

The cranial osteology of *Belebey vegrandis* (Parareptilia: Bolosauridae), from the Middle Permian of Russia, and its bearing on reptilian evolution

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The redescription of the cranial anatomy of *Belebey vegrandis*, a Permian bolosaurid reptile from southern Russia, provides valuable new information for determining the phylogenetic relationships of this enigmatic group of early amniotes. As exemplified by the superbly preserved skulls and mandibles of *Belebey*, bolosaurids are characterized by the following attributes: the presence of a unique, heterodont marginal dentition; a slender, anteroposteriorly elongate lower temporal fenestra that is bound mainly by the quadratojugal and squamosal bones; a large coronoid process formed by three bones; a splenial that is restricted to the ventral surface of the mandible; and a long anterior process of the prearticular that covers much of the medial surface of the dentary bone. The palate of *Belebey* appears to be greatly modified in the region of the snout, indicating the presence of a functional secondary palate. Phylogenetic analysis of Palaeozoic amniotes indicates that bolosaurids are parareptiles and the sister taxon to the clade comprised of *Macroleter*, *Procolophonina*, and *Pareiasauria*. This position, which is high within Parareptilia, necessitates long ghost lineages for several Late Permian Russian and South African taxa, because the oldest known bolosaurids have been found close to the Permo–Carboniferous boundary in New Mexico. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 151, 191–214.

ADDITIONAL KEYWORDS: Amniota – Palaeozoic – phylogeny.

INTRODUCTION

One of the most enigmatic clades of early amniotes is Bolosauridae, a group of small reptiles from the Lower and Middle Permian of North America and Europe (Reisz, Barkas & Scott, 2002). Originally known from cranial material and fragmentary postcranial remains, the recent discovery of an almost completely preserved skeleton of *Eudibamus cursoris*, a small bolosaurid from the Lower Permian of Germany (Berman *et al.*, 2000), revealed that these animals were apparently very agile small reptiles with the ability to run bipedally using a parasagittal gait. A further notable feature is the unique heterodont dentition, consisting of a relatively low number of highly differentiated procumbent anterior and greatly expanded cheek teeth, suggesting very specialized feeding

habits. Despite a wide stratigraphic and geographical range, the number of bolosaurid taxa is surprisingly low, with only three valid genera and five species being currently recognized: *Bolosaurus grandis* and *Bolosaurus striatus* from the Lower Permian of Oklahoma and Texas (Watson, 1954; Reisz *et al.*, 2002), *E. cursoris* from the Lower Permian of Germany (Berman *et al.*, 2000), and *Belebey maximi* and *Belebey vegrandis* from the Middle Permian of Russia (Ivakhnenko, 1973; Ivakhnenko & Tverdochlebova, 1987).

The type species of *Bolosaurus*, *B. striatus*, was established by Cope (1878) on the basis of poorly preserved skulls and jaw fragments, all apparently from a single pocket near Mt Barry, Wichita County, Texas. Watson (1954) described this taxon suggesting that it was most closely related to diadectids, although it was a highly specialized form. More recent discoveries of bolosaurid reptiles in Eastern Europe have increased our knowledge of this problematic group. These forms, although similar to the North American species,

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exhibit slight differences in the unique structure of the teeth, prompting the erection of new taxa. The first bolosaurid from Eurasia, *B. vegrandis* (Ivakhnenko, 1973), is based on a maxilla from Middle Permian sediments (latest Kazanian), near Belebey, Bashkortostan, Russia. More recently, parts of four skulls of *B. vegrandis*, one in articulation with a badly weathered postcranial skeleton, have been recovered (Ivakhnenko & Tverdochlebova, 1987). A second species of *Belebey*, *B. maximi*, was also described from the Upper Kazanian deposits near Saray-Gyr, Bashkortostan, Russia. In the eastern European bolosaurids, the cheek teeth are more transversely expanded relative to their anteroposterior dimension than in *Bolosaurus* (Ivakhnenko & Tverdochlebova, 1987). This condition is particularly striking in *B. maximi*, where the bases of the teeth beneath the crowns are compressed anteroposteriorly. In effect, these proportions give *Belebey* teeth a generally more gracile appearance than the generally rounded bulbous cheek teeth of *Bolosaurus*.

Recently, the excavations at the Bromacker quarry in Germany have yielded the remains of a small bolosaurid, *E. cursoris* (Berman *et al.*, 2000). This discovery has rekindled interest in the group because it is represented by a nearly complete skeleton. A second partial skeleton of this species has been discovered recently and is currently under study.

The available evidence indicates that the evolutionary history of bolosaurids extends from the Permian–Carboniferous boundary (Lowest Wolfcampian) of New Mexico to far into the Middle Permian (Upper Kazanian) of Bashkortostan, Russia. The taxonomic history of bolosaurids reflects our poor understanding of the phylogenetic relationships of this group. Bolosaurids were placed in Cotylosauria by Case (1911). Watson (1917) argued for a separate superfamily that he placed among the Pelycosauria. Later, Watson (1954) proposed that bolosaurids were related to diadectids, mainly on the basis of dental features. Kuhn (1969), however, erected the subclass Bolosauromorpha based on the presence of a lower temporal fenestra and distinctive calvaria. *Bolosaurus* has also been interpreted as a captorhinomorph reptile (Carroll & Gaskill, 1971). Most recently, Berman *et al.* (2000) presented a preliminary phylogeny in which bolosaurids were part of Parareptilia, the sister taxon of eureptiles. However, the lack of well-described cranial material still rendered this interpretation somewhat speculative.

The purpose of the present paper is to redescribe thoroughly the skull of *B. vegrandis* and to test the parareptilian affinities of bolosaurids, incorporating postcranial information from *Eudibamus*. This study presents a new phylogeny of early amniotes that takes advantage of our increasing knowledge of the relation-

ships among synapsids, eureptiles, and parareptiles. As these are by far the best-preserved skulls of bolosaurids, the results of this study contribute significantly to our understanding of general bolosaurid anatomy, and is likely to have a significant impact on our knowledge of early amniote phylogeny and biogeography.

MATERIAL AND METHODS

SYSTEMATIC PALAEOLOGY

BOLOSAURIDAE COPE, 1878

BELEBEY VEGRANDIS IVAKHNENKO, 1973

Holotype: PIN (Palaeontological Institute, Russian Academy of Science, Moscow, Russia) 104/50 maxillary bone with partly preserved palatine bone.

Referred specimens: SGU (Saratov Geological University, Saratov, Russia) 104/B-2020, a small complete skull that has been disarticulated (Figs 1–6); SGU 104/B-2021, a slightly larger, complete skull (Figs 7, 8); SGU 104/B-2022, a large, partial skull, preorbital region not preserved. This large individual was available for study but could not be illustrated.

Horizon and locality: Upper Kazanian, Middle Permian; Bashkortostan and Orenburg regions, Southern Russia.

Diagnosis: Bolosaurid parareptiles characterized by the presence of strongly procumbent incisiform dentition anteriorly, and linguo-labially elongated, bulbous, posterior cheek teeth with strongly developed longitudinal striations. Non-dental potential autapomorphies cannot be recognized because most of the other bolosaurid taxa are known from fragmentary cranial and mandibular elements.

DESCRIPTION

SKULL ROOF

In general, the skull has a pointed snout and is strongly expanded posterolaterally, resulting in a triangular outline in dorsal view. The postorbital region is comparatively short, much shorter than the antorbital region, whereas the orbits are very large, as is the pineal foramen. There is a single, elongate temporal fenestra in the lower part of the cheek region that is bounded ventrally by the quadratojugal. Sculpturing can be recognized on the external surface of the skull roof, but it is modest in comparison with most Palaeozoic amniotes.

The premaxilla is a small, slender, elongate element that slopes anteroventrally to form the tip of the snout. The restoration (Fig. 9) shows, however, that the snout was not downturned, and the premaxillary

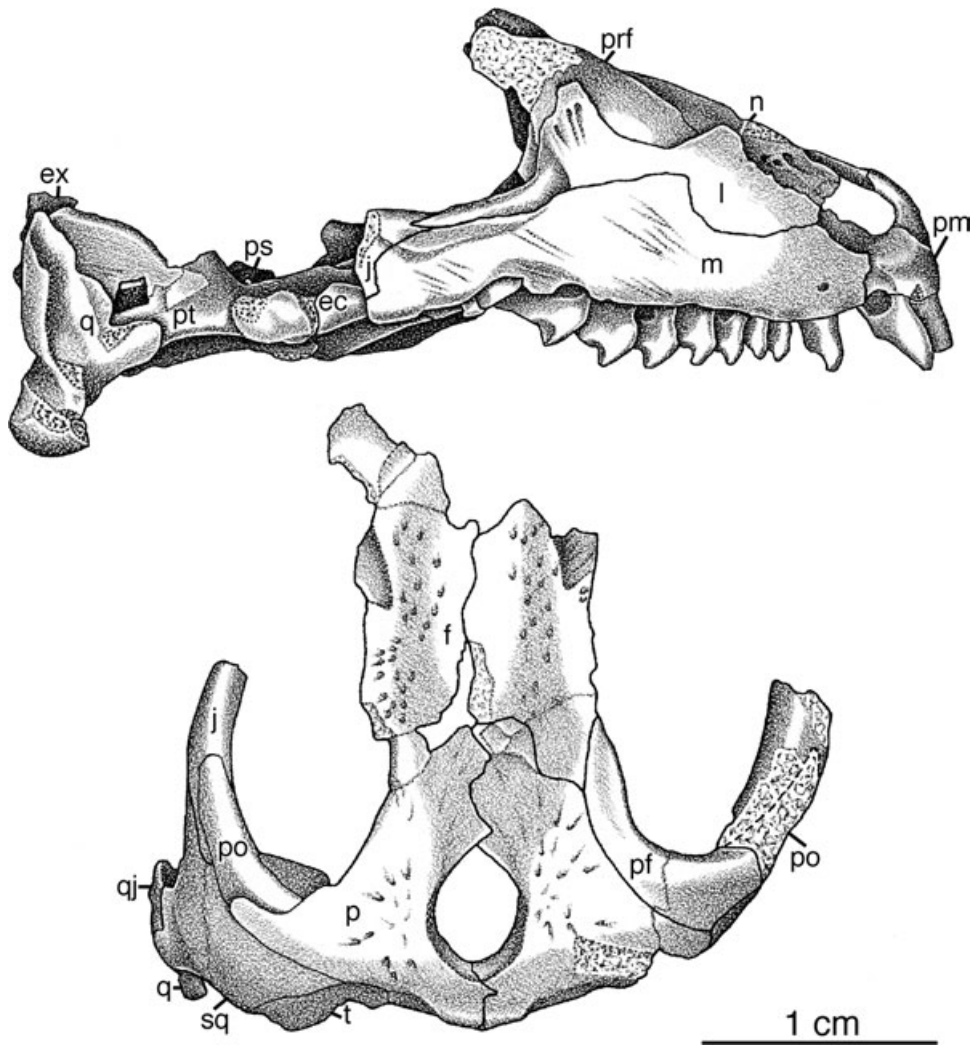


Figure 1. Skull of *Belebey vegrandis*, SGU 104/B-2020: antorbital region and palate in lateral view, and skull table and temporal region in dorsal view. These are parts of the same skull, prepared and separated from each other. Scale bar = 1 cm; see Appendix 1 for abbreviations list.

alveolar margin is in line with that of the maxilla. As seen in other early amniotes, the premaxilla has a well-developed dorsal process, but the other processes of this bone are modified from the primitive amniote condition. As in other parareptiles, the dorsal process is very slender, contributing only slightly to the anterior edge of the external nares, and attaches to the dorsal surface of the nasal on either side of the midline.

In SGU 104/B-2020, each premaxilla carries two elongate, relatively massive teeth that attach to the bone along its anterior edge (Fig. 2). The teeth are distinctly procumbent, and three of the four teeth have a large lingually facing cusp. These teeth do not show any evidence of wear, suggesting that they were not in position to occlude against the dentary teeth. The two teeth on the left premaxilla apparently have not com-

pleted their eruption at the time of death, and were not firmly attached to the premaxillary bone. In contrast, on the right side, the medial tooth is strongly worn, showing a flat occlusal surface that carries fine anteroposteriorly orientated striations (Fig. 2). The wear on this tooth appears to have exposed the pulp cavity, showing up as a small circular hole on the flat wear facet. The maxillary process of the premaxilla is greatly reduced, and does not extend posterolaterally along the ventral jaw margin beyond the second tooth position. In contrast, the palatal process extends directly posteriorly from the tooth row, and is relatively larger than the palatal process of other amniotes, bridging the ventral surface of the snout between the maxillae and overlapping the anterior tip of the vomers medially. There are therefore no distinct palatal and maxillary processes in *Belebey*, and this

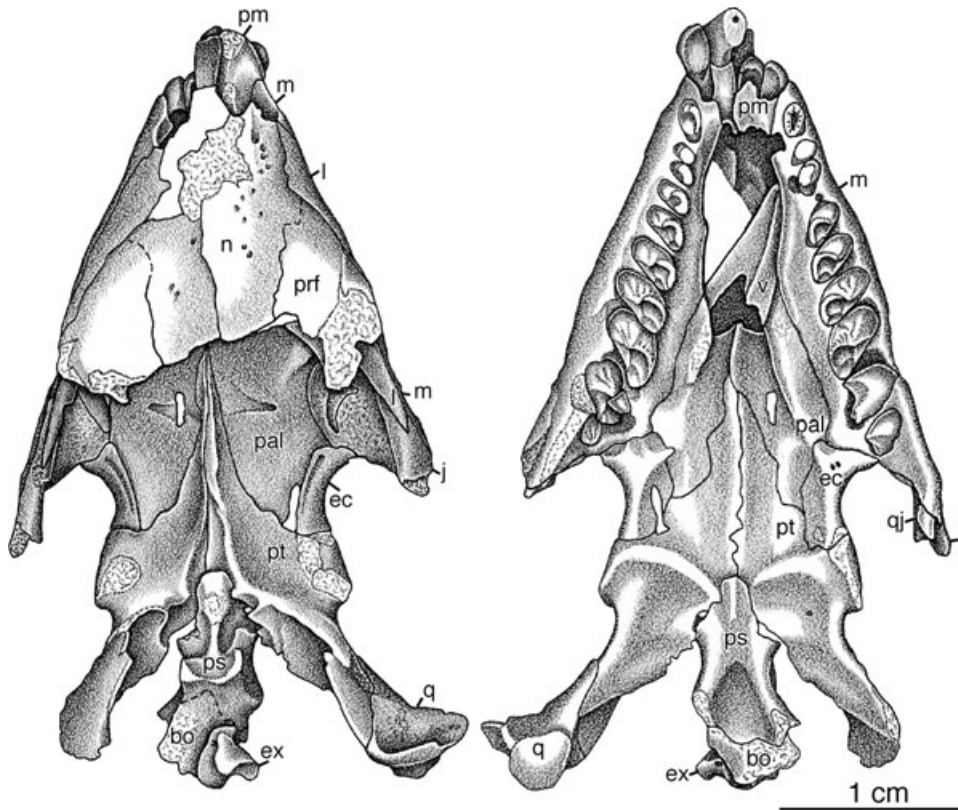


Figure 2. Skull of *Belebey vegrandis*, SGU 104/B-2020: antorbital region of the skull roof and the palate in both dorsal and ventral views. Scale bar = 1 cm; see Appendix 1 for abbreviations list.

