

MORPHOLOGY OF
THE LATE CRETACEOUS CROCODYLOMORPH
SHAMOSUCHUS DJADOCHTAENSIS AND
A DISCUSSION OF NEOSUCHIAN PHYLOGENY
AS RELATED TO THE ORIGIN OF EUSUCHIA

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ABSTRACT

We describe a new specimen of the fossil crocodyliform taxon *Shamosuchus djadochtaensis* from the Late Cretaceous Djadokhta Formation. The new specimen consists of an almost complete skull found in association with postcranial material. Because it is considerably more complete than the holotype, the new specimen permits proper diagnosis of *Shamosuchus djadochtaensis* and offers new information for exploring its phylogenetic relationships.

The phylogenetic analysis conducted here improves taxon sampling of neosuchian crocodyliforms with respect to previous approaches to crocodyliform systematics and reveals that *Shamosuchus djadochtaensis* bears important information toward an understanding of the relationships of advanced neosuchians and the evolutionary origin of Eusuchia. *Shamosuchus djadochtaensis* is found to be the sister group of *Rugosuchus nonganensis*, comprising an Asian clade diagnosed by the presence of a sagittal ridge on the dorsal surface of the frontal, confluent openings for the exit of cranial nerves IX–XI, a posterior region of the palatine bar between suborbital fenestra that is flared posteriorly, and a longitudinal ridge on the lateral surface of the angular. This clade is inferred to be the sister group of Eusuchia, to the exclusion of *Bernissartia fagesii* and the Glen Rose form, based on the absence of an acute anterior tip of the frontal that wedges between the nasals, the presence of rodlike neural spines in the posterior cervical vertebrae, procoelous cervical vertebrae, and the presence of hypapophyses in the three anteriormost dorsal vertebrae.

Incorporating the new information into the phylogenetic analysis indicates the decoupled nature of the evolutionary history of procoely in different regions of the vertebral column and the eusuchian type of palate, both traditionally considered as diagnostic of Eusuchia. All these features have complex evolutionary histories with several cases of convergences and reversals. Finally, a review of all the available evidence on the diversity of advanced neosuchians suggests this group achieved a worldwide distribution and a remarkable morphological diversity, pushing their evolutionary origins back to the Jurassic.

INTRODUCTION

Mook (1924) described *Shamosuchus djadochtaensis* based on an incomplete skull (fig. 1) found in the Shabarakh Usu (Bayn Dzak or the Flaming Cliffs) locality during the Third Asiatic Expedition of the American Museum of Natural History in 1923. Subsequent specimens found in Mongolia and Uzbekistan were described and classified into six additional species in this genus (Efimov, 1975, 1981, 1983, 1988; Nesov et al., 1989). Additionally, three species originally described as *Paralligator*, from the Late Cretaceous of Mongolia (*Paralligator ancestralis* and *Paralligator gradilifrons*; Konzhukova, 1954) and Early Cretaceous of China (*Paralligator sungaricus*; Sun, 1958), were later referred to *Shamosuchus* by Efimov (1983). Some of the described species allocated to this genus differ markedly in rostral morphology and probably represent distinct taxa, although the number of *Shamosuchus* species may have been overestimated by Efimov (1983, 1988), as recently pointed out by Storrs and Efimov (2000).

Here, we describe the first reasonably complete crocodyliform specimen found in the Ukhaa Tolgod locality (Djadokhta Formation) (Dashzeveg et al., 1995, 2005; Dingus et al., 2008; fig. 2), referring it to the type species *Shamosuchus djadochtaensis* (fig. 3). This specimen (IGM 100/1195) preserves a nearly complete skull and associated postcranial skeleton, offering new information not preserved in previously known specimens of *Shamosuchus* and contributes to a clearer understanding of this taxon and its phylogenetic relationships.

Shamosuchus djadochtaensis was initially considered a member of the Goniopholidae (Mook, 1934a; Kälin, 1955; Steel, 1973), but more recently it was interpreted as a form related to *Bernissartia fagesii* and advanced neosuchians (Clark, 1986; Benton and Clark, 1988), thus providing critical information for understanding the evolutionary origins of modern crocodiles. However, despite the abundance of material referred to this genus, it has remained understudied and usually overlooked in phylogenetic analyses of Crocodyliformes. Recently, however, Wu et al.



Fig. 1. Holotype of *Shamosuchus djadochtaensis* AMNH FR 6412.



Fig. 2. Map of Mongolia showing the Bayn Dzak and Ukhaa Tolgod localities.

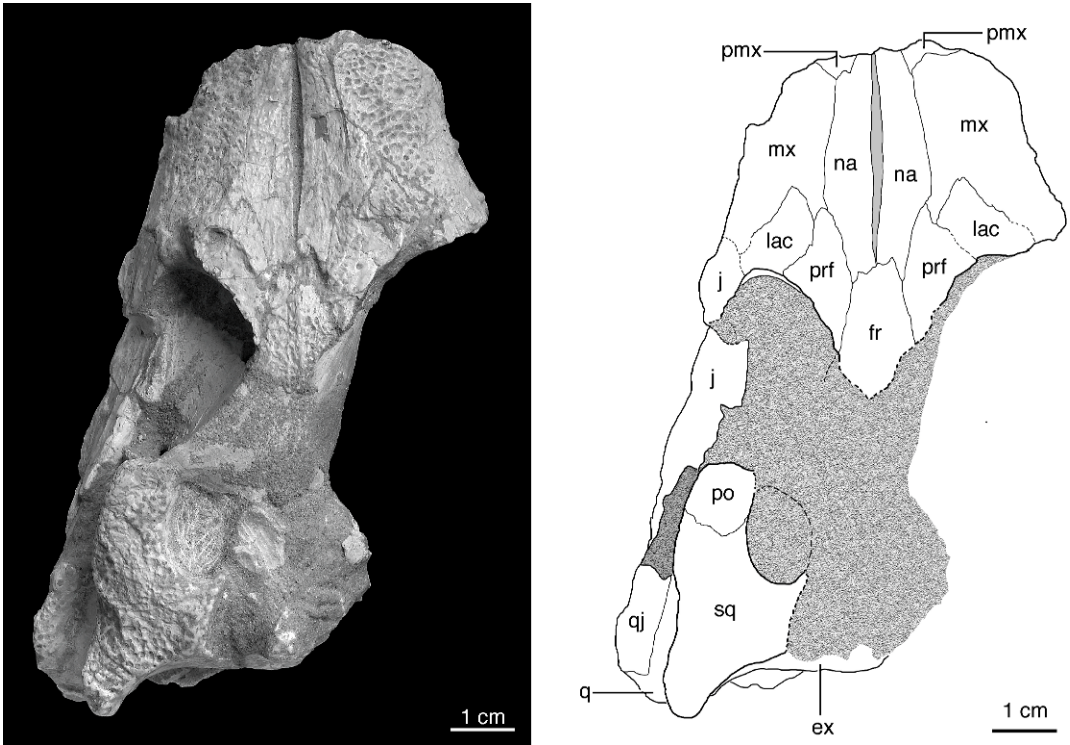


Fig. 3. Holotype of *Shamosuchus djadochtaensis* AMNH FR 6412 in dorsal view. See appendix 5 for abbreviations.

(2001a) described a new taxon from the Early Cretaceous of northeastern China, *Rugosuchus nonganensis*, pointing out derived similarities with *Shamosuchus* and suggesting these two taxa may be closely related.

Information from the new specimen of *Shamosuchus djadochtaensis* is incorporated in a comprehensive phylogenetic analysis to test the relationships of this advanced neosuchian crocodyliform and explore its implications for understanding the evolutionary origins of Eusuchia.

INSTITUTIONAL ACRONYMS

The following acronyms are used throughout this work:

- AMNH-FR American Museum of Natural History, New York, USA
Collection of fossil reptiles, amphibians and birds
- BMNH British Museum of Natural History, London, England

- BSP Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
- CNM Chongqing Natural Museum, Sichuan, People’s Republic of China
- CNMH Cleveland Museum of Natural History, Cleveland, USA
- CNRST-SUNY Centre National de la Recherche Scientifique et Technologique de Mali – Stony Brook University
- DGM Departamento de Produção Mineral, Rio de Janeiro, Brazil
- FMNH The Field Museum, Chicago, USA
- GMPKU-P School of Earth and Space Sciences, Peking University, Beijing, People’s Republic of China
- GPIT Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany
- IGM Mongolian Institute of Geology, Ulaan Bataar, Mongolia
- IRScNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium

IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China	SMF	Senckenberg Museum, Frankfurt, Germany
LACM	Los Angeles County Museum, Los Angeles, USA	SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina	SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
MAL	Malawi Department of Antiquities, Malawi	TMM	Texas Memorial Museum, Austin, USA.
MB	Institut für Palaontologie, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany	TMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA	UA	University of Antananarivo, Madagascar
MGHF	Museo Geológico H. Fuenzalida, Universidad Católica del Norte, Antofagasta, Chile	UCMP	Museum of Paleontology, University of California, Berkeley, USA
MHNSR	Museo de Historia Natural de San Rafael, San Rafael, Argentina	YPM	Yale Peabody Museum, New Haven, USA.
MLP	Museo de La Plata, La Plata, Argentina	ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland
MNHN	Musée National d'Histoire Naturelle, Paris, France		
MNN	Musée National du Niger, Niamey, Niger		
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil		
MOZ	Museo Profesor J. Olsacher, Zapala, Argentina		
MPCA-PV	Museo Carlos Ameghino, Cipolletti, Argentina		
MSU	Dunn-Seiler Museum, Mississippi State University, Starkville		
MUC-PV	Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina		
MZSP-PV	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.		
NMC	Canadian Museum of Nature, Ottawa, Ontario, Canada		
PPM	Pink Palace Museum, Memphis, Tennessee		
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		

COMPUTED TOMOGRAPHY

IGM 100/1195 was CT-scanned on a GE Systems Lightspeed 16 scanner at Stony Brook University Hospital in March 2005. The skull was scanned in air after final physical preparation was completed. Original scans were done in the coronal plane with a slice thickness of 0.625 mm, an interslice spacing of 0.310 mm, and a field of reconstruction of 96.0 mm. The original DICOM files were converted to TIFFs using Adobe Photoshop 7.0 (levels: 35, 1.00, 150). Stack movies and additional manipulation and visualization of the dataset were done using the ImageJ software package available as freeware from NIH. The complete data set is available on request from the authors.

SYSTEMATIC PALEONTOLOGY

Crocodylomorpha Hay, 1930 (sensu Walker, 1970)
 Crocodyliformes Hay, 1930 (sensu Clark, 1986)
 Neosuchia Clark, 1986
Shamosuchus djadochtaensis Mook, 1924

HOLOTYPE: AMNH FR 6412. Incomplete skull and lower jaws preserved in articulation (figs. 1, 3–6).

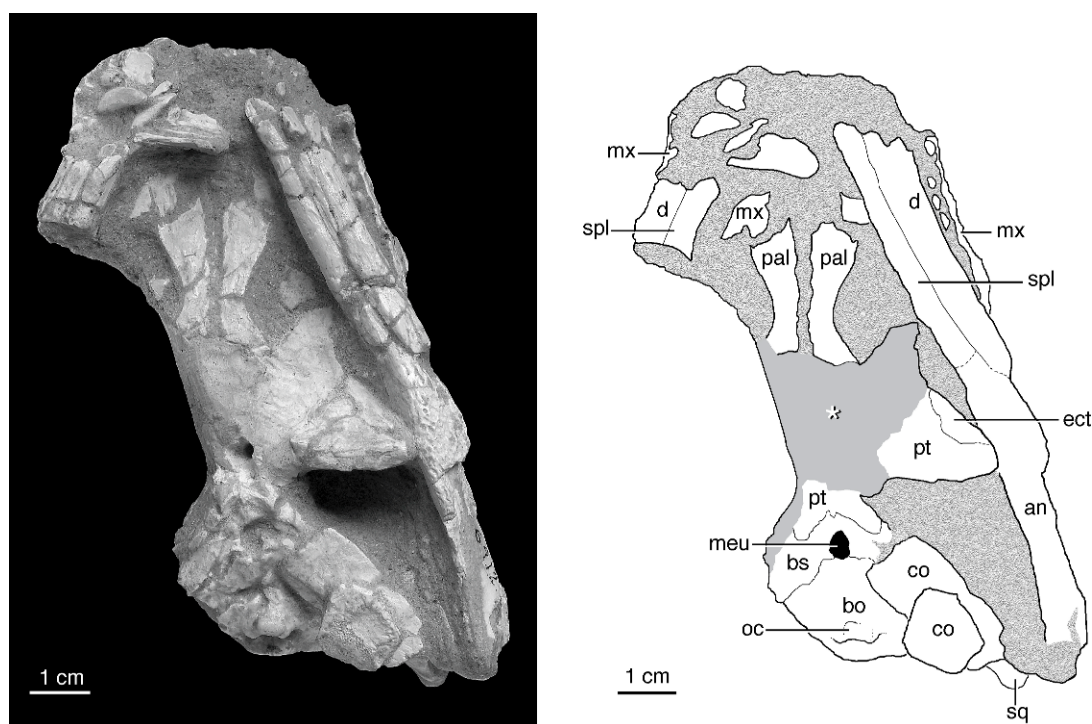


Fig. 4. Holotype of *Shamosuchus djadochtaensis* AMNH FR 6412 in ventral view. See appendix 5 for abbreviations.

REFERRED SPECIMEN: IGM 100/1195 (figs. 7–12). Nearly complete skull, lower jaws, and associated postcranial remains including; all eight cervical vertebrae with three right cervical ribs (c5–c7) and one left cervical rib (c8), dorsal vertebrae d1 through d3 with four right dorsal ribs (d1–d3) and three left dorsal ribs (d2?–d6?), five anterior caudal vertebrae and two haemal arches, a complete right humerus, the distal half of the left humerus, the proximal portion of the right radius, a complete left radius in association with the left humerus, a complete left ulna, a fragmentary right ischium, a partial right femur consisting of a damaged diaphysis and distal condyle, a complete right tibia, a nearly complete left tibia, a complete right fibula, a partial left fibula, and a single left metatarsal and phalanx.

DIAGNOSIS: A crocodyliform diagnosed by the following combination of derived characters (autapomorphic features indicated with an asterisk): absence of notch at

premaxilla-maxilla contact; enlarged third maxillary tooth; elongated lacrimal not contacting the nasal; dorsal surface of lacrimal and prefrontal bears a smooth, rounded depression bounded by elevated ridges*; frontal with elevated orbital margins and participation in supratemporal fossa; shallow and broad squamosal groove that tapers posteriorly at the level of the posterior edge of the otic aperture and reappears along the lateral edge of the posterolateral process of the squamosal*; narrow ascending process of the quadratojugal bearing a slightly developed ridge located close to its anterior margin* and a knob at the posterior margin of the infratemporal opening; small siphoneal foramen located anteroventrally to the otic aperture; well-developed crest B on ventral surface of quadrate; hourglass-shaped palatine bar between the suborbital fenestra with concave lateral margins; lateral margins of choanal opening mostly formed by ptery-

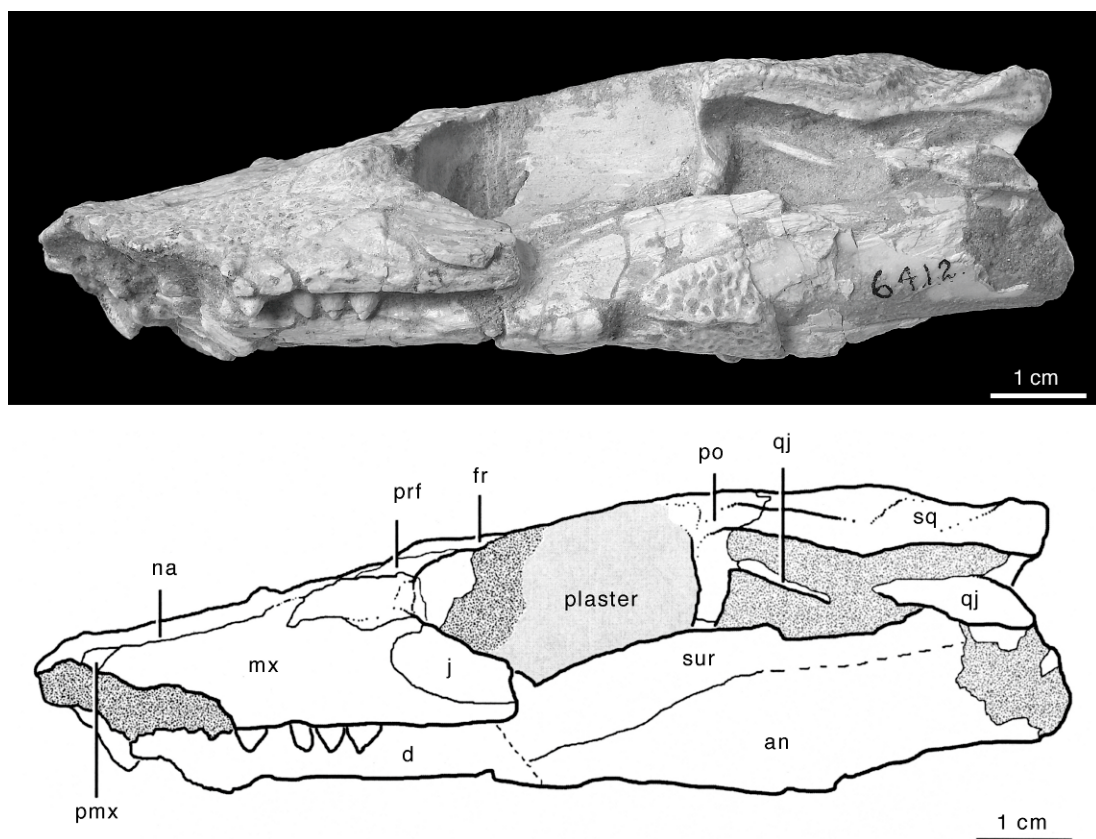


Fig. 5. Holotype of *Shamosuchus djadochtaensis* AMNH FR 6412 in lateral view. See appendix 5 for abbreviations.

goids; basisphenoid with moderate exposure on ventral surface of braincase and brief exposure on the lateral surface of the braincase; posterior opening of the cranioquadrate passage located close to the lateral margin of the paroccipital process; occipital condyle and ventral basioccipital surface slightly deflected posteroventrally; undivided foramen vagi; closed external mandibular fenestra and lateral surface of surangular and angular bearing a longitudinal groove; cervical vertebrae procoelous; first dorsal procoelous and with large neural canal; caudal vertebrae amphicoelous; imbricate dorsal osteoderms with discrete convexities on their anterior margins and extremely large keels restricted to their posterior margins*; appendicular osteoderms present.

DESCRIPTION

THE SKULL

The skull of IGM 100/1195 preserves most of its elements, except for the anteriormost region of the rostrum and the anterior region of the secondary palate (figs. 4, 9). The snout is moderately low and broad (i.e., platyrostral sensu Busbey, 1994). The rostrum of *Shamosuchus djadochtaensis* is short, approximately 43% of the anteroposterior skull length (as preserved). Because the anterior tip of the rostrum is missing, this proportion would have been slightly longer. All other *Shamosuchus* species have a noticeably longer rostrum, varying between 63% and 70% of the total skull length (Efimov, 1983, 1988). This is also the case in other advanced neosuchians, such as *Bernissartia fagesii*

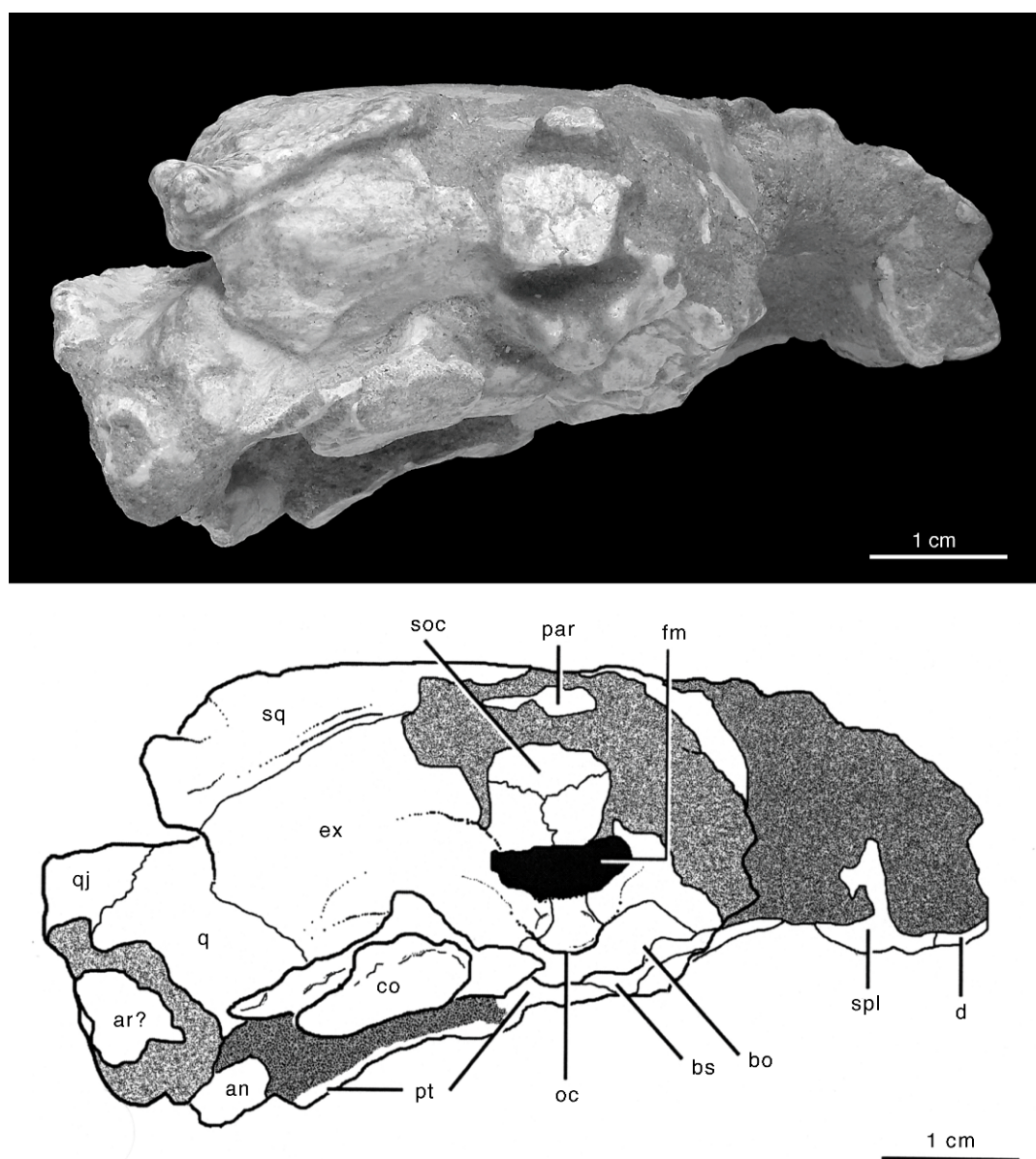


Fig. 6. Holotype of *Shamosuchus djadochtaensis* AMNH FR 6412 in occipital view. See appendix 5 for abbreviations.

(Buffetaut, 1975), *Rugosuchus nonganensis* (Wu et al., 2001a), and *Isisfordia duncani* (Salisbury et al., 2006). However, a relatively short rostrum has also been described for the basal eusuchian *Tharkutosuchus makadii* (Ösi et al., 2007); a condition probably shared with *Hylaeochampsia vectiana*. The external nares are not preserved in the holotype of

Shamosuchus djadochtaensis and only the posterolateral margins of this opening are present in IGM 100/1195. These margins are vertically oriented suggesting that the external nares faced somewhat anteriorly (or anterodorsally), in contrast to the dorsally facing nares of most neosuchian crocodyli-forms. The antorbital fenestra is completely



Fig. 7. Skull of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195.

obliterated and there is no sign of an antorbital fossa (fig. 10). The orbits of *Shamosuchus djadochtaensis* are moderately large, approximately 27% of the preserved skull length (measured from rostral end to the caudal end of the parietal dorsal surface). The supratemporal fenestrae are relatively reduced, being smaller than the orbits and subcircular in shape (fig. 8). The infratemporal fenestrae are subtriangular and longer than high. The suborbital openings are not completely preserved, although they seem to be well developed and anteroposteriorly elongate (fig. 9). The external surface of the skull is deeply ornamented with the pitted pattern characteristic of neosuchian crocodyliforms. The sculpture present in IGM 100/1195 is slightly more developed and extended than in the type specimen of *Shamosuchus djadochtaensis* (AMNH FR 6412).

The **premaxillae** are incompletely preserved in IGM 100/1195, lacking the region anterior to the external nares and most of their palatal branches. The lateral margins of

the narial opening are vertically oriented and smooth, denoting the presence of a perinarial fossa extending along the ventrolateral region of this opening. The premaxilla also forms part of the dorsal margin of the external nares, deflecting dorsally and contacting the anterior tip of the nasals.

Posterior to the perinarial region, the external surface of the premaxilla is ornamented with subcircular pits, as in most neosuchian crocodyliforms. The premaxilla extends posteriorly forming the anterior fourth of the rostrum. Its external surface has two exposure planes, a ventral region oriented vertically and a dorsal region facing dorsolaterally to dorsally. As in most platyrostral forms, the ventral region is dorsoventrally low while the dorsal region is much more extensive (figs. 8, 10). The premaxilla-maxilla suture is slightly interdigitated, extends vertically from the alveolar margin, and then deflects posteriorly, forming the ventral margin of a well-developed posterodorsal process of the premaxilla. The dorsomedial

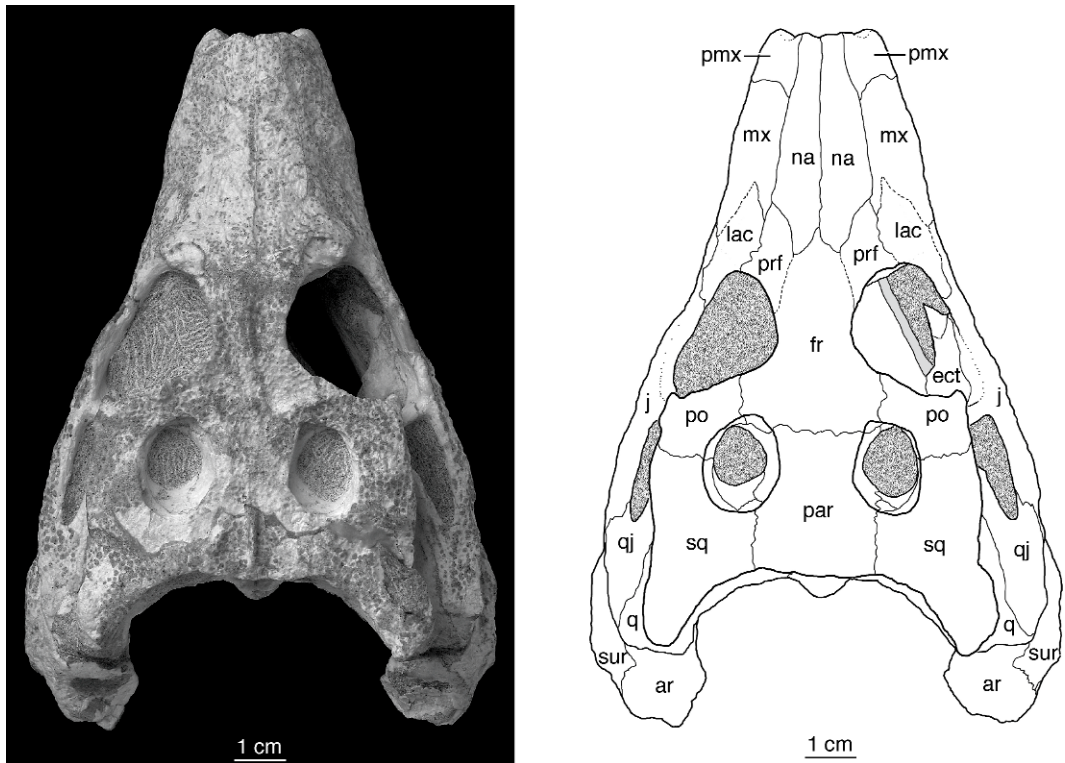


Fig. 8. Referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in dorsal view. See appendix 5 for abbreviations.

margin of the premaxilla contacts the lateral margin of the nasal on the dorsal surface of the rostrum. The anterior half of this contact forms a linear and parasagittally oriented suture (fig. 8). The posterior half of this suture is slightly deflected posterolaterally.

The alveolar margin of the premaxilla-maxilla contact is continuous and lacks a notch for the reception of the opposing dentary tooth, unlike most platyrostral neosuchians (except for alligatorids). The palatal branches of the premaxilla are only briefly preserved medial to the posteriormost alveoli. Unfortunately, the palatal sutures between the premaxillae and with the maxillae are not preserved in the type specimen or in IGM 100/1195. Only the two posteriormost alveoli of each premaxilla are preserved, bearing fragments of the subcircular tooth crowns. These alveoli are discrete and subcircular, with the posterior one significantly smaller than the anterior premaxillary alveolus (and the anterior maxillary alveoli).

The **maxillae** are well preserved in IGM 100/1195, except for their palatal branches (figs. 9, 10). The external surface of the maxilla forms most of the rostrum and is densely ornamented with subcircular pits. As in the premaxilla, the external surface has two planes of exposure, a dorsoventrally low ventral region oriented vertically and an extensive dorsal region facing dorsolaterally. The dorsomedial margin of the maxilla contacts the nasal along a straight and posterolaterally oriented suture. The alveolar margin of the maxilla bears a single outgrowth, projecting ventrally at the level of the third and fourth maxillary enlarged alveoli (fig. 10). At this point, the external surface of the maxilla is slightly bulged, forming a noticeable convexity seen in dorsal and ventral views (figs. 8, 9). Posterior to this region the buccal margin of the maxilla is straight. Variation in alveolar size closely follows the shape of the ventral margin of the maxilla, increasing in size toward the third

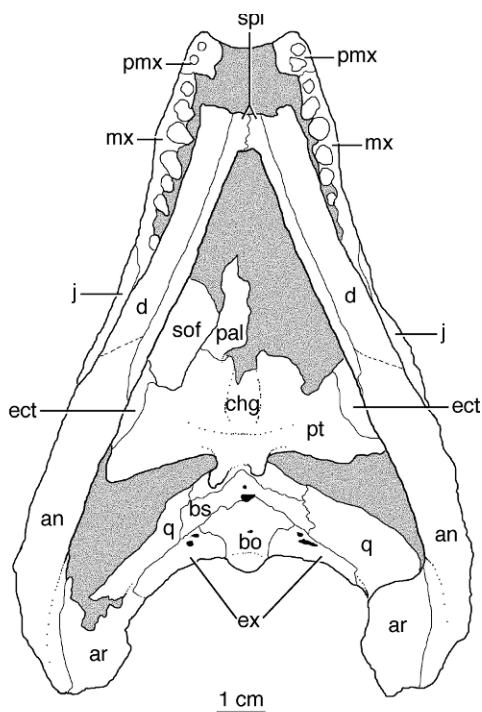


Fig. 9. Referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in ventral view. See appendix 5 for abbreviations.

and fourth teeth and decreasing posterior to these elements. In contrast, most advanced neosuchians (e.g., *Rugosuchus nonganensis* [Wu et al., 2001a], *Goniopholis simus* BMNH 41098, *Eutretauranosuchus delfsi* (Mook, 1967), *Bernissartia fagesii* (Norell and Clark, 1990), and brevirostran crocodylians) have two “waves” of maxillary tooth size variation (or festooning pattern). There are 12 preserved maxillary teeth that resemble those of most advanced neosuchians in that they are subconical and only slightly compressed lateromedially toward the tip of the crowns, bear a slightly marked constriction between root and crown, and lack serrated margins. The third maxillary alveolus is approximately 35% larger than its adjacent alveoli, which bear the second largest teeth of the maxilla. In contrast, other species referred to *Shamosuchus* (e.g., *S. major*, *S. gradilifrons*, *S. ulgicus*) have the cheek maxillary alveolus significantly larger than the others (Efimov, 1983, 1988; Storrs and Efimov, 2000). Most advanced neosuchians also have enlarged

maxillary teeth located in the fourth and/or fifth position (e.g., *Rugosuchus nonganensis* [Wu et al., 2001a], *Bernissartia fagesii*, most crocodylians [Norell, 1988]). The Glen Rose form (USNM 22039), however, shares with *Shamosuchus djadochtaensis* the presence of a distinctly enlarged third alveolus with respect to the other maxillary alveoli (Brochu, 1999). The posteriormost teeth are not well preserved, although they seem to be more robust and with shorter crowns. The maxillary alveoli are closely packed to each other, as in other neosuchians (e.g., the Glen Rose form, *Bernissartia fagesii*, *Theriosuchus pusillus*, *Goniopholis simus*), but differ from the well-separated alveoli of *Rugosuchus nonganensis*, as noted by Wu et al. (2001a).

Several small neurovascular foramina are scattered on the lateral surface of the maxilla, close to its alveolar margin. They are evenly spaced and most of them are positioned between adjacent alveoli. The posterior region of the maxilla is laterally overlapped by the anterior process of the jugal on its ventral

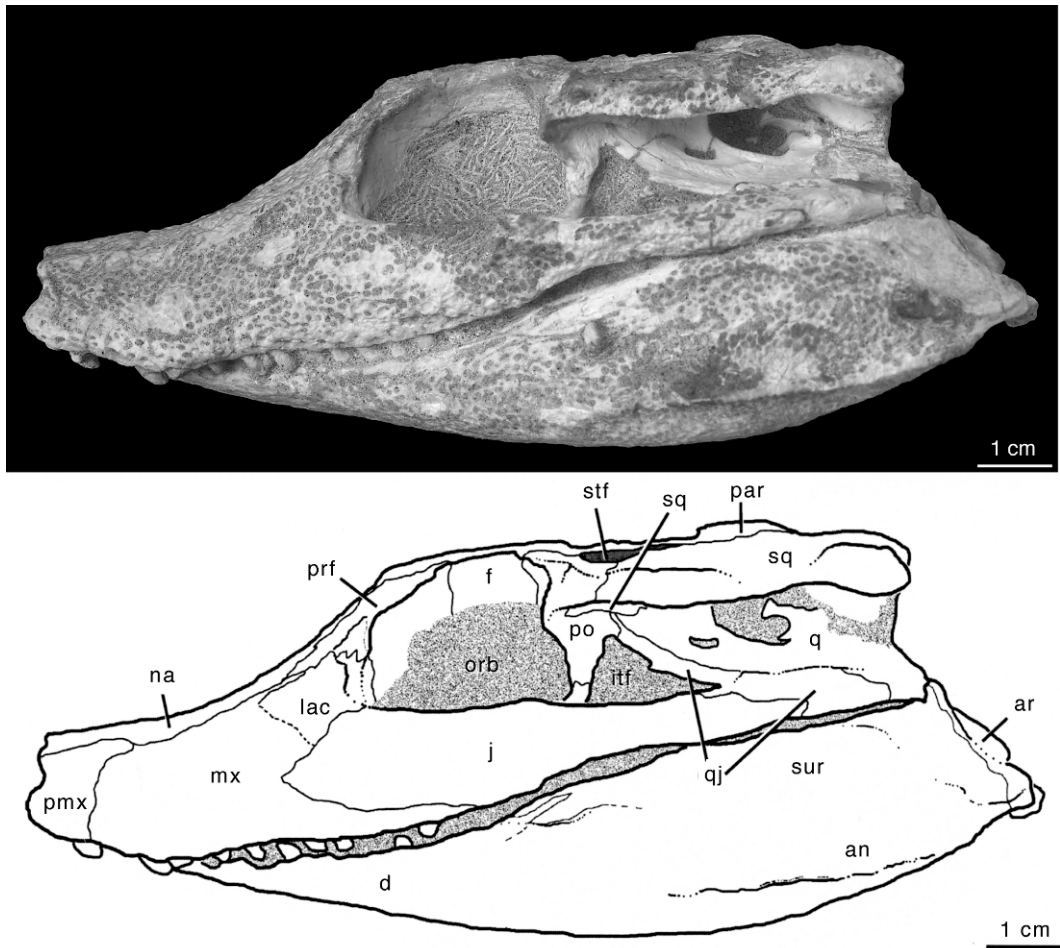


Fig. 10. Referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in lateral view. See appendix 5 for abbreviations.

region and sutured to the lacrimal dorsally. The latter suture is difficult to delimit precisely in IGM 100/1195 due to the heavy ornamentation pattern of this region, but is clearly preserved in the type specimen (see below). Here the maxilla is completely sutured to the lacrimal, lacking an antorbital fossa or opening, as in derived neosuchians. An acute branch projects from the postero-medial region of the maxilla, reaching the anterior tip of the prefrontal, excluding the lacrimal from contacting the nasal, as in *Hylaeochampsia vectiana* (Clark and Norell, 1992; BMNH R177), *Susisuchus krebsi* (Salisbury et al., 2003), and some extant eusu-

chians (e.g., *Alligator mississippiensis* FMNH 8201).

The **nasals** form the dorsal surface of the rostrum and bear a similar (although less developed) ornamentation pattern as present on the rest of the skull in IGM 100/1195. In the type specimen (AMNH FR 6412) most of the dorsal surface of the nasals is not ornamented, a difference considered here as likely due to preservational or individual variation. These elements extend from the anterior end of the preserved rostrum to the level of the anterior margin of the orbits. Their lateral margins diverge slightly posteriorly along their contact with the premaxil-

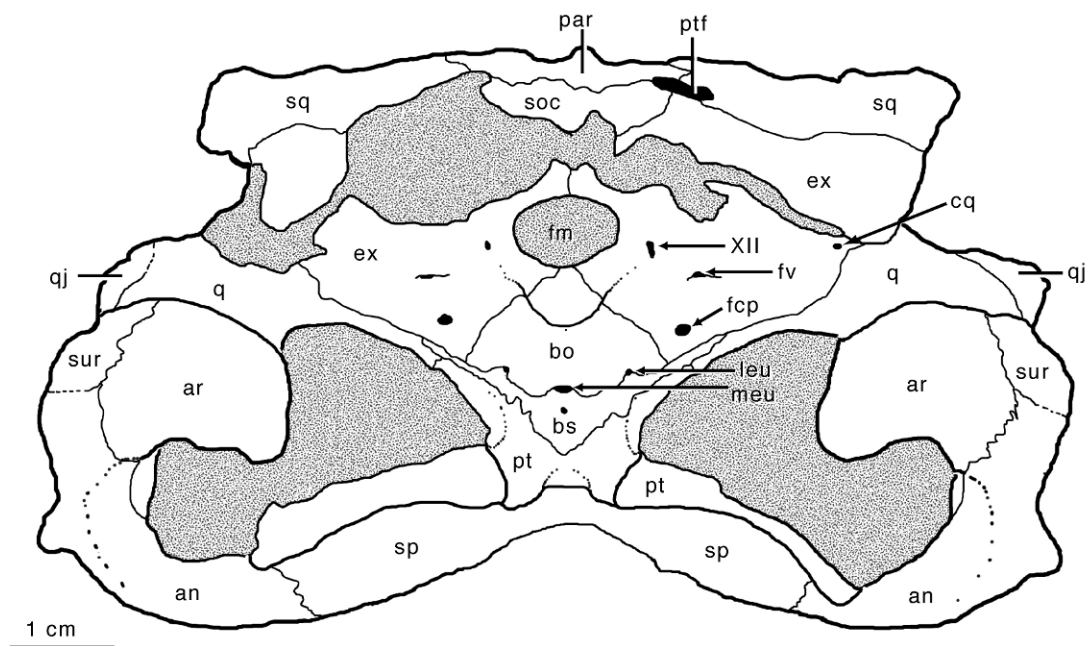
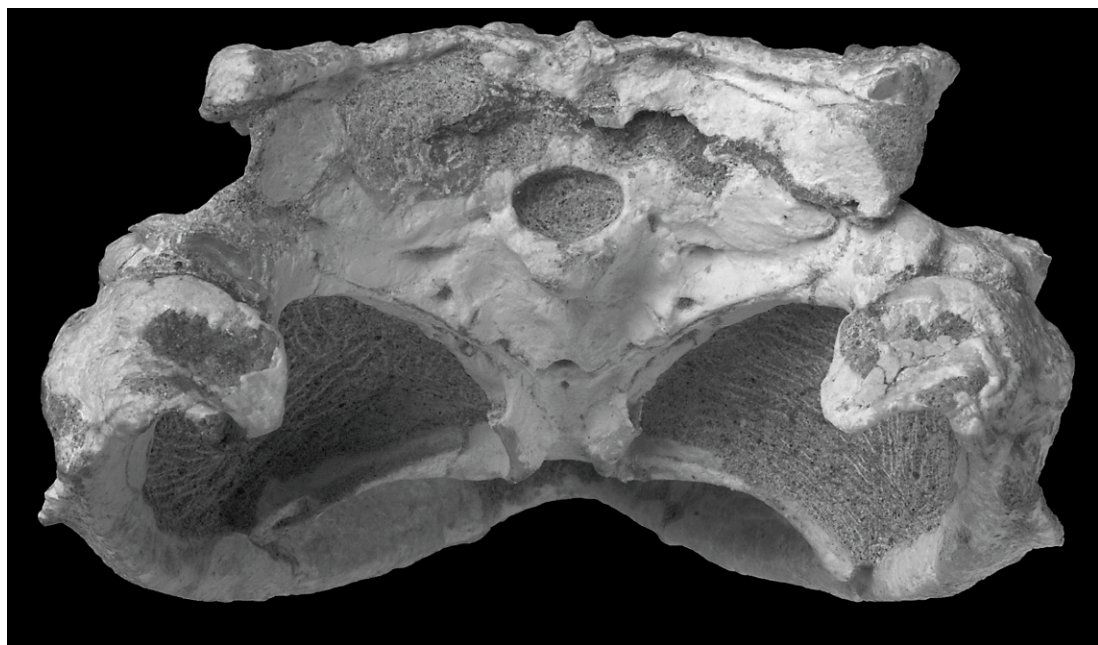


Fig. 11. Occipital surface of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

lae and maxillae (fig. 8). The nasals are sutured to each other along their medial margins forming a slightly developed medial crest (fig. 12).

