

Basal crocodyliforms from the Lower Cretaceous Tugulu Group (Xinjiang, China), and the phylogenetic position of *Edentosuchus*

Diego Pol^{a,*}, Shu-an Ji^b, James M. Clark^c,
Luis M. Chiappe^d

^aDivision of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

^bSchool of Earth and Space Sciences, Peking University, Beijing 100871, People's Republic of China

^cDepartment of Biological Sciences, George Washington University, Washington, DC 20052, USA

^dDepartment of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA

Received 28 July 2003; accepted in revised form 7 May 2004

Abstract

We report here two crocodyliform specimens from Lower Cretaceous beds of the Tugulu Group (Xinjiang Uygur Autonomous Region, People's Republic of China). One of them consists of postcranial material, while the other is a nicely preserved skull. The latter is assigned to *Edentosuchus tienshanensis*, a previously poorly known taxon from the Tugulu Group. The new specimen adds novel information on this unusual crocodyliform and allows us to test previously proposed phylogenetic relationships of *Edentosuchus tienshanensis* through a parsimony analysis within the context of Crocodyliformes. *Edentosuchus* is found to be a member of Protosuchidae, the most basal clade of crocodyliforms, thus extending the stratigraphic record of this clade from the Early Jurassic to the Early Cretaceous.

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Keywords: Crocodyliformes; Tugulu Group; Early Cretaceous; China; *Edentosuchus*; Protosuchidae

1. Introduction

Previous knowledge of the Early Cretaceous crocodyliform fauna of the Tugulu Group was restricted to the type specimen of *Edentosuchus tienshanensis*. This taxon was originally described by Young (1973) as a protosuchian, at that time considered as a member of Crocodylia. The holotype (IVPP-V 3236), the only material known to date, consists of a partially preserved skull roof associated with the lower jaws and anterior cervical vertebrae. The presence of some peculiar characters and the fragmentary nature of this specimen

rendered *Edentosuchus* an enigmatic taxon of debated phylogenetic affinities (Young, 1973; Li, 1985; Clark, 1986). This taxon was alternatively considered to be closely related to either “protosuchians” (Young, 1973; Clark, 1986; Wu and Sues, 1995) or to the more derived taxon Mesoeucrocodylia (Li, 1985). However, probably due to the incompleteness of the type specimen, the phylogenetic relationships of *Edentosuchus* were not tested in any of the cladistic analyses of Crocodyliformes performed to date (e.g., Clark, 1994; Wu et al., 1997; Buckley et al., 2000; Ortega et al., 2000; Sereno et al., 2001; Pol, 2003).

Here, we report two recently collected crocodyliform specimens from the Lower Cretaceous beds of the Tugulu Group. One of them, a partial skull and associated mandible, can be attributed to *Edentosuchus*

* Corresponding author.

E-mail address: dpol@amnh.org (D. Pol).

tienshanensis. This specimen adds critical information on the morphology and the phylogenetic relationships of this unusual taxon.

2. Geographic and stratigraphic setting

The specimens here reported were collected in 2000, during a joint expedition of the Natural History Museum of Los Angeles County and the National Geological Museum of China to the Lower Cretaceous beds of the Tugulu Group 10–20 km southeast of Urho, a village located some 85 km northeast of Karamay, northwestern Xinjiang, P.R. China (Fig. 1; GPS coordinates of GMPKU-P 200101: 46° 00' 36.1" N; 85° 50' 57.9" E and GMPKU-P 200102: 46° 00' 47.6" N; 85° 51' 14.0" E). Rocks of the Tugulu Group around Urho consist of alternating beds of mudstone, shale, and fine sandstone of fluviolacustrine origin (Brinkman et al., 2001). This facies association corresponds to hot and seasonally arid climatic conditions with a preponderance of widespread floodplains and transient ponds (Eberth et al., 2001). The specimens come from the middle of the formation in the Urho stratigraphic section. This section is dominated by isolated and partially articulated remains of dsungaripterid

pterodactyls (Young, 1964; Dong, 2001). Remains of turtles (Sinemydidae: *Sinemys wuerhoensis*; Ye, 1973), theropods (*Phaedrolosaurus ilikensis*; *Tugulusaurus faciles*; *Kelmaysaurus petolicus*; Dong, 1973), sauropods (Euhelopodidae: cf. *Asiatosaurus mongoliensis*; Camarasauridae indet.; Dong, 1973), stegosaurids (*Wuerhosaurus homheni*; Dong, 1973), psittacosaurids (*Psittacosaurus xinjiangensis*; Brinkman et al., 2001), and a putative basal ornithopod (collected during the same LACM-NGMC expedition) also occur in this section. This faunal association has been correlated to the renowned Jehol biota of the northeastern Chinese province of Liaoning (Dong, 2001).

