

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024  
Number 3445, 36 pp., 16 figures June 2, 2004

## A New Crocodyliform from Zos Canyon, Mongolia

DIEGO POL<sup>1</sup> AND MARK A. NORELL<sup>2</sup>

### ABSTRACT

Here we report on a new fossil crocodyliform from Cretaceous Redbeds in the Zos Canyon, Gobi Desert, Mongolia. This new taxon, *Zosuchus davidsoni*, is described based on the information provided by five specimens collected during expeditions of the Mongolian Academy of Sciences–American Museum of Natural History. *Zosuchus davidsoni* is identifiable by numerous characters, including a posteriorly extensive secondary palate that opens through a secondary choana bordered by the palatines and pterygoids near the posterior edge of the skull, and a lacrimal–premaxillary contact on the dorsal surface of the snout. The phylogenetic relationships of *Zosuchus davidsoni* are shown through a parsimony analysis in the context of Crocodyliformes. This new form is found to be a late-appearing basal crocodyliform, forming a monophyletic group with two other taxa from the Early Cretaceous of China. Because of the basal position of *Zosuchus* within Crocodyliformes, the marked posterior extension of the secondary palate is most parsimoniously interpreted as a convergence with the derived condition of neosuchian crocodyliforms.

### INTRODUCTION

During the last decade, expeditions from the Mongolian Academy of Sciences and the American Museum of Natural History have developed large collections of fossil vertebrates from Djadokhta and Djadokhta-like rocks in the Gobi Desert (Dashzeveg et al., 1995; Novacek, 1996, 2002). Although remains of reptiles (especially dinosaurs and

lizards) are very common, crocodyliform specimens are rare. Other expeditions have noticed this as well, and only a few crocodyliform specimens have been collected in these beds (Osmólska, 1972; Storrs and Efimov, 2000; Mook, 1924; Efimov, 1983, 1988; Osmólska et al., 1997). However, at one locality, Zos Canyon, multiple crocodyliform specimens have been collected. Re-

<sup>1</sup> Division of Paleontology, American Museum of Natural History (dpol@amnh.org).

<sup>2</sup> Division of Paleontology, American Museum of Natural History (norell@amnh.org).

mains of three taxa have been recovered, which are known from seven specimens. One of these taxa, *Zosuchus davidsoni*, n.gen. and n.sp., is surprisingly primitive for a Late Cretaceous crocodyliform.

In the following report we describe the anatomy of this new form from the Zos Canyon locality and analyze the phylogenetic relationships within the context of Crocodyliformes. This new taxa is depicted as a basal crocodyliform, forming a clade with two forms from the Early Cretaceous of China.

The following institutional abbreviations are used throughout the text:

AMNH	American Museum of Natural History, New York
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
CNM	Chongqing Natural Museum, Sichuan, People's Republic of China
DGM	Departamento de Produção Mineral, Rio de Janeiro, Brazil
GPIT	Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany
GWU	George Washington University, Washington, DC
IGM	Mongolian Institute of Geology, Ulaan Bataar, Mongolia
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China
LACM	Los Angeles County Museum, Los Angeles
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MAL	Malawi Department of Antiquities, Malawi
MB	Institut für Palaontologie, Museum für Naturkunde, Humbolt-Universität, Berlin, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MLP	Museo de La Plata, La Plata, Argentina
MOZ	Museo Profesor J. Olsacher, Zapala, Argentina
MUC-PV	Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina
PVL	Instituto Miguel Lillo, Tucumán, Argentina
RCL	Museo de Ciencias Naturales, Pontificia Universidade Católica de Minas Gerais, Brazil

SAM-K	South African Museum, Cape Town, South Africa
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
UA	University of Antananarivo, Madagascar
UCMP	Museum of Paleontology, University of California, Berkeley
ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland

## HORIZON AND LOCALITY

The Zos Canyon locality (figs. 1, 2) was first visited by Mongolian Academy of Sciences–American Museum of Natural History field parties in 1992. It had previously been visited by Mongolian and Russian paleontologists (Dashzeveg, personal commun.); however, according to Dashzeveg, little was found and nothing about this locality was ever published. The locality has also been referred to informally as Kholbot (Dashzeveg, personal commun.).

The locality lies on the southern flank of the Gilvent Ul, about 6 km northwest of the main locality at Ukhaa Tolgod (fig. 1). The canyon is at the mouth of a large north–south pass that transects the Gilvent Ul. Although topographically higher than the exposures at Ukhaa Tolgod, the rocks at the Zos locality are stratigraphically lower, as the beds dip to the south underneath the Ukhaa Tolgod beds. No geochronologic work has commenced at Zos Canyon; however, *Protoceratops* sp. remains are common throughout the exposures. Interestingly, the mammalian fauna seems to be distinct as taxa unknown at other Mongolian Djadokhta and Djadokhta-like beds have been recovered (e.g., “zhelestids” [Novacek et al., 2000]).

At Zos Canyon three distinct levels are preserved (fig. 2). The uppermost of these (the Red Rum locality) is where the zhelestid material is from. Also occurring at this locality are lizards, protoceratopsians, and dinosaur eggs. Sediments at Red Rum are bright red and very similar to classic Djadokhta rocks. Below this is a series of white beds (Zos Canyon White beds); these rocks are much more similar to sediments of the Nemegt Formation than they are to other Djadokhta sediments. The beds are white, poorly sorted, and represent a series of

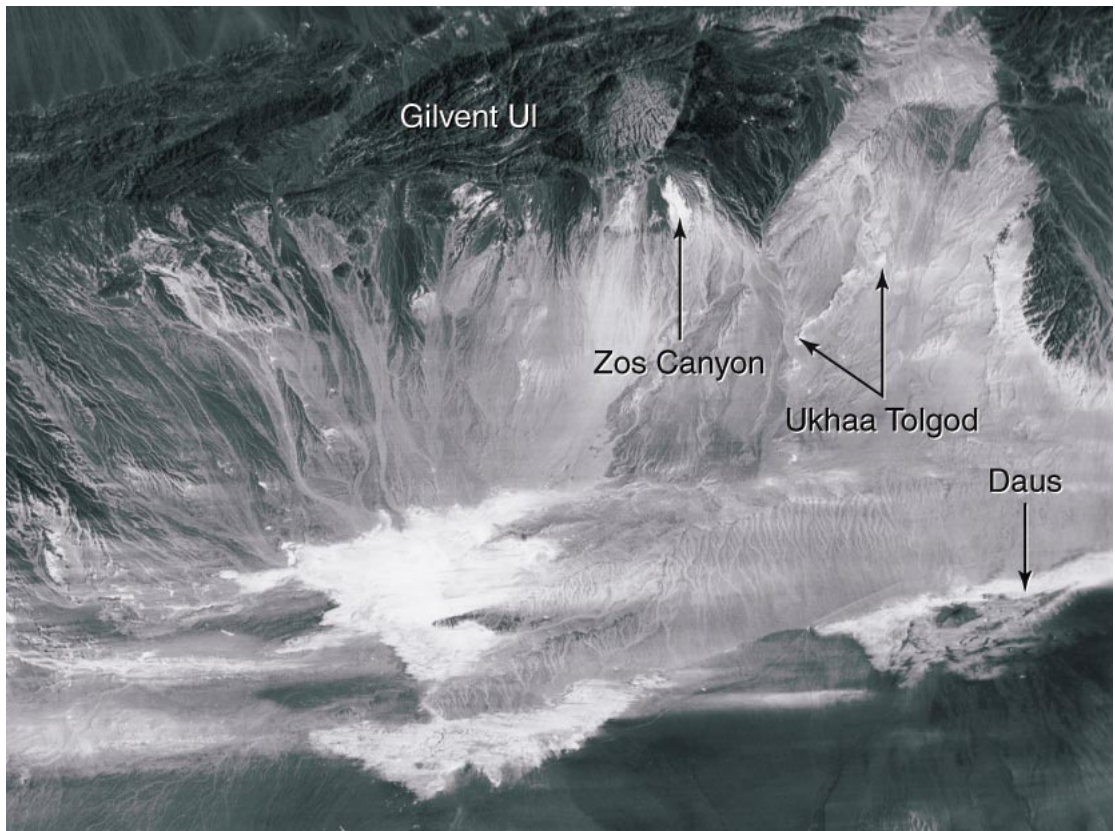


Fig. 1. Satellite photo of the Zos and Ukhaa Tolgod localities.

stream channels preserved as indurated sands and gravels. Fossils in these beds are not common, and when found include large dinosaurs (ornithischans such as hadrosaurs, sauropods, large theropods), turtle pieces, and occasional pieces of petrified wood. Below these white beds a layer of red beds similar to, but more fluvial than, classic Djadokhta beds lies atop the Paleozoic basement. The rocks have produced several poorly preserved dinosaur skeletons (dromaeosaurids and proceratopsians) and lizards. It is in these beds that all the specimens of *Zosuchus davidsoni* were collected.

#### SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMA WALKER, 1970

CROCODYLIFORMES HAY, 1930 (SENSU CLARK, 1986)

*Zosuchus davidsoni*, n.gen. and n.sp.

HOLOTYPE: IGM 100/1305, isolated skull and lower jaws.

REFERRED SPECIMENS: IGM 100/1304, 100/1306, 100/1307, and 100/1308.

ETYMOLOGY: *Zos*, from the type locality; *suchus*, Greek for crocodile; and *davidsoni*, for Amy Davidson who prepared several of these specimens and has been so instrumental in the exquisite preparation of Mongolian specimens allowing the success of our work.

DIAGNOSIS: Small and extremely short-snouted crocodyliform with an extensive anterodorsal lacrimal process wedging between the nasal and maxilla, contacting anteriorly the posterodorsal process of premaxilla. Palatines forming a posteriorly extended secondary palate, almost reaching the posterior edge of the pterygoid flanges where the secondary choana is located. Posttemporal region of the parietal extremely narrow, wedging between the squamosals (paralleled in *Gobiosuchus*). Reduced upper dentition, premaxilla with three teeth and maxilla with five

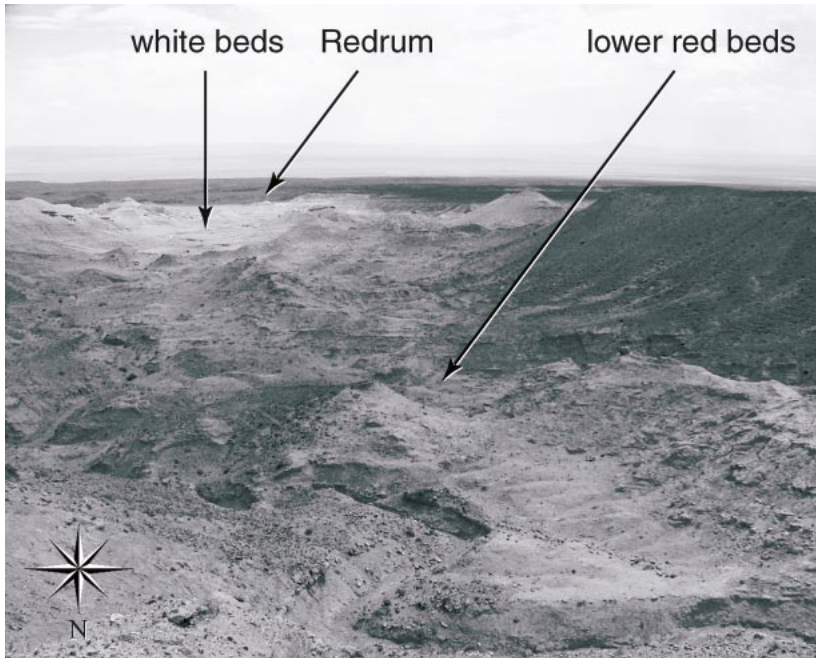


Fig. 2. Exposures of the Zos Canyon and overlying beds. Photo: G.W. Rougier.

teeth (paralleled in some mesoeucrocodylians).

#### DESCRIPTION

The skull of IGM 100/1305 has most of its elements preserved except for the palatine shelves, supraoccipital, and left side of the rostrum (figs. 3–5). However, most of these elements are nicely preserved in IGM 100/1304, 100/1306, 100/1307, and 100/1308. The snout is extremely short, high, and moderately broad (i.e., oreinirostral, sensu Busbey, 1994). The external nares are confluent and face anteriorly. The antorbital fenestrae are markedly reduced and located just anterior to the orbital margin. *Zosuchus davidsoni* has extremely large and laterodorsally facing orbits occupying 33% of the total skull length (IGM 100/1305). The supratemporal fenestrae are extremely reduced and oriented oblique to the longitudinal axis of the skull with their anterior ends pointing anterolaterally. One of the specimens (IGM 100/1304) shows minor differences in the shape and size of the supratemporal fenestra (fig. 6). IGM 100/1304 (fig. 7) is the smallest specimen, and this variation is interpreted

here as a product of ontogenetic change. Similar ontogenetic changes in supratemporal fenestra shape have been noted in extant crocodyliforms (Mook, 1921; Kälin, 1933). Moreover, this variation is congruent with other differences in IGM 100/1304 that are also subject to ontogenetic change (see below). The infratemporal fenestra is not completely preserved in any of the specimens studied here, although it probably was small due to the broadness of the dorsal process of the quadratojugal. The external surface of the skull is ornamentated with a slight pitted pattern as in most members of *Crocodyliformes*. This sculpture is missing in the smaller specimen (IGM 100/1304).

The premaxilla is a short element, yet its ventral edge occupies the anterior third of the anteroposterior extension of the snout. It forms the ventral, lateral, and dorsolateral margin of the external nares. It possesses an extremely well-developed posterodorsal process that wedges between the maxilla and nasal bones on the dorsal surface of the snout (fig. 3). The suture between these two bones does not seem to overlap, although it is not interdigitated. A large vertically oriented



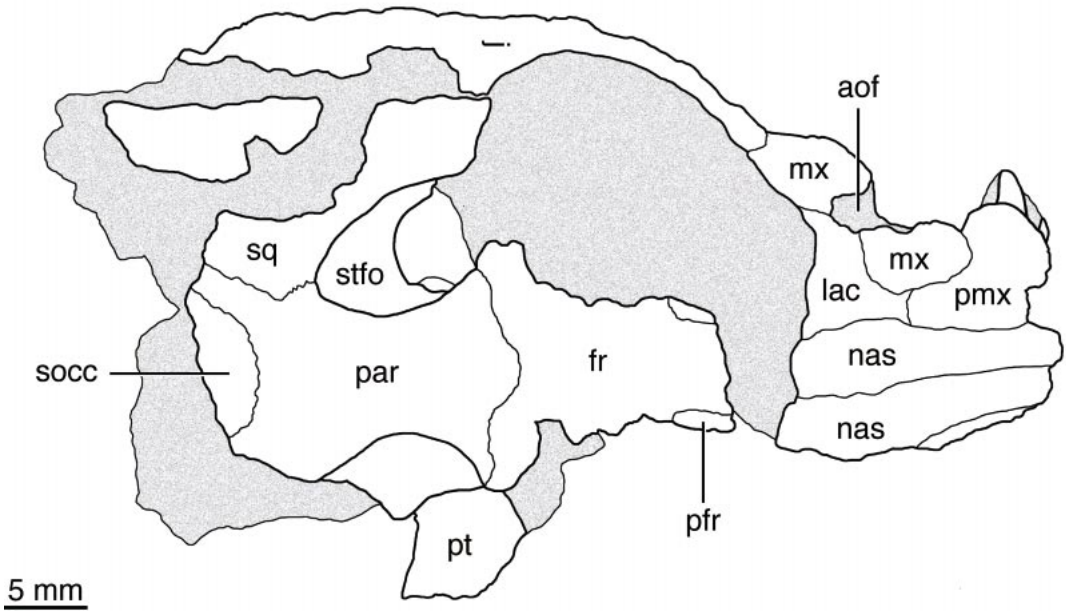
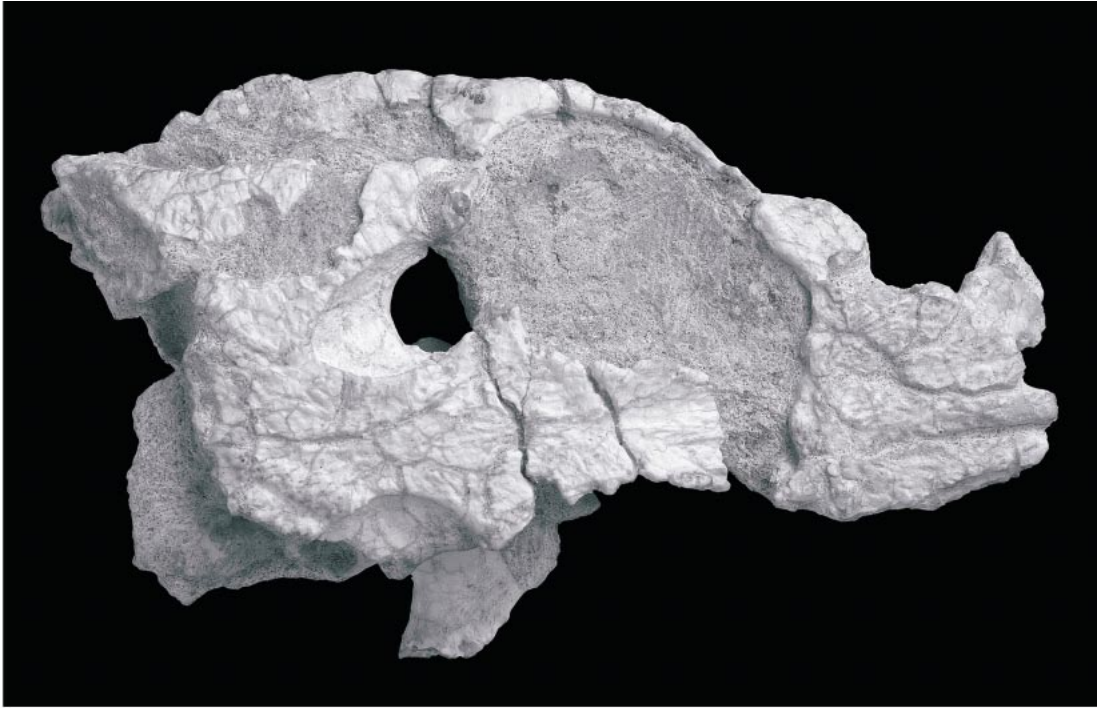


Fig. 3. Skull of the holotype of *Zosuchus davidsoni* IGM 100/1305 in dorsal view.