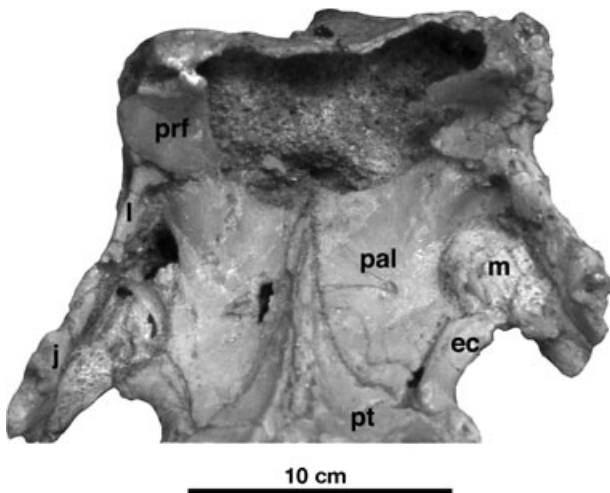


Figure 3. Skull of *Belebey vegrandis*, SGU 104/B-2020: photograph of the antorbital area of the skull in anterior view, showing details of the palate, the medial process of the prefrontal, and the palatine–prefrontal buttress. The dorsal surface of the maxilla, where the largest maxillary teeth are attached, is pockmarked. Scale bar = 1 cm; see Appendix 1 for abbreviations list.

shelf forms only the anterior border of the very slender internal naris.

A fourth, apparently new process of the premaxilla extends posterodorsally. It is visible only in lateral view through the external naris (Fig. 1), and has a wing-like posterodorsal extension along the midline that meets its pair from the other side. This new process appears to form the medial wall of the nasal passage, and its appearance suggests that the passage was no longer extending to the choana but posteriorly above the vomer. This interpretation is supported by the position and size of the vomer, as discussed below. We therefore interpret this modified configuration of the premaxilla as a secondary palate, where the air passage from the external naris to the roof of the mouth has moved posteriorly, and enters the palate between the vomer and the palatine (Fig. 9).

The maxilla (Figs 1, 7) is a comparatively long element, as is typical for many early amniotes, extending from the anterior edge of the external naris to the midpoint of the suborbital region. Along its entire dorsal margin, the bone meets and overlaps the lacrimal in a slightly undulating suture, and contributes to the posteroventral border of the external naris. The reconstruction of the skull (Fig. 9) shows clearly this

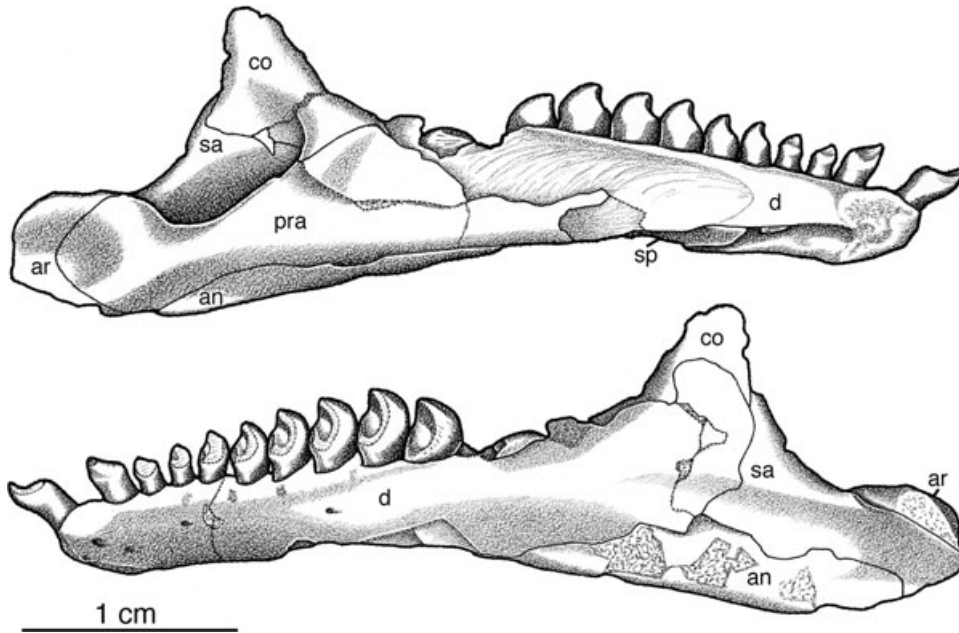


Figure 4. *Belebey vegrandis*, SGU 104/B-2020: left mandible in medial and lateral views. Scale bar = 1 cm; see Appendix 1 for abbreviations list.

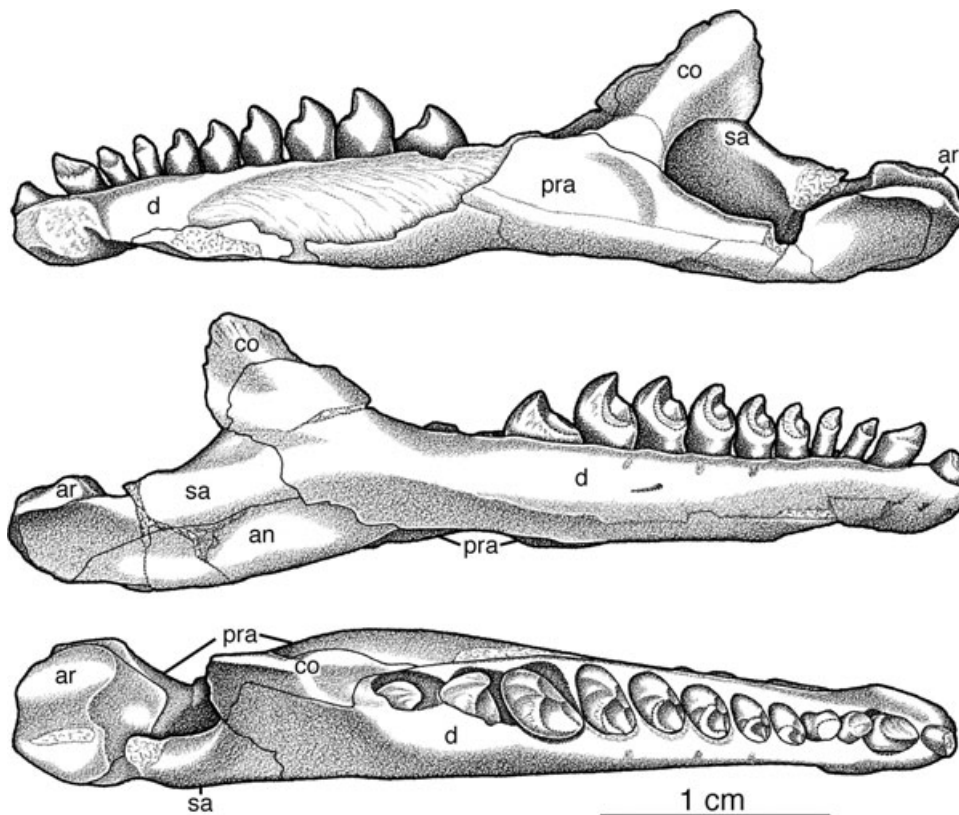


Figure 5. *Belebey vegrandis*, SGU 104/B-2020: right mandible in medial, lateral and occlusal views. Scale bar = 1 cm; see Appendix 1 for abbreviations list.



Figure 6. *Belebey vegrandis*, SGU 104/B-2020: photograph of left and right mandibular rami in occlusal view. Scale bar = 1 cm.

contribution in dorsal view, but not in lateral view, because in the latter, the new posteromedial process of the premaxilla gives the mistaken impression of excluding the premaxilla from the narial edge. The correct special relationship between these elements is best seen in the lateral view of SGU 104/B-2020 (Fig. 1). There are at least two distinct foramina in the anterolateral surface of the bone. Posteriorly, the maxilla is in contact with both jugal and quadratojugal, but in contrast to the condition in other early amniotes, the dorsal lamina of its suborbital process remains relatively tall throughout its length. This is probably related to the nature of the dentition, which does not diminish in size posteriorly.

In ventral view, the maxilla is very wide, with a well-developed alveolar shelf that is expanded both lingually and labially (Fig. 2). The lingual expansion is modest anteriorly at the level of the first four maxillary teeth, where it forms the lateral edge of the choana, but becomes a broad shelf along the rest of the maxilla, where it contacts the palatine and ectopterygoid bones. The lingual expansion is tilted slightly dor-

sally, contributing to the vaulting of the palate. Anteriorly, the maxilla is attached to the premaxilla along a long, anteroposteriorly extending suture that is best seen in palatal view (Figs 2, 9). From the level of the first maxillary tooth to the fifth, the medial edge of the alveolar shelf is strongly rounded and bears a moderately developed ridge where it formed the border of the choana. Posterior to this area, the maxilla forms a sutural contact with the palatine, with the medial ridge present along the free medial edge of the maxilla continuing onto the palatine. In this way, the posterior half of the maxilla forms, together with the palatine, a slightly vaulted and slightly rugose shelf that is located ventral to the general palatal surface formed by the rest of the palatine and the pterygoid. Posteriorly, the expanded alveolar shelf of the maxilla is buttressed by the ectopterygoid (Figs 2, 9).

Either nine or ten teeth are present on the alveolar shelf of the maxilla, most quite distinctive in shape and size. The morphology of these teeth has been previously described (Reisz *et al.*, 2002), and therefore only general features need to be given here. The first tooth is significantly larger than the second one and, like the teeth of the premaxilla, tilted slightly forward. Beginning with the second tooth, the smallest of the maxillary teeth, there is a gradual increase in size posteriorly along the series, with the posterior teeth becoming particularly massive. The last tooth, however, is again slightly smaller than the others. Each tooth has an oval, almost kidney-shaped outline in occlusal view. The long axis of the first maxillary tooth is more or less anteroposteriorly directed, in contrast to a rather anterolabial–posterolingual orientation of the remaining teeth. All teeth show a sharp, posteriorly recurved main cusp with a distinct labial and lingual ridge/cutting edge. In addition, there is a smaller ridge posterior to the tooth cusp, predominantly in the more bulbous posterior cheek teeth. Posterolingual to each tooth cusp there is a distinct wear facet, which is bordered anteriorly by the above lingual ridge. This wear facet is especially pronounced in the posterior cheek teeth. Again, the only exception is the first tooth, in which the wear facet is situated posterolabially. The posterior two cheek teeth of SGU 104/B-2020 were not fully erupted at the time of death (Fig. 2), indicating that this was probably a juvenile individual.

The nasal is an elongate, transversely domed element of the snout, slightly exceeding the length of the frontals (Figs 2, 7). Anteriorly it forms the dorsal edge of the external naris, and also appears to contribute slightly to the posterior edge of that opening. Posterolaterally the nasal meets the large prefrontal, which it overlaps slightly. The nearly straight suture between the two nasals is interrupted posteriorly by a short anteromedial process of the frontals.

