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A New Gobiosuchid Crocodyliform Taxon from the Cretaceous of Mongolia

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ABSTRACT

We describe a new fossil crocodyliform, *Zaraasuchus shepardi*, found in the Cretaceous Red Beds of Zos Canyon (Gobi Desert, Mongolia). *Z. shepardi* shares numerous derived characters with *Gobiosuchus kielanae*, also known from the Late Cretaceous of Mongolia (Bayn Dzak locality). However, it is distinguished from the latter by the presence of a moderately large infratemporal fenestra, anterior margin of infratemporal fenestra almost completely formed by the postorbital, retroarticular process with a well-developed ornamented posterolateral pointed process, and extremely well-developed keels on dorsal and lateral cervical osteoderms (the heights of which are approximately as long as the lateromedial extension of the dorsal osteoderms).

A phylogenetic analysis indicated that these two taxa form a monophyletic group located basally among crocodyliforms. This clade is diagnosed by 14 synapomorphies (e.g., anterior and posterior palpebrals sutured to each other and to the frontal, excluding it from the orbital margin, external surface of ascending process of jugal exposed posterolaterally, dorsal surface of posterolateral process of squamosal ornamented with three longitudinal ridges, dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges, cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements, and closed supratemporal fenestra).

INTRODUCTION

Numerous fossil vertebrates were found during the last decade by joint expeditions of the Mongolian Academy of Sciences and the American Museum of Natural History to Cretaceous beds of the Gobi Desert (Dashzeveg et al., 1995; Novacek, 1996, 2002). Fossil crocodyliforms from these beds are not abundant, although several taxa have

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been described (see Storrs and Efimov, 2000; Pol and Norell, 2004).

Here we report a new form from Zos Canyon, a poorly known locality, yet one that is rich in crocodyliforms. Recently we described another taxon, *Zosuchus davidsoni*, from the same beds (Pol and Norell, 2004). The phylogenetic relationships of these taxa are analyzed through a parsimony analysis in the context of Crocodyliformes. The new taxon, *Zaraasuchus shepardi*, shares several derived characters with *Gobiosuchus kielanae*, forming with the latter a basal crocodyliform clade. This is in accordance with the previous hypotheses of the relationships of *Gobiosuchus kielanae* (Clark, 1986; Ortega et al., 2000; but see Wu et al., 1997).

The following acronyms are used throughout this work:

AMNH	American Museum of Natural History, New York
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, Münich, 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, Universitat Tübingen, Tübingen, Germany
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, CA
MAL	Malawi Department of Antiquities, Malawi
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MAL	Malawi Department of Antiquities, Malawi
MB	Institut für Palaontologie, Museum fur Naturkunde, Humbolt-Universitat, 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 Catolica 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, CA
ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA WALKER, 1970

CROCODYLIFORMES HAY, 1930 (SENSU CLARK, 1986)

GOBIOSUCHIDAE OSMÓLSKA, 1972

Zaraasuchus shepardi, new genus, new species

HOLOTYPE: IGM 100/1321, posterior region of the skull and lower jaws preserved in articulation with cervical vertebrae, osteoderms, and forelimb elements.

ETYMOLOGY: *Zaraa*, Mongolian for hedgehog in reference to the spiny character of the skull and osteoderms, and *shepardi*, in reference to Dr. Richard Shepard, a friend of the expedition for many years.

DIAGNOSIS: Small crocodyliform diagnosed by the following combination of characters: sculptured skull bones that are ornamented with thin and continuous ridges; anterior margin of infratemporal fenestra almost completely formed by the postorbital; retroarticular process with a pointed, well-developed posterolateral process, the surface of which is ornamented; extremely well-developed keels on dorsal and lateral cervical osteoderms, the heights of which are approximately equal in length to the lateromedial extension of the dorsal osteoderms.

DESCRIPTION

SKULL

The skull of IGM 100/1321 has most of its dorsal and lateral postorbital elements in articulation with the posterior region of the lower jaws (figs. 1, 3). *Zaraasuchus shepardi*

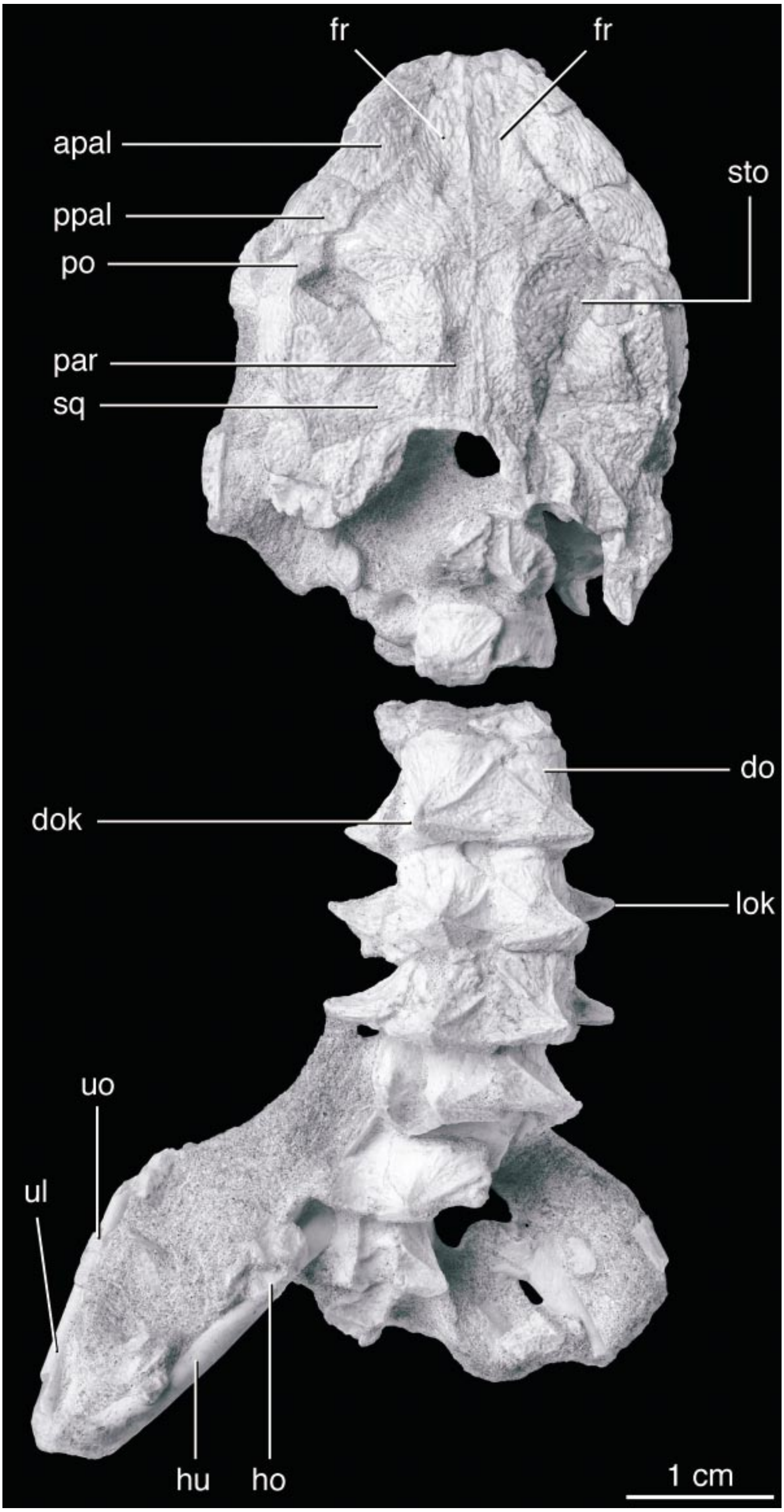

Fig. 1. Holotype of *Zaraasuchus shepardi* IGM 100/1321 in dorsal view.

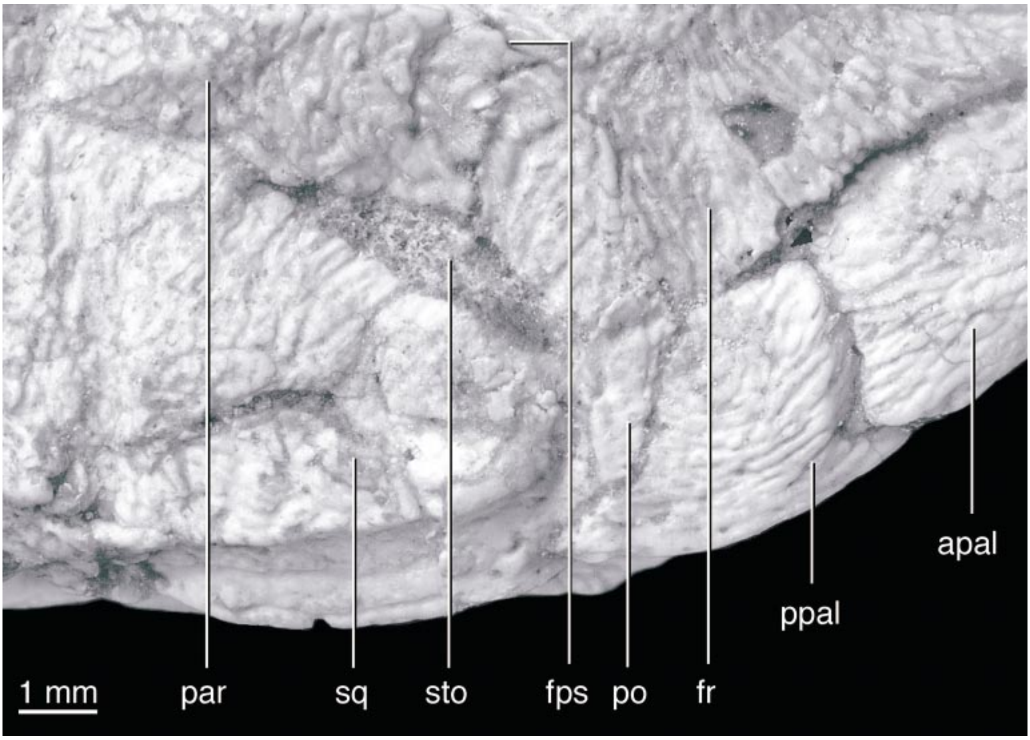

Fig. 2. Right supratemporal region of *Zaraasuchus shepardi* IGM 100/1321 in dorsal view.

has large, laterally facing orbits. The supratemporal fenestrae are almost completely obliterated by a lateral expansion of the parietals and frontals and by a medial expansion of the squamosals. These expansions are depressed in respect to the rest of the skull roof, although this could be a preservational artifact. A narrow oblique slit between the squamosal, parietal, and frontal is the only remnant of the supratemporal opening (figs. 1, 2). This differs from the derived condition seen in *Gobiosuchus kielanae*, where the supratemporal fenestra is completely closed and the squamosal and parietals are sutured along their entire length (ZPAL MgR-II/68 and 69). This character, however, is probably subject to ontogenetic change. In some living crocodylians (*Osteolaemus tetraspis* and *Paleosuchus trigonatus*) the supratemporal fenestrae may close during ontogeny. The infratemporal fenestra is reduced due to the wide ascending process of the quadratojugal (fig. 3). This fenestra, however, is not as reduced as in *Gobiosuchus kielanae* (ZPAL MgR-II/67), since the postorbital process and the infratemporal bar of the jugal are not as wide in *Zaraasuchus shepardi* as in *Gobiosuchus kielanae*. The skull table is very broad, being as wide as the infratemporal region, as in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/67, 68, and 69) and *Sichuanosuchus shuhanensis* (Wu et al., 1997; IVPP V 10594). The external surface of the skull is ornamentated with a unique pattern of extremely thin ridges and grooves. These thin ridges are more marked and continuous in comparison with the slightly marked ornamentation preserved in some of the specimens of *Gobiosuchus kielanae* (ZPAL MgR-II/67 and 69), although this difference could relate to preservational or ontogenetic causes. However the more marked sculpture of the cranium in *Zaraasuchus shepardi* suggests a more advanced ontogenetic stage than that of specimens of *Gobiosuchus kielanae*, while the previous character of an open supratemporal fenestra suggests a younger comparable stage.

