

## A NEW BURNETIAMORPH THERAPSID FROM THE TEEKLOOF FORMATION, PERMIAN, OF SOUTH AFRICA

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**ABSTRACT**—A new biarmosuchian therapsid, *Lobalopex mordax* gen. and sp. nov., from the Permian Teekloof Formation (*Tropidostoma* Assemblage Zone) of the Victoria West District, South Africa, is described on the basis of a partial skull with lower jaws and the first four cervical vertebrae. The genus is diagnosed by the following autapomorphies: median nasal eminence low and ridge-like; supraorbital boss small and unpachyostosed; posteriorly projecting supratemporal ‘horns’ present but relatively small; ventral surface of transverse flange of pterygoid edentulous and sharply ridged; and laterally-directed knob present lateral to contact between pterygoid and palatine dentigerous bosses. As in some other biarmosuchians, the cervical vertebrae are elongated, being roughly twice as long as they are wide or deep. A cladistic analysis including ten biarmosuchian taxa indicates that *Lobalopex* is the sister taxon to Burnetiidae and that *Lemurosaurus* is the most primitive burnetiamorph. These results fail to provide evidence for geographic endemism in these groups of Middle to Late Permian therapsids.

### INTRODUCTION

From 1923 to 1997, burnetiid therapsids were known from two specimens, one from South Africa and one from Russia (Broom, 1923; Tatarinov, 1968). Both specimens are skulls characterized by numerous bony outgrowths and swellings, specializations that prompted Broom (1923) to consider *Burnetia mirabilis* (the South African form) to warrant its own suborder, the Burnetiamorpha. Tatarinov (1968) named the second burnetiid, *Proburnetia viatkensis*, on the basis of a natural mold in a sandstone concretion. Despite their preservational differences, the two skulls are remarkably similar. Where they differ, it is typically with respect to the degree of expression of features held in common. For example, both taxa have a median nasal boss, which in *Burnetia* is spindle-shaped but in *Proburnetia* is ridge-like (Rubidge and Sidor, 2002).

Several new burnetiamorph taxa have been recognized in recent years. *Niuksenitia sukhonensis* was initially described by Tatarinov (1977), on the basis of an incomplete skull, as a broomicephaline gorgonopsid, but Sigogneau-Russell (1989), in her review of primitive theriodonts, suggested that the specimen preserved morphology more consistent with a placement in the Burnetiidae. More recently, Ivachnenko et al. (1997) transferred *Niuksenitia* to the Burnetiidae, although they did not provide a rationale for their taxonomic decision.

Rubidge and Kitching (2003) described *Bullacephalus jacksoni*, from the *Tapinocephalus* Assemblage Zone of South Africa, as the stratigraphically lowest burnetiamorph. Moreover, they published the first cladistic analysis of Burnetiamorpha, suggesting that *Bullacephalus* was the sister taxon to Burnetiidae (defined as including *Burnetia* + *Proburnetia*; see Rubidge and Sidor, 2002).

Sidor and Welman (2003) described a new specimen of the basal therapsid *Lemurosaurus pricei* and, on the basis of their cladistic analysis, reassigned this taxon to the Burnetiamorpha, thus removing it from the Ictidorhinidae, where it had long been placed (Sigogneau, 1970; Sigogneau-Russell, 1989). Sidor and Welman (2003) disagreed with Rubidge and Kitching (2003),

considering *Bullacephalus* to be the sister taxon of the genus *Burnetia* and not of the entire family Burnetiidae.

Finally, we are aware of two undescribed burnetiamorph specimens. The first was recovered from near the boundary of the *Tropidostoma* and *Cistecephalus* assemblage zones of South Africa by a team from the South African Museum (R. Smith, pers. comm., May 2002). The second was discovered in Malawi and is currently under study by Dr. Elizabeth Gomani (L. Jacobs, pers. comm., October 2002).

Here we describe a new burnetiamorph that preserves portions of the skull and lower jaw that are either unknown or poorly understood in other early therapsids. In addition, the cervical vertebrae in our new specimen represent the first associated postcranial remains of a burnetiamorph. We expand upon the cladistic studies of Sidor and Welman (2003) and Rubidge and Kitching (2003) to ascertain the position of our new taxon within Burnetiamorpha. A preliminary description of our new taxon was given by Sidor (2000) in his unpublished dissertation.

**Institutional Abbreviations**—**BMNH**, The Natural History Museum, London; **BP**, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; **CGP**, Council for Geosciences (formerly the Geological Survey of South Africa), Pretoria; **NMQR**, National Museum, Bloemfontein; **PIN**, Paleontological Institute, Moscow; **RC**, Rubidge Collection, Graaff-Reinet; **SAM**, South African Museum, Cape Town.

### MATERIAL

The holotype, CGP/1/61, was discovered by collectors working under the guidance of Dr. Colin MacRae of the Geological Survey of South Africa. The fossil was misidentified as a gorgonopsian and housed in the collections of the Council for Geosciences in Pretoria until it was recognized as a burnetiamorph by JAH in 1989. Before being loaned to JAH, the partially prepared specimen was severely damaged during the process of molding. It was broken into small pieces at the level of the orbits, just posterior to the transverse flanges of the pterygoid, so that contacts be-

tween the snout and braincase portions of the skull cannot be accurately made. Fortunately, several casts were made that preserve the original morphology of this region; these were used to make the figured restorations of the complete skull presented here. Additional fine-scale preparation of the specimen was undertaken by Ms. Claire Vanderslice at the University of Chicago. In addition, the cervical vertebrae were separated from the occipital portion of the skull.

The spongy and pachyostotic nature of burnetiamorph crania has made it difficult to interpret sutures (Broom, 1923; Rubidge and Sidor, 2002; Rubidge and Kitching, 2003; Sidor and Welman, 2003). Although the present skull is the least ornamented yet discovered, we also had difficulty in this regard. Sutures are drawn in Figures 1–5 only when clearly visible. Dashed lines indicate that a given suture is likely, but open to interpretation.

As burnetiamorphs are rare fossils, the comparisons made herein are based on direct observation of all described members of the clade and one undescribed specimen. The latter, SAM-PK-K10037, is currently under study by Drs. Roger Smith and Bruce Rubidge. The holotype of *Burnetia mirabilis* (BMNH R5397) was borrowed from the Natural History Museum (London) with kind permission of Dr. Angela Milner. The holotype of *Bullacephalus jacksoni* (BP/1/5387) was made available for study by Dr. Bruce Rubidge. The holotypes of the Russian burnetiamorphs, *Proburnetia viatkinsis* (PIN 2416/1) and *Niuksenitia sukhonese* (PIN 3159/1), were studied by the first author at the Paleontological Institute in Moscow. For direct comparison to the new specimen, latex molds of *Proburnetia* were provided by Dr. Robert Reisz. Finally, we have included in this study the specimen recently described by Sidor and Welman (2003) as *Leurosaurus pricei* (NMQR 1702).

## SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905  
BIARMOUCHIA Sigogneau-Russell, 1989  
BURNETIAMORPHA Broom, 1923

**Definition**—The most inclusive clade including *Burnetia mirabilis*, but excluding *Biaromosuchus tener*, *Hipposaurus boonstra*, and *Ictidorhinus martinsi* (from Sidor and Welman 2003).

**Revised Diagnosis**—Skull moderately to greatly pachyostotic; supraorbital boss present; boss on zygomatic arch present; lower canine occluding into lateral diverticulum of internal nares; palatal processes of premaxillae long and laterally bounding anterior portion of vomer.

*LOBALOPEX MORDAX*, gen. et sp. nov.

**Etymology**—*Lobos*, lobe (Greek); *alopez*, fox (Greek); *mordax*, biting (Latin).

**Holotype**—CGP/1/61, skull and lower jaws with parts of the first four cervical vertebrae in articulation.

**Type Horizon and Locality**—The holotype of *Lobalopez* was collected on the farm Quaggas Fontein 250, which is on the plateau of the Nuweveld escarpment about 90 km north of Beaufort West in the Victoria West District of South Africa. The coordinates of the type locality are 32° 40' 11" South and 22° 30' 06" East. The fossil was found in gray and purple mudstone assignable to the Hoedemaker Member of the Teekloof Formation. The beds in this area contain fossils representative of the *Tropidostoma* Assemblage Zone, which is considered to be Tatarian (Middle or Late Permian) in age (Smith and Keyser, 1995; Lucas, 2002).

**Diagnosis**—Therapsid with cranial bosses more moderately developed than in other burnetiamorphs; midline nasal boss low and ridge-like; supraorbital ridges weakly developed; squamosals

forming weakly developed, posteriorly projecting supratemporal 'horns'. Autapomorphic in possession of parietals with shallow fossae on their dorsal surface just lateral to parietal foramen; vomer deeply troughed ventrally and narrow; palatine teeth forming two longitudinal rows separated from single row of pterygoid teeth by short gap; laterally projecting knob present at junction of pterygoid and palatine bosses; transverse flange of pterygoid edentulous, with sharply ridged ventral surface; ectopterygoid with thin lamina connecting lateralmost portion of transverse flange and primary palate.

## DESCRIPTION

### Skull

The holotype of *Lobalopez* has suffered pronounced dorsoventral compression, especially in the interorbital and temporal regions (Fig. 1A). As a result, the occiput slants more anteroventrally (i.e., it is more horizontal) than in life, the zygomatic arches are splayed outwards, and the lateral surfaces of the antorbital region are crumpled.

Phylogenetically, the skull retains many primitive features, chief among which is a very broad intertemporal region and small lateral temporal fenestrae (Fig. 1:ltf). The margins of the latter indicate that the jaw adductor musculature did not pass through the fenestra to attach to the outer surface of the skull, as in eutherapsids. The palate is also primitive, with no development of a secondary palate or suborbital vacuities. Numerous bosses and protuberances adorn the skull roof, although these are less developed than in most other members of the burnetiamorph clade (e.g., Rubidge and Sidor, 2002).