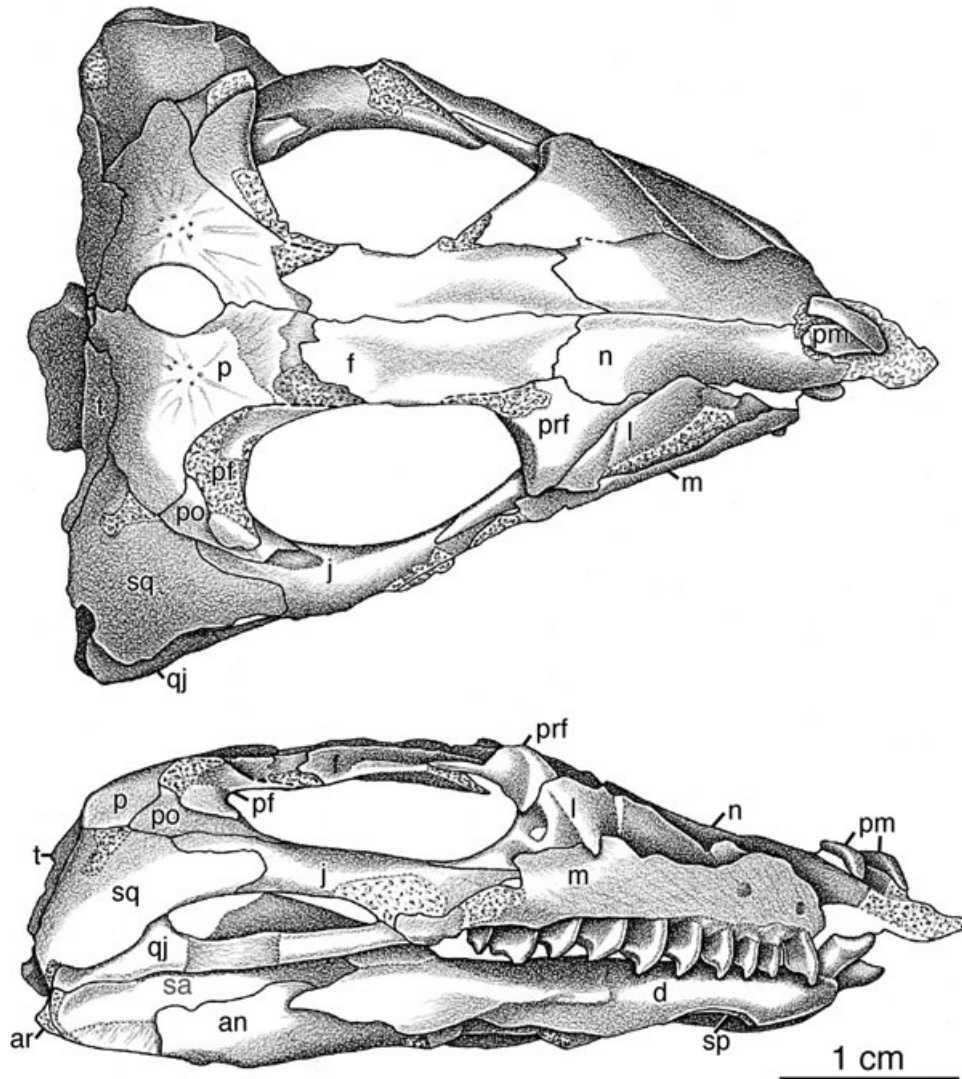


Figure 7. *Belebey vegrandis*, SGU 104/B-2021: skull and mandible in dorsal and lateral views. Scale bar = 1 cm; see Appendix 1 for abbreviations list.

The lacrimal is a prominent element of the cheek that extends from the posterior margin of the external naris to the orbit. It has a broad dorsal contact with the nasal, whereas its tall posterodorsal process extensively overlaps the prefrontal (Figs 1 and 7). Posteriorly, the lacrimal has a long, slender suborbital process that contacts the jugal, excluding the maxilla from the orbital margin (Fig. 3). Two large foramina for the lacrimal duct are exposed on the lateral surface of the lacrimal, situated near the anteroventral edge of the orbit. Some smaller foramina can also be found along the anterior orbital margin on the posteromedial surface of the bone. Medially, the lacrimal has a distinct, triangular medial process that meets both the prefrontal above and the palatine below (Fig. 3). Ventral to this process, the foramen orbitonasale is

present directly above the palate, its margins being formed by the palatine, prefrontal, and the lacrimal.

The prefrontal is a triangular element that forms the anterodorsal orbital margin, and also has a large contribution to the dorsal surface of the skull. Although slightly damaged in both specimens, its overall anatomy can be readily reconstructed. Its ventral orbital process forms part of the anterior border of the orbit, whereas the slender, pointed anterior process extends far between the lacrimal and the nasal (Figs 2, 7). The prefrontal also has well-developed medial and ventral flanges that not only form an anterior wall for the orbit, but also form an extensive contact with the lacrimal and the palatine (Fig. 3).

The frontal is a relatively elongate, subrectangular, transversely flat element that forms most of the nar-

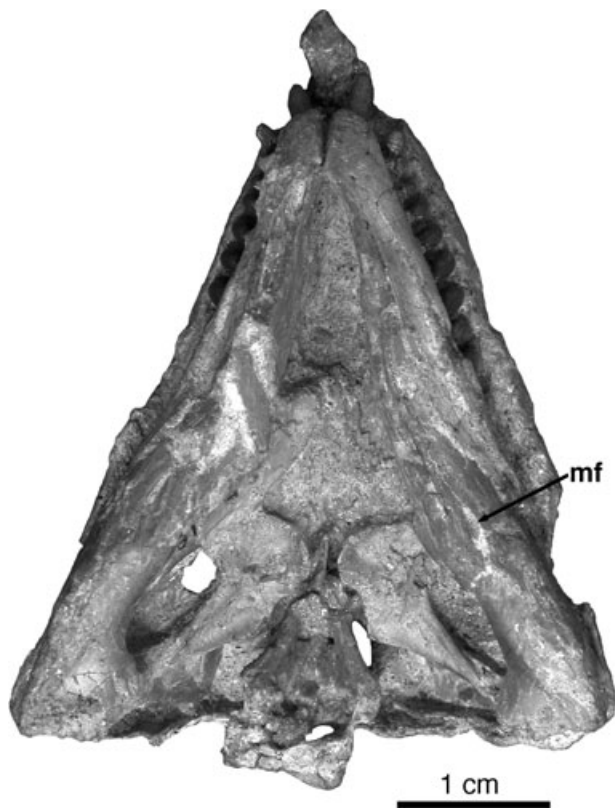


Figure 8. *Belebey vegrandis*, SGU 104/B-2021: photograph of skull and mandible in palatal view. The skull was not available for illustration in this view. Arrow points to ventral location of the mandibular foramen (mf). Scale bar = 1 cm.

row supraorbital region, but also extends anteriorly onto the snout. Anteriorly the frontal contacts the nasal, whereas anterolaterally it has a strong sutural contact with the prefrontal. The nature of this suture is clearly visible in SGU 104/B-2020 (Fig. 1), where the prefrontal has separated from the frontal, exposing a wide, deep groove on the frontal above the orbit. A narrow lateral lappet of the frontal makes a wide contribution to the dorsal orbital margin (Fig. 9). Posterolaterally, the frontal has an unusually short contact with the postfrontal, much shorter than with the prefrontal. The posterior process of the frontal is unusually short in *Belebey*, and does not extend to the level of the posterior limit of the orbit, and its posterior margin contacts the parietal in a slightly undulating transverse suture.

The postfrontal is a slender, semilunar-shaped element at the posterodorsal margin of the orbit that forms a bridge between the skull table and temporal regions of the skull roof (Figs 1, 7). Anteriorly the postfrontal extends only slightly beyond the level of the parietal bone, forming a short contact with the lateral edge of the frontal. Medially it is attached to the con-

cave lateral edge of the parietal, and posteroventrally is sutured to the postorbital. As seen in procolophonids, but in strong contrast to other amniotes, the postfrontal appears to be deeply emarginated along its border with the orbit, resulting in a posterodorsal expansion of the orbit. Consequently, the temporal region is greatly reduced in length (Fig. 9). The ventral process of the postfrontal is transversely broad, with a distinct orbital edge separating the external and orbital surfaces of the bone, and forming a broad shelf along the posterior margin of the orbit. This structure, not developed on the postfrontal of other Permian amniotes to the extent seen here, is located directly above the massive coronoid process of the mandible, and may have served for the attachment of mandibular adductor muscles. This is a reasonable interpretation when the reduced length of the temporal region and the great dorsal extension of the coronoid process, and the presence of a slender lower temporal fenestra, are taken into account.

The postorbital is an unusually small bone that appears to have been ventrally and anteriorly displaced from the position that it normally occupies in other amniotes. The bone underlies the broad ventral process of the postfrontal and forms a long ventral contact with the jugal and the squamosal (Fig. 1). Surprisingly, it is bound posteriorly by a slender lateral process of the parietal (Fig. 7). Although visible in dorsal view, this bone is largely a laterally facing element of the skull roof. In addition, it has a very small contribution to the posterior margin of the orbit.

The parietal is relatively short and broad, significantly shorter than either the nasal or the frontal (Fig. 7). In contrast to most other early amniotes, the parietal is not a flat bone that forms the skull table. Instead, it is strongly curved both anteroposteriorly and transversely, forming the domed posterior end of the skull roof. Laterally, it has a distinct, broad lappet that contacts both the postorbital and squamosal. This lateral lappet is strongly curved ventrally. The posteroventral edge of the parietal meets the tabular and the postparietal. A very large, slightly elongate pineal foramen is located near the posterior edge of the parietal and occupies nearly 50% of the length of the bone. The disarticulated skull of SGU 104/B-2020 (Fig. 1) has exposed the concave ventral surface of the parietal bone, and reveals two faint longitudinal ridges on either side of the large pineal foramen. One of these ridges has preserved a small ventral process on the right side, slightly posterior to the mid-point of the foramen. We interpret this process as the contact between the skull roof and the dorsal process of the epipterygoid.

The paired postparietal are extremely small, but are preserved on two of the skulls (SGU 104/B-2020 and 2021). They are occipital elements, and are located on

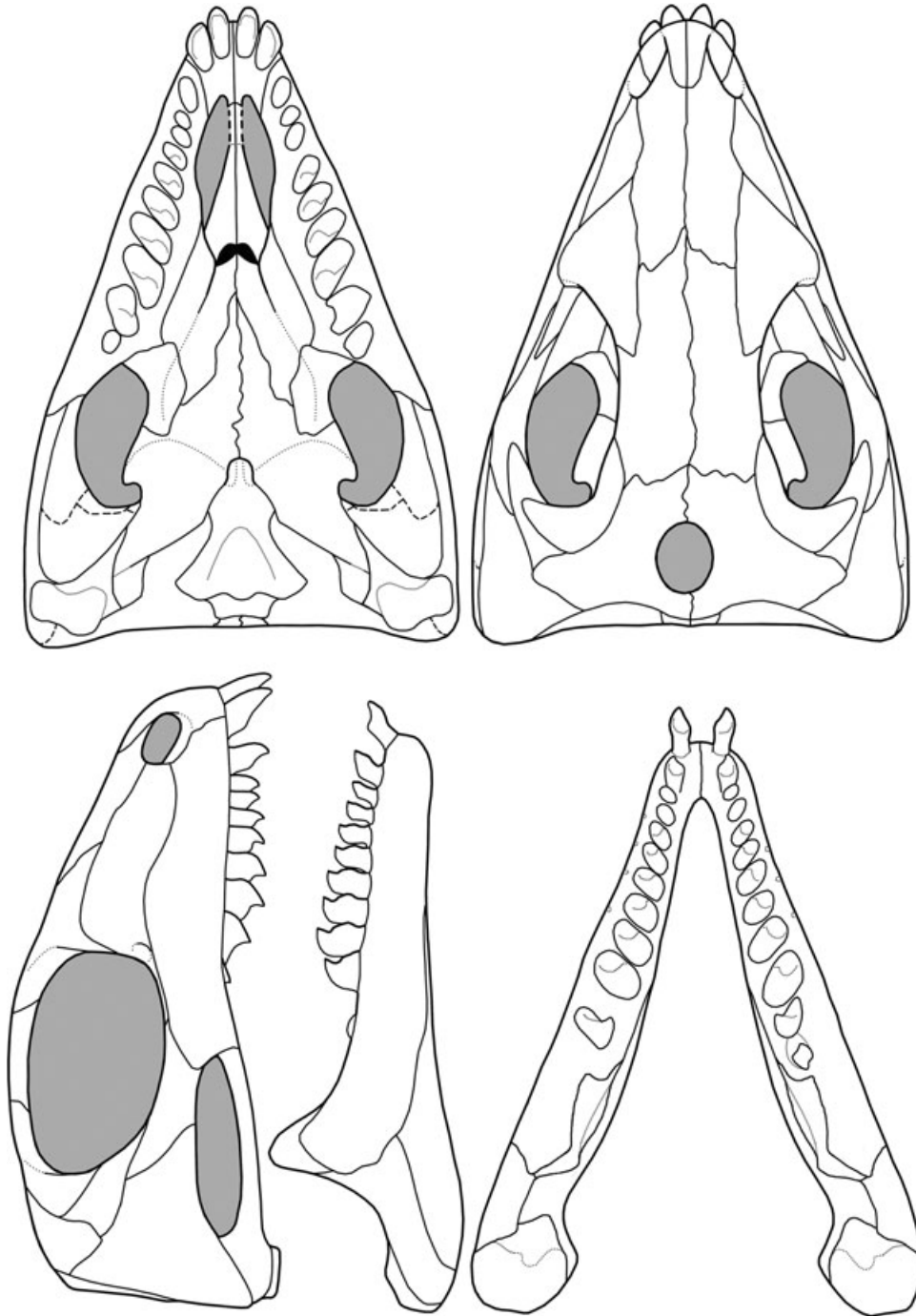


Figure 9. *Belebey vegrandis*: cranial reconstruction in palatal, dorsal, and lateral views, and reconstruction of the mandibles in occlusal view. The anterior opening in palatal view between the maxilla and the vomer, shown in grey, represents the primary internal naris, but the vomer is sutured to the palatines posteriorly, blocking off any possible air passage. It is unlikely that this opening was used for respiration. Instead, the small space between the posterior edge of the vomer and the anterior edge of the palatine, shown in black, represents a new opening (choana) for the passage of air between the nasal capsule and the throat.

either side of the midline just posterior to the parietals. Although slightly visible in dorsal view, they are clearly part of the occiput, and slightly underlie the parietals (Fig. 7).

The tabular, on the other hand, is a prominent, transversely elongate element that forms a significant portion of the posterior edge of the skull table, as well as extending far ventrally onto the occiput (Figs 1, 7). The tabular contacts the postparietal medially and the parietal anteriorly. In addition, the tabular is a very long element, and not only contacts the squamosal laterally, but also extends far ventrally along a posterior groove of the squamosal, in a position normally occupied by the supratemporal. This is in contrast to the original description by (Ivakhnenko, 1973) of a separate supratemporal bone. This peculiar morphology is interpreted as having developed in order to strengthen the short temporal region, and could have been achieved in one of two ways: either by fusion of the supratemporal with the tabular or by the loss of the supratemporal, the latter having been replaced by a posterolateral extension of the tabular bone. The first scenario is the more likely, but the second alternative cannot be rejected.

