaurus* (Figs 3, 4, 11) resembles that of the small captorhinid *Captorhinus*. Sculpturing, which is limited to the lateral surface, consists of a system of fine pits and short furrows for the most part, with one or two slightly

larger randomly positioned pits that are reminiscent of the large pits present on the dentary. These larger pits tend to cluster longitudinally close to the ventral margin, and in CM 73371 they are accompanied by larger shallow excavations. On the left mandibular ramus of CM 73371 the excavations take the form of moderately deep pits, about 9-mm long and 6-mm wide, over which is superimposed the regular pattern of small pits and furrows. In approximately the same area on the right ramus there is instead a more extensive trough-like excavation, approximately 40-mm long with a maximum width of 6 mm, which straddles the division between the smoothly finished bone of the medial surface and the sculptured bone of the lateral surface. The floor of this excavation is for the most part flat with a roughened texture, over which is superimposed a diffuse pattern of small pits and a few furrows.

The articular (Figs 2, 3, 4) is the one mandibular element of *Labidosaurus* that diverges most widely from that of *Captorhinus*. The most conspicuous difference is the relatively larger articulating surface, or glenoid. The glenoid facet in *Captorhinus* is just over 55% wider than its length, and a prominent notch separates the lateral and the medial facets (Heaton, 1979: figs 32B, C). In strong contrast, both facets of *Labidosaurus* are expanded anteroposteriorly, such that the breadth of the glenoid is no more than 20% greater than its anteroposterior length, and the posterior notch is relatively small. This size relationship is underscored by the observation that when the mandible is articulated with the skull, and the quadrate condyles are positioned back against the posterior boss of the articular, approximately 6–7 mm of condylar facet lies anterior to the midpoint of the condyles of the quadrate, which suggests that the glenoid could accommodate some fore-and-aft translation of the condyles. Furthermore, whereas the medial and lateral facets of the condylar facet in *Captorhinus* conjoin to form a slightly saddle-like articulating surface, those in *Labidosaurus* form a ridge. This ridge is aligned with the tooth row, fits snugly into the notch formed by the quadrate condyles, and seems well suited to constrain translation at the jaw suspension to fore-and-aft movement. Two further differences with the articular of *Captorhinus* include: (1) the observation that the posterior boss, the wedge-like prominence that rises dorsally from the base of the retroarticular process and supports the posterior end of the lateral condylar facet, is relatively short, and (2) the retroarticular process is reduced to a nubbin that extends no farther than the posterior tip of the surangular.

DENTITION

Contrary to previous studies (Broili, 1904; Williston, 1910; Berman & Reisz, 1986), the premaxilla possesses four or five teeth. The right premaxilla of CM 73371 has four teeth (Fig. 2), plus a gap at the second tooth position that is large enough to have accommodated a tooth of the size present in this position in the left element, but the alveolar surface does not appear to feature either an empty pit or any other sign of replacement. Whether four or five teeth are present, the first premaxillary tooth is invariably the largest in the entire marginal series. In CM 73370 the first premaxillary teeth are subequal in size and have a transverse (or mesiodistal) diameter of about 5.5 mm. The right tooth is complete and has a length (from base to apex) of about 10.0 mm. In CM 73371 the right first premaxillary is conspicuously larger than its counterpart (see below), with a transverse (mesiodistal) basal diameter of approximately 7.0 mm and a length of 13.0 mm. CM 73370 is slightly larger than CM 73371, so this slight disparity in the absolute sizes of the largest premaxillary teeth lends support to Seltin's (1959) suggestion that, as in *Captorhinus*, there is marked variation in the premaxillary tooth size in *Labidosaurus*. In the specimens at hand there is a dramatic serial decrease in premaxillary tooth size posteriorly. For example, the first left tooth is estimated to have a transverse basal diameter of just over 6.0 mm and a length of 12.0 mm, whereas these measurements for the second premaxillary tooth are 4.0 and 6.5 mm, respectively, with comparable decreases in size for succeeding teeth. The premaxillary teeth are much larger and slightly stouter versions of the teeth described for the premaxilla of *Captorhinus* (*Eocaptorhinus*: Heaton, 1979: fig. 7). Hotton *et al*. (1997: 222) described the premaxillary teeth of *Labidosaurus* as 'narrowly spatulate.' That assertion may have been influenced by Heaton's (1979) description of captorhinid premaxillary teeth with lingual 'wear facets.' However, the 'wear' facets described by Heaton (1979) for *Captorhinus* (which are actually shallow fossae that emphasize the cutting edges of the marginal teeth of small captorhinids: Modesto, 1996) are very faint, if they are present at all in *Labidosaurus*. It is possible that the fossae may have been obliterated during feeding. The enigmatic labial facet on the first premaxillary tooth, which Hotton *et al*. (1997: 222) ascribed to both *Captorhinus* and *Labidosaurus*, is neither evident in CM 73370 nor is it seen on the larger right first tooth of CM 73371. A facet appears to be present, however, on the smaller presumably older tooth on the left side, but the proximal boundary of the facet is obscured by what appears to be pathological destruction of the basal surface of the tooth.