**Dermal Skull Roof and Occiput**—The tooth-bearing ramus of both premaxillae is well preserved, but all of the dorsal (internarial) process has been lost to erosion (Figs. 1, 2). Because of this erosion, we are unable to determine whether the dorsal processes of the premaxillae were long and extended posterior to the level of the upper canine (as in *Biaromosuchus* and *Hipposaurus*), or relatively short (as in *Lycaenodon*). Nine small incisors are preserved in the premaxillae. A suture clearly separates the two premaxillae for most of their midline contact, but then appears to bisect a small median tooth. We interpret this median tooth as a retained right first incisor that has been shifted medially to partially fill the alveolus of the missing left first incisor. Below the narial region, the premaxillae are overlapped by the maxillae. When viewed from above, the premaxillae are seen to form the anterior, anteromedial, and anterolateral margins of the internal nares. The tips of the lower canines pass through the anterior portions of the internal narial openings so as to lie within the nasal cavity. In addition, because of the erosion of the dorsal rami of the premaxillae, the palatal rami of the premaxillae can be seen to clasp the median vomer for a substantial distance, as can be observed in several other biarmosuchian therapsids in ventral view (Rubidge and Sidor, 2002; Sidor, 2003).

The size of the septomaxilla is unknown, although there is a possible portion of the right septomaxilla preserved between the nasal and maxilla. *Proburnetia* shows a small facial process that extends between the nasal and maxilla for only a short distance (Rubidge and Sidor, 2002).

The maxilla in *Lobalopez* conforms to the pattern typical of sphenacodontid 'pelycosaurs' and early therapsids (Orlov, 1958; Reisz et al., 1992a). Anteriorly, a small horizontal subnarial process overlaps the premaxilla lateral to the last two incisors. Posterior to this, the ventral margin of the maxilla curves abruptly posteroventrally so that the base of the upper canine projects anteroventrally. Behind the canine, the ventral margin of the maxilla forms a gentle convex curve, which ascends posteriorly to form a short spur that overlaps the jugal near the ventral border

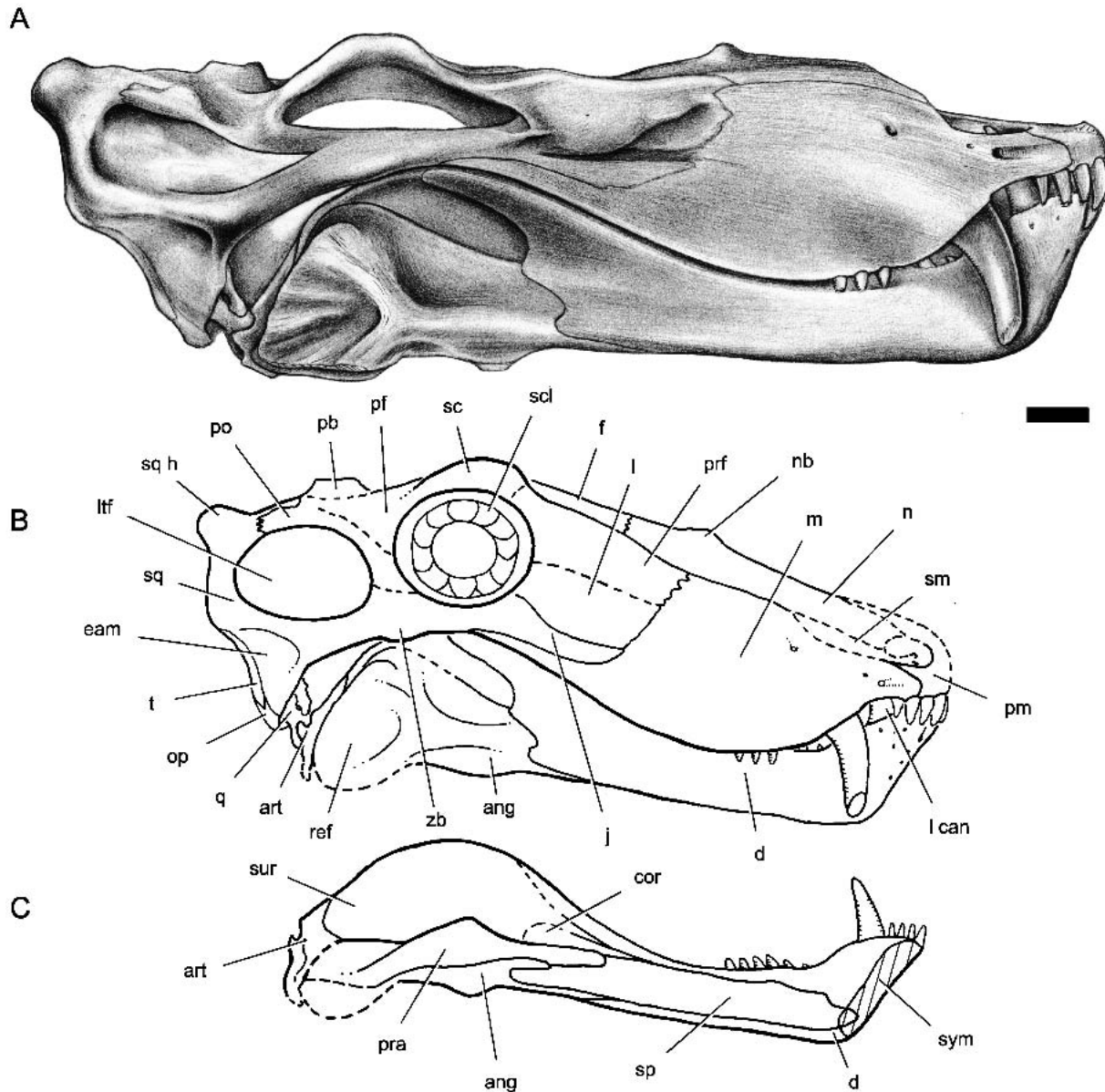


FIGURE 1. Skull and lower jaw of *Lobalopex mordax* gen. et sp. nov., CGP/1/61: **A**, specimen drawing (from cast and specimen) in lateral view (scale bar equals 1 cm); **B**, reconstruction in lateral view; and **C**, reconstruction of medial aspect of lower jaw. Parallel lines denote extent of mandibular symphysis. **Abbreviations:** **ang**, angular; **art**, articular; **cor**, coronoid; **d**, dentary; **dp**, dorsal process of articular; **eam**, external auditory meatus; **ec**, ectopterygoid; **epi**, epipterygoid; **ex**, exoccipital; **f**, frontal; **for**, foramen magnum; **ic**, internal carotid foramen; **j**, jugal; **j for**, jugular foramen; **l**, lacrimal; **l can**, lower canine; **ltf**, lateral temporal fenestra; **m**, maxilla; **n**, nasal; **nb**, nasal boss; **oc**, occipital condyle; **op**, opisthotic; **p**, parietal; **p a**, pila antotica; **pb**, parietal boss; **pal**, palatine; **pf**, postfrontal; **pm**, premaxilla; **pm p**, broken dorsal process of premaxilla; **po**, postorbital; **pp**, postparietal; **pr?**, possible proatlas; **pra**, prearticular; **prf**, prefrontal; **pro**, prootic; **pt**, pterygoid; **ptf**, post-temporal fenestra; **q**, quadrate; **q for**, quadrate foramen; **qr**, quadrate ramus of pterygoid; **qj**, quadratojugal; **ref**, reflected lamina; **rp**, broken retroarticular process; **s**, stapes; **sc**, supraorbital crest; **scl**, sclerotic ring; **sel**, sella turcica; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **sq b**, squamosal boss; **sq h**, supra-temporal 'horn' of squamosal; **sur**, surangular; **sym**, mandibular symphysis; **t**, tabular; **tp**, tympanic process of opisthotic; **v**, vomer; **vas**, vascular notch; **V n**, notch for trigeminal nerve; **zb**, boss on zygomatic arch.

of the skull. The dorsal margin of the maxilla contacts, in order from front to back, the (probable) septomaxilla, nasal, prefrontal, lacrimal, and jugal. The upper canine is relatively large and recurved, and bears serrations along its posterior (distal) margin. The anterior margin of the canine is rounded and appears to lack serrations, although its apex is not well preserved. Posterior to a diastema equivalent in length to the diameter of the canine, three small postcanine teeth are present on either side. The postcanines are separated from one another by spaces equal to their

diameters. Because the jaws are tightly closed, finding additional postcanine teeth or alveoli is impossible. It is clear, however, that there are no precanine maxillary teeth.