The squamosal is a broadly curved, sheet-like bone that forms the posterolateral part of the cheek, as well as the posterodorsal margin of the temporal fenestra (Figs 1, 7). Posteriorly the squamosal curves medially for a short distance onto the occipital surface of the skull, and forms the gently sloping posterior edge of the temporal region, whereas anteriorly it has a distinct projection that is embraced by the suborbital process of the jugal. In contrast to the condition seen in other parareptiles, where the squamosal forms either a sharp separation between the temporal region and the occiput or is emarginated for the formation of the temporal notch, there is no sharp separation between the temporal and occipital regions of the skull of *Belebey*. Instead, there is a shallow but clearly demarcated groove that extends vertically along the posteriorly facing surface of the squamosal for the ventral process of the tabular. In contrast to the condition seen in some eupelycosaurian synapsids, this groove extends far ventrally, as seen in the largest known skull of *Belebey*, nearly reaching the posteroventral edge of the squamosal. The gently curving sheet of the squamosal that forms most of the temporal region extends anteroventrally and contributes to the dorsal edge of the lateral temporal opening. Posteroventrally, the squamosal is in contact with the posterior part of the quadratojugal, and extends far ventrally, close to the level of the jaw articulation. Posteromedially the bone meets and overlaps the dorsal process of the quadrate.

The quadratojugal is a very conspicuous, elongate element of the skull roof, forming not only the ventral edge of the skull, from the jaw articulation to the level

of the mid-orbit, but also its rod-like anterior process also forms the entire ventral margin of the temporal fenestra (Fig. 7). The long anterior process of the quadratojugal makes up nearly 40% of the overall skull length. Anteriorly, it contacts the posterior edge of the maxilla, but it is not clear if it meets the jugal to exclude the maxilla from the temporal fenestra. Posteriorly the quadratojugal is more sheet-like where it covers part of the quadrate, underlies the squamosal, and forms the posterior edge of the temporal fenestra.

The jugal is a fairly massive element of the suborbital region that forms an arc between the elongate horizontal temporal fenestra below, and the unusually large orbit above (Fig. 7). Posterodorsally, it extends far between the postorbital and squamosal bones. On the right side of SGU 104/B-2020, a well-developed groove on the dorsal process of the jugal marks the anteroventral extent of the postorbital. Anteriorly, the jugal has a slender process that extends between the maxilla and lacrimal, but the anterior tip of the bone reaches in only slightly from the anterior orbital margin. A brief contact between the maxilla and the quadratojugal prevents the jugal from reaching the ventral margin of the skull.

PALATE

The palate is only partially exposed in two of the skulls (SGU 104/B-2021 and 2022) because the mandibles are tightly attached to the skull in the former, and because of damage and loss in the latter. However, in SGU 104/B-2020, the mandibles were successfully removed from the skull by Dr Michael Ivakhnenko, exposing much of the palate (Fig. 2). In addition, he disarticulated the skull, exposing much of the palate in dorsal view (Figs 2, 3). It is therefore possible to study the palate and the preserved portions of the braincase in great detail. Two particularly striking features of the palate in *Belebey* are the presence of a functional secondary palate, and the total lack of any palatal dentition. Although there are slight, slender remnants of the original internal nares, there is a well-developed secondary single choana between the posterior edge of the vomer and the anteromedian edge of the palatine. In contrast to the condition in other early amniotes, where the rounded posterior boundary of the internal naris is formed by the palatine, this bone is excluded from the narial edge by a vomer–maxillary contact, and the posterior edge of the internal naris is pinched.

The paired vomer is a relatively elongate, narrow bone that has a triangular outline. Anteriorly, the bone meets the premaxillae, whereas posterolaterally it is in contact with the palatine. Anterolaterally it forms the medial boundary of the narrow, slit-like, primary internal nares for a short distance, before it con-

tacts the massive medial shelf of the maxilla (Figs 2, 9). Posteriorly, however, the vomer has a thin, free edge that was slightly damaged during preparation, and appears to form the floor of the secondary choana. The remnants of the primary internal nares have probably lost their original function, and were possibly covered by a membranous sheet. This functional interpretation is supported by the overall morphology of this region, not only because of the unnaturally small, generally slit-like configuration of the reduced internal naris, but also because the posterior edge of the opening is pinched, and no longer rounded and reinforced by the palatine, where the functional choana would be in other early amniotes.

The paired palatine is a prominent, three-dimensional structure in *Belebey*, in contrast to the more sheet-like configuration in other early amniotes. It is best exposed in the partially disarticulated skull SGU 104/B-2021, where it is exposed in both dorsal and ventral views (Figs 2, 3). In dorsal view it has a large sheet-like surface, which carries a well-developed foramen in its central part that opens medially (Fig. 3). It overlaps the pterygoid medially and posteromedially, and the ectopterygoid posterolaterally, reinforcing these areas of the palate from above. Anterolaterally, the palatine is curved dorsally where it forms a broad, massive contact with the expanded orbital flange of the prefrontal, and also has a slender lateral extension for contact with the lacrimal. Between the orbital flanges of the prefrontal and the midline, the palatine forms a curved free edge that we interpret as the posterior edge of the internal naris (Fig. 3). Although this free edge is visible in both dorsal and ventral views, its thickness can only be inferred, with the available evidence indicating that it is slightly thickened along the short midline suture that is formed between the palatines anteriorly. The free anterior edge is relatively thinner along a segment of about 3 mm, and then becomes rapidly thick where it extends both ventrally and dorsally to reinforce the massive maxilla and prefrontal, respectively. In ventral view, the palatine has two major surfaces: a smooth palatal surface in the same plane as the pterygoid, and a slightly rugose maxillary surface that forms a distinct, anteroposteriorly elongate ventral process of the bone, and represents the medial extension of the maxillary palatal shelf (Fig. 2). The medial part of the palatal surface is offset ventrally, its anteromedial edge forming a slightly raised contact with the opposite palatine. The remaining portion of the palatal surface is in contact with the pterygoid, forming a suture running posterolaterally. We interpret the two grooves formed on either side of the midline along the ventral surfaces of the palatine and pterygoid as the air passages that extended posteriorly from the internal naris, at a significantly deeper level than the

maxillary surface of the palatine bone, where oral processing probably occurred.

The maxillary surface of the palatine is located ventral to the general palatal surface of the palatine and pterygoid, and is separated from it by a deep medially facing groove. This groove gradually diminishes in depth posteriorly, so that the two surfaces are not as widely separated posteriorly as they are anteriorly (Fig. 2). This massively ridged part of the palatine forms a deep sutural contact with the maxilla that also extends along the four largest teeth. The ventral surface of the palatine appears to have a rugose surface in this region, similar to that seen on the medial shelf of the maxilla. Thus, a relatively large rugose, slightly pitted surface is present on the palate of *Belebey* where the large cheek teeth of the lower jaw would have impacted, and represents the secondary palatal shelf. A similar structure is present in diadectids (Berman *et al.*, 1998) and in dicynodonts (Sullivan & Reisz, 2005). The maxillary process of the palatine has short contacts with the vomer anteriorly and the ectopterygoid posteriorly.

The paired pterygoid is the largest bone of the palate (Figs 2, 8). Anteromedially, it extends far between the palatines, whereas posteriorly, the bone is transversely expanded and has a prominent, very large, quadrate ramus that projects anterolaterally to meet the quadrate. The anterior process of the pterygoid is more slender in dorsal than in ventral view, extending anteriorly along the dorsal surface of the palate, almost to the modified internal naris. A slender, but well-developed longitudinal groove extends anteriorly along most of the pterygoid from the level of the basicranial articulation. This dorsal groove is widest just anterior to the basicranial articulation, and gradually becomes more slender anteriorly. The groove is separated from the general dorsal surface of the pterygoid by a slender, fairly sharp ridge, but is sufficiently wide to have held a short slender cultriform process posteriorly, and the base of the sphenethmoid anteriorly. In contrast to most other early amniotes, the anterior process of the pterygoid does not contact the vomer.

At the level of the basicranial articulation, a short semilunar-shaped emargination is exposed in dorsal view on each of the pterygoids, where the tubera of the basisphenoid and the head of the epipterygoid may have attached. This recess is covered ventrally by the medial flange of the pterygoid quadrate ramus, so that the basicranial articulation is not visible in ventral view (Figs 2, 9). Posterolateral to the basicranial recess the pterygoid forms the quadrate ramus, which is clearly divided into two flanges: a posterodorsal flange that attaches to the dorsal process of the quadrate, and a medioventral arcuate flange. A deep groove separates the two flanges, which are relatively thin sheets of bone attached to each other along the vent-

rolateral edge of the quadrate ramus (Fig. 2). Anteriorly this groove terminates in a deep pocket located next to the basicranial recess. The epipterygoid is likely to have attached to the dorsal edge of this pocket.

In ventral view, the separation between the anterior plate-like process of the pterygoid and the posterior quadrate process is marked in *Belebey* by an unusual transverse flange. As in other bolosaurids, and unlike any other early amniote, the edentulous ventral ridge of the transverse flange does not extend ventrally below the edge of the skull roof, and is not visible in lateral view. In addition the flange does not extend far laterally, creating a wide space between the free lateral edge of the flange and the suborbital ramus of the skull roof.

The quadrate process is a broad structure in ventral view because there is no strong mediolateral pinching of the pterygoid immediately posterior to the transverse flange. Instead, a broadly curving arcuate flange extends posteromedially from the transverse flange, and covers much of the space between the vertical portion of the quadrate process of the pterygoid and the braincase. Posteroventrally, the pterygoid forms an elongate sutural contact with the quadrate.

The ectopterygoid is the smallest element of the palate (Figs 2, 3). Nevertheless, it is relatively robust and has a well-developed ventral ridge that buttresses the lateral region of the palate, between the maxilla and maxillary surface of the palatine, anteriorly, and the transverse flange of the pterygoid, posteriorly. Medially the ectopterygoid contacts the palatal portions of the palatine and the pterygoid, respectively. In *Belebey*, the suborbital foramen does not appear in the normal position on the palate, but rather, two small foramina found anteriorly on the ventral surface of the ectopterygoid, along with a slightly larger foramen, and a posteriorly extending groove on the dorsal surface of the bone may have served the same purpose.

QUADRATE AND BRAINCASE

In articulated condition, the dorsal process of the quadrate is covered by the squamosal and quadratojugal. Thus, most of the bone is covered laterally, but it possesses a distinct transversely expanded ventral head for articulation with the lower jaw that extends ventrally beyond the level of the remaining skull bones (Fig. 1). The body of the quadrate is expanded anterodorsally and is in broad contact anteromedially with the pterygoid along an anteroventrally sloping suture. Although somewhat damaged the condyle of the quadrate appears to be broad, but its exact ventral surface cannot be determined either because of damage (Fig. 2) or because the mandible is in articulation, thereby obscuring the articular surfaces (Figs 7, 8).

The basioccipital is very poorly preserved in both SGU 104/B-2020 and 2021 (Figs 2, 8), but appears to have been a comparatively short element. In SGU 104/B-2020, the basioccipital is exposed in both dorsal and ventral views, and it can be discerned that it extended farther anteriorly in dorsal than in ventral view, partly because it appears to be covered by the posterior plate of the parasphenoid. Although damaged posteriorly, both specimens indicate that it had a major contribution to the occipital condyle, resulting in a broad, dorsoventrally narrow surface of articulation with the atlas.

The exoccipital is a small, vertically orientated element with a slightly expanded ventral base that was in broad contact with the basioccipital. Although only the right exoccipital is preserved in SGU 104/B-2020, the size of the ventral base indicates that it excluded the basioccipital from the border of the foramen magnum and met its pair at the midline (Fig. 2). The bone was apparently not fused to the opisthotic, which is not preserved, and did not meet the opposite exoccipital dorsally. A well-developed foramen can be recognized posteriorly and is probably the opening for the passage of the hypoglossal nerve.

The parasphenoid and basisphenoid are fused and are thus indistinguishable in all three specimens of *Belebey*, and are only partially preserved (Figs 2, 8). Even though the basiptyergoid processes can be clearly identified projecting anteriorly and slightly laterally, they appear to be too small to fit into the pterygoid recesses for the basicranial articulation. This condition indicates that the epipterygoids must have contributed to the basicranial articulation, as in other Palaeozoic amniotes. Unfortunately, only the slender dorsal process of the epipterygoid is preserved in SGU 104/B-2021, deep inside the orbit (and thus could not be illustrated), and its basal portion cannot be exposed. The anteriormost process of the basisphenoid is developed as a small, rounded projection extending between the pterygoids (Fig. 2). In dorsal view, preservation allows for the identification of the semilunar-shaped dorsum sellae in SGU 104/B-2020, along with a rostrally expanded ridge in the anteriormost region of the bone, which might be attributed to the sella turcica (Fig. 2).

In ventral view, the parasphenoid portion of the complex has a distinct triangular depression in its posterior part, which is surrounded by the posterolaterally diverging cristae ventrolaterales (Fig. 8). These ridges meet the basioccipital posterolaterally, and both bones participate in the formation of modestly developed basituberal projections. Anterior to the triangular depression, two small, carotid foramina can be recognized in SGU 104/B-2021 (Fig. 8). A delicate, slender anterior process of the parasphenoid can be recognized in SGU 104/B-2021 and 2022 as the base of

the cultriform process. Its dimensions indicate that it must have been very short, not extending far anteriorly. However, the presence of the elongate median groove on the dorsal surface of the pterygoid indicates that an elongate cultriform process may have been present.

None of the known specimens of *Belebey* have preserved the opisthotic, prootic, supraoccipital, or stapes. This is a strange occurrence, because all other elements of the skull and mandible are preserved in place, suggesting that these elements of the braincase were not strongly sutured to the rest of the skull, and were therefore readily lost after death.