3. Systematic paleontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930 (sensu Clark, 1986)

Protosuchidae Brown, 1934

Edentosuchus Young, 1973

Edentosuchus tienshanensis Young, 1973

Holotype. IVPP-V 3236. Dorsal temporal area of the skull associated with anterior end of lower jaws and cervical vertebrae.

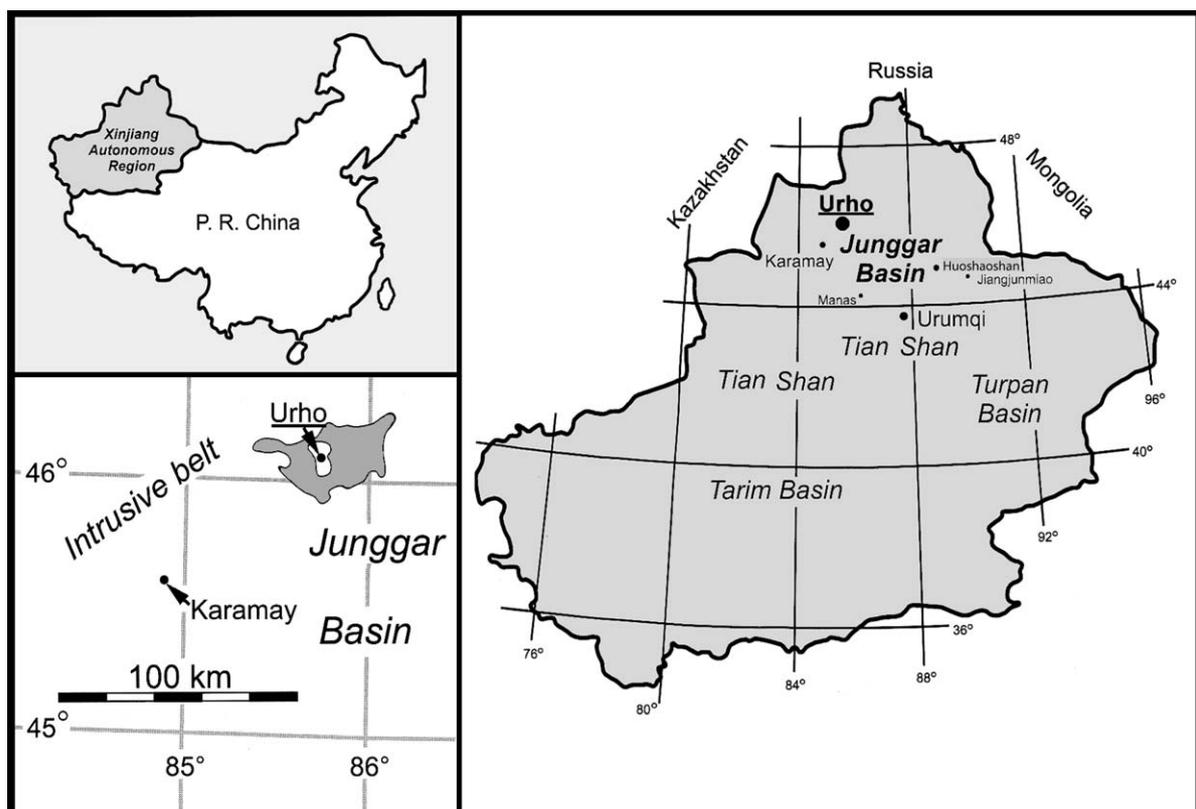


Fig. 1. Geographic setting of the fossiliferous locality where the specimens studied were found (modified from Eberth et al., 2001).

Referred specimens. GMPKU-P 200101. Anterior and infratemporal regions of the skull articulated with the lower jaws.