The nasals in *Lobalopex* appear to be partially fused, because a median suture is not visible for most of their length, and they are damaged anteriorly by erosion. The lateral margins of the nasals, however, are distinct, and bow gently inward between the dorsal margins of the maxillae and, more posteriorly, the prefrontals. Posteriorly, contact between the nasals and frontals ap-

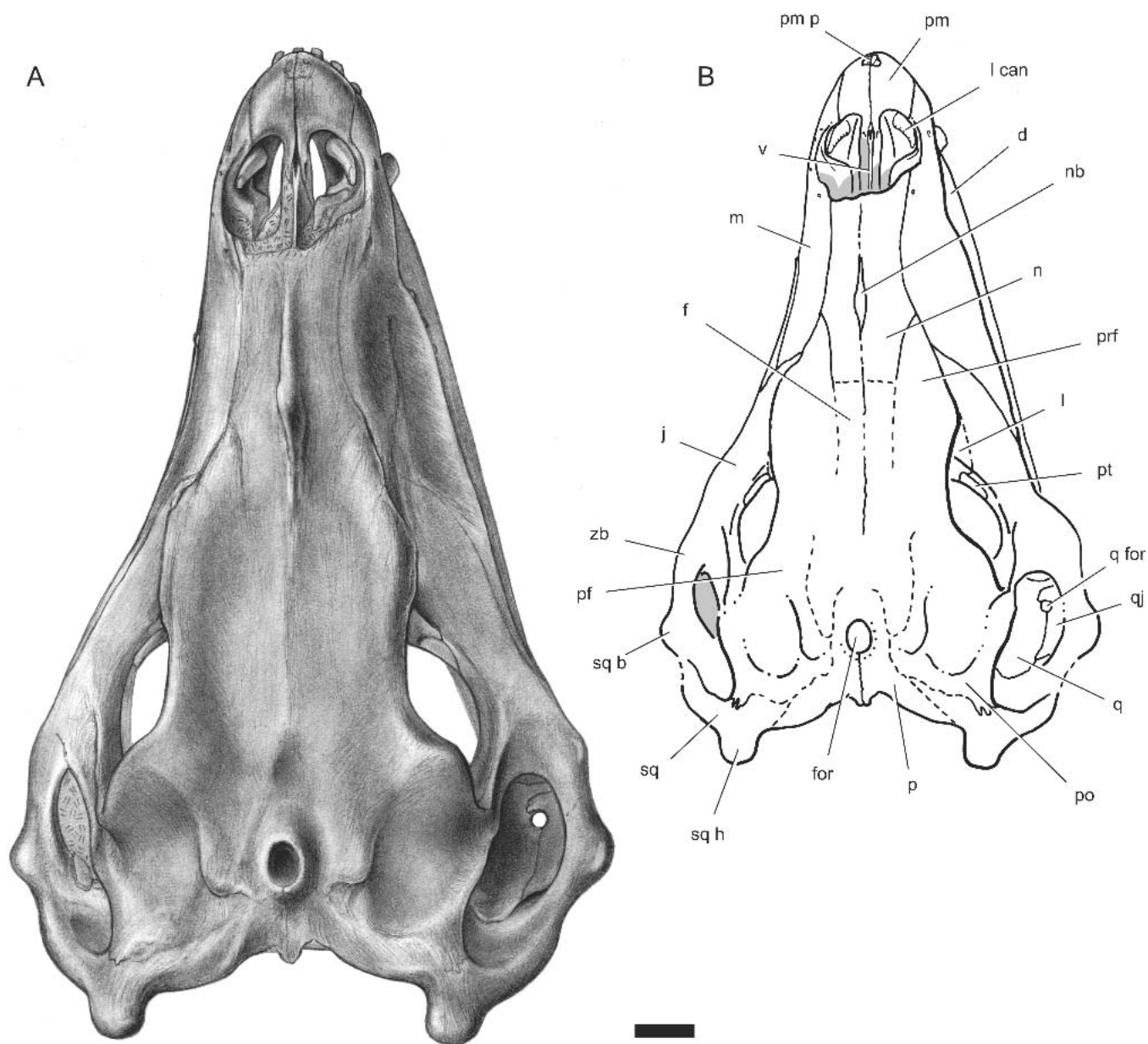


FIGURE 2. Skull and lower jaw of *Lobalopex mordax* gen. et sp. nov., CGP/1/61, in dorsal view. **A**, specimen drawing (scale bar equals 1 cm) and **B**, interpretive drawing. Check pattern (A) and gray (B) indicate areas of remaining matrix. Abbreviations given in Figure 1.

pears to be present as a roughly transverse suture located slightly rostral to the level of the orbit. Burnetiamorph nasals bear diagnostic median outgrowths. Except for *Lemurosaurus*, this outgrowth is most weakly expressed in *Lobalopex* among burnetiamorphs and takes the form of a low ridge (Fig. 2B:nb). In *Proburnetia* it is also ridge-like, whereas in *Burnetia* it is spindle-shaped, and in *Bullacephalus* it is compact and circular (although eroded).

Diagenetic crushing and damage from the molding process have both contributed to the poor preservation of the frontals. Between the prefrontals, the frontals continue the median nasal eminence as a slight ridge bounded by paired depressions. Posteriorly, the midline frontal suture is visible, but it is impossible to tell if the frontal contributed to the orbital margin because of breakage and subsequent reattachment. Rubidge and Kitching (2003) suggested that the prefrontals and postfrontals of *Bullacephalus* contact one another, although Sidor and Welman

(2003) suggested that they did not in *Lemurosaurus*. Determining the posterior extent and morphology of the frontals is also difficult, but they appear to extend to the level of the parietal foramen as tapering wedges that contact the parietals along their anterior and medial margins (Fig. 2). A similar morphology occurs in fossils assigned to the basal therapsid genera *Hipposaurus* (SAM-PK-K8950; CGP/1/66), *Lycaenodon* (RC 20), and cf. *Rubidgina* (CGP/1/67).

The prefrontal tapers anteriorly on the dorsal surface of the skull roof anterior to the orbit. The posterior border of the prefrontal is unclear, but it is likely that this element extended at least part way onto the rim of the orbit. Laterally the prefrontal is damaged, but it can be seen to contact the maxilla anterolaterally and is inferred to contact the lacrimal ventrally.

The lateral surface of the lacrimal has been crumpled because of dorsoventral crushing, such that its dorsal contact with the prefrontal is unclear. On both sides of the skull, the lacrimal

appears to accommodate two shallow fossae with a slight ridge between them. Both *Burnetia* and *Proburnetia* possess shallow depressions on the lacrimal anterior to the orbit (Rubidge and Sidor, 2002), so it is probable that the crushing experienced by the specimen of *Lobalopex* has simply accentuated these fossae. The lacrimal contacts the maxilla anteriorly and the jugal ventrally. As preserved, lacrimal foramina are not visible within the orbit.

The snout portion of the holotype preserves the anterior ramus of the jugal, which has a long contact with the maxilla before paralleling the upward sweep of the latter anterior to the orbit. The contact between the jugal and lacrimal is difficult to make out with confidence because of crushing in this region. The post-orbital and zygomatic rami of the jugal were damaged during molding, although their original form can be seen in the cast. It is uncertain to what degree the jugal contributed to the formation of the postorbital bar. It is also uncertain how far back the jugal extended on the zygomatic arch, although a break just anterior to the lateral boss on the squamosal revealed no indication of the jugal. *Burnetia* and *Proburnetia* have a large, laterally protruding boss at the junction of the zygomatic and post-orbital bars and another similar structure just anterior to this, ventral to the orbit. In *Lobalopex*, the posterior boss (Fig. 1:zb) is moderately well developed and a more anterior boss below the orbit is not present.

The postfrontals have also been affected by molding damage. Although sutures with its surrounding elements cannot be determined, it appears certain that the postfrontal contributed to at least the posterior portion of the supraorbital crest in *Lobalopex*. This crest (Fig. 1:sc) is continuous with the lateral ridge on the prefrontal, which forms the anterodorsal margin of the orbit. Whether the frontal contributed to the orbital margin cannot be determined. The postfrontal is broadly convex and overhangs the posterodorsal portion of the orbit. Also, in contrast to the condition in *Burnetia* and *Bullacephalus*, the supraorbital eminence in *Lobalopex* (as well as in *Lemurosaurus*, *Proburnetia*, and SAM-PK-K10037) is not subdivided into separate (anterior) longitudinal and (posterior) transverse portions.

The morphology of the postorbital is best preserved on the left side. In dorsal view, the postorbital forms the lateral margin of the broad intertemporal region and contacts the squamosal along a clear suture positioned at the posterodorsal corner of the temporal fenestra. It presumably contributes to the postorbital bar, which bears a ridge along the posterior border of the orbit and is triangular in cross-section. Neither the contacts of the postorbital with the jugal and squamosal at the base of the postorbital bar, nor its contact with the postfrontal at the upper end of the post-orbital bar, can be determined.

In lateral view, the squamosal forms the posterior and ventral margins of the lateral temporal fenestra. The bone in these regions is relatively thick, but does not show the pronounced pachyostosis seen in more derived burnetiamorphs. The squamosal forms a prominent boss or 'horn' above the posterodorsal margin of the temporal fenestra, at the posterolateral corners of the skull roof (Fig. 1:sq h). A similar structure occurs in *Proburnetia* and *Burnetia*, and in the dinocephalian *Styracocephalus*. Rubidge and van den Heever (1997), however, considered the dorsal aspect of the 'horns' in *Styracocephalus* to be formed by both the postorbital and squamosals, so that it was not homologous to the 'horns' in burnetiamorphs. Midway along the zygomatic arch is a weakly expressed ventrolateral thickening, although it is difficult to determine if it is present on the squamosal or jugal (Fig. 1:zb). At the posteroventral corner of the zygomatic arch, above the jaw articulation, the squamosal forms an additional, bulbous thickening (Fig. 2:sq b). In posterior view, this boss is positioned at the dorsolateral corner of the external auditory meatus and represents the confluence of the latter depression's thickened dorsal and lateral margins (Fig. 4:sq b). The squamosal extends

ventrally to form a transverse sheet behind the quadrate and quadratojugal. The occipital surface of the squamosal forms a continuous, thickened ridge between the posteroventral and 'supratemporal' (Fig. 4:sq h) bosses. The internal portion of the right squamosal is visible (Fig. 5). In anterior view this element can be seen to form much of the posterior surface of the adductor chamber. Ventrally the squamosal disappears behind the quadrate, but it can be seen to contact the prootic medially.

A distinct preparietal anterior to the parietal foramen cannot be discerned in *Lobalopex*. In all other burnetiamorph taxa where this region is preserved, the presence or absence of a preparietal is similarly equivocal. Among biarmosuchians, a preparietal is unequivocally present in *Hipposaurus*, *Lycaenodon*, and *Rubidgina* (Sidor, 2000).