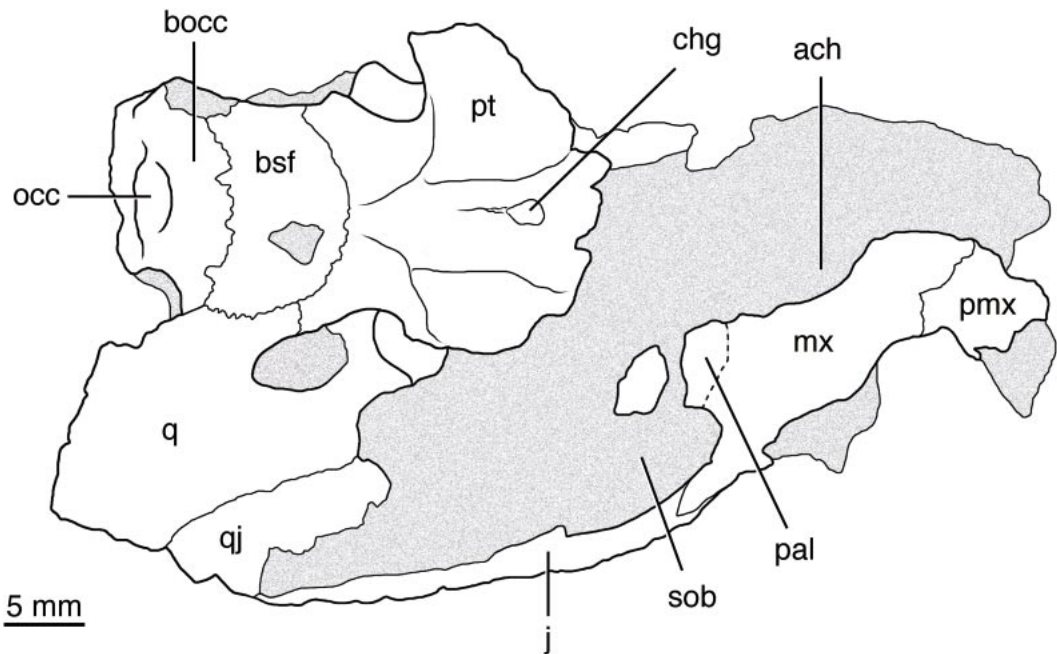
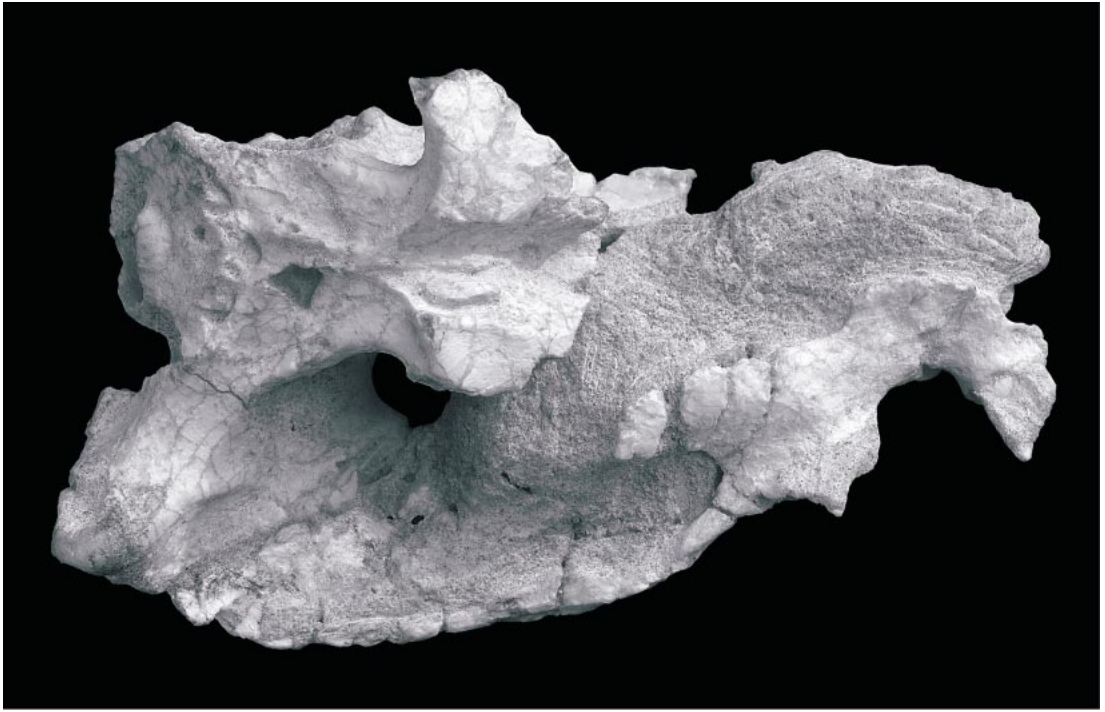


Fig. 4. Skull of the holotype of *Zosuchus davidsoni* IGM 100/1305 in ventral view.



Fig. 5. Skull of the holotype of *Zosuchus davidsoni* IGM 100/1305 in lateral view.

notch which fits the canineform dentary tooth lies at the suture between the premaxilla and the maxilla (fig. 5). A small neurovascular foramina is located on the premaxillary wall that forms the anterior edge of the premaxillary-maxillary notch. The palatal branches of the premaxillae extend medially, presumably contacting each other at the midline, although this contact has not been pre-

served. The suture with the palatal branch of the maxilla extends anteromedially (fig. 4) rather than medially as in most Crocodyli-formes.

The premaxillary dentition is well preserved in the right premaxilla of IGM 100/1305 and consists of only three slender conical teeth. None of these elements has serrations on anterior or posterior edges. The

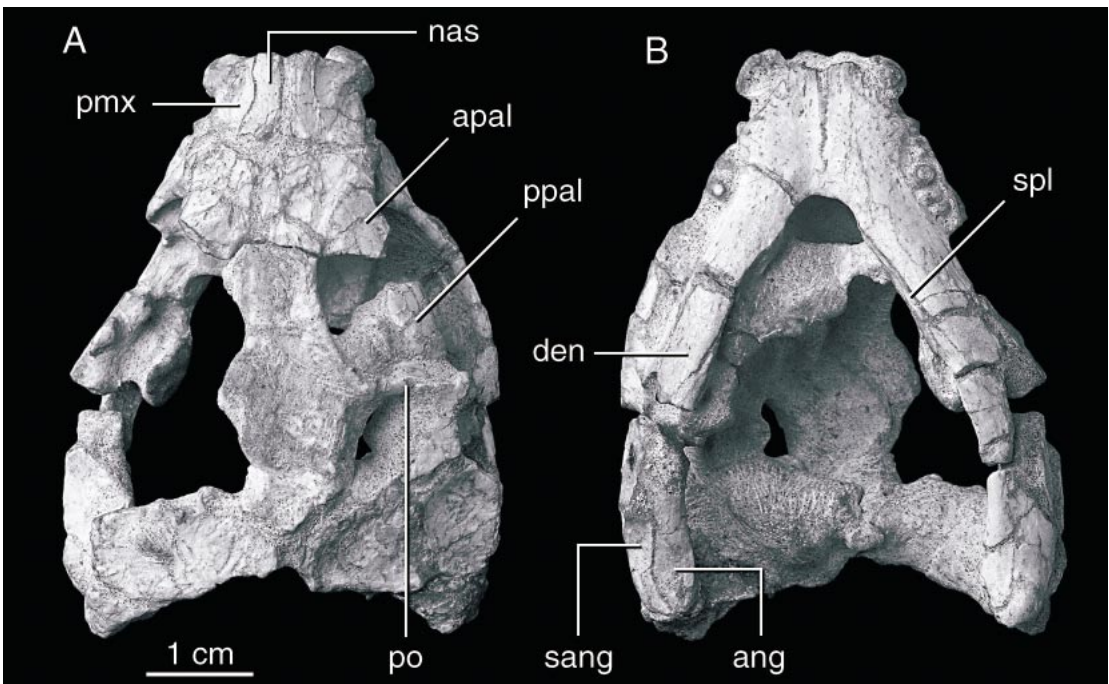


Fig. 6. Skull of specimen IGM 100/1304 in dorsal (A) and ventral (B) views.



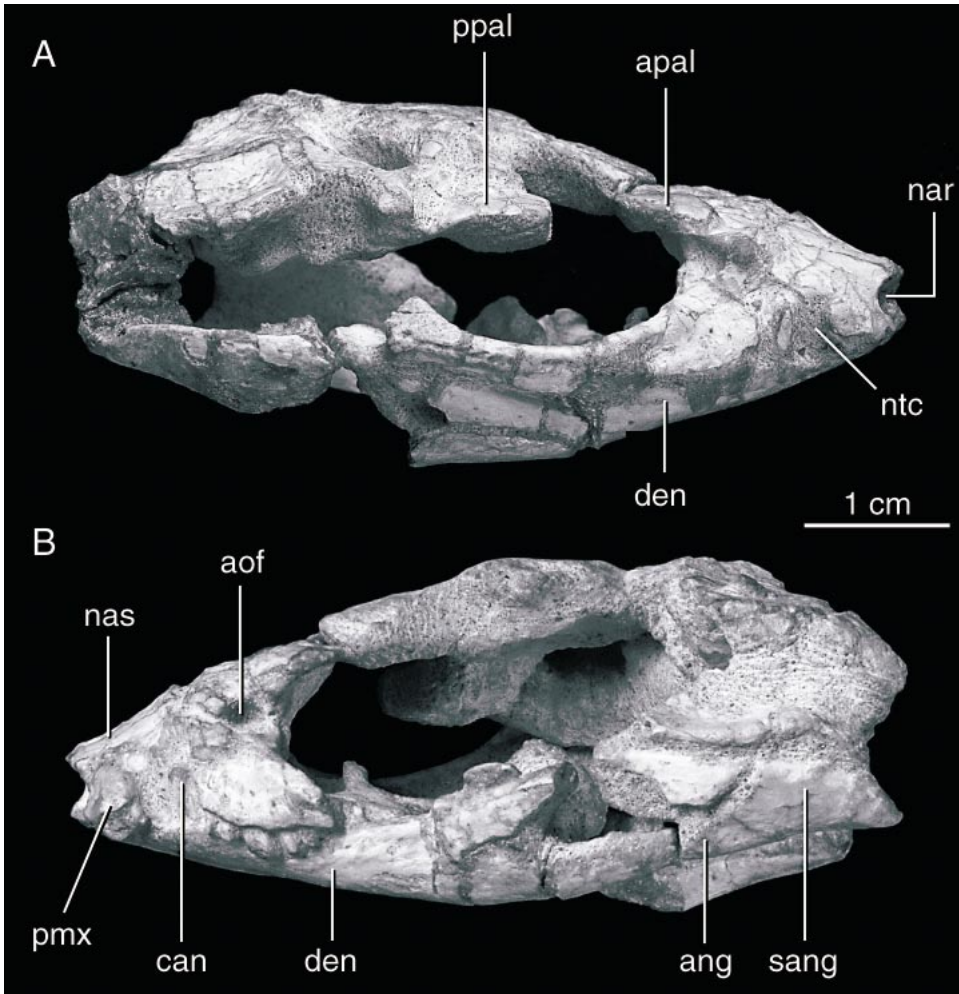


Fig. 7. Skull of specimen IGM 100/1304 in left (A) and right (B) lateral views.

first premaxillary tooth is small and located below the lateral edge of the external nares. The second tooth is more than twice the size of the more anterior teeth, causing the premaxilla to bulge at this point. The third premaxillary tooth is extremely reduced and is located just before the anterior edge of the premaxillary-maxillary notch.

The maxilla has a limited exposure on the lateral surface of the snout due to the extension of the premaxillary-maxillary notch. Dorsal to this notch the maxilla borders the premaxillary posterodorsal process. At the posterior edge of the posterodorsal premaxillary process, the maxilla contacts the anterodorsal process of the lacrimal which wedges

between the nasal and the maxilla reaching the posteromedial edge of the posterodorsal process of the premaxilla (fig. 8). Thus, the maxilla does not contact the nasals, a unique condition among Crocodylomorpha.

The maxilla borders the anterior edge of a reduced antorbital fenestra located just anterior to the anterior orbital edge (fig. 5). The maxilla and lacrimal are not depressed around the antorbital fenestra in contrast to most non-neosuchian crocodyliforms that have a marked antorbital fossa surrounding the antorbital fenestra (e.g., *Protosuchus richardsoni* MCZ 6727, *Gobiosuchus kielanae* ZPAL MgR-II/70, *Notosuchus terrestris* MACN-RN 1037). Posteriorly, the maxilla



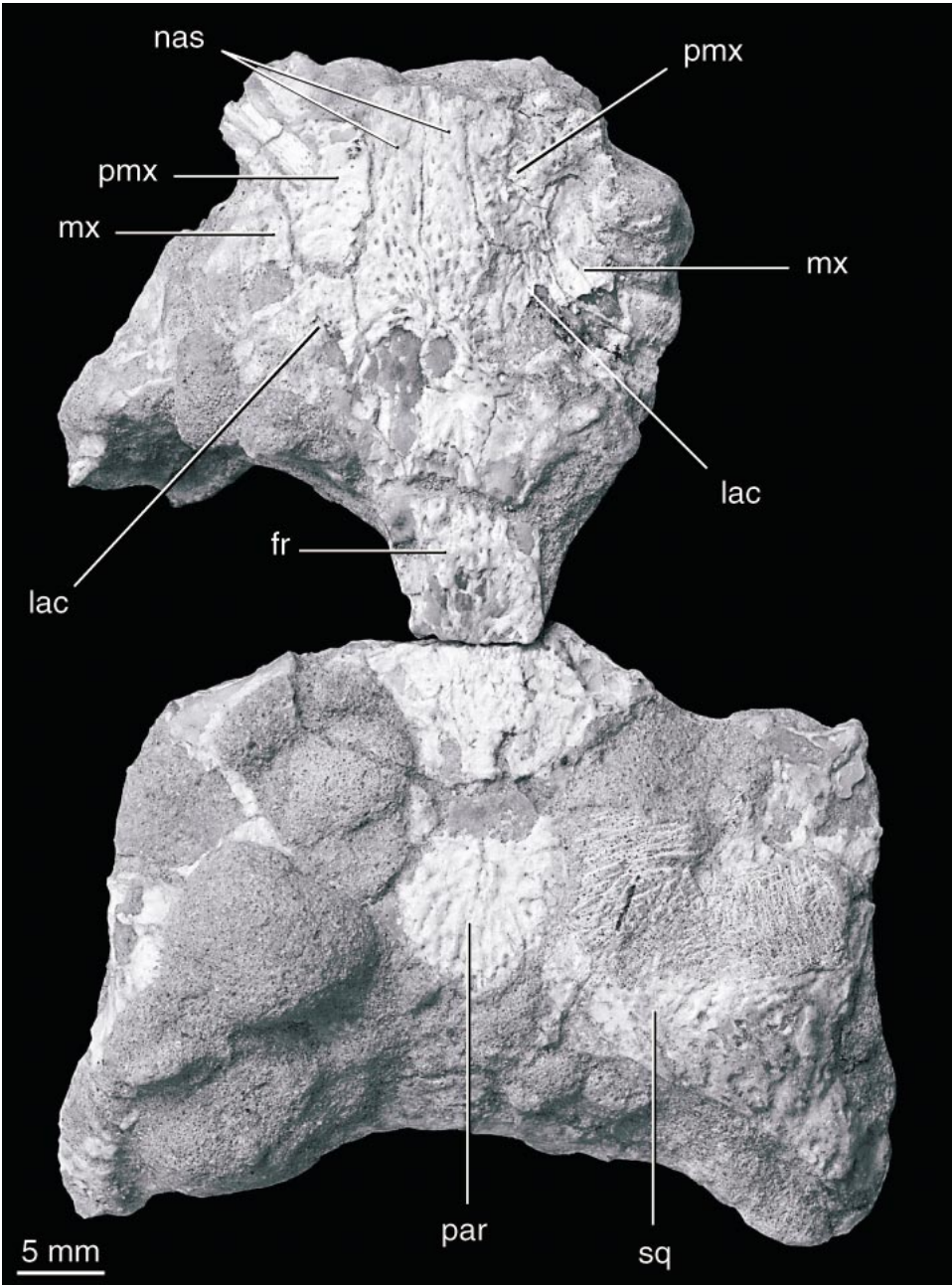


Fig. 8. Skull of specimen IGM 100/1307 in dorsal view.

borders the anteroventral margin of the enlarged orbit and contacts the jugal before the midpoint of the orbit.