Revised diagnosis. Small, short-snouted crocodyli-form lacking an antorbital fenestra; posterolaterally expanded squamosal; elongated prootic and laterospheno-oid; five maxillary and nine mandibular teeth; marked heterodonty in maxillary teeth displaying three different crown morphologies: first two maxillary teeth tricusped (central cusp with two accessory cusps), third and fourth maxillary teeth with occlusal edges formed by numerous small cusps enclosing three larger cusps aligned anteroposteriorly, fifth maxillary tooth large and bulbous with a central cusp and two reduced accessory cusps located anterolingually and posterobuccally on the tooth crown; mandibular symphysis extremely elongated encompassing all but the posteriormost dentary tooth.

This diagnosis was modified from that of Young (1973) and Li (1985), excluding some characters that are now known in other crocodyliform taxa (e.g., small supratemporal fenestra, anterodorsal branch of the quadrate enclosing the temporo-orbital passage with the parietal, platycoelus vertebrae).

Description. The specimen preserves the anterior and infratemporal regions of the skull as well as the anterior half of both lower jaws (Fig. 2). The snout is slightly crushed dorsally but is completely preserved except for its anteriormost region. The snout is markedly short, high, and moderately broad (i.e., oreinirostral, sensu Busbey, 1994), resembling the condition of other basal crocodyliforms. As in most crocodyliforms, the external surface of the skull is ornamented with closely spaced pits. The orbits are large and dorsolaterally exposed. Only the ventral half of the infratemporal fenestra is preserved, and it seems to be small relative to the orbital diameter. The suborbital fenestra is reduced and, in contrast with most basal crocodyliforms, the antorbital fenestra is closed.

The specimen preserves only the posterior half of the premaxilla, at its contact with the maxilla. The posterior region of the premaxilla has two distinct planes of exposure, a laterally facing plane located ventrally and a dorsolaterally facing plane located dorsally, but the dorsal portion has been flattened by crushing. The surface of the ventral region of the premaxilla is distinctly smooth, lacking the ornamentation present in most of the skull surface (Fig. 2C). The dorsal surface, instead, is heavily sculptured with small and closely spaced pits. This region bears a well-developed posterodorsal process that wedges between the maxilla and nasal bones and posteriorly reaches the anteroposterior midpoint of the snout as preserved (Fig. 2A). The contact with the maxilla is interrupted at its ventral edge by a well-developed notch into which the mandibular

caniniform tooth occludes. The ventral edge of this notch seems to be widely opened, lacking the posteroventral process of the premaxilla present in other forms (e.g., *Dibothrosuchus* IVPP V 7907; *Baurusuchus* DGM 299-R), but this is variable in some taxa and individuals (Clark, 1986). Above this notch, the premaxillo-maxillary suture is briefly directed dorsally and slightly interdigitated. Dorsal to this region, the suture is straight and directed posteromedially.

The external surface of the maxilla also has two distinct planes, continuing those of the premaxilla, but it too has been crushed. The buccal margin of the maxilla is straight, lacking the festooned pattern present in most neosuchian taxa. The laterally facing facial process of the maxilla extends dorsally from the buccal margin of the maxilla. As in the premaxilla, this surface is distinctly smooth, having only a few irregularly spaced pits (Fig. 2C). These differ from the ornamentation pattern of the dorsal surface of the skull, being much smaller, deeper, and with sharper edges than the ornamentation pits. The ventral maxillary pits are interpreted here as neurovascular openings, as noted in other crocodyliforms (Witmer, 1997; Soares, 2002). The dorsal region of the maxilla faces dorsolaterally and is heavily ornamented with closely spaced pits (Fig. 2A). The ventral portion of the anterior maxillary margin is concave, forming the posterior edge of the premaxillo-maxillary notch. Dorsal to this notch, the anterior maxillary edge borders the premaxillary posterodorsal process. The maxillary dorsal margin is convex and contacts the nasal, extending on the dorsal surface of the posterior half of the snout. Posterodorsally, the maxilla contacts the lacrimal in an interdigitated suture directed posterolaterally. Posteroventral to this region, the maxilla forms most of the anteroventral margin of the orbit contacting the jugal approximately at the anteroposterior midpoint of the infraorbital bar. The jugal overlaps the maxilla in this region and their contact extends ventrally down to the buccal margin of the maxilla. The posteromedial surface of the maxilla is well exposed on the medial to the anterior margin of the orbit.