There are 22 tooth positions in each maxilla but not all are occupied by teeth, with at least one gap present in each series. Some gaps are marked by empty alveoli that are accompanied by small replacement pits located posterolingual to the alveolus, which are indic-

ative of ongoing tooth replacement. Other gaps are spans of solid alveolar bone, the ventral surfaces of which are roughened but not marked by the replacement scars observed in some jaws of *C. laticeps* (Heaton, 1979: fig. 31B). The fourth or fifth maxillary tooth is the largest in the series, but it is not enlarged conspicuously enough over neighbouring teeth to be regarded as a caniniform. From this tooth position there is a progressive decrease in tooth size both anteriorly and posteriorly. There is, however, an abrupt serial change in the morphology of the maxillary dentition. The anteriormost either six or seven teeth are essentially larger versions of the anterior maxillary teeth seen in the species of *Captorhinus* (Heaton, 1979; Modesto, 1998), having the appearance of stout, slightly rounded cones in lateral aspect. Heaton (1979: fig. 6) illustrated the anterior maxillary teeth of *Labidosaurus* as larger versions of those present in an undescribed captorhinid (FMNH 183), identified by him as *Protocaptorhinus* sp., but this tooth morphology cannot be confirmed in any of the specimens at hand. The remaining either 14 or 15 posterior maxillary teeth of *Labidosaurus* are intermediate in form between the triangular-tipped chisel-shaped posterior teeth of *C. laticeps* and the characteristically ogival posterior teeth of *C. aguti* (Modesto, 1998: fig. 10). The posterior teeth in *Labidosaurus* are slightly broader mesiodistally, relative to their length (base to apex), than the posterior teeth in *C. laticeps*, but are not as broad as those in *C. aguti*. In mesial profile the posterior teeth of *Labidosaurus* are similar to the posterior teeth in *C. laticeps* (Modesto, 1998: fig. 10B), although the lingual side is more convex (but not to the degree seen in the ogival posterior teeth in *C. aguti*; Modesto, 1998: fig. 10D). In the available *Labidosaurus* specimens cutting edges on the teeth arise about halfway between the base and the apex, but all exhibit a polish that presumably represents normal wear incurred during feeding. The lateral flexure that characterizes the maxillary tooth row in small captorhinids (Heaton, 1979; Modesto, 1996) when viewed ventrally is not present in *Labidosaurus*, but rather the tooth row is slightly concave laterally. Finally, Branson (1911) reported the presence of more than one row of maxillary teeth in some specimens but this report is erroneous according to Seltin (1959).

The arrangement of the dentary teeth in *Labidosaurus* is typically captorhinid, with the largest teeth positioned anteriorly near the symphysis (Figs 2, 11). A relatively small tooth may, however, occupy the first position, and it is followed by a short series of large teeth. Dodick & Modesto (1995) ascribed the presence of a dentary caniniform tooth in the absence of a dentary caniniform region in *Labidosaurus*, but the patterns of cross-sections on the right mandibular ramus (Fig. 2B) and tooth outlines on the left ramus of CM 73371 (Fig. 3A) belie that description. The teeth succeeding the largest anterior tooth exhibit a gradual serial decrease in size posteriorly to the end of the series. Interestingly, the first either six or seven postcanine teeth are conspicuously larger than the opposing maxillary teeth. Instances of tooth replacement are rare in the specimens at hand and can be described only in the right dentary of CM 73371. Here a small but well-formed replacement pit lies in a position posterolingual to the second tooth; there are also two gaps in the tooth row that are large enough to accommodate teeth, but they are occupied by irregular alveolar bone. The available evidence suggests that tooth replacement was ongoing in *Labidosaurus*, but not as frequent as in small predatory captorhinids such as the indeterminate basal species described from Richards Spur (Modesto, 1996).

The palatal dentition (Fig. 3) comprises the three separate clusters that are typical of early amniotes. The most medial of these clusters extends along the medial edge of the pterygoid margin forming the interpterygoid vacuity. The second cluster is a narrow band, of mainly a single column of teeth, which extends anterolaterally from the posteromedial corner of the transverse flange, and across the deeply serrate section of the suture with the palatine, to end near the centre of the palatine. The remaining palatal teeth form a four- or five-tooth column that extends along the greater proximal portion of the transverse flange. All palatal teeth are small sharply pointed cones, with the tips of some being slightly curved posteriorly. Some palatal teeth achieve a maximum basal diameter of about 1.0 mm and lengths (from base to tip) of just over 1.5 mm.

PHYLOGENETIC ANALYSIS

The relationships of *L. hamatus* have been considered in every published phylogenetic analysis of captorhinid interrelationships (Gaffney & McKenna, 1979; de Ricqlès, 1984; Berman & Reisz, 1986; Dodick & Modesto, 1995; Modesto & Smith, 2001; Kissel *et al*., 2002). Gaffney & McKenna (1979) identified *Labidosaurus* and *Protocaptorhinus pricei* as sister taxa within Captorhinidae, whereas Berman & Reisz (1986) identified the former taxon as the closest relative of a clade that includes what are now regarded as species of the genus *Captorhinus* (*C. aguti* and *C. laticeps*).

Dodick & Modesto (1995) conducted the first PAUP analysis of Captorhinidae. In addition to the taxa examined by Berman & Reisz (1986), Dodick & Modesto (1995) included the moradisaurine *Labidosaurikos meachami*. The results of their analysis agree with the results of Berman & Reisz (1986), with regards to the taxa used in common, but Dodick & Modesto (1995) also discovered that *Labidosaurus* and

Labidosaurikos were sister taxa, a relationship that was supported by 15 synapomorphies. Subsequent phylogenetic analyses of the group (Modesto & Smith, 2001; Kissel *et al*., 2002), which sought to place new single-rowed taxa among other captorhinids, used augmented and/or slightly emended versions of the data matrix of Dodick & Modesto (1995).