The ventral edge of the maxilla is straight and increases its ventral extension posterior to the premaxillary-maxillary notch. Five

maxillary teeth are preserved on the left side of IGM 100/1304, although these elements are poorly preserved (fig. 6). The four posteriormost maxillary teeth are nicely preserved in IGM 100/1305 and have no serrations along their anterior or posterior edges. All of

them are conical and subequal in size, except for the third tooth, which is approximately twice the size of the other maxillary teeth (fig. 5). In contrast to neosuchian crocodyliforms, the tooth size variation of *Zosuchus davidsoni* is not matched by a sinusoidal ventral edge of the maxilla.

The palatal branch of the left maxilla of IGM 100/1305 extends posteromedially to the premaxilla-maxilla palatal contact (fig. 4). Specimen IGM 100/1306 shows the posterior region of both palatal shelves exposed in dorsal view. These contact each other, forming a brief and anteriorly located secondary palate as well as the anterior and lateral edges of the anterior (primary) choanal opening (fig. 11).

This condition clearly resembles the morphology present in basal crocodyliforms (e.g., *Gobiosuchus* ZPAL MgR-II/67, Fruita form LACM 120455a) that lack the posteriorly extended maxillary secondary palate present in mesoeucrocodylians, in which the maxillary palatal branches contact each other medially along their entire length. Lateral to this opening, the palatal branch of the maxilla forms the anterior and medial edges of a large suborbital fenestra.

The nasals form most of the the dorsal margin of the confluent external nares. Their dorsal surfaces have different degrees of ornamentation in the three specimens in which this region was preserved (IGM 100/1304, 100/1305, and 100/1307). The nasals of IGM 100/1304 are smooth, whereas those of the IGM 100/1307 are the most heavily ornamented (showing a pattern of small and well-spaced pits). This difference in ornamentation is interpreted as ontogenetic differences, which is also expressed in differences in the ornamentation of other bones, the degree of interdigitation of sutures, and skull size among the specimens studied here. The anterior region of the lateral edges of the nasals is straight (IGM 100/2 and 100/1307) or slightly concave (IGM 100/1304). In this region the lateral edges of the nasals diverge slightly posteriorly along their contact with the posterodorsal process of the premaxilla. Posterior to this area, the nasal contacts the anterodorsal process of the lacrimal that wedges between the maxilla and the nasals. The lateral edges of the nasals converge

slightly along their contact with the lacrimal and prefrontal (fig. 8). The posterior edge of the nasals contacts with the frontal in an interdigitated transverse suture.

The lacrimal is poorly preserved in most specimens. This element forms the posterior and dorsal margins of the antorbital fenestra and the dorsal half of the anterior orbital margin. Posterior to the antorbital fenestra, the lacrimal is a thin columnar bar, slightly exposed on the lateral surface of the snout (fig. 5). Therefore, the posterior edge of the antorbital fenestra is very close to the anterior orbital margin. Dorsal to the antorbital fenestra, the lacrimal extends anteromedially on the dorsal surface of the snout. As described above, this well-developed process wedges between the nasal and maxilla, reaching the posterodorsal end of the premaxilla anteriorly. A similar, anteriorly extended process is also present in other short-snouted crocodyliforms such as *Simosuchus clarki* (UA 8679) or *Navajosuchus mooki* (= "*Allognathosuchus*" *mooki* (Brochu, 1999); AMNH 6780), although in these forms the anterior process of the lacrimal does not reach the posterodorsal process of the premaxilla. Furthermore, the derived similarities between these taxa and *Zosuchus* are limited to this character and the extremely short-snouted condition.

The prefrontals are elongate, longitudinally oriented bones that form the anteromedial edge of the orbits. The medial edge of the prefrontal contacts the frontal and nasals. Anteriorly, the prefrontal is sutured to the lacrimal on the dorsal surface of the snout. They are overlapped by a large anterior palpebral preserved in IGM 100/1304 (fig. 6). The descending process of the prefrontal is not preserved in any of the specimens, and therefore it cannot be determined if they contact the palate as in mesoeucrocodylians (Clark, 1994).

Two large palpebrals are preserved above the orbit of specimen IGM 100/1304. The anterior palpebral is triangular and extends posterolaterally from the anteromedial margin of the orbit. Its anterior end overlaps the prefrontal and probably the lacrimal at its contact with the skull. In contrast with most crocodyliforms, the posterior palpebral is extremely large, being subequal to the anterior

element. This particular condition is also found in *Sichuanosuchus* (IVPP V 10594).

The frontals are fused along the midline and have a smooth and flat dorsal surface (fig. 3). The frontals are moderately narrow anteriorly and across the interorbital region (subequal to the width of the nasals). They expand at the posterior end of the orbits where they contact the postorbitals laterally and the parietals posteriorly. The suture with the postorbital on the skull roof shows that the frontals formed, at least, the anteromedial margin of the supratemporal fossa. The lateral edges of the frontals delimiting the orbits are elevated with respect to the dorsal surface of this bone, forming small supraorbital ridges. At the midpoint of the orbital margin, the frontals contact elongate posterior processes of the prefrontals. The anterior contact of the frontals with the nasals is oriented transversely, is slightly concave posteriorly, and is interdigitated (fig. 8).

The parietals are fused and wide between the supratemporal fenestrae to form a skull table with the frontal postorbital and squamosal. This surface is flat, lacks a medial ridge, and has varying degrees of ornamentation in the different specimens. In IGM 100/1304, this area is almost completely unornamented, while in IGM 100/1307 this region has a marked ornamentation composed of small pits and slightly marked grooves.

The parietal table's anterior edge contacts the frontal through an interdigitated transversal suture (IGM 100/1305). Posteriorly to this, it forms the medial and posteromedial edges of the supratemporal fossae where it contacts the squamosals, forming the roof of the anterior opening of the tempo-orbital passage. Lateral to these edges, and more ventrally located, the parietal extends as a flat and smooth flange, forming more than half the floor of the supratemporal fossa. This floor is also formed by the quadrate and the squamosal and occupies the posterior half of the supratemporal fossa, leaving a rather small supratemporal fenestra located anteriorly to it (fig. 3). Posterior to the supratemporal fossa, the parietal narrows markedly along an interdigitated suture with the squamosal (similar to the condition present in *Gobiosuchus* ZPAL MgR-II/68). Interestingly, this contact is located along a slightly de-

pressed region of the parietal dorsal surface, medially bounded by an oblique ridge parallel to the parietal-squamosal suture (fig. 3). The diminutive posterior edge of the parietals briefly contacts the anteriormost edge of the supraoccipital surface on the skull roof.

The squamosals form most of the flat skull roof characteristic of Crocodyliformes. These are distinctive elements of *Zosuchus davidsoni* due to the presence of an extremely enlarged surface which extends posteriorly and posterolaterally to the supratemporal fenestra. Like other bones of the skull roof, the squamosal shows variation in the ornamentation among the specimens studied here. In IGM 100/1307, the squamosal is densely ornamented with a pitted pattern on its dorsal surface. Its contact with the postorbital in the anterolateral region of the squamosal cannot be precisely located in any of the specimens studied here due to poor preservation. The lateral region of the squamosal overhangs the otic recess and bears a smooth and slightly developed groove on its lateral edge, presumably for the insertion of a muscular ear flap. Medially, the squamosal borders the supratemporal fossa and contributes to the extensive smooth floor of this fossa. The squamosal extends posteromedially to border the supratemporal fossa, where it contacts the parietal at the anterior opening of the tempo-orbital passage. The contact with the parietal is located more medially than in most crocodyliforms, since it originates on the posteromedial corner of the supratemporal fenestra and extends posteromedially toward the dorsal surface of the supraoccipital (fig. 3).

Posterior to the occipital edge of the skull roof, a flange of the squamosal extends posteroventrally to border the lateral edge of the occipital surface of the supraoccipital. The lateral region of this surface of the squamosal contacts the dorsal edge of the paroccipital process. As in most basal crocodyliforms (e.g., *Protosuchus* UCMP 131827, *Shantungosuchus* (Wu et al., 1994a), *Gobiosuchus* ZPAL MgR-II/67), the occipital flange of the squamosal extends laterally beyond the lateral edge of the paroccipital process. This contrasts with the condition of most mesoeucrocodylians, in which the paroccipital pro-

cess reaches the lateral edge of the occipital flange of the squamosal.

The occipital flange of the squamosal is bordered dorsolaterally by a moderately long, acute, and descending posterodorsal process of the squamosal that is ornamented in IGM 100/1307 but smooth in all the other specimens (probably because of preservational and/or ontogenetic reasons). The distal extremity of the posterolateral process contacts the occipital surface of the quadrate as well as the distal end of the paroccipital process. Interestingly, a descending and acute posterodorsal process of the squamosal is absent in the most basal crocodyliforms (*Protosuchus* AMNH 3024, *Orthosuchus* SAM-K 409, *Hemiprotosuchus* PVL 3829), but is present in *Gobiosuchus* ZPAL MgR-II/67, *Shantungosuchus* (Wu et al., 1994a), *Sichuanosuchus* IVPP V 10594, and most basal mesoeucrocodylians.

The postorbital is best preserved on the right side of IGM 100/1304. On its dorsal surface, the postorbital contacts the frontal medially on the skull roof and extends laterally as a thin cylindrical bar between the supratemporal fenestra and the orbit (fig. 6). The anterolateral corner of the postorbital bears a small anterolaterally pointed process. This process is continuous with the dorsal surface of this bone instead of being located ventrally, as in most non-neosuchian crocodyliforms (e.g., *Notosuchus* MACN-RN 1037, *Araripesuchus* AMNH 24450, *Baurusuchus* DGM 299-R) and dyrosaurids (Buffetaut, 1976). The lateral edge of the postorbital continues posteriorly to the pointed process, thus lacking the anteroventrally exposed postorbital edge that characterizes basal mesoeucrocodylians (Clark, 1994). A poorly preserved descending process of the postorbital is present only in IGM 100/1305. This process forms the dorsal half of a somewhat flattened and smooth postorbital bar. Dorsally, the postorbital bar expands abruptly to form the dorsal surface of the postorbital.

The jugal delimits the ventral margin of the enlarged orbits and, as in basal crocodyliforms, is not dorsoventrally expanded with respect to the postorbital region. The jugal's anterior end does not reach the anterior edge of the orbit (figs. 5, 6). The lateral surface of the suborbital process is poorly or-

namented in IGM 100/1305. Along this region, a slightly marked and extremely narrow groove is oriented longitudinally. Dorsal to this groove, the jugal has a rounded dorsal surface, while ventral to it, the jugal's surface is slightly concave and faces lateroventrally. The base of the postorbital process is preserved on the right jugal of IGM 100/1304 and 100/1305. As in basal crocodyliforms, this region is wide, somewhat flattened, dorsally oriented, and continuous with the lateral surface of the jugal. The jugal bar below the infratemporal fenestra is also moderately narrow and forms part of the ventral edge of the infratemporal fenestra. The infratemporal region of the jugal is dorsoventrally flattened as in *Sichuanosuchus* IVPP V 10594, although this might be accentuated as a preservational artifact. Both the posterior end and the jugal's contact with the quadratojugal are not preserved.

The quadratojugal is best preserved in IGM 100/1305 and 100/1306. The quadratojugal extends posterior to the infratemporal fenestra and has a wide and smooth surface that nearly reaches the posterior edge of the quadrate, as in basal crocodyliforms. The posterior region of the quadratojugal has a sinusoidal ventral margin that ends in a wide and round posterior edge (fig. 9), similar to the "fan-shaped" process described for *Shantungosuchus* IVPP V 10594 and *Sichuanosuchus* (Wu et al., 1994b). A unique characteristic of this posterior quadratojugal fan-shaped process is that it forms a small laterally projected shelf, which slightly overhangs the lateral surface of the quadrate (fig. 10). In other crocodyliforms, instead, this process is absent and therefore the lateral surface of the quadratojugal and quadrate is continuous.

The dorsal process of the quadratojugal extends anterodorsally as a broad sheet, as in basal crocodyliforms. This process is bordered posteriorly by the quadrate and has a moderately developed ridge running parallel to the dorsal half of the quadrate-quadratojugal suture (resembling the condition present in *Gobiosuchus kielanae* [Osmólska et al., 1997; ZPAL MgR-II/68]). The anterior edge of the quadratojugal dorsal process presumably forms the posterior edge of the infratemporal fenestra, although it is not clear



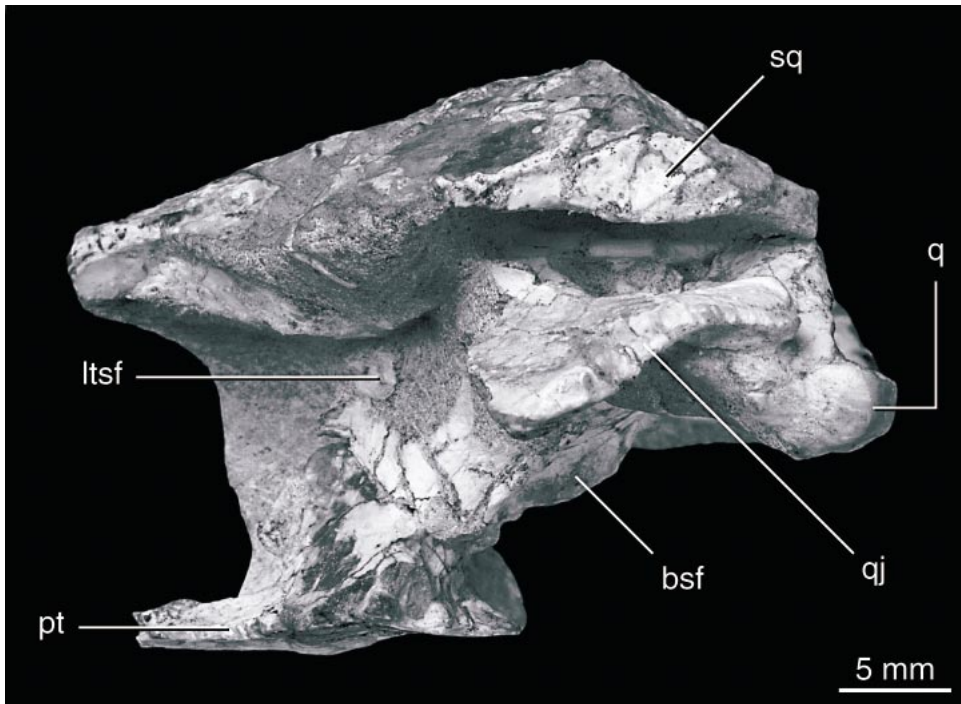


Fig. 9. Posterior region of skull of specimen IGM 100/1306 in lateral view.

if this edge was preserved in any of the specimens studied here. Dorsally, this process articulates extensively with the postorbital descending process.