The lacrimal is almost excluded from the lateral surface of the skull at the anterodorsal margin of the orbit. Medial to this region, there is a large depression on the inner surface of the orbit, where the opening of the lacrimal duct is located in extant crocodylians. Above this region, the lacrimal is exposed on the dorsal surface of the skull where it bears a concave, smooth surface for the articulation with the anterior palpebral (Fig. 2A). The lacrimal's contact with the prefrontal is not clearly preserved in this area.

The nasals are almost completely preserved, except for their anterior tip. Their dorsal surface is heavily sculpted along their entire length with the same pattern described for the dorsal surface of the maxilla. The

premaxillae overlap the nasal medial to their natural contact, and therefore the anterior width of the nasals cannot be precisely determined. However, the development of the posterodorsal premaxillary process and the orientation of the maxillo-nasal suture suggest that the nasals were transversally narrow at their anterior end and expanded posteriorly (Fig. 2A). The posterior region of the nasals is only preserved on the left side of specimen. Here, the nasal widens and contacts the lacrimal on its medial edge along a posteromedially directed suture that continues along the medial border of the left prefrontal. The contact with the frontal is not preserved.

The left jugal is completely preserved in GMPKU-P 200101, except for the dorsal part of the postorbital process. The lateral surface of the anterior process has a well-developed lateral shelf below the orbit (Fig. 2B). The edge of this shelf originates at the anterodorsal limit of the jugal and extends posteroventrally, increasing its lateral development. Dorsal to this shelf the jugal surface is dorsolaterally exposed and bears a heavily ornamented pattern. In contrast, the jugal surface ventral to the shelf is smooth and laterally exposed. The ventral margin of this surface is oriented posterodorsally while the lateral edge of the shelf is directed posteroventrally. Thus, both margins meet ventral to the posterior edge of the orbit. As in basal crocodyliforms, the base of this process is wide, sculptured, and continuous with the outer surface of the jugal (Fig. 2C). The postorbital process narrows dorsally, being cylindrical in cross section at its dorsalmost preserved region. This process is anteroposteriorly centered on the jugal and is dorsomedially directed. The infratemporal bar of the jugal is flat, ornamented, and its ventral edge is concave (Fig. 2C). The jugal forms the anteroventral margin of the infratemporal opening and is overlapped posteriorly by the quadratojugal at the anteroposterior midpoint of this fenestra. The jugal-quadratojugal suture extends posteroventrally on the lateral surface of the infratemporal bar beyond the posterior edge of the infratemporal fenestra.

The left quadratojugal is partially preserved. It is slightly ornamented at its base ventrally and posteriorly to the infratemporal fenestra (Fig. 2A, C). The dorsal process of the quadratojugal is not completely preserved, although its base is wide and lacks the ornamentation present on the ventral margin of the quadratojugal. The quadratojugal surface posterior to the infratemporal fenestra is extensive although its posterior edge and its contact with the quadrate are not preserved.

A large anterior palpebral is preserved on the left side close to its natural position (Fig. 2A). It has the same ornamentation pattern present on the dorsal surface of the skull, except for a narrow region bordering its lateral margin that seems to be smooth. Although its medial

edge is probably broken, the palpebral is roughly triangular.

Only the posterior region of pterygoids is exposed due to the occlusion of the mandible. The ventral surface of the left pterygoid is better preserved, while the dorsal surface can be seen on the right side. In ventral view the pterygoids enclose the posterior area of the choanal groove (Fig. 2B). The choana opens ventrally at the end of an elongated, narrow groove (ca. one sixth of the skull width at that level). This opening extends posteriorly to the pterygoid wings where it narrows even more. A thin, vertical choanal septum completely divides this opening extending from the roof of the pterygoids along the entire choanal exposed length. Lateral to this, the pterygoid wings are briefly extended laterally, rather than lateroventrally as in most neosuchian taxa. The pterygoid wings are dorsoventrally high rather than laminar, showing a well-developed posterior surface (Fig. 2A). In this region, the pterygoids probably enclosed pneumatic spaces as seen on some broken surfaces. The lateral edges of the pterygoid wings are convex and anterodorsally oriented. The dorsal surface of the pterygoid wings is exposed on the right side of GMPKU-P 200101. This surface is slightly concave on its lateral edge and, probably, medially, although the latter area is crushed and poorly preserved. The pterygoid contact with the ectopterygoid cannot be precisely determined due to poor preservation. The ventral surface of the pterygoid wing is flat and smooth instead of being ornamented as in some basal crocodyliforms (e.g., *Protosuchus* UCMP 131827). However, several small pits are scattered on the ventral surface of the posterior area of the pterygoid wings. The posterior edge of the ventral surface of the pterygoid wing originates anterior to the posterior end of the choanal groove and extends as a posterolaterally directed ridge (Fig. 2B). As in basal crocodyliforms, posterior to this ridge the base of the quadrate process of the pterygoids is slightly concave, extremely wide, and ventrally exposed (Fig. 2B). This contrasts with the condition present in mesoeucrocodylians, where the pterygoids are markedly constricted posterior to the pterygoid wings, and the base of the quadrate processes faces more posteriorly. The medial edges of the quadrate processes of the pterygoids form the lateral margin of the posterior end of the choanal groove, where this opening markedly narrows posteriorly. The concave surface lateral to these ridges also bears the small pits present on the pterygoid wings. The posterior end of the pterygoids and their contact with the braincase are not preserved in GMPKU-P 200101. However, on the posterior broken section, a thin anterior extension of the basisphenoid wedging between quadrate processes of the pterygoids is present on the posterior edge of the choana.