The redescription of *L. hamatus* and the resultant new data warrants a re-examination of its phylogenetic position within Captorhinidae. It also represents an opportunity to examine the monophyly of the basal genus *Romeria*, which was questioned recently by Modesto (1998). In the Dodick & Modesto (1995) analysis, this genus was assumed to be monophyletic and was coded from its two included taxa *R. texana* Price (1937) and *Romeria prima* Clark & Carroll (1973). However, the holotype of *R. texana* differs from that of *R. prima* in featuring elongate prefrontals that extend anteriorly to a point just posterior to the external naris (Clark & Carroll, 1973: fig. 11). This morphology also suggests that UT 40001-4 (University of Texas, Austin, TX, USA), a skull referred to *R. texana* by Clark & Carroll (1973), may be incorrectly assigned to that species because it has prefrontals of the same relative size as of those in *R. prima*, *P. pricei*, and *Saurorictus australis*.

Following Dodick & Modesto (1995), *Protorothyris archeri* is used as the outgroup. Although this taxon has not been placed phylogenetically within Reptilia in published cladistic analyses of Palaeozoic Amniota, it is generally regarded to be a basal eureptile. Whether *Protorothyris* is related more closely to either captorhinids or to other eureptiles is moot for the purposes of the present work. The suitability of *Protorothyris* as an outgroup is predicated on the basis that its holotype is the most complete single skeleton of a 'protorothyridid' (i.e. a nondiapsid, noncaptorhinid eureptile). *Protorothyris* is preferred to the next-best-known 'protorothyridid', the Carboniferous taxon *Palaeothyris acadiana*, the anatomy of which is drawn from several skeletons. Each of these is visible in a single aspect only, and they have been assigned to the same species on the basis of size and overall similarity. The result has been a reconstruction of the skull (Carroll, 1969) that is a composite, in which there is little consistency among the views, suggesting that all materials assigned to *P. acadiana* should be critically re-examined.

Ingroup taxa in addition to *L. hamatus* comprise (including sources): *R. texana* (Clark & Carroll, 1973), *R. prima* (Clark & Carroll, 1973), *P. pricei* (Clark & Carroll, 1973), *Rhiodenticulatus heatoni* (Berman & Reisz, 1986), *S. australis* (Modesto & Smith, 2001), *C. laticeps* (Heaton, 1979), *Captorhinus magnus* (Kissel *et al*., 2002), *C. aguti* (Fox & Bowman, 1966; Modesto, 1998), and *L. meachami* (Dodick & Modesto, 1995). The phylogenetic characters used in the analysis are from Dodick & Modesto (1995), with minor modifications of the definitions of some characters (see the Appendix). A data matrix for 10 taxa and 40 characters (see the Appendix) was constructed in MacClade (Maddison & Maddison, 1997), which was then subjected to a branch-and-bound search by PAUP (Swofford, 2002). Multistate characters were unordered and the search was run with the delayed transformation (DELTRAN) option in effect.

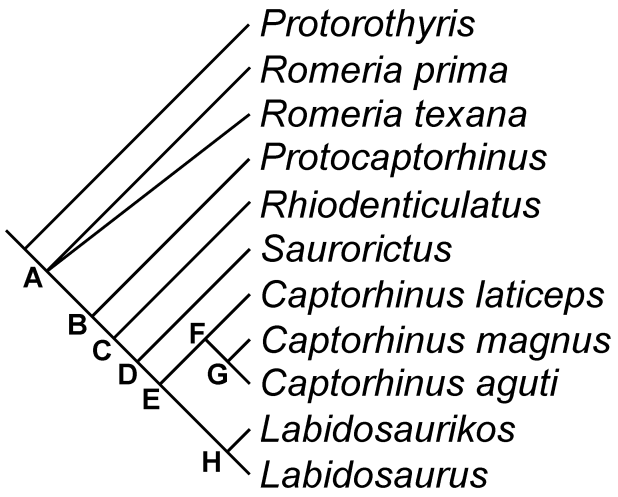

Figure 12. Strict consensus of the three shortest trees found in a PAUP analysis of the data matrix in the Appendix. Tree statistics: tree length, 55; consistency index (excluding uninformative characters), 0.80; rescaled consistency index, 0.69. Clades are diagnosed by the following synapomorphies (an asterisk denotes an ambiguous character; a minus sign indicates a reversal; numbers correspond to the characters listed in the Appendix): clade A (Captorhinidae), 1, 2, 3, 16*, 18*, 34, 35; clade B, 10(1), 14, 15, 17(1), 33(1); clade C, 5–11, 12, 19*, 31*; clade D, 4, 39; clade E, 13, 17(2)*, 20*, 21*, 25*, 29*, 38(1); clade F, 10(2), 22(1)*, 33(2), 40*; clade G, 38(2); clade H, 6, 7, 8, 9, 22(2)*, 23, 24, 26, 27, 28, 30, 32, 36.

Three shortest trees were discovered, the strict consensus of which is shown in Figure 12. The trees differ only in the relative positions of *R. texana* and *R. prima*: in one tree they are sister taxa at the base of Captorhinidae, in another tree *R. texana* is the most basal captorhinid, and in the third tree *R. prima* is the most basal captorhinid. The topology of the remainder of the tree(s) is identical to that discovered by Modesto & Smith (2001): *Labidosaurus* and *Labidosaurikos* form a clade ('H' in Fig. 12) that has a sister-group relationship with a clade formed by the three species of *Captorhinus* (clade F). *Saurorictus*, *Rhiodenticulatus*, and *Protocaptorhinus* form successively more distant outgroups to the clade of *Labidosaurus*, *Labidosaurikos*, and *Captorhinus*. The clade of *Labidosau-*

rus and *Labidosaurikos* (clade H) is the strongest grouping, requiring nine steps to collapse. The next strongest clade is Captorhinidae, which requires seven steps to collapse, followed by the clade exclusive of the two species of *Romeria* (clade B), which requires three steps to collapse. All other clades collapse with either one or two additional steps.