A large anterior **palpebral** forms most of the dorsal margin of the orbit of *Zaraasuchus*

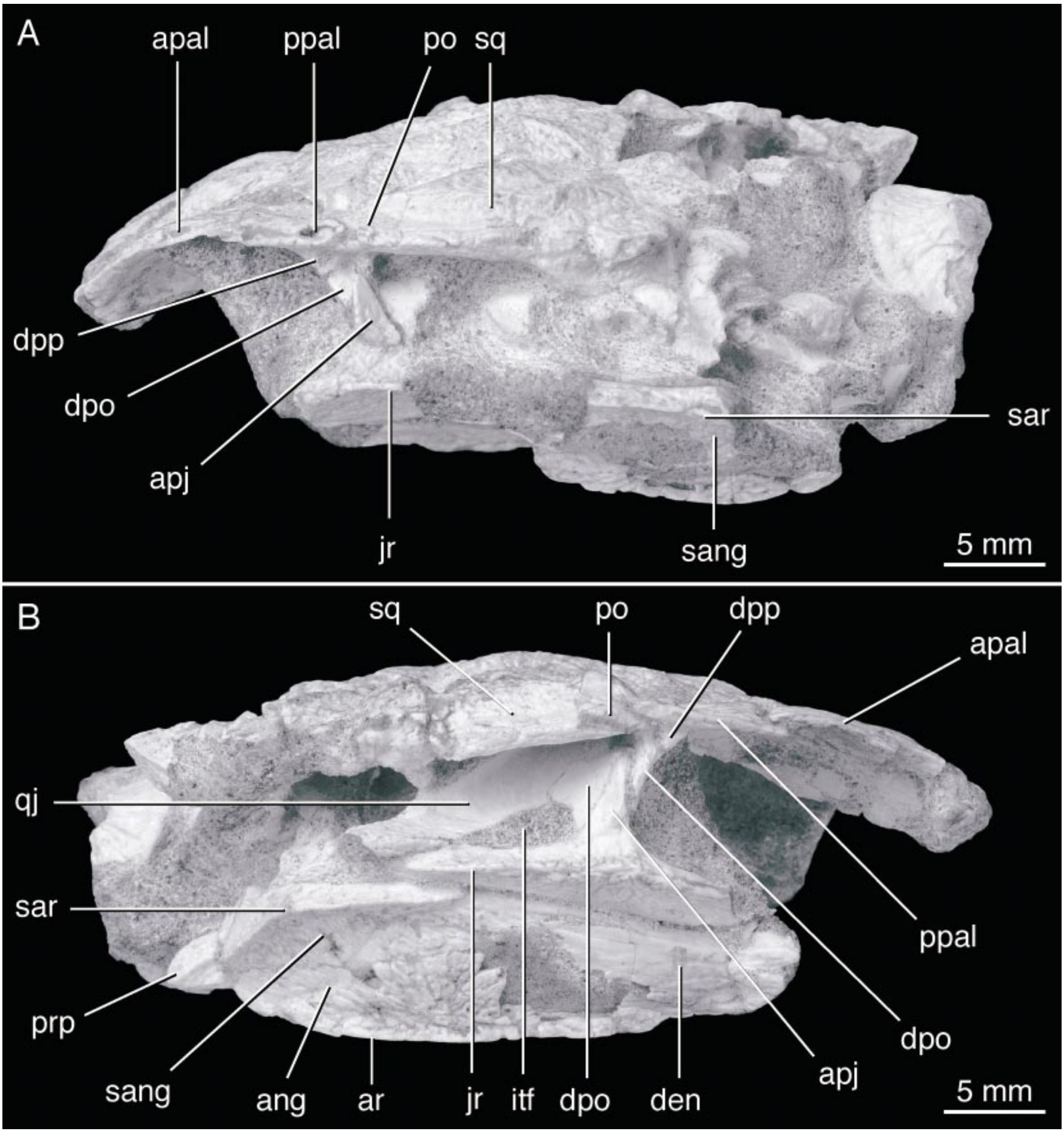

Fig. 3. Skull of the holotype of *Zaraasuchus shepardi* IGM 100/1321 in (A) left lateral view; (B) right lateral view.

shepardi. The palpebral is tabular rather than triangular as in all crocodyliforms. Its anterior contact with the prefrontal is not preserved in IGM 100/1321. The dorsal surface of this element is heavily sculptured with thin ridges and is sutured to the frontal along its medial margin (fig. 1) excluding the frontals from the orbital margin. Its posterior margin is sutured to the the posterior palpebral (fig. 1), extensively overlapping the depressed articular facet of this element (figs. 2, 3). A similar morphology is present in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/68), although in this form the two palpebrals are completely fused and more tigthly sutured to the frontal.

The posterior palpebral is much shorter than the anterior element (fig. 1). This palpebral dorsally covers the posterior part of the orbit and is firmly sutured to the postorbital and the frontal. The large anterior palpebral overlaps a depressed facet of the posterior palpebral. Its medial edge contacts the frontal along a straight and posterolaterally directed suture. The posterior edge of this palpebral overlaps the postorbital and projects a pointed posterolateral process along the lateral edge of the postorbital (figs. 1, 3). On its ventral surface, the posterior palpebral has a short descending process that anteriorly covers the dorsal end of the descending postorbital bar (figs. 3, 6).

The **frontals** are not completely fused as in some specimens of *Gobiosuchus kielanae* (ZPAL MgR-II/67 and 68) and other basal crocodyliforms (e.g., *Protosuchus* AMNH 3024; *Orthosuchus* SAM-K 409). The anterior half of the suture between the frontals is straight, while the posterior third of this suture is interdigitated (fig. 1). Between these two regions, the suture is not visible and the frontals seem to be fused, at least superficially. The interfrontal suture extends along a slightly elevated ridge, similar to that present in one of the specimens of *Gobiosuchus kielanae* that has fused frontals (ZPAL MgR-II/69) and several other basal mesoeucrocodylians. The dorsal surface of these elements is ornamented with thin ridges which radiate from the interfrontal suture. The frontals are posteriorly broad at their contact with the parietal and postorbital and they narrow anteriorly markedly, with their straight lateral edges forming an acute angle (fig. 1), resembling the condition of *Gobiosuchus kielanae* (ZPAL MgR-II/68).

The posterior contact with the parietal is transverse on the medial elevated region of the skull roof. It projects slightly anteriorly along the medial margin of the supratemporal depression and then is directed laterally, entering into the supratemporal depression where it continues to the slitlike supratemporal opening (fig. 2). The frontal forms the anterolateral margin of the supratemporal slit and meets the postorbital at the anteriormost tip of this opening. Anterior to this point, the frontal narrows, laterally contacting the palpebrals through a robust suture excluding the frontal from the orbital margin (fig. 1). The anterior tip of the frontal and its contact with the prefrontal and nasals are not preserved in IGM 100/1321.

The ventral surface of the frontal has an extremely well-developed crista cranii (fig. 4). The space between them, which enclosed the olfactory tract of the forebrain, is very narrow, and it was probably closed ventrally by a ventromedial extension of the cristae cranii or an ossification fused to them (fig. 4). This peculiar condition is also found in *Gobiosuchus kielanae* (ZPAL MgR-II/68).

The **parietals** are fused into a single element as in all crocodyliforms (fig. 1). Their dorsal surface is ornamented like the rest of the skull roof and bears a slight longitudinal ridge, which is also found in *Gobiosuchus kielanae* and several other basal crocodyliforms. The medial region of its dorsal surface is flat, resembling the condition of most crocodyliforms. This area is bordered by two laterally concave ridges which demarcate the flat dorsal surface of the skull table from the supratemporal depressions (figs. 1, 2).

The parietal is broad at its anterior edge and continuously narrows toward the occipital margin of the skull, as in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/68). The anterolateral edge of the parietal forms the posterormedial margin of the supratemporal slit opening and contacts the squamosal at the posteriormost tip of this aperture (fig. 2). Posteriorly, the squamosal-parietal suture is straight and extends posteromedially along the supratemporal depression. This suture continues in the same direction posterior to the supratemporal depression reaching the posterior edge of the skull roof (fig. 1). Only the right side of the posterior margin of the parietal is preserved in IGM 100/1321. In this region, the parietal has a posterolaterally directed crest running from the medial ridge to the squamosal-parietal suture, close to its posterior end (fig. 1). Unfortunately, in this specimen, it cannot be determined if the parietal extended onto the occipital region of the skull.