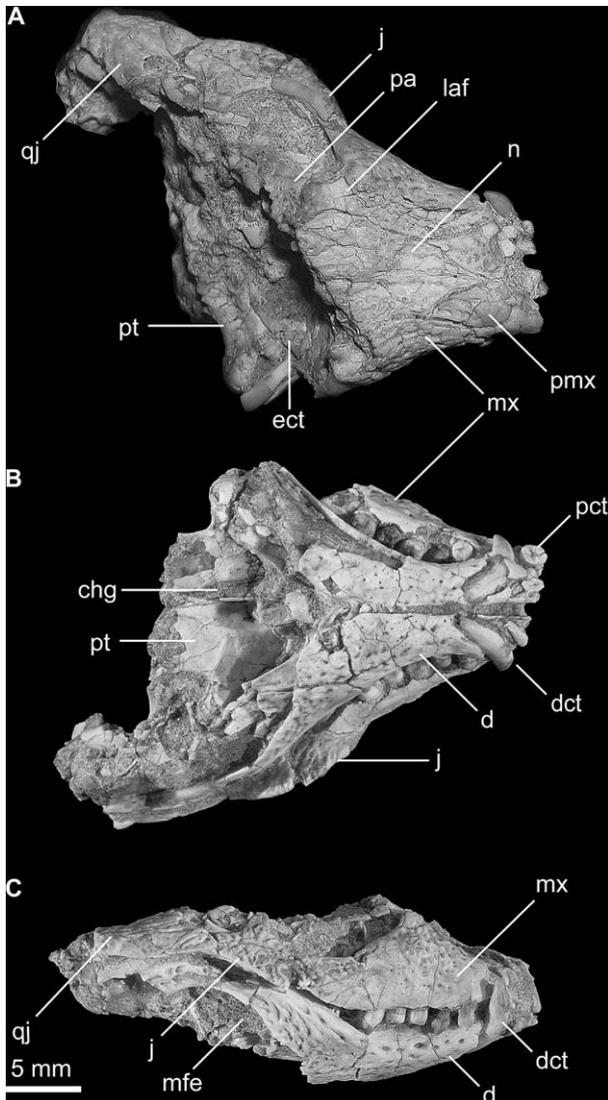


Fig. 2. Skull of *Edentosuchus tienshanensis* (GMPKU-P 200101) in A, dorsal, B, ventral, and C, lateral views: chg, choanal groove; d, dentary; dct, dentary caniniform tooth; ect, ectopterygoid; j, jugal; laf, lacrimal facet for the anterior palpebral; mfe, mandibular fenestra; mx, maxilla; n, nasal; pa, anterior palpebral; pct, premaxillary caniniform tooth; pmx, premaxilla; pt, pterygoid; qj, quadratojugal.

The right ectopterygoid is exposed in dorsal view (Fig. 2A) and, although its precise contact with the pterygoid and maxilla cannot be determined, its main axis is oriented anteriorly rather than anterolaterally (as in most crocodyliforms).

Only the posterior region of the palatines is exposed on the palate. The left palatine is a sheet-like element that underlies ventrally the anterior process of the pterygoid, rather than being strongly sutured to it as in mesoeucrocodylian taxa. The poor preservation of this region does not allow determination of whether the palatines contacted each other forming a bony secondary palate.