Posterior to their contact with the maxillae, the nasals are sutured to the prefrontals along a laterally concave suture directed posteromedially. Thus, the posterior region

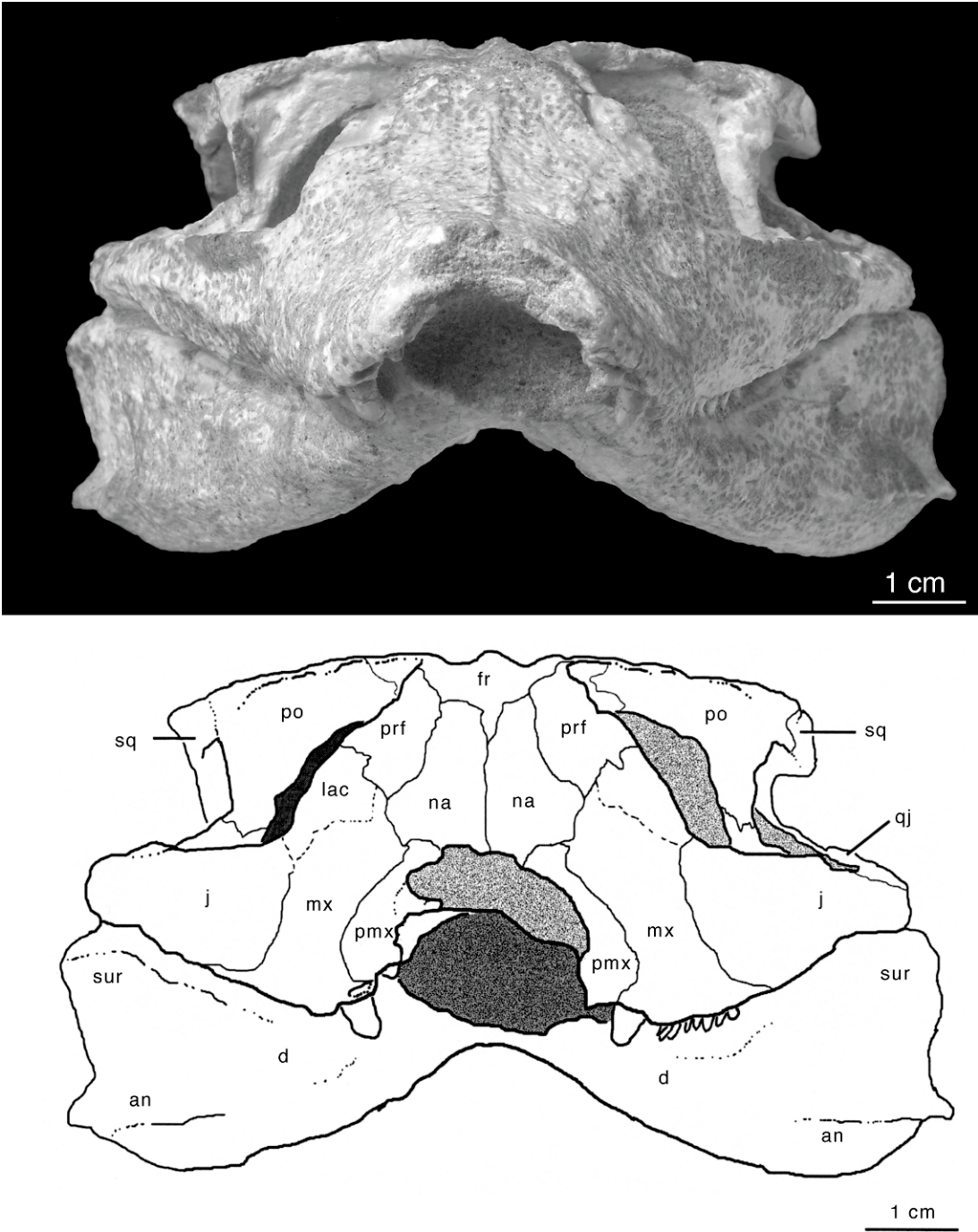


Fig. 12. Referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in anterior view. See appendix 5 for abbreviations.

of the nasals narrows gradually, being at their posterior end approximately half the width of their breadth at the midpoint of the rostrum (fig. 8). The posterior margins of the nasals are sutured to the frontals along a transversally oriented suture, although details on this suture were not preserved in IGM 100/1195 or in the type specimen AMNH FR 6412.

The **lacrimal** forms most of the anterior margin of the orbit and is sutured to the prefrontal, maxilla, and jugal. As clearly seen in the type specimen, the lacrimal is rather low dorsoventrally and slightly elongated anteroposteriorly, extending on the lateral surface of the snout (where it faces laterodorsally; figs. 3, 8). The lacrimal extends further anteriorly than the prefrontal as in *Rugosuchus nonganensis* (Wu et al., 2001a) and *Isisfordia duncani* (Salisbury et al., 2006), in contrast to the condition of some basal eusuchians such as *Hylaeochampsia vectiana* (Clark and Norell, 1992) and *Iharkutosuchus makadii* (Ösi et al., 2007). The anterior margin of this region of the lacrimal is anteriorly convex and sutured to the maxilla. As noted above, in the two specimens of *Shamosuchus djadochtaensis* studied here, there are no signs of an antorbital opening or fenestra at the maxilla-lacrimal contact. Posteroventrally, the lacrimal narrows markedly and briefly contacts the jugal at the anteroventral corner of the orbit.

The anterior half of the dorsomedial margin of the lacrimal is medially convex and bounded by the maxilla; as a result, it is excluded from contact with the nasal. This morphology contrasts with that of *Rugosuchus nonganensis* (Wu et al., 2001a) and most other neosuchians (see above), in which the elongated lacrimal contacts the nasal. Posteriorly, this margin of the lacrimal is bordered by the prefrontal, along a similarly curved suture. The posterodorsal surface of the lacrimal is horizontally exposed (lateral to its suture with the prefrontal; figs. 3, 8). In contrast to the rest of the external surface of the lacrimal, this dorsally exposed surface bears a smooth depression bounded by elevated ridges (fig. 13). This morphology is similarly present in AMNH FR 6412 for which Mook (1924) described the lacrimal ridges as diagnostic of *Shamosuchus djadoch-*

taensis. Other *Shamosuchus* species, however, also show prominent lacrimal (and prefrontal) ridges (Efimov, 1983, 1988; Storrs and Efimov, 2000). The depressed surface bounded by these ridges continues medially along the prefrontal's dorsal surface. The posterior margin of this depression is elevated, forming a slightly developed ridge at the anterodorsal margin of the orbit. This depression is located close to the position in which the anterior palpebral articulates in most crocodyliforms. However, the posterior margin of this depression in IGM 100/1195 is separated from the orbital margin by an elevated ridge of the lacrimal, rather than being confluent with the orbit as the palpebral articular facet of other crocodyliforms. This suggests that either this depression is not the palpebral articular facet, or that the anterior palpebral of *Shamosuchus djadochtaensis* is markedly distinct from that of other Crocodyliformes. Although further material and study is needed to test these options this depression seems to be diagnostic of *Shamosuchus djadochtaensis* or, alternatively, a putative synapomorphy for the higher taxon *Shamosuchus* more broadly, given the presence of a transverse prefrontal ridge in other species of *Shamosuchus* (Efimov, 1983; Wu et al., 2001a).

Inside the orbit, the lacrimal-prefrontal suture is interdigitated and directed ventrally (fig. 14). The posterior opening of the lacrimal duct opens into the orbital cavity, just lateral to this suture and ventromedial to the crest formed by the posterior margin of the lacrimal depression described above. Additionally, there is a much smaller foramen located ventrolaterally to the main lacrimal opening. The ducts that extend anteriorly from these openings merge within the lacrimal bone.

The dorsal surface of the **prefrontals** of *Shamosuchus djadochtaensis* is anteroposteriorly elongate, extending from the anteroposterior midpoint of the orbit to the level of the posteromedial branch of the maxilla. In IGM 100/1195 most of the dorsal surface of the prefrontals is ornamented, except for the depressed facet described above (fig. 13). The anterior end of the prefrontal is acute, wedging between the nasal and the posteromedial branch of the maxilla. Its anterior tip



Fig. 13. Orbit region of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in anterolateral view showing shallow hemispherical depression on the prefrontal and lacrimal (character 277.1).

does not exceed the anterior extension of the lacrimal (fig. 3), but surpasses the anterior end of the frontal, in contrast to the condition seen in longirostrine crocodyli-

forms (e.g., *Terminonaris robusta* [Wu et al., 2001b], *Sarcosuchus hartii* MNN 604, and *Rhabdognathus aslerensis* CNRST-SUNY 190).

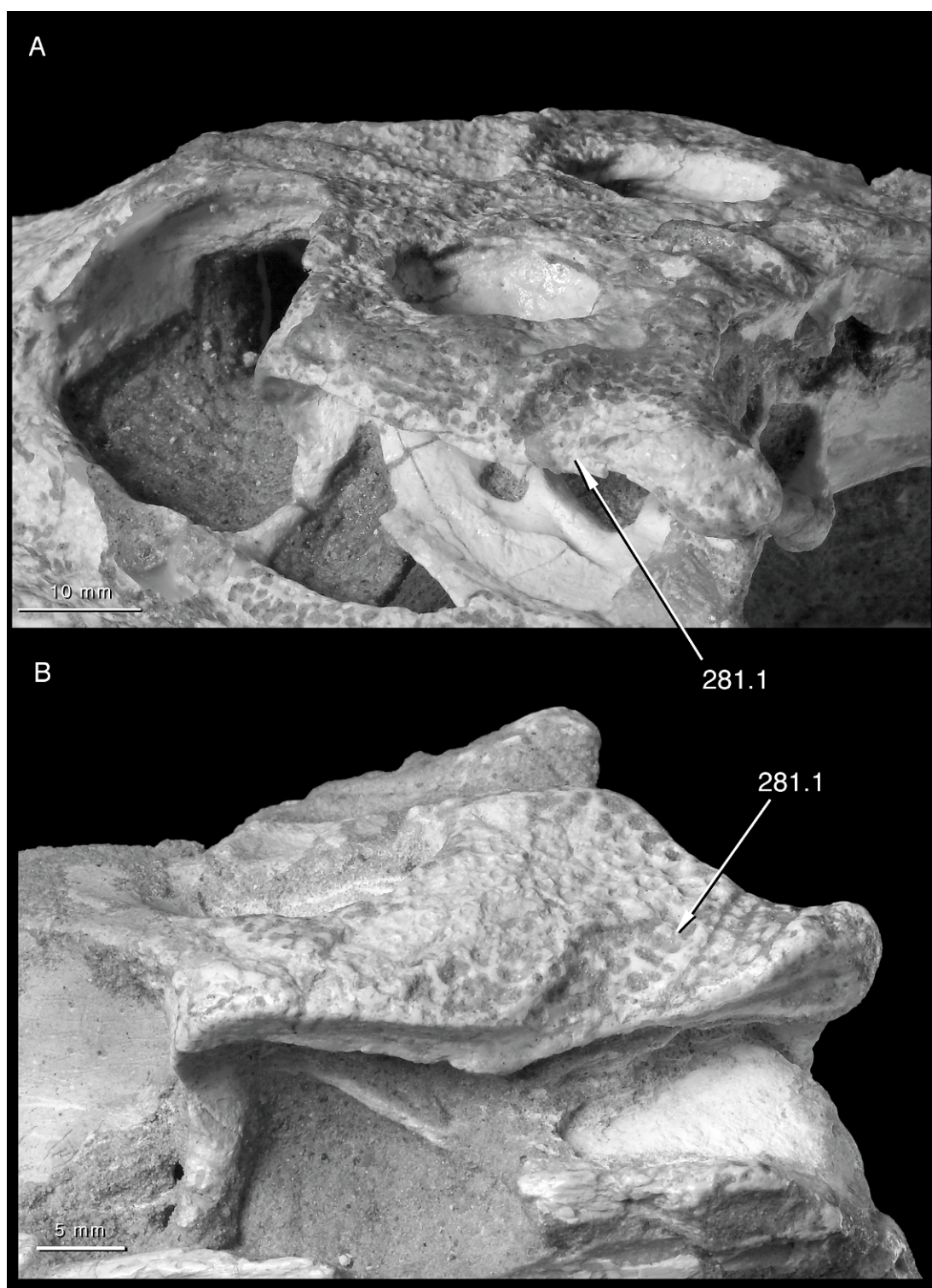


Fig. 14. Detail of *Shamosuchus djadochtaensis* autapomorphic characteristic of a prominent depressed area anterior to the posterior lobe of the squamosal. **A**, Referred specimen IGM 100/1195, and **B**, holotype specimen AMNH FR 6412.

The posterior end of the prefrontal tapers gradually, wedging between the lateral margin of the frontal and the orbital margin. The entire posterolateral region of the dorsal surface of the prefrontals is occupied by the smooth depressed surface described above. This surface extends along the anterior half of the dorsal orbital margin (figs. 3, 8), forming a posteriorly elongate, wing-shaped facet.

Within the orbital cavity, the prefrontal has a well-developed descending process that forms the prefrontal pillars, reaching the dorsal surface of the palate as in other mesoeucrocodylians (Clark, 1994). The dorsal half of the descending process is a flat surface oriented obliquely to the longitudinal axis of the skull, in contrast to the transversally oriented condition seen in basal mesoeucrocodylians (e.g., *Araripesuchus gomesii* AMNH FR 24450, *Notosuchus terrestris* MACN-RN 1041; *Sphagesaurus huenei* RCL-100). The condition of *Shamosuchus djadochtaensis* actually resembles that of *Allodaposuchus precedens* (Buscalioni et al., 2001) and extant crocodylians, which also have this surface exposed posterolaterally. The lateral region of this surface contacts the lacrimal along a ventrally directed suture.

Ventromedially, the descending process of the prefrontal forms the prefrontal pillar proper and is sutured to the palate (fig. 14). The prefrontal pillar is laminar, being anteroposteriorly thin and lateromedially expanded, except for its most distal region where it expands anteroposteriorly at the suture with the dorsal surface of the palate. IGM 100/1195 preserves the incomplete base of the prefrontal, which displays a medial process dorsoventrally centered on its medial edge.

As mentioned previously, none of the studied specimens preserve **palpebrals**. However, the presence of an anterior palpebral in *Shamosuchus djadochtaensis* cannot be rejected at the moment and further material is needed to assess this issue. The presence of a posterior palpebral that articulates with the postorbital is unlikely, due to the absence of a corresponding facet on the postorbital, which occurs in most advanced neosuchians.

The **frontals** are completely fused to each other on the midline as in all mesoeucroco-

dylans (Clark, 1994). The dorsal surface of this element is densely ornamented and bears a well-developed ridge along the sagittal plane (figs. 8, 13). The frontal ridge is clearly present in the type specimen (as described by Mook, 1924) and in IGM 100/1195. This resembles the condition of *Rugosuchus nonganensis* (Wu et al., 2001a), *Isisfordia duncani* (Salisbury et al., 2006), and some non-neosuchian crocodyliforms (e.g., *Sichuanosuchus shuhanensis* IVPP V 10594, *Simosuchus clarki* UA 8679, *Notosuchus terrestris* MACN-RN 1041). Lateral to this ridge, the dorsal surface of the frontal is flat, differing from the condition in *Rugosuchus nonganensis* (as noted by Wu et al., 2001a). The anterior end of the frontal tapers between the prefrontals and is markedly constricted above the orbits (being narrower than the width of the nasals). The lateral margins of the frontal form the posterior half of the dorsal margin of the orbits. Along this region, the lateral edges of the frontal are slightly elevated with respect to the rest of the dorsal surface of the frontal. Thus, the frontal forms supraorbital ridges similar to those of several neosuchian crocodyliforms (e.g., *Trematochampsia taqueti* MNHN-IBC 231, *Theriosuchus pusillus* BMNH R48330, *Bernissartia fagesii* [Buffetaut, 1975], *Rugosuchus nonganensis* [Wu et al., 2001a], *Hylaeochampsia vectiana* BMNH R177, and some crocodylians).

The frontal expands at the posterior end of the orbits where it contacts the postorbitals laterally and the parietal posteriorly. The suture with the postorbital is anteroposteriorly directed on the skull roof from the posteromedial margin of the orbit to the anterior edge of the antorbital fossa (fig. 8). This suture extends within the supratemporal fossa, where the frontal meets the anterolateral tip of the parietal and the postorbital is excluded from contacting the parietal by a portion of the laterosphenoid. Thus, although the frontal extends into the supratemporal fossa, it does not form part of the margin of the supratemporal (internal) fenestra, due to the existence of a laterosphenoid-parietal contact. Within the supratemporal fossa, the frontal-parietal suture is interdigitated and oriented transversely, extending onto the skull roof with the same orientation

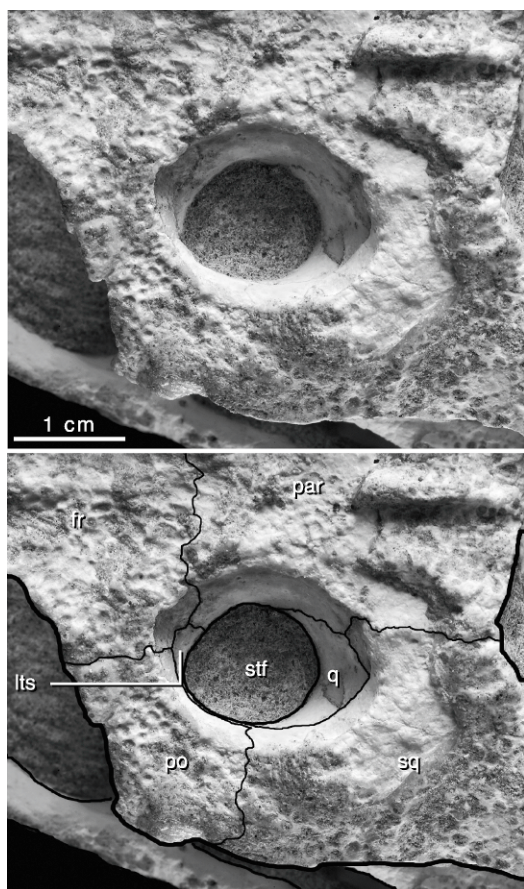


Fig. 15. Supratemporal fenestra of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 with accompanying interpretation of sutures. See appendix 5 for abbreviations.

and located just posterior to the anterior margin of the antorbital fossae. Inside the orbital cavity, the frontal is sutured to the postorbital laterally and ventrally to the anterodorsal margin of the laterosphenoid (fig. 15).

As in all crocodyliforms, the **parietals** are fused to each other forming an unpaired element. Its dorsal surface is ornamented and rather wide between the supratemporal fossae, forming part of the characteristic skull roof of most Crocodyliformes. The anterior half of this surface is flat, whereas the posterior region bears a prominent sagittal ridge (figs. 8, 15).

The lateral region of the parietal enters into the supratemporal openings, where it

forms the medial surface of the supratemporal fossae. This region is smooth and almost vertically oriented (fig. 8). The ventrolateral margins of the parietals are bounded by the laterosphenoid and the dorsal edge of the quadrate. The anterior region of the parietal fails to contact the postorbital, as in most noncrocodylian neosuchians. Posteriorly, the parietal expands slightly laterally, contacting the squamosals. The parietal-squamosal suture interdigitates and extends posteriorly from the posterior region of the supratemporal fossa onto the skull roof, reaching the occipital margin of the skull table. Within the supratemporal fossa, the parietal and squamosal enclose the anterior opening of the orbitotemporal passage. This opening is covered dorsally by a well-developed rim of the external margin of the supratemporal fossa (fig. 16). Therefore, the orbitotemporal opening is not visible in dorsal view, a character noted to be present only in advanced neosuchians (e.g., species of *Goniopholis*, *Bernissartia fagesii*, and adult eusuchians; Norell and Clark, 1990; Ortega et al., 2000). This character, however, is subject to marked ontogenetic variation in extant crocodylians and in the goniopholid *Sunosuchus junggarensis* (Wu et al., 1996a).

The dorsal surface of the **squamosals** forms the posterolateral region of the flat skull table characteristic of Crocodyliformes. This dorsal surface of the squamosal surface is triradiate, composed by a medial branch contacting the parietal, an anterior process contacting the postorbital, and a posterolateral process. The medial branch is rather short but anteroposteriorly extensive, well separating the supratemporal fossa from the occipital margin of the skull roof (figs. 3, 8, 15). The anterior branch of the squamosal is slightly curved and meets the postorbital in an interdigitated suture oriented transversely that is located at the anteroposterior mid-point of the supratemporal opening.

The posterolateral process of the squamosal is well developed and slightly curved medially toward its distal end, having a concave occipital margin and a sigmoid lateral margin (fig. 3). The dorsal surface of this process is ornamented with a pitted pattern, as is the rest of the squamosal, and is located at the same level as the skull table

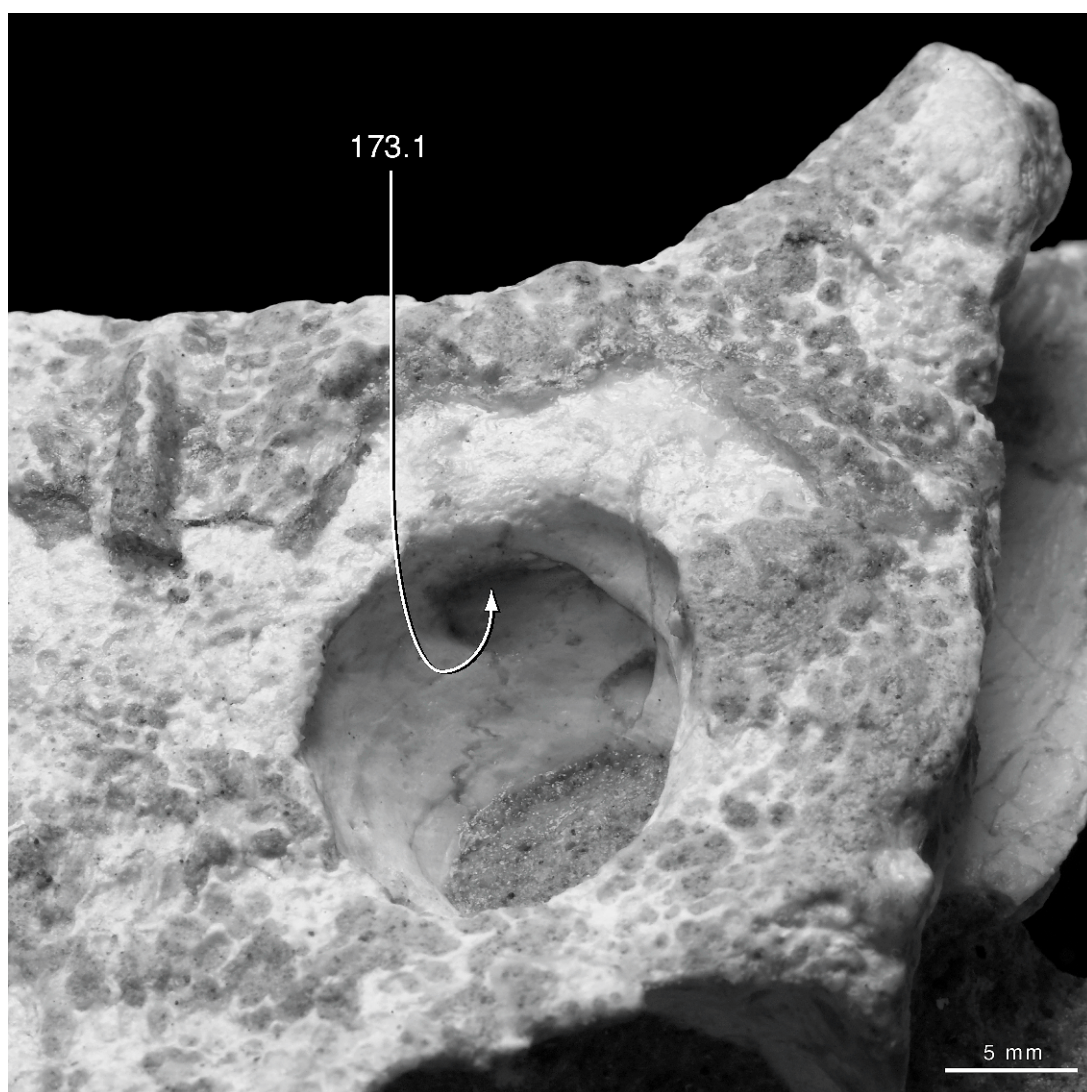


Fig. 16. Close-up of supratemporal fossa in the referred specimen IGM 100/1195 showing anterior opening of temporo-orbital opening hidden in dorsal view and overlapped by squamosal rim of fossa (character 173.1).

(figs. 8, 10). This pattern is in contrast to the ventrally deflected posterolateral process of most basal mesoeucrocodylians (*Araripesuchus gomesii* AMNH FR 24450, *Notosuchus terrestris* MACN-RN 1037, *Sebecus icaeorhinus* AMNH FR 3160). The type specimen of *Shamosuchus djadochtaensis* (AMNH FR 6412) bears two posteromedially directed grooves on this process. One of them is posteriorly concave, bordered by a weakly

developed ridge, and located at the base of the posterolateral process. The other groove is narrow, anteriorly concave, and located at the anteroposterior midpoint of this process (fig. 3). The first of these is present in IGM 100/1195, although the presence of the posterior groove cannot be corroborated in this specimen due to the poor preservation of this region. The presence of a distinct, depressed, and smooth posterolateral “lobe”

has been noted as a characteristic of some neosuchians (e.g., atoposaurids) by Clark (1994) (fig. 14). Wu et al. (1996a, 2001a), however, noted that a smooth depressed lobe of the squamosal may have a wider distribution and that it is ontogenetically variable in *Sunosuchus junggarensis*. Interestingly, *Rugosuchus nonganensis* has a morphology similar to *Shamosuchus djadochtaensis*, having the posterolateral region slightly sculpted, depressed, and separated by a weak ridge (Wu et al., 2001a). The presence of a sculpted and slightly depressed squamosal "lobe," however, may be also present in other species of *Shamosuchus* (Efimov, 1983, 1988) but not in *Shamosuchus major* (Wu et al., 2001a).

Medial to the skull roof surface, the squamosal forms the posterolateral region of the supratemporal fossa (figs. 15, 16). This surface is smooth and exposed almost vertically, forming a reduced lateral floor of the supratemporal fossa. The ventral margin of this region is bounded by the anterodorsal process of the quadrate.

The lateral margin of the squamosal overhangs the quadrate and quadratojugal forming a deep otic recess. The anterior half of the squamosal's lateral margin is laterally convex, whereas this edge is concave along the squamosal posterolateral process (fig. 3). The squamosal bears a rather broad discontinuous groove on the external surface of its lateral edge, resembling the attachment point of the movable dorsal earflap of extant crocodylians located above the otic aperture (Shute and Bellairs, 1955). The morphology of this groove in *Shamosuchus djadochtaensis* is, however, autapomorphic and differs slightly between the type specimen and IGM 100/1195. Both specimens share the presence of a shallow, but broad, groove extending from the anterior region of the lateral edge of the postorbital onto the lateral edge of the squamosal, up to the level of the otic aperture (fig. 14). At this point, the groove tapers posteriorly, disappearing and forming a sharp lateral edge of the squamosal. A similar groove reappears at the posterior edge of the otic aperture, along the lateral edge of the posterolateral process of the squamosal. This posterior region of the squamosal bulges dorsally and overhangs the posteriormost region of the otic recess

(fig. 14). This combination of characters seems to be unique among Crocodyliformes. The differences between the type specimen and IGM 100/1195 consist of the ornamentation of the anterior region of the groove (lacking in the holotype) and the depth of the posterior region of the groove, which is notably shallower in IGM 100/1195 (see figs. 3, 14). Within the otic recess, the squamosal bears a descending process that contacts the anterodorsal process of the quadrate and the postorbital. The otic aperture is located between the squamosal and quadrate and these two elements meet posteriorly to close the otic aperture as in other mesoeucrocodylians, except for *Allodaposuchus precedens* (Buscalioni et al., 2001) and *Gonipholis simus* (Salisbury et al., 1999), in which the squamosal and quadrate are not sutured posteriorly to the otic aperture and therefore the cranioquadrate passage is laterally open. The squamosal-quadrate contact is located at the dorsoventral midpoint of the posterior edge of the otic aperture, in contrast to the derived condition of alligatorids in which it is located at the posteroventral corner of the otic aperture (Brochu, 1999).

The squamosal is briefly exposed on the occipital surface of the skull. This smooth surface is vertically oriented and is dorsoventrally low. Its dorsoventral depth increases slightly toward its lateromedial midpoint and then tapers laterally along the occipital margin of the posterolateral process of the squamosal (fig. 11). This surface is bounded dorsally by a broad ridge of the skull table and ventrally by the paroccipital process.

The **postorbital** has a dorsal surface that forms the anterolateral region of the skull roof and a descending process that forms the dorsal half of the postorbital bar as in most mesoeucrocodylians (Clark, 1994). The anteromedial end of the postorbital contacts the frontal on the skull roof and both the frontal and laterosphenoid on the supratemporal fossa. The anterolateral corner of the postorbital bears a slightly developed pointed process, which extends ventrally as a thin, anteriorly convex, low lamina that merges with the anterior margin of the postorbital bar (figs. 13, 14). This process resembles the condition present in some longirostrine taxa (e.g., dyrosaurs, pholidosaurs; Buffetaut,

1979), although it is remarkably less developed than in those forms. The anterior surface of this lamina bears at least one small foramen located inside the orbital cavity. Similar structures are present in some mesoeucrocodylians (e.g., *Araripesuchus gomesii* AMNH FR 24450, *Trematochampsia taqueti* MNHN-IBC 231, *Rhabdognathus aslerensis* CNRS-ST-SUNY 190, *Allodaposuchus prece-dens* [Buscalioni et al., 2001], and crocodylians), although the homology of these foramina is poorly understood due to differences in number and precise location.

The descending process of the postorbital is a flat lamina facing posterolaterally (figs. 10, 14). This process is subdivided into a short posterior branch and an elongated anteroventral process that forms the postorbital bar. The short posterior branch extends to the anterior border of the otic recess. The dorsal region of this posterior branch contacts the ascending process of the quadrate and the squamosal. The ventral end of the short posterior branch projects as an acute tip that fits into the dorsal end of the ascending process of the quadratojugal, forming a posteroventrally directed V-shaped suture (fig. 14). The ventral margin of this acute ventral tip forms the dorsal apex of the infratemporal fenestra.

The elongate anteroventral process of the descending process of the postorbital becomes subcylindrical toward its contact with the ascending process of the jugal that delimits the posterior margin of the orbit. The postorbital-jugal suture is interdigitated on its lateral side and is located approximately at the dorsoventral midpoint of the postorbital bar.

The **jugal** of *Shamosuchus djadochtaensis* is markedly elongate, exceeding posteriorly the infratemporal fenestra and anteriorly the orbital opening. The external surface of the jugal is heavily ornamented, except for its ascending process that forms the ventral half of the postorbital bar. This element is dorsoventrally low posteriorly and increases gradually in depth toward the orbital region, being approximately twice as deep in the suborbital region as it is in the infratemporal region (as in most mesoeucrocodylians; Clark, 1994). The anterior end of the jugal is acute and overlaps laterally the posterior

end of the maxilla (figs. 5, 10). In the orbital region, it dorsally contacts the ventral extension of the lacrimal. The external surface of the jugal bears a moderately developed ridge oriented on the longitudinal axis along the suborbital region.

The base of the ascending postorbital process is located approximately at the anteroposterior midpoint of the jugal (figs. 5, 10). This process is narrow, cylindrical, posterodorsally directed, and inset from the lateral surface of the jugal. The postorbital process of the jugal forms the ventral half of the postorbital bar, separating the orbit from the infratemporal fenestra. At this region the jugal laterally overlaps the descending process of the postorbital.

The jugal bar below the infratemporal fenestra is dorsoventrally narrow and forms the ventral margin of the infratemporal fenestra (except for its posteroventral corner). Along this region, the lateral surface of the jugal is convex and bears a faint longitudinal ridge. Toward the posterior end of the infratemporal opening, the jugal becomes lateromedially flattened. Posterior to this point, the jugal narrows progressively and laterally overlaps the quadratojugal (figs. 5, 10). The posterior end of the jugal is a pointed process that reaches the level of the posterior edge of the otic aperture.

The **quadratojugal** is a triradiate element, with a notably short and broad anterior branch, an elongate and thin anterodorsal process, and a robust posterior process. The external surface of the quadratojugal is ornamented except for the thin anterodorsal process and the caudal region of the posterior process. The anterior branch forms the anteroventral corner of the infratemporal fenestra and contacts ventrally the posterior end of the jugal, through a posteroventrally directed suture. The quadratojugal ascending process extends dorsally forming the posterior edge of the infratemporal fenestra. This process is moderately thin along its ventral half and bears a slightly developed ridge located close to its anterior margin. The anterior margin of this process has a well-developed knob at the dorsoventral midpoint of the ascending process, resembling the condition of some neosuchians (e.g., *Stolokrosuchus lapparenti* [Larsson and Gado,

2000], *Sarcosuchus imperator* [Sereno et al., 2001]). This knob is interpreted as putatively homologous to the quadratojugal spine present in several neosuchians (e.g., *Terminonaris robusta* [Wu et al., 2001b], *Bernissartia fagesii* [Norell and Clark, 1990], nonalligatorid crocodylians). Dorsal to the quadratojugal knob, the ascending process of the quadratojugal is markedly narrower and contacts the postorbital (figs. 10, 14).

The posterior margin of the quadratojugal contacts the anterodorsal process of the quadrate along a straight suture. The posteroventral region of the quadratojugal is unsculpted and laterally bulged. It seems to overlap laterally the quadrate, reaching the level of the articular condyles although it apparently does not form part of the craniomandibular articulation (fig. 10), similar to *Rugosuchus nonganensis* (Wu et al., 2001a) and other advanced neosuchians (e.g., *Goniopholis simus* BMNH 41098, crocodylians). Although this region is not perfectly preserved in the two specimens studied here, the distal end of the quadratojugal does not seem to form part of the craniomandibular joint.

The **quadrates** are well preserved in IGM 100/1195 although their articular surfaces are partially covered by the articular. The anterodorsal region of the quadrate is smooth and forms most of the ventral surface of the otic recess (figs. 10, 14). The anterior edge of this process contacts the quadratojugal and its dorsal edge is sutured to the squamosal and parietal. The posterodorsal region of the anterodorsal process of the quadrate forms the anterior and ventral margins of the otic aperture. This opening is anteroposteriorly elongate with a markedly concave anterior margin. As indicated above, this notch is posteriorly closed by the squamosal-quadrate suture (fig. 10). The posteroventral corner of the otic aperture is strongly curved and the quadrate extends as a short dorsal process that bears a dorsoventrally centered protrusion delimiting the dorsal border of the anterior end of the cranioquadrate passage. A small siphoneal foramen is located anteroventrally to the otic aperture. The anterodorsal process of the quadrate bears a slightly depressed area that surrounds the ventral margins of the otic notch and siphoneal foramen (figs. 10, 14).

The distal body of the quadrate is short, robust, and directed posteroventrally. The extension of this region of the quadrate is more developed than in basal crocodyliforms (e.g., *Protosuchus richardsoni* AMNH FR 3024; *Gobiosuchus kielanae* ZPAL MgR-II/67), but less than in derived neosuchians (*Rhabdognathus* sp. CNRST-SUNY 190; *Alligator mississippiensis* FMNH 8201; *Crocodylus niloticus* FMNH 1757; *Goniopholis stovalli* AMNH FR 5782). The distal body of the quadrate is slightly wider than anteroposteriorly long, resembling the neosuchian condition. The posterior surface of the quadrate body is slightly convex and seems to lack a well-developed ridge, a condition noted by Wu et al. (2001a) to be shared with *Shamosuchus tersus*, *Rugosuchus nonganensis*, and *Bernissartia fagesii*. A similar ridge, however, is present in several basal mesoeucrocodylians (e.g., *Libycosuchus brevirostris* BSP 1912.VIII.574, *Sebecus icaeorhinus* AMNH FR 3160, *Hsisosuchus chungkingensis* CNM V 1090). The medial surface of the distal quadrate body is pierced by a small foramen aërum. The quadrate condyles are in their natural position on the articular facets of the craniomandibular joint. The dorsal region of the quadrate body is overhung laterally by the paroccipital process up to the posterior opening of the cranioquadrate passage (fig. 11). The dorsomedial region of the quadrate body contacts the otoccipital through an interdigitated suture. This contact originates near the cranioquadrate passage and runs ventromedially toward the ventral margin of the occiput. Medial to this point, the suture continues along the ventral edge of the occipital surface of the skull, forming a sharp ridge (fig. 11). The ventral surface of the quadrate extends anteriorly to this ridge and is strongly sutured to the posterolateral margins of the basisphenoid and the quadrate processes of the pterygoids. The ventral surface of the quadrates is not fully exposed although the visible region bears a well-developed crest B (sensu Iordansky, 1973) (fig. 18). Details on the quadrate contact with the rest of the braincase are not exposed, although this branch certainly extends dorsally reaching the posterior region of the supratemporal fossa, where it is sutured to the squamosal.

The **ectopterygoids** are preserved in articulation with the pterygoids in IGM 100/1195 and AMNH FR 6412, being partly occluded by the lower jaw. Their anterolateral end articulates with the maxilla and jugal through well-developed anterior and posterior processes. This element seems to lack the ascending process that extends along the medial surface of the postorbital bar in neosuchians including derived forms such as *Hylaeochampsia vectiana* (Clark and Norell, 1992), *Allodaposuchus precedens* (Buscalioni et al., 2001), and nonalligatorid crocodylians (Brochu, 1999). The posteromedial region of the ectopterygoid is sutured to the lateral edge of the pterygoid flange (figs. 4, 9, 18). This suture is sigmoidal and extends from the posterior edge of the suborbital fenestra toward the posterolateral end of the pterygoid flanges. Along this region, the ectopterygoids partially overlap the ventral surface of the pterygoids and fail to reach the posterior end of the pterygoid flanges (as in most mesoeucrocodylians). The ventral surface of these elements is flat, smooth, and broadly exposed on the palate, occupying approximately the lateral third of the lateromedial extension of the pterygoid flanges.

The **palatines** are partly preserved in the two specimens studied here. The type specimen has preserved the midsection of the palatine secondary palate (fig. 4) and the specimen IGM 100/1195 has preserved its posterior region (fig. 9). These elements are medially sutured to each other constituting a posteriorly extended secondary palate that forms the floor of the nasopharyngeal passage, characteristic of mesoeucrocodylians. The anterior ends of the palatines seem to have extended anteriorly to the suborbital fenestra, between the palatal branches of the maxillae (figs. 4, 9). However, this region is poorly preserved and details on the maxilla-palatine suture or on the degree of extension of this anterior process cannot be determined at the moment. The palatines extend between the suborbital fenestra, forming a relatively narrow palatine bar. Along this region, their lateral margins are concave, producing an hourglass-shaped ventral surface of the palatines (figs. 4, 9).

The posterolateral region of the right palatine of IGM 100/1195 projects a process

that contacts the anterolateral region of the pterygoid at the anterolateral corner of the choanal opening. Thus, the choana of *Shamosuchus djadochtaensis* is enclosed between the palatine and pterygoids (i.e., a “mesosuchian” palate) in contrast to the pterygoid bounded choana of *Isisfordia duncani* (Salisbury et al., 2006), *Hylaeochampsia vectiana* (Clark and Norell, 1992), and more derived eusuchians. Mook (1924) has originally interpreted the type specimen as having a eusuchian type choanal opening, but the holotype has this region severely damaged and restored (fig. 4) and the new specimen clearly rejects his original interpretation. The palatine forms the entire anterior margin of the choanal opening and fails to project extensively along the lateral margins of the choana (fig. 9), differing from the condition of all other noneusuchian mesoeucrocodylians (except for *Rugosuchus nonganensis* and the Glen Rose form). As in *Rugosuchus nonganensis* (Wu et al., 2001a), the posterolateral end of the palatines does not reach the posterior margin of the suborbital fenestra, resulting in a rather anterior location of the anterior margin of the choanal opening (i.e., rostral to the posterior edge of the suborbital opening). Some of the described species of *Shamosuchus* have a similar position of the choanal anterior margin (e.g., *Shamosuchus ulgicus*; Storrs and Efimov, 2000: fig. 20.8). Wu et al. (2001a), however, noted that other species (e.g., *Shamosuchus ulanicus*) have a more posteriorly located choanal opening, which is the condition found in some advanced neosuchians (e.g., *Bernissartia fagesii* [Buscalioni and Sanz, 1990], the Glen Rose form [Langston, 1973], *Isisfordia duncani* [Salisbury et al., 2006]) and Crocodylia. The medial region of the posterior end of the palatines has not been preserved in any of the studied specimens.

The **pterygoids** are completely fused to each other as in all mesoeucrocodylians. IGM 100/1195 preserves most of the ventral surface of these elements, in contrast to the fragmentary pterygoids of the holotype of *Shamosuchus djadochtaensis*. The ventral surface of the pterygoids is smooth, laterally flat along the pterygoid flanges and depressed at their medial region (figs. 9, 18). At the anterior end, the medial region has a broad

depression that extends laterally up to the caudal end of the suborbital openings (i.e., exceeding in width the lateromedial extension of the palatine bar between the suborbital fenestrae). The lateral walls of the broad depression are subvertically oriented laminae that separate the choana from the suborbital fenestra and their anterior ends contact the posterolateral projections of the palatines (fig. 9). This broad and shallow depression bears a markedly concave choanal groove, which is deep, narrow, and elongate (fig. 9). The narrow choanal groove is more clearly differentiated from the broad medial depression of the pterygoids toward the anterior end of the choanal opening (approximately at the level of the anteroposterior midpoint of the suborbital opening). Posteriorly, the narrow and deep choanal groove gradually opens into the broader medial depression of the pterygoids, at the level of the pterygoid flanges. This region is closed posteriorly by a well-developed buttress located close to the posterior edge of the pterygoid. The presence of a relatively broad choanal opening is a plesiomorphic condition for neosuchians, and clearly differs from the reduced opening present in *Hylaeochampsia vectiana* and more derived eusuchians (Salisbury et al., 2006). In IGM 100/1195 there are no signs of a pterygoid choanal septum.

The pterygoids expand laterally forming well-developed pterygoid flanges. These flanges are large, laminar, and directed laterally at their base. Along their lateromedial extension, the pterygoid wings gradually deflect ventrally (figs. 11). The pterygoid flanges seem to lack the air cavities present in some basal crocodyliforms (*Edentosuchus tienshanensis* GMPKU-P 200101, *Araripesuchus buitreaensis* MPCA-PV 235, *Notosuchus terrestris* MACN-RN 1037). The anterior edges of the pterygoid flanges are L-shaped and form the posterolateral and posterior margin of the suborbital opening. As mentioned above, their lateral edges are overlapped by the ectopterygoids. The posterior edge of the pterygoid flanges is directed posteromedially. The medial region of their posterior margin bears a deep notch bounded by the base of the quadrate processes of the pterygoids (fig. 9). The base of these processes is markedly narrow, as in most advanced

neosuchians, and extends dorsally contacting the basisphenoid and the quadrates (fig. 11). The posterior surface of this dorsal extension of the pterygoids is strongly concave and contacts the anteromedial region of the basisphenoid. The quadrate processes of the pterygoids extend dorsolaterally, bordering the lateral margins of the basisphenoid through an interdigitated suture. These processes are rather extensive and are dorsally sutured to the pterygoid processes of the quadrates.

The **basisphenoid** is preserved only in IGM 100/1195. The ventral surface of this element is crescent shaped and has a reduced exposure on the ventral surface of the braincase (figs. 9, 11). The anterior edge of the basisphenoid is convex and contacts the pterygoids through an interdigitated suture. The posterior edge of the basisphenoid is deeply concave and is similarly sutured to the basioccipital (figs. 4, 9, 11). The basisphenoid exhibits elongate dorsolateral processes that are bounded posterodorsally by the basioccipital and the ventromedial extension of the otoccipital and posteroventrally by the pterygoid processes of the quadrate and the pterygoids. The distal end of these processes is slightly expanded with respect to their base, extending for a short distance onto the lateral surface of the braincase (rather than onto the occipital surface of the skull). This expansion could be homologous with the well-developed basisphenoid exposure on the lateral surface of the braincase present in *Isisfordia duncani* (Salisbury et al., 2006) and crocodylians. The ventral surface of the basisphenoid is flat, except for its posterior edge, which bears a well-developed ridge along its contact with the basioccipital (figs. 4, 9, 11). The foramen intertympanicum is rather large and located medially on the basisphenoid-basioccipital suture. The lateral eustachian foramina are also enclosed between these two bones, but are notably smaller than the foramen intertympanicum and located at the midpoint of the posterolateral processes of the basisphenoid.