The dorsal surface of the **squamosal** is very long and roughly triangular, with its apex directed anteriorly. Its dorsal surface has the same ornamentation pattern as the rest of the skull roof (fig. 1). Anteriorly it forms the lateral part of the supratemporal depression and laterally it overhangs the otic

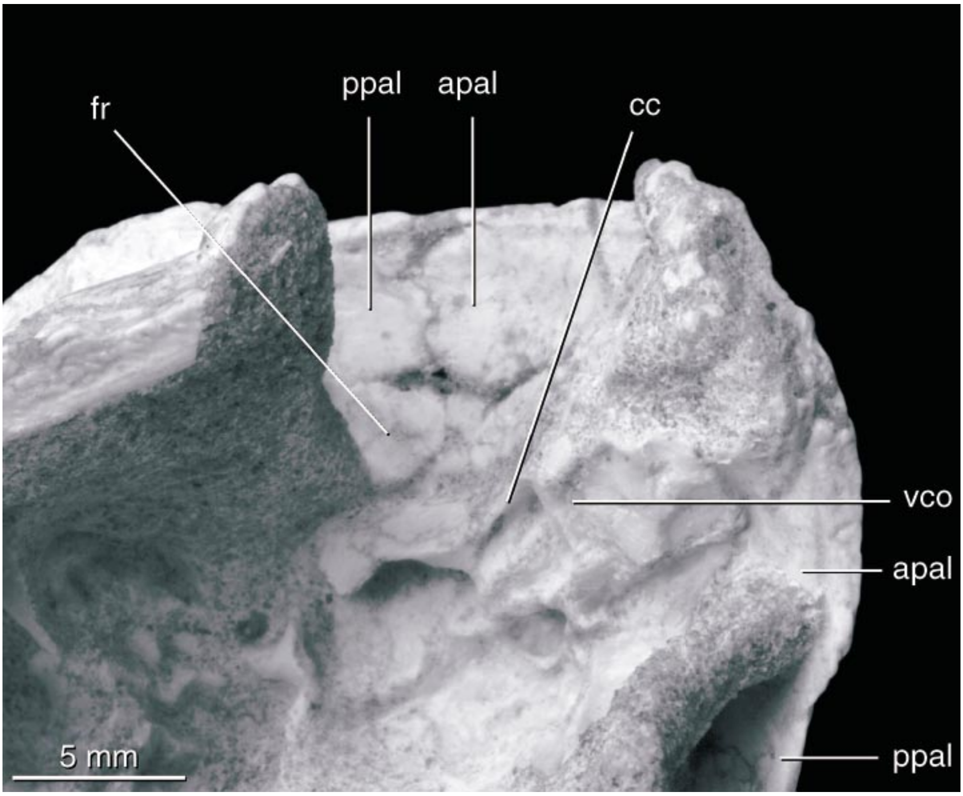

Fig. 4. Ventral surface of frontals of *Zaraasuchus shepardi* IGM 100/1321.

recess as in most crocodyliforms. As described previously, the squamosal contacts the parietal along an anterolaterally directed suture, entering the supratemporal depression near the posterior end of the supratemporal slit. Anterior to this point, the squamosal forms the lateral margin of the reduced supratemporal opening (fig. 2). The squamosal contacts the postorbital at the anterior apex of the supratemporal opening, where this bone overlaps the squamosal. The squamosal facet receiving the postorbital extends ventral to it, reaching the base of the descending process of the postorbital (fig. 3). On the dorsal surface of the skull, the postorbital-squamosal contact is directed posterolaterally within the supratemporal depression toward the lateral edge of the skull roof (fig. 2). This is in contrast to the laterally directed suture of *Gobiosuchus kielanae* (ZPAL MgR-II/69).

The skull roof is separated from the lateral edge of the squamosal by a well-developed longitudinal ridge that runs along most of the length of the squamosal (figs. 1, 3). Lateral to this ridge, the lateral edge of the squamosal has a wide, concave surface exposed laterodorsally (fig. 3A). This longitudinal ridge and the wide concave surface ventral to it closely follows the morphology preserved in one of the specimens of *Gobiosuchus kielanae* (ZPAL MgR-II/69) and resembles the groove for the attachment of the movable dorsal earflap on the squamosal of extant crocodylians. In *Zaraasuchus shepardi*, this concave surface is smooth, except for the presence of several slightly marked grooves. The ventral margin of the lateral surface of the squamosal bears a narrow and deep groove near its ventral margin which is preserved only on the right side of IGM 100/1321 (fig. 3B). Posterior to the supratemporal depression, the concave lateral surface of the squamosal opens onto the dorsal surface of the skull due to a medial deflection of the longitudinal ridge that forms its dorsal margin (figs. 1, 3A).

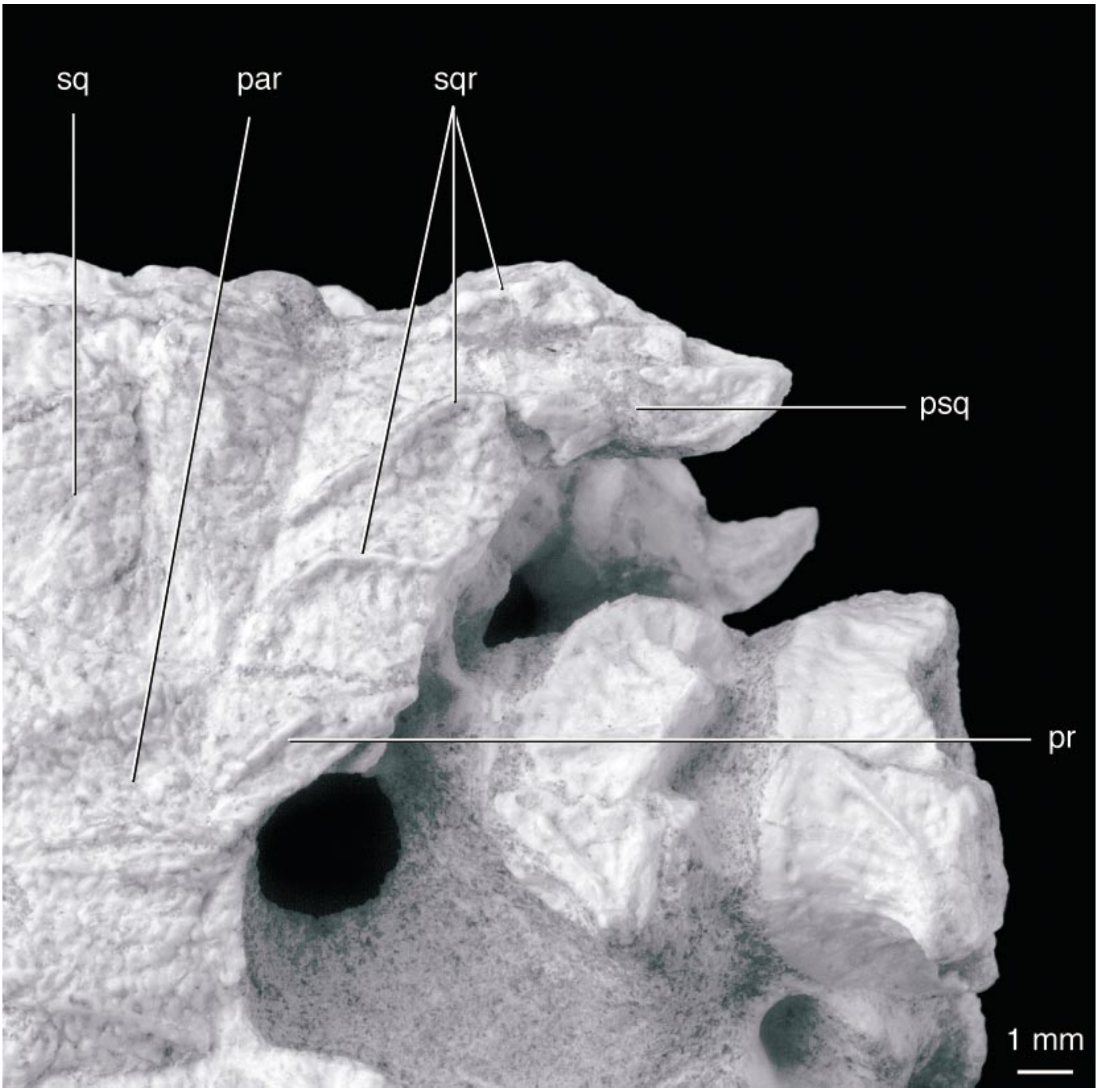

Fig. 5. Right posterolateral process of the squamosal of *Zaraasuchus shepardi* IGM 100/1321 in dorsal view.

The dorsal surface of the squamosal posterior to the supratemporal depression is bordered anteriorly by a transversal groove. This is not present in any of the *Gobiosuchus kielanae* specimens, yet it might be accentuated by preservation, although it is present on both squamosals in a symmetrical way (fig. 1). Posterior to this transverse groove, the squamosal bears a long posterolateral process that, as in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/68), extends to reach the level of the posterior end of the mandibular ramus. The dorsal surface of this long process is ornamented and bears three well-developed and sinuous crests oriented longitudinally near its base (fig. 5). This region is poorly preserved in all the specimens of *Gobiosuchus kielanae*; however, the specimen ZPAL MgR-II/68 preserves the internal mold of the posterolateral processes of the squamosals showing similar, yet not identical, ridges on its dorsal surface. The distal end of the posterolateral process of the squamosal is distinctly outurned, as in the type specimen of *Gobiosuchus kielanae* (ZPAL MgR-II/67). Despite these similarities, in *Zaraasuchus shepardi* the posterolateral process of the squamosal is directed horizontally, approximately at the same level as the skull roof, while in *Gobiosuchus kielanae* (ZPAL MgR-II/68) and more derived crocodyliforms it is ventrally deflected.

Unfortunately, the occipital flange of the squamosal and its descending process have not been preserved in IGM 100/1321.

The dorsal surface of the **postorbital** is a narrow and curved bar which forms the anterolateral margin of the skull roof (fig. 1). Posteriorly the postorbital overlaps a depressed articular surface of the squamosal. here the dorsal surface of the postorbital is smooth and slightly concave, continuous with the dorsolateral concave surface of the squamosal. Medial to this surface the postorbital surface is ornamented and borders the squamosal near the supratemporal slit opening, of which it forms the anterior apex (fig. 2). In *Gobiosuchus kielanae* (ZPAL MgR-II/68) the postorbital contacts the parietal at its posteromedial corner, while in *Zaraasuchus shepardi* this contact is not present, probably due to the presence of the vestigial supratemporal opening. Anterior to the supratemporal slit margin, the medial area of the postorbital dorsal surface contacts the frontal overlapping this element (figs. 1, 2). The anterolateral margin of the dorsal surface of the postorbital is convex and contacts the posteror palpebral along most of its anterior margin.

The descending process of the postorbital is covered anteriorly by the descending process of the posterior palpebral (fig. 6). Ventrally, the descending process of the postorbital is a flat and smooth lamina of bone that extends medially to the ascending process of the jugal, reaching almost to the base of the postorbital bar. This thin and laminar postorbital bar is not exposed laterally as in most basal crocodyliforms, but projects posteriorly (thus facing posterolaterally). A similar condition is also present in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/67). The postorbital forms most of the anterior margin of the infratemporal fenestra, a condition that differs from the interpretation

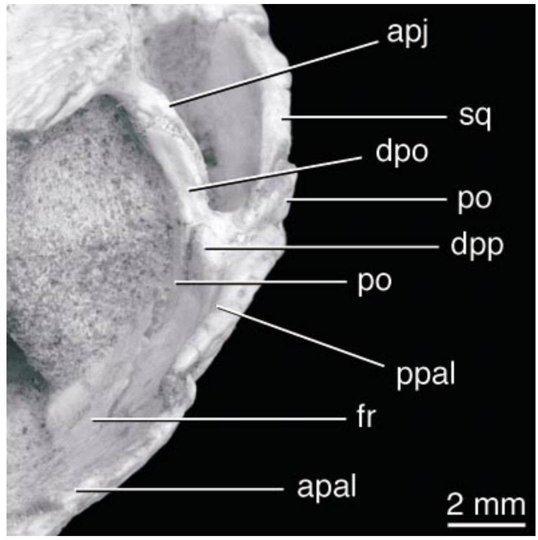

Fig. 6. Ventral surface of the postorbital of *Zaraasuchus shepardi* IGM 100/1321.

of Osmólska et al. (1997) concerning the condition in *Gobiosuchus kielanae* (although this region is poorly preserved in all the ZPAL specimens of this taxon). The posterior edge of the descending process of the postorbital extensively contacts the quadratojugal, reaching the posterodorsal margin of the infratemporal opening. The broad participation of the postorbital in the posterodorsal margin of the infratemporal fenestra in *Zaraasuchus shepardi* is very different from the condition in *Gobiosuchus kielanae* (Osmólska et al., 1997).