The anterior half of the lower jaw was preserved in GMPKU-P 200101, comprising most of the dentaries and the anterior end of the surangulars. The dentaries and the lower teeth are the only overlapping elements between GMPKU-P 200101 and the type material of *Edentosuchus tienshanensis* (IVPP V 3236), upon which the taxonomic identification was established.

Both the holotype (IVPP V 3236) and the specimen described here (GMPKU-P 200101) have an extremely long mandibular symphysis, extending posteriorly in GMPKU-P 200101 beyond the level of the anterior margin of the orbit. Consequently, in these specimens, only the posteriormost of the observed dentary teeth is implanted beyond the posterior end of the ventral surface of the symphysis. On the posterior half of this surface, both dentaries meet at an interdigitated suture; however, on the anterior half the medial edges of the dentaries are straight and meet at a straight contact. At this point the dentaries are slightly separated by a matrix filled space, probably due to post-mortem separation (Fig. 2B). The ventral surface is broken anteriorly, exposing the roots of the first two teeth. Lateral to the symphysis, the ventral surface of the dentaries is slightly ornamented with well-spaced pits both on the holotype and in GMPKU-P 200101. In ventral view, the lateral margins of the dentaries also show diagnostic characters of *Edentosuchus tienshanensis* noted for the holotype (Li, 1985). These margins are only slightly expanded below the caniniform teeth and are strongly constricted posterior to it (Fig. 2B). At this point, close to the level of the third postcaniniform dentary teeth, mandibular breadth is approximately half the lateromedial width of the snout. Posterior to this constriction, at the anteroposterior midpoint of the mandibular symphysis, the lateral edges of the dentaries strongly diverge laterally, following the post-rostral expansion of the skull (Fig. 2B).

The dorsoventral extension of the dentaries gradually increases posteriorly along the symphyseal region. This anteriorly tapering profile seen in lateral view is mainly caused by the increasing depth of the ventral edge of the dentaries, since the dorsal margin is straight and parallel to the longitudinal axis of the skull (Fig. 2C). Along the symphyseal region, the lateral surface of the dentaries also shows an unusual morphology. This surface is bordered ventrally by several large pits aligned anteroposteriorly, interpreted here as neurovascular foramina. These differ from ornamentation pits since their edges are better defined, deeper, and their diameter is not reduced internally (Fig. 2C). Furthermore, the lateral surface of the right dentary is broken at one of these pits, showing that they actually penetrate the lateral surface of this bone. Dorsal to them, the buccal surface of the dentaries is smooth and exposed dorsolaterally. Therefore, the buccal margin of the dentary tooth row is markedly inset, located medial to

the lingual margin of the maxillary tooth row. Posterior to the dentary tooth row, the smooth dorsolateral surface is reduced and disappears. In contrast to the symphyseal region, the posterior external surface of the dentaries is laterally exposed, heavily sculptured, and forms the anterodorsal margin of an enlarged mandibular fenestra (Fig. 2C). Here, the dorsal edge of the dentaries strongly curves dorsally following the development of the mandibular fenestra, contacting the surangular posteriorly. The dentaries seem to have a posteroventral process that forms the anteroventral margin of the mandibular fenestra, although this region is not well preserved in GMPKU-P 200101 or in the holotype. Posterior to the symphysis the medial surface of the dentaries is briefly preserved, exposing a medially opened meckelian groove (as noted for the holotype; Li, 1985). This groove could have been covered by the splenial as in other crocodyliforms; however this element was not preserved in GMPKU-P 200101.

The surangular is not entirely preserved in any specimen. However, in GMPKU-P 200101, it can be seen that the surangular forms the posterior half of the dorsal margin of the mandibular fenestra and that its dorsal edge is strongly bowed dorsally. At this point, the surangular is bounded dorsally by the ventrally concave jugal infratemporal bar described above (Fig. 2C). The posteriormost preserved region of the surangular deflects ventrally bordering the posterodorsal edge of the mandibular fenestra.