The lateral process of the ectopterygoid is only preserved in IGM 100/1304. This element is a delicate cylindrical bar which expands slightly at its contact with the infraorbital jugal bar. The medial branch of the ectopterygoid has not been preserved in any of the specimens studied here.

The anterior processes of the palatines have not been preserved in IGM 100/1305, although they are present but poorly preserved in IGM 100/1304 and 100/1306. IGM 100/1306 is particularly interesting since it has preserved both the anterior and posterior edges of the palatines, although the midregion of them has not been preserved.

The anterior edge of the palatine shelves extends medially to contact each other medially and form the posterior border of the anterior (primary) choana (figs. 11, 12), which is bordered anteriorly by the palatal branches of the maxillae. A similar anterior palatal morphology was reported on some

basal crocodyliforms from the Jurassic of North America (Fruita form; Clark, 1985) and Mongolia (*Nominosuchus* and *Adzhosuchus*; Efimov, 1996; Efimov et al., 2000). Unfortunately, the maxillopalatine suture is not well defined in this area but was probably located on the posterolateral edges of the anterior (primary) choana.

The posterior region of the palatines is preserved in IGM 100/1306, showing an overlapping articulation with the pterygoids over a depressed area on the lateral edges of the choanal groove (clearly seen in IGM 100/1305; fig 4). The palatines of *Zosuchus davidsoni* extend posteriorly to contact each other medially (fig. 12), forming a posteriorly located palatine secondary palate that closes the choanal groove (ventrally opened in basal crocodyliforms). The palatines of *Zosuchus davidsoni* are unique since they extend posteriorly much more than in any other basal crocodyliform, almost reaching the posterior margin of the pterygoid flanges (figs. 12, 13). At their posterior end, the palatines form the anterior edge of a posterior (secondary) choanal opening. This resembles the choanal

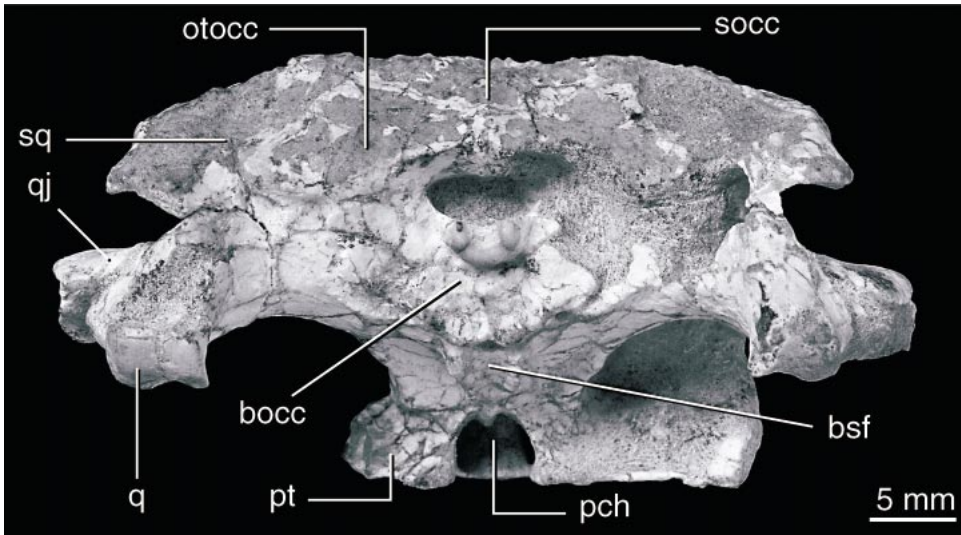


Fig. 10. Skull of specimen IGM 100/1306 in occipital view.

opening of basal mesoeucrocodylians which is enclosed between the palatines and the pterygoids. Interestingly, the palate of *Zosuchus davidsoni* is projected dramatically posteriorly, leaving the small posterior (secondary) choanal opening close to the posterior edge of the pterygoid flanges. A similar condition is present in derived neosuchians,

although it differs structurally from these taxa since the posterior (secondary) choana of *Zosuchus* is anteriorly closed by the palatines rather than being enclosed within the pterygoids as in eusuchians (fig. 12). Additionally, the posterior (secondary) choana of *Zosuchus davidsoni* opens posteriorly near the pterygoid-basisphenoid contact, while the

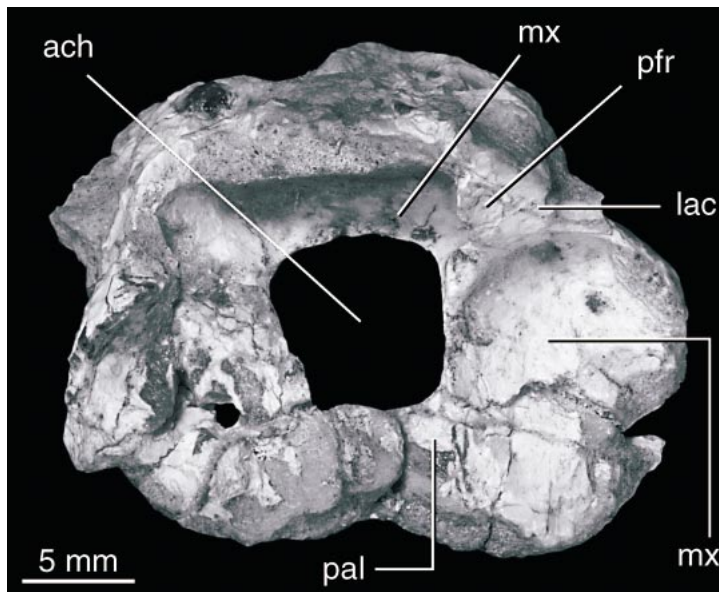


Fig. 11. Palatal region specimen of IGM 100/1306 in posterodorsal view.

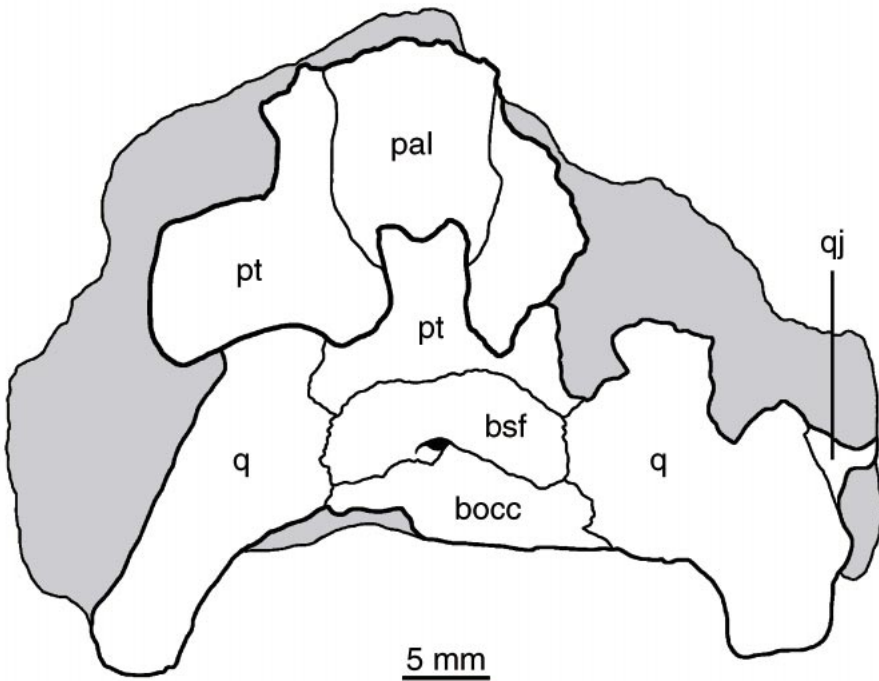
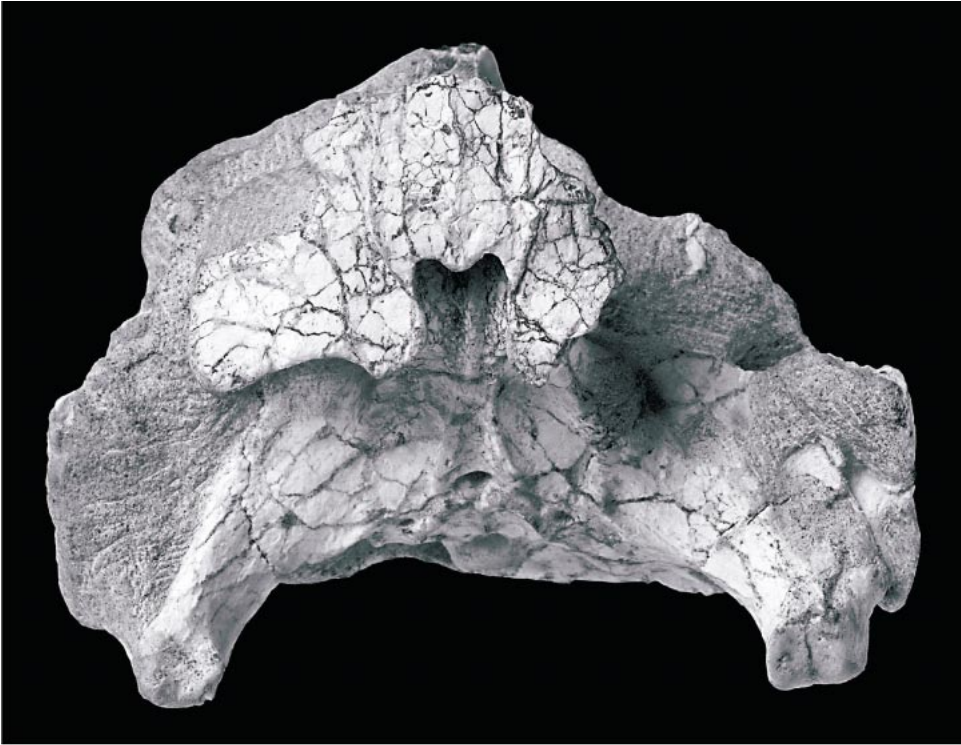


Fig. 12. Posterior region of skull of specimen IGM 100/1306 in ventral view.

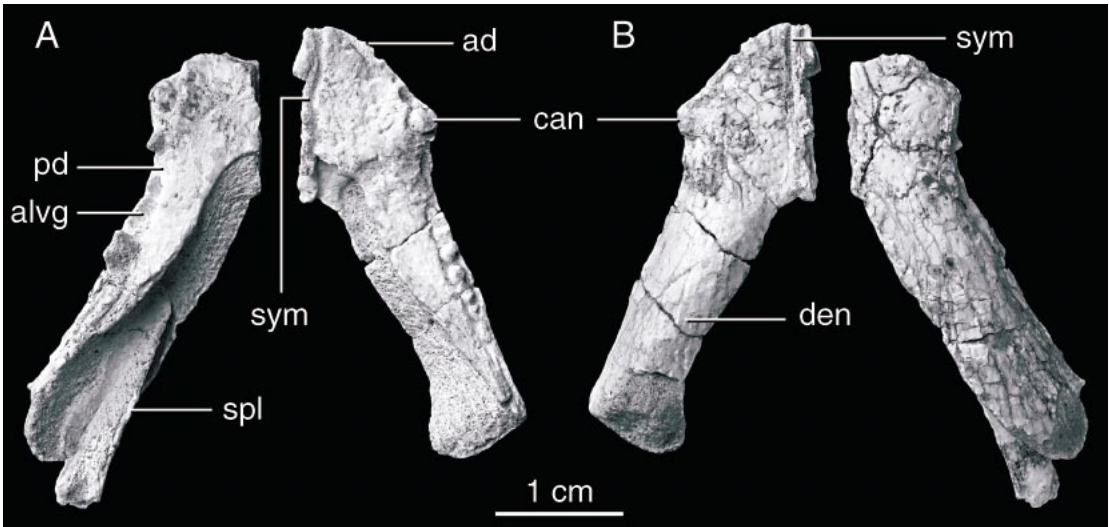


Fig. 13. Lower jaws of the holotype of *Zosuchus davidsoni* IGM 100/1305 in dorsal (A) and ventral (B) views.

secondary choana of eusuchians is posteriorly closed by a posterior wall of the pterygoids (fig. 12).

The pterygoids are almost completely preserved in IGM 100/1305 and 100/1306. As in most basal crocodyliforms, the pterygoid wings are reduced, directed laterally on a transverse plane, dorsoventrally thick, and filled with pneumatic spaces (fig. 10). The ventral surface of the pterygoids is flat and smooth, except for the medial region, which is markedly depressed, forming a narrow and longitudinally oriented trough-shaped groove that narrows posteriorly to the pterygoid flanges toward the basisphenoid-ptyerygoid contact (fig. 4). The pterygoids contact each other along this depression and are apparently fused posteriorly. The posterior half of the pterygoideal groove bears a longitudinal ridge that forms an incipient septum in the posterior (secondary) choanal opening (fig. 12). This ridge extends posteriorly to the pterygoid wings, reaching the anterior edge of the basisphenoid. The base of the quadrate processes of the pterygoids is lateromedially wide and faces posteroventrally (fig. 4), as in most basal crocodyliforms. These processes are sutured strongly to the basisphenoid and quadrates.

The basisphenoid is semicircular and widely exposed on the ventral surface of the

braincase (figs. 4, 12), as in basal crocodyliforms. The anterior margin of the basisphenoid is transversally oriented, lacking the acute anterior process that wedges between the pterygoids in most basal crocodyliforms (*Protosuchus* UCMP 131827, *Gobiosuchus* ZPAL MgR-II/67, *Shantungosuchus* [Wu et al., 1994b]). The basisphenoid has two well-developed longitudinal ridges located medially on its ventral surface (figs. 4, 12). Anteriorly, at the pterygoid-basisphenoid contact, these ridges approach one another (separated by 1.3 mm) and are continuous with the lateral edges of the choanal groove of the pterygoids. The basisphenoidal ridges diverge posteriorly and disappear at the basisphenoid-basioccipital contact, between the foramen intertympanicum and the lateral eustachian foramina (fig. 10). At this point, these ridges are separated by 3.3 mm. Several basal crocodyliforms have paired ridges on the ventral surface of the basisphenoid (e.g., *Protosuchus richardsoni* UCMP 130860); however, in these forms, the ridges are usually located laterally on the ventral surface of the basisphenoid, at the lateral edges of this element. Paired basisphenoidal ridges located medially on the ventral surface of the basisphenoid similar to those of *Zosuchus* are present in *Sichuanosuchus* (IVPP V 10594) and *Shantungosuchus* (Wu et al.,



1994b). The lateral eustachian foramina and the foramen intertympanicum are located on the basisphenoid posterior edge, at its contact with the basioccipital.

The basioccipital is best preserved in IGM 100/1306. This bone is exposed posterovertrally on the occipital surface of the skull (figs. 10, 12). Anteriorly, it contacts the basisphenoid in a wide U-shaped suture that delimits the posterior edge of the foramen intertympanicum and the lateral eustachian foramina. The basioccipital surface is elevated at this point, forming a marked ridge along the basisphenoidal suture. The lateral ends of this ridge are slightly more elevated, forming small and delicate basioccipital tubera. Posterior to the foramen intertympanicum, the basioccipital bears a medially located longitudinal ridge which extends onto the ventral half of this bone (fig. 10). The remainder of the basioccipital surface is flat or slightly concave. The basioccipital forms only the ventral half of the occipital condyle (fig. 10), in contrast to the condition seen in most crocodyliforms where the basioccipital forms nearly all of the occipital condyle. The basioccipital-otoccipital contact is not well defined except for sutures at the occipital condyle.

The otoccipitals are also best preserved in IGM 100/1306. These are exposed widely on the occipital surface of the skull and, in contrast to the typical crocodyliform condition, they form the dorsal half of the lateral region of the occipital condyle (fig. 10). Dorsal to the condyle, the otoccipitals form the lateral and dorsal margins of the foramen magnum, contacting each other medially (excluding the supraoccipital from the dorsal margin of the foramen magnum). Lateral to this region the otoccipitals are exposed along two different planes, separated by a transverse ridge that runs from the dorsal margin of the foramen magnum to the ventrolateral edge of the paroccipital process (fig. 10). Ventral to this ridge the otoccipitals are slightly exposed posterovertrally and lack the enlarged ventrolateral process that characterizes most basal crocodyliforms (e.g., *Protosuchus* UCMP 131827; Clark, 1986). Along the lateral edge of this region the otoccipitals extensively contact the quadrates in an interdigitated suture that extends dorsolaterally.