MANDIBLE

The mandible is a relatively slender structure, with a nearly straight tooth-bearing region that occupies only about 60% of the jaw length, a very small mandibular fossa, a prominent coronoid process, and a large articular surface (Figs 4–6). There is no retroarticular process. In occlusal view, the labial surface of each mandible is nearly straight throughout the length of each ramus. Many elements of the mandible are greatly modified in bolosaurids, and represent autapomorphies of this clade of reptiles. Most of these autapomorphies are probably related to the unusual dentition and the unique feeding adaptations of bolosaurids.

The dentary can be readily subdivided into three major areas, the tooth-bearing region that forms the lateral wall of the mandible, a posterodorsally expanded coronoid process, and a ventrally expanded medial blade of the alveolar shelf (Figs 4, 5). Anteriorly, the tooth-bearing region of the dentary is relatively straight in dorsal view, and curves medially, but only slightly, at the symphysis. Laterally, the bone shows a smooth, unsculptured surface with few small foramina.

The tooth-bearing portion of the dentary is continued posterodorsally, so that the bone meets the angular ventrally, and the surangular posteriorly, in an overlapping suture. The dentary has a large posterodorsal process that contributes to the coronoid process, almost completely covering the large coronoid laterally by means of a broadly overlapping suture. Perhaps the most striking bolosaurid feature of the dentary is the presence of a flat medioventral flange that extends below the level of the dental implantation, and matches in height the lateral wall of the dentary. In transverse section the dentary has the rough outline of an inverted U. Thus, the broad Meckelian canal that normally faces lingually or medially, and is covered by the sheet-like splenial in other early amniotes, is reduced to a slender ventral groove in *Belebey* and other bolosaurids. Much of the medial

wall of the dentary is flat and slightly striated, with a slightly raised edge that clearly indicates the dorsal, anterior, and ventral boundaries of its extensive sutural overlap with the sheet-like anterior process of the prearticular. The narrow ventral groove of the Meckelian canal is covered by the short, slender splenial.

The symphysis is entirely formed by the dentary, and its slightly rounded surface indicates that the two rami may have been able to move relative to each other through an arc of nearly 5°.

The dentary bears 11 or 12 heterodont teeth that were described previously (Reisz *et al.*, 2002). The first tooth is similar in shape to the first premaxillary, and it is a relatively slender, procumbent tooth that has a slightly expanded crown, and a sharply pointed, posteriorly recurved cusp. The next two teeth also show a somewhat anterodorsal orientation, and both teeth possess distinctively constricted heels. The third and fourth teeth are smaller than the anterior two, whereas from the fifth tooth onwards an anteroposterior increase in size is observed, comparable with the condition seen in the maxilla. The last tooth, however, is again slightly smaller than the others. In occlusal view, the fifth to the 11th or 12th teeth have a kidney-shaped outline, but the orientation is different from that of the maxilla, with the long axis now posterolabially anterolingually directed. Also, the tooth cusps in these cheek teeth show an anterior orientation instead of a posterior curvature, and the wear facets, which again consist of two depressions, are now situated anterolingually to the tooth cusps, which again possess distinct labial and lingual ridges/cutting edges, as well as a less well-developed posterior crest. Only the three anteriormost teeth show wear facets that are situated posteriorly to the cusp. In conclusion, these features suggest that there must have been extensive dental occlusion between the upper and the lower teeth. In addition, striations on the wear facets on the dorsolateral surface of the dentary teeth indicate that the lower teeth moved posteriorly during contact with the upper teeth.

The splenial is poorly preserved in all known specimens. It can, however, be discerned that it was only a small splint-like bone that covered the ventral part of the Meckelian groove, and it did not reach the symphysis (Figs 4, 5, 7, 8). This is in strong contrast to the condition in all other Palaeozoic amniotes, where the splenial is a sheet-like, large element that covered the medial wall mandible at the level of the dentary.

The coronoid of *Belebey* is only exposed in SGU 104/B-2020 in the isolated mandibles (Figs 4, 5). The coronoid is preserved in articulation with the surrounding elements, and forms not only the strongly ridged anterior border of the adductor fossa, but also the prominent coronoid process. The coronoid process extends

far dorsally, showing a somewhat posterodorsal inclination, and is strongly supported by the dentary and surangular laterally, and the prearticular medially. The apex of this process is developed into a sharp crest, indicating that an aponeurotic sheet ('bodenaponeurosis') probably inserted there. The medial surface of the coronoid process has a well-developed, broad ridge that extends posterodorsally from the prearticular contact to the apex of the process (Figs 4, 5). In contrast, the lateral surface of the coronoid process has a slightly concave surface posterodorsally. It is not possible to determine the exact nature of the contact between the surangular and the coronoid, but its posteroverentral edge clearly meets the surangular where the two bones contribute to the walls of the adductor (mandibular) fossa.

The angular is an elongate element that covers the posteroverentral region of the mandible, and is trough-shaped, forming the ventral wall of the mandibular fossa (Figs 4, 5). Anterolaterally it underlies the dentary, posterodorsally it contacts the surangular, and medially it underlies the large prearticular. It does not seem to have a superficial contact with the splenial. A slender, slit-like mandibular foramen (Fig. 8) is present on the ventral surface of the mandible at the contact between the angular and the prearticular at the level of the coronoid eminence.

The exposed portion of the surangular indicates that it is a short, massive element that forms the lateral wall of the mandibular fossa, and contributes to the large coronoid process (Figs 4, 5). In dorsal view, this bone has a massive ridge that forms the dorsal edge of the lateral mandibular wall, and slightly overhangs the mandibular fossa. Posteriorly the surangular overlaps the lateral surface of the articular bone, and is sandwiched between the angular below and the expanded articular surface of the articular bone above.

The prearticular is a very long element, nearly equal in length to the dentary. It extends along the medial (lingual) surface of the mandible from the level of the jaw articulation to the level of the fifth dentary tooth. Anterior to the coronoid process, the prearticular covers most of the medial surface of the mandible, as indicated by the striated sutural surface of the dentary, where it is overlain by this bone (Figs 4, 5). However, this anterior part of the prearticular has been largely lost in both rami of SGU 104/B-2020. The prearticular contacts the expanded base of the coronoid bone, but more posteriorly, the prearticular has a free, ridged dorsal edge where it forms the medial wall and medial border of the mandibular fossa. In medial view the free dorsal edge of the prearticular is concave in outline. Posteriorly, the prearticular curves medially and contacts the articular, which it covers almost completely on its medial surface.

The articular is a transversely broad element that forms the surface of articulation with the quadrate. As in other early amniotes, the articular surface possesses both a lateral and a medial ridge, separated from each other by a depression. However, these two ridges are not as tall as in other amniotes, and the depression is not a narrow longitudinal groove, but a broad, gently concave area. The long axis of this combination of ridges and the shallow groove is approximately in line with the straight tooth row. When compared with the much shorter condyle of the quadrate, it becomes obvious that extensive propalinal movement was possible in the mandible. As revealed by the right mandible of SGU 104/B-2020 (Fig. 5) and in occipital view of SGU 104/B-2021 (studied by RRR but not available for illustration), the overall surface of articulation was sloping slightly ventromedially.

SKULL RECONSTRUCTION

A previous reconstruction of *Belebey* correctly interpreted many aspects of the skull morphology (Ivakhnenko & Tverdochlebova, 1987), but also incorporated numerous inaccuracies. We therefore summarized the cranial anatomy of this bolosaurid with a new set of precisely drafted skull reconstructions (Fig. 9). These reconstructions differ markedly from the previous interpretations in the overall shape of the skull roof, one that is relatively narrow in dorsal view, matching precisely the outline of the lower jaws. In addition, the current reconstruction shows the presence of a postorbital that is distinct and separate from the postfrontal, the presence of an elongate frontal, a large prefrontal with a well-developed medioventral process along the anterior edge of the orbit, and a distinct, elongate maxillary-premaxillary suture. Contrary to previous interpretations there is no supratemporal bone, and the tabular has a large ventral process that is visible in lateral view at the posterior edge of the skull. There are also marked differences in palatal view, including the increased medial extent of the maxilla, the reduced size of the ectopterygoid, the reduced length and width of the pterygoid palatal process, the presence of a functional secondary palate, and the posterior position of the choana, marked in black (Fig. 9). Most strikingly the anterior part of the palatine bone is suturally attached to the vomer, and there is no pterygoid-vomer contact. In addition the palatine forms not only part of a large palatal shelf, but also a deep median groove that would have formed the air passage from the internal naris towards the throat.

As a result the current skull reconstruction is quite different from previous interpretations of bolosaurid skulls, one that emphasizes the procumbent nature of

the anterior premaxillary and dentary teeth, the large orbit, the elongate temporal fenestra, the large size of the pineal foramen, and the presence of a functional secondary palate.

PHYLOGENETIC ANALYSIS

In order to evaluate the phylogenetic relationships of *Belebey* and bolosaurids, a cladistic analysis was performed using the data matrix of Modesto (2000), which actually represents a modified version of the character set (1–124) of Laurin & Reisz (1995). Modesto added two characters to that data matrix (125, 126). A few new characters were added for evaluating parareptilian relationships (127–129). Finally, characters that were not duplicates of any of the above were also added from the deBraga & Reisz (1996) analysis of parareptilian relationships (130–140). The following taxa were included in the analysis: Limnoscelidae, Diadectidae, Synapsida, Mesosauridae, Millerettidae, *Eunotosaurus*, *Acleistorhinus*, *Lanthanosuchus*, *Eudibamus*, *Belebey*, *Macroleter*, Pareiasauria, Procolophonidae, Captorhinidae, *Paleothyris*, Araeoscelidia, and Younginiformes. Five of these taxa were newly added, whereas turtles were taken out of the data set because of the recent controversy about their phylogenetic position (see e.g. Rieppel & Reisz, 1999). The scoring of *Acleistorhinus* and *Lanthanosuchus* are based on the information provided by deBraga & Reisz (1996), whereas *Eudibamus*, *Belebey*, and *Macroleter* were coded on the basis of personal observations. Limnoscelids and diadectids were used as outgroups. The data matrix consists of 140 characters (see Appendix 3 for the character list).

After excluding 18 uninformative characters, a branch-and-bound search using PAUP* 4.0b10 (Swofford, 2002) resulted in a single most parsimonious tree (TL = 332, CI = 0.5000, HI = 0.5000, RI = 0.6311, and RC = 0.3156) in which bolosaurids are nested within the clade of Ankyramorpha (deBraga & Reisz, 1996) (node A, Fig. 10), and the sister taxon of the clade of *Macroleter* + Pareiasauria + Procolophonidae (Node B, Fig. 10). Bolosaurids unequivocally share with these parareptiles the presence of massive prefrontal–palatal contact [character 6, (2)], the presence of a large prefrontal medial flange [character 7, (0)], posterior expansion of the orbit [character 37, (1)], the reduced interpterygoid vacuity [character 39, (1)], the reduced anterior process of the pterygoid [character 44, (1)], the reduced cultriform process [character 52, (1)], and palatine not extending to the anterior border of the interpterygoid vacuity [character 127, (1)]. Unequivocal autapomorphies of *Belebey* include the low anterodorsal process of the maxilla [character 19, (1)] and the straight posterior skull margin [character 125, (0)]. Bootstrap support

(10 000 replicates) is high for many clades, including the Amniota (93%), Reptilia (89%), Lanthanosuchidae (94%), Bolosauridae (100%), and the clade of parareptiles comprised of the Lanthanosuchidae + Bolosauridae + *Macroleter* + Pareiasauria + Procolophonidae (97%). The clade of Parareptilia is less well supported (58%). Results of the decay analysis indicate that one additional step produces three equally parsimonious trees (EPTs), two additional steps produce six EPTs, and three additional steps produce 18 EPTs. Four additional steps produce 39 EPTs, collapsing most reptilian nodes, but the position of bolosaurids within the Ankyramorpha (deBraga & Reisz, 1996) is maintained. Thus, the position of bolosaurids within parareptiles is very well supported.

DISCUSSION

This phylogenetic analysis provides strong support for the parareptilian affinities of bolosaurids that was originally suggested by Reisz in Berman *et al.* (2000). The result of our analysis is particularly interesting because bolosaurids are grouped with *Macroleter* and the clade of pareiasaurs and procolophonids. This pattern of phylogenetic relationships is startling within a biogeographical context because the three basal parareptiles, Mesosauridae, *Eunotosaurus*, and Millerettidae, are restricted to Gondwana, whereas the stratigraphically older Bolosauridae and Lanthanosuchidae are known from Laurasian strata (Fig. 11). Given the above pattern, or relationships, the biogeographical origin of parareptiles cannot be unequivocally assigned to Gondwana, as has been proposed by Modesto (2000). The present phylogeny provides an ambiguous biogeographical history, with two equally parsimonious patterns of dispersal. The amniote and diadectomorph outgroups to the parareptiles clearly have equatorial origins and early histories. The two basal parareptile taxa (mesosaurids and the clade of *Eunotosaurus* + Millerettids) are restricted to the Gondwanan part of Pangaea, whereas the two more apical parareptile taxa (bolosaurids and lanthanosuchids + *Acleistorhinus*) have a Laurasian distribution. Thus, it is equally parsimonious to have Laurasian origins for parareptiles, with two independent invasions of Gondwana by mesosaurs and millerettids + *Eunotosaurus*, or to have a Gondwanan origin for parareptiles with a subsequent invasion of Laurasia by bolosaurids and by lanthanosuchids + *Acleistorhinus*.