The dentition of *Edentosuchus tienshanensis* was previously known only by poorly preserved lower teeth of the type material. The beautifully preserved dentition of GMPKU-P 200101 is unique among Crocodyliformes, showing an extremely high degree of heterodonty. Only the posteriormost right tooth was preserved on the premaxillae. The apex of this element is missing, but the base of its crown is conical, lacks serrations on its edges, and its cross section is similar in size to the mandibular caniniform teeth (Fig. 2A). The five

maxillary teeth have unusual crown morphologies. The first two teeth have crowns slightly compressed lateromedially and bear three cusps aligned anteroposteriorly on their apex (Fig. 3A). The central cusp is the largest and occupies most of the tooth crown, while the other two accessory cusps are much smaller and located on the anterior and posterior edges of the crown. These cusps are more developed in the second maxillary tooth (Fig. 3A). The third and fourth maxillary teeth are subquadrangular in cross section and their crowns are covered with a heavy enamel coat. At their apex, these teeth bear a distinctive pattern of multiple cusps. Six small enamel cusps are located along the buccal and lingual edges of the occlusal surfaces of these teeth (Fig. 3B). These cusps are disposed anteroposteriorly following slightly arched rows. The buccal row of cusps is laterally convex, while the lingual row is medially convex, enclosing a strongly concave occlusal surface. Within this concave surface there are three large cusps anteroposteriorly aligned and mediolaterally centered. The posteriormost maxillary tooth is the largest maxillary element and shows a different morphology than the preceding elements. The crown is markedly bulbous and has a large central cusp on its apex (Fig. 3B). There are two accessory cusps, although the three cusps are not anteroposteriorly aligned as in the anterior maxillary teeth. On this tooth, the anterior accessory cusp is located anterolingually, while the posterior accessory cusp is located posterobuccally. Additionally, the accessory cusps of the last maxillary tooth are much smaller relative to the central cusp. All maxillary teeth are implanted within a continuous groove, rather than in separate alveoli.

The lower dentition is not entirely exposed since it lies medial to the upper tooth rows. As in the type specimen, nine mandibular teeth were preserved in GMPKU-P 200101 although more may have been present anteriorly. The most anterior tooth is identical to that of the holotype, being small and projected anterolaterally. Its

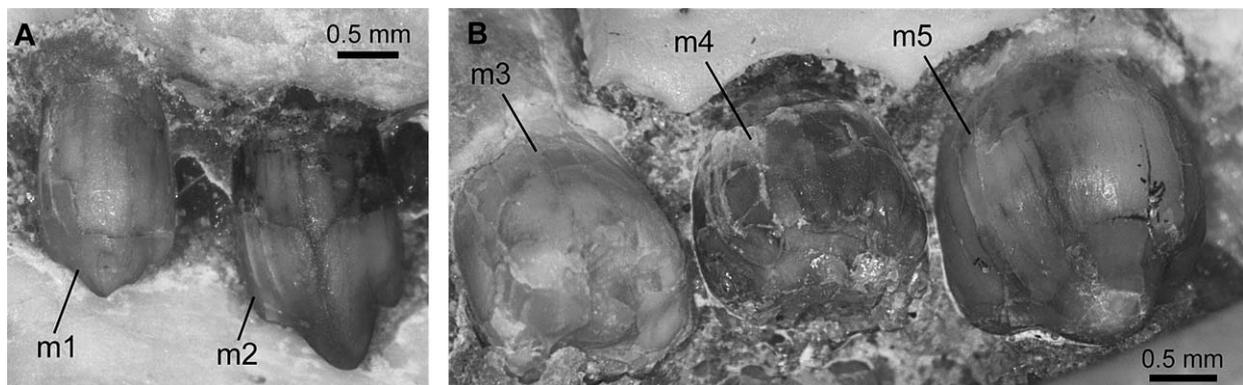


Fig. 3. Maxillary dentition of *Edentosuchus tienshanensis* (GMPKU-P 200101) in lateral view. A, first two left maxillary teeth; B, posteriormost three right maxillary teeth: m1–m5, first maxillary tooth to fifth maxillary tooth.