Unfortunately, none of the specimens of *Zosuchus davidsoni* has preserved details on the cranial nerve and vascular foramina which open on the occiput. The dorsal planes of the otoccipitals contact each other medially through a vertical suture. Dorsal to the transverse ridge, the otoccipitals are exposed posterodorsally. Their dorsomedial edges contact the supraoccipital along an interdigitated suture directed dorsolaterally. At this point the otoccipitals extend laterally to form a rather narrow and short paroccipital process (fig. 10). Dorsally, the paroccipital process is bounded by a ventrolaterally directed suture along a large occipital flange of the squamosal. The paroccipital process is dorsoventrally narrow and curves slightly posteriorly at its lateral end. In this region, the paroccipital process overhangs the ventral region of the otoccipital (fig. 10), forming a notch similar to the cranioquadrate passage of *Crocodylia*. The identification of this structure as the cranioquadrate passage cannot be determined since it is dependent on the identification of the other nerve and vascular openings of the occipital region (see Clark, 1986).

The supraoccipital is well preserved in IGM 100/1305, 100/1306, and 100/1308. It is exposed both on the occipital and dorsal surfaces of the skull. The occipital region is best preserved in IGM 100/1308 where it is triangular-shaped and exposed posterodorsally. Its surface is smooth and flat and bears a medial sagittal ridge, as in several other crocodyliforms. The dorsal surface of the supraoccipital is best preserved in IGM 100/1305. The supraoccipital region is smaller than the occipital surface, semicircular-shaped, and slightly ornamented (fig. 4). The posttemporal fenestra cannot be observed in any specimen due to poor preservation.

The quadrate of *Zosuchus davidsoni* is best preserved in IGM 100/1305 and 100/1306. Its anterodorsal region is clearly exposed on the left quadrate of IGM 100/1305. The otic recess is very deep and roofed by a large lateral flange of the squamosal (figs. 5, 9). On its posterodorsal surface, the quadrate's anterior edge contacts the quadratojugal along an overlapping suture that is slightly concave posteriorly. Posterior to this suture the quadrate surface is perforated by several foramina (fig. 5), as is commonly

found in basal crocodyliforms (e.g., *Protosuchus* AMNH 3024, *Orthosuchus* SAM-K 409, *Gobiosuchus* ZPAL MgR-II/67, *Shantungosuchus* [Wu et al., 1994b]). Hecht and Tarsitano (1983) and Nash (1975) described these fenestrae in *Protosuchus richardsoni* and *Orthosuchus stormbergi* and they were later found to be present in other basal crocodyliforms (Busbey and Gow, 1984; Clark, 1985, 1986). In *Zosuchus davidsoni* (IGM 100/1305) only three fenestra can be identified, closely resembling the condition described for *Shantungosuchus* (Wu et al., 1994b). The most distal fenestra is very elongate, extending anterodorsally on the posterodorsal surface of the quadrate (fig. 5). Within this fenestra lie several delicate bony struts. This fenestra could be homologized with fenestra A of *Protosuchus*, due to its location, shape, and the presence of numerous internal bony struts, although in most forms this fenestra is not as elongated as in *Zosuchus davidsoni*. Notably, *Shantungosuchus* presents a fenestra A that is remarkably similar to that of *Zosuchus davidsoni*. Anterodorsal to this large fenestra are two well-defined and rounded fenestrae. The first contains an oblique bony strut while the second one does not seem to be subdivided (fig. 5). Again, the number and shape of these fenestrae are remarkably similar to those of *Shantungosuchus*, in contrast to the condition of other basal crocodyliforms that have four distinct fenestrae in addition to fenestra A. Posterior to this area the quadrate is poorly preserved, and therefore it is not possible to determine the morphology of the otic notch and confirm the presence of a posteriorly closed otic meatus. The sutures with the squamosal and postorbital are not preserved on any of the specimens.

The distal region of the quadrate is best preserved in IGM 100/1306. The distal body of the quadrate extends ventral to its contact with the posterolateral process of the squamosal on the occipital surface of the skull (figs. 9, 10). Most basal crocodyliforms do not have a differentiated distal body of the quadrate, which contrasts with the incipient development of this process in *Zosuchus davidsoni*. A similar morphology is also present in *Sichuanosuchus* IVPP V 10594, although the development of the quadrate body

in these taxa is much less extensive than in most mesoeucrocodylians. The distal body of the quadrate is posteroventrally directed and is about as wide as long (fig. 9).

The posterior surface of the quadrate body has a vertical ridge that divides this surface (fig. 10). The articular condyles face posteroventrally and are horizontally aligned. The medial condyle is narrower and sharper than the rounded lateral condyle.

The anteroventral surface of the quadrate of *Zosuchus davidsoni* (IGM 100/1305) is convex rather than flat as in most crocodyliforms. A single, oblique crest runs from the lateral condyle to the midpoint of the anteroventral surface of the quadrate. Anteroventrally, the quadrate is tightly joined to the quadrate process of the pterygoids via an interdigitated suture. Dorsal to this suture the quadrate contacts the laterosphenoid to form the posterior edge of the trigeminal foramen (at this point the quadrate probably contacted the prootic on its medial surface, although this contact is not exposed). The quadrate extends dorsally to wedge between the parietal and squamosal on the floor of the supratemporal fossa, reaching the posterior edge of the supratemporal fossa.

The laterosphenoid is partially preserved in IGM 100/1305, 100/1306, and 100/1308. Posteriorly, it contacts the quadrate enclosing the trigeminal foramen (it probably also contacted the prootic at this region, although this element is not exposed). At the ventral edge of the trigeminal foramen, the laterosphenoid briefly contacts the ascending process of the pterygoid at an interdigitated suture located on the lateral surface of the braincase wall. Anterior to this region the laterosphenoid's lateral surface curves medially and bears a slightly developed ventral notch (which extends ventrally onto the pterygoids, lateral to the area occupied by the basisphenoid cultriform process in Crocodylia). Although the anteriormost surface of the laterosphenoid is not exposed, it seems that the external surface of the laterosphenoid of *Zosuchus davidsoni* is convex, lacking the large ridge that separates the lateral and anterior laterosphenoid surfaces as in Crocodylia. No details on the notches and foramina for the passage of nerves II, III, and IV are preserved in any of these specimens. Dorsally, the anteromedial

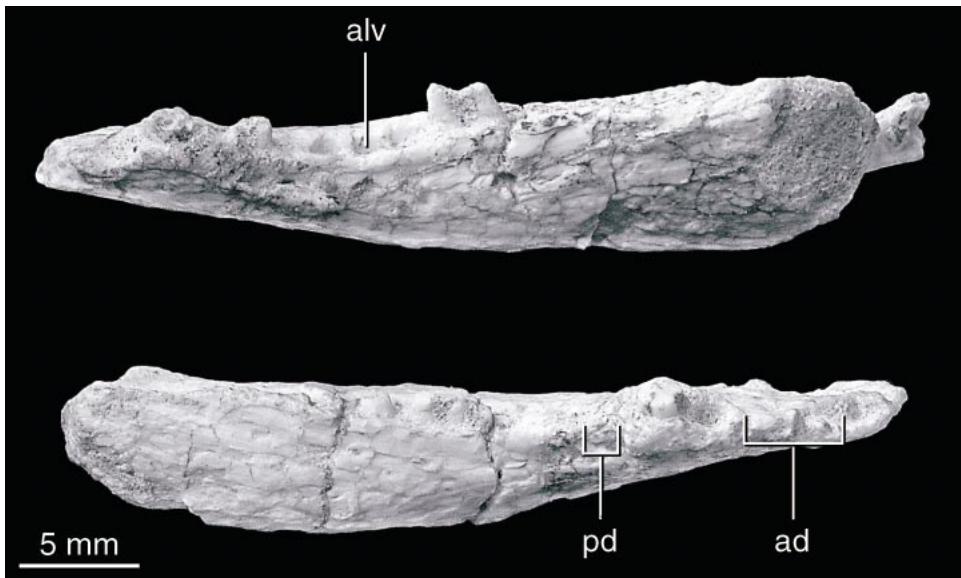


Fig. 14. Lower jaws of the holotype of *Zosuchus davidsoni* IGM 100/1305 in lateral view.

flange of the laterosphenoid is tightly sutured to the frontals and presumably the parietals (IGM 100/1305). The capitulate process of the laterosphenoid and its contact with the post-orbital is not preserved in any of the specimens.

The dentaries are very low and broad at the symphyseal region (figs. 13, 14). The mandibular symphysis is elongate, extending posteriorly to the level of the enlarged maxillary teeth and anterior edge of the orbit. The dorsal surface of the mandibular symphysis is wide, flat, and horizontally exposed (fig. 13). Several neurovascular foramina are located on this surface, close to the lateral edges of the dentaries. These edges bulge at the midpoint of the symphysis where the lower caniniform tooth is located (fig. 13). At this region the ventral surface is flat and slightly ornamented with well-spaced small pits (IGM 100/1304 and 100/1307). Posterior to the mandibular symphysis, the dentaries increase in dorsoventral height and have a convex lateral surface. In this region the dentaries are smooth (IGM 100/1304) or slightly ornamented (IGM 100/1305). The dorsal edge of the dentary is slightly elevated at the lower caniniform tooth (fig. 14). Posterior to this area, the dorsal edge is slightly concave, lacking the sinusoidal margin that character-

izes neosuchian crocodyliforms. The dentaries have well-developed posterodorsal and posteroventral processes that extend above and below the mandibular fenestra (fig. 6).

The lower dentition is best preserved in IGM 100/1305. All preserved teeth are thin, conical, and apparently unserrated. The anterior tip of the dentaries lack preserved teeth, although in IGM 100/1305 there are two poorly preserved cavities that are probably the anteriormost alveoli. Posterior to this region, the dentary has a small diastema of 2.0 mm. This edentulous region extends to the next dentary tooth that precedes the lower caniniform tooth (fig. 13). This tooth is small judging from the alveolar dimensions in IGM 100/1305 and from the base of a small crown poorly preserved in IGM 100/1307. The next dentary tooth is the lower caniniform, which is well preserved in IGM 100/1304 (fig. 6). This enlarged tooth is approximately twice the size of the other dentary teeth. The first postcaniniform dentary tooth is small and conical as preserved in the left dentary of IGM 100/1305. Posterior to this tooth, the dentaries have a short posterior diastema (1.6 mm) that is present in both dentaries of IGM 100/1305 (fig. 13). This region accommodated the enlarged maxillary tooth. Posterior to the second diastema, the

dentary bears several alveoli showing a single wave of size variation. The dimensions of these teeth increase along the first three alveoli and decrease posteriorly (fig. 13). The first three alveoli are partially divided by septa located ventral to the lateral and medial edges of the toothrow. Therefore, these alveoli are superficially continuous, resembling the tooth groove present in some basal mesoeucrocodylians (e.g., *Notosuchus* MACN-RN 1040). The posterior half of the toothrow lacks internal septa between the tooth sockets (fig. 13). The precise number of postcaniniform dentary teeth is difficult to determine because none of the specimens preserves the entire toothrow; however, this number probably was either seven or eight.

The splenials do not form part of the mandibular symphysis (at least as can be determined from the ventral surface). Posterior to this area, they overlap the ventral surface of the dentaries medially and are only slightly exposed in ventral view. The medial surface of the splenials is thin and very convex (IGM 100/1304 and 100/1305).

The angular forms most of the ventral border of the mandibular fenestra (fig. 6). This element extends anteriorly beyond the mandibular fenestra and ventrally borders the posteroventral process of the dentary. The angular forms the ventral edge of the posterior half of the mandibular ramus, which deflects dorsally only slightly posterior to the mandibular fenestra. In this region, the lateral extension of the angular is extremely reduced and, thus, the surangular forms most of the lateral surface of the mandible (fig. 6). This condition is also present in *Sichuanosuchus* and *Shantungosuchus* (Wu et al., 1994b, 1997).

The surangular anteriorly contacts the posteroventral process of the dentary above the mandibular fenestra. It posteriorly forms the dorsal edge of the this fenestra, where it is slightly arched (fig. 6). As noted, posterior to the mandibular fenestra, the surangular extends ventrolaterally much more than in any other crocodyliform (except *Shantungosuchus* and *Sichuanosuchus*), reaching the ventral surface of the posteriormost region of the mandibular ramus, where it contacts the angular (fig. 6).

## PHYLOGENETIC RELATIONSHIPS

A dataset of 183 characters with the addition of seven new characters was gathered from previous studies (Clark, 1994; Wu and Sues, 1996; Gomani, 1997; Wu et al., 1997; Buckley et al., 2000; Ortega et al., 2000; Pol, in press). These characters were scored across 44 taxa. The taxon-sampling regime focused on non-neosuchian crocodyliforms, although 15 representatives of the neosuchian clade were included. This dataset was analyzed under equal-weighted parsimony using Nona (Goloboff, 1993). A heuristic tree search was performed consisting of 1000 replicates of RAS + TBR with a final round of TBR (mult\*1000; max\*), holding 20 trees per replication (hold/20;). Zero-length branches were collapsed using the strictest criterion (i.e., when any possible states are shared between the ancestor and descendant node; amb-). Six most parsimonious trees of 615 steps (CI = 0.36, CI<sub>inf</sub> = 0.35, RI = 0.67) were found in 863 of 1000 replications. Further searches employing 10,000 iterations of the Parsimony Ratchet (Nixon, 1999) implemented in Nona resulted in the same set of topologies (hitting the best length in 9351 times).

In all most parsimonious hypotheses, *Zosuchus* is depicted as the sister taxon of a clade composed by *Sichuanosuchus* and *Shantungosuchus*, both from the Early Cretaceous of China (fig. 15). This Cretaceous Asian clade is located basally within the crocodyliform clade and is diagnosed by four unambiguous synapomorphies (quadratojugal posterior end not reaching the quadrate condyles [char. 141]; angular shifted to the ventral surface mandibular rami posterior to the mandibular fenestra [char. 171]; paired basisphenoid ridges located medially on the ventral surface of basisphenoid [char. 179]; “fan-shaped” posterior process of the quadratojugal [char. 180]).

*Zosuchus* is depicted as the sister taxon of the *Sichuanosuchus*-*Shantungosuchus* clade since these taxa share the presence of a ventrally deflected posterior region of the mandibular rami (char. 172): Other characters, such as the palatines excluded from the margins of the suborbital fenestra (char. 170),



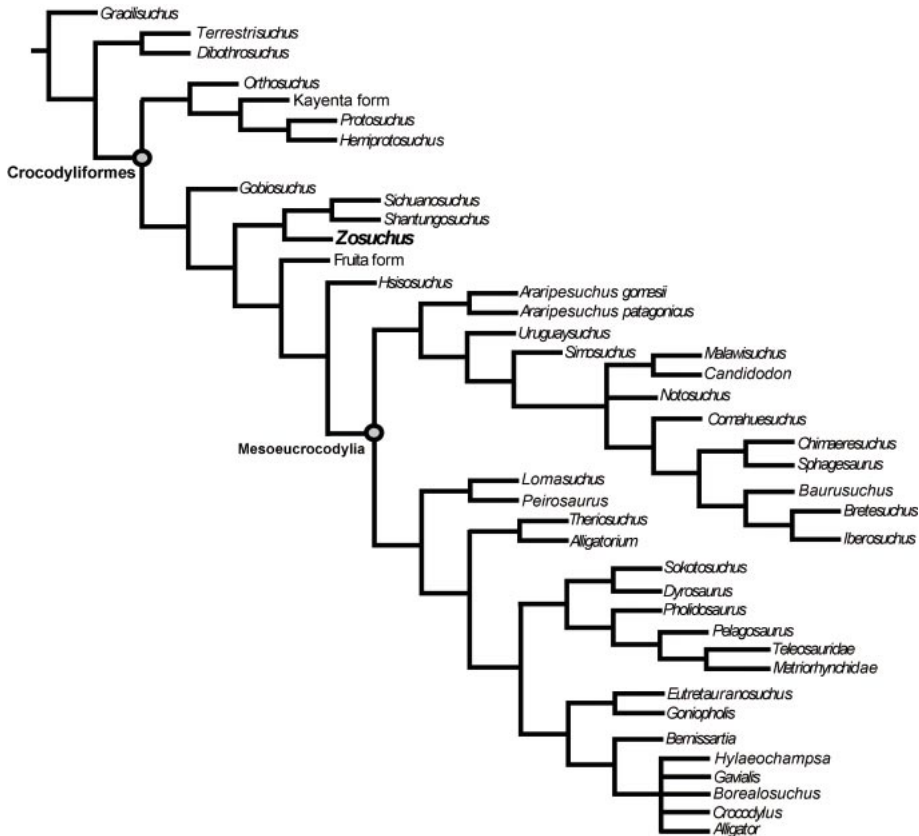


Fig. 15. Strict consensus of the six most parsimonious hypotheses obtained with Nona.

may diagnose this clade but are unknown in *Zosuchus*.