The dorsal surface of the parietals is dominated by a volcano-shaped eminence that surrounds the parietal foramen (Fig. 1:pb). In *Proburnetia*, SAM-PK-K10037, and *Bullacephalus*, the parietals form a broad swelling around the pineal foramen, but do not form a tall projection; this area is damaged in *Burnetia*. The exact margins of the parietals are difficult to determine with confidence. Lateral to the parietal foramen, the parietals contact the long posterior processes of the frontals. Posterolaterally, the parietals presumably contact the postorbitals and squamosals, but clear sutures are not present. In occipital view, the parietals form small parasagittal embayments that border a median ridge that descends onto the postparietal. Dorsoventral crushing has accentuated the degree to which the parietals overhang the tabulars, so that deep fossae are formed just lateral to the embayments.

The postparietal extends ventrally from the dorsal border of the occiput midway to the foramen magnum (Fig. 4:fm). As in the majority of early synapsids (except for some varanopids and caseids), the postparietal is unpaired. The postparietal has a rhomboidal outline and supports a small median ridge that diminishes in relief ventrally. This median ridge is most strongly expressed in *Bullacephalus*, *Proburnetia*, and SAM-PK-K10037. Suture contacts with the parietals dorsally, tabulars laterally, and median supraoccipital ventrally are clearly visible.

On the occipital surface, the tabulars form L-shaped elements whose rami parallel the dorsal and lateral surfaces of the skull. The descending process wedges between the paroccipital process of the opisthotic and the squamosal as a thin spur. The tabular contacts the dorsal margin of the supraoccipital along a roughly transverse suture and contacts the postparietal medially. Dorsally and dorsolaterally the tabular contacts the parietal and squamosal, respectively.

**Dermal Palate**—In ventral view (Fig. 3), the anterior portion of the vomer remains obscured by matrix. More posterior portions show that the interchoanal portion of this bone was extremely narrow, as in all burnetiamorphs except *Burnetia* (the condition in *Niuksenitia* is unknown). The lateral margins of the vomer are turned downward to produce the median ventral trough characteristic of most non-theriodont therapsids (except tapinocephalian dinocephalians). Deformation has caused the margins of the lateral ridges of the vomer to contact one another so that much of the main body of the vomer's ventral surface is hidden. Where this surface is visible anteriorly, the vomer appears paired. Only a small portion of the postnarial part of the vomer is preserved contacting the anteromedial surface of the palatines and presumably the pterygoids between the toothed bosses.

The palatines are large bones that form most of the anterior half of the palate. The lateral margins of the internal nares are formed by a short section of the maxillae anteriorly and by long anterolateral processes of the palatines more posteriorly. Posterior to the internal nares, the palatines contribute to the formation of prominent palatal bosses. These bosses take the form of elongate ridges that extend far ventral to the palatal portion of

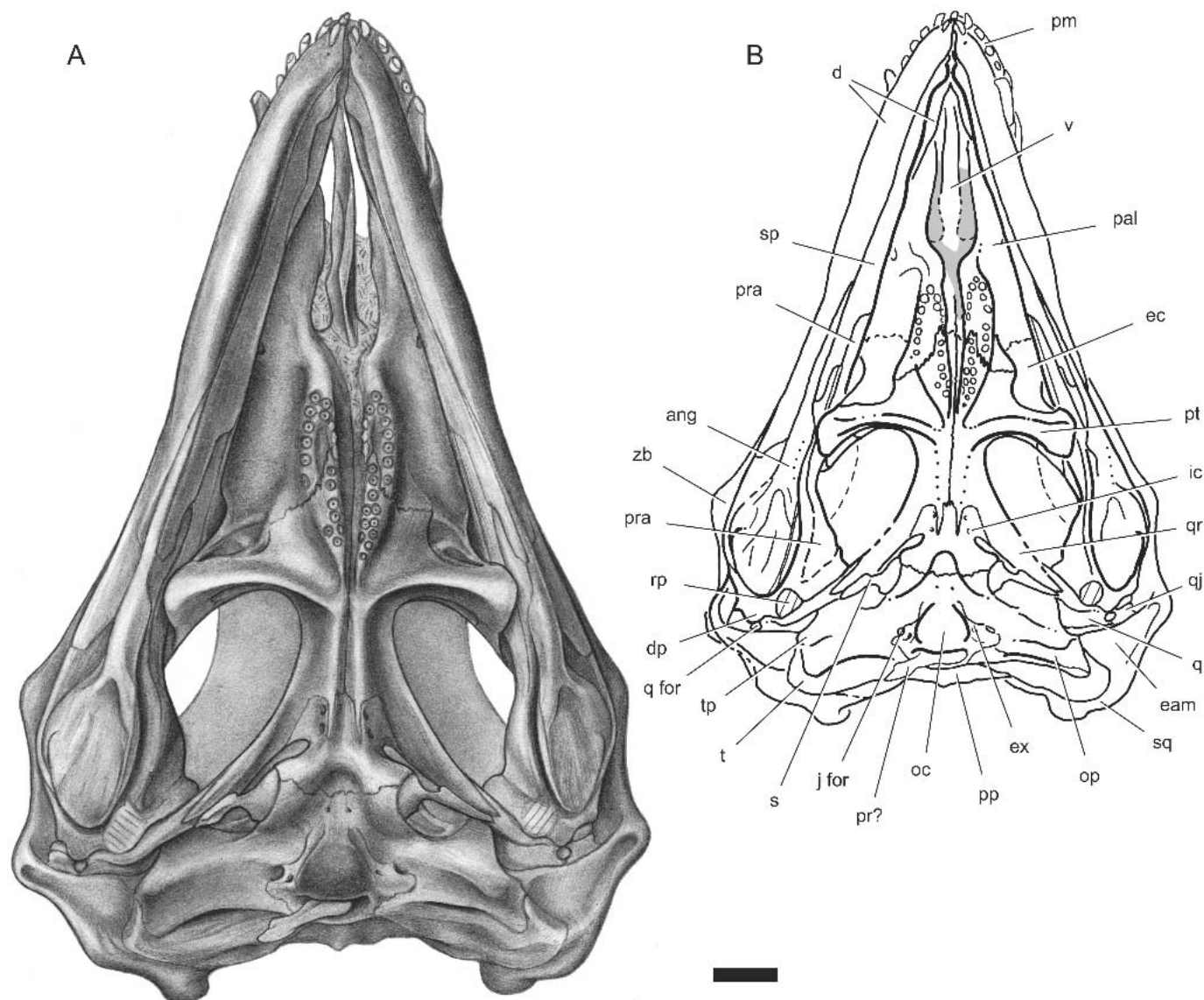


FIGURE 3. Skull and lower jaw of *Lobalopex mordax* gen. et sp. nov., CGP/1/61, in ventral view. **A**, specimen drawing (scale bar equals 1 cm) and **B**, interpretive drawing. Parallel lines denote broken surfaces; check pattern (**A**) and gray (**B**) indicate areas of remaining matrix. The left lower jaw has been partially restored based on the anatomy preserved on the right side. Abbreviations given in Figure 1.

the palatine, and below the ventral surface of the maxillae (although the latter condition may be a diagenetic artifact). On the left ridge can be seen the roots of eleven small teeth arranged in two longitudinal rows: an anteromedially-placed row of four teeth, and a longer, lateral row of seven teeth. These two tooth rows are probably the result of transversely deforming the semi-circular arc of teeth present on the palatines of biarmosuchian therapsids (e.g., Sidor and Welman, 2003). The palatine bosses widen posteriorly towards their contact with the pterygoids, and a small laterally directed knob is present at the sutural junction of these two bones. The area between the palatine bosses is deeply troughed. The trough is presumably roofed by the vomers anteriorly and the pterygoids posteriorly.

The limits of the ectopterygoid are difficult to discern. In *Proburnetia* this bone is a large, well-defined triangular element that lies at the posterolateral corner of the primary palate, just in front of the transverse flange of the pterygoid. In *Burnetia*, the ectopterygoid is much smaller but still contacts the anterior surface of the transverse flange. Because of numerous cracks in this

area of the palate, only the posterior margin of the ectopterygoid in *Lobalopex* is clear. Here, the ectopterygoid and pterygoid form a transverse suture across the anterior face of the transverse flange. Medially and anteriorly this suture disappears. On its lateral border, the ectopterygoid forms a prominent dorso-ventrally directed ridge.

The pterygoid can be described as being composed of four portions: the anterior, or palatal ramus, the transverse flange, the basicranial portion, and the quadrate ramus. The palatal ramus contacts the palatine by means of a transverse suture on the parasagittal dentigerous ridges (Fig. 3). In *Proburnetia*, the pterygoid also sends a long anterior process between the ridges to contact the vomer (Rubidge and Sidor, 2002, contra Tatarinov, 1974; Ivachnenko, 2000), but a similar condition cannot be determined with certainty in *Lobalopex*. The transverse flange of the pterygoid is oriented almost perfectly orthogonal to the long axis of the skull. It forms a remarkably thin, edentulous ridge along the medial two-thirds of its ventral edge, but becomes thicker more laterally. In dorsal view, the transverse flange of the

pterygoid can be seen to possess a small dorsal ramus that appears on the ventral margin of the orbit as a rectangular element between the jugal and lacrimal.

Both pterygoid quadrate rami (Fig. 3:qr) were damaged during molding so that a gap exists between the snout and braincase portions in the holotype. Based on the condition present both anterior and posterior to this gap, the interpterygoid vacuity appears to have been closed. Near their origin from the transverse flanges, the basicranial rami are relatively narrow and have a total of four ridges along their ventral surface. The medial pair of ridges bounds a midline trough, which is roofed by medial lappets of the pterygoids (Fig. 3). This trough appears to be characteristic of most biarmosuchians except *Biarmosuchus*. In dinocephalian, anomodont, and gorgonopsian therapsids, the pterygoids form a median keel in this region (Sidor, 2000). Anteriorly, the medial ridges are confluent with the ventral ridge of the transverse flanges and continue forward onto the toothed palatal bosses. Posteriorly, the pterygoids extend back as slender prongs lateral to the parasphenoid rostrum and medial to the internal carotid foramina. The lateral pair of pterygoid ridges emerges from the posterior surface of the transverse flanges and extends posterolaterally onto the quadrate rami. These ridges deepen as they approach the quadrates and form the medial margins of the adductor fossae. A broad trough is therefore formed between the lateral ridge and the medial ridge where it contacts the parabasisphenoid. The posterior margin of the trough is poorly preserved, but as opposed to the condition in dinocephalians and other primitive therapsids, a relatively large cranio-quadrate passage is present between it, the basisphenoid, and the anteroventral surface of the paroccipital process. The pterygoid makes an extensive contact with the pterygoid ramus of the quadrate along the latter's posteromedial surface.