The degree of exposure of the basisphenoid is intermediate between the plesiomorphic condition of basal crocodyliforms and the derived condition of crocodylians (fig. 9). The anteromedial region of the

basisphenoid is reduced, contrasting with the broad basisphenoid of basal crocodyliforms (e.g., *Gobiosuchus kielanae* ZPAL MgR-II/67, *Sichuanosuchus shuhanensis* IVPP V10594; *Zosuchus davidsoni* IGM 100/1305). The basisphenoid of IGM 100/1195 (in particular its posterolateral process), however, is more exposed in ventral view than in crocodylians (e.g., *Alligator mississippiensis* FMNH 8021, *Crocodylus niloticus* FMNH 17157) and most neosuchians (e.g., *Rhabdognathus* CNRST-SUNY 190, *Sarcosuchus hartii* MNN 604, *Isisfordia duncani* [Salisbury et al., 2006], *Hylaeochampsia vectiana* BMNH R177). The condition of *Shamosuchus djadochtaensis*, with a moderately exposed anteromedial region and well-exposed posterolateral processes, resembles the morphology of the basal neosuchian *Theriosuchus pusillus* (Clark, 1986) and several basal mesoeucrocodylians (e.g., *Notosuchus terrestris* MACN-RN 1037, *Simosuchus clarki* UA 8679, *Baurusuchus pachecoi* DGM 299-R, *Lomasuchus palpebrosus* MOZ-P 4084). The condition of IGM 100/1195, however, seems to be more derived than in these forms in two features. First, the exposure of the basisphenoid of *Shamosuchus djadochtaensis* is slightly less developed in ventral view. Second, the anteromedial region of the basisphenoid projects further ventrally in *Shamosuchus djadochtaensis*, so that it is visible in posterior view (fig. 11), as in extant forms. The latter feature can be interpreted as an incipient stage in the development of the strong verticalization of the basicranium that characterizes crocodylians (Tarsitano, 1985).

The **basioccipital** of *Shamosuchus djadochtaensis* is subrhomboidal and is laterodorsally bounded by the otoccipitals and ventrally by the basisphenoid. At its dorsal end, the basioccipital forms most of the occipital condyle. The occipital condyle lacks a well-developed neck and is slightly deflected posteroventrally, as is the rest of the basioccipital surface extending ventrally from the condyle. This orientation of the basioccipital surface is also found in *Isisfordia duncani* (Salisbury et al., 2006), although it is also present (and more developed) in non-neosuchian crocodyliforms (e.g., *Gobiosuchus kielanae* ZPAL MgR-II/67, *Zosuchus davidsoni* IGM 100/1305, *Notosuchus terrestris* MACN-

RN 1037, *Araripesuchus gomesii* AMNH FR 24450, *Simosuchus clarki* UA 8679). Other neosuchians, however, have a more vertically oriented basioccipital that faces posteriorly (*Lomasuchus palpebrosus* MOZ-P 4084, *Sarcosuchus hartii* MNN 604, *Rhabdognathus* CNRST-SUNY 190, *Goniopholis simus* BMNH 41098). This condition is also present in eusuchians (including *Hylaeochampsia vectiana* BMNH R177), due to the strong verticalization of the braincase (Tarsitano, 1985).

Ventral to the occipital condyle, the basioccipital bears a slightly developed medial depression and a moderately developed sagittal ridge extending along the ventral half of the basioccipital. This ridge reaches the posterior margin of the foramen intertympanicum, where it bifurcates surrounding the posterolateral edges of this opening (fig. 9). The lateral region of the basioccipital expands along their contact with the otoccipital, giving the subrhomboid shape to this bone (figs. 9, 11). The basioccipital-otoccipital suture is slightly interdigitated and reaches the ventral margin of the occipital surface of the skull, at the triple contact between the basioccipital, otoccipital, and basisphenoid (located just ventral to the foramen for the internal carotid artery). Ventromedially to this point, the basioccipital is sutured to the basisphenoid as described above. The basioccipital lacks well-developed tubera, a character usually present in long snouted crocodyliforms and consequently it is not expected here.

The **otoccipitals** are partially preserved in both specimens studied here, although those of IGM 100/1195 are more complete. The otoccipitals extend along most of the occipital surface of the skull (fig. 11). Their medial margins form the lateral and dorsal margins of the foramen magnum and contact each other medially above this opening. Dorsally to this point, the otoccipitals contact the supraoccipital, although details on this contact cannot be determined due to the poor preservation of this region. Most of the lateral extension of the otoccipitals is exposed on two different planes. The ventral half of the otoccipital is exposed posteroventrally, although this region is slightly more vertical than the basioccipital. This morphology

resembles the condition of *Rugosuchus non-ganensis* (Wu et al., 2001a) and several other noneusuchian crocodyliforms. The ventral region of the otoccipital narrows ventrally, lacking the enlarged ventrolateral process that characterizes most basal crocodyliforms and thalattosuchians (Clark, 1986). The lateral margin of this region of the otoccipital contacts the quadrate, forming the ventral ridge of the occipital surface of the skull (as described above). The ventral end of the otoccipital is acute and wedges between the basioccipital and the basisphenoid (figs. 9, 11). The ventral end of this surface is pierced by the foramen for the internal carotid artery. Dorsolaterally to this foramen, the otoccipital bears a slightly larger opening for the cranial nerves IX–XI (fig. 11). A single foramen for the cranial nerve XII is located just lateral to the foramen magnum.

The dorsal half of the otoccipital forms a relatively short paroccipital process, which briefly extends laterally to the posterior opening of the cranioquadrate passage. A similarly reduced lateral extension of the paroccipital process is also present in other advanced neosuchians (e.g., *Gonipholis stovalli* AMNH FR 5782, *Isisfordia duncani* [Salisbury et al., 2006], *Allodaposuchus precedens* [Buscalioni et al., 2001], *Hylaeochampsia vectiana* BMNH R177), but differs from the relatively long paroccipital process of crocodylians. This process is subtabular in shape and vertically oriented. The dorsal margin of this region of the otoccipital is sutured to the occipital flange of the squamosal (as described above). The lateral end of the paroccipital process is slightly narrower and curved posteriorly, but forms a relatively blunt lateral end as in most mesoeucrocodylians. The ventral margin of the paroccipital process forms a transverse ridge that overhangs the cranioquadrate passage (fig. 11). Above this margin, the paroccipital process displays slightly marked striations.

Only the dorsalmost region of the **supra-occipital** is preserved in IGM 100/1195 (fig. 11). This region bears a poorly developed sagittal ridge and does not seem to extend onto the skull table, as in other noneusuchian neosuchians (and *Alligator*; Brochu, 1999). The laterodorsal region of

the supraoccipital bulges slightly close to the location of the posttemporal fenestra.

The **laterosphenoid** forms the anterolateral wall of the braincase. The left laterosphenoid is exposed and well preserved in IGM 100/1195. It is divided into distinct anterior and posterior surfaces by a prominent cotylar crest, with the posterior surface forming the anteromedial wall of the supratemporal fenestra. The laterosphenoid contacts the quadrate posteriorly in a robust suture enclosing the trigeminal foramen. The ventroposterior margin of the trigeminal foramen is obscured, so it is unclear whether, or to what extent the prootic participated in the nerve foramen. Anterior to the trigeminal foramen, the laterosphenoid has a moderate suture with the basisphenoid medially and the pterygoid ventrally. This area corresponds to the location of the laterosphenoid bridge in Crocodylia. In IGM 100/1195 this area is broad and clearly lacks a distinct passage for the ophthalmic branch of cranial nerve V. This is also the case in the basal eusuchian *Hylaeochampsia vectiana* (Clark and Norell, 1992), which indeed lacks a laterosphenoid bridge. On the posterior side of the cotylar crest, just anterior to the trigeminal foramen there is a shallow groove that may correspond to the path of the ophthalmic branch of cranial nerve V as it passes over the laterosphenoid body. Anteriorly the laterosphenoids converge toward the midline; however, IGM 100/1195 does not preserve details of the notches and/or foramina for the passage of cranial nerves II, III, and IV. Anterodorsally, the laterosphenoid sutures broadly with the frontal. The capitate process is well preserved and contacts the postorbital near the midpoint of the anterior body of the bone.

Posterior to the basisphenoid rostrum, CT imagery indicates small sellae turcicae on the basisphenoid (fig. 19). Although artifacts obscure the exact location of the anterior border of the dorsum sellae, the foramina passing through the dorsum sellae are well preserved and clear in CT images. Posterior to the sellae two pairs of foramina pierce the basisphenoid. The medial pair mark the passage of the anterior carotid artery into the tympanic cavity (fig. 19; see also Colbert, 1946). Lateral to the anterior carotid fora-

mina smaller opening are present corresponding to the exit of cranial nerve VI from the braincase. Ventral to these passages, a large cavity corresponding to the anterior branch for the median Eustachian tube is preserved. Moving posterolaterally, the anterior and posterior branches of the median Eustachian tube open into a large rhomboidal sinus. Dorsal to the posterior border of the rhomboid sinus the metotic fissure is seen dividing the opisthotic from the basioccipital. The opisthotic is generally well preserved, but its exact suture with the exoccipital (forming the otoccipital) is not clearly defined. The opisthotic forms the posteroventral border of the tympanic bulla, delineates the dorsal border of the metotic fissure, and forms the dorsal wall of the perilymphatic foramen. The anterior portion of the lateral semicircular canal passes within the opisthotic. Also, the canal for the foramen vagi is well defined. The canal is undivided, unlike that in living crocodylians (Iordansky, 1973) and passes posterolaterally from the metotic fissure toward its exit from the skull near the posterior carotid foramen.

The area surrounding the **prootic** is not exposed; thus, it is uncertain whether the bone is visible on the lateral side of the braincase. Internally, it forms the anterior portion of the bulla tympani (cochlear prominence) and part of the lateral wall of the braincase (fig. 19). The prootic contains the common crus of the anterior and posterior semicircular canals, the ventral portion of the anterior semicircular canal, and the anterior half of the lateral semicircular canal, although the lateral semicircular canal is very poorly preserved.

THE MANDIBLE

The mandible is dorsoventrally shallow anteriorly and a solid and robust element posteriorly. The external mandibular fenestra is completely obliterated, as in other species described for *Shamosuchus* and several non-crocodylian neosuchians such as *Theriosuchus pusillus* (BMNH R48328), *Gonipholis simus* (Salisbury et al., 1999), *Bernissartia fagesii* (Norell and Clark, 1990), *Rugosuchus nonganensis* (Wu et al., 2001a), and the Glen Rose form (Brochu, 1999). *Isisfordia duncani*

(Salisbury et al., 2006) and most crocodylians instead have a well-developed external mandibular fenestra. The symphysis is only partly preserved and posterior to it, the mandibular rami diverge at an angle of approximately 40°.

The **dentaries** are almost complete in IGM 100/1195, having only the anterior symphyseal region missing. The anterior half of the dentaries is inset between the maxillae, whereas the posterior region of the dentaries is aligned with the lateral edge of the maxillae. Anteriorly, the height of the dentary is markedly low, forming a shallow mandibular symphysis (figs. 9, 10, 12). Posteriorly the mandibular rami diverge continuously and the dentaries gradually increase their dorsoventral depth. The ventral and lateral surfaces of the dentaries of IGM 100/1195 are deeply ornamented with the pitted pattern present on most skull bones, whereas the preserved portion of the dentaries of the holotype is smooth. The ventral end of the dentary is medially deflected, forming the lateral half of the ventral surface of the mandibular rami. This margin of the dentary is sutured to the ventrolateral margin of the splenial through a linear suture. The lateral surface of these elements is laterally convex, as in most neosuchian crocodyliforms (Ortega et al., 2000). The buccal margin of the dentaries is mostly occluded by the maxillae, except for their posterior region. At this point, specimen IGM 100/1195 shows a smooth laterodorsally exposed surface bordering the posteriormost region of the lower tooth row. In this smooth surface there are no signs of neurovascular foramina in IGM 100/1195.

The posterior ends of the dentaries are entirely sutured to the surangular and angular, thus forming the absence of an external mandibular fenestra (figs. 9, 10). The posterodorsal margin of the dentaries borders the acute anterior process of the surangular, along a straight suture directed posteroventrally. Ventral to this point, the posterior region of the dentary is sutured to the angular, although details on this contact cannot be determined in the two specimens studied here. The lower dentition cannot be observed in any of the specimens reported

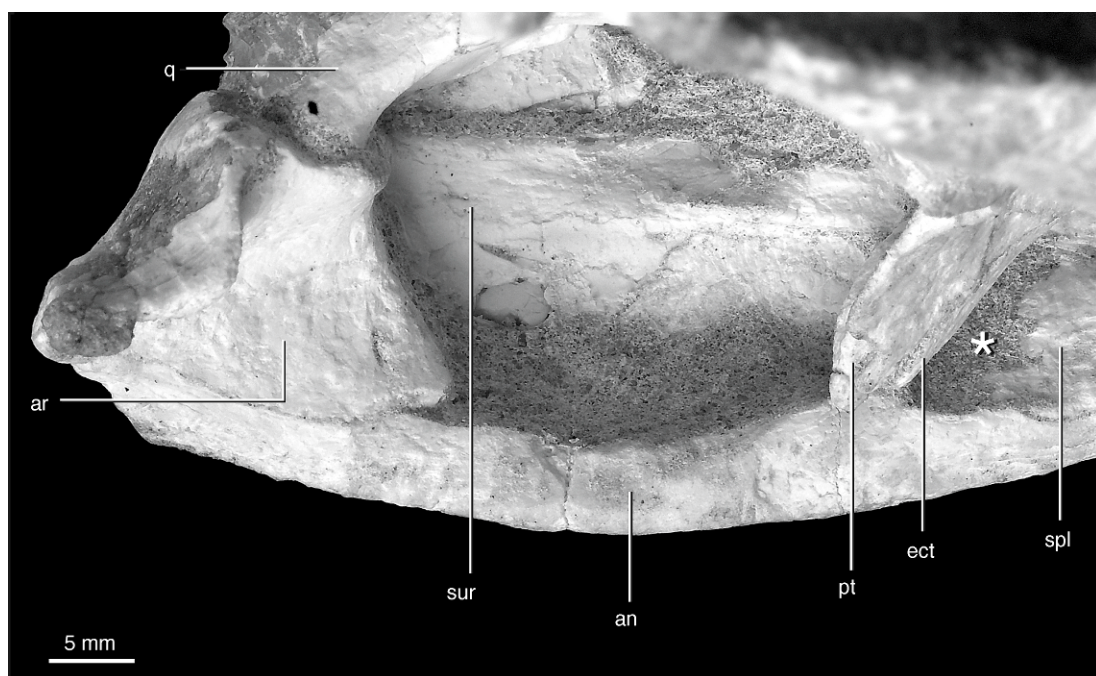


Fig. 17. Posterior mandible of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in medial view. See appendix 5 for abbreviations. Asterisk indicates likely position of coronoid had it been present or preserved.

here due to the inset position of the mandibular rami between the maxillae.

The **splenials** form part of the mandibular symphysis (at least on its ventral surface). Along this region, the splenials form the medial third of the ventral surface of the mandibular symphysis. The participation of the splenials on the mandibular symphysis is also present in basal crocodylians (Brochu, 1999) and most noncrocodylian neosuchians (e.g., *Rugosuchus nonganensis* [Wu et al., 2001a], *Terminonaris robusta* [Wu et al., 2001b], *Sarcosuchus imperator* MNN 604, *Hyposaurus rogersii* [Denton et al., 1997], *Theriosuchus pusillus* BMNH R48330). Posteriorly, the splenials cover the medial surface of the mandibular rami and the medial half of their ventral surface (figs. 4, 9). The ventrolateral edge of the splenial is sutured to the dentary along a straight suture that extends on the anterior half of the mandibular ramus. The medial surfaces of the splenials are smooth and slightly convex. Although this surface is slightly damaged anteriorly in IGM 100/1195, there are no

signs of a foramen intermandibularis oralis. Similarly, the foramina intermandibularis medius and caudalis seem to be absent in IGM 100/1195. The posteroventral margin of the medial lamina of the splenial is sutured to the anteromedial surface of the angular, through a slightly interdigitated suture running posterodorsally. The posterodorsal margin of the splenial lamina seems to be slightly broadened and deflected medially. Presumably, this surface formed a broad medial margin of the posterior region of the lower tooth row, a morphology also present in several basal globidontans (Brochu, 1999). The **coronoids** have not been preserved as isolated elements, although at the moment we cannot determine whether these elements were fused to the splenials or were lost during preservation (fig. 17).

The **angular** forms more than half of the lateral surface of the posterior mandibular ramus (figs. 5, 9, 10, 17). In the two specimens studied here, the lateral surface of this element is heavily ornamented and bears a well-developed longitudinal ridge

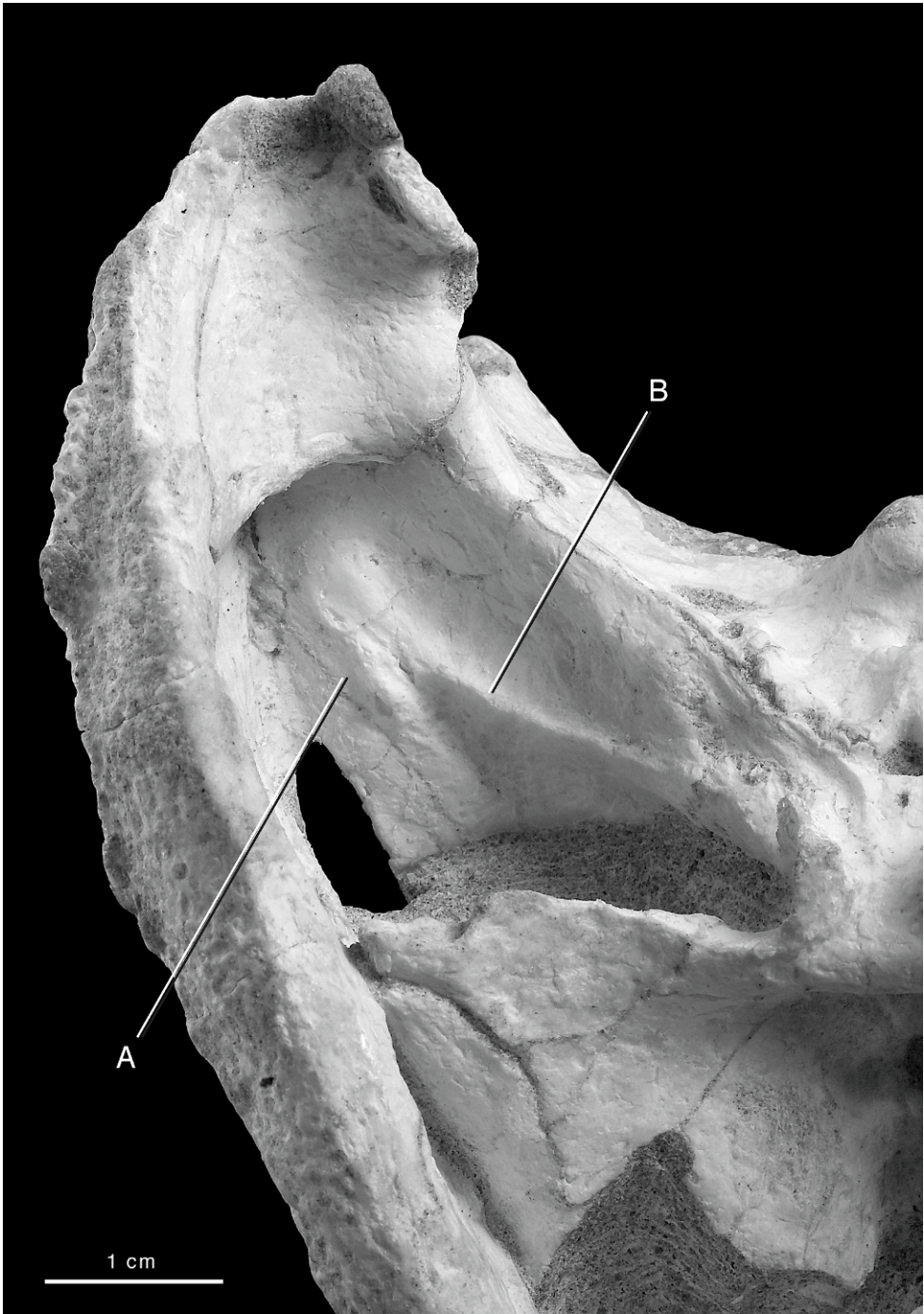


Fig. 18. Cranoquadrate articulation of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in ventral view. See appendix 5 for abbreviations.

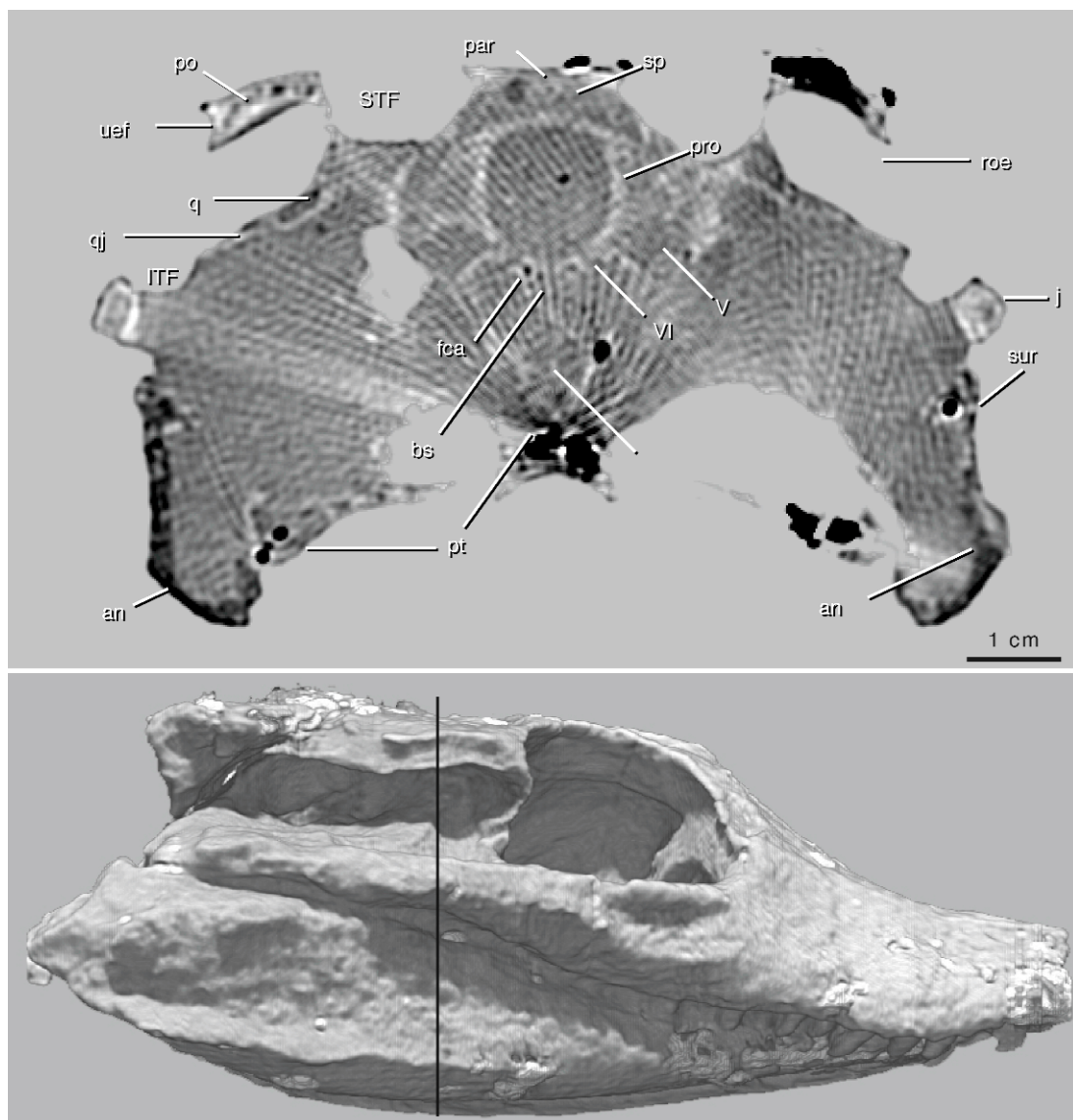


Fig. 19. Coronal CT section through the braincase of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

located at its dorsoventral midpoint. This ridge extends from its anterior margin to the posteroventral end of the mandibular ramus, where it is deflected ventrally (fig. 10). This ridge is absent in crocodylians, but a similar structure has been noted as present in *Shamosuchus gradilifrons* (Wu et al., 2001a) and is also recorded in some forms that lack an external mandibular fenestra, such as the neosuchians *Rugosuchus nonganensis* (Wu et

al., 2001a), *Theriosuchus pusillus* (BMNH R48328), and the Glen Rose form. Additionally, an angular ridge is also present in some basal crocodylians (e.g., *Zaraasuchus shepardi* IGM 100/1321, *Gobiosuchus kielanae* ZPAL MgR-II/68) although their ridge is located at the ventral margin of the mandibular ramus, rather than on its lateral surface as in the above-mentioned neosuchians. The presence of this ridge, however, is not strictly

correlated with the absence of an external mandibular fenestra since it is similarly present in forms that have this opening (e.g., *Simosuchus clarki* UA 8769) and absent in others that lack this fenestra (e.g., *Bernissartia fagesii* [Wu et al., 2001a], *Geosaurus araucanensis* MACN-N 95). Due to its position on the lower jaw, this ridge may have served as the posterior insertion point of the m. pterygoideus posterior.

The dorsal margin of the angular contacts the ventral margin of the surangular through an interdigitated suture oriented longitudinally along the lateral surface of the lower jaw (fig. 5). This suture is located slightly above the dorsoventral midpoint of the mandibular ramus and extends horizontally to the caudal end of the lower jaw, reaching the lateral margin of the retroarticular process (fig. 18). A horizontal and dorsally located angular-surangular suture is also present in *Rugosuchus nonganensis* (Wu et al., 2001a) and *Bernissartia fagesii* (Buscalioni and Sanz, 1990). The posteriormost region of the angular that borders the retroarticular process lacks the ornamentation present in the rest of the angular's lateral surface. The medial surface of the angular is smooth and seems to be dorsoventrally low, although it is not completely exposed in IGM 100/1195. Posteriorly, the ventral surface of the angular contacts the articular, covering the lateral region of the ventral surface of the retroarticular process (extending up to its posterior end; fig. 18). The ventral margin of the angular of *Shamosuchus djadochtaensis* is slightly deflected dorsally, in contrast to the highly curved angular of *Rugosuchus nonganensis* (Wu et al., 2001a) and *Bernissartia fagesii* (Buscalioni and Sanz, 1990; Norell and Clark, 1990) that form angles of 110–120° (see Wu et al., 2001a, for a discussion).

The **surangular** extends anteriorly as an acute process that contacts the posterodorsal region of the dentary, reaching the level of the anteroposterior midpoint of the orbit. At this point, the lateral surface of the surangular is pierced by a moderately large surangular foramen (figs. 5, 10). Posterior to this point, the surangular increases its dorsoventral depth along its suture with the dentary and angular. The dorsal surface of the surangular of IGM 100/1195 is rather flat

and not dorsally bowed as it seems to be in the poorly preserved holotype of *Shamosuchus djadochtaensis*. Except for the anterior process, the lateral surface of the surangular is heavily ornamented. This element bears a rounded ridge that extends along the posterior half of its dorsal margin. Posteriorly, this ridge curves ventrally following the outline of the caudal end of the mandibular ramus (figs. 7, 10). Like the angular ridge, this structure is also present in other forms that lack an external mandibular fenestra (e.g., *Zaraasuchus shepardi* IGM 100/1321, *Gobiosuchus kielanae* ZPAL MgR-II/68). The surangular ridge, however, is absent in other crocodyliforms that lacks such fenestra (e.g., *Geosaurus araucanensis* MACN-N 95). The posterior end of the lateral surface of the surangular reaches the posterolateral end of the retroarticular process, as in *Rugosuchus nonganensis* (Wu et al., 2001a) but in contrast to the condition of other advanced neosuchians (e.g., *Bernissartia fagesii*). This region is smooth and continuous with the smooth posterior end of the angular (fig. 10).

The **articular** is exposed only on its ventral, medial, and posterior surfaces. The lateral surface is completely covered by the angular and surangular and its dorsal surface occluded by the quadrate. The rostral end of the articular tapers anteriorly into a rod-shaped anterior process, as in most crocodyliforms. Posteriorly, the medial surface of the articular is concave and expands medially to support the articular facets for the quadrate (fig. 9). At its medial margin, the process that supports the internal articular facet for the quadrate is dorsoventrally thin. The caudal margins of these facets are bounded by a posterior buttress as in most crocodyliforms. Posteriorly, the articular continues into a broad and short retroarticular process (figs. 8, 17, 18). This process projects posterodorsally and its dorsal surface is slightly concave, smooth, and lacking the longitudinal ridge present in several crocodyliforms. Most of this surface faces posteriorly, but its posteromedial end is slightly deflected medially. The morphology of the retroarticular process of *Shamosuchus djadochtaensis* resembles that of some neosuchian taxa (e.g., *Theriosuchus pusillus* [Clark, 1986], *Rugosuchus nonganensis* [Wu et al., 2001a]). This

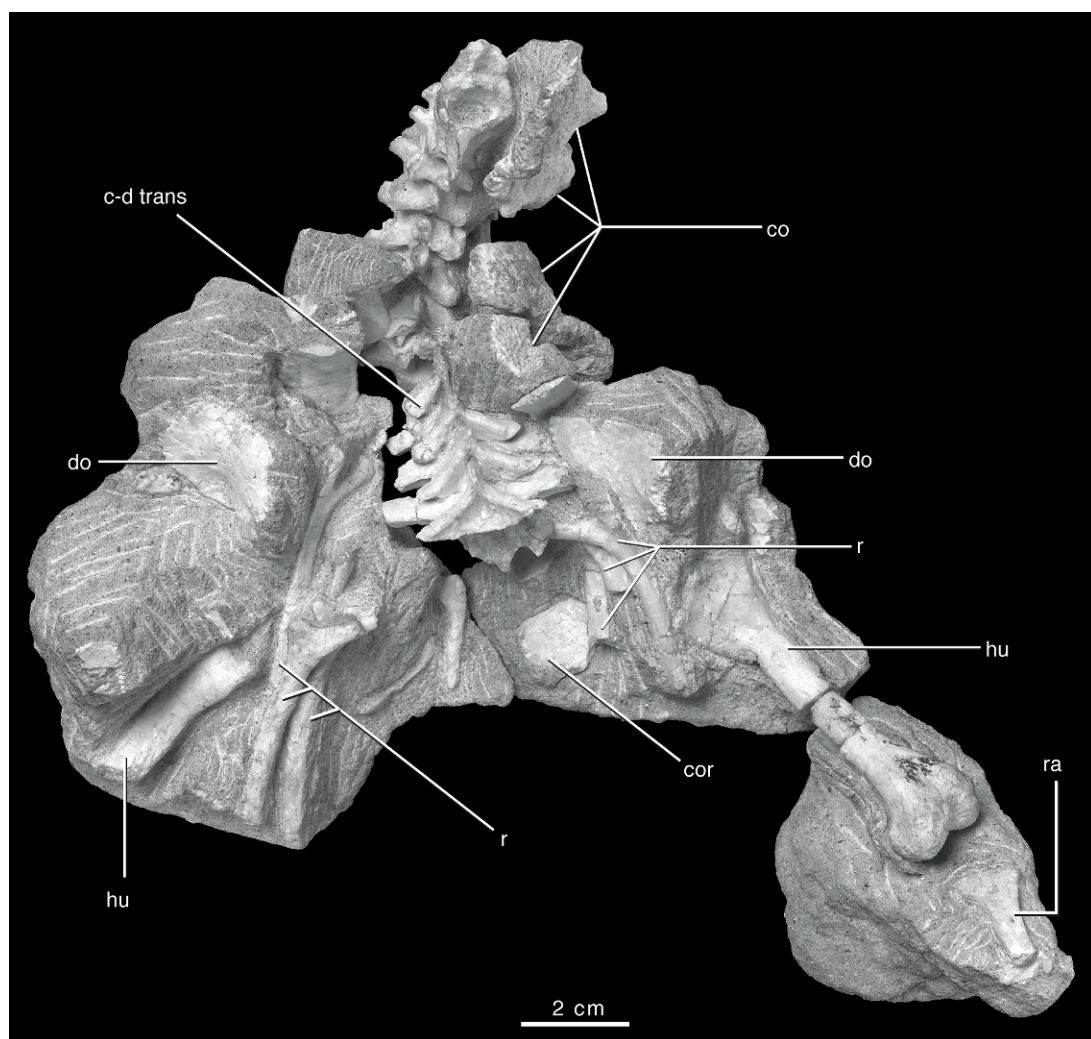


Fig. 20. Anterior postcranial remains of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

condition, however, contrasts that of eusuchians (e.g., *Alligator mississippiensis* FMNH 8021, *Paleosuchus palpebrosus* FMNH 69867, *Crocodylus niloticus* FMNH 17157) and longirostrine forms (e.g., *Terminonaris robusta* [Wu et al., 2001b], *Sarcosuchus imperator* MNN 604), which have an elongated, dorsally facing, and dorsally recurved process.

THE AXIAL SKELETON

A well-preserved cervical series was found associated with the skull of IGM 100/1195 and removed during preparation (figs. 20,

21). All eight cervical vertebrae are preserved with the exception of the neural arches of the atlas (fig. 21). The right side of the cervical series is obscured by three lateral cervical osteoderms, of which the two anteriormost are in overlapping articulation. The left side of the seventh cervical is slightly obscured by a partial lateral osteoderm. All other surfaces and views of the cervical column are well exposed. A proatlas is not present or was not preserved. In addition to this, the first three dorsal vertebrae with associated ribs were recovered, as well as five caudal vertebrae (figs. 22–24). Prior to discovery of IGM 100/

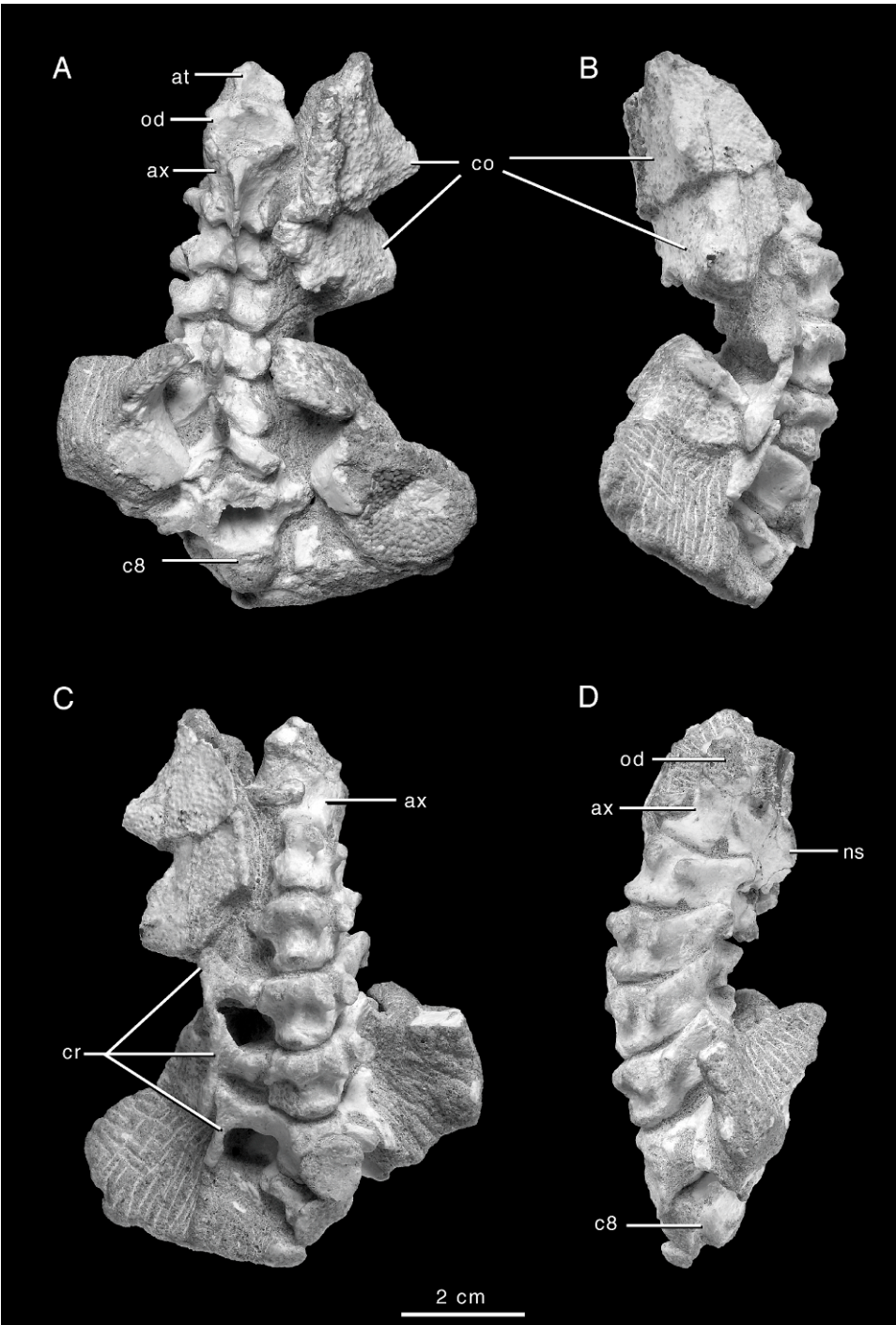


Fig. 21. Cervical vertebrae and osteoderms of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195, in **A**, dorsal view; **B**, right lateral view; **C**, ventral view; and **D**, left lateral view. See appendix 5 for abbreviations.

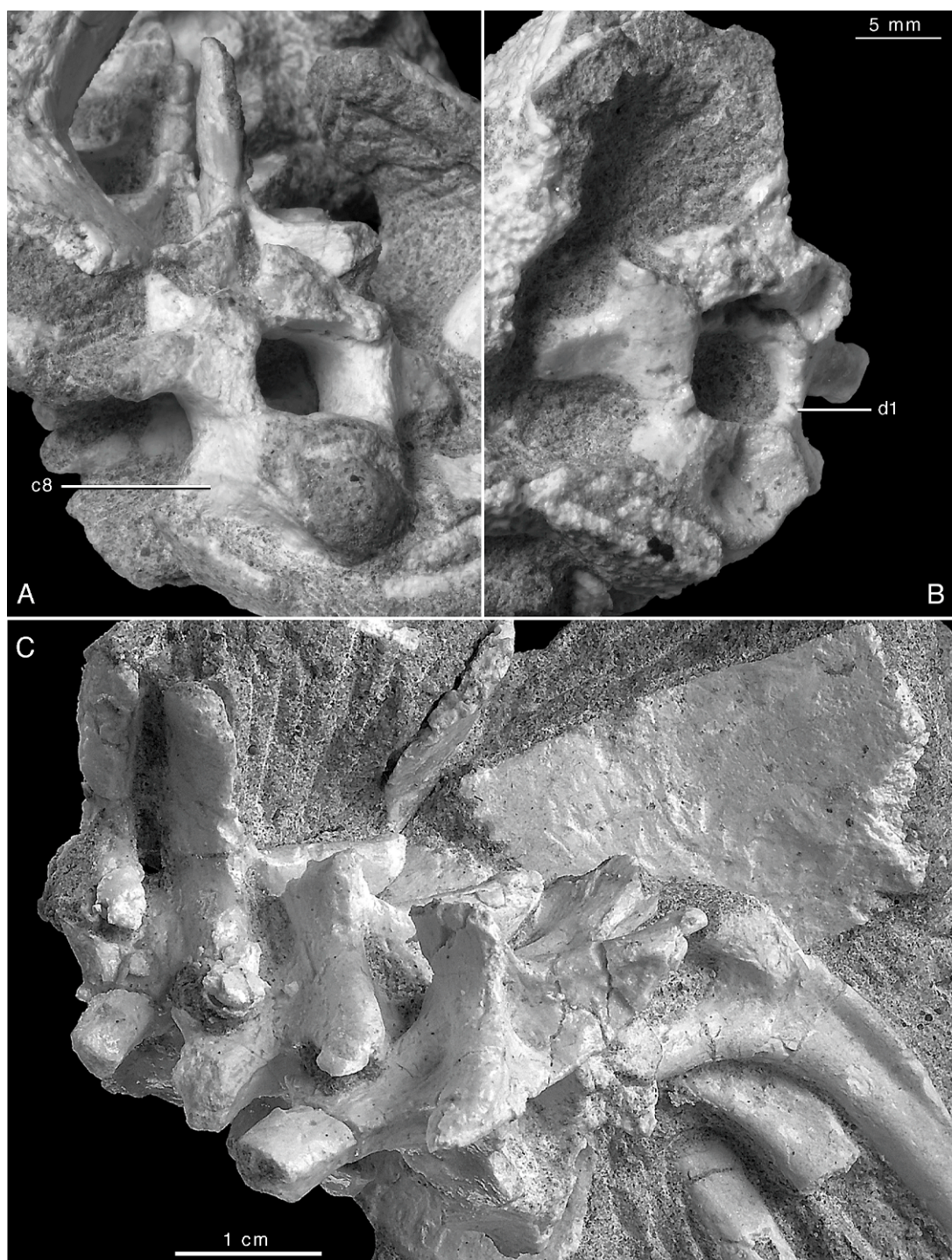


Fig. 22. Cervicodorsal vertebrae of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. **A**, eighth cervical vertebra in posterolateral view; **B**, first dorsal vertebra in anterolateral view; **C**, anterior dorsal vertebrae in posterolateral view.

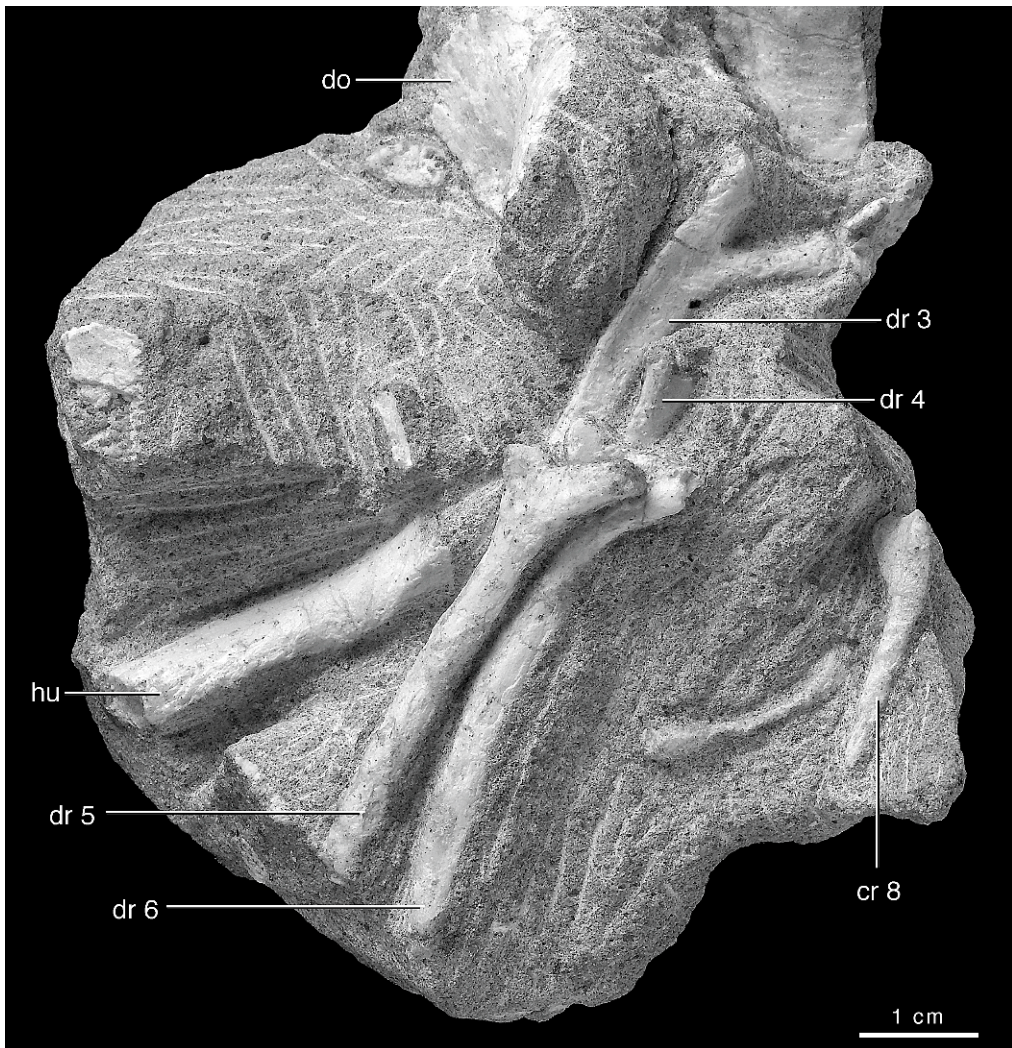


Fig. 23. Anterior dorsal ribs of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

1195, the only reported vertebrae from species referred to *Shamosuchus* were amphicoelous (i.e., “*Paralligator*” spp.; Konzhu-kova, 1954). The cervical vertebrae and the first dorsal of IGM 100/1195, however, are procoelous. Unfortunately, the condition in the remaining dorsal vertebrae cannot be determined and all the preserved caudals are amphicoelous. Since the first caudal vertebra is not unequivocally identified among the preserved caudals, it cannot be ruled out that this vertebra is biconvex like in *Bernissartia fagesii* and eusuchians.