The clade composed by *Zosuchus*, *Sichuanosuchus*, and *Shantungosuchus* is supported to be more closely related to derived mesoeucrocodylians than *Gobiosuchus* and protosuchids by five synapomorphies (presence of palatine shelves extended below narial passage [char. 37]; choana opens posteriorly into a midline depression (choanal groove) [char. 39]; fusion of pterygoids posterior to choana [char. 41]; presence of one enlarged maxillary tooth [char. 79]; presence of a well-developed posterodorsal process of premaxilla [char. 125]).

All the most parsimonious hypotheses depict *Gobiosuchus*, the Fruita form, and the *Zosuchus* clade as more closely related to derived crocodyliforms than to protosuchids. However, the best tree that supports a monophyletic clade formed by protosuchids and

all these basal forms (traditionally referred as “Protosuchia”) is only two steps longer than the most parsimonious hypotheses.

## DISCUSSION

*Zosuchus davidsoni* is depicted as a late-appearing basal crocodyliform in the outcome of the phylogenetic analysis. Note that the presence of this new taxon in Late Cretaceous sediments provides another case of a Mongolian basal crocodyliform registered unusually late in the stratigraphic record (Efimov et al., 2000; Storrs and Efimov, 2000). *Gobiosuchus kielanae* (Osmólska, 1972; Osmólska et al., 1997) is also known from the Late Cretaceous of Mongolia (Bayn Dzak locality) and, although it is not closely related to *Zosuchus*, it also shows a basal position among crocodyliforms (fig. 15). A related taxon, *Gobiosuchus parvus*, was also de-

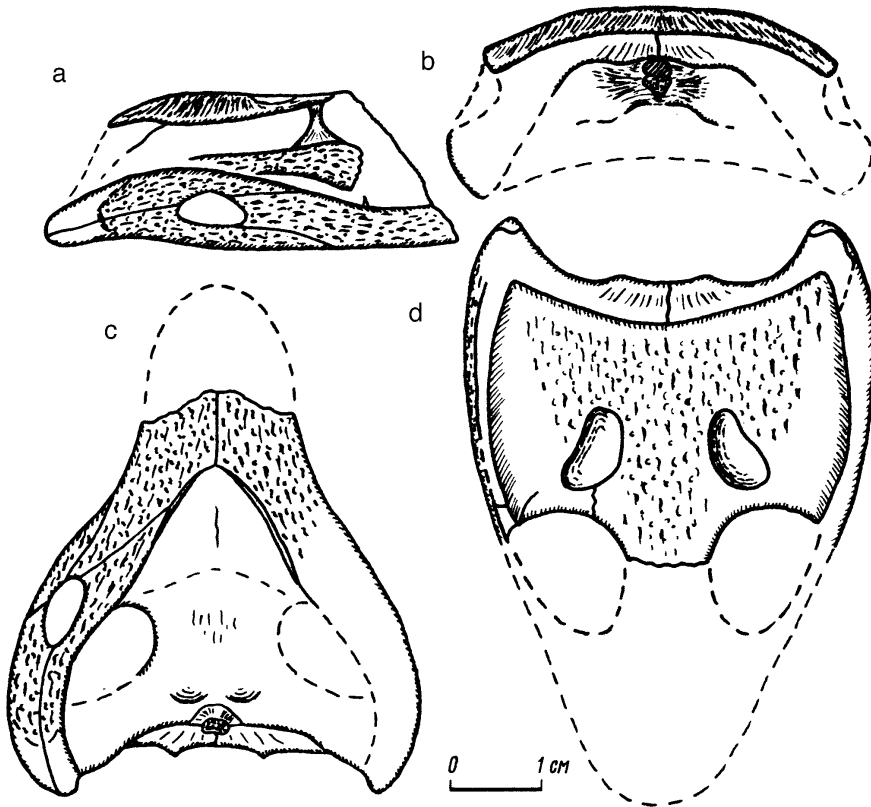


Fig. 16. *Artzosuchus brachycephalus* GIN PST 10/23, taken from Efimov (1983).

scribed from the Late Cretaceous beds of Mongolia (Efimov, 1983), although there are some doubts on the validity of this species (Osmólska et al., 1997; Storrs and Efimov, 2000). Efimov (1983) also described *Artzosuchus brachycephalus* (fig. 16), another crocodyliform from the Udan Sair locality that differs from *Gobiosuchus* in numerous characters. According to the information provided by Efimov (1983), *Artzosuchus* also differs from *Zosuchus* in several characters (e.g., inset postorbital bar, angular exposed on the lateral surface of the mandibular ramus, absence of posterodorsal and posteroventral processes of the dentaries extending above and below the mandibular fenestra, posterolaterally directed processes on the posterior squamosal corners). Unfortunately, *Artzosuchus* was briefly described from an incomplete and unprepared skull (Efimov, 1983; Storrs and Efimov, 2000), and its phylogenetic affinities are not clear at present.

*Zosuchus davidsoni* also provides interesting information on the evolutionary history of the secondary palate of Crocodyliformes. Since Victorian times the position of the choana in crocodylians has been used as an important character in classifying the group. The posterior migration of the palate has been considered a specialization for aquatic existence and/or a structural requirement of the feeding behavior present in modern crocodyles (Busbey, 1994). In extant forms the secondary palate is posteriorly extensive, the choanal opening is located near the glottis, and therefore the oral cavity can be closed by the palatal valve, allowing the animal to breath while the mouth cavity is full of water or to breath while eating.

In Eusuchia the posterior region of the secondary palate is composed both of the palatines and the pterygoids (the vomers also form part of the palate but they are rarely exposed externally), while in more basal taxa

(i.e., noneusuchian mesoeucrocodylians or "mesosuchians") the choana lies in a more anterior position on the border between the palatines and the pterygoids. It is doubtful that this more anterior position would have rendered a modern type palatal valve functional (Busbey, 1994).

Curiously, *Zosuchus davidsoni* mimics the eusuchian condition. Yet instead of a secondary palate formed posteriorly by the pterygoids, *Zosuchus* exhibits a drastically long posterior region of the palate exclusively formed by the palatines. While in no way homologous to the condition in Eusuchia, this posterior extension of the palatines yields the posterior (secondary) choanal opening close to the posterior edge of the pterygoid flanges as in eusuchians. Interestingly, another case of convergent extension of the secondary palate was also noted in a clade of noneusuchian mesoeucrocodylians (e.g., *Bretesuchus*, *Iberosuchus*; Gasparini et al., 1993; Ortega et al., 2000; see fig. 15).

Considering the new information presented here and the phylogenetic position of *Zosuchus*, it seems clear that the posterior extension of the secondary palate has an evolutionary history much more complex than previously thought.

#### ACKNOWLEDGMENTS

We thank Amy Davidson for the skillful preparation of several specimens described here (IGM 100/2, 100/3, 100/5). We also thank Jane Shumsky for the preparation of IGM 100/1. Mick Ellison masterfully prepared the illustrations and figures. Our thanks are extensive to the Mongolian Academy of Sciences—American Museum of Natural History field crews that collected the specimens reported here. Financial support to D.P. was provided by the Department of Earth and Environmental Sciences of Columbia University and the American Museum of Natural History. Access to collections was possible thanks to:) M. Moser (BSP), M. Maisch (GPIT), X. Xing (IVPP), J.M. Clark (GWU), J.F. Bonaparte (AMNH), E. Goman (MAL), D. Unwin (MB), L.E. Ruigomez and R. Cuneo (MEF), Z.B. Gasparini and M. Reguero (MLP), F.L. de Broin (MNHN), A. Kellner

(MNUFRJ), S. Cocca (MOZ), J.O. Calvo and L. Salgado (MUC-PV), J. Powell (PVL), C. Cartelle (RCL), A. Chinsamy (SAM), R. Wild (SMNS), D. Krause and G. Buckley (UA), A. Buscalioni and F. Ortega (UAM), I.S. Carvalho (UFRJ), and H. Olsmólska (ZPAL).

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## APPENDIX 1

### CHARACTER LIST CORRESPONDING TO DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Character definitions 1–101 were taken from Clark (1994) and have the same numeration as in the original publication. Character 5 was excluded from the analysis (due to dependence with the modified definition of character 6); however, its inclusion does not affect the outcome of the analysis (except for the tree length). The additional characters are also listed here and their respective sources are cited along with the character numbers of the original publication. Characters 1, 3, 6, 37, 45, 49, 65, 67, 69, 73, 77, 79, 83, 90, 91, 97, 103, 104, 105, 121, 126, 139, 143, 150, and 167 were set as ordered characters (also marked “+” in this list).

Character 1 (modified from Clark, 1994: char. 1): + External surface of dorsal cranial bones: smooth (0), slightly grooved (1), or heavily ornamented with deep pits and grooves (2).

Character 2 (modified from Clark, 1994: char. 2): Skull expansion at orbits: gradually (0), or abruptly (1).

Character 3 (modified from Clark, 1994: char. 3): + Rostrum proportions: narrow oreinrostral (0), broad oreinrostral (1), nearly tubular (2), or platyrostral (3).

Character 4 (Clark, 1994: char. 4): Premaxilla participation in internarial bar: forming at least the ventral half (0), or with little participation (1).

Character 5 (Clark, 1994: char. 5): Premaxilla anterior to nares: narrow (0), or broad (1).

Character 6 (modified from Clark, 1994: char. 6): + External nares facing: anterolaterally or anteriorly (0), dorsally not separated by premaxillary bar from anterior edge of rostrum (1), or dorsally separated by premaxillary bar (2).

Character 7 (Clark, 1994: char. 7): Palatal parts of premaxillae: do not meet posterior to incisive foramen (0), or meet posteriorly along contact with maxillae (1).

Character 8 (Clark, 1994: char. 8): Premaxilla-maxilla contact: premaxilla loosely overlies maxilla (0), or sutured together along a butt joint (1).

Character 9 (modified from Clark, 1994: char. 9): Ventrally opened notch on ventral edge of rostrum at premaxilla-maxilla contact: absent (0), present as a notch (1), or present as a large fenestra (2).

Character 10 (Clark, 1994: char. 10): Posterior ends of palatal branches of maxillae anterior to palatines: do not meet (0), or meet (1).

Character 11 (Clark, 1994: char. 11): Nasal-lacrimar contact: contact (0), or do not contact (1).

Character 12 (Clark, 1994: char. 12): Lacrimal contacts nasal along: medial edge only (0), or medial and anterior edges (1).

Character 13 (Clark, 1994: char. 13): Nasal contribution to narial border: yes (0), or no (1).

Character 14 (Clark, 1994: char. 14): Nasal-premaxilla contact: present (0), or absent (1).

Character 15 (modified from Clark, 1994: char. 15): Descending process of prefrontal: does not contact palate (0), or contacts palate (1).

Character 16 (Clark, 1994: char. 16): Postorbital-jugal contact: postorbital anterior to jugal, or postorbital medial to jugal (1), or postorbital lateral to jugal (2).

Character 17 (Clark, 1994: char. 17): Anterior part of the jugal with respect to posterior part: as broad (0), or twice as broad (1).

Character 18 (Clark, 1994: char. 18): Jugal bar beneath infratemporal fenestra: flattened (0), or rod-shaped (1).

Character 19 (Clark, 1994: char. 19): Quadrate-jugal dorsal process: narrow, contacting only a small part of postorbital (0), or broad, extensively contacting the postorbital (1).

Character 20 (Clark, 1994: char. 20): Frontal width between orbits: narrow, as broad as nasals (0), or broad, twice as broad as nasals (1).

Character 21 (Clark, 1994: char. 21): Frontals: paired (0), unpaired (1).

Character 22 (Clark, 1994: char. 22): Dorsal surface of frontal and parietal: flat (0), or with midline ridge (1).

Character 23 (modified from Clark, 1994: char. 23 by Buckley and Brochu, 1999: char. 81): + Parieto-postorbital suture: absent from dorsal surface of skull roof and supratemporal fossa (0), absent from dorsal surface of skull roof but broadly present within supratemporal fossa (1), or present within supratemporal fossa and on dorsal surface of skull roof (2).

Character 24 (Clark, 1994: char. 24): Supratemporal roof dorsal surface: complex (0), or dorsally flat "skull table" developed, with postorbital and squamosal with flat shelves extending laterally beyond quadrate contact (1).

Character 25 (modified from Clark, 1994: char. 25): Postorbital bar: sculpted (if skull sculpted) (0), or unsculpted (1).

Character 26 (modified from Clark, 1994: char. 26): Postorbital bar: transversely flattened (0), or cylindrical (1).

Character 27 (Clark, 1994: char. 27): Vascular opening in dorsal surface of postorbital bar: absent (0), present (1).

Character 28 (modified from Clark, 1994: char. 28): Postorbital anterolateral process: absent or poorly developed (0), or well developed, long, and acute (1).

Character 29 (Clark, 1994: char. 29): Dorsal part of the postorbital: with anterior and lateral edges only (0), or with anterolaterally facing edge (1).

Character 30 (Clark, 1994: char. 30): Dorsal end of the postorbital bar broadens dorsally, continuous with dorsal part of postorbital (0), or dorsal part of the postorbital bar constricted, distinct from the dorsal part of the postorbital (1).

Character 31 (Clark, 1994: char. 31): Bar between orbit and supratemporal fossa broad and solid, with broadly sculpted dorsal surface (0), or bar narrow, sculpting restricted to anterior surface (1).

Character 32 (modified from Clark, 1994: char. 32): Parietal: with broad occipital portion (0), or without broad occipital portion (1).

Character 33 (Clark, 1994: char. 33): Parietal: with broad sculpted region separating fossae (0), or with sagittal crest between supratemporal fossae (1).

Character 34 (Clark, 1994: char. 34): Postparietal (dermosupraoccipital): a distinct element (0), or not distinct (fused with parietal?) (1).

Character 35 (Clark, 1994: char. 35): Postero-dorsal corner of the squamosal: squared off, lacking extra "lobe" (0), or with unsculptured lobe (1).

Character 36 (modified from Clark, 1994: char. 36): Posterior edge of the squamosal: nearly flat (0), or with elongated and posteriorly directed process (1).

Character 37 (Clark, 1994: char. 37): + Palatines: do not meet on palate below the narial passage (0), form palatal shelves that do not meet (1), or meet ventrally to the narial passage, forming part of secondary palate (2).

Character 38 (Clark, 1994: char. 38): Pterygoid: restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0), or pterygoid extends dorsally to contact laterosphenoid and form ventrolateral edge of the trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1).

Character 39 (modified from Clark, 1994: char. 39): Choanal opening: continuous with pterygoid ventral surface except for anterior and anterolateral borders (0), or opens into palate through a deep midline depression (choanal groove) (1).

Character 40 (Clark, 1994: char. 40): Palatal surface of pterygoids: smooth (0), or sculpted (1).

Character 41 (Clark, 1994: char. 41): Pterygoids posterior to choanae: separated (0), or fused (1).

Character 42 (modified from Clark, 1994: char. 42 by Ortega et al., 2000: char 139): Depression on primary pterygoidean palate posterior to choana: absent or moderate in size being narrower

than palatine bar (0), or wider than palatine bar (1).

Character 43 (Clark, 1994: char. 43): Pterygoids: do not enclose choana (0), or enclose choana (1).

Character 44 (modified from Clark, 1994: char. 44): Anterior edge of choanae situated near posterior edge of suborbital fenestra (or anteriorly) (0), or near posterior edge of pterygoid flanges (1).

Character 45 (Clark, 1994: char. 45): + Quadrate: without fenestrae (0), with single fenestrae (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2).

Character 46 (Clark, 1994: char. 46): Posterior edge of quadrate: broad medial to tympanum, gently concave (0), or posterior edge narrow dorsal to otoccipital contact, strongly concave (1).

Character 47 (Clark, 1994: char. 47): Dorsal, primary head of quadrate articulates with: squamosal, otoccipital, and prootic (0), or with prootic and laterosphenoid (1).

Character 48 (Clark, 1994: char. 48): Ventrolateral contact of otoccipital with quadrate: very narrow (0), or broad (1).

Character 49 (Clark, 1994: char. 49): + Quadrate, squamosal, and otoccipital: do not meet to enclose cranioquadrate passage (0), enclose passage near lateral edge of skull (1), or meet broadly lateral to the passage (2).