The endochondral basisphenoid is fused to the underlying dermal parasphenoid, and so this complex is termed the parabasisphenoid for descriptive purposes. In ventral view (Fig. 3), the parasphenoid rostrum of this element projects between the medial ridges of the pterygoid for a short distance. More laterally, the basiptyergoid processes can be seen to contact the medial margin of the pterygoid's quadrate rami. Internal carotid foramina pierce the basisphenoid lateral to the medial pterygoid ridges. The parabasisphenoid forms the anterior half of a bowl-shaped fossa between the fenestrae ovals. A transversely oriented suture is present near the midpoint of this fossa, and represents the contact between the parabasisphenoid and basioccipital. In addition, the former element can be seen to contact the

opisthotic diagonally across the anteroventral face of the fenestra ovalis.

Approximately half of the sclerotic ring (Fig. 5:sc) is preserved in the left subtemporal fossa between the epipterygoid and quadrate. The thin, individual elements are difficult to distinguish, although we estimate that six are present. Another small patch of disarticulated sclerotic ossicles is preserved on top of the left prootic. Among biarmosuchians, a sclerotic ring is otherwise known in *Biarmosuchus* (Ivachnenko, 1999) and *Leurosaurus* (Sidor and Welman, 2003).

**Endochondral Skull Elements**—As is common for early synapsids, the endochondral elements forming much of the braincase in *Lobalopex* are fused to a greater degree than are the dermal bones (Romer and Price, 1940). For example, the occipital condyle is presumably formed by a combination of the median basioccipital and paired exoccipital bones, but these three elements are indistinguishable in the holotype (Fig. 4:oc). When viewed end-on, the occipital condyle is subtriangular, but it does not display the more extreme trefoil shape common among dicynodonts, where the basioccipital and paired exoccipitals each visibly contribute a bulbous one-third to the condyle. Furthermore, in contrast to the condition in *Burnetia* and *Proburnetia*, where the occipital condyle is extremely small, that of *Lobalopex* is relatively large.

The exoccipitals are visible as discrete elements dorsolateral to the occipital condyle (Fig. 4). On the right side, the connection between the exoccipital and opisthotic is perforated by the jugular foramen (Fig. 3:j for). Medial to this foramen a single hypoglossal foramen is contained entirely within the exoccipital. On the left side, the exoccipital can be seen to contact the supraoccipital well up the sides of the foramen magnum. Although the holotype of *Proburnetia* preserves distinct proatlantal facets on the exoccipitals, these are obscured by damage in *Lobalopex*.

As noted earlier, the unpaired supraoccipital is difficult to distinguish from surrounding elements. In addition, the relatively low dimensions of the supraoccipital are probably influenced by the degree of dorsoventral compression experienced by the holotype. In occipital view, the supraoccipital forms the dorsal margin of the foramen magnum. More laterally on either side, a suture is present between the supraoccipital above and the paroccipital process of the opisthotic below. The lateral process of the supraoccipital forms the dorsal margin of the post-temporal foramen (Fig. 4:ptf). The supraoccipital contacts the tabulars dorsally and laterally and the postparietal dorsally. On the pos-

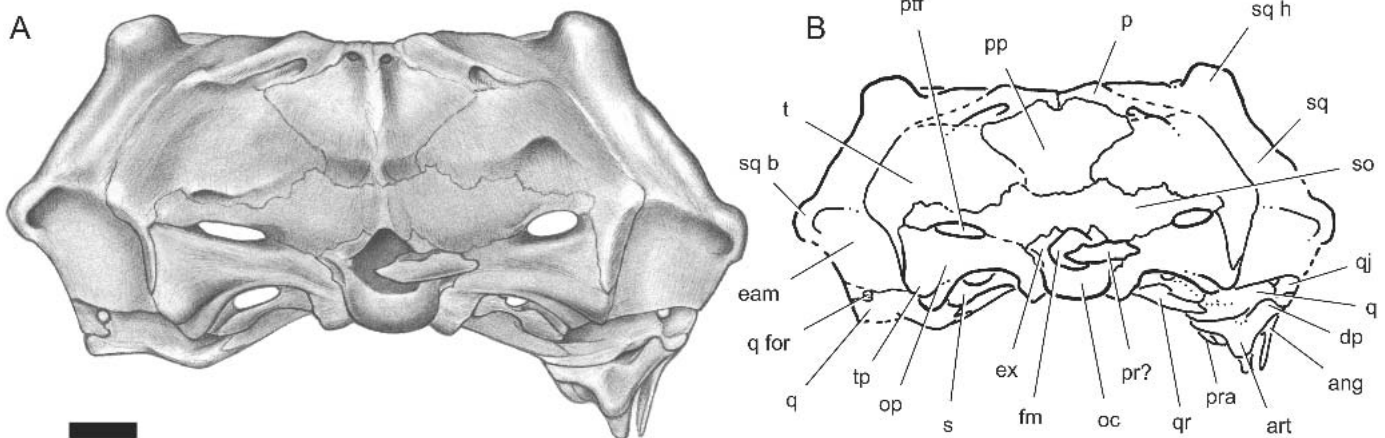


FIGURE 4. Skull and lower jaw of *Lobalopex mordax* gen. et sp. nov., CGP/1/61, in occipital view. **A**, specimen drawing (scale bar equals 1 cm) and **B**, interpretive drawing. The right retroarticular process has been restored, as well as the left quadrate and quadratojugal. Abbreviations given in Figure 1.



terior surface of the adductor chamber, the lateral process of the supraoccipital is fused to the prootic, but can be seen to contact the squamosal laterally.

The opisthotic forms the laterally directed paroccipital process. In posterior view, this process expands slightly at its distal end and contacts the tabular, squamosal, and, on its anteroventral surface, the quadrate. Ventral to the contact between tabular and squamosal, the opisthotic forms a small, posteroventrally directed knob (Fig. 4:tp). A more pronounced tuberosity occurs in many dicynodonts and has been termed the tympanic process (Cox, 1959). The paroccipital process forms the ventral margin of the post-temporal fenestra and the posterodorsal margin of the cranio-quadrato passage. Also in ventral view, the paroccipital process can be seen to extend anteriorly such that its distal end

is approximately as long anteroposteriorly as it is deep dorsoventrally. The rim of the fenestra ovalis is a prominent ventrolaterally-directed structure that is connected to its respective paroccipital process by a web of bone just posterior to the cranio-quadrato passage. Both stapes are preserved in situ, so that the internal surface of both fenestrae is obscured.

In anterior view, the lateral portion of the braincase is a complicated structure that shows no trace of separate prootic and opisthotic ossifications (Fig. 5). Furthermore, our interpretation of the anatomy of the region is hampered by the dorso-ventral crushing experienced by the specimen. The more anterior, presumably prootic portion forms much of the lateral surface of the braincase and can be seen to contact the basisphenoid just lateral to the sella turcica. A weak, median ridge divides the floor of the