During the course of reappraising the characters of Dodick & Modesto (1995) for this analysis, it became apparent that several characters that had been identified as synapomorphies for *Labidosaurus* and *Labidosaurikos* may have been influenced by allometric scaling effects. For example, both taxa were the largest captorhinid taxa used in the analysis of Dodick & Modesto (1995), with skull lengths of approximately 20 and 28 cm, respectively, whereas the next largest captorhinids were the species of *Captorhinus*, with maximum skull lengths of up to 8 cm (Seltin, 1959). The size of the braincase and of the sensory structures such as eyes (of which the orbits serve as a rough approximation) are relatively larger in smaller members of groups than in larger representatives (Carroll, 1990). The converse of this observation is that although the braincase and orbits of very large captorhinids, such as *Labidosaurus* and *Labidosaurikos*, would be absolutely much larger than in *Captorhinus* and other small captorhinids, these structures would be smaller with respect to the rest of the skull.

Accordingly, the relatively smaller size of the orbit in both *Labidosaurus* and *Labidosaurikos* is reflected by three synapomorphies discovered in the first analysis: prefrontal anterior process elongate (character 7), frontal anterior process elongate (character 8), and jugal subtemporal process dorsoventrally deep (character 9). Similarly, the braincase is expected to be relatively smaller in *Labidosaurus* and *Labidosaurikos*, manifesting as two synapomorphies: supraoccipital dorsolateral processes tall (character 23) and occipital condyle positioned anteriorly (character 24). If all these characters are excluded and the phylogenetic analysis is rerun, the same shortest trees are discovered as those found in the original analysis. The sister-group relationship between *Labidosaurus* and *Labidosaurikos* is still relatively robust, requiring five additional steps to collapse. These results suggest that despite the removal of characters that might reflect allometric scaling effects, there is still good phylogenetic evidence that *Labidosaurus* is related more closely to large multiple-tooth-rowed taxa such as *Labidosaurikos* rather than to other single-tooth-rowed captorhinids.

The clade of *Labidosaurus* and *Labidosaurikos* remains the strongest grouping within Captorhinidae. Future work on captorhinids should focus not only on the anatomy and interrelationships of moradisaurines other than *Labidosaurikos*, but on the weaknesses (as the Bremer analysis reveals) apparent in the relationships of the basal captorhinids, such as the species of *Romeria* and *Protocaptorhinus*. The current work and recent anatomical studies provide a fresh perspective on the anatomy of captorhinids that should result in a more rigorous understanding of the anatomy of the earliest captorhinids. For example, the present work on *Labidosaurus* and new information on *Captorhinus* (Modesto, 1998) indicate that the parietals of these captorhinids do not possess occipital flanges, and that these bones can be excluded from the occipital rim. Such information will be valuable when re-investigating the putative occipital parietal flanges of *R. texana* (Clark & Carroll, 1973). If these flanges are confirmed in *R. texana*, this and other features might help to resolve the weaknesses at the base of the captorhinid tree.

DIET

Whereas there are inherent difficulties in identifying the diet of early vertebrates, high-fibre herbivory (a diet of plant leaves, stems and other cellulose-rich plant structures; Hotton *et al.*, 1997) can be attributed to early terrestrial vertebrates with identifiable morphological structures that are correlative with herbivory (Reisz & Sues, 2000). A caveat to this kind of endeavor, particularly with fossil taxa with no close living relatives, is that it is impossible to infer the full range of food items eaten by fossil tetrapods. For example, Munk & Sues (1993) described a specimen of *Protorosaurus speneri*, a Late Permian archosauromorph reptile characterized by a dentition consonant with carnivory, with gut contents that included a large number of seeds. Presumably the converse can be expected, as suggested by Hotton *et al*. (1997), for many early tetrapods that appear to be well adapted to high-fibre herbivory.

The large multiple-tooth-rowed captorhinids have been regarded as (presumably high-fibre) herbivores since the work of Olson (1955), but it was only relatively recently that the osteological evidence for herbivory was reviewed comprehensively for captorhinids. Dodick & Modesto (1995) identified several cranial characters, such as propaliny, that were strongly suggestive of high-fibre herbivory in *L. meachami* and other moradisaurines. Hotton *et al*. (1997) presented additional dental evidence from their SEM studies in support of the hypothesis of herbivory in *L. meachami*. The Dodick & Modesto (1995) discussion of moradisaurine herbivory included comparisons with *L. hamatus*, which now can be reassessed in light of the present redescription of the osteology of this single-tooth-rowed form.

Propaliny is thought to be an important feature of early amniote herbivory because it would have

allowed a herbivore to slide its upper and lower dentitions past one another, thereby making possible the oral processing, or communition, of plant materials (King *et al.*, 1989; Reisz & Sues, 2000; Rybczynski & Reisz, 2001). Dodick & Modesto (1995) proposed that, among captorhinids, only moradisaurines and species of the genus *Captorhinus* were capable of effecting propalinal jaw movements. However, our examination and description of the quadrate and the articular of *Labidosaurus* indicates that the articulating surface of the articular is more extensive than that of the quadrate. Moreover, this jaw joint would have facilitated only anteroposterior translation of the mandible because of the tongue-and-groove-like contact between the articular and the quadrate.