The **jugal** is preserved anterior to the postorbital bar and closely resembles the morphology of *Gobiosuchus kielanae*. The lateral surface of this region is exposed lateroventrally, resembling *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/67). This surface is distinctly ornamented with slightly marked, thin grooves, except for its ventral margin, which is smooth (fig. 3A, B).

The ascending process of the jugal is, like the descending process of the postorbital, a flat lamina facing posterolaterally. Its anterolateral edge is sharp and superficial, while its posterior edge is inset medially from the lateral ridge of the jugal (fig. 3). This laminar process is compressed anteromedial–posterolaterally, but is wide along its posteromedial–anterolateral axis. This peculiar morphology is identical to that of *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/67, 69). The base of the postorbital process of the jugal is ornamented along its anterolateral edge, as in basal crocodyliforms, but it is distinctly smooth on its posteromedial region (fig. 3). The ornamentation of this region cannot be determined in any specimen of *Gobiosuchus kielanae* due to poor preservation.

Below the postorbital ascending process, the external surface of the jugal bears a well-defined longitudinal ridge that divides the jugal into a dorsal surface facing dorsomedially and a ventral surface facing ventrolaterally (fig. 3). The latter is continuous with the external surface of the suborbital process of the jugal and bears the same ornamented pattern bordered ventrally by a smooth margin. The dorsal surface is less ornamented, although there are some slightly marked ridges and grooves on its anterior end. The dorsal edge of this region of the jugal forms the entire ventral margin of the infratemporal fenestra and contacts the quadratojugal at the posterior corner of this opening (fig. 3). Posterior to the infratemporal fenestra, the extensive jugal-quadratojugal projects posteroventrally, probably approaching the quadrate condyles (not preserved in IGM 100/1321).

This region of the jugal is also identical to that of *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/68 and 69), except for the ornamentation pattern that is barely present in this taxon (possibly due to preservational causes). A similar longitudinal ridge on the infratemporal region of the jugal is also present in *Sichuanosuchus shuhanensis* (IVPP V 10594), but this taxon lacks the other similarities of the jugals of *Zaraasuchus shepardi* and *Gobiosuchus kielanae*.

The **quadratojugal** is preserved on the right side of IGM 100/1321. The quadratojugal's posteroventral region is thickened and sculpted at its contact with the jugal (fig. 5B). The ascending process is broad and directed anterodorsally as in basal crocodyliforms. This region forms most of the posterior edge of the infratemporal fenestra and its surface is smooth. It contacts the postorbital extensively dorsally to the infratemporal fenestra (fig. 5B). Unfortunately, its posterior contact with the quadrate has not been preserved.

MANDIBLE

Only the posterior regions of the mandibular rami of *Zaraasuchus shepardi* are preserved in IGM 100/1321. Most of the lateral and ventral surfaces are ornamented with a similar pattern to the skull bones (fig. 3). The mandibular ramus is dorsoventrally high and the external mandibular fenestra is completely closed, a condition only present in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/69) among basal crocodyliforms, but also present in some derived mesoeucrocodylians (e.g., atoposaurids, some goniopholids, *Bernissartia*).

Only the posterior end of the right **dentary** is preserved in IGM 100/1321. Its lateral surface is smooth and bears a single, small neurovascular foramen. The dorsal region of the lateral surface of the dentary below the orbits is projected medially, being exposed laterodorsally rather than laterally (figs. 3, 4). This would produce an inset mandibular toothrow, similar to the condition of most non-neosuchian crocodyliforms. Posteriorly, the dentaries contact the surangular to the level of the postorbital bar and they seem to extensively overlap the angular, although this contact is not well preserved.

The **angular** is heavily ornamented and forms most of the ventral half of the lateral surface of the mandibular ramus (fig. 3). Dorsally, the angular is bordered by the surangular, and the suture between them extends posteriorly and is deflected slightly ventrally near the posterior end of the mandibular ramus (fig. 3). The ventral edge of the angular bears a sharp and well-defined longitudinal ridge dividing the lateral surface from a ventromedially facing surface of the angular (fig. 7B). This morphology is not known in other crocodyliforms except for *Gobiosuchus kielanae* (ZPAL MgR-II/68), although *Shantungosuchus hangjinensis* seems to have a similar, but less developed condition (Wu et al., 1994a). This ridge is directed posteriorly along a horizontal plane (fig. 3), in contrast to the condition in derived crocodyliforms where the angular is deflected dorsally. The

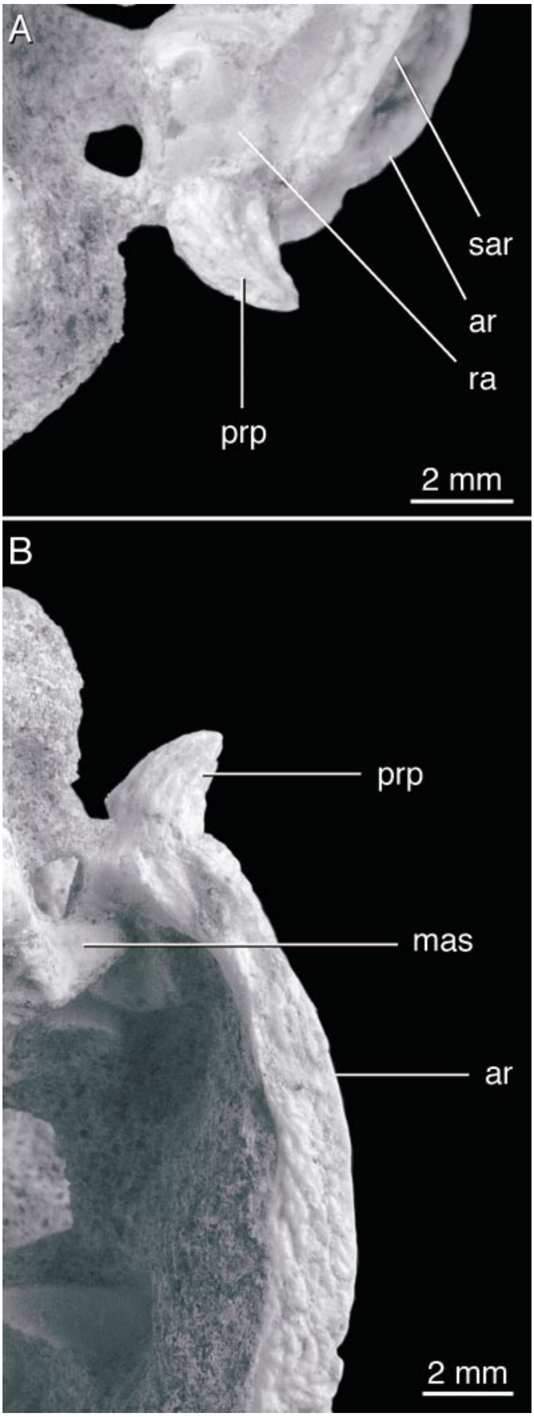

Fig. 7. Posterior region of the mandibular ramus of *Zaraasuchus shepardi* IGM 100/1321 in (A) posterolateral view; (B) ventral view.

posterior end of the angular reaches the level of the quadrate-mandibular articulation.

The **surangular** anteriorly contacts the posterodorsal region of the dentary near the dorsal margin of the lower jaw at the level of the postorbital bar. Posterior to this point the surangular bows slightly to form the dorsal margin of the mandible. The lateral surface of the surangular is heavily ornamented and has a sharp, prominent ridge that extends posteroventrally from its dorsal margin (at the level of the posterior edge of the infratemporal fenestra) up to the level of the cranio-mandibular articulation (figs. 3, 7A). Posterior to this point, the ridge ventrally deflects abruptly, forming the lateral border of the reduced retroarticular process (figs. 3, 7A). A similar feature is also present in *Gobiosuchus kielanae* (Osmólska et al., 1997; ZPAL MgR-II/68) and *Sichuanosuchus shuanensis* (IVPP V 10594). Medial to this ridge, the surangular is exposed laterodorsally and is slightly ornamented (fig. 7A). Its dorsomedial edge is smooth and forms the lateral wall of the articular surface for the quadrate condyles. Posterior to this point, this smooth surface of the surangular deflects ventrally, contacting the retroarticular process medially and the surangular ridge laterally (fig. 7A).

The dorsal surface of the **articular** is exposed posteriorly to the articular facets for the quadrate. The lateromedial extension of the articular surface is reduced although its medial extent is poorly preserved. Posteriorly, a reduced, flat, and triangular-shaped retroarticular process extends ventrally, resembling the condition seen in most basal crocodyliforms. The distal (posteroventral) end of the retroarticular process of *Zaraasuchus shepardi*, however, is uniquely autapomorphic in that it has a laterally curved conical process ornamented with slight ridges and grooves and four well-developed apically converging ridges. This condition is absent in *Gobiosuchus kielanae* (fig. 7).

The ventral surface of the articular has a dorsomedially directed shelf forming the support for the articular facet with the quadrate. This shelf is subtriangular and is slightly concave on its ventral surface. A similar process is present in *Gobiosuchus kielanae* (medial process of Osmólska et al., 1997);

however, it cannot be determined if the dorsomedial tip of this process contacted the basisphenoid in *Zaraasuchus shepardi*. Unlike in *Gobiosuchus kielanae*, the entire retroarticular region of the lower jaw of *Zaraasuchus shepardi* projects medially and is not ''squared-off'' (fig. 7B).

Postcranium

Several postcranial elements were found in association with the skull of IGM 100/1321. Some fragmentary cervical vertebral elements were crushed underneath the posterior end of the skull roof, including partially preserved neural arches and cervical ribs. A series of cervical osteoderms and a posterior cervical were found in articulation with the skull. Posterior to these elements, the left humerus and ulna were also preserved in association with appendicular osteoderms.