The intercentrum of the **atlas** is a simple bone that is wedge shaped and broader than long, with a shallow concavity separating the two capitular facets (fig. 21). This morphology is fairly conserved among crocodylomorphs. The atlantal intercentra known in *Hesperosuchus agilis* AMNH FR 6758 (Clark et al., 2000), *Mahajangasuchus insignis* (Buckley and Brochu, 1999), *Araripesuchus tsangatsangana* (Turner, 2006), *Sunosuchus junggarensis* (Wu et al., 1996a), and *Crocodylus porosus* FMNH 15529 share similar shapes and proportions. This is in

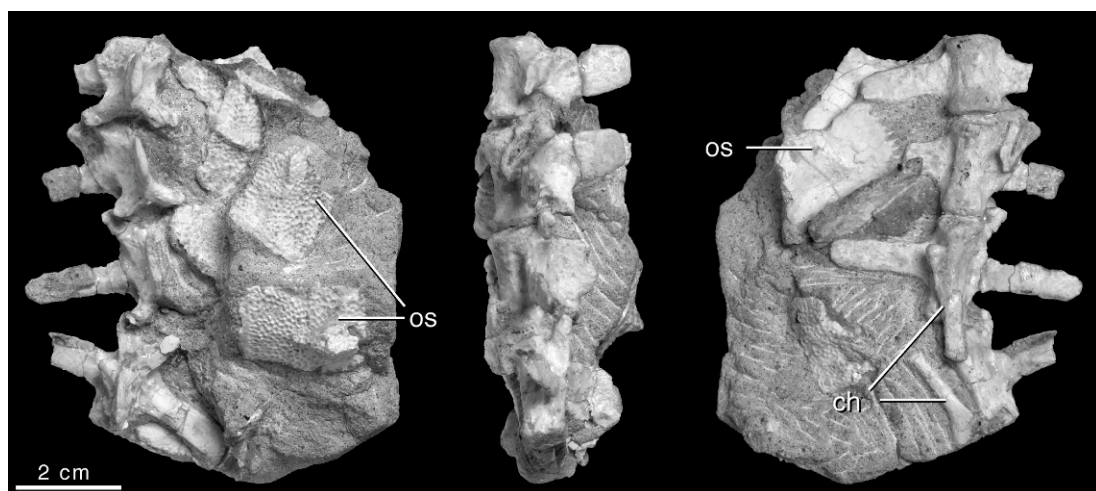


Fig. 24. Caudal vertebrae of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

contrast to the relatively platelike atlas of alligatoroids.

The dorsal surface of the bone is weakly concave for the reception of the occipital condyle. The anteriormost portion of the dorsal surface is formed by the short knob-like anterior margin of the atlas. The neurapophyses were not preserved in the specimen.

The **odontoid process** is strongly sutured to the axis (fig. 21D). It is nearly 13 mm wide and 6 mm deep at its extremes, making it wider than the body of the axis. In dorsal view, the odontoid process is similar to that figured for *Sunosuchus junggarensis* (Wu et al., 1996a). There is a midline lingulate surface projecting from the otherwise gently curved anterior margin. The ventral surface of the odontoid is obscured by the atlas.

The centrum of the **axis** is approximately 11 mm long, similar in length to the postaxial cervicals (fig. 21). The axial centrum is constricted medially and depressions are present on either side of the vertebra. Most of the ventral surface of the centrum is covered by a small, partly preserved osteoderm. Nonetheless, an anterior hypapophysis appears not to be present. The suture between the neural arch and the centrum is closed. In lateral profile, the neural arch is as tall as the axial centrum. A small notch is located posteriorly between the neural arch

and centrum. This notch is superficially similar to that of the eusuchian *Diplocynodon hantoniensis* (Brochu, 1999), but does not extend to the ventral margin of the postzygapophysis as in the later taxon. The right prezygapophysis is damaged. The left prezygapophysis is small and poorly developed, but appears to be complete. The postzygapophyses are robust, small, and curved laterally. The articular facets are approximately on level with the prezygapophyses and face ventrolaterally. The neural spine is anteroposteriorly broad, running the entire length of the neural arch. In lateral view, the dorsal surface of the spine has a horizontal profile. The axis neural arch lacks a lateral process ("diapophysis"). The facet for the tuberculum of the axial rib is located on the odontoid process. The capitular facets appear to be divided between the axial centrum and the ventrolateral surface of the odontoid process. Neither atlantal nor axial ribs are preserved.

All six postaxial **cervical vertebrae** are preserved in an articulated death posture (fig. 21). As a result the dorsal surface of these vertebrae are not well exposed. The centra are similar to those of most mesoeucrocodylians, being slightly longer than they are tall. As all the cervicals are in articulation, the nature of the articulation cannot be determined for most. The eighth cervical

possesses a partly weathered condyle on its posterior articular surface. Therefore, at the very least, the eighth cervical was procoelous (fig. 22A). Because of the surface of the posterior condyle of the eighth cervical is partially weathered, it cannot be determined at the moment whether the condyle was hemispherical (as in crocodylians) or slightly less developed.

The ventral surface of the cervical vertebra is constricted at the midpoint and bears a weakly developed keel (hypapophysis) anteriorly. This keel is very small on c3, with them becoming progressively larger moving posteriorly. The tip of the keel on c5 is damaged but the posterior aspect of the keel is marked by a shallow groove (fig. 21C). A very similar groove is present on the keel of c6 in *Araripesuchus tsangatsangana* (Turner, 2006) and *Mahajangasuchus insignis* UA 8654, and Wu et al. (1996a) noted a groove present anteriorly on the ventral ridges of c7 and c8 in *Sunosuchus junggarensis*. The anterior margins are notably more expanded than the posterior margins due largely to the well-developed parapophyses. Moving posteriorly through the cervical series, the centrum bodies become wider and the parapophyses broader with larger contact facets. The lateral surfaces of c3, c4, and c5 bear shallow depression between the parapophyses and diapophyses. The diapophysis of c3 is small and cylindrical. The remaining diapophyses are longer and flatter, with oval contact facets. The diapophyses present on c7 and c8 are roughly twice the length of the others and are located entirely on the surface of the neural arch.

The prezygapophyses are well developed. On c3, the prezygapophyses are smaller than succeeding ones and strongly curve medially. The remaining prezygapophyses are larger and project more laterally. The surface of the articular facets are not exposed, but are directed more dorsally than medially. The postzygapophyses are on level with, and roughly equal in size to, the prezygapophyses. These processes curve laterally, and the articular facets face ventrolaterally. A poorly developed ridge extends from the posterior surface of the postzygapophyses onto the posteroventral margin of the neural spines (fig. 21A). These ridges do not resemble the

suprapostzygapophyseal laminae seen in *Notosuchus terrestris* (Pol, 2005), *Araripesuchus gomesii* AMNH FR 22450, or *Araripesuchus tsangatsangana* (Turner, 2006).

Neurocentral sutures are completely closed on the lateral surfaces of the cervical vertebrae (fig. 21D), although this suture is visible on the internal surface of the neural canal of the eighth cervical vertebra. The neural canal is large, square, and about as large as the condylar surface of the centrum. The neural spines are damaged on c3 through c6 and c8. The neural spine of c7 is tall and anteroposteriorly narrow, with the posterior distal surface slightly curved. Very small median laminae are preserved on the posterior surface of the spine.

Four cervical ribs are preserved (c5, c6, c7, and c8) (fig. 21C). These vertebrae exhibit a highly conserved crocodyliform morphology (Mook, 1921; Whetstone and Whybrow, 1983). In c5–c7, the tuberculum and capitulum are roughly equal in size and the shaft of the rib is perpendicular to these processes. The shaft consists of a tapered anterior process and a dorsoventrally broad posterior process, which narrows posteriorly. Ventrally, the shaft is distinct from the capitular process, marked by a slight ventral development. The c8 is transitional in form between typical cervical and dorsal rib morphologies, as in many crocodyliforms (fig. 23). The tubercular process is small and the capitulum is represented by a small, thin process. These processes are closely spaced as in cervical ribs. Unlike other cervical ribs, the shaft of rib c8 is not perpendicular to the rib process. The rib shaft is short and weakly curved if at all.

The three anteriormost **dorsal vertebrae** are preserved articulated with one another and the cervical series (fig. 22C). The first dorsal vertebra is procoelous (fig. 22B). The centra of the other two are not well enough preserved to determine their condition. In ventral view, the centrum of d1 is about as broad as long. All three dorsals possess a distinct hypapophysis. The hypapophysis becomes less robust and more keellike by d3.

Distinct parapophyses are present and located near the neurocentral suture in all three vertebrae, although the left parapophysis on d3 is unpreserved. In d1 the para-

pophysis is located just below the suture and is anteriorly displaced relative to the diapophysis. In d2 and d3, the parapophyses rest on or just above the suture and are aligned anteroposteriorly with the diapophyses. The parapophyses are shorter and stouter than those on the cervical centra. The diapophyses of d1 are nearly cylindrical and short, just extending beyond the margin delimited by the postzygapophyses. The diapophyses increase in size posteriorly, becoming more dorsoventrally flattened.

The first dorsal vertebra of IGM 100/1195 is very similar to *Sunosuchus junggarensis* (Wu et al., 1996a) with respect to a number of features. The neural canal is extremely large in both taxa, roughly equal in size to the anterior contact surface of the centrum. This is in contrast to the condition in Crocodylia where the neural canal is markedly smaller than the anterior surface of the centrum. Consequently, the neural arch is tall and slanted dorsolaterally. This causes wide separation of the prezygapophyses on the arch, lateral to the edge of the centrum and parapophysis (fig. 22B). They do not extend anteriorly beyond the margin of the centrum, however. The articular facets face medially, with the surface slanted at about a 45° angle. The postzygapophyses are also widely spaced and extend just slightly beyond the posterior margin of the centrum.

On d2 and d3, the prezygapophyses are broad, very weakly slanted medially, and again widely spaced on the neural arch and proximal diapophyses. This differs from the closely spaced and strongly slanted prezygapophyses in mesoeucrocodylians like *Araripesuchus gomesii* AMNH FR 22450, *Araripesuchus tsangatsangana* (Turner, 2006), *Notosuchus terrestris* (Pol, 2005), and *Mahajangasuchus insignis* UA 8654 (Buckley and Brochu, 1999), as well as in Crocodylia (Mook, 1921). The widely spaced prezygapophyses in *Shamosuchus djadochtaensis* correspond to the widely spaced postzygapophyses. The postzygapophyseal facets are ovular and offset laterally from the main body of the postzygapophysis. Unlike crocodylians, the postzygapophyses are positioned at the same level as the prezygapophyses (fig. 22C). Viewed dorsally, a thin lamina connects the postzygapophysis with the

posterior surface of the diapophysis. Located posteriorly between the postzygapophyses is a relatively deep median small triangular fossa.

Only d1 preserves a complete neural spine (fig. 22). The spine is tall and anteroposteriorly narrow. Similar to *Notosuchus terrestris* (Pol, 2005), *Araripesuchus gomesii* AMNH 22450, *Araripesuchus tsangatsangana* (Turner, 2006), and *Sunosuchus junggarensis* (Wu et al., 1996a), but unlike crocodylians and *Mahajangasuchus insignis* UA 8654, the spine does not slant posteriorly. A distinct posterior thin lamina appears lacking. The dorsal terminus of the spine flares slightly, but not to the extent seen in Crocodylia. Although the remaining spines are missing near the base, it is apparent that the spines become anteroposteriorly broader in the more posterior dorsal vertebrae.

Three right and four left dorsal ribs were preserved (figs. 22, 23). The anterior two right ribs correspond to d1 and d2, but are largely obscured by matrix (fig. 22C). The third right rib is nearly complete, with its posterior surface well exposed. The tuberculum is short and stout, forming a robust contact with the diapophysis. The capitulum is very long and cylindrical. The shaft of the rib curves away slightly from the head of the rib, with the remainder of the shaft straight. The proximal lateral edge of the rib appears as a thin flange. This is formed in part by a longitudinally running depression near this lateral edge.

The four left dorsal ribs are isolated from their complementary vertebrae, making their exact identification equivocal (fig. 23). The anteriormost of the four is interpreted as the left rib of d3. This is based on its relative position within the block containing the dorsal vertebrae and its close similarity to the right d3 rib. The remaining three left ribs corroborate this identification. The tubercula of these ribs are small to completely absent, which is what is predicted given the changes in rib morphology seen in Crocodylia (Mook, 1921). The shafts of these three ribs (d4–d6) are straight to very weakly flexed. No lateral flanges are preserved on the ribs' shafts.

The five **caudal vertebrae** are likely from the anterior part of the tail, although exact identification is not possible (fig. 24). This

interpretation is based on their long transverse processes, anteroposteriorly broad neural spines, relatively short centrum bodies, and the presence of a partial ischium near the anteriormost of the five caudals. The anteriormost caudal vertebra is heavily damaged, missing most of the left side and both transverse processes. All of the caudal centra are amphicoelous. The centra of the anteriormost two caudals are stout, being anteroposteriorly short but still slightly longer than broad. The posterior three preserved caudal vertebrae are much more spool shaped. They are about twice as long as wide, and are broadly constricted along their length. The ventral surfaces of the centra are smooth like in those of *Pachycheilosuchus trinqueti* (Rogers, 2003) and *Sunosuchus junggarensis* (Wu et al., 1996a), and they lack the parallel ridges seen in basal mesoeucrocodylians like *Araripesuchus gomesii* AMNH FR 22450 and in modern crocodylians (e.g., *Alligator sinensis* FMNH 197946).

Where preserved, the transverse processes are long (at least slightly longer than the vertebral body) and roughly 0.5 cm wide. The region of the neural arch connecting the transverse process to the prezygapophysis bears a semicircular depression. Prezygapophyses are long, narrow, and extend laterally at approximately a 45° angle. This angle decreases in the posteriormost preserved caudal vertebra, where the prezygapophyses are directed more anteriorly. The prezygapophyses extend beyond the anterior border of the centrum. Postzygapophyses are short, the contact facets ovular, and they sit more dorsally than the prezygapophyses. They project laterally in the anterior caudals (complementing the prezygapophyses), becoming more posteriorly directed in the more distal vertebrae. The neural spines are anteroposteriorly broad. They are not, however, particularly tall—less than the length of the transverse processes. Neither anterior nor posterior thin laminae can be discerned in any of the preserved caudal vertebrae. The distal ends of the neural spines are slightly expanded, as in the dorsal vertebrae.

Two chevrons are preserved with the caudal vertebrae (fig. 24). The first lies between the second and third preserved caudals. This chevron is heavily damaged.

The second chevron is more complete and located between the third and fourth preserved caudals. This chevron is just over 3 cm long. The haemal canal is less than a centimeter tall. The anterior surface of the chevron below the haemal canal bears a pronounced ridge along its length.

THE SHOULDER AND FORELIMB

Appendicular remains are more scarce than axial or cranial elements. The left and right humerus and radius are preserved, as well as the left ulna. No identifiable carpal or manual elements are present among the preserved postcranial material. The distal end of the right **coracoid** is exposed in medial view (fig. 20). This bone is flat and noticeably expanded at its distal terminus. The shaft of the coracoid, however, is obscured by a series of articulated dorsal ribs.

The right **humerus** is complete, but fractured at the middiaphysis (fig. 25). Proximally, only the dorsal surface is exposed. The left humerus is less complete. Only the distal half is preserved, with the lateral and ventral surfaces exposed. The humerus of *Shamosuchus djadochtaensis* is expanded to a similar extent at both ends. The shaft is relatively straight like in *Alligatorium meyeri* (Wellnhofer, 1971), and not as sharply bent medially as in more derived neosuchians like “thoracosaur” or species of *Alligator*. At the end of the shaft, the humeral head begins to gently curve dorsally. Medially on the head, a prominent internal tuberosity is present. The dorsal surface of the humeral head is broad, bearing a wide but shallow depression near its proximalmost edge. A fairly prominent angle delimits the dorsal surface from the lateral surface and the deltopectoral crest (fig. 25). Lateral to this angle, the attachment surface for the m. teres major is marked by a thin raised surface.

The distal articular surfaces are similar in size. The medial, ulnar hemicondyle, is slightly smaller than the capitulum (fig. 26). It is narrow and squarish, separated from the more rounded capitellum by a moderately deep trochlea. The ulnar hemicondyle extends distally farther than the capitellum forming a slight slant to the overall articular surface. Like other crocodyliforms, the artic-

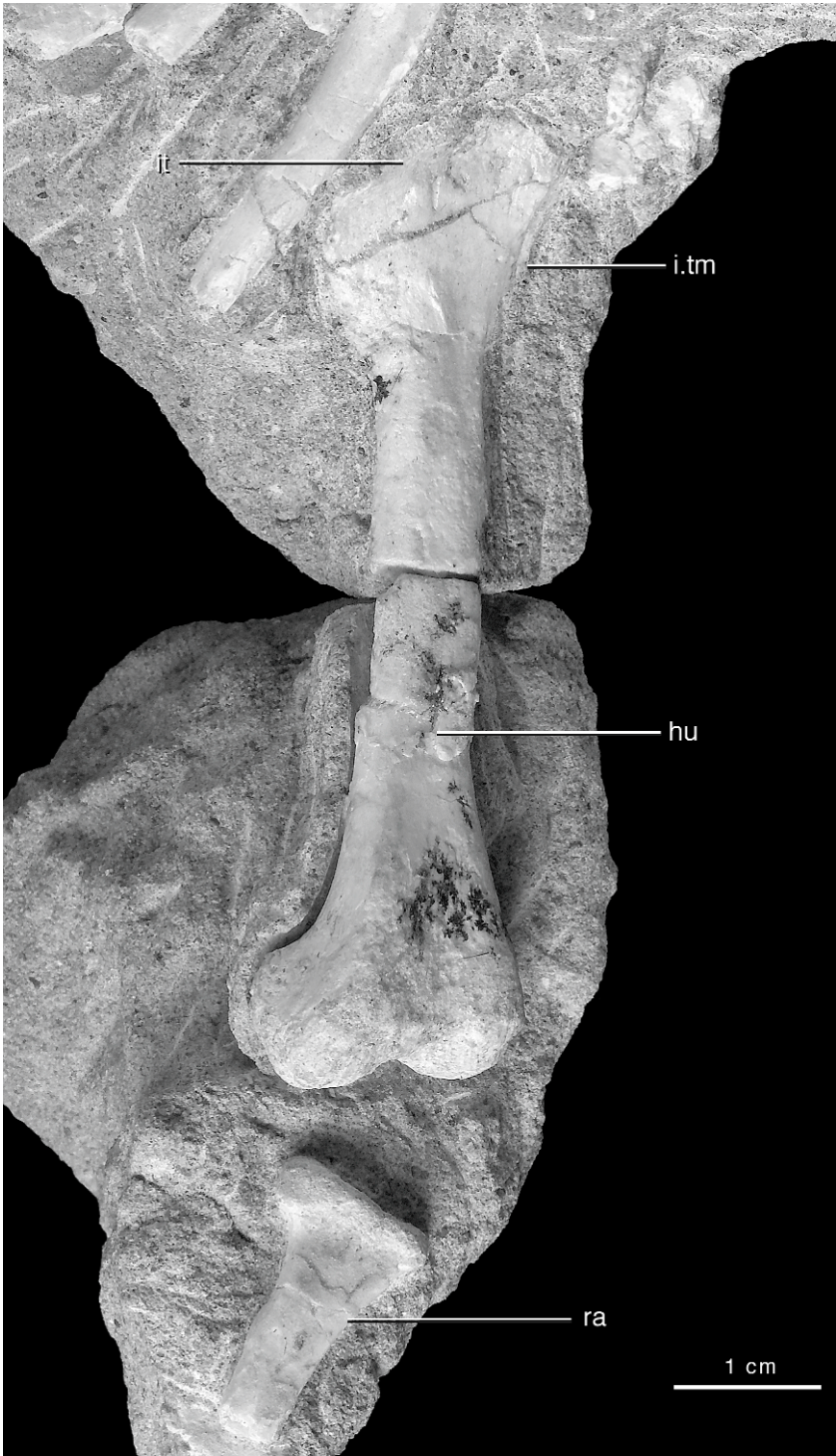


Fig. 25. Left humerus and proximal left radius of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in dorsal view. See appendix 5 for abbreviations.

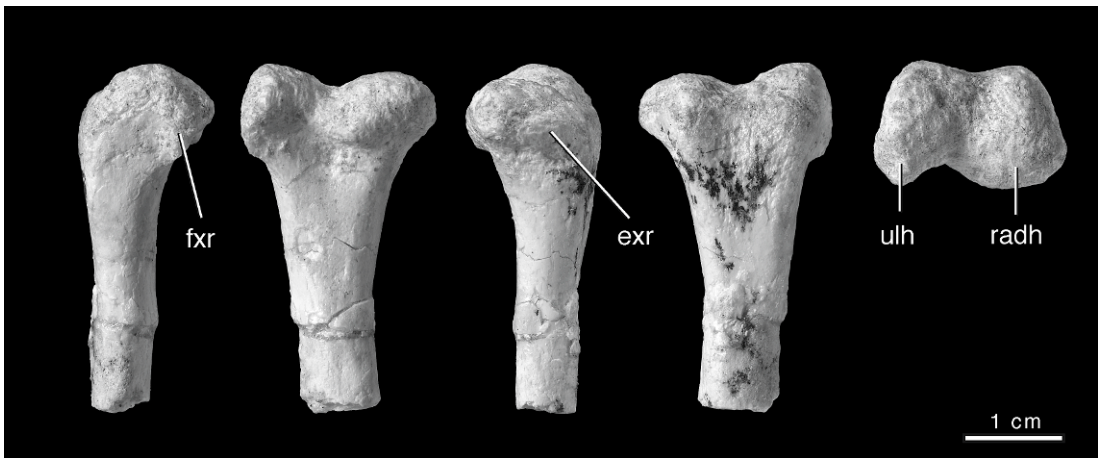


Fig. 26. Distal half of left humerus of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in all views. See appendix 5 for abbreviations.

ular surface of the capitellum curves ventrally, developing a short process that extends proximally. In dorsal view, the distal end is generally triangular in outline and prominent supracondylar ridges are absent. Laterally, an extensor ridge runs from near the dorsal edge ventrally to the terminus of the capitellum. Medially, a prominent flexor ridge is present on the ulnar hemicondyle near its ventral edge. This forms a triangular raised surface. In ventral view, the flexor ridge is expressed as a flat, lateral continuation of the ventral surface onto the edge of the hemicondyle.

The left **ulna** is preserved (fig. 28). Only the lateral and part of the anterior surfaces are exposed. In general shape it is typical of crocodylians, expanded and triangular proximally while narrow and reduced distally. The ulna is bowed anteroposteriorly as in crocodylians, but not as pronounced as in the mesoeucrocodylian *Pachycheilosuchus trinquei* (Rogers, 2003). In lateral view, the proximal end bears a distinct process contacting the radius. The medially directed surface of this process may represent the dorsolateral almost extent of the m. pronator quadratus (Brochu, 1992; Meers, 2003), but this interpretation remains equivocal. Distal to this, the shaft begins to narrow gradually, narrowing more rapidly after midshaft and ending in an anteroposteriorly flat surface. Just proximal to the midpoint of the shaft, a ridge traverses the length of the ulna, distally

becoming indistinct from the flattened end. In crocodylians, a similar ridge marks the division between the m. flexor ulnaris attachment posteriorly from the m. extensor carpi radialis brevis attachment anteriorly (Meers, 2003).

A complete left **radius** is preserved articulated to the ulna and humerus, while the right radius is represented only by the proximalmost portion (fig. 27). The radius is relatively slender. The proximal end expands abruptly from the shaft and is a long rectangle in cross-section. The distal end is also expanded, however this expansion is more gradual. Additionally, the expansion of the distal end is unequal as the medial portion is broader and thicker, while a thin lingular process comprises the lateral portion. The ventral articular surface is weakly concave. The radius shaft is narrow and the medial edge strongly concave while laterally it is nearly straight edged. Only anterior and lateral aspects of the left radius are visible, revealing little in the way of muscle scarring. The preserved portion of the right radius is better preserved and bears a protuberance medially corresponding the insertion of the m. humeroradialis (Fürbringer, 1876; Meers, 2003) (fig. 28).

THE PELVIS AND HINDLIMB

The right **ischium** is largely complete (fig. 29). It is fractured in two places and

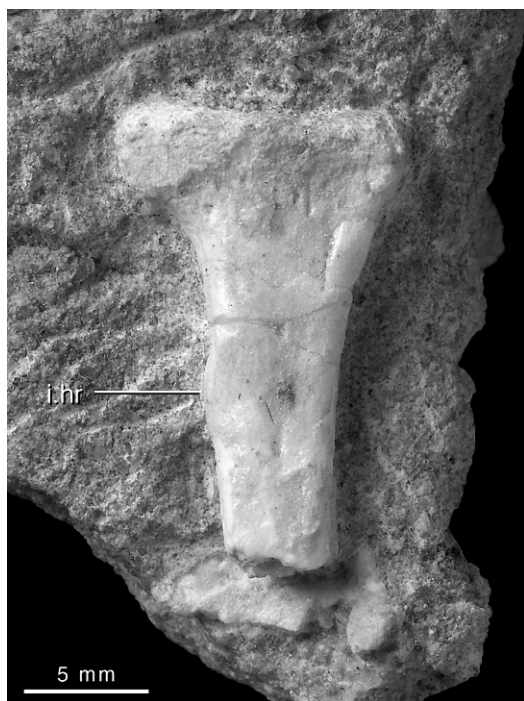


Fig. 27. Close-up of proximal portion of left radius of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in lateral view. See appendix 5 for abbreviations.

lacks the anterior margin of the blade. The anterior iliac process is robust like other neosuchians (e.g., *Theriosuchus* sp. IVPP V10613 [Wu et al., 1996b], *Sunosuchus* sp. [Averianov, 2000], *Sunosuchus junggarensis* [Wu et al., 1996a], *Alligator sinensis* FMNH 197946). The process is nearly cylindrical, expanding slightly as it extends proximally. Although badly damaged and incomplete, it is clear that the blade of the ischium extended posteriorly and very slightly curved medially. The preserved portion of the anterior margin is more straight and thin than the posterior margin. Proximally below the posterior iliac process, the posterior margin of the ischial blade is weakly concave, straightening distally on the blade. Little can be said regarding the lateral surface of the ischial blade as it is poorly preserved. What is discernible is a small, shallow longitudinal depression running ipsilateral to the anterior margin.

A partial, highly fragmentary element was recovered near the caudal vertebrae, ischium,

and left tibia. It is interpreted here as the proximal shaft and distalmost end of the left **femur**. The bone was recovered in three pieces and is heavily effaced. A small, slightly rugose protuberance on the medial surface of the proximal portion likely corresponds to the fourth trochanter. The distal end of the femur consists of two large condyles separated by a shallow, triangular popliteal space (fig. 30). On the lateral hemicondyle a faintly developed crista tibiofibularis delimits a shallow groove.

The left and right **tibiae** are well preserved with little distortion beyond cracking (fig. 31). The proximal ends are broken at approximately the same location on each one—just before the proximal shaft begins to expand. The right proximal end is missing, the left preserved. The proximal end of the tibia is composed of two depressions for reception of the distal femoral condyles. The buttresses for these depressions are unequally developed; the medial is larger and more posteriorly directed than the lateral. A triangular depression divides the two buttresses along the posteromedial surface of the tibia. Viewed anteromedially, the proximal end of the tibia is flat sided. A rugose tuberosity is present on this surface. Brochu (1992) interpreted a topographically equivalent structure in *Alligator mississippiensis* as the attachment for the internal lateral ligament. Laterally, just around the anterior face of the tibia, another protuberance is present and likely served as the insertion of m. tibialis anterior.

The cross-section of the shaft is triangular both proximally and distally, becoming more circular throughout the diaphysis. The margin of the shaft is straight anteriorly and curves along the posterior margin. The medial face of the shaft is flat. Distal to the break surface, an angle distinguishes this surface from the more rounded posterior and lateral surfaces. This angle marks the origin of m. flexor digitorum longus (Brochu, 1992). At a similar level, but on the anterolateral surface, the tibia bears a low, centimeter-long ridge that is weakly fluted on the lateral aspect of the ridge. Topographically, this corresponds to the insertion of m. flexor tibialis internus (interior sensu Romer [1923] and Brochu [1992]).

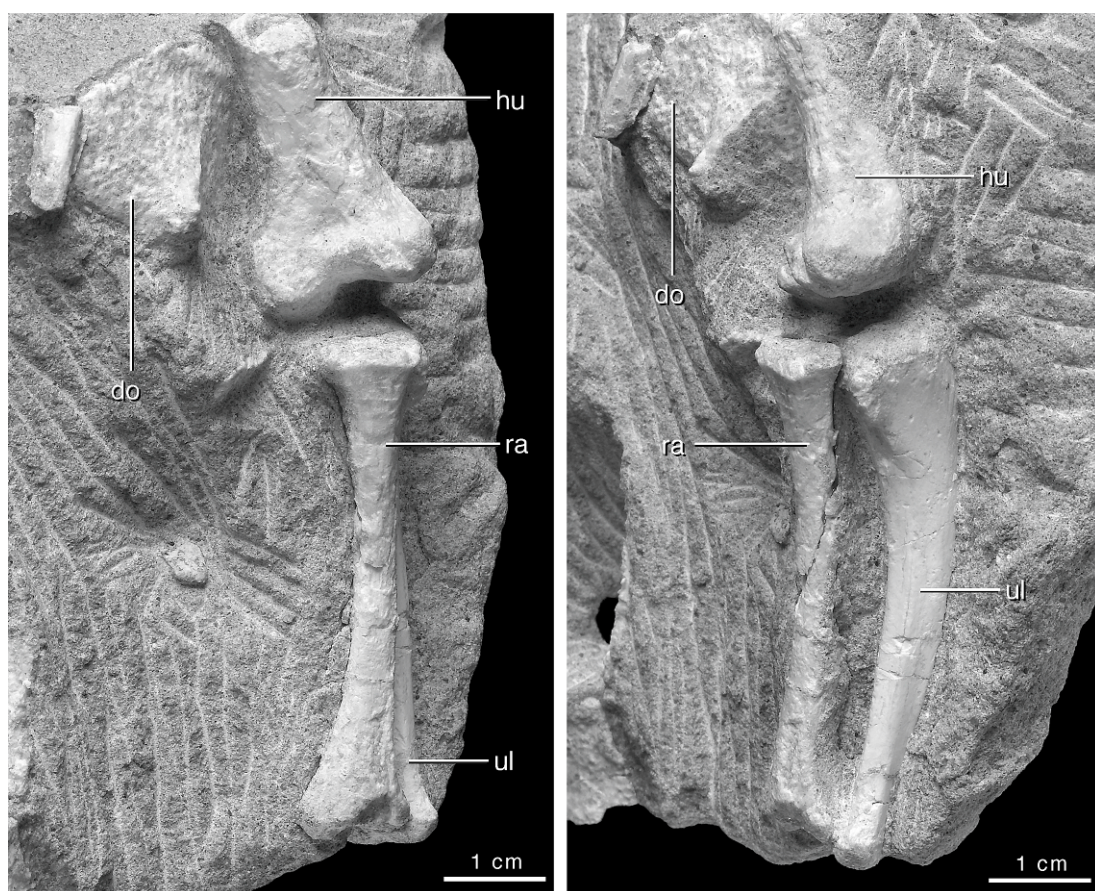


Fig. 28. Right distal half of humerus, right radius, and right ulna of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in medial (left) and lateral (right) views. See appendix 5 for abbreviations.

The tibia widely flares distally. The posteromedial surface remains generally flat, though it becomes weakly depressed prior the lateral margin (fig. 31D). The anterolateral surface expands greatly into a round head when viewed laterally or distally. Normally, a depression for the attachment of the medial tibioastragalar ligament would be located on this surface (Brochu, 1992). However, its presence cannot be confirmed because the distal extent of this rounded surface is damaged. The distal tibia is divided into two contact surfaces for the tarsus. The larger, more developed facet contacts the astragalus. A small surface on the anteromedial aspect of the distal tibia articulates with the calcaneum. The astragalus contact extends distally, considerably farther than the

contact with the calcaneum. Additionally, the facet for contact with the astragalus is far more developed distally than is the same contact surface in *Crocodylia* or the neosuchian *Pachycheilosuchus trinquei* (Rogers, 2003). The facet, in fact, terminates in an acute process similar to that of *Araripesuchus gomesii* AMNH FR 22450, *Araripesuchus tsangatsangana* (Turner, 2006), or *Mahajangasuchus insignis* UA 8654 (Buckley and Brochu, 1999).

The right **fibula** is complete but very heavily cracked and shattered. It was recovered loosely articulated to the right tibia. Nevertheless, some morphology is present and it can be determined that it bears a prominent proximodistal oriented ridgelike iliofibularis trochanter that slants anteropos-

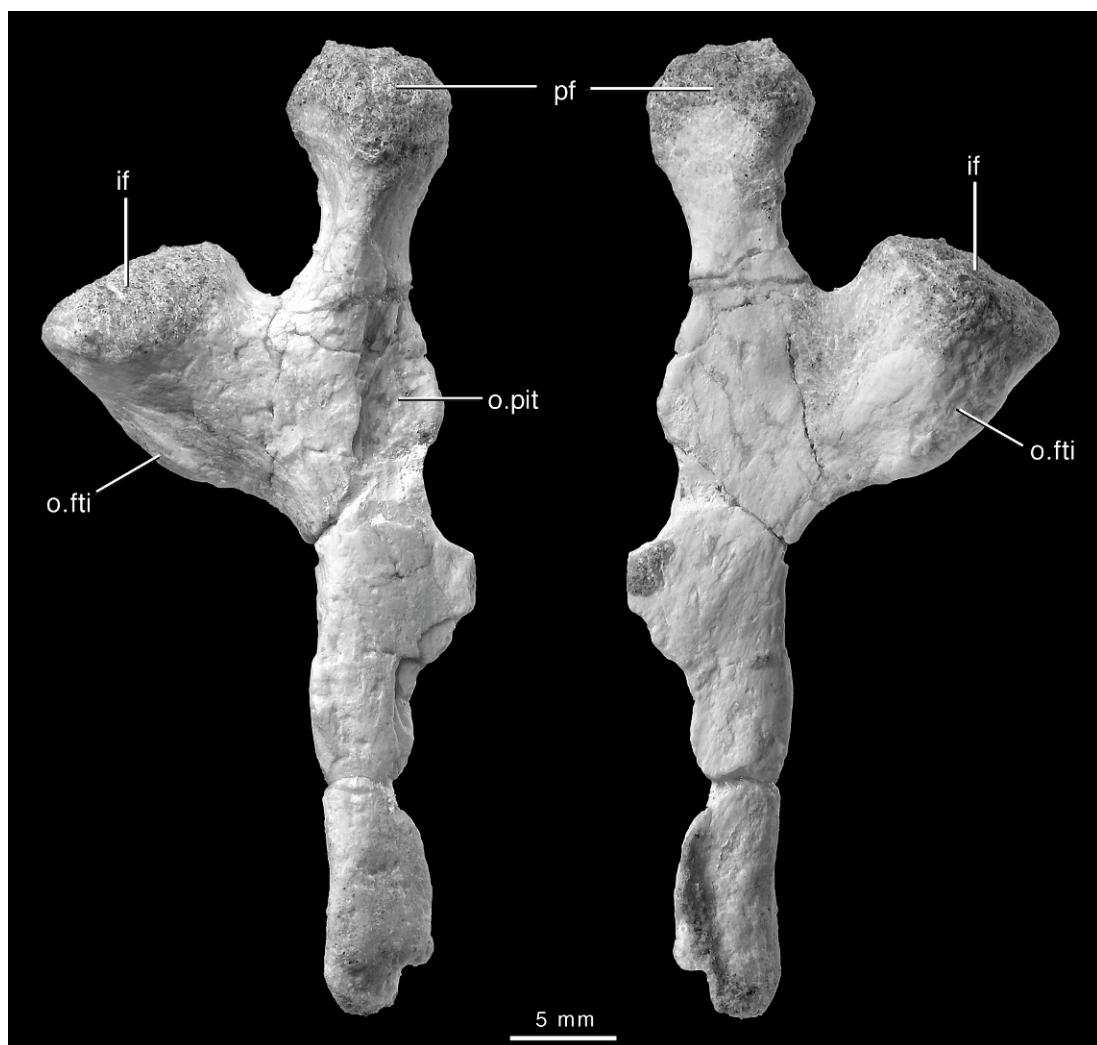


Fig. 29. Partial right ischium of referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in lateral (left) and medial (right). See appendix 5 for abbreviations.

teriorly and is located roughly one quarter of the way down the fibular shaft. As in *Sunosuchus junggarensis* (Wu et al., 1996a) and *Goniopholis* sp. AMNH FR 620, the trochanter is bordered proximally by a broad, but shallow depression leading into the head of the fibula. The anterior border of the depression bulges medially, marking the origin of *m. flexor digitorum longus* (Brochu, 1992). Distally, an additional ridge, separated from the trochanter by a small hiatus, extends down the shaft of the fibula. The fibularis longus muscle originates from this

longer and more developed ridge (Reese, 1915; Brochu, 1992). The cross-section of the shaft is triangular distally. In axial view, the distal surface of the fibula is rectangular. The medial portion of the distal articular surface curves upward forming the “distal hook,” which contacts the lateral edge of the tibia.

The lateral surface of the left fibula is also exposed (fig. 32). It suggests that the fibular shaft was not completely straight (e.g., *Alligator mississippiensis* AMNH 1106CA, *Araripesuchus gomesii* AMNH FR 22450), but was bowed posterior slightly (e.g.,



Fig. 30. Distal end of left femur of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in all views.

Goniopholis sp. AMNH FR 620, *Pachycheilosuchus trinqueti* [Rogers, 2003]). Immediately distal to the iliofibularis trochanter, an oval-shaped scute is present adjacent to the fibular shaft. Opposite to the left fibula in the block, the left tibia was removed. A small portion of the calcaneal contact facet of the left tibia remains in the block. In contact with this portion of the tibia, and lying less than a half of centimeter from the distal articular surface of the left fibula, a bone fragment is present that is interpreted here as the left calcaneum. This bone is poorly preserved and little can be said of its morphology.

The **pes** of IGM 100/1195 is only partially preserved. A single left metatarsal and phalanx were recovered near the left fibula (fig. 32). Also, three metatarsals and three phalanges are preserved with the right hindlimb elements. The metatarsals of this pes are interpreted as metatarsals III (specimen C15), IV (specimen C16), and V (specimen C11), respectively (fig. 33, 34). This identification is based on the short, hooked shape of the lateralmost metatarsal. This metatarsal is roughly 1.5 cm long. Metatarsal V is shorter in other neosuchians such as *Alligatorium meyeri* (Wellnhofer, 1971; pl. 11) and *Alligator mississippiensis* (AMNH 18707, AMNH 18697) (fig. 34). In this regard, *Shamosuchus djadochtaensis* bears closer resemblance to basal crocodyliforms (e.g., *Protosuchus richardsoni* AMNH FR 3024). The proximal articular surface is weakly convex, with a shallow midpoint depression. The shaft of the metatarsal is narrow distally, expanding and curving medial as one moves proximally. The medial

surface bears a triangular contact surface for distal tarsal IV near the posterior border.

The metatarsals are slender and long—slightly more than half the length of the tibia. The proximal articular surface is fan shaped. Laterally, the surface is nearly as thick as the main shaft of the metatarsal, while medially the proximal surface thins into a lamina underlying the proximoposterior surface of the preceding metatarsal. The cross-section of the metatarsal shafts is nearly circular. The distal ends are trochleated. Anteriorly, an extensor fossa is present above the trochlea. The preserved phalanges appear to pertain to digit three. The proximal articular surface is concave for the reception of the preceding pedal element. The distal articular surface is trochleated with the medial and lateral surfaces bearing ligament fossae.

OSTEODERMS

Numerous **osteoderms** displaying a wide range in morphology are present in partial articulation with the postcranial remains of IGM 100/1195. In the cervical region, several large osteoderms are present along the lateral margins of the specimen (fig. 21). The right side is best preserved, retaining at least six osteoderms laterally. The anteriormost two are adjacent to the axis and articulated to one another, likely representing the first two lateral cervical osteoderms. The posteriormost preserved osteoderms are located adjacent to the second and third dorsal vertebrae. These osteoderms are articulated via a cranially sloping imbrication. A discrete convexity is present along the anterior

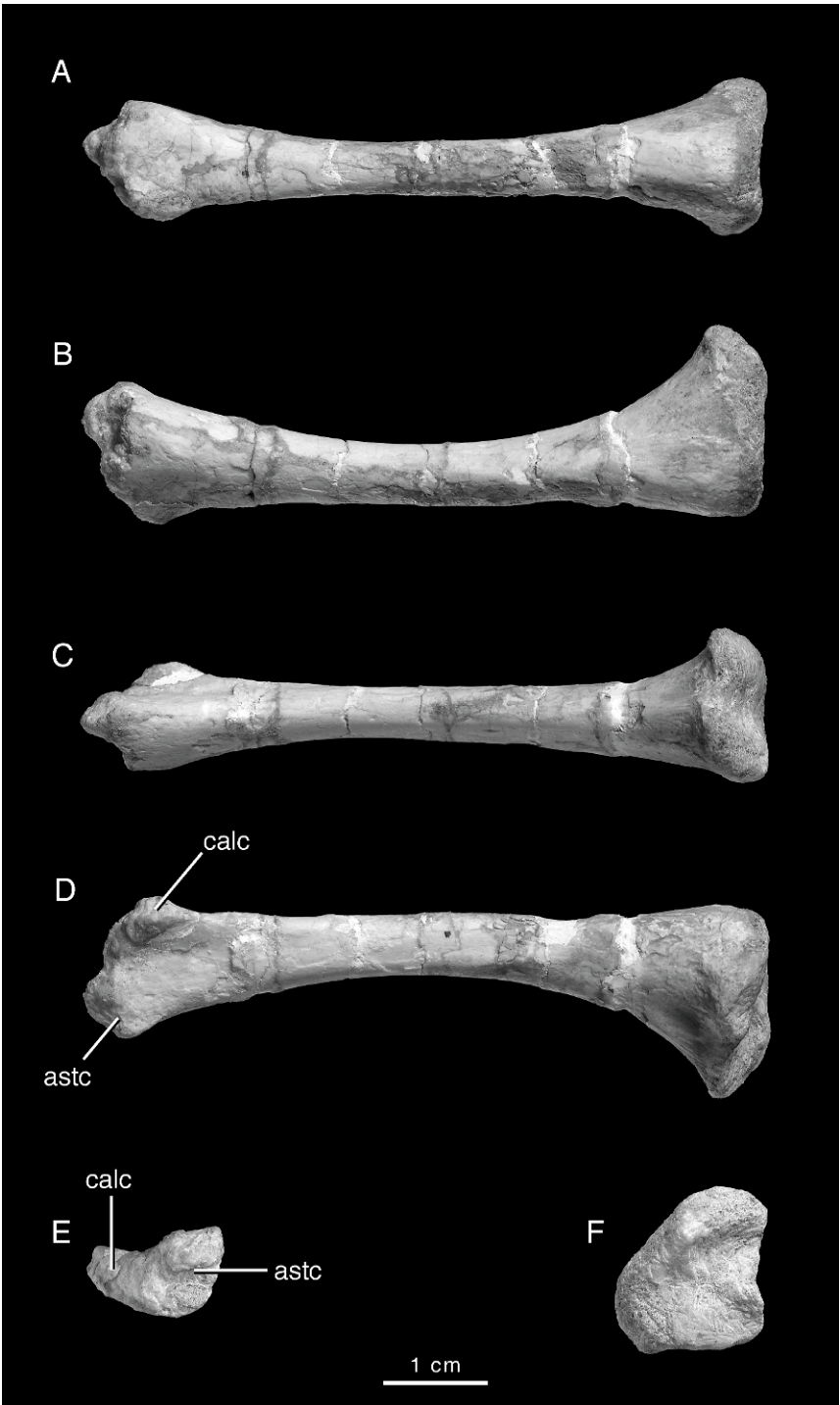


Fig. 31. Left tibia of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in **A**, anterior; **B**, lateral; **C**, posterior; **D**, medial; **E**, distal; and **F**, proximal views. See appendix 5 for abbreviations.