Labidosaurus possesses most of the cranial correlates of high-fibre herbivory that were attributed to the large multiple-tooth-rowed captorhinids by Hotton *et al*. (1997), including the absence of caniniform maxillary teeth and the presence of chisel-like teeth. The one conspicuous attribute that *Labidosaurus* lacks is the presence of multiple rows of marginal teeth. If *Labidosaurus* was a high-fibre herbivore, or had herbivorous tendencies, it would not have been capable of the fine communition of plant material attributed to its moradisaurine relatives. Instead it may have been limited to swallowing unprocessed partial or whole leaves and other plant structures, and propalinal movements of the marginal teeth would therefore have served to section plant materials for immediate ingestion.

There is no evidence of facetting of the marginal teeth in support of the interpretation that *Labidosaurus* was capable of propalinal jaw movements, but Hotton *et al*. (1997) presented evidence that some individuals of *C. aguti* exhibited wear facets indicative of propaliny, and that other individuals clearly did not (Hotton *et al*., 1997: fig. 2B). We conclude either that propaliny did not manifest itself as wear facetting on the marginal teeth of *Labidosaurus*, or that we lack the sample size for this captorhinid that was available to Hotton *et al*. (1997) for *C. aguti*. Circumstantially, Hotton *et al*. (1997) observed that extant herbivorous lizards do not undertake oral processing and lack wear on their marginal teeth, despite a capability for propalinal jaw movement and feeding on abrasive plant materials.

Anomalous wear facets are present on the labial surface of the apex of the first (and largest) premaxillary teeth of *Labidosaurus* and *Captorhinus*. Hotton *et al*. (1997) attributed these to a 'grubbing' action. If these reptiles dug in soils with their premaxillary teeth, however, one would expect that the whole of the apices of the largest premaxillary teeth would display more-or-less even wear. Accordingly, we feel that the presence of a distinct labial facet is not consistent with the hypothesis of grubbing action. We can think of no modern analogue that would help to explain the facetting of the first premaxillary teeth of *Labidosaurus* and *Captorhinus*. Judging from the great size of the first premaxillary teeth, it seems possible that the wear was incurred during normal foraging movements: these captorhinids may have inclined their heads with their snouts held close to the ground while walking, thereby bringing premaxillary teeth in contact with the ground surface; periodic contact between the largest premaxillary teeth and the ground would have resulted in the beveling of the apices of the teeth. If this hypothesis is correct, it would suggest that both *Labidosaurus* and *Captorhinus*, not surprisingly, relied to a great extent on olfactory cues when foraging. This behaviour may have been used equally to detect either plant fructifications or animal carcasses. Accordingly, the presence of distinctive labial facets on the largest premaxillary teeth, whatever their origin, does not serve to support the hypothesis of high-fibre herbivory in *Labidosaurus*.

The postcranial skeleton of *Labidosaurus* has been documented recently by Sumida (1987, 1989), whereas information on the structure of the trunk ribs is lacking to the point where we cannot determine whether this captorhinid had a barrel-like rib cage, suggestive of the presence of an elaborated gut tract housing cellulolytic microbes, as is present in early herbivorous tetrapods such as the species of *Diadectes* and *Edaphosaurus*. The postcranial skeleton of *Labidosaurus* appears more heavily built than that of a smaller captorhinid such as *C. laticeps* (Heaton & Reisz, 1980; Dilkes & Reisz, 1986). This difference could be attributed to an allometric scaling effect. O'Keefe *et al*. (2005) argue, however, that allometric scaling effects may not necessarily explain differences in skeletal construction in early tetrapods of less than 300 kg, a weight limit under which living *Labidosaurus* doubtless fell, because tetrapod skeletons generally scale isometrically up to this figure, and extant tetrapods compensate for increased mass with postural changes (Biewener, 2000). O'Keefe *et al*. (2005) suggest that allometric scaling effects are probably not sufficient to account for the relatively more massive build of the larger captorhinids as compared with the smaller basal members of the group, but that the adaptation to herbivory by moradisaurines might partially explain the more robust build of its skeleton because most early herbivorous tetrapods share a similar massive construction. In such aspects as femoral morphology, *Labidosaurus* appears intermediate in structure between species of *Captorhinus* and the moradisaurine *Moradisaurus* (O'Keefe *et al*., 2005), an observation that could be interpreted to mean that *Labidosaurus* was intermediate in habitus, including diet, between the smaller and the larger captorhinid taxa. A complication with this interpretation, and the suggestion by O'Keefe *et al*. (2005) that the robustness of the skeleton of *Moradi-*

saurus grandis is partly a result of herbivorous adaptation and not of the large size alone, is the attribution of herbivory to the relatively small captorhinid *C. aguti* by Hotton *et al*. (1997), which, with the exception of large size, shares all of the morphological correlates of herbivory that Hotton *et al*. attributed to the moradisaurines, including the presence of tooth plates and propalinal jaw movement.

The osteological evidence is not conclusive with regards to the diet of *Labidosaurus*. The relatively large body size (for an early reptile) and the presence of propalinal jaw action are consonant with an adaptation to herbivory; yet the absence of multiple rows of teeth suggests that *Labidosaurus* was not capable of processing ingested plant material orally, as is interpreted for its close relatives *C. aguti* and moradisaurines. The available evidence suggests that *Labidosaurus* was omnivorous, consuming whatever plant or animal foods that it encountered and could swallow, and in whatever proportions were available either in a given region or during a particular season. If this interpretation is correct, *L. hamatus* would represent a transitional taxon, in terms of diet, between the plesiomorphically faunivorous basal captorhinids (Modesto, 1996) and the herbivorous moradisaurines (Reisz & Sues, 2000).