The best preserved postcranial elements are eight transverse rows of cervical **osteoderms** found in life articulation with the skull of IGM 100/1321. The first two rows of osteoderms seem to be composed exclusively of two dorsal osteoderms as in most basal crocodyliforms. These are heavily sutured to each other and have rounded lateral and anterior edges (fig. 8A). The dorsal surface of these osteoderms is ornamented with shallow and sinous grooves and have, near their posterior edge, a well-developed medial keel (fig. 8A, B). Five ridges radiate from this keel (two laterally, one anterolaterally, one medially, and one anteromedially). The posterior edge of the osteoderms imbricates with a thin smooth area of the posterior osteoderms.

Posterior to this first pair of osteoderms, six transverse rows are composed of two dorsal and two lateral osteoderms that are strongly sutured to each other. The dorsal pair of osteoderms has the same ornamentation pattern as the anterior ones, although the medial keel is much more developed and is directed dorsolaterally (fig. 8A, B). Additionally, an accessory ridge is present on the posterior surface of the medial keel (fig. 8A). The lateral osteoderms also have a well-developed lateral keel. This keel, however, is located extremely close to the sutures with the dorsal osteoderms, and the radiating ridges are not as developed and seem to be absent in some of the lateral osteoderms (fig. 8B).

Several ventral osteoderms are preserved in the cervical region, although slightly disarticulated. The ventral osteoderms are notably different from the dorsal elements. The ventral surface lacks well-developed keels and is ornamented with slightly marked grooves, except for the anteriormost region which is smooth and imbricates with the preceding element. A slight ridge is present on its ventral surface extending obliquely to the longitudinal axis of the osteoderm, which projects anterolaterally. These osteoderms were probably contacted to a corresponding pair along their medial margins, as in *Gobiosuchus kielanae* (ZPAL MgR-II/71).

The cervical dermal armor of *Zaraasuchus shepardi* is unique among crocodyliforms; however, it shares with *Gobiosuchus kielanae* several derived characters (fig. 8). First, the derived presence of lateral cervical osteoderms that are strongly sutured to a pair of dorsal osteoderms, and the presence of five radiating ridges on the dorsal surface of the osteoderms (fig. 8). The three anterior ridges were described as displaying a ''fleur de lys'' pattern by Osmólska et al. (1997). Other crocodyliforms have multiple ridges on their osteoderm dorsal surface (e.g., *Pristichampsus*), but their similarities with the osteoderms of *Zaraasuchus shepardi* and *Gobiosuchus kielanae* are only superficial.

Despite these similarities, the cervical dermal armor of *Zaraasuchus shepardi* is distinguished from that of *Gobiosuchus kielanae* by the presence of extremely elevated keels on the posterior edge of each osteoderm rather than a low ridge (ZPAL MgR-II/68, 71), the presence of a thin ridge directed parasagittally on the posterior surface of the osteoderm, and the ornamentation pattern of the dorsal surface of osteoderms composed by shallow grooves rather than by discrete pits (ZPAL MgR-II/71). Additionally, the first pair of osteoderms preserved in *Zaraasuchus shepardi* differs in being notably narrower and in lacking a lateral spur, although this pair of osteoderms might not be actually the first pair of *Zaraasuchus shepardi* (i.e., the ''nuchal'' osteoderms sensu Osmólska et al., 1997).

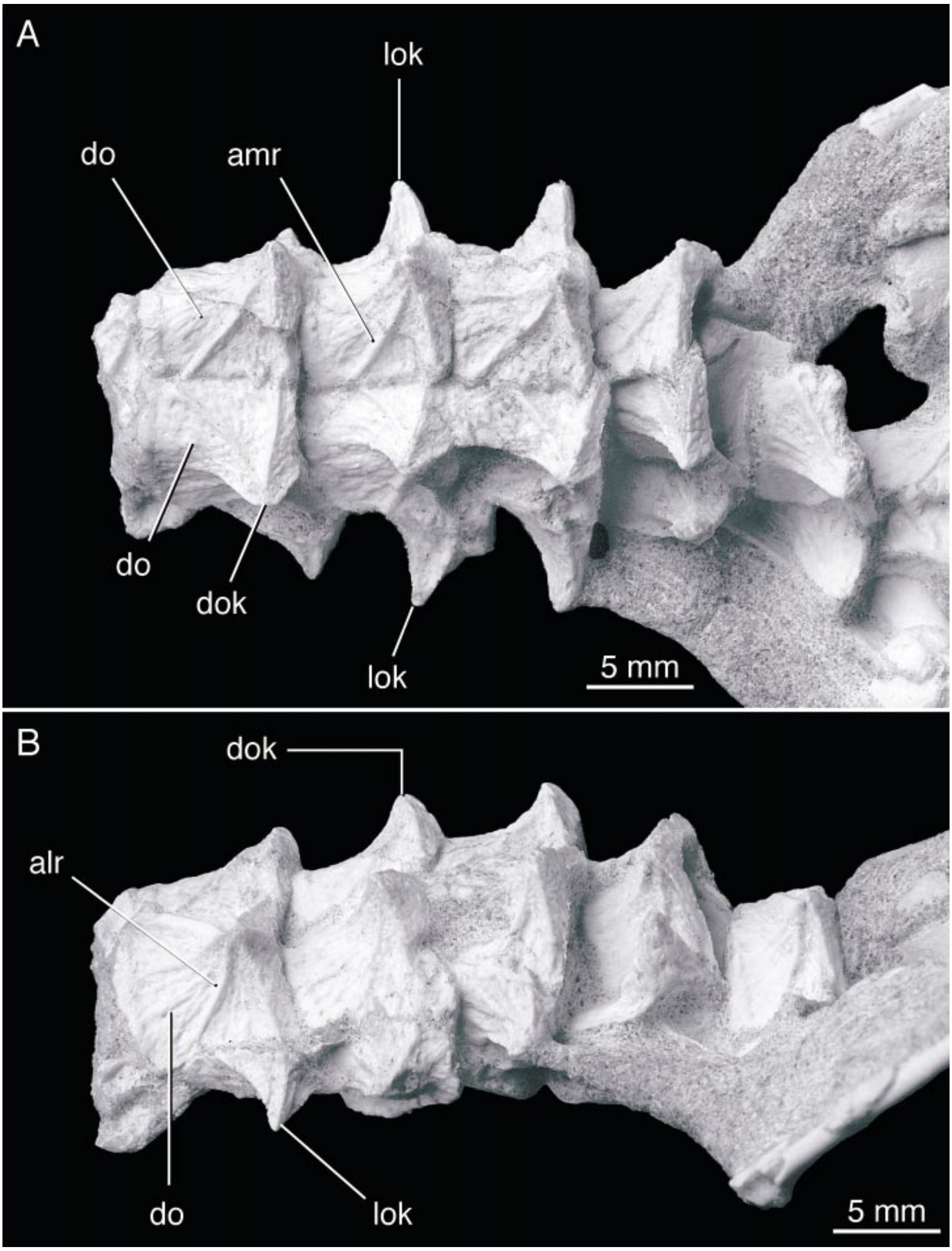

Fig. 8. Cervical osteoderms of *Zaraasuchus shepardi* IGM 100/1321 in (A) dorsal view; (B) lateral view

In *Gobiosuchus kielanae*, four smooth ventral osteoderms close the cervical region ventrally (Osmólska et al., 1997; ZPAL MgR-II/68), while in *Zaraasuchus shepardi* these elements are ornamented. This difference, however, is subject to ontogenetic variation and it is not possible to determine how many ventral osteoderms composed each transverse row in *Zaraasuchus shepardi* due to its poor preservation. It is important to note, however, that some features of *Gobiosuchus kielanae* are ontogenetically more ad-

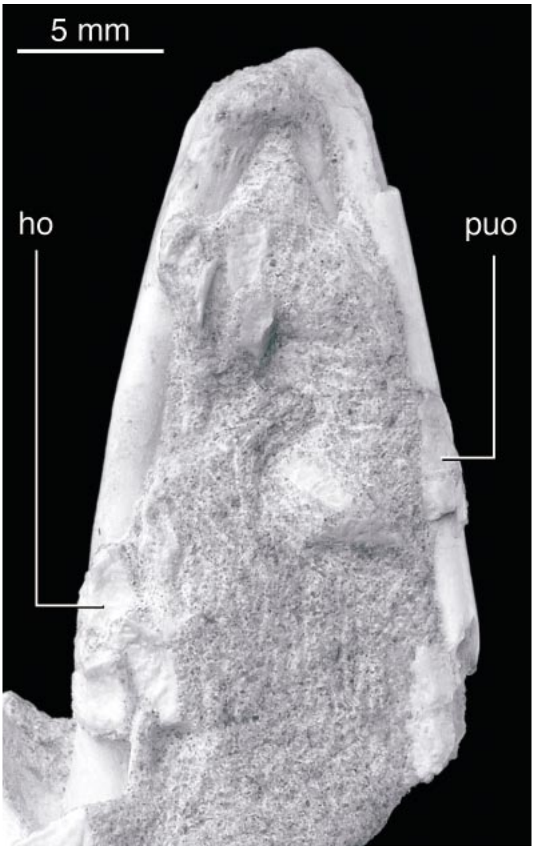

Fig. 9. Appendicular osteoderms of *Zaraasuchus shepardi* IGM 100/1321.

vanced (e.g., complete closure of the supratemporal fenestrae), than in *Zaraasuchus shepardi*.

In addition to the dorsal osteoderms, several small and subrectangular osteoderms were found on the dorsal surface of the humeral and ulnar shafts (fig. 9). The preserved humeral osteoderms are located near the proximal end of the humeral shaft. These are slightly ornamented with shallow grooves and a slightly marked ridge. The proximal osteoderm overlaps the element distal to it, although this might not be its natural position (fig. 9). Two osteoderms were preserved on the distal section of the ulnar shaft. These elements are less ornamented and more elongate than the humeral osteoderms (fig. 9). *Gobiosuchus kielanae* has appendicular osteoderms along the hindlimbs (ZPAL MgR-II/67 and 68); however, as noted by Osmólska et al. (1997), both limbs were probably covered by osteoderms, as suggested by the postition of similar disarticulated appendicular elements. The distribution of appendicular osteoderms among crocodyliforms has not been extensively studied, although it has been reported in some taxa, ranging from basal forms (CUP 2083; Wu, personal comun.) to goniopholids (*Sunosuchus*; Wu et al., 1996) and alligatorids (Cong et al., 1998).