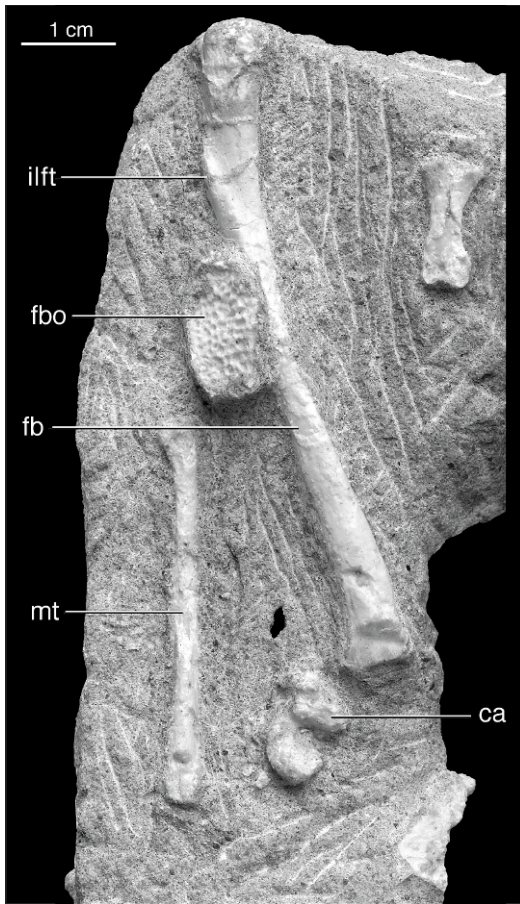


Fig. 32. Left fibula and accompanying appendicular osteoderms of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

margin as in *Bernissartia fagesii* IRScNB n° R 46 (Buffetaut, 1975: fig. 4; Norell and Clark, 1990) and nonbrevirostran eusuchians (Brochu, 1999). The dorsal surface of these osteoderms is ornamented with a series of very small and shallow pits, and has a well-developed medial keel near their posterior margin. The dorsal ornamentation continues onto the surface of the keel. The anterior osteoderms, lying adjacent to the cervical vertebrae, bear the largest keels and are strongly curved to form a concave medial surface. The lateromedial curvature of the osteoderms lessens caudally until the level of the first dorsal vertebrae where curvature is extremely slight to nearly flat, and the medial

keels become less developed. It is unclear whether a paired row of dorsal osteoderms were present between the lateral rows of osteoderms. However, a longitudinally running discontinuity zone is present near the dorsal margin of the lateral osteoderms. This zone may mark a suture with what might be interpreted as fragmentary dorsal osteoderms. Given that no unambiguous osteoderms in this location preserving a second distinctive morphology were recovered, it is unclear whether additional osteoderms were present.

Posteriorly, two osteoderm morphotypes are present along the right side of the caudal vertebrae as well as in two blocks corresponding to the left flank (fig. 35). This last set is located dorsal to the humerus but appears unassociated with it. The first type is rectangular in shape, being anteroposteriorly longer than it is wide and weakly bowed mediolaterally (fig. 35B). The second type is also rectangular, but these osteoderms are wider than they are long—the more pervasive condition among crocodyliforms (fig. 35A, C). These, like the other posterior osteoderms, are weakly bowed mediolaterally. Both posterior morphologies have the same ornamentation pattern as the anterior ones, although the medial keels diverge slightly to one side of the osteoderm. Laterally near the preserved left dorsal ribs, two osteoderms are preserved side by side articulated to one another. One of these two osteoderms displays the first posterior morphotype discussed above. The second one is too poorly preserved to determine its overall shape. Additionally, it is unclear whether these osteoderms are preserved in their life position.

Several ventral osteoderms are preserved between the two humeri, patches of which remain articulated (fig. 36). Additionally, fragments of ventral osteoderms are present along the posterior end of the cervical vertebrae and the proximal dorsal vertebrae. The ventral dermal armor is clearly distinct from the dorsal armor. The osteoderms are generally smaller and more square shaped in outline, except in some more laterally placed contacts where the osteoderms can take on less regular shapes. The ornamentation is similar to the dorsal elements in that it consists of a series of small, closely clustered

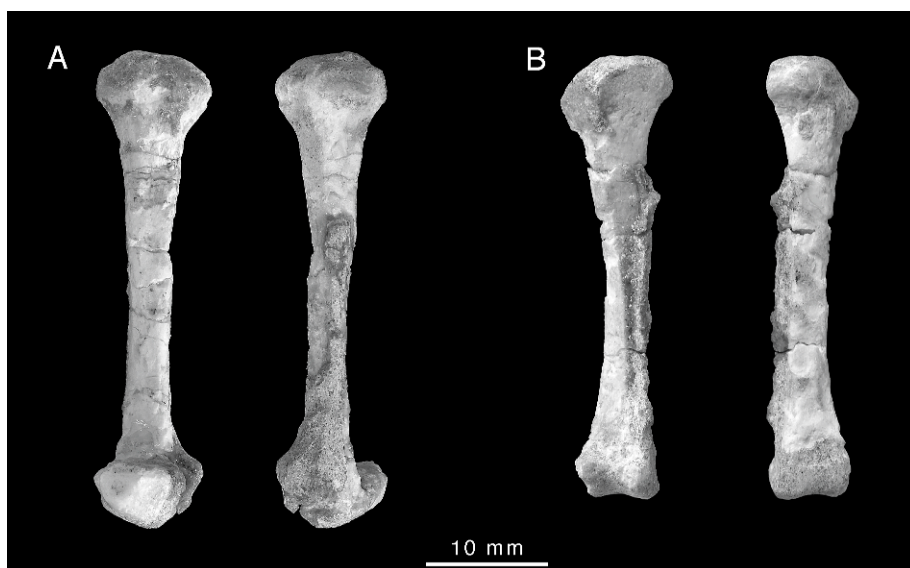


Fig. 33. Metatarsal III (A) and metatarsal IV (B) of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in anterior and posterior views.

pits. No keels are present on the preserved ventral elements. The anteriormost region lacks the smooth imbrication area present in the dorsal elements. This morphology is consistent with the fact that the ventral osteoderms, where articulated, are sutured to each other with no evidence of imbrication.

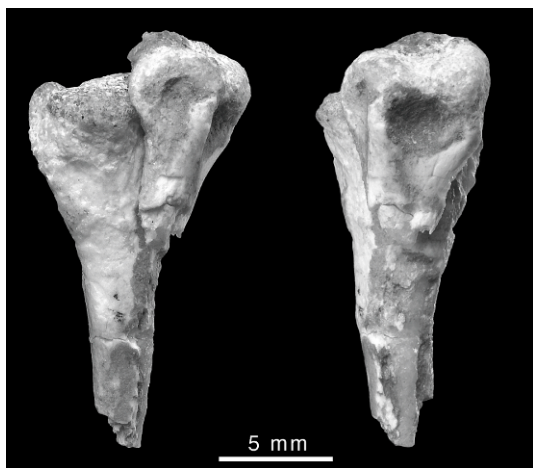


Fig. 34. Partial proximal ends of metatarsal IV and V of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195 in lateral and posterior views.

The cervical osteoderms of *Shamosuchus djadochtaensis* are peculiar among crocodyli-forms. They are most similar to the basal crocodyli-form *Zaraasuchus shepardi* (Pol and Norell, 2004b), due to the presence of an extremely large lateral keel located along the posterior margin of each osteoderm. This similarity is largely superficial, however, as *Shamosuchus djadochtaensis* lacks the radiating anterior ridges and shallow grooved ornamentation present in the *Zaraasuchus shepardi*. Additionally, the cervical dermal armor of *Shamosuchus* is distinguished from *Zaraasuchus shepardi* and other crocodyli-forms by being wider than long and more strongly flexed medially. *Sunosuchus junggarensis* also has dorsolateral neck osteoderms that bear a single medial keel (Wu et al., 1996a). These osteoderms, however, are largely dissimilar to *Shamosuchus djadochtaensis*. The osteoderms are small and leaf shaped, and the medial keel runs the entire length of the osteoderm in *Sunosuchus junggarensis* (Wu et al., 1996a). In this respect, the lateral dermal neck armor of *Sunosuchus junggarensis* is more similar to *Alligator sinensis* than *Shamosuchus djadochtaensis*.

Shamosuchus djadochtaensis shares with *Bernissartia fagesii* and nonbrevirostran eu-

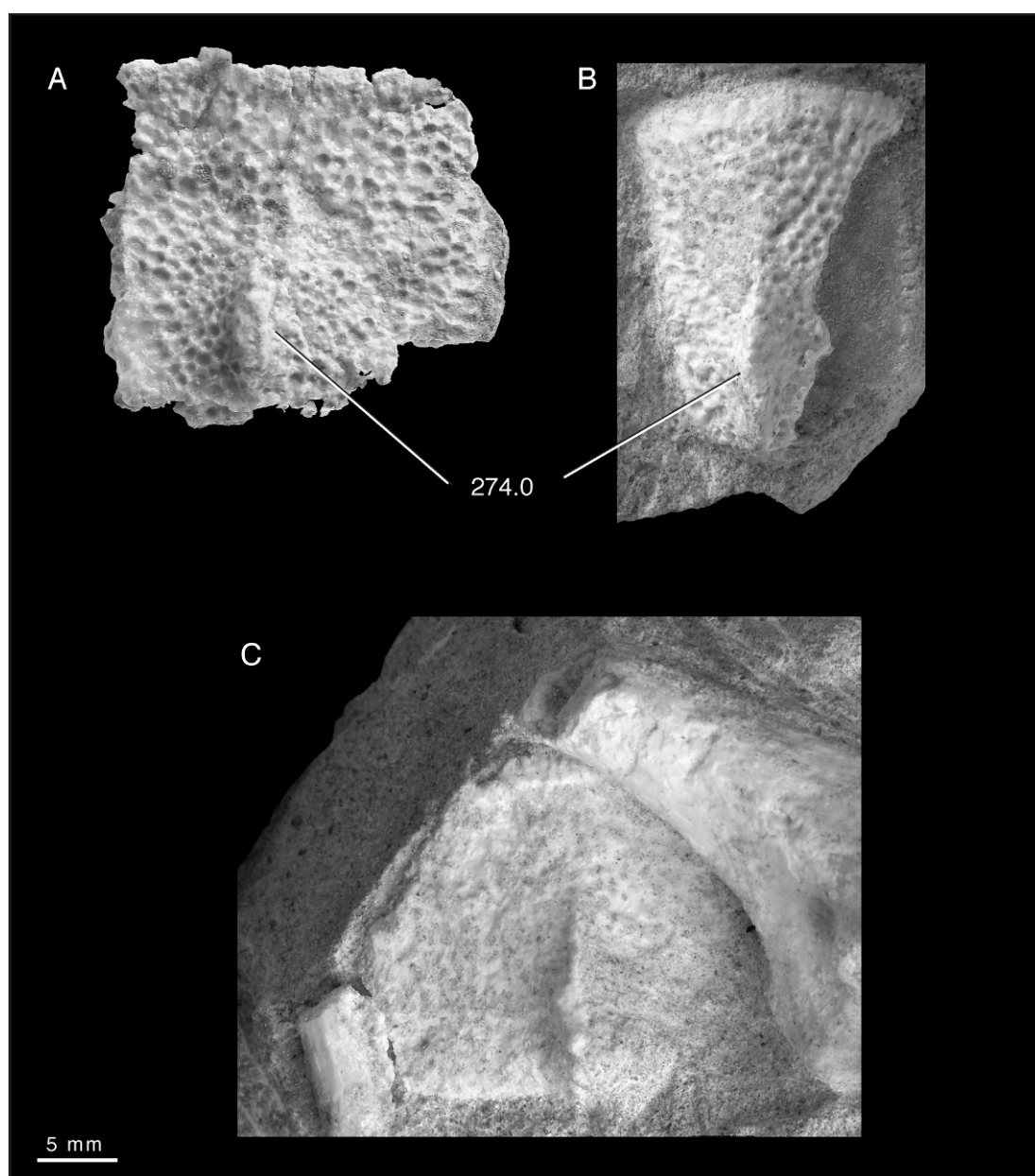


Fig. 35. Individual and systematic variation in the dorsal osteoderms of *Shamosuchus djadochtaensis*. Paramedian or near paramedian osteoderms (A and C) and more laterally located osteoderms (B). Note the posteriorly restricted location of median ridge (character 274.0).

schians the derived presence of a discrete convexity on the anterior margin of each osteoderm, in addition to the lack of a peglike anterolateral process. The two osteoderm morphologies present in the trunk and caudal dermal series is inconclusive as to the

number of rows of scutes that were present in *Shamosuchus djadochtaensis*. Eusuchians and some derived neosuchians closely related to this clade have more than two rows of dorsal osteoderms, flanked by accessory rows of osteoderms (Salisbury et al., 2006). Most

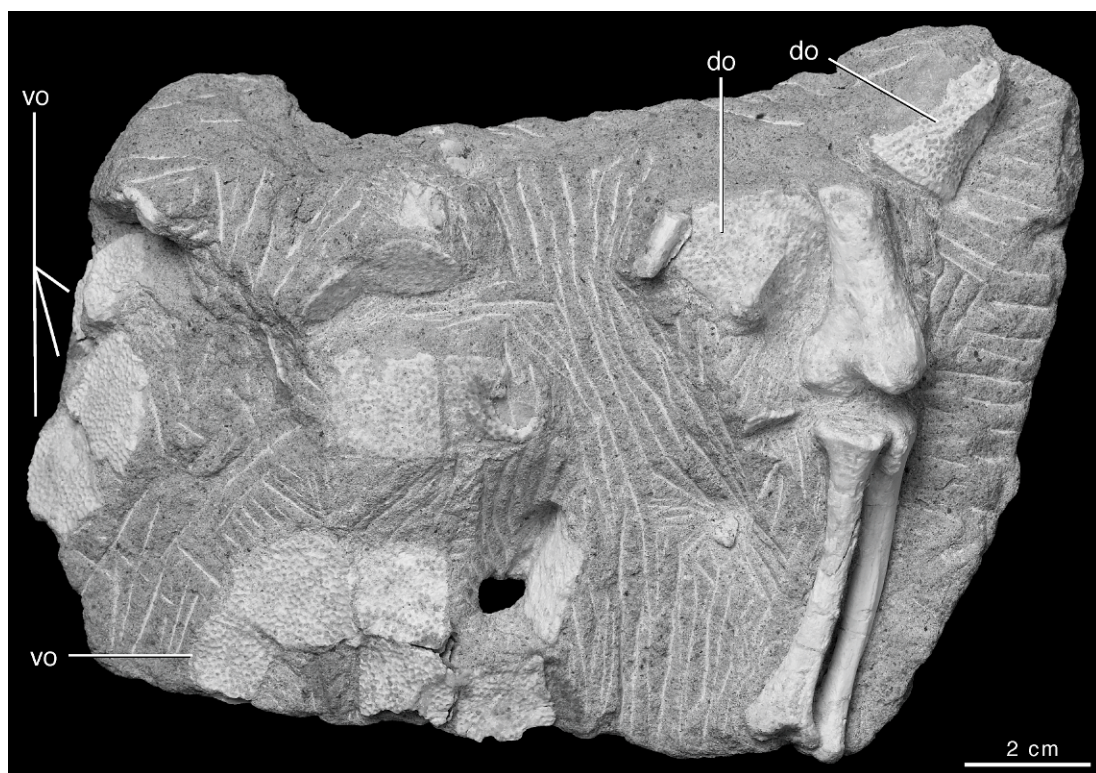


Fig. 36. Ventral osteoderms of the referred specimen of *Shamosuchus djadochtaensis* IGM 100/1195. See appendix 5 for abbreviations.

other crocodylomorphs possess a single paired row (Clark, 1994), although some notosuchians are known to have more than two rows—e.g., *Malawisuchus mwakayasyungutiensis* (Gomani, 1997) and *Simosuchus clarki* UA 8679.

The dorsal armor of *Shamosuchus djadochtaensis* can be distinguished from most other crocodyliforms by its possession of a set of osteoderms that are longer than they are wide, although this condition also occurs in some basal crocodylians (e.g., *Stangerochampsia maccabei*; Wu et al., 1996c). The dorsal armor of *Shamosuchus djadochtaensis* is distinguished from all other mesoeucrocodylians by the presence of keels restricted to the posterior edge of each osteoderm.

In addition to the axial osteoderms, a number of small osteoderms were found adjacent to the radial and ulnar, tibial and fibular, and femoral shafts. Those associated with the radius and ulna are only partly preserved but appear subrectangular in out-

line. The osteoderms have the small-sized alveolar ornamentation present in the dorsal osteoderms. However, no keel is present on any of the preserved forelimb osteoderms. Only one femoral osteoderm is preserved and is partial and poorly exposed. Five osteoderms were recovered along the shafts of the left tibia and fibula. Opposed to the forelimb osteoderms, these hindlimb elements are narrow and elongated axially. The ornamentation consists of small pits, and at least one of them possesses a low longitudinal ridge near the distal edge of the osteoderm. The nature of the articulation in these elements is unclear, given that no appendicular osteoderm is preserved overlapping or even contacting another osteoderm. The phylogenetic significance of appendicular osteoderms is currently unclear because the distribution of this character within Crocodyliformes is poorly understood. They have been reported in widely disparate taxa with crocodyliformes, including the goniopholid *Sumosu-*

chus junggarensis (Wu et al., 1996a), alligatorids (Cong et al., 1998), and the basal crocodyliforms *Gobiosuchus kielanae* and *Zaraasuchus shepardi* (Osmólska et al., 1997, and Pol and Norell, 2004b, respectively).

PHYLOGENETIC RELATIONSHIPS

As mentioned above, *Shamosuchus djadochtaensis* was traditionally considered a member of Goniophoridae (Mook, 1934a; Kälin, 1955; Steel, 1973) or, alternatively, in its own family (Efimov, 1983). Clark (1986; Benton and Clark, 1988), in the first global approach to the evolution of Crocodyliformes based on cladistic methods, depicted *Shamosuchus djadochtaensis*, *Bernissartia fagesii*, and the clade composed by the Glen Rose form and Eusuchia in an unresolved trichotomy of advanced neosuchians. This position was mainly supported by the presence of apomorphic characters, such as the multiple rows of dorsal osteoderms lacking a well-developed anterolateral process, reported in the type specimen of *Shamosuchus gradilifrons* (Konzhukova, 1954). The simultaneous presence of these derived features with characters showing the plesiomorphic neosuchian condition (e.g., “mesosuchian” palate) suggested *Shamosuchus* was a critical taxon for understanding the evolutionary origin of Eusuchia. Since then, *Shamosuchus* has usually been regarded as closely related to this clade (Norell, 1989; Clark and Norell, 1992; Wu et al., 2001a; Salisbury et al., 2006), although it has been excluded from subsequent phylogenetic analyses of Crocodyliformes. A recent exception to this trend is the inclusion of *Shamosuchus* in the phylogenetic analysis presented by Jouve et al. (2006), in which this taxon is depicted in a polytomy along with other neosuchians (e.g., *Theriosuchus*, *Rugosuchus*). The data used for *Shamosuchus* in this study, however, is based on the multiple species of this genus described by Efimov (Jouve et al., 2006: 642). This could be problematic as some characters suggest the monophyly of all the species referred to this genus may not be justified (see below). The reasons underlying the exclusion of this important taxon from most phylogenetic datasets were probably centered on the incompleteness of the type material

(AMNH FR 6412) and the lack of firsthand revision of the abundant material described by Efimov (1983, 1988) housed at the Paleontological Institute of Moscow.

The completeness of the specimen described here, including abundant postcranial remains that were almost unknown for this taxon, allows testing of the phylogenetic relationships of *Shamosuchus djadochtaensis* through a comprehensive cladistic analysis. The phylogenetic analysis conducted here is based on an extension of previous datasets (Pol and Norell, 2004b; Gasparini et al., 2006; Pol and Gasparini, 2009). Differences with these analyses consist of the addition of taxa, characters, and modification of some character definitions and scorings. Due to the large number of derived characters and similarities with advanced neosuchians (e.g., *Bernissartia fagesii*, *Rugosuchus nonganensis*, the Glen Rose form) described above, the taxon-sampling effort was focused on derived neosuchians. The extended dataset include these three taxa (see next section for a discussion on the information used for the Glen Rose form and *Bernissartia fagesii*), as well as more representatives of Goniophoridae and Eusuchia.

The complete dataset included 71 crocodylomorph taxa plus the most external out-group (*Gracilisuchus stipanicicorum*) used to root the phylogenetic trees. The character sampling was also increased with respect to previous datasets, in order to represent the morphological variation observed among neosuchians, resulting in a dataset of 282 characters (see appendices 1–3).

This phylogenetic dataset was analyzed with equally weighted parsimony using TNT v. 1.0 (Goloboff et al., 2003). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences) followed by TBR branch swapping (holding 10 trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed if they lack support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). This analysis resulted in 18 most parsimonious trees of 1031 steps (CI = 0.343, RI = 0.734), found in 913 out of the

1000 replicates. TBR branch swapping of these 18 trees did not find additional optimal topologies. Branch support of clades was evaluated examining the most parsimonious trees in which the monophyly of a given group is rejected (Bremer, 1994). These tests were conducted using negative constraints in TNT, focusing on the clades of interest. The taxon *Candidodon itapecurens* was excluded from the constrained searches as it takes one extra step to place this taxon anywhere within nonlongirostrine crocodyliforms putting a bound on the Bremer values for almost all tree nodes (see Wilkinson et al., 2000). This uncertainty is produced by the large amount of missing data rather than by character conflict (scorings on the type specimen have 98% data missing). The exclusion of *Candidodon itapecurens* therefore allows a comparison on differences in branch support irrespective of the alternative positions of this highly incomplete terminal taxon.

The most parsimonious hypotheses of this analysis places *Shamosuchus djadochtaensis* as the sister taxon of *Rugosuchus nonganensis* from the Early Cretaceous of China (node 1 in fig. 37). This Asian clade is diagnosed in all most parsimonious trees by the presence of a sagittal ridge on the dorsal surface of the frontal (character 22.1; also present in *Isisfordia duncani* and notosuchians), a unified opening for the exit of cranial nerves IX–XI (character 59.0; resembling the condition of basal crocodyliforms), the posterior region of palatine bar between suborbital fenestra flared posteriorly (character 279.1), and the presence of a longitudinal ridge on the lateral surface of the angular (character 219.2). The latter condition is also present in the Glen Rose form, although in the most parsimonious trees is optimized as acquired convergently.

Several other characters may diagnose this group although they have not been clearly preserved (or described) in *Rugosuchus nonganensis* and therefore are currently ambiguously optimized as synapomorphies of this clade. The buccal edge of the premaxillamaxilla suture of *Shamosuchus djadochtaensis* lacks the notch (character 9.1) present in all neosuchians (except for alligatorids). Wu et al. (2001a) noted this region is damaged in

Rugosuchus and the lateral notch has been greatly exaggerated and therefore we have scored this taxon with a missing entry. Unlike other neosuchians, the ectopterygoid fails to contact the postorbital on the medial surface of the postorbital bar (character 144.1) in *S. djadochtaensis*, but this condition is unknown in *Rugosuchus nonganensis* and therefore the character is ambiguously optimized. The orbital margin of the jugal of *Shamosuchus djadochtaensis* is emarginated, forming a distinct ridge with an associated elongate depression located ventrally to it (character 275.1). It is currently unclear whether this condition is also present in *Rugosuchus nonganensis* and therefore it is uncertain whether this character diagnoses the Asian clade or it is autapomorphic of *Shamosuchus*. A similar case occurs with the lateral surface of the squamosal, in which *Shamosuchus* has an unusual morphology because of the presence of a discontinuous groove for the ear valve (character 281.1), but is uncertain in *Rugosuchus nonganensis*. The presence of appendicular osteoderms (character 223.1) in *Shamosuchus djadochtaensis* is also an uncommon feature for a neosuchian and, if present in *Rugosuchus nonganensis*, it may also diagnose this clade. Finally, the dorsal cervical and osteoderms of *Shamosuchus djadochtaensis* bear their longitudinal keels restricted to their posterior halves, tapering on their anterior regions (character 274.0) instead of tapering both anteriorly and posteriorly as in other neosuchians. The dorsal osteoderms of *Rugosuchus nonganensis* had not been described in detail (Wu et al., 2001a) and therefore this condition could not be determined at the moment.

The monophyly of this Asian clade is only moderately supported (Bremer, 1994); in some trees with only two extra steps the monophyly of the clade is rejected. In these trees, the Glen Rose form is depicted as the sister taxon of *Shamosuchus djadochtaensis*. The monophyly of the Asian clade, however, agrees with previous ideas regarding the close relationship of *Shamosuchus* and *Rugosuchus nonganensis* (Wu et al., 2001a). This clade could be referred to as Paralligatoridae (Konzhukova, 1954), although the taxon sampling of this analysis is not sufficiently complete to evaluate whether the use of such

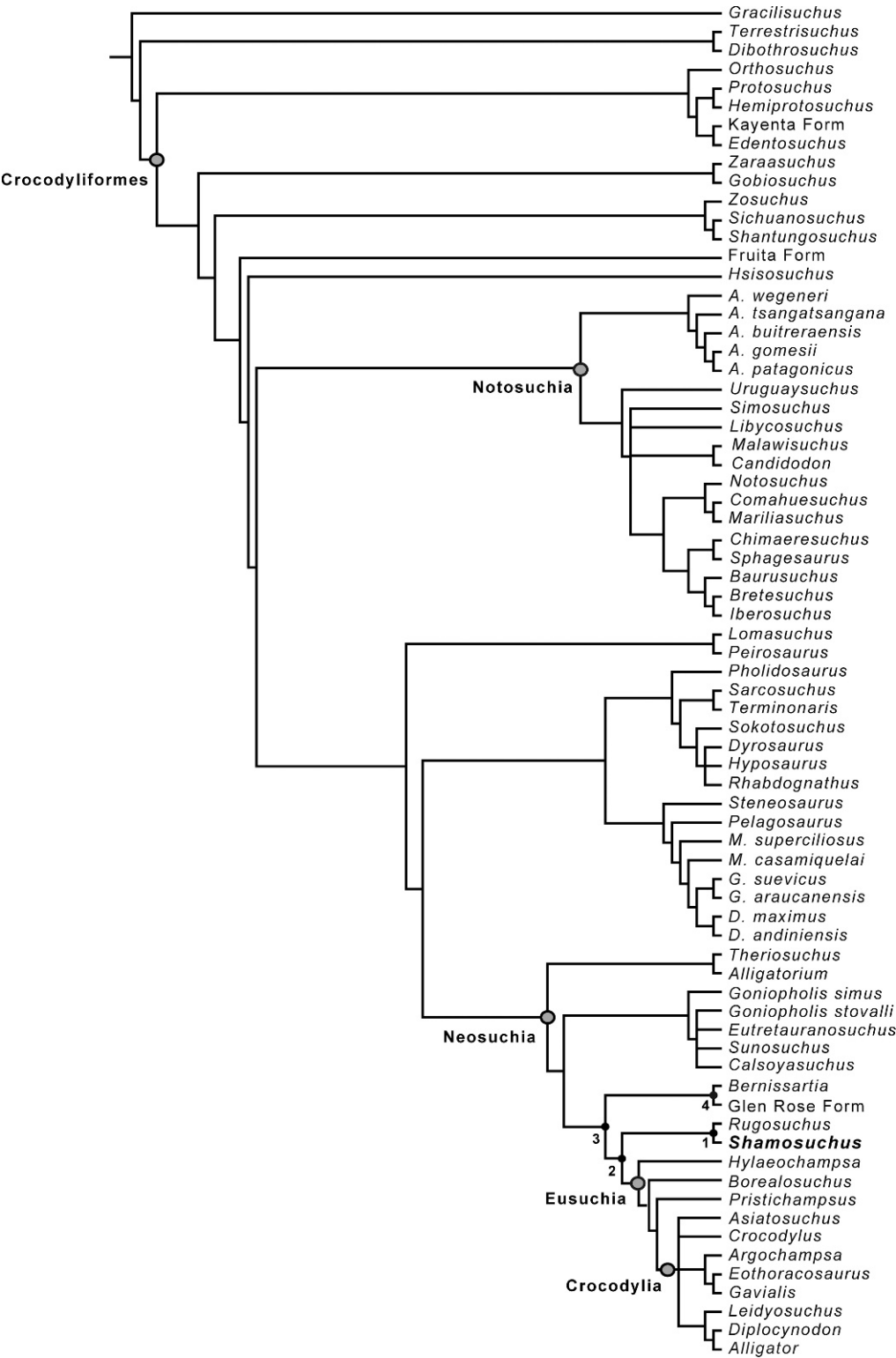


Fig. 37. Strict consensus of 18 most parsimonious trees obtained in the phylogenetic analysis.

name is appropriate. Future studies, including a careful revision of the alpha taxonomy of all the species referred to *Shamosuchus* (including “*Paralligator*” spp.) and their inclusion in a phylogenetic analysis, are needed to assess whether these forms constitute a monophyletic group together with *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis* (for which the name *Paralligatoridae* may be appropriate). Two relevant characters present in the *Shamosuchus djadochtaensis* specimen described here, however, contrasts with the morphology described for *Shamosuchus gradilifrons* (Konzhukova, 1954): the presence of platycoelous vertebrae and nonoverlapping osteoderms. These differences suggest that some of the species referred to *Shamosuchus* may not form a monophyletic clade, with some of them more closely related to Eusuchia than others. Given their character-state distribution, however, these two features would be in conflict with each other, and we consider it premature to establish any conclusion at this point. Furthermore, these two characters vary within the body segments of IGM 100/1195 (e.g., cervical versus caudal elements) and a careful comparison of these materials is therefore needed.

The Asian clade composed by *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis* is depicted as the sister group of Eusuchia, represented by *Hylaeochampsia vectiana* and more derived neosuchians (node 2 in fig. 37). This node is supported in all most parsimonious trees by four unambiguous synapomorphies centered on the morphology of the frontal and the cervicodorsal vertebrae. The frontal of *Shamosuchus djadochtaensis* tapers anteriorly and lacks a pointed anterior tip that wedges between the nasals (character 165.0) as it occurs in eusuchians but not in more basal neosuchians. This region, however, is poorly preserved in the type specimen of *Rugosuchus nonganensis* and a character state could not be determined. The neural spines of the posterior cervical vertebrae of *Shamosuchus djadochtaensis* are rodlike, resembling the condition of eusuchians (character 90.1), whereas more basal forms have anteroposteriorly long neural spines in the posterior cervicals. The neck vertebrae of *Shamosuchus*

djadochtaensis are procoelous as in crocodylians (character 92.1), whereas in other noneusuchian mesoeucrocodylians the cervical vertebrae are amphicoelous. This plesiomorphic condition was scored for *Bernissartia fagesii* based on the information of the holotype (Norell and Clark, 1990), although a cervical vertebra of a referred specimen seems to have an incipiently developed procoelous condition with a convex but flattened posterior condyle (see Buscalioni and Sanz, 1990). This character was scored as uncertain in the Glen Rose form given the recent suggestion that the procoelous vertebrae previously referred to this taxon may actually belong to *Pachycheilosuchus trinquei* (Rogers, 2003). Finally, hypapophyses are present in the three anteriormost dorsal vertebrae of the members of node 2 (character 91.3), including crocodylians, which have these processes up to the third or fourth dorsal vertebra (Brochu, 1997a). The condition of the fourth dorsal vertebrae cannot be determined in IGM 100/1195, but the first three dorsal vertebrae of *Shamosuchus djadochtaensis* bear hypapophyses. The closest outgroup to this node (*Bernissartia fagesii*) was noted to have hypapophyses only in the first two dorsals (Brochu, 1997a), whereas more basal forms usually lack well developed hypapophyses in the dorsal vertebrae.

Other relevant characters provide ambiguous support for this node because of the uncertainty in the condition of either *Shamosuchus* or its most immediate outgroup (the clade formed by *Bernissartia fagesii* and the Glen Rose form). Most crocodylians are characterized by the presence of a reduced anterior palpebral (character 65.1; with the notable exception of some derived forms such as *Paleosuchus* and *Osteolaemus*), whereas basal neosuchians (goniopholidids, atoposaurids) usually have a much larger anterior palpebral (a plesiomorphic condition given that this character state is also found in non-neosuchian crocodyliforms). Given the lack of precise information in several advanced neosuchians (e.g., *Bernissartia fagesii*, *Shamosuchus djadochtaensis*, *Rugosuchus nonganensis*, *Hylaeochampsia vectiana*), it is currently unclear if the drastic reduction of the anterior palpebral can be traced back to node 2 or to a less inclusive clade within Eusuchia.

Procoelous dorsal vertebrae (character 93.1) have also long characterized Eusuchia (Huxley, 1875), although this condition has also been described in a eusuchian close relative (i.e., *Isisfordia duncani*; Salisbury et al., 2006). The presence of procoelous condition cannot be verified in all the dorsal vertebrae of *Shamosuchus djadochtaensis* because of the incompleteness of the vertebral series, although the first dorsal of IGM 100/1195 is certainly procoelous. This character state is therefore ambiguously optimized in the present analysis and may diagnose either node 2 (fig. 37) or Eusuchia, given that *Bernissartia fagesii* (Dollo, 1883; Buffetaut, 1975; Norell and Clark, 1990; Salisbury and Frey, 2001) and goniopholidids have amphicoelous dorsal vertebrae (and the condition of the Glen Rose form was considered uncertain). This clade is not robust, as in some trees with one extra step the Glen Rose form is depicted as the sister taxon of the Asian clade or, alternatively, the sister group of Eusuchia. Trees with one extra step are needed to depict *Bernissartia fagesii* as closer to Eusuchia than the Asian clade.

The monophyly of Eusuchia (*Hylaeochampsia vectiana* and more derived neosuchians) is supported in this analysis by four unambiguous synapomorphies present in all most parsimonious trees. As mentioned above, one apomorphic palatal morphology that traditionally diagnosed Eusuchia is the presence of a choanal opening completely enclosed by the pterygoids (Huxley, 1875). This character is also shown in this study as a synapomorphy of this clade (character 43.2), because of its presence in *Hylaeochampsia vectiana* and more derived forms. More basal forms, including the Asian clade, *Bernissartia fagesii* (Buscalioni and Sanz, 1990), and the Glen Rose form (Brochu, 1999), have palatine participation of the choanal opening. The recently described *Isisfordia duncani* also shows the eusuchian condition, supporting a close phylogenetic relationship of this taxon with Eusuchia postulated recently by Salisbury et al. (2006; see below).

The second synapomorphy concerns the relative position of the anterior margin of the choanal opening relative to the suborbital fenestra. All eusuchians have a posteriorly positioned choana, the anterior margin of

which is well displaced caudally from the suborbital opening (even reaching the posterior edge of the pterygoid flanges in some forms; character 44.2). Other advanced neosuchians have the choanal anterior margin located more rostrally, either anteriorly or at the posterior edge of the suborbital opening (character 44.0 and 44.1, respectively). As noted by Brochu (1999), all eusuchians share the absence of a shallow fossa at the anteromedial corner of the supratemporal fenestra—instead this region is flat or slightly convex (character 265.1). Finally, the lateral margins of the anterior end of the palatine bar, located between the suborbital fenestrae, are subparallel to each other in Eusuchia (character 278.0), whereas in its most immediate outgroups (the Glen Rose form, *Shamosuchus djadochtaensis*, *Rugosuchus nonganensis*, and goniopholidids) this region flares anteriorly. The character-state distribution of this feature is, however, not free of conflict within Neosuchia, as *Theriosuchus pusillus*, *Terminonaris robusta*, and dyrosaurids also have subparallel margins of the anterior region of the palatine bar. Therefore, Eusuchia is diagnosed by a reversion in this character to the condition present in these more basal forms. Furthermore, within Crocodylia, several alligatoroids have a flared anterior region of the palatine bar (optimized as a derived transformation back to the condition present in the Glen Rose form, *Shamosuchus*, and goniopholidids).

Three additional characters also may diagnose Eusuchia, although the lack of information in *Hylaeochampsia vectiana* hampers an unambiguous optimization in the present analysis. The presence of an external mandibular fenestra (character 75.0) characterizes extant crocodylians and contrasts with the complete closure of this opening in most neosuchians closely related to Eusuchia (e.g., *Shamosuchus djadochtaensis*, *Rugosuchus nonganensis*, the Glen Rose form, *Bernissartia fagesii*, *Theriosuchus pusillus*). The condition of *Hylaeochampsia vectiana* is unknown and therefore this character is optimized as an ambiguous synapomorphy of Eusuchia within the context of this dataset. However, as noted by Brochu (2004), the evolutionary history of the external mandibular fenestra is likely to be

more complicated than previously thought as it is reduced to a narrow slit in some crocodylians (Brochu, 2004) and is well developed in *Isisfordia duncani* (Salisbury et al., 2006). The shape of the retroarticular process of crocodylians is anteroposteriorly elongated and subtriangular and faces dorsally (character 71.3; convergently acquired in longirostrine forms), whereas *Shamosuchus djadochtaensis*, *Rugosuchus nonganensis*, *Bernissartia fagesii*, goniopholids, and *Theriosuchus pusillus* have a much shorter process that is paddle shaped and projected posteriorly or posteroventrally (character 71.4). Unfortunately, the morphology of this process is not known in *Hylaeochampsa vectiana* and therefore the crocodylian condition may be diagnostic of Eusuchia or a more restricted clade within this group (fig. 37). The presence of a clearly demarcated insertion area for m. pterygoideus posterior on the lateral surface of angular shows a similar pattern of character-state distribution. A smooth and concave surface is present in species of *Borealosuchus* and more derived crocodylians included in this study (character 76.1). The lack of information for *Hylaeochampsa vectiana* also renders this character as ambiguously optimized at Eusuchia or a less inclusive clade (fig. 37). The absence of longitudinal keels on dorsal osteoderms (character 101.1) shows numerous instances of homoplastic transformations across the tree (both outside and inside Neosuchia), but it is currently optimized as an ambiguous synapomorphy of Eusuchia because of the absence of this structure in basal crocodylians (e.g., *Borealosuchus*, *Pristichampsus*, *Eothoracosaurus*). A more complete taxonomic sampling, however, would be critical to test the evolution of this feature given the character conflict displayed within Crocodylia (e.g., a longitudinal keel is present in *Gavialis* and several brevirostrans). The support of the node identified here as Eusuchia is relatively good in comparison with those of other neosuchian nodes. The monophyly of this taxon is rejected in trees with four extra steps, placing *Hylaeochampsa vectiana* in a more basal position within Neosuchia.

Shamosuchus djadochtaensis, *Rugosuchus nonganensis*, the Glen Rose form, and *Bernissartia fagesii* are clustered with Eusuchia

to the exclusion of other neosuchians (node 3 in fig. 37). This group, herein referred to as advanced neosuchians, is supported by four unambiguous synapomorphies. These forms share the presence of a large pterygoid contribution to the choanal margins. All noneusuchian members of this clade have their choanal opening enclosed by the pterygoids and palatines (i.e., “mesosuchian palate”). However, these forms show an intermediate condition between the choanal opening of most other “mesosuchians” and eusuchians, given that the lateral margins of the choanal opening are mostly (if not completely) formed by the pterygoids and therefore the palatine contribution is restricted to the anterior margin of the choanal opening (character 43.1). In eusuchians, the palatines do not contribute to the choanal margins (character 43.2). More basal neosuchians (and outgroups) instead have a significant contribution of the palatines to the lateral margin of the choanal opening (e.g., *Goniopholis simus*, *Theriosuchus pusillus*; character 43.0). This character is ordered and therefore the character state 1 diagnoses node 3 (fig. 37). It must be noted that the condition of this character in *Bernissartia fagesii* has been the subject of debate due to the poor preservation of the type material (Buffetaut, 1975, 1982; Buscalioni and Sanz, 1990; Norell and Clark, 1990). In our analysis *Bernissartia fagesii* was scored with character state 1 based on the morphology described by Buscalioni and Sanz (1990) for the Spanish specimen. The second character concerns the internal choanal septum formed by the pterygoids, which is absent in *Shamosuchus djadochtaensis* (character 69.0), the Glen Rose form, and nonalligatorid eusuchians (Brochu, 1999). The two remaining synapomorphic characters concern osteoderm morphology. The dorsal osteoderms of *Bernissartia fagesii*, *Shamosuchus djadochtaensis*, and nonbrevirostran crocodylians share the presence of a discrete convexity on the lateral region of their anterior margin (character 96.1), whereas more basal neosuchians (e.g., *Theriosuchus pusillus*, goniopholids) have a well-developed anterolateral articular peg (character 96.2). As also noted previously, the dorsal dermal armor of *Bernissartia fagesii* is composed by more

than two rows (character 97.1), as in more derived neosuchians (*Isisfordia duncani*, crocodylians). The composition of the dorsal armor of *Shamosuchus djadochtaensis* is currently unknown, yet it is suggestive of multiple rows because of the two morphologies of dorsal osteoderms found with IGM 100/1195. Other species of *Shamosuchus* have been described as having multiple rows of osteoderms (Konzhukova, 1954). Finally, the presence of an elevated ridge on the orbital margins of the frontal (character 266.1) provides ambiguous support for this clade. This character shows a conflictive character-state distribution, as it is present in basal members of this clade but is also present in *Theriosuchus pusillus* (but absent in goniopholids, dyrosaurids, and pholidosaurids). Furthermore, these ridges are optimized as secondarily lost in crocodylians (except for *Pristichampsus vorax* and some alligatorids and gavialids; Brochu, 1999). Two extra steps are required to reject the monophyly of this node, placing the Glen Rose form more basally within Neosuchia (as the sister taxon of goniopholids plus advanced neosuchians). One additional extra step (i.e., three extra steps) is required to place *Bernissartia fagesii* basal to goniopholids.