Character 50 (Clark, 1994: char. 50): Pterygoid ramus of quadrate: with flat ventral edge (0), or with deep groove along ventral edge (1).

Character 51 (Clark, 1994: char. 51): Ventromedial part of quadrate: does not contact otoccipital (0), or contacts otoccipital to enclose carotid artery and form passage for cranial nerves IX–XI (1).

Character 52 (Clark, 1994: char. 52): Eustachian tubes: not enclosed between basioccipital and basisphenoid (0), or entirely enclosed (1).

Character 53 (Clark, 1994: char. 53): Basisphenoid rostrum (cultriform process): slender (0), or dorsoventrally expanded (1).

Character 54 (Clark, 1994: char. 54): Basipterygoid process: prominent, forming movable joint with pterygoid (0), or basipterygoid process small or absent, with basisphenoid joint sutured closed (1).

Character 55 (modified from Clark, 1994: char. 55 by Ortega et al., 2000: char. 68): Basisphenoid ventral surface: shorter than the basioccipital (0), or wide and similar to, or longer in length than, basioccipital (1).

Character 56 (Clark, 1994: char. 56): Basisphenoid: exposed on ventral surface of braincase (0), or virtually excluded from ventral surface by pterygoid and basioccipital (1).

Character 57 (Clark, 1994: char. 57): Basioccipital: without well-developed bilaterally tuberosities (0), or with large pendulous tubera (1).

Character 58 (Clark, 1994: char. 58): Otoccipital: without laterally concave descending flange ventral to subcapsular process (0), or with flange (1).

Character 59 (Clark, 1994: char. 59): Cranial nerves IX–XI: pass through common large foramen vagi in otoccipital (0), or cranial nerve IX pass medial to nerves X and XI in separate passage (1).

Character 60 (Clark, 1994: char. 60): Otoccipital: without large ventrolateral part ventral to paroccipital process (0), or with large ventrolateral part (1).

Character 61 (Clark, 1994: char. 61): Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0), or horizontal (1).

Character 62 (Clark, 1994: char. 62): Supraoccipital: forms dorsal edge of the foramen magnum (0), or otoccipitals broadly meet dorsal to the foramen magnum, separating supraoccipital from foramen (1).

Character 63 (Clark, 1994: char. 63): Mastoid antrum: does not extend into supraoccipital (0), or extends through transverse canal in supraoccipital to connect middle-ear regions (1).

Character 64 (Clark, 1994: char. 64): Posterior surface of supraoccipital: nearly flat (0), or with bilateral posterior prominences (1).

Character 65 (modified from Clark, 1994: char. 65): + One small palpebral present in orbit (0), one large palpebral (1), or two large palpebrals (2).

Character 66 (Clark, 1994: char. 66): External nares: divided by a septum (0), or confluent (1).

Character 67 (Clark, 1994: char. 67): + Antorbital fenestra: as large as orbit (0), about half the diameter of the orbit (1), much smaller than the orbit (2), or absent (3).

Character 68 (modified from Clark, 1994: char. 68 by Ortega et al., 2000: char. 41): Supratemporal fenestrae extension: relatively large, covering most of surface of skull roof (0), or relatively short, fenestrae surrounded by a flat and extended skull roof (1).

Character 69 (modified from Clark, 1994: char. 69): + Choanal groove: undivided (0), partially septated (1), or completely septated (2).

Character 70 (Clark, 1994: character 70): Dentary: extends posteriorly beneath mandibular fenestra (0), or does not extend beneath fenestra (1).

Character 71 (modified from Clark, 1994: char. 71): Retroarticular process: absent or extremely reduced (0), very short, broad, and robust (1), with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally (2).



trally and facing dorsomedially (2), posteriorly elongated, triangular-shaped and facing dorsally (3), or posteroventrally projecting and paddle-shaped (4).

Character 72 (Clark, 1994: char. 72): Prearticular: present (0), or absent (1).

Character 73 (modified from Clark, 1994: char. 73): + Articular without medial process (0), with short process not contacting braincase (1), or with process articulating with otoccipital and basisphenoid (2).

Character 74 (Clark, 1994; character 74): Dorsal edge of surangular: flat (0), or arched dorsally (1).

Character 75 (Clark, 1994: char. 75): Mandibular fenestra: present (0), or absent (1).

Character 76 (Clark, 1994: char. 76): Insertion area for *M. pterygoideus posterior*: does not extend onto lateral surface of angular (0), or extends onto lateral surface of angular (1).

Character 77 (modified from Clark, 1994: char. 77): + Splenial involvement in symphysis in ventral view: not involved (0), involved slightly in symphysis (1), or extensively involved (2).

Character 78 (Clark, 1994: char. 78): Posterior premaxillary teeth: similar in size to anterior teeth (0), or much longer (1).

Character 79 (modified from Clark, 1994: char. 79): + Maxillary teeth waves: absent, no tooth size variation (0), one wave of teeth enlarged (1), or enlarged maxillary teeth curved in two waves ("festooned") (2).

Character 80 (Clark, 1994: char. 80): Anterior dentary teeth opposite premaxilla-maxilla contact: no more than twice the length of other dentary teeth (0), or more than twice the length (1).

Character 81 (modified from Clark, 1994: char. 81): Dentary teeth posterior to tooth opposite premaxilla-maxilla contact: equal in size (0), or enlarged dentary teeth opposite to smaller teeth in maxillary tooththrow (1).

Character 82 (modified from Clark, 1994: char. 82 by Ortega et al., 2000: char. 120): Anterior and posterior scapular edges: symmetrical in lateral view (0), anterior edge more strongly concave than posterior edge (1), or dorsally narrow with straight edges (2).

Character 83 (modified from Clark, 1994: char. 83 by Ortega et al., 2000: char. 121): Coracoid length: up to two-thirds of the scapular length (0), or subequal in length to scapula (1).

Character 84 (Clark, 1994: char. 84): Anterior process of ilium: similar in length to posterior process (0), or one-quarter or less the length of the posterior process (1).

Character 85 (Clark, 1994: char. 85): Pubis: rodlike without expanded distal end (0), or with expanded distal end (1).

Character 86 (Clark, 1994: char. 86): Pubis: forms anterior half of ventral edge of acetabulum (0), or pubis at least partially excluded from the acetabulum by the anterior process of the ischium (1).

Character 87 (Clark, 1994: char. 87): Distal end of femur: with large lateral facet for the fibula (0), or with very small facet (1).

Character 88 (Clark, 1994: char. 88): Fifth pedal digit: with phalanges (0), or without phalanges (1).

Character 89 (Clark, 1994: char. 89): Atlas intercentrum: broader than long (0), or as long as broad (1).

Character 90 (modified from Clark, 1994: char. 90): + Cervical neural spines: all anteroposteriorly large (0), only posterior ones rodlike (1), or all spines rodlike (2).

Character 91 (modified from Clark, 1994: char. 91 by Buscalioni and Sanz, 1988: char. 37 and by Brochu, 1997a: char. 7): + Hypapophyses in cervicodorsal vertebrae: absent (0), present only in cervical vertebrae (1), present in cervical and the first two dorsal vertebrae (2), present up to the third dorsal vertebra (3), or up to the fourth dorsal vertebrae (4).

Character 92 (Clark, 1994: char. 92): Cervical vertebrae: amphicoelous or amphiplatian (0), or procoelous (1).

Character 93 (Clark, 1994: char. 93): Trunk vertebrae: amphicoelous or amphiplatian (0), or procoelous (1).

Character 94 (Clark, 1994: char. 94): All caudal vertebrae: amphicoelous or amphiplatian (0), first caudal biconvex with other procoelous (1), or procoelous (2).

Character 95 (Clark, 1994: char. 95): Dorsal osteoderms: rounded or ovate (0), rectangular, broader than long (1), or square (2).

Character 96 (modified from Clark, 1994: char. 96 and Brochu, 1997: char. 40): + Dorsal osteoderms without articular anterior process (0), with a discrete convexity on anterior margin (1), or with a well-developed process located anterolaterally in dorsal parasagittal osteoderms (2).

Character 97 (modified from Clark, 1994: char. 97 by Ortega et al., 2000: chars. 107, 108): + Rows of dorsal osteoderms: two parallel rows (0), more than two (1), or more than four with "accessory ranges of osteoderms" (sensu Frey, 1988) (2).

Character 98 (Clark, 1994: char. 98): Osteoderms: Some or all imbricated (0), or sutured to one another (1).

Character 99 (Clark, 1994: char. 99): Tail osteoderms: dorsal only (0), or completely surrounded by osteoderms (1).

Character 100 (Clark, 1994: char. 100): Trunk

osteoderms: absent from ventral part of the trunk (0), or present (1).

Character 101 (Clark, 1994: char. 101): Osteoderms: with longitudinal keels on dorsal surfaces (0), or without longitudinal keels (1).

Character 102 (Wu and Sues, 1996: char. 14): Jugal: participating in margin of antorbital fossa (0), or separated from it (1).

Character 103 (modified from Wu and Sues, 1996: char. 23): + Articular facet for quadrate condyle: equal in length to the quadrate condyles (0), slightly longer (1), or close to three times the length of the quadrate condyles (2).

Character 104 (modified from Wu and Sues, 1996: char. 24 and Wu et al., 1997: char. 124): + Jaw joint: placed at level with basioccipital condyle (0), below basioccipital condyle about above level of lower toothrow (1), or below level of toothrow (2).

Character 105 (modified from Wu and Sues, 1996: char. 27 and Ortega et al., 2000: char. 133): + Premaxillary teeth: five (0), four (1), three (2), or two (3).

Character 106 (modified from Wu and Sues, 1996: char. 29): Unsculptured region along alveolar margin on lateral surface of maxilla: absent (0), or present (1).

Character 107 (Wu and Sues, 1996: char. 30): Maxilla: with eight or more teeth (0), or seven or fewer teeth (1).

Character 108 (Wu and Sues, 1996: char. 33): Coracoid: without posteromedial or ventromedial process (0), with elongate posteromedial process (1), or distally expanded ventromedial process (2).

Character 109 (Wu and Sues, 1996: char. 40): Radiale and ulnare: short and massive (0), or elongate (1).

Character 110 (Wu and Sues, 1996: char. 41): Postacetabular process: directed posteroventrally or posteriorly (0), or directed posterodorsally and much higher in position than preacetabular process (1).

Character 111 (modified from Gomani, 1997: char. 4): Prefrontals anterior to orbits: elongated, oriented parallel to anteroposterior axis of the skull (0), or short and broad, oriented posteromedially–anterolaterally (1).

Character 112 (modified from Gomani, 1997: char. 32): Basioccipital and ventral part of otocipital: facing posteriorly (0), or posteroventrally (1).

Character 113 (Buscalioni and Sanz, 1988: char. 35): Vertebral centra: cylindrical (0), or spool-shaped (1).

Character 114 (modified from Buscalioni and Sanz, 1988: char. 39): Transverse process of posterior dorsal vertebrae: dorsoventrally low and laminar (0), or dorsoventrally high (1).

Character 115 (Buscalioni and Sanz, 1988: char. 44): Number of sacral vertebrae: two (0), or more than two (1).

Character 116 (Buscalioni and Sanz, 1988: char. 49): Supra-acetabular crest: present (0), or absent (1).

Character 117 (Buscalioni and Sanz, 1988: char. 54): Proximal end of radiale expanded symmetrically, similarly to the distal end (0), or more expanded proximomedially than proximolaterally (1).

Character 118 (Ortega et al., 1996: char. 5): Lateral surface of the dentary: without a longitudinal depression (0), or with a longitudinal depression (1).

Character 119 (Ortega et al., 1996: char. 9): Ventral exposure of splenials: absent (0), or present (1).

Character 120 (Ortega et al., 1996: char. 11, 2000: char. 100): Tooth margins: with denticulate carinae (0), or without carinae or with smooth or crenulated carinae (1).

Character 121 (modified from Pol, 1999a: char. 133 and Ortega et al., 2000: char. 145): Lateral surface of anterior process of jugal: flat or convex (0), or with broad shelf below the orbit with triangular depression underneath it (1).

Character 122 (Pol, 1999a: char. 134): Jugal: does not exceed the anterior margin of orbit (0), or exceeds margin (1).

Character 123 (Pol, 1999a: char. 135): Notch in premaxilla on lateral edge of external nares: absent (0), or present on the dorsal half of the external nares lateral margin (1).

Character 124 (Pol, 1999a: char. 136): Dorsal border of external nares: formed mostly by the nasals (0), or by both the nasals and premaxilla (1).

Character 125 (Pol, 1999a: char. 138): Posterodorsal process of premaxilla: absent (0), or present extending posteriorly wedging between maxilla and nasals (1).

Character 126 (Pol, 1999a: char. 139 and Ortega et al., 2000: char. 9): + Premaxilla-maxilla suture in palatal view: projected markedly forward (0), projected slightly anteriorly (1), or projected posteriorly (2).

Character 127 (Pol, 1999a: char. 140): Nasal lateral border posterior to external nares: laterally concave (0), or straight (1).

Character 128 (Pol, 1999a: char. 141): Nasal lateral edges: nearly parallel (0), parallel but the anterior end oblique to each other (1), or entirely oblique to each other (2).

Character 129 (Pol, 1999a: char. 143): Palatine anteromedial margin: exceeding the anterior margin of the palatal fenestrae wedging between the

maxillae (0), or not exceeding the anterior margin of palatal fenestrae (1).

Character 130 (Pol, 1999a: char. 144): Dorsoventral height of jugal antorbital region respect to infraorbital region: equal or lower (0), or antorbital region more expanded than infraorbital region of jugal (1).

Character 131 (Pol, 1999a: char. 145): Maxilla-lacrimal contact: partially included in antorbital fossa (0), or completely included (1).

Character 132 (Pol, 1999a: char. 146): Lateral eustachian tube openings: located posteriorly to the medial opening (0), or aligned anteroposteriorly and dorsoventrally (1).

Character 133 (Pol, 1999a: char. 147): Anterior process of ectopterygoid: developed (0), or reduced-absent (1).

Character 134 (Pol, 1999a: char. 148): Posterior process of ectopterygoid: developed (0), or reduced-absent (1).

Character 135 (Pol, 1999a: char. 149 and Ortega et al., 2000: char. 13): Small foramen located in the premaxillo-maxillary suture in lateral surface (not for big mandibular teeth): absent (0), or present (1).

Character 136 (Pol, 1999a: char. 150): Jugal posterior process: exceeding posteriorly the infra-temporal fenestrae (0), or not (1).

Character 137 (Pol, 1999a: char. 151): Compressed crown of maxillary teeth: oriented parallel to the longitudinal axis of skull (0), or obliquely disposed (1).

Character 138 (Pol, 1999a: char. 152): Large and aligned neurovascular foramina on lateral maxillary surface: absent (0), or present (1).

Character 139 (modified from Pol, 1999a: char. 153): + External surface of maxilla and premaxilla: with a single plane facing laterally (0), or with ventral region facing laterally and dorsal region facing dorsolaterally (1).

Character 140 (Pol, 1999a: char. 154 and Ortega et al., 2000: char. 104): Maxillary teeth: not compressed laterally (0) or compressed laterally (1).

Character 141 (Pol, 1999a: char. 155): Posteroventral corner of quadratojugal: reaching the quadrate condyles (0), or not reaching the quadrate condyles (1).

Character 142 (Pol, 1999a: char. 156): Base of postorbital process of jugal: directed posterodorsally (0), or dorsally (1).

Character 143 (Pol, 1999a: char. 157): + Postorbital process of jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2).

Character 144 (Pol, 1999a: char. 158 and Ortega et al., 2000: char. 36): Postorbital-ectopterygoid contact: present (0), or absent (1).

Character 145 (Pol, 1999a: char. 161): Quad-

ratojugal: not ornamented (0), or ornamented in the base (1).

Character 146 (Pol, 1999a: char. 162): Prefrontal-maxillary contact in the inner anteromedial region of orbit: absent (0), or present (1).

Character 147 (Pol, 1999a: char. 163): Basisphenoid: without lateral exposure (0), or with lateral exposure on the braincase (1).

Character 148 (Pol, 1999a: char. 164): Posteriorly facing notch between the base of pterygoid wing: absent (0), or present (1).

Character 149 (Pol, 1999a: char. 165): Quadrate process of pterygoids: well developed (0), or poorly developed (1).

Character 150 (modified from Pol, 1999a: char. 166 and Ortega et al., 2000: char. 44): + Quadrate major axis directed: posteroventrally (0), ventrally (1), or anteroventrally (2).