The posterior cervical vertebra was found underneath the posteriormost preserved cervical osteoderms and was removed during preparation (fig. 10). The neural spine is dorsoventrally short and located posteriorly on the neural arch, although the anterior edge is poorly preserved (fig. 10A). The prezygapophyses are not preserved. The postzygapophyses are robust, short, and barely curved laterally (fig. 10A). Their articular facets are elevated and facing lateroventrally. A well-developed ridge extends anteriorly from the postzygapophyseal articular facets on the dorsal region of the lateral surface of the neural arch (fig. 10B). The neural canal is large in comparison with most crocodyliforms. The neurocentral suture is visible on the lateral surfaces of this cervical vertebra. Diapophyses are not well preserved, but a long ridge extends posteriorly from them, ventrally on the lateral surface of the neural arch (fig. 10C). Ventral to the diapophyseal ridges, a narrow concavity extends anteriorly on the lateral surface of the centrum between them and the parapophyses. The parapophyses are extremely well developed and projected laterovetrally (fig. 10B, D). A long ridge extends posteriorly to these, reaching the anteroposterior midpoint of the lateral surface of the centrum. The centrum of this vertebra is unusually long for a crocodyliform, being approximately three times longer than high. Its anterior end is notably more expanded than its posteiror end, mainly due to the well-developed parapophyses (fig. 10D). Its ventral surface is constricted at its midpoint and bears a small keel anteriorly, between the parapophyses (fig. 10D). None of the specimens of *Gobiosuchus kielanae* has well-exposed cervical vertebrae; however, as noted by Osmólska et al. (1997), the length of the neck in specimen ZPAL MgR-II/68 is remarkalbly long and composed by

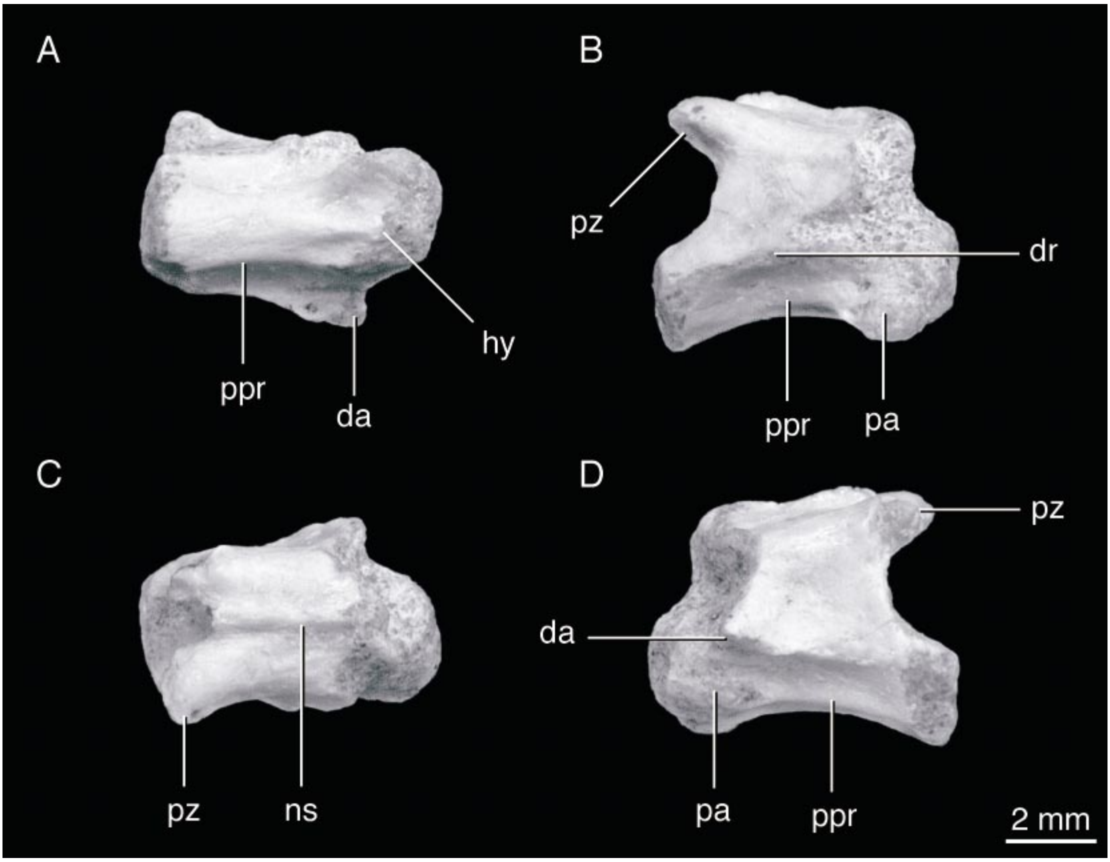

Fig. 10. Posterior cervical vertebra of *Zaraasuchus shepardi* IGM 100/1321 in (A) ventral view; (B) right lateral view; (C) left lateral view; (D) dorsal view.

seven postaxial vertebrae. This suggests that at least some of the cervical vertebrae of *Gobiosuchus kielanae* must be unusually long, as in *Zaraasuchus shepardi*.

Unfortunately, only the shafts of the humerus and the ulna are preserved in IGM 100/1321. As in *Gobiosuchus kielanae*, these forelimb elements are extremely long and slender (fig. 1), even longer than the elongate forelimbs of most basal crocodyliforms.

PHYLOGENETIC ANALYSIS

The phylogenetic relationships of *Zaraasuchus shepardi* were analyzed using a modification of a recently published dataset (Pol and Norell, 2004), which was based on the addition of several new characters to previously published matrices (Clark, 1994; Wu and Sues, 1996; Gomani, 1997; Wu et al., 1997; Buckley et al., 2000; Ortega et al., 2000). Twelve new characters were added to this dataset, resulting in a matrix of 192 characters scored across 45 taxa. As in our previous study, the taxon-sampling regime is focused on non-neosuchian crocodyliforms. In our analysis characters had equal weights 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-).

Two most parsimonious trees of 633 steps (CI = 0.37, CI_{inf} = 0.36, RI = 0.67) were found in 797 of 1000 replications. Further

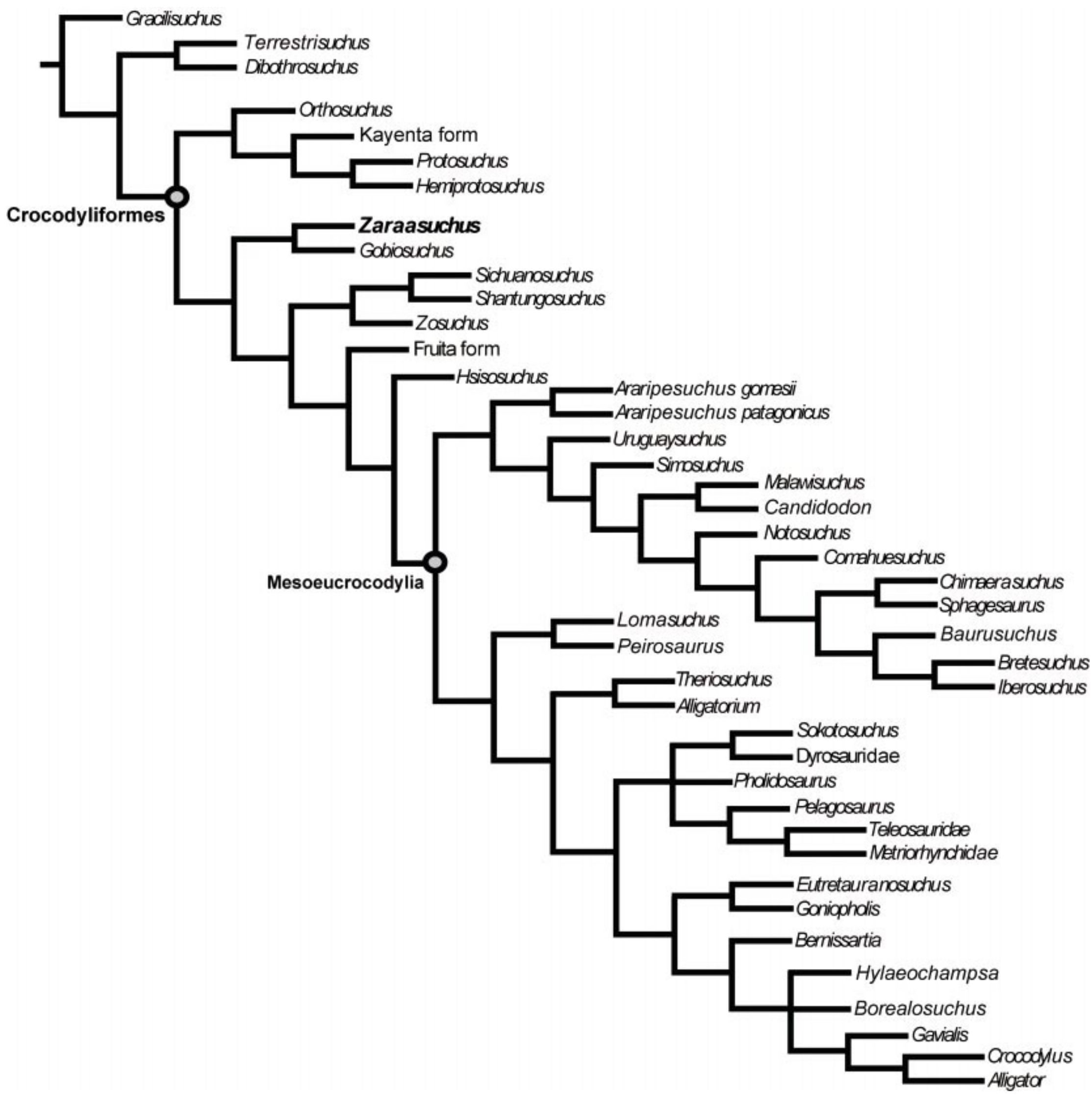

Fig. 11. Strict consensus of the two most parsimonious hypotheses obtained with Nona.

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 6190 times).

In all most parsimonious hypotheses, *Zaraasuchus shepardi* is depicted as the sister taxon of *Gobiosuchus kielanae*. Both of these gracile armored corcodyliforms are from the Late Cretaceous of Mongolia (fig. 11). This is a basal clade within Crocodyliformes and is diagnosed by 14 unambiguous synapomorphies (parietal without broad occipital portion [character 32]; absence of external mandibular fenestra [character 75]; more than two parallel rows of dorsal osteoderms [character 97]; cranial table as wide as ventral portion of skull [character 174; paralleled in *Sichuanosuchus*]; palpebrals sutured to each other and the frontal, excluding it from the orbital margin [character 181]; external surface of ascending process of jugal exposed posterolaterally [character 182]; longitudinal ridge on lateral surface of jugal below infratemporal fenestra [character 183; paralleled in *Sichuanosuchus*]; dorsal surface of posterolateral process of squamosal ornamented with three longitudinal ridges [character 184]; presence of a sharp ridge along ventral surface of angular [character 186; paralleled in *Shantungosuchus*]; surangular with a longitudinal ridge on its dorsolateral surface [character 187; paralleled in *Sichuanosuchus*]; dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges [character 188]; cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements [character 189]; presence of appendicular osteoderms [character 190; also present in other crocodyliforms, see above]; closed, or incipiently close, supratemporal fenestra [character 191]). Despite the large number of synapomorphies, support for this clade is low (Bremer support = 2). Most other nodes of these hypotheses also have minimal Bremer support values.