The present analysis retrieved the Glen Rose form as the sister taxon of *Bernissartia fagesii*, in contrast with previous cladistic analyses (e.g., Benton and Clark, 1988; Brochu, 1997a, 1999) but in agreement with previous comments on the relationships of these forms by Buscalioni and Sanz (1990). Our analysis, however, restricts the scorings to the skull characters of the Glen Rose form (see next section), which prove decisive in depicting this taxon as the sister group of *Bernissartia fagesii*. This position is supported in this analysis by only one unambiguous synapomorphy: the ectopterygoid of these two forms extends up to the posterior edge of the pterygoid flange (character 269.0), in contrast to that of all other neosuchians in which the ectopterygoid does not reach the caudal end of the pterygoid. Additionally, as mentioned above the anterior edge of the choanal opening of the Glen Rose form (USNM 22039) and the Spanish specimen of *Bernissartia fagesii* (Buscalioni and Sanz, 1990) is located at the posterior edge of

suborbital fenestrae, providing another feature that may diagnose this clade. The sister group status of these two forms is clearly weak and needs to be tested with the addition of new information on these forms as well as additional taxa (see below). This clade has minimal Bremer support value, as trees with a single extra step depict either of these taxa as closer to the Asian clade and/or to Eusuchia.

DISCUSSION

SHAMOSUCHUS, *BERNISSARTIA*, AND THE GLEN ROSE FORM

The new information provided by IGM 100/1195 allows postulating a novel phylogenetic arrangement on the interrelationships of *Shamosuchus djadochtaensis* and two other advanced neosuchians: the Glen Rose form and *Bernissartia fagesii*.

GLEN ROSE FORM: The so-called Glen Rose form is an undescribed taxon originally mentioned by Langston (1973, 1974) as a eusuchian close relative from the Early Cretaceous Glen Rose Formation. Several specimens have been informally referred to this form, including two skulls (USNM 22039; MCZ 4453) and several postcranial remains. Among the latter there are isolated vertebrae (e.g., TMM 40595, TMM 41306, TMM 41307) and partly articulated remains (e.g., TMM 42995-2, TMM 40644-1). The key features of these materials were the presence of an intermediate condition between “mesosuchians” and eusuchians in the choanal morphology and the procoely of the referred vertebrae. Although these remains have never been described, the Glen Rose form has been included in several phylogenetic analyses and has been consistently retrieved as the closest eusuchian outgroup (Clark, 1986; Benton and Clark, 1988; Brochu, 1997a, 1999) or as a basal eusuchian (Buscalioni et al., 2001). The phylogenetic position of this form was, however, influenced by the association of the skull material with isolated procoelous vertebrae from the same formation (i.e., forcing its putative affinities with Eusuchia).

Rogers (2003) described *Pachycheilosuchus trinquei*, a neosuchian crocodyliform from

the same unit with procoelous vertebrae, as closely related to Atoposauridae (see below). Rogers (2003) considered that the isolated procoelous vertebrae originally referred to the Glen Rose form belong to *Pachycheilosuchus trinquei*, suggesting the phylogenetic position of the former taxon should be revised. We have taken a conservative approach in evaluating the relationships of the Glen Rose form by ignoring the postcranial remains as they are not clearly associated with the diagnostic skull remains studied by Langston (1973, 1974). Thus, the scorings of the Glen Rose form in our analysis are restricted to craniomandibular and dental characters taken from the specimens USNM 22039 and MCZ 4453.

The exclusion of postcranial material from the scorings of the Glen Rose form results in a more basal position of this taxon in comparison with previous results based on scorings of both cranial and postcranial material (e.g., Clark, 1986; Benton and Clark, 1988; Brochu, 1997a, 1999; Buscalioni et al., 2001). The new phylogenetic position of the Glen Rose form should be taken as a preliminary result for two main reasons. First, a thorough study on the Glen Rose form still needs to be conducted, including a careful revision of all postcranial material available from the Glen Rose Formation. In particular, detailed comparisons of the postcranium of *Pachycheilosuchus trinquei* and the partly articulated remains originally referred to the Glen Rose form (TMM 42995-2, TMM 40644-1) will help determine whether their original taxonomic assignment was correct. If so, these remains could provide information on the osteoderm and vertebral morphology of the Glen Rose form, which will be valuable from a phylogenetic point of view. Second, even within the context of the present analysis (considering only skull material), the new position of the Glen Rose form is not free of character conflict. This taxon indeed bears two skull characters that suggest it may be more closely related to Eusuchia than the Asian clade (i.e., *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis*).

The first character, as originally recognized by Langston (1973), the position of the choanal opening in the Glen Rose form is

located at the posterior edge of the suborbital fenestra (character 44.1), approaching the caudally displaced choanal opening of Eusuchia (character 44.2). In contrast, *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis* have the anterior edge of the choana located more anteriorly, between the suborbital fenestra (character 44.0), resembling the condition of most noneusuchian mesoeucrocodylians. This character distribution suggests a more derived position of the Glen Rose form. Irrespective of the phylogenetic position of this taxon, the evolutionary history of this character appears to have been complicated. Character state 1 is also present in other advanced neosuchians (e.g., *Bernissartia fagesii*, *Isisfordia duncani*; Buscalioni and Sanz, 1990; Salisbury et al., 2006), as well as in some longirostrine neosuchian crocodyliforms (e.g., *Sarcosuchus imperator*, *Terminonaris robusta*, dyrosaurids). The second character is the presence of a dorsal exposure of the supraoccipital on the skull roof (character 171.1). Although this feature is present in several basal mesoeucrocodylians (e.g., notosuchians), most basal neosuchians lack the dorsal exposure of the supraoccipital (e.g., *Pholidosaurus*, *Sarcosuchus*, dyrosaurids, thalattosuchians, gonio-pholids). This character is unknown in *Shamosuchus djadochtaensis*, but the supraoccipital is not exposed on the skull roof of *Rugosuchus nonganensis*. The presence of a dorsal supraoccipital exposure in the Glen Rose form (Brochu, 1999), *Hylaeochampsia vectiana* (Clark and Norell, 1992), and most crocodylians provide evidence toward a more derived position of the Glen Rose form with respect to the Asian clade.

Further study and materials of the Glen Rose crocodyliforms are needed to provide a solid alpha taxonomy, confident association of skull and postcranial material, and to provide a more complete understanding of its phylogenetic relationships of the Glen Rose form.

BERNISSARTIA: *Bernissartia fagesii* was originally described by Dollo (1883) based on two specimens from the Early Cretaceous Wealden beds of Bernissart (Belgium). Fragmentary additional remains have been reported from temporally equivalent beds in England (Buffetaut and Ford, 1979) and a

young specimen from the Early Cretaceous of Spain has also been referred to this taxon (Buscalioni et al., 1984; Buscalioni and Sanz, 1990). *Bernissartia fagesii* has been the subject of much disagreement and intensive study by numerous authors for over a century (Dollo, 1883; Lydekker, 1888; Kälin, 1955; Buffetaut, 1975; Buscalioni and Sanz, 1990; Norell and Clark, 1990), which alternatively considered this form as more closely related to Eusuchia or to Goniophoridae. Once the debate on the choanal and vertebral morphology of *Bernissartia fagesii* was settled (Buffetaut, 1975; Buscalioni and Sanz, 1990; Norell and Clark, 1990), a general consensus was reached, considering this form as an advanced neosuchian closely related to Eusuchia but clearly outside this group. The present analysis and the new information on *Shamosuchus* allows resolution of the relative position of *Shamosuchus djadochtaensis* and *Bernissartia fagesii* relative to Eusuchia, which were collapsed into a trichotomy in the first phylogenetic analysis that have included both *Shamosuchus* and *Bernissartia fagesii* (Clark, 1986; Benton and Clark, 1988). As described above, *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis* are depicted here as more closely related to Eusuchia than *Bernissartia fagesii* in the consensus of the shortest trees presented here. This resolution contradicts the phylogenetic result obtained by Jouve et al. (2006) depicting *Shamosuchus* as more basal than *Bernissartia fagesii*.

As in the case of the Glen Rose form, *Bernissartia fagesii* shares derived characters with eusuchians that are absent in *Shamosuchus djadochtaensis*. One of them is the posterior position of the choana, relative to the suborbital opening. The type material of *Bernissartia fagesii* is difficult to determine but the Spanish specimen shows the anterior margin of the choana at the posterior edge of the suborbital fenestra (Buscalioni and Sanz, 1990), approaching the eusuchian condition (character 44.1; see above). Additionally, the morphology of the caudal vertebrae centra of *Bernissartia fagesii* is more derived than that of *Shamosuchus djadochtaensis*. In the former taxon the first caudal is biconvex (character 94.1) and at least the second caudal vertebra is procoelous, as in eusuchian crocodyliforms

(see discussion by Norell and Clark, 1990). In contrast, the caudal vertebrae of *Shamosuchus djadochtaensis* preserved in IGM 100/1195 are amphicoelous as in most non-eusuchian neosuchians (and outgroups).

These characters do not perfectly fit the most parsimonious hypotheses proposed here, indicating either reversals in the Asian clade or convergences between Eusuchia and *Bernissartia fagesii* (or the Glen Rose form). These (and other) characters traditionally used as diagnostic of Eusuchia seem to have had a more complicated evolutionary history than previously thought (see below), highlighting the character conflict present in the relationships of advanced neosuchians.

TAXON SAMPLING AND THE PHYLOGENY OF ADVANCED NEOSUCHIANS

The cladistic analysis presented here helps to clarify the phylogenetic position of *Shamosuchus djadochtaensis* as a closer relative to Eusuchia than to other advanced neosuchians, such as *Bernissartia fagesii* or the Glen Rose form. This analysis, however, is far from complete in terms of the taxonomic sampling. A large number of advanced neosuchians and basal eusuchians from Cretaceous beds of different regions of the world could not be included in this analysis for several reasons. Many of them are fragmentary forms, known for several decades. Others are recently discovered taxa, and though relatively complete and well preserved, they have been only briefly described or are still unpublished. In this section we briefly review the record of these forms according to the geographic regions where they had been found, pointing toward future directions that will help to understand more thoroughly the phylogeny of advanced neosuchians and the origin of Eusuchia. Furthermore, some of these taxa are preliminarily included in the phylogenetic analysis in order to conduct an exploratory test on their relationships as well as to assess the robustness of the topology presented above for advanced neosuchians. The results are discussed for each of these taxa and a summary is provided at the final remarks of this section.

AUSTRALIA: Until recently, the evidence of advanced neosuchians from the Southern Hemisphere was restricted to fragmentary forms of uncertain affinities, leading some authors to treat the origin of Eusuchia as if it had taken place in the Northern Hemisphere (Sill, 1968; see also Salisbury et al., 2006). However, the Cretaceous record of Gondwana has recently offered important new information on advanced neosuchians.

Among these, one of the most recently described and probably one of the most relevant taxa for understanding the evolutionary origins of Eusuchia is *Isisfordia duncani* from the Cretaceous of Australia (Salisbury et al., 2006). Several specimens of this taxon, some of which are remarkably complete, have been found in the Winton Formation (late Albian–early Cenomanian). This taxon bears a unique combination of characters that suggest close affinities with basal eusuchians. In fact, Salisbury et al. (2006) interpreted this form as the most basal member of Eusuchia (see below). Among the derived features of *Isisfordia duncani* are the presence of weakly procoelous vertebrae in both the presacral and the caudal series. In contrast to some noneusuchians with procoelous vertebrae (e.g., *Theriosuchus*, *Pachycheilosuchus*), the vertebral condyle of *Isisfordia duncani* lacks a central depression on the articular facets (Salisbury et al., 2006). The morphology of the dermal armor also shows a derived condition as it is composed by four parasagittal rows of dorsal osteoderms (two on each side of the trunk), in contrast to the two parasagittal rows representing the plesiomorphic neosuchian condition. Moreover, the central region of the paravertebral shield is flanked by a longitudinal row of accessory osteoderms, a derived feature of advanced neosuchians (e.g., *Bernissartia fagesii*, *Susisuchus anatoceps*) and Eusuchia. The skull of *Isisfordia duncani* also bears derived characters that suggest a close relationship with Eusuchia. The most remarkable one is the presence of a choanal opening completely enclosed by the pterygoids (Salisbury et al., 2006), one of the long-standing diagnostic characters of Eusuchia (Huxley, 1875). This opening, however, is not as posteriorly displaced as in the *Hylaeochampsia vectiana* and more derived forms,

but is located close to the caudal margin of the suborbital fenestra (Salisbury et al., 2006), as in some noneusuchian neosuchians (i.e., *Bernissartia fagesii* and the Glen Rose form). Thus, *Isisfordia duncani* shows a combination of plesiomorphic and apomorphic characters previously unrecorded among advanced neosuchians (although see comments on the Las Hoyas neosuchian below).

Given the unique combination of characters present in *Isisfordia duncani* and its putative close relationships with Eusuchia (Salisbury et al., 2006), we have scored this taxon in our dataset using the published information in order to preliminarily test whether its inclusion has any impact on the phylogenetic hypothesis presented here (see appendix 4). Since we have not examined this material and its description is relatively brief (Salisbury et al., 2006), the scoring of this form was conducted using a conservative approach that assigned missing entries for those characters not explicitly described in the text or the data matrix published by Salisbury et al. (2006). Admittedly, many of the missing entries using this approach are likely to be scorable after a firsthand study of the specimen, but the risk of introducing spurious information into this exploratory analysis is reduced.

An exploratory phylogenetic analysis including *Isisfordia duncani* retrieves 60 most parsimonious trees (1044 steps) that show the same basic topology as the analysis presented above (excluding *Isisfordia duncani*). The only topological difference among these 60 trees regarding the relationships of advanced neosuchians consists of two alternative positions for *Isisfordia duncani*. Both of these corroborate the hypothesis of the close relationship of *Isisfordia duncani* to eusuchians recently proposed by Salisbury et al. (2006). Half of the most parsimonious trees depict *Isisfordia duncani* as the sister group of *Hylaeochampsia vectiana* and more derived eusuchians, identical to the analysis of Salisbury et al. (2006). The other half of the optimal trees, however, depict an alternative position for this taxon: as the sister group of the Asian clade (fig. 38). This alternative position is also compatible with the results of Salisbury et al. (2006), as they did not include the Asian forms in their study.

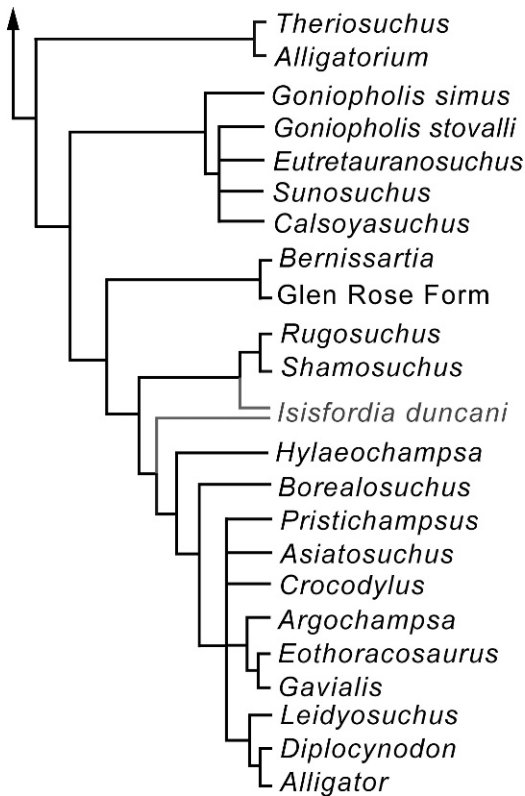


Fig. 38. Reduced strict consensus of the 60 most parsimonious trees obtained in the exploratory analysis including *Isisfordia duncani* (based on the information provided by Salisbury et al., 2006), showing only the relationship among neosuchians. The two alternative positions retrieved for *Isisfordia duncani* are indicated with grey lines.

The former position is supported by two unambiguous synapomorphies. The first is the condition of the choanal opening of *Isisfordia duncani*: completely bounded by the pterygoids (character 43.2). As mentioned above, this condition is exclusively shared by *Isisfordia duncani* and eusuchians. The second synapomorphy is the absence of a shallow depression at the anteromedial corner of the supratemporal fossa (character 265.1), a condition shared by *Isisfordia duncani*, *Hylaeochampsa vectiana*, and crocodylians. Other advanced neosuchians (e.g., *Shamosuchus djadochtaensis*, the Glen Rose form, *Goniopholis simus*, *Eutretauranosuchus delfsi*, *Theriosuchus pusillus*) have a distinct

rounded depression within the supratemporal fossa (Brochu, 1999). The absence of such fossa, however, seems to have a rather complex evolutionary history as it is optimized as convergently lost in some neosuchian taxa, such as *Calsoyasuchus valliceps* and the *Sarcosuchus* + *Terminonaris* clade. Furthermore, this condition is also present in some basal mesoeucrocodylians (e.g., *Araripesuchus*, *Libycosuchus*) and basal crocodyli-forms (e.g., protosuchids).

In those trees in which *Isisfordia duncani* is depicted as the sister taxon of the Asian clade there are also two unambiguous synapomorphies supporting this arrangement. First, *Isisfordia duncani* and *Shamosuchus djadochtaensis* are the only advanced neosuchians that lack a notch at the ventral edge of the premaxilla-maxilla suture (character 9.0). As mentioned in the previous section the condition in *Rugosuchus nonganensis* is uncertain. Determining the condition of this character for this taxon is a critical issue, given that within the context of this dataset, if *Rugosuchus nonganensis* actually has a premaxillary-maxillary notch, *Isisfordia duncani* would be the sister group of *Hylaeochampsa vectiana* and crocodylians. The second synapomorphic feature is the presence of a well-developed sagittal ridge on the dorsal surface of the frontal (character 22.1). In contrast to the previous character, the frontal ridge is present in *Isisfordia duncani*, *Shamosuchus djadochtaensis*, and *Rugosuchus nonganensis* but is absent in other advanced neosuchians (including eusuchians). It must be noted, however, that other taxa that are not closely related also have a sagittal ridge on the dorsal surface of the frontal (e.g., *Theriosuchus pusillus*, some notosuchians).

In sum, the exploratory analysis shows that including the recently described *Isisfordia duncani* does not alter the pattern of relationships proposed in this study for advanced neosuchians. Furthermore, it underscores the relevance of the Australian taxon for understanding the early evolution of Eusuchia given that: (1) it undoubtedly represents a close relative of *Hylaeochampsa vectiana* and more derived forms and (2) its inclusion is critical for the character optimization of several important characters (e.g., choanal morphology). However, more infor-

mation on this taxon (and others such as *Rugosuchus nonganensis*) is needed to resolve the uncertainties obtained in this exploratory analysis.

SOUTH AMERICA: The most interesting and informative advanced neosuchian described from the Early Cretaceous of South America is *Susisuchus anatoceps* (Salisbury et al., 2003). This taxon is known from a single specimen found in the Nova Olinda member of the Crato Formation (Aptian) of northeastern Brazil. The holotype consists of a skull and a partly articulated postcranium preserved in a limestone slab and only exposed in dorsal view, precluding the determination of several important characters (e.g., palate morphology). However, the available skull and postcranial information suggests this taxon represents another advanced neosuchian from the Southern Hemisphere. As noted by Salisbury et al. (2003, 2006), the dorsal dermal armor of *Susisuchus anatoceps* bears several derived features absent in other neosuchians, except for eusuchians and their closest relatives (e.g., *Isisfordia duncani*, *Rugosuchus nonganensis*). First, the dorsal dermal armor is composed of four longitudinal rows of parasagittal osteoderms (i.e., tetraserial paravertebral shield sensu Salisbury et al., 2006) flanked by two rows of accessory osteoderms. Second, the dorsal paravertebral osteoderms are square, rather than rectangular (lateromedially broader than anteroposteriorly long) as in more basal neosuchians. Third, the anterolateral process of these osteoderms is straight, lacking the distinct convexity present in some advanced neosuchians (e.g., *Bernissartia fagesii*) or the well-developed articular peg of other neosuchians (e.g., goniopholids, *Theriosuchus pusillus*). The skull of *Susisuchus anatoceps* also shows several neosuchian characters, such as the absence of an antorbital fenestra and quadrate condyles located at the level of the occipital condyle (Salisbury et al., 2003).

Susisuchus anatoceps, however, seems to be more distantly related to eusuchians than *Isisfordia duncani* because of the presence of some plesiomorphic characters (Salisbury et al., 2006). Most notably, the presacral vertebrae of *Susisuchus anatoceps* are amphicoelous (Salisbury et al., 2003), instead of the

derived procoelous cervical and dorsal vertebrae of *Isisfordia duncani*, *Shamosuchus djadochtaensis*, and eusuchians. *Susisuchus anatoceps* also has a sagittal anterior projection of the frontals that separates the caudal end of the nasals (character 165.1), as in *Bernissartia fagesii*, goniopholids, and longirostrine crocodyliforms. In contrast, *Shamosuchus djadochtaensis*, *Isisfordia duncani*, and basal eusuchians (including *Hylaeochampsia vectiana* and the recently described *Iharkutosuchus makadii*; Ösi et al., 2007) have a blunt anterior end of the frontal that does not project between the nasals (character 165.0). More derived forms (e.g., crocodylians), however, also have an anterior process of the frontal wedging between the nasals (resembling the condition of *Susisuchus anatoceps* and basal neosuchians). This combination of plesiomorphic and apomorphic characters is reflected in the phylogenetic analysis of Salisbury et al. (2006), in which the Brazilian taxon was retrieved as more derived than *Bernissartia fagesii* but more basal than *Isisfordia duncani*. A preliminary analysis on the phylogenetic position of *Susisuchus anatoceps* in our dataset was conducted using a similar coding strategy as the one described above for *Isisfordia duncani*. In all of the most parsimonious trees *Susisuchus anatoceps* is more derived than *Bernissartia fagesii* (and the Glen Rose form) but more basal than *Isisfordia duncani*. In fact, *Susisuchus anatoceps* is placed as the sister taxon of a group composed by the Asian clade, *Isisfordia duncani*, and eusuchians (fig. 39). This arrangement is topologically compatible with the results of the phylogenetic study of Salisbury et al. (2006), given that *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis* were not included in their study. The inclusion of *Susisuchus anatoceps* in this exploratory analysis does not affect the proposed relationships of advanced neosuchians presented previously, although it is decisive for determining the position of *Isisfordia duncani* as the sister taxon to the Asian clade (see Final Remarks at the end of this section). As interpreted by Salisbury et al. (2006), *Susisuchus anatoceps* indeed represents a previously unknown stage in the evolutionary history of advanced neosuchians, showing a lineage with a more

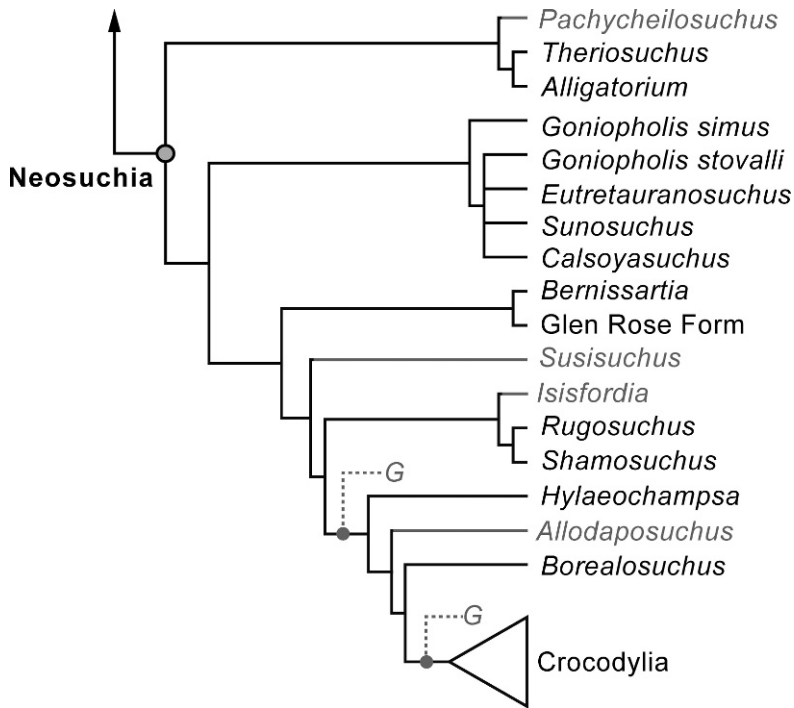


Fig. 39. Reduced strict consensus of the 39 most parsimonious trees obtained in the exploratory analysis with the addition of five taxa (highlighted in grey) that have been preliminary scored to test their positions as well as the robustness of the relationships proposed in figure 37. This analysis includes *Isisfordia duncani*, *Susisuchus anatoceps*, *Pachycheilosuchus trinquei*, *Glichristosuchus palatinus*, and *Allodaposuchus precedens*, in addition to the previously included taxa. Two of the alternative positions retrieved for *Glichristosuchus palatinus* are indicated with a dashed grey line. Other optimal positions depict this taxon nested within Crocodylia.

plesiomorphic condition than *Isisfordia duncani* and the Asian clade but more advanced than *Bernissartia fagesii*.

Another putatively relevant taxon from South America is *Dolichochampsia minima* (Gasparini and Buffetaut, 1980) from the Yacoraite Formation (Late Cretaceous), northwestern Argentina. This taxon is much more fragmentary than the two other forms mentioned above, and consequently its affinities are much harder to test. The type specimen consists of a small but extremely narrow and elongate dentary (MLP 73-II-28-16) with well-spaced everted alveoli, resembling of those of longirostrine crocodyliforms (e.g., dyrosaurids, gavialoids). Several isolated crocodyliform elements (cranial and postcranial) found at the same locality (or formation) have been referred to this taxon by Gasparini and Buffetaut (1980). The

postcranial materials include procoelous vertebrae, a feature that prompted Gasparini and Buffetaut (1980) to include *Dolichochampsia minima* within Eusuchia. Unfortunately, the available remains do not provide much information for establishing the phylogenetic relationships of *Dolichochampsia minima*. The presence of procoely is now known to occur not only in Eusuchia, but also in closely related forms (e.g., *Shamosuchus djadochtaensis*, *Isisfordia duncani*) and other neosuchians (e.g., atoposaurids). Therefore, the affinities of this form must be considered dubious pending the discovery of more complete remains.

AFRICA: The Cretaceous record of continental Africa has provided remains of three taxa with valuable information concerning the diversity and distribution of advanced neosuchians. The first of these is *Brillianceau-*

suchus babouriensis (Michard et al., 1990) from the Lower Cretaceous beds of Babouri-Figuli Basin of northern Cameroon. Although some authors have regarded this taxon as closely related to atoposaurids (Michard et al., 1990; Rogers, 2003; Salisbury et al., 2006), its remains display not only procoelous vertebrae (as *Theriosuchus*) but also lack the anterolateral articular peg on the parasagittal row of osteoderms (Salisbury and Frey, 2001) and have been interpreted as having a pterygoid bounded choanal opening (Michard et al., 1990; Brochu, 1999; Buscaglioni et al., 2001). Despite the simultaneous presence of these derived characters (the first two of which have traditionally been considered eusuchian synapomorphies), this taxon has never been thoroughly described or included in extensive phylogenetic analyses. Further study of this material is needed to understand its anatomy and thoroughly test its phylogenetic affinities.

The second taxon from the Cretaceous of continental Africa is *Stomatosuchus inermis* (Stromer, 1925) from the Bahariya Formation (Cenomanian) of Egypt. This large animal represents one of the most bizarre crocodyliforms, and is characterized by an elongate, flat, and parallel-sided rostrum and a possibly edentulous lower jaw. Most authors have considered this form as related to Eusuchia based on the presence of procoelous vertebrae and a choanal opening enclosed by the pterygoids (Stromer, 1925, 1933; Steel, 1973). The only phylogenetic analysis that has included this form supported the eusuchian affinities of *Stomatosuchus inermis* (Benton and Clark, 1988), depicting it as a noncrocodylian eusuchian (forming a polytomy with *Hylaeochampsia vectiana* and *Borealosuchus*). Unfortunately, only the original descriptions remain, as the only known specimen was destroyed during World War II. New material is needed to further understand the anatomy and relationships of this enigmatic taxon, although available information suggests affinities with advanced neosuchians (or basal eusuchians). This suggests that this "grade" was morphologically diverse and widely distributed in the Cretaceous of Gondwana. The third taxon is *Aegyptosuchus payeri* (Stromer, 1933), also found in the Bahariya Formation of Egypt.

The only known specimen is fragmentary (a skull roof with part of the occipital table; BSP 1912.VIII.177) but has fortunately been preserved in the BSP collections. This is a poor specimen and it cannot be determined whether this taxon is closely related to eusuchians or not. Several characters of the skull roof, however, resemble the condition described for *Stomatosuchus inermis*. These include the extremely reduced supratemporal fossa located anteriorly on the skull roof leaving an anteroposteriorly extensive surface of the squamosal that occupies the posterior half of the skull table, orbital openings facing dorsally and separated by a narrow bar of the frontal, dorsal surface of skull roof with a slightly developed sculpture (rather than the well-developed subcircular pits of other neosuchians), and the elongate posterolateral process of the squamosal. This combination of characters is unusual for a neosuchian crocodyliform and suggests a close affinity of *Aegyptosuchus payeri* and *Stomatosuchus inermis*, in agreement with Romer's (1956) inclusion of both taxa in the family Stomatosuchidae. The fragmentary nature of this taxon and the current lack of material of *Stomatosuchus inermis*, however, preclude resolving their affinities with certainty. Further materials from the Bahariya Formation will undoubtedly help to understand these unusual crocodyliforms.

NORTH AMERICA: The most relevant advanced neosuchian from North America is the Glen Rose form, which still needs to be described in detail, including a thorough evaluation of the postcranial material previously referred to this taxon (see above). The Cretaceous record of North America has provided other taxa that need to be considered to achieve a more complete picture on the evolution of advanced neosuchians. The first of these is *Pachycheilosuchus trinquei* described by Rogers (2003) from the Early Cretaceous Glen Rose Formation. This taxon is based on several hundred isolated crocodyliform elements collected from a single locality of the Glen Rose Formation in Texas (SMU 331; Rogers, 2003). Although these elements were not found in articulation, their referral to a single taxon seems a reasonable hypothesis based on anatomical and taphonomic bases (see Rogers, 2003).

The craniomandibular remains distinguish *Pachycheilosuchus* from the Glen Rose form based on the presence of a more dorsoventrally compressed maxilla with an expanded and unfestooned buccal margin and a more gracile dentary (Rogers, 2003). *Pachycheilosuchus trinqueti* is also a neosuchian crocodyliform but has been interpreted as closely related to atoposaurids, because of the presence of a jugal anterior ramus subequal in depth to posterior ramus and the presence of procoelous presacral vertebrae (Rogers, 2003). Furthermore, *Pachycheilosuchus trinqueti* shares with *Theriosuchus* the presence of a relatively large central pit (dimple) on the condyle of most procoelous vertebra (Rogers, 2003; Clark, 1986). The phylogenetic position of this taxon, however, is weakly supported and *Pachycheilosuchus trinqueti* shares some derived characters with neosuchians more advanced than *Theriosuchus*, such as the presence of procoelous dorsal vertebrae, a biconvex first caudal vertebra, and the absence of a well-developed articular peg in the anterolateral corner of each dorsal osteoderm. Despite the evident conflict among these characters, a preliminary scoring of *Pachycheilosuchus trinqueti* in our dataset retrieves this taxon as the sister group of Atoposauridae (fig. 39), as originally proposed by Rogers (2003). As we have not examined the specimens, these scorings have been taken from the original publication with the same coding strategy described above for *Isisfordia duncani* and *Sisisuchus anatoceps* (and therefore the results should be taken with similar caveats; see appendix 4 for these scorings).

Another relevant neosuchian from North America is *Glichristosuchus palatinus* (Wu and Brinkman, 1993) from the Milk River Formation (Santonian-Campanian) of Canada. Although this taxon is known from an incomplete small specimen (partial skull and cervical vertebra) it has been interpreted as an advanced neosuchian, purportedly more closely related to Eusuchia than *Bernissartia fagesii* (Wu and Brinkman, 1993). This interpretation is based on the presence of a unique combination of derived and plesiomorphic characters. The single cervical vertebra known for *Glichristosuchus palatinus* is procoelous, a feature known to occur (among

neosuchians) in only two groups: eusuchians and related forms (e.g., *Isisfordia duncani*, *Shamosuchus djadochtaensis*) and *Theriosuchus pusillus* and related forms (i.e., *Pachycheilosuchus trinqueti*; Clark, 1986; Salisbury and Frey, 2001; Rogers, 2003). Among the most advanced cranial features of *Glichristosuchus palatinus* is the postorbital-parietal suture extending slightly onto the skull roof, with the frontal almost reaching the anterior margin of the supratemporal fossae. This feature resembles the derived condition of some crocodylian clades (e.g., crocodylids, alligatorids) but differs from the morphology present in the most basal eusuchians and outgroups. The choanal opening of *Glichristosuchus palatinus* is unique among Crocodyliformes because of the simultaneous presence of two characters. First, it is located posterior to the caudal margin of the suborbital opening, an advanced feature present in eusuchians but not in other advanced neosuchians (including *Isisfordia duncani*, *Shamosuchus djadochtaensis*, and the Glen Rose form). Second, in contrast to the condition of eusuchians (and *Isisfordia duncani*) the pterygoids do not enclose the choana, but they form the entire lateral margin of this opening, resembling the condition in some advanced neosuchians (e.g., *Shamosuchus djadochtaensis*, *Bernissartia fagesii* [Buscalioni and Sanz, 1990], the Glen Rose form).

The simultaneous presence of these skull features in *Glichristosuchus palatinus* generates some conflict in the character-state distribution among advanced neosuchians. Therefore the proposed phylogenetic position of this taxon (Wu and Brinkman, 1993) needs to be tested within a comprehensive phylogenetic context. Although the available information on this taxon is limited because of the incompleteness of the type specimen (Wu and Brinkman, 1993) and we have not examined the specimens, a preliminary scoring of this taxon in our dataset was performed following the same coding strategy described above (see appendix 4). The exploratory analysis on the position of *Glichristosuchus palatinus* retrieves this taxon in multiple equally parsimonious positions (fig. 39). The most basal of them depicts this taxon as the sister group of *Hylaeochampsia*

vectiana and more derived crocodyliforms (e.g., *Eusuchia* sensu Brochu, 1999), being more derived than any other noneusuchian neosuchian (including *Isisfordia duncani*). Other most parsimonious trees of this exploratory analysis invariably depict *Glichristosuchus palatinus* clustered with Crocodylia (either as its sister taxon or nested within this clade; see fig. 39). The position of *Glichristosuchus palatinus* allied with eusuchians is supported (in all most parsimonious trees) by the posterior location of the rostral margin of the choanal opening with respect to the caudal border of the suborbital opening (character 44.2).

The unstable behavior of *Glichristosuchus palatinus* in the phylogenetic analysis is undoubtedly influenced by the large proportion of missing data in the scorings of this taxon (approximately 87%). However, the alternative positions retrieved for this taxon are supported by conflicting character-state distributions. For instance, the participation of the palatine in the choanal opening (character 43) supports the exclusion of *Glichristosuchus palatinus* from the clade formed by *Hylaeochampsia vectiana* and more derived forms in some trees. Alternatively, *Glichristosuchus palatinus* is nested within Crocodylia in other trees because of the presence of a postorbital-parietal contact in the supratemporal fossa (character 23). The most basal eusuchians included in this analysis (e.g., *Hylaeochampsia vectiana*, *Borealosuchus formidabilis*) and their outgroups (e.g., *Shamosuchus djadochtaensis*, the Glen Rose form) have an extensive participation of the frontal in this opening, precluding the postorbital to contact the parietal. As has been noted for many other cases dealing with incompletely known taxa, character conflict produces alternative positions for an incomplete taxon and the lack of information (i.e., missing entries) precludes resolving such conflict (Kearney, 2002).

The derived position of *Glichristosuchus palatinus* in this exploratory analysis suggests this form may play a critical role in understanding the sequence of evolutionary transformations toward the derived choanal condition of Eusuchia. Salisbury et al. (2006) had rightfully suggested, based on their phylogenetic results, that the choanal mor-

phology of *Isisfordia duncani* (enclosed by the pterygoids but located relatively anteriorly on the palate) represents an intermediate stage in the choanal evolution of eusuchians (pterygoid bounded and posteriorly located). The choanal condition of *Glichristosuchus palatinus* (posteriorly located but with a palatine participation) and its sister group relationship with Eusuchia (sensu Brochu, 1999) in some of the most parsimonious trees suggests a possible alternative scenario: a posteriorly positioned choana may have appeared before the complete enclosure of this opening by the pterygoids in the early evolution of the eusuchian lineage. Under such a scenario, the pterygoid-bounded choana of *Isisfordia duncani* must be interpreted as convergent with that of eusuchians. A detailed firsthand study of the available remains, a denser taxon sampling within Eusuchia, and more complete material of *Glichristosuchus palatinus* are needed to clarify the affinities of this taxon and to achieve a more complete understanding on the evolutionary origins of the eusuchian palate.

EUROPE: As discussed above, *Hylaeochampsia vectiana* and *Bernissartia fagesii* are the most critical taxa for understanding the origins of Eusuchia in most studies conducted during the last century. The Cretaceous record of Europe, however, has provided remains of other forms that should play an equally important role in future studies.

The first of these is *Allodaposuchus precedens*, originally known from relatively fragmentary material found in the Late Cretaceous beds of the Hateg Basin, Romania (Nopsca, 1928). A recent revision and redescription of the type material was conducted by Buscalioni et al. (2001), who also referred several more complete specimens to this taxon from the Late Cretaceous of France and Spain. The type material of *Allodaposuchus precedens* is currently restricted to a skull roof and occipital region (Buscalioni et al., 2001), whereas the rest of the original material from Romania consists of isolated postcranial remains that include several procoelous vertebrae. The material from Spain and France referred to *Allodaposuchus precedens* by Buscalioni et al. (2001) consists of five fragmentary skulls that

provide a more complete understanding of the anatomy of this taxon, including critical information to test its phylogenetic relationships (e.g., pterygoid-bounded choana located posteriorly on the palate, interdigitating occlusion of dentary teeth). Although Salisbury et al. (2006) question the taxonomic validity of this taxon as defined by Buscalioni et al. (2001), these authors noted the presence of two autapomorphic characters in the type material and the referred specimens (i.e., posterior bottom of supratemporal fossa formed by the quadrate without contribution of squamosal or parietal and extensive prefrontal contribution of the orbital margin, with the frontal restricted to the caudomedial edge of orbit).

The phylogenetic position of *Allodaposuchus precedens* was tested by Buscalioni et al. (2001) through a cladistic analysis focusing on the relationships of eusuchians, expanding the dataset published by Brochu (1997, 1999). This study retrieved *Allodaposuchus* as one of the most basal eusuchians, specifically as the sister taxon of the Crocodylia crown group (i.e., more derived than *Hylaeochampsa vectiana*). A similar result has been obtained by Delfino et al. (2005) in a slightly modified version of the same dataset and has been accepted by Brochu (2003) in a recent review of crocodylian phylogeny. Salisbury et al. (2006) also included *Allodaposuchus precedens* in their phylogenetic analysis but obtained this taxon as the sister group of *Hylaeochampsa vectiana*, whereas Ösi et al. (2007) retrieved this taxon in a trichotomy together with Crocodylia and the clade formed by *Hylaeochampsa vectiana* and *Iharkutosuchus makadai* (see below). Irrespective of these minor disagreements, the combination of characters present in the *Allodaposuchus precedens* material described by Buscalioni et al. (2001) clearly suggests a basal position within Eusuchia for this taxon. The published information on *Allodaposuchus precedens* was used to score this taxon in our dataset (following the same coding strategy described above; see appendix 4), as we have not examined these specimens. The inclusion of *Allodaposuchus precedens* in an exploratory analysis along with the other preliminary scored taxa unequivocally places this taxon as more derived than *Hylaeo-*

champsia vectiana, being the sister group of *Borealosuchus* and crocodylians (fig. 39). This position is equivalent to the results obtained by some previous authors (Buscalioni et al., 2001; Delfino et al., 2005). In addition to the evidence cited by Buscalioni et al. (2001), the derived position of *Allodaposuchus precedens* as closer to Crocodylia than *Hylaeochampsa vectiana* is supported in our exploratory analysis by the presence of lateral margins of the frontal flush with the dorsal skull surface (character 266.0). Most advanced neosuchians (e.g., the Glen Rose form, *Susisuchus anatoceps*, *Shamosuchus djadochtaensis*) and *Hylaeochampsa vectiana*, in contrast, have elevated orbital ridges on the lateral margins of the frontal. *Allodaposuchus precedens* is however excluded from the clade formed by *Borealosuchus* and more derived eusuchians because of the short extension of the paroccipital process lateral to the cranioquadrate opening (character 268.0), thus resembling the short paroccipital process of *Hylaeochampsa vectiana*, *Shamosuchus djadochtaensis*, *Isisfordia duncani*, and the Glen Rose form.

Another basal eusuchian recently described from Europe is *Iharkutosuchus makadai* (Ösi et al., 2007) found in the Late Cretaceous Csehbánya Formation of Hungary (Ösi, 2004). This taxon is highly autapomorphic, including unusual features such as the complete closure of the supratemporal fenestra, elongate posterior process of the pterygoid, and complex multicusped posterior teeth with wear facets indicating buccolingual jaw movement during occlusion. Although complex teeth and extensive wear facets have been reported in some non-neosuchian crocodyliiforms (e.g., Clark et al., 1989; Carvalho, 1994; Wu and Sues, 1996; Pol, 2003; Pol et al., 2004), the presence of such features was unknown within Neosuchia prior to the description of *Iharkutosuchus makadai*. Moreover, the multicusped teeth of this taxon differ markedly from other multicusped crocodyliiform teeth (e.g., the posteriormost teeth are flat and bear radial rows of small cusps surrounding a row of three central cusps; Ösi et al., 2007). The phylogenetic position of this taxon has been tested by Ösi et al. (2007) expanding the dataset previously used by Buscalioni et al. (2001),

which was itself based on Brochu (1997a, 1999). The results of this analysis depicted *Iharkutosuchus makadai* as the sister taxon of *Hylaeochampsia vectiana*, forming the clade Hylaeochampsidae. According to these authors several characters, including the presence of a linear frontoparietal suture, a prefrontal longer than the lacrimal, and a vertical ridge on the paroccipital process, support the monophyly of this group. We have tested the inclusion of this taxon in our dataset, performing a preliminary scoring based on the information published by Ösi et al. (2007). Unfortunately, the published description is brief and several key features cannot be scored and this taxon is depicted as unstable collapsing most nodes of advanced neosuchians and basal eusuchians (although in many of the MPTs it clusters with *Hylaeochampsia vectiana* as proposed by Ösi et al. [2007]). The uncertainty in these results will likely be solved when a more extensive description of this taxon becomes available.

Although the precise position of *Iharkutosuchus makadai* within Eusuchia should be further tested using more extensive taxon sampling, this taxon will probably become highly relevant in future studies on the relationships of advanced neosuchians and the origin of Eusuchia. First, the combination of characters described for this taxon clearly suggests strong affinities with basal eusuchians adding a new taxon known from relatively complete and abundant materials (see Ösi et al. 2007). Second, if its inclusion in Hylaeochampsidae is corroborated in future studies, the multiple skulls of *Iharkutosuchus makadai* reported by Ösi et al. (2007) would significantly increase our anatomical knowledge on this peculiar group, which has been historically pivotal for understanding the origins of eusuchians despite being known from a single fragmentary skull described by Owen (1874; the holotype of *Hylaeochampsia vectiana*). Third, the unusual craniodental features of *Iharkutosuchus makadai* broaden the known morphological and ecological diversity of advanced neosuchians.

Another neosuchian taxon from the Cretaceous of Europe that may play a critical role in future studies is the "Las Hoyas neosuchian," found in the Calizas de la Huéguina Formation (Barremian) at the

Las Hoyas locality in Spain (Ortega and Buscalioni, 1995). Although it remains undescribed, it has been discussed and included in a number of recent phylogenetic analyses. One of the most remarkable features is its derived osteoderm morphology and arrangement, including the presence of double-keeled osteoderms (Ortega and Buscalioni, 1995; Salisbury and Frey, 2001). Other skull characters suggest this form is closely related to advanced neosuchians and basal eusuchians. For instance, the choanal opening of this taxon has been scored as completely enclosed by the pterygoids but located relatively far from the posterior margin of the skull (Ortega et al., 2000; Buscalioni et al., 2001), resembling the choanal condition of *Isisfordia duncani* (Salisbury et al., 2006).