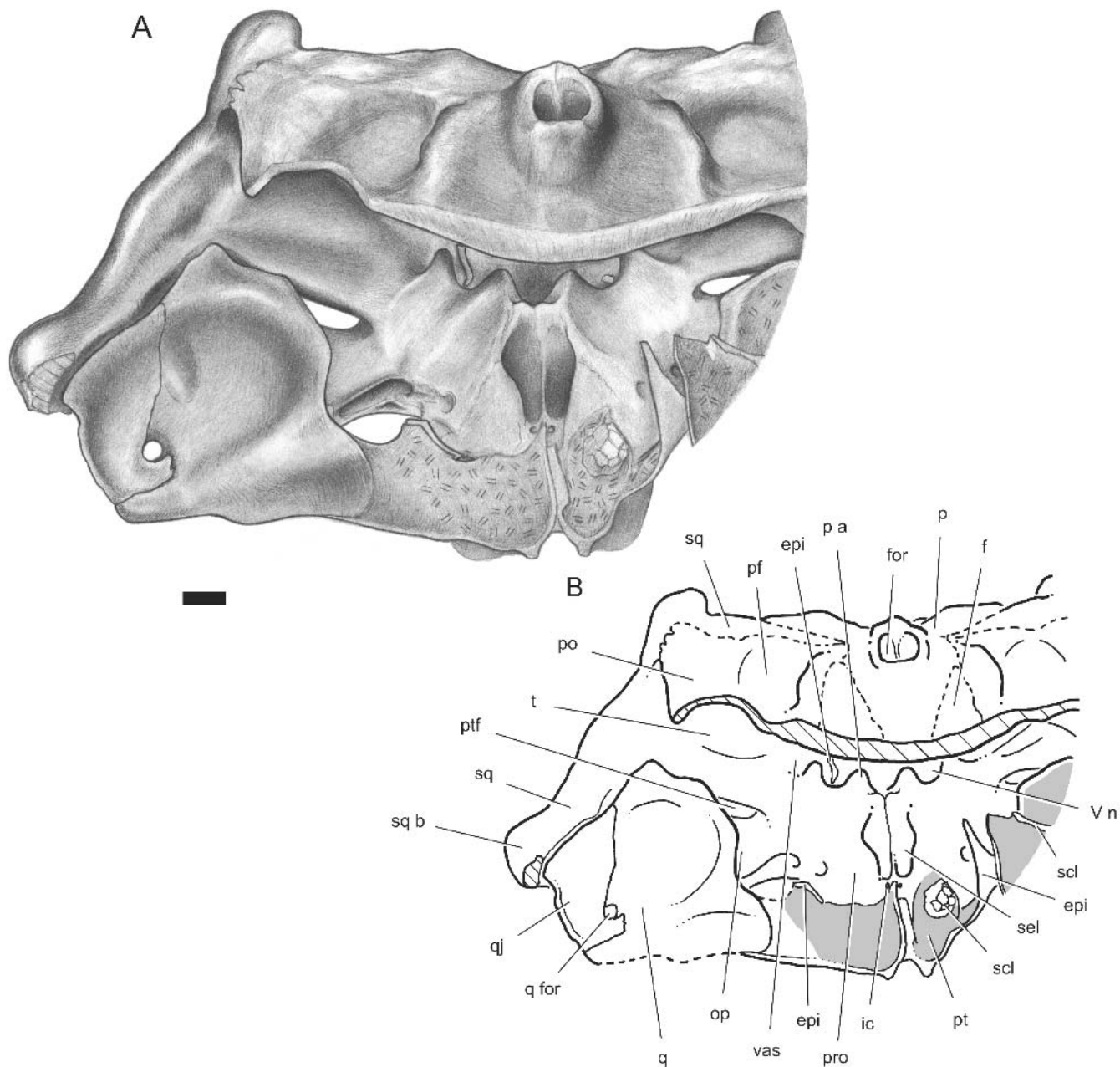


FIGURE 5. Braincase region of *Lobalopex mordax* gen. et sp. nov., CGP/1/61, in anterodorsal view. **A**, specimen drawing (scale bar equals 1 cm) and **B**, interpretive drawing. Parallel lines denote broken surfaces; check pattern (A) and gray (B) indicate areas of remaining matrix. The right lower jaw is not drawn and the ventral portions of the quadrate and quadratojugal have been restored (compare to Sidor, 2000:fig. 3.8). Abbreviations given in Figure 1.



sella (Fig. 5:sel). It is impossible to determine the junction between the basisphenoid and prootic within the sella, although the latter clearly forms its posterior wall, the dorsum sellae. Posterodorsally, the prootic and supraoccipital are fused, but two notches are present between them high on the lateral wall of the braincase. Romer and Price (1940:fig. 10) show two notches in this area in *Dimetrodon* and proposed that the more anterior, which is bounded in front by the base of the pila antotica (Fig. 5:p a), was for the trigeminal nerve and the more posterior and dorsal, which is bounded in front by a short rounded process, transmitted a vascular component. On the ventral surface of the skull roof, the prootics have their dorsal surfaces splayed outwards because of crushing.

The dorsal ramus of the epipterygoid is preserved just anterior to the trigeminal notch on the right side. This element is remarkably slender, resembling the columella cranii of modern lizards (Oelrich, 1956), and, as preserved, contacts the ventral surface of the parietal. However, because of the pronounced crushing suffered by this region of the skull, it is not possible to determine whether the epipterygoid and parietal met in life. Tatarinov (1974:fig. 8) figured such a contact in *Proburnetia*. The prootic bears an indentation in which lay the central portion of the right epipterygoid and shows that the latter remained narrow for its entire length. The footplate and a portion of the ascending ramus of the epipterygoid is exposed on the left side lying on the quadrate ramus of the pterygoid.

Both dumbbell-shaped stapes are preserved, extending from the fenestra ovalis to the medial side of the quadrate and quadrate ramus of the pterygoid. The proximal portion is poorly preserved and was probably capped with cartilage in life. The distal end is well ossified as an elongate process that contacts the quadrate ramus of the pterygoid anteriorly and the pterygoid ramus of the quadrate posterolaterally. Neither a stapedia foramen nor a dorsal process can be recognized. Tatarinov (1974) suggested that *Proburnetia* possessed a perforated stapes, but Rubidge and Sidor (2002) could not confirm this observation. In pelycosaur-grade synapsids, where the skull may be very deep and the jaw articulation typically depressed relative to the braincase, the stapes is a massive, obliquely elongated element. Because the jaw articulation and fenestra ovalis lie at nearly the same level in therapsids, the stapes is a smaller element with a more horizontal orientation.

The quadrate and quadratojugal are intimately coupled and may be best described together even though the latter is not an endochondral element. Both elements are well preserved on the right side and together have their long axis oriented almost orthogonal to that of the skull. The quadratojugal is an L-shaped element in anterior view (Fig. 5), the dorsal ramus of which contacts the quadrate on its lateral surface. A small medial extension overlies the lateral process of the quadrate condyle and forms the lower border of the quadrate-quadratojugal foramen. The anterior surface of the quadrate forms a broadly concave plate. The posterior surface of the quadrate's dorsal ramus contacts the squamosal dorsally and laterally, but overlaps much of the paroccipital process of the opisthotic medially. A moderately-sized pterygoid process projects anteromedially from the lower third of the quadrate's medial margin and extends along the lateral surface of the quadrate ramus of the pterygoid, as in many therapsids (Olson, 1944; Kemp, 1969). The pterygoid ramus of the quadrate also contacts the distal end of the stapes (Fig. 3). As the quadrate and articular are still in articulation, the morphology of quadrate condyles is hidden. In posterior view (Fig. 4), the quadrate and quadratojugal project below the lower margin of the squamosal. The lateral condyle is obscured by the dorsal process of the articular, but appears to have been separated from the larger, medial condyle by a non-articulating trough.

## Lower Jaw

The dentary is the largest element of the lower jaw, extending posterior to about the middle of the orbit. Anteriorly, it and the splenial combine to form a deep, unfused symphysis that has been slightly separated in this specimen (Fig. 1:sym; Fig. 3). As in other primitive therapsids, the root of the lower canine is accommodated by a deepened symphyseal region, which is about twice the height of the horizontal ramus of the dentary. This deep anterior region raises the anterior tooth-bearing margin of the dentary well above the level of the postcanines, and its sigmoid dorsal curvature parallels that of the ventral border of the premaxilla and maxilla. The mandible is constricted just behind the region of the lower canine to accommodate the upper canines. The dentary becomes reduced in depth posteriorly, reaching a minimum at the point where the maxilla is deepest (just anterior to the midpoint of the preorbital region). Posterior to this, the dentary begins to deepen, eventually making sutural contact with the angular ventrally and the surangular dorsally. Posterodorsally, an elongate prong of the dentary overlies the surangular and forms the anterior half of the broad coronoid eminence. Lateral to the angular, the posterior margin of the dentary bears two short processes that are separated by a shallow notch. The lower margin of the dentary is relatively straight but curves up onto the lateral surface of the angular at its posterior end. In ventral view (Fig. 3), the dentary is most robust lateral to the choana, behind which it tapers to a thin lamina.

Only the first lower incisor on each side is visible. Based on its size, there would probably be room for four incisors in each lower jaw. As preserved, the lower incisors pass completely medial to the uppers, and therefore do not interlock as in dinocephalians and some biarmosuchians (e.g., *Lemurosaurus*; Sigogneau-Russell, 1989; Sidor and Welman, 2003). The lower canines are approximately half the length of the uppers and are approximately two-thirds of their diameter. Six very small postcanine teeth are visible in the right ramus of the lower jaw, but more might be present. As preserved, the upper postcanines extend slightly farther posteriorly than do the lowers. Serrations were probably present on all of the teeth. They can be seen on both the anterior and posterior edges of the lower canines and along the posterior edge of the postcanines.

The lateral surface of the angular is dominated by the reflected lamina (Fig. 1:ref), which, as in most basal therapsids, is a large, plate-like structure characterized by a series of broad ridges and depressions. The reflected lamina extends posteriorly almost to the level of the jaw articulation, so that only a sliver of the articular is visible in lateral view. Although somewhat damaged around its periphery, the reflected lamina appears to have had a long, free dorsal margin. Anteriorly, the angular underlies the dentary on the lateral surface of the lower jaw and medially continues forward as a narrow finger between the dentary and splenial (Fig. 3).

As preserved, the lateral surface of the surangular forms a deep fossa between the dentary and angular. The depth of the fossa is probably exaggerated because of the dorso-ventral compression of the specimen. The reflected lamina is missing on the left side, exposing the lateral surface of the surangular and the body of the angular. Distinguishing the contact between these two elements is difficult, but, based on comparison with *Proburnetia* and other therapsids, it appears that the surangular forms a thin, laterally-projecting ridge that caps the dorsal margin of the postdentary region, with the angular overlapping its more ventral surface. In contrast to the condition in *Titanophoneus* (Orlov, 1958) and some other dinocephalians (e.g., *Ulemosaurus*; Efremov, 1940), where the surangular surmounts the dentary, the surangular and dentary of *Lobalopex* abut one another along the dorsal margin of the coronoid eminence. The right surangular is also visible in medial view (Fig. 1C) and can be seen to sit

atop the prearticular just posterior to the transverse flange of the pterygoid.

As in *Lemurosaurus* (Sidor and Welman, 2003), the splenial in *Lobalopex* is confined exclusively to the medial surface of the mandible. Anteriorly, the splenial expands medially and dorsally to form a small triangular process in the symphyseal region when viewed from below. Just posterior to the symphysis, the splenial forms a thin, vertical lamina attached to the medial surface of the dentary. Farther back, it contacts the angular ventrally, the prearticular posterodorsally, and the coronoid dorsally.