Modesto (2000) argued correctly that the evolutionary history of the most basal parareptiles is recorded in Gondwana. However, bolosaurids and lanthanosuchids are stratigraphically the oldest representatives of the parareptilian clade, indicating the presence of long ghost lineages, and much unrecorded

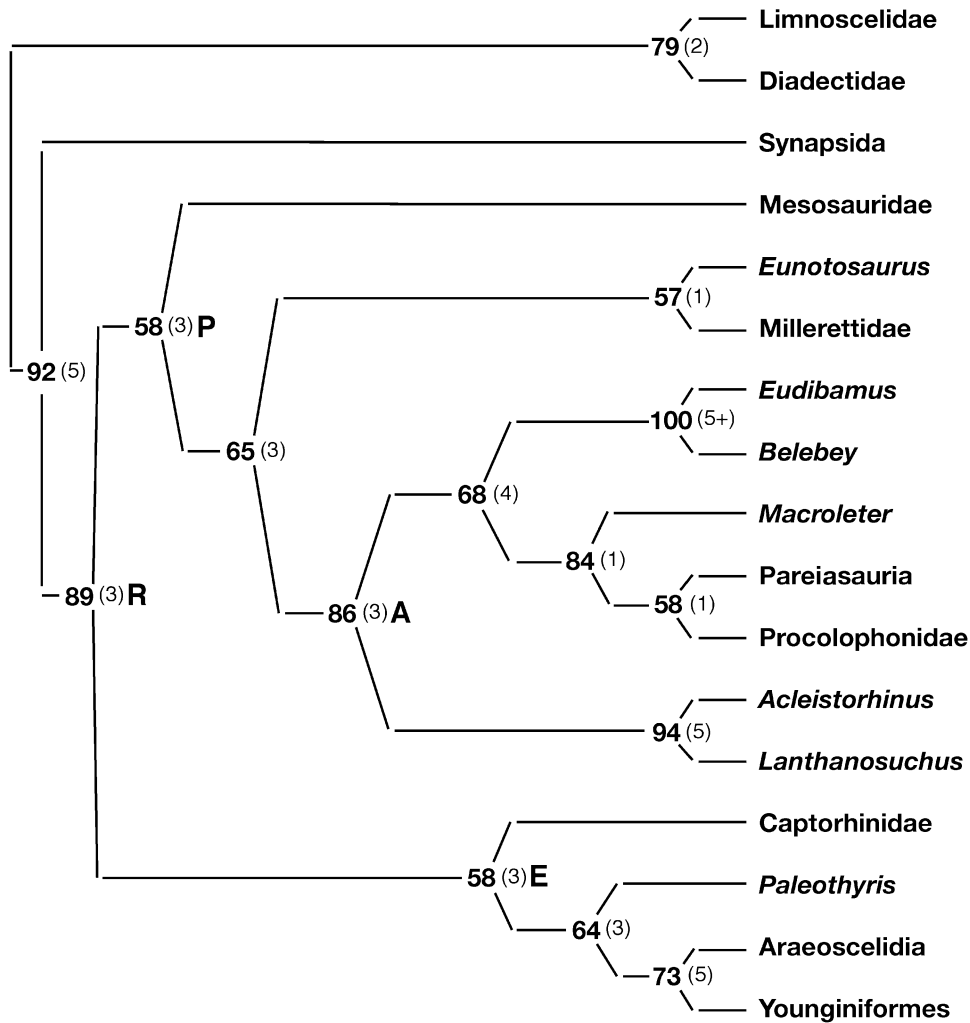


Figure 10. Cladogram showing patterns of bolosaurid relationships: bold numbers indicate bootstrap values; numbers in brackets are decay indices. A, Ankyramorpha; E, Eureptilia; P, Parareptilia; R, Reptilia.

early parareptilian history. A biogeographical pattern that is at odds with its phylogeny is inconsistent with the evidence provided by the other clades of amniotes, in particular synapsids and eureptiles. These major amniote clades have a fossil record that indicates that their early history and geographical ranges were restricted to the equatorial regions of Pangaea, indicating that their origin and early history occurred in the Laurasian part of the super continent during the Carboniferous Ice Age. In light of a highly probable Laurasian origin of all these early amniote taxa, a parareptilian origin in the same area would appear to be a reasonable assumption, but the phylogeny does not support this hypothesis unequivocally. It is clear that additional work on early parareptiles, including the enigmatic Nyctiphruetids, and new finds will be required before this interesting controversy can be resolved.

CONCLUSIONS

The cranial anatomy of *Belebey*, based upon three superbly preserved skulls, has provided important new insights into the biology and evolutionary history of bolosaurid reptiles. These Permian reptiles show numerous striking cranial features, pre-dating many innovations that occur much later in other groups of amniotes. For example, dental heterodonty, great expansion of the coronoid process on the mandible, and the complete loss of palatal dentition represent evolutionary innovations that only occur much later in synapsids and reptiles. Perhaps most remarkable of all, the modifications in the anterior part of the palate, with the apparent partial closure of the primary internal naris that is typically found between the premaxilla, vomer, palatine and maxilla, and its replacement with a more posteriorly

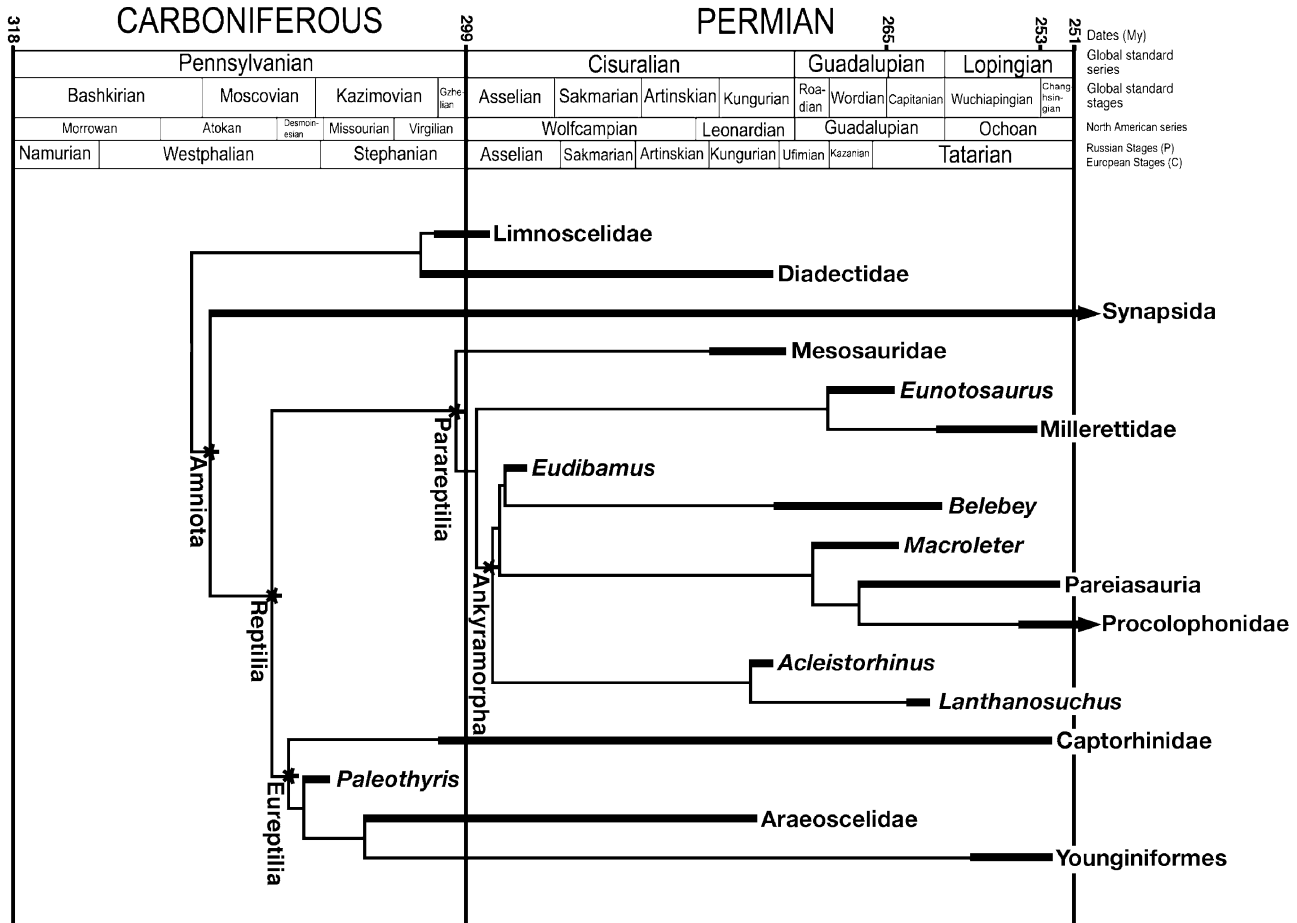


Figure 11. Phylogenetic relationships of Bolosauridae within a temporal context: thick lines represent the known fossil record of particular taxa; thin lines represent reconstructed histories of individual lineages (ghost lineages).

located internal naris and a functional secondary palate, is not found anywhere else among Palaeozoic tetrapods. This apparent modification of the anterior part of the skull is coupled with the presence of a new flange of the premaxilla, and a free anterior border of the palatine, creating an extended posterior floor for the olfactory capsule and an effective secondary palate. This is the oldest known occurrence of a functional secondary palate, one that is dramatically different from those seen in crocodiles and mammals of the Mesozoic, but one that is entirely consistent with an animal that used its highly modified, occluding cheek dentition for extensive oral processing.

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APPENDIX 1

Abbreviations used in the figures: an, angular; ar, articular; bo, basioccipital; co, coronoid; d, dentary; ec, ectopterygoid ex, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; mf, mandibular foramen; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; t, tabular; v, vomer.

APPENDIX 2

Character–taxon matrix for the phylogenetic analysis of Parareptilia and basal Amniota

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Limnoscelidae	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0
Diadectidae	0	0	0	1	1	1	0	0	0	?	0	1	1	1	1	0
Synapsida	0 & 1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0
Mesosauridae	0	1	0	0	1	0	0	0	0	?	0	1	1	1	1	0
Eunotosaurus	?	1	0	0	1	?	?	?	?	?	0	1	1	1	1	1
Millerettidae	0	1	0	0	1	1	0	0	0	2	0	1	1	1	1	0
Eudibamus	0	1	0	?	?	2	1	0	0	?	0	0	0	1	2	?
Belebey	0	1	0	2	1	2	1	0	0	2	0	0	0	1	2	?
Acleistorhinus	0	1	1	1	1	?	?	?	1	?	0	1	0	1	1	1
Lanthanosuchidae	0	1	0	2	1	1	0	0	1	?	0	0	0	1	1	?
Macroleter	0	1	0	0	1	2	1	0	1	2	1	1	0	1	1	?
Pareiasauria	0	0	1	0 & 1	0	1	0	0	0	2	1	1	0	1	1	?
Procolophonidae	1	1	1	2	0	2	1	1	1	2	1	1	0	1	1	?
Captorhinidae	0	1	0 & 1	0	1	1	0	0	0	1	1	0	0	1	2	?
Palaeothyris	0	1	0	0	1	0	0	0	0	?	0	0	0	1	2	1
Araeoscelidia	0	1	0	0	1	0	0	0	0	0	0 & 1	0	0 & 1	1	2	1
Younginiformes	0	1	0	0	1	0	0	0	1	0	1	0	1	1	2	1

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Limnoscelidae	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0
Diadectidae	0	0	0	0	0	0	1	1	0	0	3	0	0	0	1	0
Synapsida	0	0	0	0	0	1	0 & 1	0	1	0	1	0	0	1	0	0
Mesosauridae	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1
Eunotosaurus	1	0	1 & 2	?	?	1	1	1	0	1	2	1	0	0	2	0
Millerettidae	1	0	0	1	?	0	1	0 & 1	0	0	2	1	0	0 & 1	2	0
Eudibamus	?	2	0	0	?	?	0	1	0	1	1	?	0	2	0	1
Belebey	0	2	0	0	0	0	0	1	0	1	1	0	0	2	0	1
Acleistorhinus	1	0	2	1	0	0	1	0	1	1	1	1	0	1	3	0
Lanthanosuchidae	1	0	1	?	?	1	1	1	0	1	4	1	0	1	3	0
Macroleter	2	0	2	1	1	1	1	1	0	0	5	1	0	1	2	0
Pareiasauria	2	0	1	1	1	1	0	1	0	0	4	1	0	0	3	0
Procolophonidae	2	0	2	1	1	0	0	1	0	0	5	1	0	0	2	0
Captorhinidae	2	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0
Palaeothyris	1	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0
Araeoscelidia	1	1	0	0	0	0	0 & 1	0	1	0 & 1	1	0	1	1	0	0
Younginiformes	1	1	2	0	0	0	1	0	0	1	3	0	1	1	0	0

APPENDIX 2 *Continued*

	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Limnoscelidae	0	0	0	1	0	0	2	0	?	0	0	0	0	1	0	0
Diadectidae	0	1	1	1	0	1	0	1	?	0	0	0	1	0	0	0
Synapsida	0 & 1	0	0	1	0	0	0 & 2	0	?	0	0	0	0	1	0	0
Mesosauridae	1	0	0	1	0	0	0	0	?	1	?	0	0	1	2	?
Eunotosaurus	2	1	0	2	0	1	2	?	?	?	?	?	0	1	?	?
Millerettidae	1	1	0	2	0	1	2	0	?	0	0	0	0	1	1	1
Eudibamus	?	0	0	0	?	0	0	?	?	?	?	1	2	2	1	1
Belebey	0	0	0	1	1	0	0	0	?	0	?	1	2	2	1	1
Acleistorhinus	1	0	0	2	0	1	2	0	?	0	1	0	0	1	0	1
Lanthanosuchidae	1	0	0	0	0	2	2	0	?	0	1	0	0	1	0	1
Macroleter	1	0	0	2	1	2	0	0	?	0	1	1	1	1	1	?
Pareiasauria	0	0	0	2	0	2	0	1	?	0	1	1	1	1	1	1
Procolophonidae	2	0	0	2	1	0	0	0	?	0	1	1	1	2	1	1
Captorhinidae	1	0	1	1	0	3	2	0	?	1	0	0	0	0	2	?
Palaeothyris	1	0	1	1	0	0	2	0	?	1	0	0	0	1	0	0
Araeoscelidia	1	0	1	1	0	0	2	0	?	1	0	0	1	0 & 1	1	0
Younginiformes	1	1	1	1	0	0	2	0	?	1	0	0	0	1	0	1