The phylogenetic position of this form has been tested in several phylogenetic analyses (Ortega et al., 2000; Buscalioni et al., 2001; Hua and Jouve, 2004; Company et al., 2005; Delfino et al., 2005). In most of these analyses the Las Hoyas neosuchian was retrieved as the sister taxon of *Hylaeochampsia vectiana* and more derived forms (i.e., Eusuchia sensu Brochu, 1999). Alternatively, the analysis of Buscalioni et al. (2001) depicted this taxon as the sister group of *Hylaeochampsia vectiana*. Despite this difference in results, a close relationship with the most basal nodes of Eusuchia has been consistently retrieved in previous studies, even in analyses based on a markedly different taxon and character-sampling schemes (e.g., Ortega et al., 2000; Company et al., 2005). Ever since its discovery the Las Hoyas neosuchian has been recognized as an important form (e.g., Ortega and Buscalioni, 1995) and a detailed description and revision of this taxon is needed. This information, added to that of the other advanced neosuchians commented above, needs to be gathered before a full understanding on the evolutionary origins of Eusuchia can be achieved.

The Cretaceous record of Europe has also provided remains of basal crocodylians that bear relevant information for understanding the origins of Eusuchia in future studies. One of these forms is *Acynodon iberoccitanus*, formerly known from an isolated maxilla (Buscalioni et al., 1997) and recently rede-

scribed based on a series of six individuals (Martin, 2007). *Acynodon iberoccitanus* was originally referred to Alligatoridae (Buscaglioni et al., 1997) and later considered a basal alligatoroid based on a phylogenetic analysis (Martin, 2007). As noted by this author, this taxon resembles in many features other short- and blunt-snouted basal globidontans (e.g., *Stangeorchamps*, *Brachychamps*, *Albertochamps*), but it also bears several plesiomorphic characters that may be relevant for understanding the evolution of some features among basal eusuchians. For instance, in *Acynodon iberoccitanus* the external mandibular fenestra is absent, the frontal enters the supratemporal fossa, and the frontal has elevated orbital ridges. These conditions occur in basal eusuchians and advanced neosuchians (e.g., *Hylaeochamps vectiana*, *Iharkutosuchus makadii*, *Shamosuchus djadochtaensis*, *Rugosuchus nonganensis*, *Bernisartia fagesii*, the Glen Rose form) but also are present in some basal gavialoids and/or alligatoroids (as well as some species of *Borelaosuchus*). Additionally, the absence of premaxilla-maxillary notch and the flared anterior half of the palatine bar is present in *A. iberoccitanus* (and alligatorids) and in basal eusuchians and some advanced neosuchians (e.g., *Iharkutosuchus makadii*, *Isisfordia duncani*, *Shamosuchus djadochtaensis*).

The presence of these plesiomorphic characters in *Acynodon iberoccitanus* suggests it may play an important role in future studies of eusuchian origins. At the very least, this and other basal crocodylians are relevant because they can affect the character optimizations and influence evaluations of alternative hypotheses of relationships among basal eusuchians and advanced neosuchians. On the other hand, the numerous plesiomorphies and the evident character conflict in the distribution of these characters suggest the need of a more extensive evaluation on the relationships of this taxon and other basal forms of Crocodylia.

ASIA: *Rugosuchus nonganensis* and *Shamosuchus djadochtaensis* are, as shown in this contribution, critical forms for understanding the relationships of advanced neosuchians and the origins of Eusuchia. Current knowledge on the cranial anatomy of these two forms is relatively complete, although more

complete postcranial remains of *Shamosuchus djadochtaensis* are needed to define some relevant characters related to vertebral and osteoderm morphology. The postcranial anatomy of *Rugosuchus nonganensis* will also offer important information, as noted by Wu et al. (2001a: 1660). Other forms from the Cretaceous of Asia, however, are still less studied and often ignored in recent phylogenetic approaches to the relationships of advanced neosuchians, despite their importance in understanding the relationships of neosuchians. Among these, the most significant materials are the abundant remains referred to different species of *Shamosuchus* found in Late Cretaceous beds of Mongolia and Uzbekistan (Efimov, 1988). Storrs and Efimov (2000) noted that some of the 10 species described for *Shamosuchus* might be synonymous, although some of them differ markedly with respect to the remains of *Shamosuchus djadochtaensis* described here. In particular, *Shamosuchus gradiliformis* (Konzhukova, 1954) and *Shamosuchus tersus* (Efimov, 1983) are known from almost complete skulls (holotypes) that have a much longer and platyrostral snout compared to the specimen described here. Other remains can provide useful phylogenetic information because of the association of almost complete skulls with articulated postcranial remains, such as *Shamosuchus ulgicus* (Efimov, 1988; Storrs and Efimov, 2000), that shows a posteriorly placed choanal opening in combination with an osteoderm shield arranged in more than two parasagittal rows. A detailed revision of these materials is needed to achieve a solid alpha taxonomy. This will not only provide a more complete understanding of the diversity of advanced neosuchians from the Late Cretaceous of Central Asia, but will also form the basis for evaluating their evolutionary relationships and impact on the phylogeny of advanced neosuchians.

FINAL REMARKS: The overview presented in this section aims to acknowledge a number of taxa that bear relevant information for assessing the relationships of advanced neosuchians and the origin of Eusuchia. Several points are made here. First, many advanced neosuchians with eusuchian affinities have been published during the last six years (e.g.,

Rugosuchus nonganensis, *Susisuchus anatoceps*, *Pachycheilosuchus trinquei*, *Isisfordia duncani*, *Iharkutosuchus makadii*). These taxa are represented by well-preserved material and, along with some forms yet to be formally described (e.g., Las Hoyas neosuchian, the Glen Rose form), increase our knowledge on the diversity of advanced neosuchians. Their information undoubtedly helps to broaden previous discussions about the evolutionary origins of Eusuchia, which have traditionally been centered on the information provided by a few key taxa (e.g., *Hylaeochampsa vectiana*, *Bernissartia fagesii*, *Theriosuchus pusillus*). Second, adding the new records to previously known specimens, even if represented by fragmentary remains (e.g., *Aegyptosuchus payeri*, *Dolichochampsa minima*), results in a remarkably widespread distribution of advanced neosuchians during the Cretaceous. Except for Antarctica, advanced neosuchians have been found on all major continental landmasses. As previously noted by Salisbury et al. (2006) such a broad distribution of advanced neosuchians argues against the hypothesis of Laurasian origins of Eusuchia, suggesting that hypotheses of ancestral areas for this group should be taken with caution. Third, although most advanced neosuchians are relatively similar in terms of body size and general morphological features, there are cases of extensive morphological disparity. These include the recently described *Iharkutosuchus makadii* with multicusped teeth and presumably herbivorous diet (Ösi et al., 2007) and the gigantic *Stomatosuchus inermis* with a toothless mandible (Stromer, 1925). Such cases suggest advanced neosuchians (and early eusuchians) could have been among the most ecologically diverse groups of crocodyli-formes (probably rivaled only by notosuchians in their morphological disparity).

In relation to the extended exploratory phylogenetic analysis presented in this section, several conclusions can be drawn. Five of the taxa listed above were preliminarily scored in our datasets: *Isisfordia duncani*, *Susisuchus anatoceps*, *Glichristosuchus palatinus*, *Pachycheilosuchus trinquei*, and *Allodaposuchus precedens*. The first objective of this analysis was to test to determine whether their inclusion affects the relative position of

other advanced neosuchians. The results show that the basic topology presented in the previous section (fig. 37) is maintained in the exploratory analysis, depicting the Asian clade (*Shamosuchus* + *Rugosuchus nonganensis*) as closer to Eusuchia (*Hylaeochampsa vectiana* and more derived forms) than the clade composed by *Bernissartia fagesii* and the Glen Rose form. None of the five additional included taxa alter this basic result. This indicates that, within the context of this dataset, this topology is robust despite the relatively low values of branch support.

The second objective was to preliminarily test the phylogenetic relationships of these five neosuchian taxa. In general terms, the results of the exploratory analysis retrieved topologies that are highly congruent with previous hypotheses on the position of these five taxa (fig. 39). *Pachycheilosuchus trinquei* was retrieved as the sister group of atoposaurids, as interpreted by Rogers (2003). *Susisuchus anatoceps* and *Isisfordia duncani* are depicted as successively more closely related to *Hylaeochampsa vectiana* and eusuchians than *Bernissartia fagesii*, as interpreted by Salisbury et al. (2006). *Glichristosuchus palatinus* is similarly depicted as closer to eusuchians than *Bernissartia fagesii*, in agreement with the hypothesis presented by Wu and Brinkman (1993) and *Allodaposuchus precedens* is retrieved as closer to crocodylians than *Hylaeochampsa vectiana* as in Buscalioni et al. (2001). This consistency of results was not expected given that our dataset differs in terms of taxon and character sampling with respect to the various datasets used in previous studies of the relationships of these five taxa. However, it should be noted that the scorings of these five taxa in our dataset were based on the descriptions and datasets of previous authors, hence following their interpretations.

Within the context of our dataset, the phylogenetic placement of the five added neosuchians is relatively stable to variations in the taxon sampling scheme: they are retrieved in the same position irrespective of the inclusion or exclusion of the other added taxa. The only exception occurs for *Susisuchus anatoceps* and *Isisfordia duncani*, which vary their position when they are not simultaneously included. When *Susisuchus*

anatoceps is not included in the analysis *Isisfordia duncani* is retrieved in two alternative positions (see fig. 38), whereas only one of these positions is obtained for the Australian taxon when *Susisuchus anatoceps* is included in the dataset (see fig. 39). Conversely, *Susisuchus anatoceps* is allied with *Hylaeochampsia vectiana* and crocodylians when *Isisfordia duncani* is excluded from the analysis but occupies a more basal position if the latter is included (fig. 39). Irrespective of these caveats, the results of the exploratory analysis provides novel phylogenetic information, such as the relative position of these five taxa and other neosuchian crocodylians, most of which had never been simultaneously included in a cladistic study. For instance, the position of *Isisfordia duncani* and *Susisuchus anatoceps* relative to the Asian clade or *Glichristosuchus palatinus* (see fig. 39) had not been tested in previous studies (e.g., Wu and Brinkman, 1993; Salisbury et al., 2006).

In addition to a more thorough study of the relationships of these advanced neosuchians and basal eusuchians, future analyses should aim to expand the taxon sampling to include other taxa that bear critical information for understanding the origins of Eusuchia. A critical point will be the addition of more basal representatives of the major crocodylians clades, as our analysis has a reduced sampling on these taxa in comparison with other studies (e.g., Brochu 1997a, 1999, 2004). As noted above, several conflictive character-state distributions are present among these forms (see discussion of *Acynodon iberoccitanus*), which need to be tested by character congruence in a phylogenetic analysis within an extensive character and taxon sampling regime. Progress here will help to clarify critical issues concerning the relationships of advanced neosuchians and to achieve a more complete picture on the evolution of important features among advanced neosuchians and basal eusuchians.

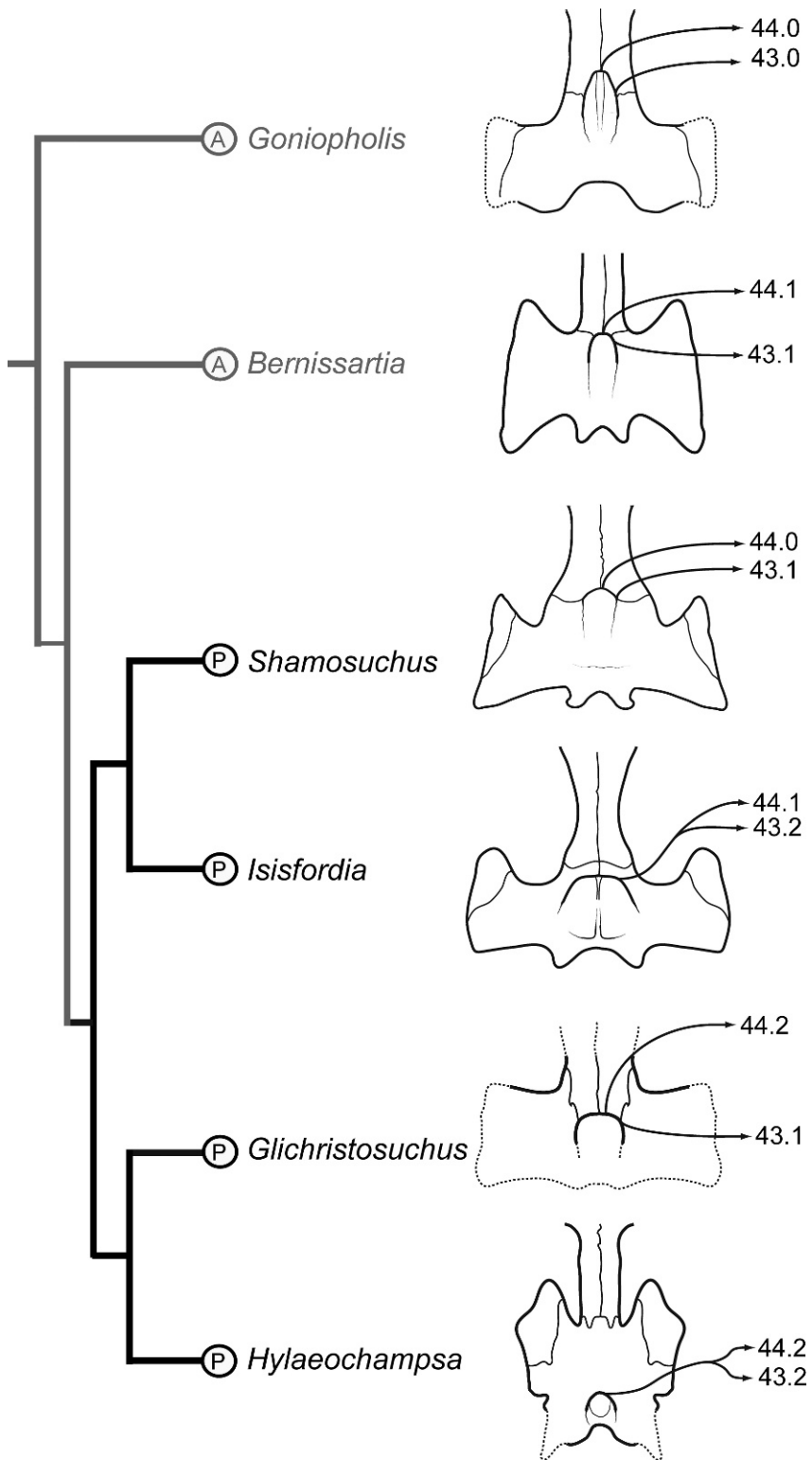
SHAMOSUCHUS AND THE EVOLUTIONARY ORIGINS OF EUSUCHIA

Eusuchia has likely been the most stable and widely recognized group of crocodylians since the original classification scheme

provided by Huxley (1875). Unlike the other major groups of Crocodyliformes (e.g., Protosuchia, Mesosuchia, Metamesosuchia, Metasuchia), eusuchian monophyly has never been seriously questioned, either in traditional or cladistic analyses. As originally conceived, this group was diagnosed by the presence of two key characters: the procoelous vertebrae and the choanal opening completely enclosed by the pterygoids. Although the origins of this clade and its relationships with other crocodylians have never been thoroughly understood, a clear morphological gap existed between eusuchians and other fossil forms (i.e., “mesosuchians”). Two taxa from the Early Cretaceous of Europe have long been considered key for understanding the origin of Eusuchia, representing the condition at both ends of this gap: *Bernissartia fagesii* (Dollo, 1883) and *Hylaeochampsia vectiana* (Owen, 1874). As noted above most authors consider *Bernissartia fagesii* as an advanced neosuchian more closely related to Eusuchia than to other neosuchians (e.g., goniopholid, atoposaurids), whereas *Hylaeochampsia vectiana* has been considered as the earliest and most basal eusuchian (Steel, 1973; Buffetaut, 1975; Clark, 1986; Benton and Clark, 1988; Clark and Norell, 1992). This morphological gap between Eusuchia and other neosuchians has been partly filled through the discovery of several Cretaceous fossils during the last few decades (see above). The new specimen of *Shamosuchus djadochtaensis* provides novel anatomical information that further contributes to our knowledge of this gap.

Although we consider premature the postulation of a robust and comprehensive scenario for the evolutionary origins of Eusuchia given the incomplete taxon sampling of our analysis (see previous section), the new information and the phylogenetic analyses presented here highlight two relevant issues that deserve further comments: (1) choanal and procoely evolution and (2) ghost lineages among advanced neosuchians.

CHOANAL AND PROCOELY EVOLUTION: The new material of *Shamosuchus djadochtaensis* has a previously unknown combination of characters for a eusuchian close relative: the presence of derived procoelous presacral vertebrae in combination with two



plesiomorphic characters—amphicoelous caudal vertebrae and a secondary palate anteriorly located and bounded by the palatines and pterygoids. This combination of characters, added to the phylogenetic analysis presented above, provides new insights into the evolution of the two characters that have traditionally characterized Eusuchia.

The evolution of the choana in Crocodyliformes had traditionally been postulated as one of the most remarkable examples of gradual change across the evolutionary history of a major group. This classic scenario portrays a gradual shift of the location of the choanal opening from an anterior position in basal forms to a posterior placement in modern crocodyliforms. Within this hypothesis the progressive shift in the position of the choana is reflected in the architecture of different palatal bones forming the anterior margin of this opening, which defined three evolutionary grades: the protosuchian condition (anterior margin bordered by maxillae), the mesosuchian condition (anterior margin formed by palatines), and the eusuchian condition (anterior margin formed by pterygoids).

Several authors have pointed to the presence of parallel trends toward a posteriorly located choana in addition to the one present in the lineage leading to extant crocodyliforms. Such cases have been noted to occur among basal crocodyliforms (e.g., *Zosuchus*; Pol and Norell, 2004a), basal mesoeucrocodylians (e.g., *Iberosuchus*; Ortega et al., 2000, and *Mahajangasuchus*;

Turner and Buckley, 2008), and dyrosaurids (Jouve et al., 2006). Thus, the progressive nature of choanal evolution within the entire diversity of Crocodyliformes had already been questioned. The evolutionary pattern within advanced neosuchians was however, up to now, free of homoplasy. The new information provided by *Shamosuchus djadochtaensis* (and *Rugosuchus nonganensis*) combined with the derived position of the Asian clade as closer to *Hylaeochampsia vectiana* and more derived forms than *Bernissartia fagesii* and the Glen Rose form introduces some homoplasy in the optimization of choanal morphology among advanced neosuchians.

Early changes are inferred to occur in the choana of advanced neosuchians reflected in the relatively posterior position of this opening (i.e., at the posterior margin of the suborbital fenestra; character 44.1) and the pterygoids forming the entire lateral margin of the choana (character 43.1; see fig. 40). Examples of this primitive condition are present in *Bernissartia fagesii* (Buscalioni and Sanz, 1990) and the Glen Rose form. Although eusuchians extend this trend by having an even more posteriorly positioned choana completely enclosed by the pterygoids (fig. 40), the choanal morphology of the Asian clade implies a reversal to the plesiomorphic position of the anterior margin of the choanal opening present in most other mesoeucrocodylians (fig. 40). The degree of pterygoid participation from the lateral margin of the choana, however, does

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Fig. 40. Simplified cladogram of advanced neosuchians showing the decoupled nature of the evolution of choanal and vertebral condition previously considered diagnostic of Eusuchia (based on the extended exploratory phylogenetic analysis discussed in the text). Only six selected taxa are shown in this tree representing the different combinations of character states among advanced neosuchians. The most parsimonious optimization of presacral vertebral morphology is shown in the cladogram. Grey lines indicate the plesiomorphic amphicoelous vertebrae (denoted with an A) and black lines represent the derived procoelous condition (denoted with a P). The vertebrae of *Hylaeochampsia* are unknown but the procoelous condition is marked for this figure representing the morphology known in all other eusuchians. Schematic drawings for the choanal morphology of selected taxa are shown to the right of the cladogram, with arrows indicating the condition of the two choanal characters discussed in the text (characters 43 and 44; see appendix 1 for character-state definitions). *Goniopholis* is based on *G. simus* (BMNH 41098), *Bernissartia* modified from Buscalioni and Sanz (1990), *Shamosuchus* based on *S. djadochtaensis* (IGM 100/1195), *Isisfordia* modified from Salisbury et al. (2006), *Glichristosuchus* modified from Wu and Brinkman (1993), *Hylaeochampsia* modified from Clark and Norell (1992), with pterygoid process reconstructed based on *Iharkutosuchus makadai* (Ösi et al., 2007). Images not to scale.

not show such a reversal in the Asian clade, maintaining its extensive participation from this edge of the opening. Thus, the choanal morphology of both *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis* shows the phylogenetic history of the neosuchian choana was more complicated than ordinarily supposed, as anticipated by Langston (1973). The eusuchian choana (both posteriorly located and pterygoid bounded), however, still seems to be diagnostic of *Hylaeochampsia* and more derived neosuchians, although the pterygoid bounded choanal opening of *Isisfordia duncani* may have been acquired independently. The palatine participation in the choanal opening of *Glichristosuchus palatinus* and its derived position in the tree (see fig. 39) add additional homoplasy to the choanal evolution in Neosuchia (fig. 40).

The presence of procoelous vertebrae has also traditionally characterized Eusuchia, although this feature had been noted to recurrently appear in other crocodyliforms, such as atoposaurids (Buffetaut, 1975; Clark, 1986; Salisbury and Frey, 2001; Rogers, 2003), basal mesoeucrocodylians (Clark, 1985), and basal crocodylomorphs (Clark et al., 2004). The presence of this character among advanced neosuchians has been considered exclusive of Eusuchia, despite the debated presence of an incipient procoely in some vertebrae of *Bernissartia fagesii* (e.g., Buffetaut, 1975; Buscalioni and Sanz, 1990; Norell and Clark, 1990; Salisbury and Frey, 2001). The new information provided by *Shamosuchus djadochtaensis* suggests procoelous presacral vertebrae had appeared before the origin of Eusuchia in the evolution of advanced neosuchians (fig. 40). This feature may have an even earlier appearance than currently optimized if the debated procoelous condition seen in both *Bernissartia fagesii* and the Glen Rose form are confirmed in future studies. The simultaneous presence of procoelous presacral vertebrae and amphicoelous caudal vertebrae in *Shamosuchus djadochtaensis* also suggests that the evolutionary origin of procoely had progressively appeared craniocaudally, which is reflected in the different degrees of procoely recorded among extant crocodylians (Salisbury and Frey, 2001). The presence of such craniocau-

dal trend may not be exclusive of Eusuchia and its closest relative, as a differential degree of procoely has also been noted in *Pachycheilosuchus trinqueti* (Rogers, 2003), which presumably has independently acquired the procoelous condition.

The new information and the phylogenetic results imply the traditional diagnostic choanal and vertebral conditions of Eusuchia appeared at different times during the evolutionary history of advanced neosuchians (fig. 40). The eusuchian-type palate is still a synapomorphy of this clade, but the procoelous presacral vertebrae diagnose a broader group. The decoupling of the evolutionary history of these two features is hardly unexpected, as has been proposed in early cladistic studies of this group (Benton and Clark, 1988; Norell and Clark, 1990; Wu and Brinkman, 1993) and has been predicted by previous authors (Lydeker, 1887; Buffetaut, 1975). The decoupled evolution of these two conditions, however, contrasts with the results of the most recent review of the evolutionary history of Eusuchia (Salisbury et al., 2006), which postulated the appearance of both conditions at the same node in the tree.

This new interpretation on the evolution of the choanal and vertebral morphology has bearings on the three alternative definitions of Eusuchia that have been defended in recent years. The first of them restricted the name to those forms with a pterygoid bounded choanal opening (Benton and Clark, 1988; Clark and Norell, 1992), given that the Glen Rose form was then considered to have procoelous vertebrae. The second proposal was offered by Brochu (1999), who argued for a node-based definition of Eusuchia, as the clade that includes the last common ancestor of *Hylaeochampsia vectiana* and Crocodylia. The choice of *Hylaeochampsia vectiana* as the anchor or specifier taxon made by Brochu (1999) was based on the fact that this form has been considered the most primitive eusuchian by most authors (Owen, 1874; Huene, 1933; Clark and Norell, 1992). Brochu (1999) discussed the convenience of using a node-based definition given that apomorphy-based definitions can be problematic when further studies reveal homoplastic instances of the chosen charac-

ter within the group of interest (Rowe and Gauthier, 1992; Bryant, 1994; Holtz, 1996). This position was echoed by Buscalioni et al. (2001), given the presence of conflicting characters and missing data throughout the evolution of neosuchian taxa that conform the stem group of Crocodylia, including the pterygoidean choana, procoely, and dorsal armor. More recently, Salisbury et al. (2006) obtained in their phylogenetic analysis both procoely and the pterygoid-bounded choana as synapomorphic features of the same node. This resulted, in part, because of their simultaneous presence in *Isisfordia duncani* (and because the procoely of the Glen Rose form was no longer accepted). This result led these authors to argue for an apomorphy-based definition based on the simultaneous presence of the two characters, based on the historical (Huxley, 1875) and biomechanical (Salisbury and Frey, 2001) significance attached to these features.

The disparity of the choanal and vertebral optimization in our phylogenetic analysis poses some problems to the apomorphy-based definitions. The decoupled evolution of both diagnostic features is a minor part of the problem and only applies to the definition proposed by Salisbury et al. (2006). The most important problem is the homoplasy involved in the posterior migration of the choanal opening and the participation of the pterygoids from the anterior margin of this opening. These homoplastic patterns coupled with the alternative positions of some taxa in our exploratory analyses suggest the optimization of these features is still unstable. For instance, the pterygoid-bounded choana of *Isisfordia duncani* is depicted as a convergence in some trees and the participation of the palatines from the anterior margin of the choana in *Glichristosuchus palatinus* requires a reversal to the plesiomorphic state in trees that depict this taxon as more derived than *Hylaeochampsia vectiana*. These issues are not likely to be completely solved in the near future given the fragmentary nature of some specimens and the presence of so much character conflict among advanced neosuchians. Therefore, we consider the use of an apomorphy-based definition of Eusuchia premature, as the relationships of its most basal members and

outgroups are not sufficiently well established to produce relatively stable optimizations in the relevant characters.

GHOST LINEAGES AMONG ADVANCED NEOSUCHIANS: In addition to the changes in the traditional diagnosis of Eusuchia, the Laurasian origin of this clade (Salisbury et al., 2006) has also been challenged. Historically, the best-known advanced neosuchians (atoposaurids, goniopholidids, *Bernissartia fagesii*) and basal eusuchians (*Hylaeochampsia vectiana*) have been found in Early Cretaceous (or Late Jurassic) beds of Europe and North America. This distribution suggested a Laurasian diversification of advanced neosuchians and basal eusuchians (Sill, 1968). Salisbury et al. (2006) have recently argued that the biogeographic origins of Eusuchia are ambiguous, postulating either eastern Gondwana (Australia) or Laurasia (western Europe) as equally likely candidates for an ancestral area. They noted, however, that the close phylogenetic relationship of *Susisuchus anatoceps* and *Isisfordia duncani* with eusuchians might be cited as evidence supporting a Gondwanan placement for the transition from Neosuchia to Eusuchia.

The increased taxon sampling of our phylogenetic analysis and the review of the distribution and diversity of advanced neosuchians (see above) allow a critical revision of this issue. In particular, combining the geographic distribution of advanced neosuchians with their chronostratigraphic information provides interesting insight into this problem.

Advanced neosuchians first appear in the fossil record by the Aptian (approximately 112–125 mya; Early Cretaceous), although this date may extend back to the Barremian (approximately 125–130 mya) based on the age of Las Hoyas neosuchian as well as on the new palynological data of the Bernissart beds in which *Bernissartia fagesii* was found (Yans et al., 2005). By the end of the Early Cretaceous, advanced neosuchians are present in virtually all major landmasses. This widespread distribution coupled with their striking morphological disparity suggests a significant part of their evolution may have occurred well before their first appearance in the fossil record. A calibration of our phylogenetic tree with the chronostrati-

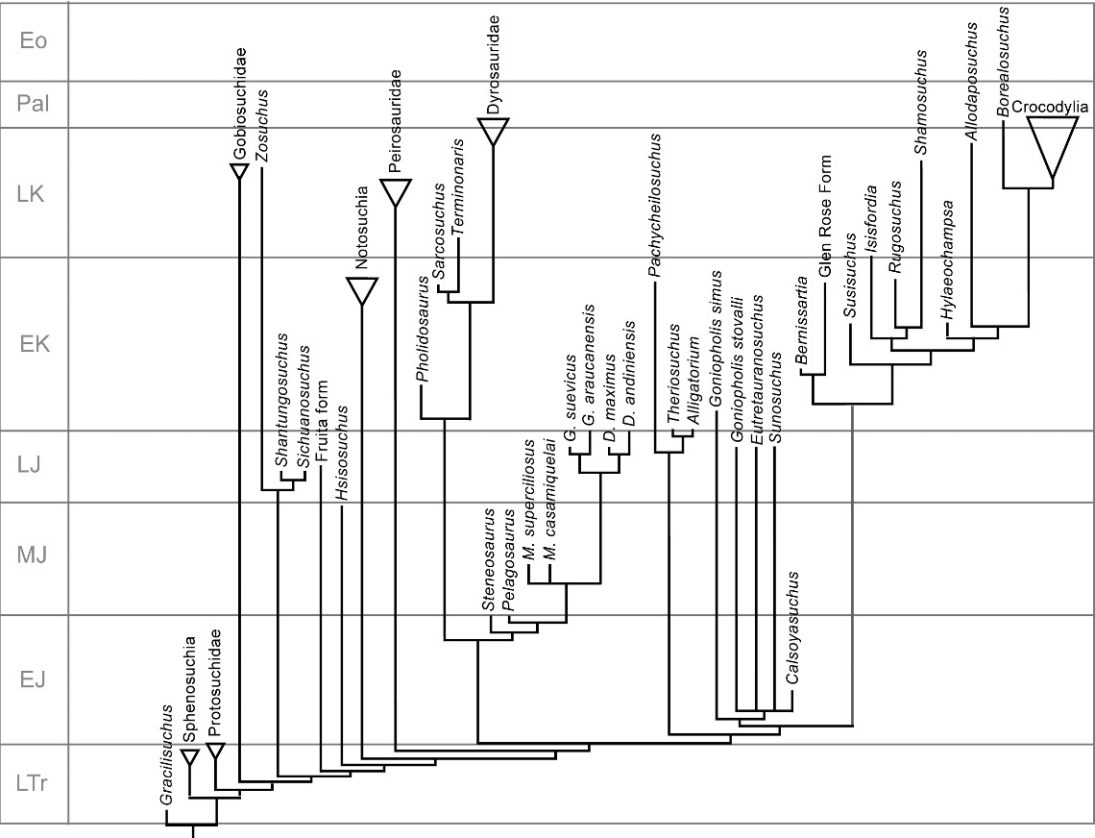


Fig. 41. Phylogeny of Crocodyliformes calibrated against geological time. The solid grey line highlights the presence of an extensive ghost lineage that trace the origins of advanced neosuchians back to the Early Jurassic. This extension implies a long unknown period in their history that predates their first appearance by more than 50 million years. Such a remote origin, coupled with the worldwide distribution of the group can be indicative of an initial diversification prior to the effective separation of the major continental landmasses.

graphic information of the fossil taxa lends support to this interpretation (fig. 41). In particular, the recent discovery of the goniopholid *Calsoyasuchus vallicept* in the Early Jurassic Kayenta Formation (Tykoski et al., 2002) has important consequences for this issue. Although the ages of most previously known neosuchians are either Late Jurassic or Early Cretaceous (e.g., *Theriosuchus*, *Goniopholis*, *Eutretauranosuchus*), the early occurrence of *Calsoyasuchus vallicept* (Sinemurian-Pliensbachian; approximately 183–190 mya) places a minimum age of origin for the lineage leading to advanced neosuchians more than 50 million years before their first appearance in the fossil record. This yet unknown significant part of the early

evolutionary history of advanced neosuchians may explain their morphological disparity and worldwide distribution by the Early Cretaceous (as some of their major lineages could have diversified before the effective isolation of some regions caused by the breakup of Pangea).

An Early Jurassic origin of the advanced neosuchian lineage, however, does not necessarily mean all their groups had diversified by that time. Therefore, the origin and diversification of Eusuchia may still have taken place in the Early Cretaceous, as traditionally thought. It is interesting to note that all the noncrocodylian eusuchians included in our phylogenetic analysis are forms from the northern hemisphere, particularly in

the Early Cretaceous of Europe. Even in our extended phylogenetic analysis the added taxa that fall within Eusuchia are Laurasian forms (e.g., *Glichristosuchus palatinus*, *Allo-daposuchus precedens*), as well as other taxa proposed as basal eusuchians (e.g., *Iharkutosuchus makadii*, Las Hoyas neosuchian). Thus, the analyzed data still seems to indicate the origin and diversification of Eusuchia was a strictly Laurasian event. Despite this result, we agree with Buscalioni et al. (2001) and Salisbury et al. (2006) in that the Laurasian origin of Eusuchia can only be seriously proposed after the phylogenetic relationships of several southern taxa are better understood (e.g., *Stomatosuchus inermis*, *Brillan-ceosuchus babouriensis*, *Dolichochampsia minima*). At any rate, even if Eusuchia turns out to be distributed worldwide, its diversity and abundance in Cretaceous beds of the Northern Hemisphere seem to be much higher than in Gondwana.

CONCLUSIONS

The new specimen of *Shamosuchus djadochtaensis* from the Late Cretaceous Djadokhta Formation of Mongolia allows for a proper apomorphy-based diagnosis of this taxon and offers new information to explore its phylogenetic relationships. With respect to previous studies of crocodyliform systematics, the phylogenetic analysis presented in this contribution improves both the taxon and character sampling relevant to neosuchian crocodyliforms. *Shamosuchus djadochtaensis* was found to be a close sister group to Eusuchia, and in conjunction with a detailed global review of relevant advanced neosuchians resulted in: (1) the discovery of a novel clade of Asian neosuchians comprised of *Shamosuchus djadochtaensis* and *Rugosuchus nonganensis*; (2) a more basal position relative to Eusuchia for *Bernissartia fagesii* and the Glen Rose Form than previously thought; (3) the postulation of a decoupled evolutionary history between procoely and the eusuchian-type palate—historically considered “key” features of Eusuchia; and (4) the understanding that advanced neosuchians achieved a worldwide distribution and a remarkable morphological diversity early in the clade’s

history with their evolutionary origins likely extending back to the Jurassic.

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APPENDIX 1

CHARACTER LIST CORRESPONDING TO DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Character list of the data matrix used in the phylogenetic analysis. The character list is adapted from Pol and Gasparini (2009), which in turn is based on Pol and Norell (2004a, 2004b), Pol and Apesteguia (2005), and includes characters from Turner (2006) and Brochu (1999). 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 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 number of the original publication. Characters 1, 3, 6, 10, 23, 37, 43, 44, 45, 49, 65, 67, 69, 73, 77, 79, 86, 90, 91, 96, 97, 104, 105, 106, 108, 126, 142, 143, 149, 167, 182, 197, 226 represent nested sets of homologies and/or entail present and absence information. These characters were set as additive (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), or 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 (i.e. posterodorsal process of the premaxilla overlaps anterodorsal surface of the 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 (modified from Clark, 1994: char. 10): + Posterior palatal branches of maxillae anterior to

palatines: do not meet (0), or meet extensively but posteriormost parts fail to meet (1), or meet entirely (2).

- 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), or 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 unsulpted (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 if sculpture present (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): 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, narrower than palatine bar (0), or wider than palatine bar (1).
- Character 43 (modified from Clark, 1994: char. 43): + Primary pterygoidean palate: forms posterior half of the choanal opening (0), or forms posterior, lateral, and part of the anterior margin of the choana (1), or completely enclose choana (2).
- Character 44 (modified from Pol and Norell, 2004a; Clark, 1994: char. 44): + Anterior edge of choanae situated between the suborbital fenestra (or anteriorly) (0), situated near the posterior edge of suborbital fenestra (1), or posterior to the suborbital fenestra (reaching in some cases the edge of pterygoid flange) (2).
- 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 (Modified from 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 lateral to the passage with otoccipital contacting the quadrate lateral to the posterior opening of 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 dorso-ventrally 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 bilateral 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 paroc-

- cipital 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): + Palpebrals: absent (0), or one small palpebral present in orbit (1), or one large palpebral (2), or two large palpebrals (3).
- 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), partly 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. 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 tooth row (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 contacting the ilium but partially excluded from the acetabulum by the anterior process of the ischium (1), or pubis completely excluded from the acetabulum by the anterior process of the ischium (2).
- 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 amphiplatyan (0), or procoelous (1).

- Character 93 (Clark, 1994: char. 93): Trunk vertebrae: amphicoelous or amphiplatyan (0), or procoelous (1).
- Character 94 (Modified from Clark, 1994: char. 94): First caudal vertebrae: amphicoelous or amphiplatyan (0), biconvex (1), or opisthocoelous (2), or procoelous (3).
- Character 95 (Clark, 1994: char. 95): Dorsal osteoderms: rounded or ovate (0), or rectangular, broader than long (1), or square (2), or rectangular, longer than broad (3).
- Character 96 (modified from Clark, 1994: char. 96; 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. 17): Mandibular symphysis in lateral view: shallow and tapering anteriorly (0), deep and tapering anteriorly (1), deep and anteriorly convex (2), or shallow and anteriorly convex (3).
- Character 104 (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 105 (modified from Wu and Sues, 1996: char. 24; Wu et al., 1997: char. 124): + Jaw joint: placed at level with basioccipital condyle (0), below basioccipital condyle about above level of lower tooth row (1), or below level of tooth row (2).
- Character 106 (modified from Wu and Sues, 1996: char. 27; Ortega et al., 2000: char. 133): + Premaxillary teeth: five (0), four (1), three (2), or two (3).
- Character 107 (modified from Wu and Sues, 1996: char. 29): Unsculptured region along alveolar margin on lateral surface of maxilla: absent (0), or present (1).
- Character 108 (Wu and Sues, 1996: char. 30): + Maxilla: with eight or more teeth (0), seven (1), six (2), five (3), or four teeth (1).
- Character 109 (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 110 (Wu and Sues, 1996: char. 40): Radiale and ulnare: short and massive (0), or elongate (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 proximolaterally than proximomedially (1).
- Character 118 (Ortega et al., 1996: char. 5): Lateral surface of the anterior region of surangular and posterior region of 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; 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; 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 extending anteriorly 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-lacrima contact: partly 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 to absent (1).
- Character 134 (Pol, 1999a: char. 148): Posterior process of ectopterygoid: developed (0), or reduced to absent (1).
- Character 135 (Pol, 1999a: char. 149; 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 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; 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 (modified from Pol, 1999a: char. 156): + Base of postorbital process of jugal: directed posterodorsally (0), or dorsally (1), or anterodorsally (2).
- 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; 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; 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 transversally 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 (Buckley and Brochu, 1999: char. 102): Surangular forms only the lateral wall of glenoid fossa (0) or forms approximately one-third of the glenoid fossa (1).
- Character 157 (Buckley and Brochu, 1999: char. 102): Anterior margin of femur linear (0), or bears flange for coccygeofemoralis musculature (1).
- Character 158 (modified from Buckley and Brochu, 1999: char. 105): Dentary smooth lateral to seventh alveolus (0), or with lateral concavity for the reception of the enlarged maxillary tooth (1).
- Character 159 (modified from Ortega et al., 1996: char. 1; Buckley and Brochu, 1999: char. 107): Dorsal edge of dentary slightly concave or straight and subparallel to the longitudinal axis of skull (0), straight with an abrupt dorsal expansion, being straight posteriorly (1), with a single dorsal expansion and concave posterior to this (2), or sinusoidal, with two concave waves (3).
- Character 160 (modified from Ortega et al., 1996: char. 2; Buckley and Brochu, 1999: char. 108): Dentary compression and lateroventral surface

- anterior to mandibular fenestra: compressed and vertical (0), or not compressed and convex (1).
- Character 161 (Ortega et al., 1996: char. 7; Buckley and Brochu, 1999: char. 110): Splenial: thin posterior to symphysis (0), or splenial robust dorsally posterior to symphysis (1).
- Character 162 (Ortega et al., 1996: char. 13; Buckley et al., 2000: char. 117): Cheek teeth: not constricted at base of crown (0), or constricted (1).
- Character 163 (Ortega et al., 2000: char. 10): Ventral edge of premaxilla located: at the same height that ventral edge of maxilla (0), or located deeper, with the dorsal contour of anterior part of dentary strongly concave (1).
- Character 164 (modified from Ortega et al., 2000: char. 19): Maxillary dental implantation: teeth in isolated alveoli (0), or located on a dental groove (1).
- Character 165 (Ortega et al., 2000: char. 24): Caudal tip of nasals: converge at sagittal plane (0), or caudally separated by anterior sagittal projection of frontals (1).
- Character 166 (Ortega et al., 2000: char. 33): Relative length between squamosal and postorbital: squamosal is longer (0), or postorbital is longer (1).
- Character 167 (modified from Ortega et al., 2000: character 34): + Jugal portion of postorbital bar: flushes with lateral surface of jugal (0), anteriorly continuous but posteriorly inset (1), or medially displaced and a ridge separates postorbital bar from lateral surface of jugal (2).
- Character 168 (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 169 (Ortega et al., 2000: char. 47): Quadratojugal spine at caudal margin of infratemporal fenestra: absent (0), or present (1).
- Character 170 (modified from Ortega et al., 2000: char. 53): Quadrate condyles with poorly developed intercondylar groove (0), or medial condyle expands ventrally, separated from the lateral condyle by a deep intercondylar groove (1).
- Character 171 (Ortega et al., 2000: char. 62): Exposure of supraoccipital in skull roof: absent (0), or present (1).
- Character 172 (Ortega et al., 2000: char. 70): Nasal participation in antorbital fenestra: yes (0), or no (1).
- Character 173 (Ortega et al., 2000: char. 75): Anterior opening of temporo-orbital in dorsal view exposed (0), or hidden in dorsal view and overlapped by squamosal rim of supratemporal fossa (1).
- Character 174 (Ortega et al., 2000: char. 90): Foramen intramandibularis oralis: small or absent (0), or big and slotlike (1).
- Character 175 (modified from Ortega et al. 2000: char 98): Coronoid size: short and located below the dorsal edge of the mandibular ramus (0), or anteriorly extended with posterior region elevated at the dorsal margin of the mandibular ramus (1).
- Character 176 (Ortega et al., 2000: char. 101): Width of root of teeth respect to crown: narrower or equal (0), or wider (1).
- Character 177 (Ortega et al., 2000: char. 109): Gap in cervicothoracic dorsal armor: absent (0) or present (1).
- Character 178 (Ortega et al., 2000: char. 130): Lateral contour of snout in dorsal view: straight (0) or sinusoidal (1).
- Character 179 (Ortega et al., 2000: char. 138): Pterygoidean flanges: laminar and expanded (0) or barlike and elongated (1), or barlike and poorly developed (2).
- Character 180 (Ortega et al., 2000: char. 146): Ectopterygoid medial process: single (0), or forked (1).
- Character 181 (modified from Ortega et al., 2000: char. 157): Skull roof: rectangular shaped in dorsal view (0), or trapezoidal shape (1).
- Character 182 (Ortega et al., 2000: char. 30): + Prefrontal pillars when integrated in palate: pillars transversely expanded (0), transversely expanded in their dorsal part and columnar ventrally (1), or longitudinally expanded in their dorsal part and columnar ventrally (2).
- Character 183 (Ortega et al., 2000: char. 21): Ventral edge of maxilla in lateral view: straight or convex (0), or sinusoidal (1).
- Character 184 (modified from Ortega et al., 2000: char. 156): Position of first enlarged maxillary teeth: second or third alveoli (0), or fourth or fifth (1).
- Character 185 (Pol and Apesteguia, 2005: char. 180): Splenial-dentary suture at symphysis on ventral surface: V-shaped (0), or transversal (1).
- Character 186 (Pol and Apesteguia, 2005: char. 181): Posterior peg at symphysis: absent (0), or present (1).
- Character 187 (Pol and Apesteguia, 2005: char. 182): Posterior ridge on glenoid fossa of articular: present (0), or absent (1).
- Character 188 (modified from Gomani, 1997: char. 46; 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 189 (Pol and Apesteguia, 2005: char. 184): Dorsal surface of mandibular symphysis: flat or slightly concave (0), or strongly concave and narrow, trough shaped (1).
- Character 190 (Pol and Apesteguia, 2005: char. 185): Medial surface of splenials posterior to symphysis: flat or slightly convex (0), or markedly concave (1).
- Character 191 (modified from Pol and Apesteguia, 2005: char. 186): Choanal septum shape: narrow vertical bony sheet (0), or T-shaped bar expanded ventrally (1).
- Character 192 (Pol and Norell, 2004a: char. 164): Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).
- Character 193 (Pol and Apesteguia, 2005: char. 188): Lateral surface of dentaries below alveolar margin, at mid to posterior region of tooth row: vertically oriented, continuous with rest of lateral surface of