The phylogeny indicates that this clade is more closely related to mesoeucrocodylians than to *Protosuchus* and its allies (Protosuchidae sensu Clark, 1986) due to the presence of five synapomorphic characters (posterolateral process of squamosal elongated, posterolaterally directed, and ventrally deflected [character 36]; squamosal contacts quadrate and otoccipital lateral to cranioquadrate passage [character 49]; maxilla and premaxilla with ventral region facing laterally and dorsal region facing dorsolaterally [character 139]; quadratojugal ornamented at its base [character 145]; thick, pneumatic pterygoid flanges [character 166]).

Our results conflict with those of Wu et al. (1997), where *Gobiosuchus* was the sister taxon of two taxa from the Early Cretaceous of China (i.e., *Sichuanosuchus* and *Shantungosuchus*). Here, the clade composed by *Zosuchus*, *Sichuanosuchus*, and *Shantungosuchus* is depicted as more closely related to derived mesoeucrocodylians than to *Gobiosuchus kielanae* and protosuchids. This position is supported by six synapormorphies (fused frontals [character 20]; palatine shelves that extend below narial passage [character 37]; choana opens posteriorly into a midline depression (choanal groove) [character 39]; fusion of pterygoids posterior to choana [character 41]; presence of one enlarged maxillary tooth [character 79]; presence of a well-developed posterodorsal process of the premaxilla [character 125]). In our dataset, forcing a monophyletic group composed by this clade, *Gobiosuchus kielanae*, and *Zaraasuchus shepardi* requires five extra steps. Despite these signs of support for the derived position of this clade, there are a considerable number of shared derived similarities between *Gobiosuchus*, *Zaraasuchus shepardi*, and these taxa. In particular, *Sichuanosuchus* shares 3 of the 14 synapomorphies of the *Gobiosuchus kielanae* + *Zaraasuchus shepardi* clade (interpreted here as convergences, see above).

The monophyly of the clade traditionally referred as Protosuchia (i.e., including protosuchids, gobiosuchids, and the *Shantungosuchus* clade) is rejected in this analysis, although this clade is present in trees only two steps longer than the most parsimonious trees.

DISCUSSION

The presence of *Zaraasuchus shepardi* in Cretaceous beds of Mongolia provides further insight into the diversity achieved by basal crocodyliforms during the Cretaceous. This record, together with previously known taxa such as *Gobiosuchus kielanae* (from the Bayn Dzak locality), *Zosuchus davidsoni* (also from the Zos Canyon beds), and probably the very poorly known *Artzosuchus brachycephalus* (Efimov, 1983), represents a diverse assemblage of basal forms recorded exclusively in the Late Cretaceous of Mongolia. *Gobiosuchus parvus* (Efimov, 1983) would also form part of this list, although there are serious doubts on the validity of this species as noted by previous authors (Osmólska et al., 1997; Storrs and Efimov, 2000).

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APPENDIX 1

Character List Corresponding to Data Matrix Used in Phylogenetic Analysis

Character definitions 1–101 are from Clark (1994) and have the same numeration as in the original publication. Character 5 was excluded from the analysis (due to dependence on the modified definition of character 6); however, its exclusion 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 number of the original publication. Characters 1, 3, 6, 23, 37, 45, 49, 65, 67, 69, 73, 77, 79, 83, 90, 91, 96, 97, 103, 104, 105, 107, 126, 143, 149, and 165 were set as ordered characters (also marked with a ''+'' in this list).

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

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

Character 3 (modified from Clark, 1994: char. 3): + Rostrum proportions: narrow oreinirostral (0), broad oreinirostral (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 contacts lacrimal (0), or does 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 (0), 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): Quadratojugal 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), or 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 restriced 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): Posterodorsal corner of the squamosal: squared off, lacking extra ''lobe'' (0), or with unsculptured ''lobe'' (1).

Character 36 (modified from Clark, 1994: char. 36): Posterolateral process of squamosal: poorly developed and projected horizontally at the same level of the skull (0), elongated, thin, and posteriorly directed, not ventrally deflected (1), or elongated, posterolaterally directed, and ventrally deflected (2).

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 suturally 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 biltaeral 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 passes 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: char. 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 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: char. 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. pterygoideous 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 toothrow (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 of 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 present up to the fourth dorsal vertebrae (4).

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

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

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

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

Character 96 (modified from Clark, 1994: char. 96, and Brochu, 1997a: 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 and 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), seven (1), six (2), five (3), or four teeth (4).

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 otoccipital: 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, medial to alveolar region: anteromedially directed (0), sinusoidal, posteromedially directed on its lateral half and anteromedially directed along its medial region (1), or posteromedially directed (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), oblique to each other converging anteriorly (1), or oblique to each other diverging anteriorly (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 infratemporal 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 maxilary 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): Quadratojugal: 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. 165): Quadrate process of pterygoids: well developed (0), or poorly developed (1).

Character 149 (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 150 (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 151 (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 152 (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 153 (Pol, 1999a: char. 170): Postzygapophyses of axis: well developed, curved laterally (0), or poorly developed (1).

Character 154 (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 transversaly oriented anterior edge (2).

Character 155 (Pol, 1999b: char. 213): Unsculpted region in the dentary below the tooth row: absent (0), or present (1).

Character 156 (Ortega et al., 1996: char. 13 and Buckley et al., 2000: char. 117): Cheek teeth: not constricted at base of crown (0), or constricted (1).

Character 157 (Ortega et al., 2000: char. 42): Outer surface of squamosal laterodorsally oriented: extensive (0), or reduced and sculpted (1), or reduced and unsculpted (2).

Character 158 (Ortega et al., 2000: char. 74): Length/height proportion of infratemporal fenestra: higher than long or subequal (0), or very anteroposteriorly elongated (1).

Character 159 (Ortega et al., 2000: char. 90): Foramen intramandibularis oralis: small or absent (0), or big and slotlike (1).

Character 160 (Ortega et al., 2000: char. 146): Ectopterygoid medial process: single (0), or forked (1).

Character 161 (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), several cusps of equal size arranged in more than one row (3), or multiple small cusps along edges of occlusal surface (4).

Character 162 (Pol and Norell, 2004: char. 164): Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).

Character 163 (Pol and Norell, 2004: char. 165): Palatine-pterygoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).

Character 164 (Wu et al., 1997: char. 103): Squamosal descending process: absent (0), or present (1).

Character 165 (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 166 (Wu et al., 1997: char. 106): Pterygoid flanges: thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).

Character 167 (Wu et al., 1997: char. 108): Postorbital participation in infratemporal fenestra: almost or entirely excluded (0), or bordering infratemporal fenestra (1).

Character 168 (Wu et al., 1997: char. 109): Palatines: form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).

Character 169 (Wu et al., 1997: char. 110): Angular posterior to mandibular fenestra: widely exposed on lateral surface of mandible (0), or shifted to the ventral surface of mandible (1).

Character 170 (Wu et al., 1997: char. 112): Posteroventral edge of mandibular ramus: straight or convex (0), or markedly deflected (1).

Character 171 (modified from Wu et al., 1997: char. 119): Quadrate ramus of pterygoid in ventral view: narrow (0), or broad (1).

Character 172 (Wu et al., 1997: char. 121): Pterygoids: not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).

Character 173 (Wu et al., 1997: char. 122): Olecranon: well developed (0), or absent (1).

Character 174 (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 175 (Wu et al., 1997: char. 127): Depression on posterolateral surface of maxilla: absent (0), or present (1).

Character 176 (Wu et al., 1997: char. 128): Anterior palatal fenestra: absent (0), or present (1).

Character 177 (Pol and Norell, 2004: char. 179): Paired ridges located medially on ventral surface of basisphenoid: absent (0), or present (1).

Character 178 (Pol and Norell, 2004: char. 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 179 (Pol and Norell, 2004: char. 181): Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0), or ventrolaterally (1).

Character 180 (Gasparini et al., 1993: char. 3): Wedgelike process of the maxilla in lateral surface of premaxilla-maxilla suture: absent (0), or present (1).

Character 181: Palpebrals: separated from the lateral edge of the frontals (0), or extensively sutured to each other and to the lateral margin of the frontals (1).

Character 182: External surface of ascending process of jugal: exposed laterally (0), or exposed posterolaterally (1).

Character 183: Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: absent (0), or present (1).

Character 184: Dorsal surface of posterolateral region of squamosal: without ridges (0), or with three curved ridges oriented longitudinally (1).

Character 185: Ridge along dorsal section of quadrate-quadratojugal contact: absent (0), or present (1).

Character 186: Sharp ridge along the ventral surface of angular: absent (0), or present (1).

Character 187: Longitudinal ridge along the dorsolateral surface of surangular: absent (0), or present (1).

Character 188: Dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges (fleur de lys pattern of Osmólska et al., 1997): absent (0), or present (1).

Character 189: Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: absent (0), or present (1).

Character 190: Appendicular osteoderms: absent (0), or present (1).

Character 191 (Ortega et al., 2000: character 72): Supratemporal fenestra: present (0), or absent (1).

Character 192 (Pol and Norell, 2004: char. 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

Gracilisuchus stipanicicorum
000000??0?000000000000?0?000000000?0??0?0
?00000?000???0000?0???00000?100000?000000
00?0???0000?0?000001012?00?00????0?01?010
00??1?01???000001002?0???0000?????0??0??00
00?00000?0?00000000?0?00000

Terrestrisuchus gracilis
000??00??0??000000?000?0?00?000?110?00000
?00000?000??0?000?000????00???010??0?00000
0?010?0000?0200000101??01100??00000?00100
??10?00?110?0?0??[01]110???00000????00?0??0
????00??0?0???0?????????????00

Dibothrosuchus elaphros
000?00?020??001???000000??????00110000000
?00000?0000?00000?0?0101000?010100?0010?0
00?????2000?0?????01010?01100?0?000000010
01?10?00?1?000101011100??000001??00000010
001000100?0?00000000?0000000

Protosuchus richardsoni
2100000120?00001101000210000010001000101
0?002010011111100101011020 11?11021000101
0100011100[1234]00?120011010111021001010 0
00[01]000000?01??01??10010[01]0101000000??
?01000000000120000011110??01000?010?00000

Hemiprotosuchus leali
?00?00?10??????10010?0??00?0010?11?0??01??
0020?00?11?1100101??1?2?11??1?21????01????
?????0????1200?1?101??0??????????000?000??1
0?00???00000??10?????00???????0?000?12???0
01??10?0?00?01??00???00

Orthosuchus stormbergi
21100001201?0001001000[01]10000010001000?
000?002011001111100??1?1?02011?0?0?0?0010
00100011100000?120010010211421001?10010?
100000001?01010000000000?0???00001???0000
00?12?000011110?001000?0?000?000

Kayenta form
[12]01110?1200000?10010?0??00????0?0???111
10?00201001111110000101 1?2011?0102100?10
10??0????00??0?1200101101112?????0????0110

0?00?01000111?101001?01?10000000011?0??40
012??00011??0?00???00?????????0

Zaraasuchus shepardi
10??????????????1?01?01?1000001?10?02???????
?????????????????????2?????1??010???????????
???[1234]0??1010??0???????????0?????????????
?????????0?????1??1?????????1?00????????1?00
???0??????1111111111?