	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Limnoscelidae	0	0	0	0	1	?	1	0	0	1	?	?	0	0	0	0
Diadectidae	0	?	0	0	0	?	1	0	1	1	1	?	0	0	0	0
Synapsida	0	0 & 1	0	0	0 & 1	?	1	0	2	0 & 1	0	?	0	1	0	0
Mesosauridae	?	0	0	0	0	?	2	0	?	?	?	?	?	1	0	?
Eunotosaurus	?	1	0	0	0	?	1 & 2	1	?	?	?	?	?	?	?	?
Millerettidae	1	1	1	0	1	?	2	0	3	0	?	?	1	1	0	0
Eudibamus	?	0	1	1	0	?	?	?	?	?	?	?	?	0	?	?
Belebey	0	0	1	1	0	?	?	?	?	?	?	?	0	?	?	0
Acleistorhinus	1	?	1	0	1	?	1	0	4	0	?	?	0	0	0	0
Lanthanosuchidae	0	1	1	0	1	?	1	0	4	0	?	?	?	0	?	?
Macroleter	1	1	1	1	0	?	2	1	?	0	?	?	?	1	?	0
Pareiasauria	1	1	1	1	0	?	3	1	3	0	0 & 1	?	0	1	0	1
Procolophonidae	1	1	1	1	0	?	3	1	4	0	?	?	1	1	1	0
Captorhinidae	1	1	0	0	0 & 1	?	2	2	6	0	?	?	0	1	0	0
Palaeothyris	?	0	1	0	1	?	2	0	6	?	?	?	?	1	0	?
Araeoscelidia	2	1	1	0	0 & 1	?	2	0	?	0	?	?	?	1	0	0
Younginiformes	2	1	1	0	0	?	2	2	6	0	?	?	?	1	0	0

	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Limnoscelidae	0	?	?	0	1	1	0	0	0	0	0	0	0	0	0	0
Diadectidae	0	0	0	0	1	0	0	?	0	1	0	0	0	0	0	0
Synapsida	0	0	0	1	0, 1, 2	0	0	0 & 1	0 & 1	0	0	0	0	0	0	0
Mesosauridae	0	0	0	1	?	?	0	0	0	1	?	1	0	0	0	?
Eunotosaurus	?	0	1	1	?	?	?	0	?	?	?	0	?	?	0	?
Millerettidae	0	0	1	1	?	0	0	0	0	1	0	0	0	0	0	0
Eudibamus	?	?	?	1	2	?	?	?	?	?	2	0	0	?	2	0
Belebey	0	?	?	1	2	0	1	1	0	1	2	0	?	0	2	1
Acleistorhinus	1	0	?	1	?	?	?	1	0	1	1	0	1	0	?	1
Lanthanosuchidae	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Macroleter	1	1	1	1	2	1	1	1	?	1	1	0	?	?	1	0
Pareiasauria	1	?	?	1	2	1	1	1	0	1	1	1	0	1	1	0
Procolophonidae	1	1	1	1	2	1	1	1	1	1	1	1	1	0	1	1
Captorhinidae	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0
Palaeothyris	0	0	0	1	?	?	0	0	0	1	?	0	0	?	0	0
Araeoscelidia	0	0	0	1	?	0	0	0	0	1	0	0	0	0	0	0 & 1
Younginiformes	0	0	1	1	?	?	0	?	0	1	?	0	0	0	0	0

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APPENDIX 2 *Continued*

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
Limnoscelidae	0	0	1	1	1	0	0	1	0	0	?	0	0	0	0	0
Diadectidae	0	0	1	1	1	0	0	1	0	?	?	0	0	0	0	0
Synapsida	0	1	1	0	0 & 1	1	0 & 1	1	0	0	0	0	0	1	1	0
Mesosauridae	0	1	1	0	1	0	0	1	0	0	1	0	0	1	1	0
Eunotosaurus	1	?	?	?	?	1	0	1	1	?	?	0	0	?	?	1
Millerettidae	0	1	1	0	1	1	0	1	1	?	?	0	0	1	1	0
Eudibamus	0	?	?	?	0	2	?	0	?	0	?	1	1	?	0	0
Belebey	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanosuchidae	?	?	?	?	?	2	?	?	?	?	?	1	1	?	?	0
Macroleter	0	1	1	0	1	2	?	2	1	?	?	1	1	1	1	1
Pareiasauria	1	1	1	0	0	2	0	2	1	1	1	1	1	1	1	1
Procolophonidae	0	1	1	0	1	2	2	2	1	1	0	1	1	2	1	1
Captorhinidae	0	1	1	0	1	0	0	1	0	0	0	0	0	1 & 2	1	0
Palaeothyris	0	1	1	0	1	1	1	1	0	0	0	0	0	1	1	0
Araeoscelidia	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1	0
Younginiformes	?	?	1	0	?	1	1	1	0	1	0	1	0	1	0	0

	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112
Limnoscelidae	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Diadectidae	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Synapsida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosauridae	1	0	0	0	1	0 & 1	0	2	1	0	0	0	0	1	1	0
Eunotosaurus	1	0	0	0	1	1	0	0	?	0	0	1	0	?	0	0
Millerettidae	1	0	0	0	1	1	0	0	?	0	0	1	?	?	0	0
Eudibamus	1	?	0	0	1	3	1	2	?	?	1	0	1	0	1	1
Belebey	?	?	?	?	1	?	?	?	?	?	0	0	?	?	?	?
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanosuchidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macroleter	1	?	0	0	1	2	0	0	1	?	0	1	1	0	0	1
Pareiasauria	1	1	1	0	2	2	0	1	0	2	0	1	1	0	0	1
Procolophonidae	1	1	0	0	2	3	0	0	1	0 & 1	0	1	1	0	1	1
Captorhinidae	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0
Palaeothyris	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0
Araeoscelidia	0	0	0	1	1 & 2	0 & 1	0	2	0	0	0	0	0	1	0	0
Younginiformes	1	0	0	1	1	0 & 1	0	0	1	0	0	1	1	1	0	0

	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
Limnoscelidae	0	0	1	?	?	0	?	0	?	0	0	0	1	0	0	0
Diadectidae	0	0	1	?	0 & 1	0	?	0	0	0	0	0	2	0	0	0
Synapsida	0 & 1	0 & 1	2	0	0	0	0	0	0	0	0	0	2	0	0	0
Mesosauridae	1	0	2	0	0	1	0	0	0	0	0	0	1	1	0	0
Eunotosaurus	0	0	2	0	0	1	0	0	0	0	0	0	1	?	0	?
Millerettidae	1	1	2	0	0	1	0	0	?	0	1	0	1	0	0	0
Eudibamus	1	1	2	0	0	1	0	0	0	0	1	0	0	?	1	1
Belebey	1	?	?	?	?	?	?	?	?	?	?	0	0	?	1	?
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?
Lanthanosuchidae	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Macroleter	1	0	2	0	1	1	1	?	0	?	0	0	1	1	1	1
Pareiasauria	0	0	2	0	1	1	1	1	0	2	0	1	1	1	1	1
Procolophonidae	1	0	2	0	0/1	1	1	0	1	0 & 1	0	0 & 1	0	1	1	1
Captorhinidae	0	0	2	0	0	1	0	0	0	0	0	0	2	0	0	0
Palaeothyris	1	1	2	0	0	1	0	0	1	0	0	0	2	1	0	0
Araeoscelidia	1	1	2	1	0	1	0	0	1	0	1	0	2	0	0	0
Younginiformes	1	1	2	1	0	1	0 & 1	0	1	0	1	0	1	0	0	1

APPENDIX 2 *Continued*

	129	130	131	132	133	134	135	136	137	138	139	140
Limnoscelidae	0	0	0	1	?	?	0	0	0	0	0	0
Diadectidae	0	0	0	?	?	?	0	?	0	0	0	0
Synapsida	0	0	0	1	0	0	0	0	0	0	0	0
Mesosauridae	0	0	0	?	?	?	0	0	?	0	0	0
Eunotosaurus	0	?	0	0	?	?	?	?	?	0	0	0
Millerettidae	0	0	0	0	0	0	0	0	0	0	0	0
Eudibamus	1	1	0	1	1	1	1	?	?	0	1	0
Belebey	1	1	0	1	1	1	1	1	1	0	?	0
Acleistorhinus	0	1	1	1	1	1	1	1	1	1	1	1
Lanthanosuchidae	?	1	1	1	1	1	1	1	1	1	1	1
Macroleter	0	1	0	1	1	1	1	1	?	0	0	0
Pareiasauria	0	1	0	1	?	?	1	1	1	0	0	0
Procolophonidae	0	1	0	1	?	?	1	1	1	0	0	0
Captorhinidae	0	0	0	1	?	?	0	0	?	0	0	0
Palaeothyris	0	0	0	?	?	?	0	?	0	0	0	0
Araeoscelidia	0	?	0	0	1	0	0	?	0	0	0	0
Younginiformes	0	?	0	0	1	0	0	?	1	0	0	0

APPENDIX 3

LIST OF CHARACTERS USED FOR STUDY

- Narial shelf: absent (0); present (1). (Laurin & Reisz, 1995)
- Frontal orbital contact: absent (0); present (1). (Laurin & Reisz, 1995)
- Pineal foramen position: in centre of parietal or further posteriorly (0); close to frontoparietal suture (1). (Laurin & Reisz, 1995)
- Postparietal: paired (0); median (1); absent (2). (Laurin & Reisz, 1995)
- Postparietal position: dorsally exposed (0); occipital (1). (Laurin & Reisz, 1995)
- Prefrontal–palatal contact: absent (0); weak (1); strong (2). (Laurin & Reisz, 1995)
- Prefrontal medial flange: narrow (0); wide (1). (Laurin & Reisz, 1995)
- Bulbous medial process of prefrontal: absent (0); present (1). (Laurin & Reisz, 1995)
- Lacrimal narial contact: present (0); absent (1). (Laurin & Reisz, 1995)
- Foramen orbitonasale: absent (0); represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine (1); enclosed between prefrontal, lacrimal, and palatine (2). (Laurin & Reisz, 1995)
- Jugal anterior process: does not extend to anterior orbital rim (0); extends at least to level of anterior orbital rim (1). (Laurin & Reisz, 1995)
- Postorbital–supratemporal contact: absent (0); present (1). (Laurin & Reisz, 1995)
- Postorbital: far from occiput (0); close to occiput (1). (Laurin & Reisz, 1995)
- Intertemporal: present (0); absent (1). (Laurin & Reisz, 1995)
- Posterolateral corner of skull roof: formed by tabular (0); formed mostly by supratemporal (1); formed by parietal and small supratemporal (2). (Laurin & Reisz, 1995)
- Tabular and opisthotic: in contact (0); separated (1). (Laurin & Reisz, 1995)
- Tabular size: large (0); small (1); absent (2). (Laurin & Reisz, 1995)
- Supratemporal size: large (0); small (1); absent (2). (Laurin & Reisz, 1995)
- Anterodorsal process of the maxilla: absent (0); low, does not reach nasal or mid-height of external naris (1); high, reaches nasal and mid-height of external naris (2). (Laurin & Reisz, 1995)
- Anterior lateral maxillary foramen: equal in size to other maxillary foramina (0); larger than other foramina (1); the lateral surface of the maxilla lacks large foramina (2). (Laurin & Reisz, 1995)
- Maxillary anterior narial foramen: absent (0); present in either the maxilla only or between maxilla and premaxilla (1). (Laurin & Reisz, 1995)
- Maxilla and quadratojugal: in contact (0); separated (1). (Laurin & Reisz, 1995)
- Quadratojugal: reaches orbit (0); does not reach orbit (1). (Laurin & Reisz, 1995)
- Caniniform region: present (0); absent (1).
- Caniniform maxillary tooth: absent (0); present (1). (Laurin & Reisz, 1995)
- Squamosal and post-temporal fenestra: separated (0); in contact (1). (Laurin & Reisz, 1995)
- Occipital flange of squamosal: in otic notch and overlaps pterygoid (0); gently convex all along the