Character 151 (Pol, 1999a: char. 167): Quadrate distal end: with only one plane facing posteriorly (0), or with two distinct faces in posterior view, a posterior one and a medial one bearing the foramen aereum (1).

Character 152 (Pol, 1999a: char. 168): Anteroposterior development of neural spine in axis: well developed covering all the neural arch length (0), or poorly developed, located over the posterior half of the neural arch (1).

Character 153 (Pol, 1999a: char. 169): Prezygapophyses of axis: not exceeding anterior edge of neural arch (0), or exceeding the anterior margin of neural arch (1).

Character 154 (Pol, 1999a: char. 170): Postzygapophyses of axis: well developed, curved laterally (0), or poorly developed (1).

Character 155 (modified from Pol, 1999b: char. 212): Shape of dentary symphysis in ventral view: tapering anteriorly forming an angle (0), U-shaped, smoothly curving anteriorly (1), or lateral edges longitudinally oriented, convex anterolateral corner, and extensive transversally oriented anterior edge (2).

Character 156 (Pol, 1999b: char. 213): Unsculpted region in the dentary below the toothrow: absent (0), or present (1).

Character 157 (Ortega et al., 1996 and Buckley et al., 2000: char. 13): Cheekteeth: not constricted at base of crown (0), or constricted (1).

Character 158 (Ortega et al., 2000: char. 42): Outer surface of squamosal laterodorsally oriented: extensive (0), reduced and sculpted (1), or reduced and unsculpted (2).

Character 159 (Ortega et al., 2000: char. 74): Length/height proportion of infratemporal fenestra: higher than wide or equal (0), or very anteroposteriorly elongated (1).

Character 160 (Ortega et al., 2000: char. 90):

Foramen intramandibularis oralis: small or absent (0), or big and slotlike (1).

Character 161 (Ortega et al., 2000: char. 146): Ectopterygoid medial process: single (0), or forked (1).

Character 162 (modified from Gomani, 1997: char. 46 and Buckley et al., 2000: char. 113): Cusps of teeth: unique cusp (0), one main cusp with smaller cusps arranged in one row (1), one main cusp with smaller cusps arranged in more than one row (2), or several cusps of equal size arranged in more than one row (3).

Character 163. Posterolateral edge of squamosal: without descending ornamented process (0), or with descending ornamented process (1).

Character 164. Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).

Character 165. Palatine-pterygoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).

Character 166 (Wu et al., 1997: char. 103): Squamosal descending process: absent (0), or present (1).

Character 167 (modified from Wu et al., 1997: char. 105): + Development of distal quadrate body ventral to otoccipital-quadrate contact: distinct (0), incipiently distinct (1), or indistinct (2).

Character 168 (Wu et al., 1997: char. 106): Pterygoid flanges: thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).

Character 169 (Wu et al., 1997: char. 108): Postorbital participation in infratemporal fenestra: almost or entirely excluded (0), or bordering infratemporal fenestra (1).

Character 170 (Wu et al., 1997: char. 109): Palatines: form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).

Character 171 (Wu et al., 1997: char. 110): Angular posterior to mandibular fenestra: widely ex-

posed on lateral surface of mandible (0), or shifted to the ventral surface of mandible (1).

Character 172 (Wu et al., 1997: char. 112): Posteroventral edge of mandibular ramus: straight or convex (0), or markedly deflected (1).

Character 173 (modified from Wu et al., 1997: char. 119): Quadrate ramus of pterygoid in ventral view: narrow (0), or broad (1).

Character 174 (Wu et al., 1997: char. 121): Pterygoids: not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).

Character 175 (Wu et al., 1997: char. 122): Olecranon: well developed (0), or absent (1).

Character 176 (Wu et al., 1997: char. 123): Cranial table width respect to ventral portion of skull: as wide as ventral portion (0), or narrower than ventral portion of skull (1).

Character 177 (Wu et al., 1997: char. 127): Depression on posterolateral surface of maxilla: absent (0), or present (1).

Character 178 (Wu et al., 1997: char. 128): Anterior palatal fenestra: absent (0), or present (1).

Character 179: Paired ridges located medially on ventral surface of basisphenoid: absent (0), or present (1).

Character 180: Posterolateral end of quadratojugal: acute or rounded, tightly overlapping the quadrate (0), or with sinusoidal ventral edge and wide and rounded posterior edge slightly overhanging the lateral surface of the quadrate (1).

Character 181: Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0), or ventrolaterally (1).

Character 182 (Gasparini et al., 1993: char. 3): Wedgelike process of the maxilla in lateral surface of premaxilla-maxilla suture: absent (0), or present (1).

Character 183: Choanal opening: opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1).

APPENDIX 2

DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

This matrix is available electronically at <http://research.amnh.org/vertpaleo/norell.html>

*Gracilisuchus*

000000??0?000000000000?0?000000000?0  
 ??0?0?00000?000??0000?0??00000?100  
 000?00000000?0??0000?0?000001012?00  
 ?00??0?0?01?01000??1?01??000001002?  
 0??00000????0?0?0??0000?00000?0?00  
 000

*Terrestrisuchus*

000?00??0?000000?000?0?00?000?1100

00000?00000?000??0?000?000????00????  
 10??0?000000?010?0000?0200000101??01  
 100??00000?00100??10?00?110?0?0??[0  
 1]110????00000????00?0??0????00??0?  
 0??0?0?

*Dibothrosuchus*

000?00?020??001??000000?????001100  
 00000?00000?0000?00000?0?0101000?010  
 100?0010?000?????2000?0?????01010?01  
 100?0?00000001001010?00?1?0001010111  
 00??0000001??00000?010001000100?0?00  
 000





??  
??  
??  
????

*Simosuchus*

10301011000000100010111110?011000101  
1?10100011?11011?1000010?1?020112121  
010110000??????02100?2010?10002010C  
???01??????1101101012000010100111002  
11000120???211[12]00011111011001[01]  
1?10000001

*Sphagesaurus*

101?000101?00??100?????110?????????  
21101?00?????011?1000?????????13?2???  
?????100?????????1?????????????????312?  
???0?????????111110111111111111111001  
11011111?0?11?0?0?11?0?10?01??0000  
001

*Bretesuchus*

1[01]0??01121??00?????????????0??????  
???2??10011?????????1011?1??????13?1  
?1?00?10110?????????????????????0?1  
00?????1??????01??0????01??0??0??1?  
0?????????????01]0[01]?1?10??1??1??  
001??00?????1

*Baurusuchus*

100??0?121??00?1101?????111?0110?????  
2?10110011112011?1000?10??10??311121  
010111111?????????????????????12103?  
???1?????110111010101110011001111011  
0?01111???[01]0[01]11110?11101?00001  
?00010001

*Iberosuchus*

1?0?00012?0?00111000111111?01?000?00  
??10100111?12??1?101??10?1????111??1  
0?0?1011011??????[12][1234]00??00???  
00?[12][01]0?2??0000??11001101010?1  
?0??100?11001?0??0101??[01]?0111?01  
01101?0??01?10000101

*Araripesuchus gomesii*

201000110100001110001011111011[01]00  
1002110100011112011?10000?0?11020112  
1210001101[01][01]1[01]11111?1[234]0  
001000100111100210010010101001001001  
000000100110002100010110?0011[01]000  
01111101000011100?0001

*Araripesuchus patagonicus*

201000?1010000?1[01]000101111?011100  
1002?10100011?12?11?1000??0?1?02?112  
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11100??01????0?01?01101?010000??1001  
10102?0??101????0??[01]10001111?0100  
001110?00001

*Lomasuchus*

201????1211?00?11000101111??11000100

2?1010001??12??1?101??1??1??2?21????  
?00??0[12]11????????????????????1???  
00????00?????0?00??1?110?00??00011?  
0??1??0?????010????01?11??10??01?10  
00??11

*Peirosaurus*

201?011??1??00??????10?1?????????0??  
2?10?????????????????????????????1????  
??????[12]1?????????????????????????0  
00?????????????0????1??0??????0?1??  
??????????????[01]?????0?????????????  
???00??1?

*Theriosuchus*

201101111101001100001101111001100110  
211010001?11?01111000?????1?20211?41  
00101010110111100011112001001010002  
?00?10?110110[01]001?1100?00?0?00100  
??01??00?00??10100000??11?010??01?10  
000??1

*Alligatorium*

?0??????1?0000?1000010?1111?0?100?1?  
???0?00??11??1??1000?????????20?1????  
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????10??1?????????????????????0????????  
?????????????????0????????????????????  
?0?

*Goniopholis*

203?1211110010111000100111?001000100  
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00[01]0[12]02011?1??1??0?00?1200?11?  
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10001?1??0000110020000001100100001  
1110?0101

*Eutretauranosuchus*

203?????1?10010111000100111?00?000100  
1110?000?1112011?1010??0?1?0?121204?  
00001020111??1?0??0?1?????????000?  
??00?????0?100??110??????0??00???  
1????0?????10?2??0001?0?000?1?110?  
1?1

*Pholidosaurus*

212?111101??11?11101100111?001000100  
211?100001112111?101??10?100?1311?30  
0??2?0??11?1??0??0??2?0?????????  
?????????????1??11110?????0?0010????  
?????????????0?1?00001??10?001?100?0  
101

*Sokotosuchus*

2?2????1101??10????001001???101001?01  
2?1??????1112?11?1?11??0??1?1?0????  
?????01?????????????????????????????  
?????????????1?????????????????0??0????  
?????????????????00?????????????????  
???

*Dyrosaurus*

002??1?101?010?11?00100011?101001101  
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00??2?000??????0?00?????1??????  
?????????1??????????????0??0?????  
????????????021?00001????0?????00??  
1?1

*Pelagosaurus*

202?1111?10011020101000000000000100  
211010000001101111001001?10001200?30  
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0??1?00????0001000?01120100001100000  
1?1

Teleosauridae

012?1111010011010100100000000001100  
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??10??01001101??1011000011000010100?  
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101

Metriorhynchidae

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?100?01001101??1011?000??000010102?0  
??0?000????001000?011?01000?11000001  
01

*Bernissartia*

203??21111??00111000?00111?001000?00  
2?????0001112?11?10100?0?1???1?1?41  
0010102011?1?11??020021110110100000?  
?00??????1????1????????0??0?10??0  
1????0??1?120000001????0?????00??  
101

*Hylaeochamps*

00?????11?????1?01????0??0?0?  
2?1?1011????????101??1??1????10???  
?????????????????????????????????  
??0?????10????????????0??0?????  
????????????2??000??????????????  
??1

*Borealosuchus*

203?1211110010111000100111?001000100  
21101011111211111010010?110?1310031  
000110?011111111113111?110?00?000002  
110?100100?101??11110??00000010001?  
1??1?0000110?20?00001100100001110000  
101

*Gavialis*

212?1211100111111011011111001000100  
2110101101112011110110101110[01]1310  
03100012000001111110131112111100?000  
002110?100100?101??121100?0000000100  
0101?10?00001?0?20?00001100100001110  
0001?1

*Crocodylus*

203012111100[01]01110001?21111001000  
1002110?01111112011110100101110[01]  
[01]31003100010010121111110131112021  
100?0000021100100100?101??111100?000  
00001001101011100001?0?2000000110010  
0001110000101

Alligator

203112?101?0[01]01110001021111001000  
?00211010111112011110100101110[01]  
[01]3120310001002012111111131112021  
1?0?0000211001001001101??111000?000  
00001001[12]010111000011[01]12000000  
1100100001110000101

APPENDIX 3

FOSSIL TAXA USED IN PHYLOGENETIC ANALYSIS  
Collection numbers of the specimens that were revised first-hand by the authors are added after the bibliographic reference.  
*Gracilisuchus stipanicorum* (Romer, 1972)  
*Terrestrisuchus gracilis* (Crush, 1984)  
*Dibothrosuchus elpahros* (Wu and Chatterjee, 1993; IVPP V 7907)  
*Protosuchus richardsoni* (Colbert and Mook, 1951; AMNH 3024, MCZ 6727, UCMP 130860, UCMP 131827)  
*Hemiprotosuchus leali* (Bonaparte, 1971; PVL 3829)  
Kayenta form (Clark, 1986; UCMP 97638, 125359, 125871)

*Orthosuchus stormbergi* (Nash, 1975; SAM-K 409)  
*Gobiosuchus kielanae* (Osmólska, 1972; ZPAL MgR-II/67, MgR-II/68, MgR-II/69, MgR-II/70, MgR-II/71)  
*Shantungosuchus hangjinensis* (Wu et al., 1994b)  
*Sichuanosuchus shuhanensis* (Wu et al., 1997; IVPP V 10594)  
*Zosuchus davidsoni* (IGM 100/1304, 100/1305, 100/1306, 100/1307, 100/1308)  
Fruita form (Clark, 1985, 1994; LACM 120455a)  
*Hsisosuchus chungkingensis* (Young and Chow, 1953; Li et al., 1994; Wu et al., 1994a; cast of CNM V 1090)  
*Notosuchus terrestris* (Gasparini, 1971; MACN-RN 1037)  
*Comahuesuchus brachybuccalis* (Bonaparte,

- 1991; MUC-PV 202; MACN-N 30, 31; MOZ P 6131)  
*Uruguaysuchus aznarezi* (Rusconi, 1933)  
*Chimaeresuchus paradoxus* (Wu and Sues, 1996; IVPP V8274)  
*Malawisuchus mwakasyunguti* (Clark et al., 1989; Gomani, 1997; MAL 45, 49)  
*Candidodon itapecurensis* (Carvalho, 1994)  
*Simosuchus clarki* (Buckley et al., 2000; UA 8679)  
*Sphagesaurus huenei* (Price, 1950; Pol, in press; RCL 100)  
*Araripesuchus gomesii* (Price, 1959; AMNH 24450)  
*Araripesuchus patagonicus* (Ortega et al., 2000; MUC-PV 269, 270)  
*Baurusuchus pachecoi* (Price, 1945; DGM 299-R)  
*Bretesuchus bonapartei* (Gasparini et al., 1993; PVL 4735)  
*Iberosuchus macrodon* (Antunes, 1975; Ortega et al., 2000)  
*Theriosuchus pusillus* (Owen, 1879; Clark, 1986, 1994; Ortega et al., 2000)  
*Alligatorium* (Wellnhofer, 1971; Clark, 1986, 1994)  
*Eutretauranosuchus delfsi* (Mook, 1967; Clark, 1986, 1994; AMNH 570)  
*Goniopholis* (Mook, 1942; Clark, 1986, 1994; Salisbury et al., 1999; AMNH 5782)  
*Pholidosaurus decipiens* (Owen, 1878; Clark, 1986, 1994)  
*Dyrosaurus phosphaticus* (Buffetaut, 1978; Clark, 1986, 1994)  
*Pelagosaurus typus* (EudesDeslongchamps, 1863; BSP 1890.I.5)  
Teleosauridae (Buffetaut, 1982; Clark 1986, 1994; AMNH 5138, BSP 1945.XV.1, GPIT Auer-1909-f.22, MB 1921.12)  
Metriorhynchidae (Kälin, 1955; Gasparini and Diaz, 1977; AMNH 997, BSP AS.I.504, MACN-N 95, SMNS 10116)  
*Hylaeochampsia vectiana* (Clark and Norell, 1992; Ortega et al., 2000)  
*Bernissartia fageysi* (Buscalioni and Sanz, 1990; Norell and Clark, 1990)  
*Borealosuchus formidabilis* (Erickson, 1976; Brochu, 1997b)  
*Gavialis gangeticus* (Clark, 1994; Brochu, 1997a)  
*Crocodylus niloticus* (Clark, 1994; Brochu, 1997a)  
*Alligator mississippiensis* (Clark, 1994; Brochu, 1997a)

## APPENDIX 4

## ANATOMICAL ABBREVIATIONS

ach	anterior choana	occ	occipital condyle
ad	anterior diastema	otocc	otoccipital
alv	alveolar groove	pal	palatine
ang	angular	par	parietal
aof	antorbital fenestra	pch	posterior choana
apal	anterior palpebral	pd	posterior diastema
bocc	basioccipital	pmx	premaxilla
bsf	basisphenoid	po	postorbital
can	lower caniniform tooth	ppal	posterior palpebral
chg	choanal groove	prf	prefrontal
den	dentary	pt	pterygoids
fr	frontal	q	quadrate
j	jugal	qf	quadrate fenestrae
lac	lacrimal	qj	quadratojugal
ltsf	laterosphenoid	sang	surangular
mx	maxilla	sob	suborbital fenestra
nar	external nares	socc	supraoccipital
nas	nasal	spl	splenic
ntc	premaxilla-maxilla notch	sq	squamosal
		stfo	supratemporal fossa
		sym	mandibular symphysis