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REFERENCES

Berman DS, Reisz RR. 1986. Captorhinid reptiles from the Early Permian of New Mexico, with a description of a new genus and species. *Annals of Carnegie Museum* **55:** 1–28.

Biewener AA. 2000. Scaling of terrestrial support: differing solutions to mechanical constraints of size. In: Brown JH, West GB, eds. *Scaling in Biology*. Oxford: Oxford University Press, 51–66.

deBraga M, Rieppel O. 1997. Reptile phylogeny and the interrelationships of turtles. *Zoological Journal of the Linnean Society* **120:** 281–354.

Branson EB. 1911. Notes on the osteology of the skull of *Pariotichus*. *Journal of Geology* **19:** 135–139.

Broili F. 1904. Permische Stegocephalen und Reptilien aus Texas. Zweite Hälfte. *Palaeontolographica* **1904:** 49–120.

Carroll RL. 1969. A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology* **43:** 151–170.

Carroll RL. 1990. A tiny microsaur from the Lower Permian of Texas: size constraints in Palaeozoic tetrapods. *Palaeontology* **33:** 1–17.

Case EC. 1911. A revision of the Cotylosauria of North America. *Carnegie Institute of Washington* **145:** 1–122.

Clark J, Carroll RL. 1973. Romeriid reptiles from the Lower Permian. *Bulletin of the Museum of Comparative Zoology* **144:** 353–407.

Cope ED. 1895. The reptilian order Cotylosauria. *Proceedings of the American Philosophical Society* **34:** 436–457.

Cope ED. 1896. Second contribution to the history of the Cotylosauria. *Proceedings of the American Philosophical Society* **35:** 122–139.

Dilkes DW, Reisz RR. 1986. The axial skeleton of the Early Permian reptile *Eocaptorhinus laticeps* (Williston). *Canadian Journal of Earth Sciences* **23:** 1288–1296.

Dodick JT, Modesto SP. 1995. The cranial anatomy of the captorhinid reptile *Labidosaurikos meachami* from the Lower Permian of Oklahoma. *Palaeontology* **38:** 687–711.

Fox RC, Bowman MC. 1966. Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). *University of Kansas Paleontological Contributions, Vertebrata* **11:** 1–79.

Gaffney ES, McKenna MC. 1979. A Late Permian captorhinid from Rhodesia. *American Museum Novitates* **2688:** 1–15.

Gow CE. 2000. A captorhinid with multiple tooth rows from the Upper Permian of Zambia. *Palaeontologia Africana* **36:** 11–14.

Heaton MJ. 1979. Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian [of] Oklahoma and Texas. *Oklahoma Geological Survey Bulletin* **127:** 1–84.

Heaton MJ, Reisz RR. 1980. A skeletal reconstruction of the Early Permian captorhinid reptile *Eocaptorhinus laticeps* (Williston). *Journal of Paleontology* **54:** 136–143.

Holmes RB. 1977. The osteology and musculature of the pectoral limb of small captorhinids. *Journal of Morphology* **152:** 101–140.

Holmes RB. 2003. The hind limb of *Captorhinus aguti* and the step cycle of basal amniotes. *Canadian Journal of Earth Sciences* **40:** 515–526.

Hotton N III, Olson EC, Beerbower R. 1997. Amniote origins and the discovery of herbivory. In: Sumida SS, Martin KLM, eds. *Amniote Origins*. San Diego: Academic Press, 207–264.

Ivakhnenko MF. 1990. Elements of the Early Permian tetrapod faunal assemblages of Eastern Europe. *Paleontological Journal* **24:** 104–112.

Jalil N-E, Dutuit J-M. 1996. Permian captorhinid reptiles from the Argana Formation, Morocco. *Palaeontology* **39:** 907–918.

Jin Y, Wardlaw BR, Glenister BF, Kotlyar GV. 1997. Permian chronostratigraphic subdivisions. *Episodes* **20:** 6–10.

King GM, Oelofsen BW, Rubidge BS. 1989. The evolution of the dicynodont feeding system. *Zoological Journal of the Linnean Society* **96:** 185–211.

Kissel RA, Dilkes DW, Reisz RR. 2002. *Captorhinus magnus*, a new captorhinid (Amniota: Eureptilia) from the Lower Permian of Oklahoma, with new evidence on the homology of the astragalus. *Canadian Journal of Earth Sciences* **39:** 1363–1372.

Kutty TS. 1972. Permian reptilian fauna from India. *Nature* **237:** 462–463.

Laurenti JN. 1768. Classis Reptilium. Specimen medicum. Exhibens synopsis Reptilium emendatum, cum experimentis circa venena et antidote Reptilium Austriacorum. Vienna: J. Thom. & Trattnern.

Lucas SG. 2002. Tetrapods and the subdivision of Permian time. In: Hills LV, Henderson CM, Bamber EW, eds. *Carboniferous and Permian of the World*. Calgary: Canadian Society of Petroleum Geologists 19: 479–491.

Maddison WP, Maddison DR. 1997. *MacClade: Analysis of Phylogeny and Character Evolution*, Version 3.07. Sunderland: Sinauer Associates.

Modesto SP. 1996. A basal captorhinid reptile from the Fort Sill fissures, Lower Permian of Oklahoma. *Oklahoma Geology Notes* **56:** 4–14.

Modesto SP. 1998. New information on the skull of the Early Permian reptile *Captorhinus aguti*. *Paleobios* **18:** 21–35.