- posterior edge of the skull (1); convex above quadrate emargination and concave medial to tympanic ridge (2); absent (3); medial to tympanic ridge, facing posterodorsally (4); medial to tympanic ridge, concave, facing either posterolaterally or ventrolaterally (5). (Laurin & Reisz, 1995)
28. Quadratojugal shape: narrow (0); dorsally expanded (1). (Laurin & Reisz, 1995)
 29. Upper temporal fenestra: absent (0); present (1). (Laurin & Reisz, 1995)
 30. Lower temporal fenestra: absent (0); present, oval (1); present, slit-like (2). (Modified from Laurin & Reisz, 1995)
 31. Temporal emargination: absent (0); with squamosal and supratemporal (1); with quadratojugal and squamosal (2); facing posteriorly and exposed on occiput, bordered by squamosal, quadratojugal, and quadrate (3). (Laurin & Reisz, 1995)
 32. Postorbital region of skull: long (more than 15% of skull length) (0); short (15% of skull length or less) (1). (Laurin & Reisz, 1995)
 33. Ventral margin of postorbital region of skull: expanded ventrally (0); rectilinear (1); emarginated (2). (Laurin & Reisz, 1995)
 34. Quadrate lateral exposure: absent (0); present (1). (Laurin & Reisz, 1995)
 35. Quadrate anterior process: long (0); short (1). (Laurin & Reisz, 1995)
 36. Jaw articulation position: posterior to occiput (0); even with occiput (1); anterior to occiput (2). (Laurin & Reisz, 1995)
 37. Posterior extension of orbit: absent (0); present (1). (Laurin & Reisz, 1995)
 38. Dermal sculpturing: absent (0); tuberosities (1); tuberosities and pits (2). (Modified from Laurin & Reisz, 1995)
 39. Interpterygoid vacuity: short, less than 15% of skull length (0); absent (1); long, at least 15% of skull length (2). (Laurin & Reisz, 1995)
 40. Choana: parallel to maxilla; palatine forms its posterior edge only (0); curved posteromedially; palatine forms its posterior and part of its lateral edge (1). (Laurin & Reisz, 1995)
 41. Suborbital foramen: bordered by either maxilla or jugal laterally (0); bordered by palatine, pterygoid, and in some cases by ectopterygoid, laterally (1). (Laurin & Reisz, 1995)
 42. Arcuate flange of pterygoid: present (0); absent (1). (Laurin & Reisz, 1995)
 43. Cranio-quadrate space: small, quadrate ramus of pterygoid and paraoccipital process of opisthotic converge posterolaterally (0); large, quadrate ramus of pterygoid and paraoccipital process of opisthotic are parallel with each other (1). (Laurin & Reisz, 1995)
 44. Pterygoid anterior extent: reaches level of posterior end of choana (0); posterior to choana (1). (Laurin & Reisz, 1995)
 45. Transverse flange of pterygoid orientation: directed either posterolaterally or transversely (0); directed anterolaterally (1); laterally, reduced (2). (Modified from Laurin & Reisz, 1995)
 46. Transverse flange of pterygoid dentition: shagreen of denticles, no ventral ridge (0); edentulous with ventral ridge (2). (Laurin & Reisz, 1995)
 47. Ectopterygoid: large (0); small (1); absent (2). (Laurin & Reisz, 1995)
 48. Ectopterygoid dentition: present (0); absent (1). (Laurin & Reisz, 1995)
 49. Suborbital foramen: absent (0); present (1); fenestra present (2). (Laurin & Reisz, 1995)
 50. Parasphenoid pocket for cervical musculature: present (0); absent (1). (Laurin & Reisz, 1995)
 51. Parasphenoid wings: present, parasphenoid broad posteriorly (0); absent, parasphenoid narrow posteriorly (1). (Laurin & Reisz, 1995)
 52. Cultriform process: long (0); short (1). (Laurin & Reisz, 1995)
 53. Parasphenoid teeth: absent (0); present (1). (Laurin & Reisz, 1995)
 54. Supraoccipital anterior crista: absent (0); present (1). (Laurin & Reisz, 1995)
 55. Supraoccipital plate: absent (0); antero-posteriorly expanded (1); narrow (2); tabular, composed of opisthotic (3). (Laurin & Reisz, 1995)
 56. Paroccipital process: vertically broad (0); antero-posteriorly expanded (1); narrow (2); tabular, composed of opisthotic (3). (Laurin & Reisz, 1995)
 57. Contact between paroccipital process and dermatocranium: to tabular (0); to supratemporal and tabular (1); to tabular and squamosal (2); to squamosal and supratemporal (3); to supratemporal (4) to squamosal and quadrate (5); ends freely (6). (Laurin & Reisz, 1995)
 58. Otic trough in ventral flange of opisthotic: absent (0); present (1). (Laurin & Reisz, 1995)
 59. Medial wall of inner ear (made of prootic): unossified (0); ossified with acoustic nerve foramina (1). (Laurin & Reisz, 1995)
 60. Post-temporal fenestra: small (0); large (1). (Laurin & Reisz, 1995)
 61. Osseous contact between basioccipital and basisphenoid: present (0); absent (1). (Laurin & Reisz, 1995)
 62. Occipital condyle shape: transversely broad (0); reniform to circular (1). (Laurin & Reisz, 1995)
 63. Basioccipital tubera: absent (0); paired (1); median (2). (Laurin & Reisz, 1995)
 64. Lateral flange of exoccipital: absent (0); present (1). (Laurin & Reisz, 1995)

65. Quadrate condyle articular surfaces: strongly convex, antero-posteriorly long (0); nearly flat, antero-posteriorly short (1). (Laurin & Reisz, 1995)
66. Stapes: massive, perforated (0); slender, imperforate (1). (Laurin & Reisz, 1995)
67. Stapedial dorsal process: ossified (0); unossified (1). (Laurin & Reisz, 1995)
68. Labrynthodont infolding: present (0); absent (1). (Laurin & Reisz, 1995)
69. Foramen intermandibularis: anterior symphyseal foramen (0); two foramina, a symphyseal and a posterior foramen located anterior to coronoid process (1); two foramina, a symphyseal and a posterior foramen located either posterior to or at the level of coronoid process (2). (Laurin & Reisz, 1995)
70. Meckelian fossa orientation: faces mediodorsally, prearticular narrow (0); faces dorsally, prearticular broad (1). (Laurin & Reisz, 1995)
71. Fossal meckelii: long, occupies at least 20% of lower jaw length (0); short, occupies less than 20% of lower jaw length (1). (Laurin & Reisz, 1995)
72. Surangular length: extends beyond coronoid eminence (0); does not extend beyond coronoid eminence (1). (Laurin & Reisz, 1995)
73. Accessory lateral shelf on surangular anterior to articular region: absent (0); present (1). (Laurin & Reisz, 1995)
74. Coronoid number: two or three (0); one (1). (Laurin & Reisz, 1995)
75. Prearticular: extends beyond the coronoid eminence (0); does not extend beyond coronoid eminence (1). (Laurin & Reisz, 1995)
76. Retroarticular process: either absent or small and narrow (0); transversely broad, dorsally concave (1). (Laurin & Reisz, 1995)
77. Retroarticular process composition: articular body (0); three or more elements (articular, prearticular, angular, and surangular) (1). (Laurin & Reisz, 1995)
78. Lateral shelf on articular region: absent (0); on articular (1); on surangular (2). (Laurin & Reisz, 1995)
79. Coronoid process: small eminence composed of several elements (0); high process composed of coronoid process only (1). (Laurin & Reisz, 1995)
80. Splenial: contributes to symphysis (0); excluded from symphysis (1). (Laurin & Reisz, 1995)
81. Presacral vertebral count: more than 20 (0); 20 or less (1). (Laurin & Reisz, 1995)
82. Axial centrum orientation: in plane of axial skeleton (0); sloping anterodorsally (1). (Laurin & Reisz, 1995)
83. Atlantal neural spine size: nearly as tall as axial spine (0); reduced to small spinous process (1). (Laurin & Reisz, 1995)
84. Axial intercentrum: with rounded anteroventral edge (0); with strong anterior process (1). (Laurin & Reisz, 1995)
85. Atlantal pleurocentrum and axial intercentrum: separate elements (0); either attached or fused (1). (Laurin & Reisz, 1995)
86. Trunk neural arches: swollen with wide zygapophyseal buttresses (0); narrow (1); swollen with narrow zygapophyseal buttresses (2). (Laurin & Reisz, 1995)
87. Ventral surface of anterior pleurocentra: rounded (0); keeled (1); with double ridge (2). (Laurin & Reisz, 1995)
88. Number of sacral vertebrae: one (0); two (1); three or four (2). (Laurin & Reisz, 1995)
89. Sacral rib distal overlap: broad with narrow gap between ribs (0); small or absent with wide gap between ribs (1). (Laurin & Reisz, 1995)
90. Transverse process or ribs: present only on a few anterior caudals (0); present on at least 13 caudals (1). (Laurin & Reisz, 1995)
91. Caudal haemal arches: wedged between centra (0); attached to anterior centrum (1). (Laurin & Reisz, 1995)
92. Interclavicle: diamond-shaped (0); T-shaped, with long, slender lateral processes (1). (Laurin & Reisz, 1995)
93. Interclavicle attachment for clavicle: ventral sutural area (0); anteriorly directed groove (1); tightly sutured into plastron (2). (Laurin & Reisz, 1995)
94. Cleithrum: caps scapula anterodorsally (0); does not cap scapula at all (1); absent (2). (Laurin & Reisz, 1995)
95. Scapulocoracoid ossifications: two (0); three (1). (Laurin & Reisz, 1995)
96. Scapula: broad (0); narrow, thin (1); narrow, cylindrical (2). (Laurin & Reisz, 1995)
97. Supraglenoid foramen: present (0); absent (1). (Laurin & Reisz, 1995)
98. Glenoid: anteroposteriorly long, helical (0); short, bipartite (1). (Laurin & Reisz, 1995)
99. Acromion: absent (0); present (1). (Laurin & Reisz, 1995)
100. Sternum: not mineralized (0); mineralized (1). (Laurin & Reisz, 1995)
101. Supinator process: strongly angled relative to shaft, separated from it by groove (0); parallel to shaft, separated from it by groove (1); parallel to shaft, not separated from shaft (2). (Laurin & Reisz, 1995)
102. Ectepicondylar foramen: only groove present (0); groove and foramen present (1); only foramen present (2); both absent (3). (Laurin & Reisz, 1995)
103. Entepicondylar foramen: present (0); absent (1). (Laurin & Reisz, 1995)

104. Humerus: with robust heads and a short shaft (0); short and robust, without a distinct shaft (1); slender with long shaft (2). (Laurin & Reisz, 1995)
105. Olecranon process: large, proximal articular facet of ulna faces medially (0); small, proximal articular facet of ulna faces proximally (1). (Laurin & Reisz, 1995)
106. Manual phalangeal formula: 2 3 4 5 3 (0); 2 3 4 4 3 (1); 2 3 3 3 3 or less (2). (Laurin & Reisz, 1995)
107. Dorsolateral shelf on iliac blade: absent (0); present (1). (Laurin & Reisz, 1995)
108. Iliac blade: low, with long posterior process (0); dorsally expanded, distally flaring (1). (Laurin & Reisz, 1995)
109. Acetabular buttress: small, overhangs acetabulum only moderately (0); large, overhangs acetabulum strongly (1). (Laurin & Reisz, 1995)
110. Oblique ventral ridge of femur (adductor crest): present (0); absent (1). (Laurin & Reisz, 1995)
111. Femoral proximal articulation: antero-posteriorly long (0); round (1). (Laurin & Reisz, 1995)
112. Greater trochanter of femur: absent (0); present on posterior edge of femur (1). (Laurin & Reisz, 1995)
113. Femoral shaft: short and broad (0); long and slender (1). (Laurin & Reisz, 1995)
114. Carpus and tarsus: short and broad (0); long and slender (1). (Laurin & Reisz, 1995)
115. Astragalus: absent (0); incorporates incompletely fused tibiale, intermedium, and perhaps centrale 4 (1); without traces of compound origin (2). (Laurin & Reisz, 1995)
116. Tibio-astragalar joint: flat (0); tibial ridge fits into astragalar groove (1). (Laurin & Reisz, 1995)
117. Astragalus and calcaneum: separate (0); sutured or fused (1). (Laurin & Reisz, 1995)
118. Medial pedal centrale: present (0); absent (1). (Laurin & Reisz, 1995)
119. Number of distal tarsals: five (0); four or less (1). (Laurin & Reisz, 1995)
120. Fifth pedal digit: longer than first digit (0); more slender and not longer than first digit (1). (Laurin & Reisz, 1995)
121. Metapodials: not overlapping (0); overlapping (1). (Laurin & Reisz, 1995)
122. Pedal phalangeal formula: 2 3 4 5 4 or 3 (0); 2 3 4 4 3 (1); 2 3 3 4 3 or less (2). (Laurin & Reisz, 1995)
123. Ratio between length of metatarsal one to length of metatarsal four: at least 0.5 (0); less than 0.5 (1). (Laurin & Reisz, 1995)
124. Dorsal dermal ossifications: absent (0); present (1). (Laurin & Reisz, 1995)
125. Posterior skull margin form: flat (0); concave (1); double concave (Modesto, 2000)
126. Atlantal epiphysis: present (0); absent (1) (Modesto, 1999)
127. Interpterygoid vacuity/palatine relation: vacuity extends to level of palatine (0); vacuity does not extend to level of palatine (1)
128. Clavicle head: diamond shaped (0); cruciform (1).
129. Transverse flange of pterygoid: large, extending far laterally (0), reduced, to nubbins (1).
130. Premaxillary dorsal process: broad, narial opening faces predominantly laterally (0); narrow, narial opening faces anteriorly (1). (deBraga & Reisz, 1996)
131. Frontal lateral lappet: absent (0); large, occupies at least one-third of the dorsal margin of the orbit (1). (deBraga & Reisz, 1996)
132. Postorbital posterior process shape: slender, half as wide as it is long (0); increased width, parallelogram outline in lateral aspect (1). (deBraga & Reisz, 1996)
133. Quadratojugal-lateral temporal fenestra contribution: quadratojugal excluded from posterior border (0); quadratojugal contributes to lateral temporal fenestra (1). (deBraga & Reisz, 1996)
134. Postorbital contribution to lateral temporal fenestra: bordered by jugal, quadratojugal, squamosal, and postorbital (0); no contribution by postorbital (1). (deBraga & Reisz, 1996)
135. Quadratojugal ramus of pterygoid: merges smoothly into transverse flange without distinctive excavation (0); deep excavation on posterolateral surface (1). (deBraga & Reisz, 1996)
136. Palatine contribution to palate: narrow, restricted to lateral margins of palate (0); broad, exceeds 50% of the width of the pterygoid (1). (deBraga & Reisz, 1996)
137. Ectopterygoid relationship to transverse flange: ectopterygoid distal to transverse flange, does not contribute to flange (0); ectopterygoid makes contact with tooth-bearing region of transverse flange (1). (deBraga & Reisz, 1996)
138. Length of basicranial articulation: restricted to anterolateral margin of the parasphenoid (0); extends over much of length of main body of parasphenoid (1). (deBraga & Reisz, 1996)
139. Ventral exposure of basioccipital: contributes extensively to ventral surface of the braincase (0); restricted to condylar region (1). (deBraga & Reisz, 1996)
140. Paraoccipital process orientation: directed primarily laterally (0); orientated obliquely, extends dorsolaterally to contact the supratemporal (1). (deBraga & Reisz, 1996)