- the dentaries (0), or flat surface exposed laterodorsally, divided by a ridge from rest of the lateral surface of the dentaries (1).
- Character 194 (Pol and Norell, 2004a: char. 165): Palatine-pterygoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).
- Character 195 (Pol et al., 2004: char. 164): Ectopterygoid main axis oriented: laterally or slightly anterolaterally (0), or anteriorly, subparallel to the skull longitudinal axis (1).
- Character 196 (Wu et al., 1997: char. 103): Squamosal descending process: absent (0), or present (1).
- Character 197 (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 198 (Wu et al., 1997: char. 106): Pterygoid flanges: thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).
- Character 199 (Wu et al., 1997: char. 108): Postorbital participation in infratemporal fenestra: almost or entirely excluded (0), or bordering infratemporal fenestra (1).
- Character 200 (Wu et al., 1997: char. 109): Palatines: form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).
- Character 201 (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 202 (Wu et al., 1997: char. 112): Posteroventral edge of mandibular ramus: straight or convex (0), or markedly deflected (1).
- Character 203 (modified from Wu et al., 1997: char. 119): Quadrate ramus of pterygoid in ventral view: narrow (0), or broad (1).
- Character 204 (Wu et al., 1997: char. 121): Pterygoids: not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).
- Character 205 (modified from Wu et al., 1997: char. 122): Olecranon: well developed (0), or reduced or absent (1).
- Character 206 (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 207 (Wu et al., 1997: char. 127): Depression on posterolateral surface of maxilla: absent (0), or present (1).
- Character 208 (modified from Wu et al., 1997: char. 128): Anterior palatal fenestra: absent (0), or present (1).
- Character 209 (Pol and Norell, 2004a: char. 179): Paired ridges located medially on ventral surface of basisphenoid: absent (0), or present (1).
- Character 210 (Pol et al., 2004: char. 179): Ventral margin of infratemporal bar of jugal: straight (0), or dorsally arched (1).
- Character 211 (Pol and Norell, 2004a: 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 212 (Pol and Norell, 2004a: char. 181): Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0), or ventrolaterally (1).
- Character 213 (Gasparini et al., 1993: char. 3): Wedgelike process of the maxilla in lateral surface of premaxilla-maxilla suture: absent (0), or present (1).
- Character 214 (Pol and Norell, 2004b: char. 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 215 (Pol and Norell, 2004b: char. 182): External surface of ascending process of jugal: exposed laterally (0), or exposed posterolaterally (1).
- Character 216 (Pol and Norell, 2004b: char. 183): Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: absent (0), or present (1).
- Character 217 (Pol and Norell, 2004b: char. 184): Dorsal surface of posterolateral region of squamosal: without ridges (0), or with three curved ridges oriented longitudinally (1).
- Character 218 (Pol and Norell, 2004b: char. 185): Ridge along dorsal section of quadrate-quadratojugal contact: absent (0), or present (1).
- Character 219 (modified from Pol and Norell, 2004b: char. 186): Sharp ridge on the surface of the angular: absent (0), or present on the ventralmost margin (1), or present along the lateral surface (2).
- Character 220 (Pol and Norell, 2004b: char. 187): Longitudinal ridge along the dorsolateral surface of surangular: absent (0), or present (1).
- Character 221 (Pol and Norell, 2004b: char. 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 222 (Pol and Norell, 2004b: char. 189): Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: absent (0), or present (1).
- Character 223 (Pol and Norell, 2004b: char. 190): Appendicular osteoderms: absent (0), or present (1).
- Character 224 (Ortega et al., 2000: character 72): Supratemporal fenestra: present (0), or absent (1).
- Character 225 (modified from Pol and Apesteguía, 2005: char. 220): Flat ventral surface of internal nares septum: parallel sided (0), or tapering anteriorly (1), or expanding anteriorly (2).
- Character 226 (Pol and Apesteguía, 2005: char. 221): + Perinarial fossa: restricted extension (0), extensive, with a distinctly concave surface facing anteriorly (1), or large concave surface facing anteriorly, projecting anteroventrally from the external nares opening toward the alveolar margin (2).
- Character 227 (modified from Sereno et al., 2001: char. 67): Premaxillary palate circular paramedian depressions: absent (0), present located anteriorly on the premaxilla (1), or present located at the premaxilla-maxilla suture (2).
- Character 228 (Pol and Gasparini, 2009: char. 223): Posterolateral region of nasals: flat surface facing

- dorsally (0), or lateral region deflected ventrally, forming part of the lateral surface of the snout (1).
- Character 229 (Zaher et al., 2006: char. 193): Ventral half of the lacrimal: extending ventroposteriorly widely contacting the jugal (0), or tapering ventroposteriorly, does not contact or contacts the jugal only slightly (1).
- Character 230 (Zaher et al., 2006: char. 194): Large foramen on the lateral surface of jugal, near its anterior margin: absent (0), or present (1).
- Character 231 (modified from Zaher et al., 2006: char. 195): Procumbent premaxillary alveoli absent (0) or present (1).
- Character 232 (modified from Martinelli, 2003: char. 36; Zaher et al., 2006: char. 196; Turner, 2006: char. 119): Posterolateral end of palatines, completely sutured to the pterygoids (0) or project posterolaterally as rodlike palatine bars (1).
- Character 233 (Zaher et al., 2006: char. 197): Participation of ectopterygoid in palatine bar: no (0), or yes (1).
- Character 234 (Pol and Norell, 2004a: char. 183): Choanal opening: opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1).
- Character 235 (Zaher et al., 2006: char. 198): Ectopterygoid projecting medially on ventral surface of pterygoid flanges: barely extended (0), or widely extended covering approximately the lateral half of the ventral surface of the pterygoid flanges (1).
- Character 236 (Pol and Gasparini, 2009: char. 236): Evaginated maxillary alveolar edges: absent (0), or present as a continuous sheet (1), or present as discrete evaginations at each alveoli (2).
- Character 237 (Pol and Gasparini, 2009: char. 237): Foramen in perinarial depression of premaxilla: absent (0), or present (1).
- Character 238 (Serenio et al., 2001: char. 27): Frontal anterior ramus with respect to tip of prefrontal: ending posteriorly (0), or ending anteriorly (1).
- Character 239 (modified from Serenio et al., 2001: char. 68): Premaxillary anterior alveolar margin orientation: vertical (0), or inturned (1).
- Character 240 (Serenio et al., 2001: char. 69): Premaxillary tooth-row orientation: arched posteriorly from midline (0), or angled posterolaterally, at 120 degree angle (1).
- Character 241 (Serenio et al., 2001: char. 70): Last premaxillary tooth position relative to tooth row: anterior (0), or anterolateral (1).
- Character 242 (Pol and Gasparini, 2009: char. 242): Posterior teeth with rings of undulating enamel: absent (0), or present (1).
- Character 243 (modified from Brochu, 1999: char. 108 by Pol and Gasparini, 2009: char. 243): Maxilla-palatine suture: palatine anteriorly rounded (0), or palatine anteriorly pointed (1), or palatine invaginated (2).
- Character 244 (Pol and Gasparini, 2009: char. 244): Lateral surface of postorbital bar: formed by postorbital and jugal (0), or only by postorbital (1).
- Character 245 (Pol and Gasparini, 2009: char. 245): Enlarged foramen at anterior end of surangular groove: absent (0), or present (1).
- Character 246 (Pol and Gasparini, 2009: char. 246): Shape of antorbital fossa: subcircular or subtriangular (0), or elongated, low, and oriented obliquely (1).
- Character 247 (Pol and Gasparini, 2009: char. 247): Prefrontal lateral development: reduced (0), or enlarged, extending laterally over the orbit (1).
- Character 248 (Pol and Gasparini, 2009: char. 248): Foramen for the internal carotid artery: reduced, similar in size to the openings for cranial nerves IX–XI (0), or extremely enlarged (1).
- Character 249 (Pol and Gasparini, 2009: char. 249): Squamosal posterolateral region, lateral to paroccipital process: narrow (0), or bearing a subrounded subcircular flat surface (1).
- Character 250 (Pol and Gasparini, 2009: char. 250): Posteromedial branch of squamosal oriented: transversely (0), or posterolaterally (1).
- Character 251 (Pol and Gasparini, 2009: char. 251): Dorsal margin of squamosal occipital flange: straight (0), or dorsally concave (1).
- Character 252 (Pol and Gasparini, 2009: char. 252): Sculpture in external surface of rostrum: absent (0), or present (1).
- Character 253 (Pol and Gasparini, 2009: char. 253): Longitudinal depressions on palatal surface of maxillae and palatines: absent (0), or present (1).
- Character 254 (Pol and Gasparini, 2009: char. 254): Angle between medial and anterior margins of supratemporal fossa: approximately 90° (0), or approximately 45° (1).
- Character 255 (Pol and Gasparini, 2009: char. 255): Transverse process of sacral vertebrae directed: laterally (0), or markedly deflected ventrally (1).
- Character 256 (Pol and Gasparini, 2009: char. 256): Prefrontal and lacrimal around orbits: forming flat rims (0), or evaginated, forming elevated rims (1).
- Character 257 (Pol and Gasparini, 2009: char. 257): Nasal bones: paired (0), or partially or completely fused (1).
- Character 258 (Brochu, 1997: char. 3): Posterior half of axis neural spine wide (0) or narrow (1).
- Character 259 (Brochu, 1997: char. 19): Axial hypapophysis without (0) or with (1) deep fork.
- Character 260 (Brochu, 1997: char. 27): Olecranon process of ulna narrow and subangular (0) or wide and rounded (1).
- Character 261 (Brochu, 1997: char. 29): M. teres major and M. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1).
- Character 262 (modified from Brochu, 1997: char. 53): Anterior dentary alveoli project anterodorsally (0) or weakly procumbent (1) or strongly procumbent (2).
- Character 263 (Brochu, 1997: char. 84): Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1).
- Character 264 (Brochu, 1997: char. 91): Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1).

Character 265 (Brochu, 1997: char. 92): Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa; anteromedial corner of supratemporal fenestra smooth (1).

Character 266 (modified from Brochu, 1997: char. 103): Lateral margins of frontal: flush with skull surface (0), or elevated, forming ridged orbital margins (1).

Character 267 (Brochu, 1997: char. 130): Capitate process of laterosphenoid oriented laterally (0) or anteroposteriorly (1) toward midline.

Character 268 (modified from Brochu, 1997: char. 141): Paroccipital process development lateral to cranioquadrate opening: short (0) or long (1).

Character 269 (modified from Norell, 1988: char. 32 by Brochu, 1997: char. 149): Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity.

Character 270 (Brochu, 1997: char. 153): Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) or projects between first premaxillary teeth (2).

Character 271 (modified from Turner, 2006: character 126): Ventral surface of choanal septum smooth to slightly depressed (0) or marked by an acute groove (1).

Character 272 (modified from Turner, 2006: char. 128): Proximalmost portion of fibular head straight sided to weakly developed posteriorly (0) or very sharply projecting posteriorly, forming distinct extension (1).

Character 273 (Turner, 2006: char. 129): Posterior process of cervical rib shaft lacks (0) or possesses (1) a posterodorsally projecting spine at the junction with the tubercular process.

Character 274: Longitudinal keels on dorsal surface of osteoderms restricted to the posterior edge of osteoderm (0) or are not (1).

Character 275: Jugal below the anteroventral corner of the orbit: lacks (0) or possesses an emarginated orbital margin and an associated depression located on the dorsal region of the jugal (1).

Character 276: Transverse ridge crossing the frontal anteromedial to the orbits: absent (0) or present (1).

Character 277: Shallow hemispherical depression on the lacrimal and/or prefrontal anterior to the orbital margin (not articulation facet for palpebral): absent (0), or present (1).

Character 278: Anterior half of palatine bar between suborbital fenestrae: lateral margins are parallel to subparallel (0) or flared anteriorly (1).

Character 279: Posterior half of palatine bar between suborbital fenestrae: lateral margins are parallel to subparallel (0) or flared posteriorly (1).

Character 280: Posteroventral margin of the angular straight or gently arched dorsally (0) or strongly arched dorsally (1).

Character 281: Lateral margin of dorsal surface of squamosal squared off with continuous ear valve groove (0), or bears a prominent depressed area just anterior to the posterior lobe of the squamosal, groove for ear valve discontinuous (1). The posterior end of the squamosal lobe as flares distally.

Character 282: Fibular shaft distal to iliofibularis trochanter straight (0) or bowed posteriorly (1).

APPENDIX 2

DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Character states enclosed between parentheses represent conditions found to be variable within a terminal taxon (i.e., polymorphic scorings). Multiple states enclosed in braces indicate uncertainty or ambiguity in the condition of a terminal taxon (among these states, but not among the remaining character states). This dataset is also available in Nexus and TNT formats at: <http://research.amnh.org/users/dpol/crocs/shamosuchus> or <https://research.amnh.org/users/turner>.

Gracilisuchus stipanicicorum

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0?0?00?1?0?0?001???0?110??1?01000?0?0?

Terrestrisuchus gracilis

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Dibothrosuchus elaphros

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011100?000001?00?0?0011102101010000{0,1}0000
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?0?000000?0000?00?0?0?000?0?0?1101?01?01000?0?0?

Protosuchus richardsoni

2100000120?000011010002100000100010001010?002
0100111110010101103011?11021000101010000110
0{1,2,3,4}00?120011010011102101010000{0,1}0000
00?01?01??10010{0,1}010100000??011000000000
0000001?00000000?0??0000?0100120000011110?0
01000?010?0000?0?0000?0?0000000?000000001000
00??0?0?10????00?000?0000

Hemiprotosuchus leali

200?00?10????10010?0?00?0010?11?0?01?00020?00?
11?1100101??13?11??121????01????????0????1200?1
?1001??0????????000?0000?10?00??00000??10????00
??????0?0?0?00?0?????0?0000?0????0?0?0?12??00
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?00????0?10??????0?0?0?

Orthosuchus stormbergi

21100001201?0001001000{0,1}10000010001000?000?
002011001111100??1?1?03011?0?0?0?001000100011
100000?120010013021142101?10010?100000001?010
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000?0???0?000?012?000011110?0001000?0?000?00?
00?0?0?0?000?0?0?0000?000100?00???100110?01?0
?0?0?0?0

Kayenta form

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00010112?000011?0?010?0?00????????000?0???0???
?0?0???0?0?1?000?0?0?1?1????????????0???

Edentosuchus tienshanensis

201????{1,2}????0??{0,1}0??1?0100?0?0???02?110?00
????????????????{2,3}?311???10?01010?0?????
{2,3,4}????????0???1{2,3}????????00110?1?01?1?
??1000110?11?1??????01?0001?1?1?00?0?0?0?000?
0?0???4?0?0101??1???11?0?0?1?00000?0?0?0?0?0??
0?0?0?0?0?0?0?01?0?00?0?0?10?101????000?0???

Zaraasuchus shepardii

10?????????1?01?01?1000001?10?02?????????????
????????3????1?010????????????{1,2,3,4}0??1010
?0?????????0????????????????????0????1??1?????
?10????????0000?0???0?0?0?0?0?0?1????1?00?0?
??0??1111111111????????????0?0?00?0?0?0?0?
??0?10?0?0?0?1000?00?

Gobiosuchus kielanae

101000?110000011001?{0,1}{0,1}?1?00001?10?02010
00?002011201111000?0?0?301???1?20100{0,1}010
?0?1?????0?1010110{0,1}3012002?0000?00010{0,1
{00001000000?00001001211?0000???11000000001?0
0000?1?0010000000?000?0?01?0121000011?00?00?0
01111111111?000000?000000000?0000?00010?00
????001?0?1????10?0?0?0?

Sichuanosuchus shuhanensis

{1,2}01?0?1200{0,1}00?10010{0,1}?110?0?1?00?021
?10?00020?1011?1100?0?0?3?110???1?000011?1?1
????000?0?0?0?10?11?0?1?0?0?100100?1?10?0?0?
0011?{0,1}1210?00?0?0?1?0000?00100?00?10?0?000
?0?00?0?00010?111011111100?1010000100?1?0?0?
?0?00?00?0?000?000?001?000?0?00?0?0?0?0?0?00
0?00?

Shantungosuchus hangjinensis

2?1????10?0?0?1?1?1????1????????21?1{0,1}100020?1
?011?1100?10?0?0?0?101?1?000?10?0?0?0?0?0?0?0?
?0?1?????1????00100?0?0?0?0?10?00?0?1211?0001?
????00000000?0?0?0?1?0?0?0?0?0?0?0?0?0?0?10111
11?0?1{0,1}10?0?0?1?1????????0?0?0?0?0?0?0?0?0?
0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?

Zosuchus davidsoni

201?0?1200000?001010{0,1}110?001110?022110100
22?1?011?11000?0?1?0311110?0?0?0111?????????
????????10?1223???1????00100011011?0001?0?00101
12?{0,1}?0001???0?0010001{0,1}000?{0,1}111????
0??0?00??000?1000111??1011?101101000000100???0
?000?000?0000000?0?00?0?000100?00?0??10?10?0?0?
?0?0?0?00?

Fruita form

201?001200100010000100100000110010221?11?0120
112?1???0?0?0?1?3?31????1?0111101011?1?000111
12?0?1?0?0?{0,1}00?1?1001?001?0?0100100??101?00
11?01110?0?00?10?0?001?00?0?0?000?0000?0?0?
0???110???000???101??0?00000?000?0?00?0?0?00?
????0?????0?100?00?0?01?1????????0?0???

Hsisosuchus chungkingensis

211?0????000000100001100011000?022?101001{1,2}
??12?11?10000?0?1?0{2,3}?11114?00{0,1}01?1??10?0?
??000?1000??0?01?1021?1????01001????0?0000?000
1011?1?001????10??0?0?0?00020?10??0000?0?000000?
00?10??{0,1}00?00011111100{0,1}?0000?0000?0?0?00?
0?10?0?0?0?000?0001?0?00?0?00?0?0?0?0?0?0?0?0?

Notosuchus terrestris

101?00110201001110001111110011000102211011002
1112011?1000010?1103111112?0101110001{0,1}112
?1?200001000?01122011??1100101{0,1}1101{0,1}0
1001000000111111111?00011110010100000011000
011100?0?001000?1110000111010110000111011?000
00000000000?100000111{0,1}10000?0000?000100
0000?0100100101????100001000

Comahuesuchus brachybuccalis

103?0?102??00????0112??????0010?2????1?011?1????
????????????131?????0?10101????????????????0??
{0,1}13??1?????0?10?101201?01????011??0?1????11??
?11?020?00{0,1}0?0011?01?0?00?1011?000?110?
0?000???100???0?000?0?0?0?1?01110?1{0,1}{0,1}0
0000?0?0?0?100?00?0?0?22110101????000?01?0?

Mariliasuchus amarali

101?00?10200001110001{0,1}01110001100102211011
0121?12011?1000010?1?0313111210{0,1}0?11000?0?
????????????22111?11?1????0{0,1}0001010010?1
100{0,1}0011110110?0011??01?????1????0?0?0?0?0?
?1?????0?0?0?1?100100001?1010?0000000000?0?0?
??11110?10100000?00?00000100?00?0?020000?010??
0?0010??

Uruguaysuchus aznarezi

201?001102?00?0?10?1?1?1???1???01022?101?0011???
1????0?0?0?02111{1,2}??000110100??1?2????0000?
0?010?2100210?00?000?{0,1}??01?1?00?0?1?0111?1
1????11????100?10?{0,1}00?0?100?0?0000?001?1
????????????0?0?10?0?0?00?0?0?0?0?0?0?0?0?0?0?
????????1?000?0?0?0?0?0?0?1?10000?000

Lomasuchus palpebrosus

201????1221?00?11000101111??110001022?1010001??
12??1?100??1??1??3?21????00??0{1,2}11?????????
??????1???00?00????0?00??1?110?00??00011?0??
1?0?0????0?0??10000?0??10???00?0?00??0?0?01
?1??10?01?10000??11000?0?0??0?0?0?100?0??00
00?0?00100?00??001?0????0??0000000?

Peirosaurus torminni

201?011?22?00?000?10?1??????0??2?10?????????
??????????1?????????{1,2}1????????????????000?
????????0??1?00?0??0?1??????????{0,1}??????0
????????000????000????????????00??1????????
0?0????00?0?0??????1???0???0????????0?????

Theriosuchus pusillus

20110111120100110000110111100110011?211010001
?11?01111000?????1?20211?410010101011011211000
11{1,2}120010013010002?0?10?110110{0,1}001?110
0?00?0?00110?0?1??0?00??10{0,1}00210100{0,1}020
00?100?0?10001110{0,1}0?0?0?0101?010?01?1000?0
?00000?2??0?0?0?0??0?10?0000?0??000?100?00??0
?0?0011?1??0?100000?00

Alligatorium

?0?????1?0000?1000010?111??0?100?1????0??00??11??
1??1000?000??20?1???00101?101?0111211000??1?00
100?????????10??1??????????????0?????????????
??????1????????????????????0?????????????????
????0????????????????????0??????????1??00?????
????????????????

Pelagosaurus typus

202?{0,1}111?20011020101{0,1}00000000000{0,1}10
02110100000011011?1001001?10001201?3000002000
01101?1?00000012000111?011002100???101?101??1?
?10000?00001010110??{0,1}00??100000?00011020
00100?000200?0??0?0?00001011010000110000001??0
000000?0??10?00?10{0,1}000000210001100110?00?
????11000?1???10000000?

Steneosaurus bollensis

{0,1,2}02?{0,1}111?20011020100{0,1}000100000001
10021101000?0011011?1001011?1?00120103?000?20
000110111100000?120001{0,1}1?011?02100{0,1}00
1001101??10?10000?0?00101??0?00000110000010
000110?0001001000200?0?000000000101{1,2}01000
{0,1}1100010010?0000000000?0010?00?100000000?
1000010?0{0,1}0100?00??1000?11?0?1000000?0

Metriorhynchus superciliosus

{0,2}02?1211020011?201001000100000001100211010
00?0011011?1001011?1?001201?30001020000?01111
?0000????0?0?012?02?100001?11101??10?1000?0?00
10????0??000????00000110?00?00010?0200?0?000
000000101101000?1100000010?000000??0?0010000?1
0000000020011111010100????00?0000?000?0??

Metriorhynchus casamiquelai

0?2?1??10?0011?20?0010?010?00????02?101001?0??1
?1????0?0??0?1201????010?0000????????????????
0?01?0??10?????1101??1?1?0????0010????????0??
?????0??00110?0?0????0?0?0?0?0?00?0??11???0?
1?00?001????0????0??1????1?0?00?00??111?110?
0?00????00????????0?0??

Geosaurus araucanensis

002012?10200111201001000100000001100211010000
0?1101??10010{0,1}1?1?000200?3?001020000??????
0000??????0?012?0?01000??11101??10?1001??0?00
10?{0,1}2?00?00??0?0?0010000110?00000010?0??0
{0,1}0?00?000?00??1?1000?1?000?0010?000000??0?
0010000??0000000211111110?1?00????0?00??????
?000000??

Geosaurus suevicus

0?2012?10???11?01?0100010?000001?00????????????
????????????00{2,3}0?3?01020000????????????????
???0?{1,2}0??1????011101??1??1????0?0010?02?0??
?0?0010?000??000110????0??0?0?0?0??0????0????
?000?1?0?00?0?000?00?0?0?10?0???0?00000??11?
11?0?1?00????0?00?00000000?0??

Dakosaurus maximus

001?12?1????11?0?0?010?0?00?001????????????????
????????01?0????01?00000??????????????????2?
0?1?????1?00??1?11????0?0011????????????000?
?00011??????0?0???0???0???0????????000?????
????00??0?0???000???00001??1?1???011100????0?
0????????????

Dakosaurus andiniensis

001????1020011?200001000100000001?002?10100?00?
?1?1????{0,1}0??1?00?200????010?0000?????????
??????0?012?0?10????11001?1?1?01??010011112?
0??00001?0?00?0000110?00?00?0?0?0?0????0?00
??{0,1}1?0001?00?00?0000?0???0??11000?11???00
01?11111110?1?00??0?00?000000000000?

Sokotosuchus ianwilsoni

2?2??21112??10???001001???101001?012?1?????1112?
11?1?11?0???1?1?0??????01?????????????????
1?0?????????1??????0??????0?10????????0????????
????0??????????1??????0??????0????????????1??
??????0?????????2?000?0??0?001?0?11?????????
??????????

Rhabdognathus

202????200??11100010011011010011012110101{0,1}
01112011?10110101?111?302??????0?????????????
????????1?10?00?00000100????00?000?0{0,1}1002
0?001?00????1????0?01{0,1}22000?0??0?000000????
??0?1010010?01?1000001?0000????0?0000??112?
1???010??00000000?11????0000111?0??0000000?

Dyrosaurus

202?12?102?010?11?010011??101001?012?10101{0,1}
 ?1112011?1011?10?101113021???00?2?000? ???????0
 0?????????1?10?000?????10????00??00?0010020?
 0???0?????1000?00001?0200????0?0?00?0???000000
 10?0?000?1?00?001?000000??0?0?0?00?11201000
 010??00000?0?1?0010011100??00000?0?

Hyposaurus rogersii

?02?12?102??1?????1????0101????2??????1?12011
 ?101??10?1?1??3????0???2?000??112????00????????
 01?0?0?0??1?0110? ???????????0?1002?0?0?00??1
 ?1000100?0???00??0?0?????0?000000?00??0?????
 ??0??01????0????0????????2????0????0???0???1?
 ???00?0?1?????000?00?

Pholidosaurus purbeckensis

212?121102??1??1110?10011?0010001012110101?0
 1112?11?101??10?100?131{1,2}??0??2?0?1?2??
 ?0??0?200? ???????0?0? ??????1?0??1?110? ??0?00
 100? ??????00? ?????000?0000102?100???0?0000?0?
 ?000?00?10?0?10?01?100?0010??0?0???0?0??0?
 10??1????1???0?0001?0?00? ?????00? ???????0?????

Sarcosuchus imperator

203?12?10200101?100010011001010001012?10101101
 ?12?1??10100?0?100?131213?000210101?112???{0,
 1}00?1200?00?010{0,1}0?00{0,1}001?0?101??1211
 00??00000010010?1???00??110?0{0,1,2}11010{0,1}0
 22{0,1}00?0000?000000?000000?00?01001000?1?100
 ?0010?00000000?0?0100000?100011110100?0?000100
 ?10????00110?1100?0?0001000?

Terminonaris robusta

202??{0,1}2?1020010?11??01001???1010001012?1010{0
 ,1}1?????11?1010?0?0??13{0,1}{1,2}13?000?21000
 11112?00000?1200?10?0?010210?1001001101??1??1
 0?0?0?0010????1???000011100?0??101{0,1}2{1,2}1
 0????0?000?0?0000?0001?0?00?0?0?11100?00?0?00?
 ?00?0?0100?00?1020111101?0?00?100?00?00?0?10
 11?000100000000

Goniopholis simus

203?1211120010111000100111?0010001002?101000?1
 112011?1010?10?1?021312?4100{0,1}0{1,2}02011?1?1?
 ?0?00?1200?1?30000210010?1101101??101100?000010
 010001?1???00001110003110001022100?10?001000111?
 0000000101001000011110?00100000000000?0000000?
 10000{0,1}00000?0?000100?00????000? ??????0100??

Goniopholis stovalli

203?121111?101?1000100111?0010001001?1?000?11
 12011?10?0?0?1?021312?410?02????????????????
 ?????00100?00? ?????101??1?1100?000?0010001?1?
 ?00? ?????0?00001022?00????0?1?0?11?00?00?10?
 0?0?0?01?110000100000?000?0?000000?1?00000000
 ???0?000100?00?00?0010?100?000?0001

Eutretauranosuchus delfsi

203????1?10010111000100111?00?0001001110?000?11
 12011?1010?0?1?0?121204?00001020111??1??0?0?
 1??????3?000?000????0?101???110?????0?00???1?
 ?0????11??{0,1,2}1??01022100?1???10?0?1???000
 00010?0?000?1?110?01?0000000??0?000?00??100?0
 ?000?00?0?00100?00?0?010010?0?0?0001000?

Calsosuchus valliceps

203?0201110210?110?01021111001000?001?1???00?11
 12?11??0?0?0?1?0?111(1,2)??????01?????????????
 ?????0?0000?000? ?????101??1110?0?0?0010001?1?
 ?00? ?????????001022?001????1????01???0?00?00??
 ??????1100?0100000?000?0?000000??0000000?0?10
 0?0?100?00?00?0?1010?0?0?1000?0?0?

Sumosuchus junggarensis

203?0201111?10?1100010011110010001002210100011
 112011110100?0?11011312?41000110101??1111?0?20
 001200?11????????????????????????????????????
 ?????????????????????????????????????????????
 ?????????????????????????????????????????????
 ?????????????????????????????????????????????10?
 ?0?011???00?00?1000?

Bernissartia fagesii

203??21112?00111000?00111?001000?002????110111
 2?11?10100?0?1??1?1??410010102011?1?21?020011
 1101101300000?0??????1???1??????0?0?10??01?
 ?0????1?0??31?100102210?1100001000111?000?0?1
 ?????0?000?00??10000?0?0?0?0?0?0?10??0?0?????
 0?001?0?001000001?1?0010?01000?010?

Shamosuchus djadochtaensis

203????10?1??0111000110111000100010021101?10111
 1??1111010000?10??310?4100101?1??????1101{3,4}
 1?{0,1}(1,3)1?0?10?{0,3}00{0,1,2}002?000(0,1)????011
 00??1?11?0?0000000100011101?00001?0?0?10?00002
 2{0,1}???1??01000?100000?0001010010?001?10?00
 01000000210?1??0000?0100?0?00?00?000001?0?00
 0??1?0?01101?00010111011

Rugosuchus nonganensis

203??{1,2}1?20?00??1?0110111???00010{0,1}2110?
 010?1112?11?1010000?1?0??31??4?0010102?????????
 ?????2?{1,2}0??0?{0,3}0?000?0?0????01?01??1?1000?0
 ?00?0100?1?1??00??100?0?1?100??2??0?10??10??
 110000?0?0???0?100001?100?0010?000020???0?0?00
 000?1?0?0000000?00000100?01????0????????????01
 11??

Glen Rose Form

2030001112?0011???0100111?001100?0?2110?011??1
 12?11?10100?0?1?030310??0?1?0211?????????????
 ?????3?000?000?000?01100?01?1?00?0000?010?0??
 ?1????10??13101001022??1?10?0?10?0?1000?000?0
 1?1?010?0?1?1000???000?0?2??0?000000001000000
 000?0?00?00100?00?000001001??1?1?1000?

- Gobiosuchus kielanae* (Osmólska, 1972; ZPAL MgR-II/67, ZPAL MgR-II/68, ZPAL MgR-II/69, ZPAL MgR-II/70, ZPAL MgR-II/71)
- Sichuanosuchus shuhanensis* (Wu et al., 1997; IVPP V 10594)
- Shantungosuchus hangjinensis* (Wu et al., 1994b)
- Zosuchus davidsoni* (Pol and Norell, 2004a; IGM 100/1304, IGM 100/1305, IGM 100/1306, IGM 100/1307, IGM 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; MLP 64-IV-16-1, MLP 64-IV-16-5, MLP 64-IV-16-6, MLP 64-IV-16-10, MLP 64-IV-16-11, MLP 64-IV-16-12, MLP 64-IV-16-13, MLP 64-IV-16-23, MACN-RN 1037, MACN-RN 1040, MACN-RN 1041, MACN-RN 1042, MACN-RN 1043, MACN-RN 1044, MUC-PV 287, MPCA-PV 249, MPCA-PV 250)
- Comahuesuchus brachybuccalis* (Bonaparte, 1991; MUC-PV 202, MACN-N 30, MACN-N 31, MOZ 6131P)
- Mariliasuchus amarali* (Carvalho and Bertini, 1999; MZSP-PV 50, MZSP-PV 51, MNRJ 6298-V, MNRJ 6756-V)
- Uruguaysuchus aznarezi* (Rusconi, 1933)
- Chimaeresuchus paradoxus* (Wu and Sues, 1996; IVPP V8274)
- Malawisuchus mwakayasyungutiensis* (Clark et al., 1989; Gomani, 1997; MAL 45, MAL 49)
- Candidodon itapecurense* (Carvalho, 1994)
- Simosuchus clarki* (Buckley et al., 2000; UA 8679)
- Sphagesaurus huenei* (Price, 1950; Pol, 2003; RCL 100)
- Baurusuchus pachecoi* (Price, 1945; DGM 299-R)
- Bretesuchus bonapartei* (Gasparini et al., 1993; PVL 4735)
- Iberosuchus macrodon* (Antunes, 1975; Ortega et al., 2000; UAM)
- Libycosuchus brevirostris* (Stromer, 1914; BSP 1912.VIII.574)
- Araripesuchus gomesii* (Price, 1959; AMNH 24450)
- Araripesuchus patagonicus* (Ortega et al., 2000; MUC-PV 269, MUC-PV 270, MUC-PV 283)
- Araripesuchus buitreaensis* (Pol and Apesteguía, 2005; MPCA-PV 235)
- Araripesuchus wegneri* (Buffetaut, 1981; MNHN-GDF 700)
- Araripesuchus tsangatsangana* (Turner, 2006; UA 8720, FMNH PR 2297, FMNH PR 2298, FMNH PR 2299)
- Lomasuchus palpebrosus* (Gasparini et al., 1991; MOZ 4084 PV)
- Peirosaurus torminni* (Price, 1955; Gasparini et al., 1991; MOZ 1750 PV)
- Theriosuchus pusillus* (Owen, 1879; Clark, 1986, 1994; Ortega et al., 2000; BMNH R48328, BMNH R48330)
- Alligatorium* (Wellnhofer, 1971; Clark, 1986, 1994)
- Pelagosaurus typus* (Eudes-Deslongchamps, 1864; BMNH R32599, BSP 1925.I.34, BSP 1990.VIII.68, MB 1925.1, MB R.2883, SMNS 8666, SMNS 80066)
- Steneosaurus bollensis* (Jaeger, 1828; Westphal, 1962; AMNH 5138, BSP 1890.I.510, BSP 1945.XV.1, BSP 1949.XV.1, BSP 1972.V.11, BSP 1973.VII.592, GPIT Re.1193-6, GPIT Re.1193-12, MB 1878.262, MB 1921.12, MB R.1953, SMNS 115, SMNS 4554, SMNS 9427, SMNS 9428, SMNS 15951, SMNS 16848, SMNS 17484, SMNS 18878, SMNS 20280, SMNS 20282, SMNS 20283, SMNS 53422)
- Metriorhynchus superciliosus* (Blainville, 1853; Wenz, 1968; AMNH 997, SMNS 10116)
- Metriorhynchus casamiquelai* (Gasparini and Diaz, 1977; cast of MGHF 1.08573)
- Geosaurus araucanensis* (Gasparini and Dellapé, 1976; MLP 72-IV-7-1, MLP 72-IV-7-2, MLP 72-IV-7-3, MLP 72-IV-7-4, MLP 72-IV-7-4, MLP 86-XI-5-7, MACN-N 95, MACN-N 64)
- Geosaurus suevicus* (Fraas, 1902; SMNS [Fraas specimen])
- Dakosaurus maximus* (Fraas, 1902; SMNS 8203, BSP AS.VI.1, BMNH R486)
- Dakosaurus andiniensis* (Vignaud and Gasparini, 1996; MHNSR PV 344, MOZ 6146P)
- Sokotosuchus ianwilsoni* (Halstead 1975; Buffetaut, 1979; Clark, 1986, 1994)
- Rhabdognathus* (Brochu et al., 2002; CNRST-SUNY 190)
- Dyrosaurus* (Buffetaut, 1978; Clark, 1986, 1994; Jouve, 2005; BSP 1993.IX.400)
- Hyposaurus rogersii* (Troxell, 1925; Denton et al., 1997; YPM 985, YPM 764)
- Pholidosaurus purbeckensis* (Owen, 1878; Clark, 1986, 1994; Salisbury, 2002; BMNH R3414)
- Sarcosuchus imperator* (Broin and Taquet, 1966; Sereno et al., 2001; MNN 604, MNN 603)
- Terminonaris robusta* (Mook, 1934b; Wu et al., 2001a; AMNH 5850, AMNH 5849)
- Goniopholis simus* (Mook, 1942; Clark, 1986, 1994; Salisbury et al., 1999; BMNH 41098)
- Goniopholis stovalli* (Mook, 1964; AMNH 5782)
- Eutretauranosuchus delfsi* (Mook, 1967; Clark, 1986, 1994; CMNH 8028; AMNH 570)
- Calsosuchus valliceps* (Tykoski et al., 2002)
- Simosuchus junggarensis* (Wu et al., 1996a)
- Bernissartia fagesii* (Buscalioni and Sanz, 1990; Norell and Clark, 1990; Brochu, 1999)
- Shamosuchus djadochtaensis* (Mook, 1924; AMNH 6412, IGM 100/1195)
- Rugosuchus nonganensis* (Wu et al., 2001a)
- Glen Rose Form (Brochu 1997a, 1999; USNM 22039, MCZ 4453)
- Hylaeochampsia vectiana* (Clark and Norell, 1992; BMNH R177)
- Borealosuchus formidabilis* (Erickson, 1976; Brochu, 1997b, 1999)
- Argochampsia krebsi* (Hua and Jouve, 2004)
- Eothoracosaurus mississippiensis* (Brochu, 2004; MSU 3293, PPM p2000.1.60)
- Gavialis gangeticus* (Clark, 1994; Brochu, 1999; MLP s/n, FMNH 82681, FMNH 98864)
- Leidyosuchus canadensis* (Brochu, 1997b, 1999, 2003; Wu et al., 2001c; AMNH 5352, TMP 74.10.8, NMC 2279)
- Pristichampsus vorax* (Brochu, 1999; UCMP 154329, FMNH PR 399, FMNH PR 479, FMNH PR 74)

Asiatosuchus germanicus (Brochu, 1999, 2003; SMF Me 1801, SMNK uncat.)
Crocodylus niloticus (Clark, 1994; Brochu, 1999; FMNH 17157, FMNH 217153)
Diplocynodon hantoniensis (Brochu, 1999; BMNH 30392, BMNH 30393, BMNH 30397, BMNH 30394, BMNH 25199, BMNH 25178, BMNH 30391, BMNH 30250, BMNH 30362, BMNH 30289, BMNH 30368, BMNH 30414, BMNH 30402, BMNH 30219, BMNH 30210, BMNH 30206, BMNH 30236, BMNH 25245, BMNH R1046, BMNH R1050, BMNH R5230)
Alligator mississippiensis (Clark, 1994; Brochu, 1999; FMNH 8201)

APPENDIX 4

SCORINGS FOR ADDITIONAL TAXA USED IN EXTENDED ANALYSES

Isisfordia duncani

203?02110200?0??1?00110111?00100010021101021?1
112011?10100?0?1?0?131{12}0??00?00?0??1?????
{1234}1122?20110??00?0?100100?0??101?111100?
000000011001?1?1?000?0??00?0?000022101????10
000?0??0?0?00010100100?1110000000?0000?0000
?0000000?10000000000?00000100?00?0?001?01?
00?100?10?0?

Susisuchus anatoceps

203?12?1??1?10??1??0100111?001000100?0??0??1??
????????1??131?23?0??0??1??????0002020110?
??0?0?10??0??0??0??1?11?0??00001??1?0??0????
??????0?1022?1????1{01}??0?????0??????1?0??
110??0?0?0000?00000?0?0000??000?000?0?0?00?1
?0000?0??0?11?????01000?0?

Pachycheilosuchus trinquei

203????????00?10?111??10001??????01?1????
????????2????01?0?0?101111?021111{01}00??
0?3??0021??1000?0?10????????0?1?0??????
?10?00010?0?2??0??01????1??00??0?????0??
1?0????????00?0?0??????0?0????????01}??
????{01}??????001????0?

Allodaposuchus precedens

203??2?11?0????1?0?10{01}1111001000?00?11??2??
?110?11?1?00?0?1?0?131????????{12}????????1
1????????0?0?0??0????101?????0?00?000100?
1?1?1?00????????00?022?01????1?00?????0??0
??010?1??0??10??001??0000????0?0??000?1?{01}0
?000?0?00000?0?0????0000101?????0????

Glichristosuchus palatinus

2????????????10{12}1????10001??2?10?12??11?
1??????0?1?0??1????????????????1????????
????0?0????????????????????????????????

?????01?0??????????????0?1??0?0????????????
??????????0?0????????????0?00?0?0????????????
???????

APPENDIX 5

ANATOMICAL ABBREVIATIONS

an	angular
ar	articular
astc	astragalar condyle
at	atlas
ax	axis
bo	basioccipital
bs	basisphenoid
c	cervical vertebra
ca	calcaneum
calc	calcaneal condyle
ch	choana
chg	choanal groove
co	cervical osteoderm
cor	coracoid
cr	cervical rib
cq	cranioquadrate canal
d	dentary
do	dorsal osteoderm
ect	ectopterygoid
ex	exoccipital
exr	extensor ridge
fb	fibula
fbo	fibular osteoderm
fca	anterior carotid foramen
fcp	posterior carotid foramen
fm	foramen magnum
fr	frontal
fv	foramen vagi
fxr	flexor ridge
hu	humerus
if	ilial facet of ischium
i.hr	insertion for m. humeroradialis
ilft	iliofibularis trochanter
itf	infratemporal fenestra
it	internal tuberosity
i.tm	insertion for m. teres major
j	jugal
lac	lacrimal
leu	lateral Eustachian tube
meu	median Eustachian tube
mt	metatarsal
mx	maxilla
na	nasal
ns	neural spine

od	odontoid	radh	radial hemicondyle of humerus
o.fti	origin of m. flexor tibialis inter- nus	roe	external otic recess
o.pit	origin of m. puboischiotibialis	soc	supraoccipital
orb	orbit	sof	suborbital fenestra
os	osteoderm	sp	parietal sinus
pal	palatine	spl	splénial
par	parietal	sq	squamosal
pf	pubic facet of ischium	st	sella turcica
pmx	premaxilla	stf	supratemporal fenestra
po	postorbital	sur	surangular
prf	prefrontal	uef	groove for upper ear valve
pro	prootic	ul	ulna
pt	pterygoid	ulh	ulnar hemicondyle of humerus
ptf	posttemporal fenestra	vo	ventral osteoderm
q	quadrate	V	passage for trigeminal nerve
qj	quadratojugal	VI	passage for abducens nerve
r	rib	VII	passage for facial nerve