A single coronoid is present in both lower jaws (Fig. 1C:cor). When preserved in basal therapsids, this bone has been traditionally considered to represent the posterior coronoid of pelycosaur-grade synapsids (e.g., Romer and Price, 1940:pl. 15) because of its location and size. As preserved, the coronoid in *Lobalopex* extends forward from behind the transverse flange of the pterygoid as a thin triangular sheet that tapers anteriorly to contact the splenial at its apex (Fig. 1; Sidor, 2000:fig. 3.12). The coronoid does not reach the level of the lower postcanines, and is not visible posterior to the transverse flange of the pterygoid.

The slender prearticular lies between the surangular and the angular and pinches out anteriorly between the splenial and coronoid. Posteriorly, where the skull was damaged, the prearticular can be seen in cross-section to contact the angular ventrally and laterally, although it has been separated slightly from the surangular dorsally. The prearticular is deepest in the region of the pterygoid flange and then twists about its long axis a short distance anterior to the jaw articulation (Fig. 3:pra).

The anatomy of the jaw joint is difficult to interpret because of the probable fusion of several elements. In medial view, the prearticular is partially fused to the corresponding articular and angular. In ventral view, the fusion of these elements makes it difficult to establish the limits of the articular. However, it is likely that the articular bone bears a small 'dorsal process' (sensu Parrington, 1955) that projects upwards behind the lateral condyle of the quadrate (Fig. 3:dp). As in gorgonopsians, this process indicates that the articular had to slide laterally on a screw-

shaped quadrate condyle in order to depress the mandible. Although this process was considered diagnostic for gorgonopsians by Hopson and Barghusen (1986), a similar structure occurs in cf. *Rubidgina* (personal observation, CGP/1/67) and *Hipposaurus* (personal observation, CGP/1/66) as well, and so this character may have a more widespread distribution among therapsids. In addition, the articular bears the eroded base of a retroarticular process. Despite the exaggerating effects of dorso-ventral crushing, the level of the jaw articulation appears to be set slightly below that of the dentary tooth row.

### Cervical Vertebrae

The holotype of *Lobalopex* preserves portions of the first four cervical vertebrae (Fig. 6), which, except for an isolated vertebra referred to *Niuksenitia* (PIN 3709/2), represent the only known burnetiamorph postcranial remains. A small, irregularly shaped fragment, perhaps representing a proatlas, remains attached to matrix in the foramen magnum (Figs. 3, 4). The cervical vertebrae are in articulation, but were slightly displaced from the skull so that the atlas-axis complex had lost contact with the occipital condyle. Where preserved, the neural arches have been plastically deformed so that they lie to the left and a little forward of their respective centra.

The atlas is composed of paired atlantal neural arches, an atlantal intercentrum, and an atlantal pleurocentrum. The latter two elements appear at least partially fused to one another. The atlantal pleurocentrum is relatively deep and is exposed ventrally between the atlantal and axial intercentra. The anterior portion of the right atlantal neural arch is damaged. The atlantal postzygapophyses extend posteriorly to articulate with the axial prezygapophyses at an angle of approximately 40° to the horizontal. The right atlantal neural arch preserves a well-developed diapophysis, but the only remnant of its associated rib is a small shard located at the junction of the atlantal intercentrum, atlantal pleurocentrum, and atlantal neural spine.

The axis includes the standard complement of early synapsid

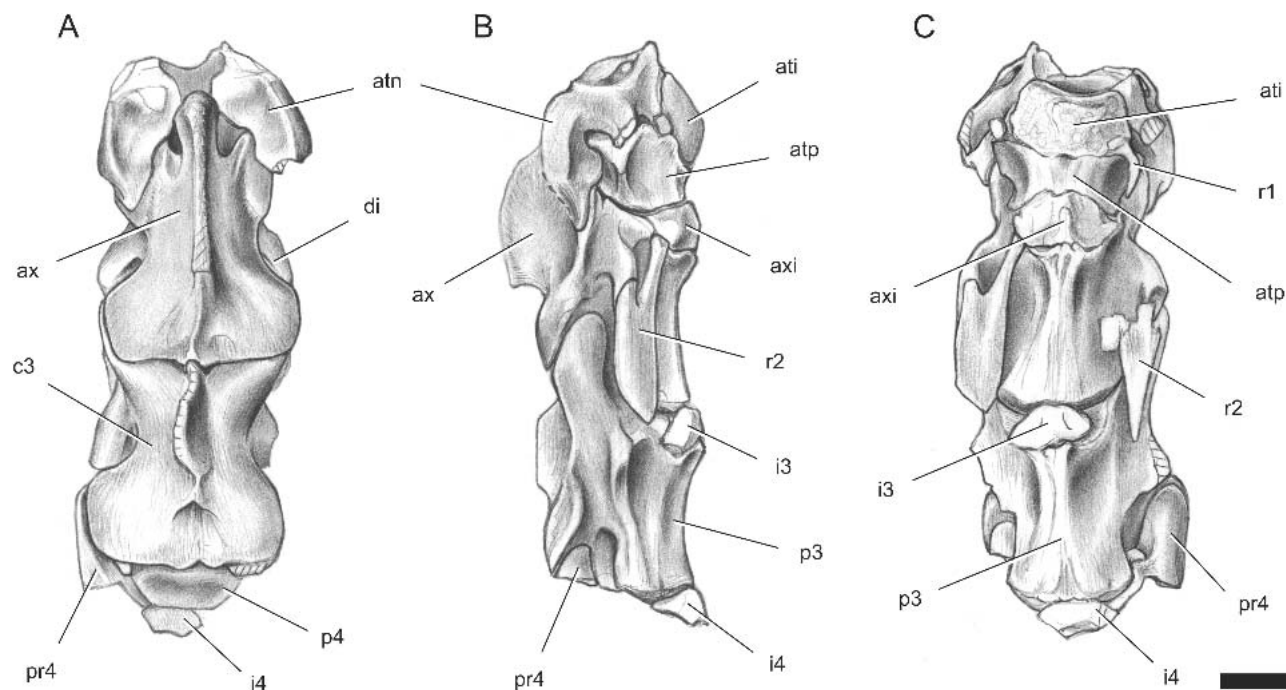


FIGURE 6. Illustration of first four cervical vertebrae of *Lobalopex mordax* gen. et sp. nov., CGP/1/61, in **A**, dorsal, **B**, right lateral, and **C**, ventral views. **Abbreviations:** *ati*, atlantal intercentrum; *atn*, atlantal neural arch; *atp*, atlantal pleurocentrum; *ax*, axial neural arch; *axi*, axial intercentrum; *di*, diapophysis; *i3–4*, intercentra for post-axial cervical vertebrae; *p3–4*, pleurocentra for post-axial cervical vertebrae; *pr4*, prezygapophysis for fourth cervical vertebra; *r1–2*, ribs. Scale bar equals 1 cm.

elements: an axial intercentrum, pleurocentrum, neural arch, and paired ribs (Reisz et al., 1992b). The axial pleurocentrum is elongated, as in *Hipposaurus* and *Biarmosuchus* (Hopson, 1991), has a gentle midline ridge on its ventral surface, and is completely fused to its neural arch. The axial neural spine is hatchet shaped and inclined slightly forwards so that it overhangs the atlantal intercentrum anteriorly. The plane of the zygapophyseal facets is inclined anteroventrally approximately 40 degrees to the horizontal in the frontal plane, so that the neck was probably habitually oriented anterodorsally. In combination with an anteroventrally sloping occiput and posteroventrally directed occipital condyle, the head was probably held at about a right angle with respect to the neck, so that the anterior part of the skull was directed somewhat downwards. As in the third vertebra, the axial postzygapophyses are connected by a horizontal lamina of bone behind the neural spine, the posterior margin of which is oriented transversely and is notched on the midline to accommodate the anterior edge of the succeeding neural spine. Both axial ribs are in place, but poorly preserved. On the right side, the tuberculum articulates with a posterolaterally-projecting diapophysis whereas the rod-like capitulum projects forward to contact the axial intercentrum. The better-preserved left rib is very thin (dorsoventrally compressed), tapering posteriorly to a point slightly beyond the third intercentrum.

The third and fourth cervical vertebrae are less complete than the axis and lack preserved ribs. The third intercentrum is small and crescentic. As with the axis, the third pleurocentrum is elongate, being approximately two-and-a-half times as long as it is deep, and is fused to its neural arch. Its neural spine is damaged, but has a smaller base than that of the axial neural spine. A midline foramen is present behind the neural spine. The zygapophyseal facets are slanted anteroventrally, as occurs in the axis. However, the prezygapophyses are much more massively constructed and extend anteriorly almost to the midpoint of the axial pleurocentrum. In contrast, the postzygapophysis of the third cervical vertebra fails to reach the posterior border of its own pleurocentrum.

Only the prezygapophyses and intercentrum of the fourth cervical vertebra are preserved. As with the third vertebra, the fourth pair of prezygapophyses extends anteriorly to approximately to the middle of the third pleurocentrum.