Modesto SP, Rybczynski N. 2000. The amniote faunas of the Russian Permian: implications for Late Permian terrestrial vertebrate biogeography. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN, eds. *The Age of Dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press, 17–34.

Modesto SP, Smith RMH. 2001. A new Late Permian captorhinid reptile: a first record from the South African Karoo. *Journal of Vertebrate Paleontology* **21:** 405–409.

Munk W, Sues H-D. 1993. Gut contents of *Parasaurus* (Pareiasauria) and *Protorosaurus* (Archosauromorpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany. *Paläontologische Zeitschrift* **67:** 169–176.

O'Keefe FR, Sidor CA, Larsson HCE, Maga A, Ide O. 2005. The vertebrate fauna of the Upper Permian of Niger—III, morphology and ontogeny of the hindlimb of *Moradisaurus grandis* (Reptilia, Captorhinidae). *Journal of Vertebrate Paleontology* **25:** 309–319.

Olson EC. 1955. Parallelism in the evolution of Permian reptilian faunas of the old and new world. *Fieldiana Zoology* **37:** 385–401.

Olson EC. 1984. The taxonomic status and morphology of *Pleuristion brachycoelus* Case; referred to *Protocaptorhinus pricei* Clark and Carroll (Reptilia: Captorhinomorpha). *Journal of Paleontology* **58:** 1282–1295.

Price LI. 1935. Notes on the brain case of *Captorhinus*. *Proceedings of the Boston Society of Natural History* **40:** 377–386.

Price LI. 1937. Two new cotylosaurs from the Permian of Texas. *Proceedings of the New England Zoölogical Club* **16:** 97–102.

Reisz RR, Sues H-D. 2000. Herbivory in late Palaeozoic and Triassic terrestrial vertebrates. In: Sues HD, ed. *Evolution of Herbivory in Terrestrial Vertebrates*. Cambridge: Cambridge University Press, 9–41.

de Ricqlès A,. 1984. Remarques systématiques et méthodologiques pour servir à l'étude de la famille des captorhinidés (Reptilia, Cotylosauria, Captorhinomorpha). *Annales de Paléontologie* **70:** 1–39.

de Ricqlès A, Bolt JR. 1983. Jaw growth and tooth replacement in *Captorhinus aguti* (Reptilia: Captorhinomorpha) – a morphological and histological analysis. *Journal of Vertebrate Paleontology* **3:** 7–24.

de Ricqlès A, Taquet P. 1982. La faune de vertébrés de Permien Supérieur du Niger. I. Le captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria) – le crane. *Annales de Paléontologie* **68:** 33–106.

Rieppel O. 1985. The recessus scalae tympani and its bearing on the classification of reptiles. *Journal of Herpetology* **19:** 373–384.

Rybczynski N, Reisz RR. 2001. Earliest evidence for efficient oral processing in a terrestrial herbivore. *Nature* **411:** 684–687.

Seltin RJ. 1959. A review of the family Captorhinidae. *Fieldiana Geology* **10:** 461–509.

Sues H-D, Munk W. 1996. A remarkable assemblage of terrestrial tetrapods from the Zechstein (Upper Permian: Tatarian) near Korbach (northwestern Hesse). *Paläontologische Zeitschrift* **70:** 213–223.

Sumida SS. 1987. Two different forms of the vertebral column of *Labidosaurus* (Captorhinomorpha, Captorhinidae). *Journal of Paleontology* **61:** 155–167.

Sumida SS. 1989. The appendicular skeleton of the Early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. *Journal of Vertebrate Paleontology* **9:** 295–313.

Sumida SS. 1991. Vertebral morphology, alternation of neural spine height, and structure in Permo-Carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. Berkeley: University Of California Publications in Zoology. 122, 1–133.

Swofford DL. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sunderland: Sinauer Associates.

Williston SW. 1910. The skull of *Labidosaurus*. *American Journal of Anatomy* **10:** 69–84.

APPENDIX

ANATOMICAL ABBREVIATIONS

Anatomical abbreviations used in Figures 1–11: an, angular; ar, articular; ax, axis; bo, basioccipital; c, coronoid; cp, cultriform process of parabasisphenoid; ch, ceratohyal; col, columella; con, condyle; d, dentary;

d pr, dorsal process; ec, ectopterygoid; eo, exoccipital; ex s s, sutural surface for exoccipital; f, frontal; f int ca, foramen intermandibularis caudalis; f int me, foramen intermandibularis medius; f int or, foramen intermandibularis oralis; ftpl, footplate; j, jugal; l, lacrimal; lag rec, lagenar recess; m, maxilla; n, nasal; op, opisthotic; p, parietal; par, paroccipital process; pbs, parabasisphenoid; pf, postfrontal; pl, palatine; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; prm, premaxilla; pt, pterygoid; pt s s, sutural surface for pterygoid; q, quadrate; q f, quadrate foramen; q fl, quadrate flange of pterygoid; qj, quadratojugal; qj s s, sutural surface for quadratojugal; s, stapes; sa, surangular; se, sphenethmoid; sm, septomaxilla; so, supraoccipital; sp, splenial; sq, squamosal; sq s s, sutural surface for squamosal; st, supratemporal; st f, stapedial foramen; st rec, stapedial recess; tr fl, transverse flange of pterygoid; v, vomer.

Characters used in phylogenetic analysis

Most are from Dodick & Modesto (1995); characters 2, 9, 18, 19, and 34 are new.