Gobiosuchus kielanae
101000?110000011001?[01][01]?1?00001?10?02
01000?00201120111111000?1????201???1?20100
[01]010?0?1???????0?1010110[01]012002??0000
???0010[01]00001000000?00001001211?0000??
?110000000?121000011?00?0?00111111111110

Sichuanosuchus shuhanensis
[12]01??0?1200[01]00?10010[01]1?110???1?00?
021?10?00020?1?011?1100???????2?11????1?00
0011?1??1?????000????????1?11?0?1????0??100
100??1??10?0????00111[01]1210??00?????1????
?01011101111100?110000100?1???00

Shantungosuchus hangjinensis
2?1????1?0???0?1??1???11?????????21?1[01]1
00020?1?011?1100?10????????101?1?000??10??
?????0???????????????1???????1?????0010??????
?00??10?00??111211??001?????0?0?00????1011
111??0?110??0???1?????0

Zosuchus davidsoni
201??0?1200000??001010[01]110?001110?0221
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11?????????????????????1?12?3????1?????00100
011011?0001?0?0010112?[01]?0001???0?00???0
10111??1011?10111000000100???00

Fruita form
201??00120010001000010010000001100102 21?1
1?0020112?1???0?0??0??1?2?31?????1?0111101
011?1?00011112?0??1???[01]00???1?1001?001?
0?0100100??101?0011?01110??0??00?10?0000?
1???000????101?0?00000?000??0?

Hsisosuchus chungkingensis
211??????1??000000100001100011000?0221101
000[12]??12?11?10000?0?1?0??111?4?00[01]02?
1??10???????000?1000???101?0021??1?????010
01???????0000??00??1?11?1??00????????0??0??
??10?0?0111[01]?00??00?0?1000?01

Notosuchus terrestris
101?00110101001110001111110011000102 2110
110021112011?1000010?1102111112?01011100
01[01]111?1?200001000??0122011???1100101[0
1]1101[01]0100100000011111111111?000111100
10000101110110000111011000000000000001

Comahuesuchus brachybuccalis
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?11?1???????????????????131??????0?10101??????
??????????????????[01]13???1??????0?10?101201

?01?????011??0?1????11???11?00100?1?0??000
???100??0?000??0????0?

Uruguaysuchus aznarezi
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0011????1?????0??0???01111[12]???000110100?
?1?1??????0000?0??01?21002100?00?000?[01]?
??01?1?00????1?0111?11?????11?????1?0001???
?????0???10?????00????????01

Simosuchus clarki
10301011000000100010111110?0110001021?10
100011?11011?1000010?1?02011212101011000
0???????02100?2010?10002010???01??????1101
101212000010100111002110012 0???211[12]000
1111011001[01]1?1000000000001000001

Malawisuchus mwakayasyunguti
101?00?1110000?[01]10001[01][01]1100?11000
1?22110100011??20???1000?10?1?02?111[01]2?
0101110001????1??210000010??01[12]2111???0
1?0???01100101?11000???110110101?0?0001??
?0?100??21110?1000011100000000000000???01

Candidodon itapecurense
??
??
????????????????????????????????1???????????????
?0??0?????????????????1????2????????????????????
?????????????

Chimaerasuchus paradoxus
101?0001111?00????????????????????????????????
?????????????????????????12??0110?01010??1?1???
??2100?00????11[12]?314210??00?0100111111 0
11??????0?0110????????????10?11?????3?????????
??1?00???0????????????0?

Sphagesaurus huenei
101?000101??00??100?????110?????????21101?
00?????011?1000?????????13?2?????????100?????
???1??????????????????312????0????????111111011
1111111111111001110111 1?0?11?0??011?0?10?
?01??000000?00???????01

Baurusuchus pachecoi
100??0?121??00?1101????111?0110??????2?1011
0011112011?1000?10??10??3111210101111111??
??????????????????????12103????1?????110111010
101110011001111011 0?0111???[01]0[01]111101
1101?00001?00010000000000???01

Bretesuchus bonapartei
1[01]0??01121??00?????????????0????????????2???1
0011?????????1011?1??????13?1??1?00?10110??
??????????????????????????100????1????????01??0???
?01??0???0??1?0????????????[01]0[01]?1?10?1??
?1??001??00????????????0????1

Iberosuchus macrodon
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00111?12??1?101??10?1????111??10?0?1011011
??????[12][1234]00??00???00?[12][01]0?2??000

0???11001101010?1?0??100?11001?0??101???[0
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Araripesuchus gomesii
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1010001111201 1?10000?0?11020112121000110
1[01][01]1[01]11111?1[234]00010001001111002
1001001010100100100100000010011000210000
110?0011[01]0000111101000011100?000000000
000001

Araripesuchus patagonicus
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Lomasuchus palpebrosus
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?110?00???00011?0??1??0??????010???0?11??1
0??01?1000??11000??0???01

Peirosaurus tormini
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???????0?1???????????????[01]??????0??????????
????00??1???????????0?

Theriosuchus pusillus
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10001?11?01111000?????1?20211?41001010101
1011111000111120010010100 02?00?10?110110
[01]001?1100?00?0?00100??01??0?00??1010000
0?11?010??01?10000??0000??????01

Alligatorium
?0??????1?0000?1000010?111??0?100?1????0??
00??11??1??1000???????20?1????00101?101?01
1111000???1?00100???????????10??1??????????
?????????0????????????????????????0???????????
???????0????????????

Pelagosaurus typus
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1010000001101111001001?10001200?30000020
000110111?000000120001 1101?00???10???????
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011201000011000001?0000000???01

Teleosauridae
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?01000?0011011110010 11?1?00120003?000?200
002101111?0000?12000101011?0???10??010011
01??1011000011000010100?0??0000??10001000
011?010?0111000101000000000000001

Metriorhynchidae
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002101?11?0000??????0??012?0???100?0100110
1??1011?000??000010102?0???000????0010000
11?01000?1100000100000000???01

Sokotosuchus ianwilsoni
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Dyrosauridae
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????00??1?0000000???01

Pholidosaurus decipiens
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110?????0?0010????????????????0?1?0001???10?
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Goniopholis
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0000011001000011110?010000000000001

Eutretauranosuchus delfsi
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?110???????0??00???1???0????10?2???001?0??0
00?1?110?01?0000000???01

Bernissartia fagessi
203??21111??00111000?00111?001000?002????
?0001112?11?10100?0?1???1?1??410010102011
?1?11??020021110110100000??00????????1????
1????????0??0?10???01???0????1?12000001????
0??????00??10000????0??01

Hylaeochampsa vectiana
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?????????????????????????0???????10???????????
?0??0??????0?????????????2??00???????????????
??????????????01

Borealosuchus formidabilis
203?12111100101110001001 11?0010001002110
1011111121111010010?110?13100310001 10?0
11111111113111?110?00?000002110?100100?1
01??11110??000000010001?1???0000110?20?00
011001000011100001000000000000001

Gavialis gangeticus
212?12111100111111011011111001000 1002110
101101112011110110101110[01]1310031000120

0000111111013111211110 0?000002110?100100
?101??121100?0000000100 0101?1?00001?0?20?
0001100100000111 00001?000000000001

Crocodylus niloticus
203012111100[01]011100010211110010001 0021
10?0111111201111010010 1110[01]13100310001
001012111111013111202110 0?00000211001001
00?101??121100?0000000100110101100001?0?2
0000001100100001110000100000000000001

Alligator mississippiensis
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10111111201111010010 1110[01]0312031000100
2012111111113111202 11?0?0000021100100100
1101??111000?00000001001[12]01011000011[0
1]120000011001000011100001000000000000 1

APPENDIX 3

Fossil Taxa Used in Phylogenetic Analysis

Collection numbers of the specimens that were first-hand revised by the authors are added after the bibliographic reference.

Gracilisuchus stipanicicorum (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, 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/67–71)
Zaraasuchus shepardi (IGM 100/1321)
Shantungosuchus hangjinensis (Wu et al., 1994b)
Sichuanosuchus shuhanensis (Wu et al., 1997; IVPP V 10594)
Zosuchus davidsoni (Pol and Norell, 2004; IGM 100/1304–1308)
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, 1040, 1041)
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 mwakayasyunguti (Clark et al., 1989; Gomani, 1997; MAL 45, 49)
Candidodon itapecurense (Carvalho, 1994)
Simosuchus clarki (Buckley et al., 2000; UA 8679)
Sphagesaurus huenei (Price, 1950; Pol, 2003; 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)
Lomasuchus palpebrosus (Gasparini et al., 1991; MOZ 4084 PV)
Peirosaurus tormini (Price, 1955; Gasparini et al., 1991; MOZ 1750 PV)
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)
Dyrosauridae (Buffetaut, 1978; Clark, 1986, 1994; CNRST-SUNY 190)
Sokotosuchus ianwilsoni (Halstead 1975; Buffetaut, 1979; 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 (Gasparini and Diaz, 1977; AMNH 997, BSP AS.I.504, MACN-N 95, SMNS 10116)
Hylaeochampsa vectiana (Clark and Norell, 1992; Ortega et al., 2000)
Bernissartia fagessi (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

alr	anterolateral ridge of dorsal osteoderm
amr	anteromedial ridge of dorsal osteoderm
ang	angular
apal	anterior palpebral
apj	ascending process of jugal
ar	angular ridge
cc	crista cranii
den	dentary
do	dorsal osteoderm
dok	dorsal osteoderm keel
dpo	descending process of posterior palpebral
dpp	descending process of postorbital
dr	diapophyseal ridge
fps	fronto-parietal suture
fr	frontal
ho	humeral osteoderms
hu	humerus
hy	hypapophysis
itf	infratemporal fenestra
j	jugal
jr	jugal infratemporal ridge
lok	lateral osteoderm keel
mas	ventral surface of medial articular shelf
ns	neural spine
pa	parapophysis
par	parietal
pho	proximal humeral osteoderm
po	postorbital
ppal	posterior palpebral
ppr	parapophyseal ridge
pr	parietal posterolateral ridge
prp	posterolateral process of retroarticular
psq	posterolateral process of squamosal
puo	proximal ulnar osteoderm
pz	postzygapophysis
qj	quadratojugal
ra	retroarticular process
sang	surangular
sar	surangular ridge
sq	squamosal
sqr	ridges of posterolateral process of squamosal
sto	remnant of supratemporal opening
ul	ulna
uo	ulnar osteoderm
vco	ventral closure of olfactory tract

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