## DISCUSSION

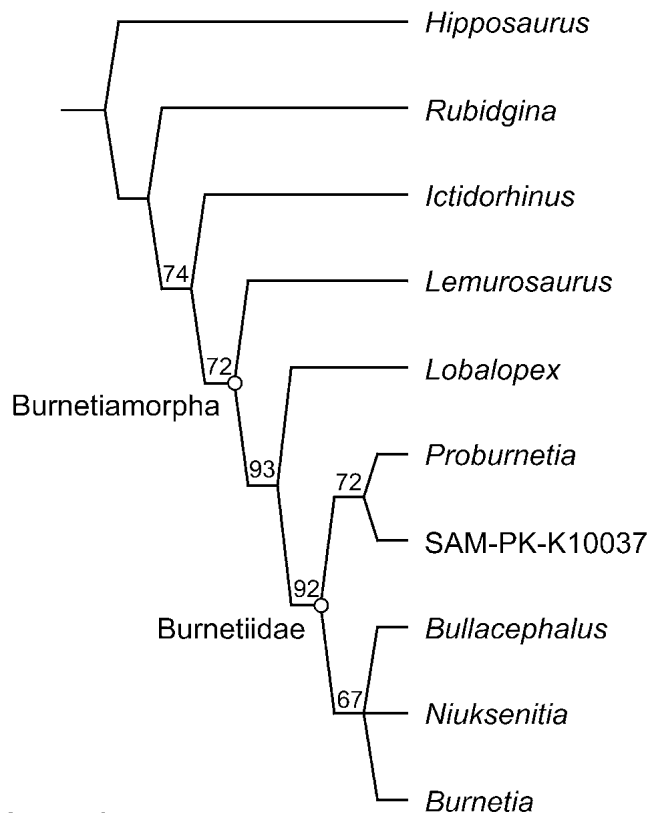
As a consequence of several recent studies, biarmosuchian morphology and systematics have become reasonably well understood (Rubidge and Sidor, 2002; Rubidge and Kitching, 2003; Sidor, 2003; Sidor and Welman, 2003). Here we use the cladistic analysis of Sidor and Welman (2003) as a basis for evaluating the position of *Lobalopex* within Burnetiamorpha. The following genera were included as ingroups in this analysis: *Bullacephalus*, *Burnetia*, *Ictidorhinus*, *Lemurosaurus*, *Lobalopex*, *Niuksenitia*, *Proburnetia*, and a newly discovered specimen (SAM-PK-K10037). Based on the cladistic results of Sidor and Welman (2003) and Sidor and Rubidge (in press), we used cf. *Rubidgina* (CGP/1/67) and *Hipposaurus* (CGP/1/66) as successive outgroups to polarize character state transformations. It is important to note that because these two taxa have been relegated to an outgroup position, we are not testing the position of burnetiamorphs among biarmosuchian therapsids. Instead, we are assessing the interrelationships of the seven taxa within Burnetiamorpha and their presumed nearest relative, *Ictidorhinus*.

The matrix in Appendix 1 was subjected to an exhaustive search using PAUP 3.0.1 (Swofford, 1993). Appendix 2 describes the characters and character states used. All characters, except for numbers four and eleven, were run unordered. When *Niuksenitia* is included, three minimum length trees were recovered. In these trees, *Niuksenitia* is resolved as the sister taxon to either

(1) *Bullacephalus*, (2) *Burnetia*, or (3) *Bullacephalus* + *Burnetia*. A strict consensus of these trees is given in Figure 7. If *Niuksenitia* is excluded from the analysis, the remaining taxa are arranged in the same topology as given in Figure 7. In both analyses, *Lobalopex* is positioned as the sister taxon to Burnetiidae.

A phylogenetic analysis incorporating stratigraphic data (e.g., Fisher, 1992) was not performed here because of the poor means of correlating the South African and Russian sediments without relying on biostratigraphic information (Modesto and Rybczynski, 2000). Within each region, however, the relationship between the stratigraphic and phylogenetic position of its constituent burnetiamorph taxa is generally good. For example, within the Karoo Basin of South Africa, *Burnetia* is known from the highest portion of the Beaufort Group, the *Dicynodon* Assemblage Zone, whereas *Lobalopex*, *Bullacephalus*, and SAM-PK-K10037 are each from lower in the section. Detailed locality information, however, indicates that the *Bullacephalus*-*Burnetia* clade requires the latter taxon to have a ghost lineage spanning most of the lower Beaufort Group. As all burnetiamorphs are known from single specimens, such that sampling is poor, it is likely that observed first appearances do not precisely duplicate true first appearances.

The most plesiomorphic member of the Burnetiamorpha, *Lemurosaurus*, as well as the group's most immediate outgroup, *Ictidorhinus*, is from the Beaufort Group of South Africa. This result contrasts with the pattern proposed by Olson (1962), who considered that the most primitive members of each therapsid



## Strict Consensus

FIGURE 7. Strict consensus cladogram of burnetiamorph relationships. Each of the three fundamental minimum-length trees has the following statistics: tree length = 27, CI = 0.78, RI = 0.85. Bootstrap percentages (out of 500 replicates) are shown above each ingroup node. When *Niuksenitia* is excluded, one tree is found with the same topology as the strict consensus and has the same tree statistics. Regardless of taxon sampling, Burnetiamorpha are diagnosed by characters 4(2) and 6 and Burnetiidae are diagnosed by characters 7, 9, and 11(2) and reversals in characters 14 and 18.

group tended to be from Russian sediments (see also Sigogneau and Tchudinov, 1972; Rubidge and Hopson, 1996). More detailed phylogenetic work on other therapsid clades will be needed to determine which pattern, if either, is prevalent.

*Lobalopex* preserves a combination of characters intermediate between those manifest in less atypical biarmosuchian therapsids, such as *Hipposaurus*, and the first described and most apomorphic burnetiamorph, *Burnetia*. Based on the cladistic data presented here, 14 character-state changes separate *Burnetia* from the primitive condition (as represented by the outgroups). Burnetiamorpha are diagnosed by only half this number when *Lobalopex* is included, demonstrating that the addition of new taxa has been able to bridge the morphological distance separating burnetiamorphs from more basal therapsids. Obviously, the minimum number of characters that could separate taxa on a cladogram is one. If the rate of character evolution did not deviate substantially from an overall constant, then the size and number of morphological gaps should point to the relative quality of a clade's fossil record; i.e., a well-sampled lineage would be predicted to have characters appearing sequentially one at a time (Sidor and Hopson, 1998). As parsimony posits numerous character changes along most branches of burnetiamorph phylogeny, the discovery of additional fossil taxa should be expected.

#### ACKNOWLEDGMENTS

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#### APPENDIX 1

Data matrix used in the cladistic analysis of burnetiamorph interrelationships. *Hipposaurus* and CGP/1/67 (cf. *Rubidgina*) were used as outgroups to polarize character-state transformations. A complete list of specimens used in this analysis is provided in the Materials section. Characters and character-state definitions are provided in Appendix 2. “?” denotes missing data. Electronic copies of this matrix will be provided upon request.

	12345	1 67890	11111 12345	111 678
<i>Hipposaurus</i>	00?00	00000	00010	001
CGP/1/67	00?00	00000	00010	111
<i>Ictidorhinus</i>	?0?10	00?00	0??1?	?1?
<i>Lemurosaurus</i>	10020	1?000	01010	111
<i>Lobalopex</i>	11010	10101	10011	111
<i>Proburnetia</i>	11020	11111	22001	110
SAM-PK-K10037	01020	11111	22001	110
<i>Bullacephalus</i>	11121	?011?	2010?	00?
<i>Niuksenitia</i>	?????	??1??	2???1	0??
<i>Burnetia</i>	11121	11111	21101	?1?

#### APPENDIX 2

The following is a list of the characters and character states used to construct the cladogram in Figure 7. The number preceding the character definition corresponds to that of the columns in Appendix 1. An ° preceding the character number denotes that the character was ordered. Following the last character state for each character is a citation for previous uses of the character in the recent literature. When an asterisk

follows the citation, it means that the character definition has been modified or that a character state has been added or deleted. Citations are in the form: (author:character number), except for those of Sidor (2000), which are (author:appendix number, character number). **Abbreviations for authors:** RK, Rubidge and Kitching (2003); S, Sidor (2000); SW, Sidor and Welman (2003).

- 1) Lateral surface of lacrimal bearing one or more deep fossae: absent (0), present (1). (RK:8\*; S:3.2,5\*; S:4.2,13; SW:4)
- 2) Median nasal boss or crest: absent (0), present (1). (RK:7\*; S:3.2,3; S:4.2,14; SW:6\*)
- 3) Shape of median nasal boss: narrow and ridge-like (0), transversely expanded (1). (RK:7\*; SW:6\*)
  - °4) Supraorbital margin: thin (0), moderately thickened (1), greatly thickened into boss (2). (RK:13\*; S:3.2,7; S:4.2,22\*; SW:7)
- 5) Boss at posterodorsal margin of orbit, near origin of postorbital bar: absent (0), present (1). (RK:14\*; S:3.2,6; S:4.2,22\*; SW:8)
- 6) Ventrolateral surface of zygomatic arch: smooth (0), with boss positioned near base of postorbital bar (1). (RK:9\*; S:3.2,9\*; SW:9\*)
- 7) Ventrolateral surface of suborbital bar: smooth (0), with boss (1). (RK:9\*; S:3.2,9\*; SW:9\*)
- 8) Squamosal thickened on ventral surface of zygomatic arch lateral to position of quadrate: absent (0), present (1). (S:3.2,12; S:4.2,29; SW:10)
- 9) Pachyostosis of zygomatic arch: absent (0), present (1).
- 10) Squamosal ‘horns’ directed posterodorsally from skull roof: absent (0), present (1). (RK:6\*; S:3.2,10; S:4.2,28; SW:12)
  - °11) Squamosal thickened along its posterior border with tabular: absent (0), present, but only moderately developed (1), present and well developed (2). (S:3.2,11; SW:13\*)
- 12) Shape of dorsal surface of frontals: flat (0), with low ridge (1), with tall, thickened ridge (2). (S:4.2,16; SW:14)
- 13) Position of parietal foramen relative to occipital border of skull: close (within three diameters of foramen) (0), far (greater than four diameters of foramen) (1).
- 14) Shape of parietal bone surrounding parietal foramen: flat or low swelling (0), or with well-defined chimney (1). (SH:21\*; S:4.2, 24\*; SW:16\*)
- 15) Ridge connecting squamosal to paroccipital process of opisthotic: absent (0), present (1).
- 16) Row of teeth on transverse flange of pterygoid: present (0), absent (1). (RK:16\*; S:3.2,17; SW:21)
- 17) Palatine dentition broadly distributed (0), restricted to small area (1) on palate. (RK:24\*; S:4.2,45; SW:23)
- 18) Ratio of dentary height in canine versus anterior postcanine regions: nearly equivalent (0), showing pronounced difference (1). (S:4.2,58; SW:30)