1. Premaxilla: ventral margin aligned horizontally (0) or anteroventrally (1) in lateral aspect.
2. Premaxilla: alary process absent (0) or present (1) on posterodorsal process.
3. Maxilla: relatively straight (0) or posterior end flexed laterally (1) in ventral aspect.
4. Maxilla: posterior tooth positioned at the level of the posterior margin of orbit (0) or at the level of the orbital midpoint (1).
5. Lacrimal: suborbital process absent (0) or present (1) resulting in extensive contact with jugal.
6. Snout: broad (≥ 35% of the skull length) (0) or narrow (≤ 24% of the skull length) (1).
7. Prefrontal: anterior process is short, extending no more than half way to the external naris, (0) or long, extending to at least two-thirds of the way to the external naris, (1).
8. Frontal: anterior process is short (< 40% of the frontal sagittal length) (0) or long (~ 55% of the frontal sagittal length) (1).
9. Jugal: subtemporal process is dorsoventrally low (≤ 25% of skull height through the orbital midpoint) (0) or dorsoventrally deep (at least 40% of the skull height through the orbit) (1).
10. Jugal/ectopterygoid: ectopterygoid present and alary process absent (0); ectopterygoid absent and alary process present, but is no higher than the midpoint of the suborbital process of the jugal and is distinct from the orbital margin (1); or ectopterygoid absent and alary process present and positioned dorsally on the medial surface of the jugal, flush with the orbital margin (2).
11. Quadratojugal: anteroposteriorly elongate (0) or short, not extending anteriorly beyond the midpoint of the postorbital region, (1).
12. Quadratojugal anterior end: acuminate (0) or square-tipped (1).
13. Postorbital cheek: relatively straight (0) or expanded laterally (1) in the dorsal aspect.
14. Pineal foramen: positioned at (0) or anterior to (1) the midpoint of the interparietal suture.
15. Postparietal: contacts mate fully along height (0) or mainly dorsally, such that paired postparietals are separated slightly ventrally by the supraoccipital, (1).
16. Postparietal: transversely narrow, with tabular present, (0) or transversely broad, occupying the area of the absent tabular, (1).
17. Skull table occipital margin: embayed bilaterally (0), roughly straight (1), or with a single median embayment (2).
18. Vomer: denticulate (0) or edentulous (1).
19. Vomer–pterygoid contact: extensive, at least 50% of the median border of the vomer, (0) or short, no more than 33% of the median border of the vomer, (1).
20. Pterygoid: tranverse flange broad based and distinctly angular (0) or narrow and tongue-like (1) in ventral view.
21. Parasphenoid: deep ventral groove absent (0) or present (1) anteriorly between cristae ventrolaterales.
22. 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).
23. Supraoccipital: lateral ascending processes account for either ≤ 50% (0) or ≥ 66% (1) of the height of the bone.
24. Occipital condyle: at the level of the posterior margin of quadrate condyles (0) or at the level or anterior to the anteriormost point of quadrate condyles (1).
25. Paroccipital process: short (0) or rod-like (1).
26. Sculpturing: consists of small honeycombing pits and grooves (0) or of pits and grooves with notably larger and randomly positioned pits on posterior skull table (1).
27. Mandibular ramus: relatively straight (0) or sigmoidal (1) in ventral view.
28. Mandibular ramus: narrow (≤ 8% of the total jaw length) (0) or broad (> 14% of the total jaw length) (1).
29. Mandibular ramus: posterior end rectilinear (0) or acuminate (1) in lateral view.
30. Mandibular ramus: lateral shelf absent (0) or present (1) below coronoid process.
31. Coronoid: anterior process short (0) or elongate (1).

32. Meckelian foramen: small (anteroposterior length ~9% or less of the total jaw length) (0) or large (anteroposterior length ≥14% of the total jaw length) (1).
33. Retroarticular process: absent (0), present but broader transversely than long (1), or present and longer anteroposteriorly than broad (2).
34. Premaxillary dentition: first tooth relatively small compared with the maxillary caniniform (0) or subequal to maxillary caniniform (1). In taxa lacking maxillary caniniforms, state 1 applies when the first premaxillary tooth is the largest marginal tooth present.
35. Maxillary dentition: tooth positions number 30 or more (0) or 25 or less (1); for multiple-rowed taxa only those teeth with unobstructed lateral profiles are considered.
36. Maxillary caniniform teeth: one or more teeth that are conspicuously taller than both preceding and succeeding teeth are present (0) or absent (1).
37. Multiple tooth rows: absent (0) or present (1).
38. Marginal dentition: posterior 'cheek' teeth conical (0), chisel-shaped (1), or ogival in section (2).
39. Dentary caniniform teeth: absent, and dentition isodont, (0), or one or more anterior teeth that are conspicuously taller than succeeding teeth are present (1).
40. Dentary: first tooth orientated mainly vertically (0) or leans strongly anteriorly (1).

DATA MATRIX

Uncertainty for states 1 and 2 for character 17 is indicated by 'A'.

Protorothyris	00000000000000000000000?0?100000000000000
Romeria prima	11101000?1000010???00?00?0000??01100010
Romeria texana	11100010001000??0100???0?????????11000?0
Protocaptorhinus	11100000011001111??00000110000??111000?0
Rhiodenticulatus	11101010010101111?1000000?00001??0100000
Saurorictus	?1?110000?010?11A????????1???????1100010
Captorhinus laticeps	11111000020111112111110011001010211001111
Captorhinus magnus	11111000?0111???????????100101?2110021?
Captorhinus aguti	11111000020111112111110011001010211012111
Labidosaurikos	11111111110111112111121112111101111111110
Labidosaurus	11111111110111112111121112111111111110111