crown is cylindrical at its base but lateromedially compressed at its apex, where three extremely reduced cusps are anteroposteriorly aligned. The second dentary tooth is an extremely enlarged caniniform that fits into the notch at the premaxilla-maxilla contact (Fig. 2C). This element lacks serrations along its margins and bears longitudinal striations on the enamel, matching the morphology of the holotype material. As in the holotype, GMPKU-P 200101 has seven postcaniniform dentary teeth, although these are only partially exposed on the right side since the mandible is in occlusion. The crowns of these elements follow the morphology found in the holotype material, although they are better preserved. All postcaniniform dentary teeth are much smaller than the caniniform but they increase in size posteriorly. The first postcaniniform is similar in size to the first dentary tooth. Its crown is cylindrical at the base and bears three anteroposteriorly aligned cusps on its apical region. The second postcaniniform tooth is similar in size to the preceding element but it is only partially exposed. Two cusps are present on the anterobuccal and posterobuccal corners of its crown. The following three teeth are almost completely embedded in the matrix and therefore it can only be noted that they increase in size posteriorly. The sixth postcaniniform is partially exposed and shows a similar morphology to its opposite (i.e., fourth) maxillary tooth, having an arched row of multiple small cusps that lie on the buccal margin of the occlusal surface of its crown. The most posterior dentary tooth is barely exposed; it lies lingual to the bulbous fifth maxillary tooth.

Crocodyliformes Hay, 1930 (sensu Clark, 1986)
incertae sedis

Specimen. GMPKU-P 200102. This specimen consists of nicely articulated postcranial elements, including 18 articulated vertebrae (13 presacrals, 2 sacrals, and the 3 most proximal caudals) found in articulation with the pelvis and most of the left hindlimb. This second crocodyliform specimen was found at the same locality. The taxonomic identity of this specimen cannot be established at the moment due to the lack of overlapping elements with the only other known crocodyliform from the Tugulu Group (i.e., *Edentosuchus tienshanensis*), although as discussed below, several characters suggest that GMPKU-P 200102 belongs to a non-neosuchian basal crocodyliform.

Presacral vertebrae. Most of these elements are preserved with only the dorsal surface of their neural arches exposed, although some vertebrae have also exposed the lateral region of the neural arches and vertebral centra. The neural spine of the anteriormost vertebra, an anterior dorsal, is well-developed, tall, and subrectangular in lateral view. The height of the neural

spines decreases posteriorly along the presacral series, being a slightly developed ridge in the last four vertebrae.

The transverse processes of the anteriormost vertebrae are thin, laminar, and well developed in their mediolateral extension but reduced in their anteroposterior dimensions (Fig. 4A). The mid-section of the preserved presacral vertebrae shows, in contrast to advanced neosuchian crocodyliforms, a large anteroposterior development in the transverse processes. The lateromedial extension of the transverse processes of these vertebrae cannot be precisely determined due to poor preservation, although they do not seem to be as elongated as in neosuchian crocodyliforms. The dorsal surfaces of these transverse processes have a marked depression located anteriorly to the postzygapophyseal processes (Fig. 4A). This condition is also present in some basal mesoeucrocodylians [e.g., *Notosuchus* MACN-RN 1037, *Mahajangasuchus* UA 8654; cf. *Theriosuchus* (Wu et al., 1996)], but is absent in most derived neosuchians. The transverse processes of the four most posterior presacral elements have not been preserved.

The prezygapophyses of the preserved presacral vertebrae are poorly developed and their articular surfaces are exposed lying in the horizontal plane. The dorsal surfaces of the prezygapophyseal processes are almost continuous with the anterior margin of the transverse process, and the prezygapophyseal articular facets are located at the same level as the transverse processes. The anterior edges of the prezygapophyseal processes do not exceed the anterior margin of the vertebral centra (as seen in the fourth and fifth preserved vertebrae).

The postzygapophyses are well developed, directed posterolaterally, and moderately curved laterally along their extension (Fig. 4A). The postzygapophyseal processes are well developed, robust, and extend from the caudal margin of the neural spines, although they lack the postzygapophyseal lamina present in basal mesoeucrocodylians (e.g., *Arapesuchus* AMNH 24450; *Notosuchus* MACN-RN 1037). The articular facets of the postzygapophyses are dorsoventrally located at the same level as the dorsal surface of the transverse processes, in contrast to the condition of most crocodyliforms in which the articular facets are located dorsally to the transverse processes (e.g., *Protosuchus* AMNH 3024; *Sichuanosuchus* IVPP V 1095; *Arapesuchus* AMNH 24450; *Hyposaurus* AMNH 2390; *Crocodylus* AMNH CA20). Between the postzygapophyseal processes the incisura vertebralis caudalis is mediolaterally wide and shallow (Fig. 4A).

The exposed vertebral centra are poorly constricted at their midpoint and lack hypapophyses. The neurocentral suture is visible in the fourth and fifth preserved presacral vertebrae, but is absent in the two most posterior presacral elements.

Sacral and caudal vertebrae. The two sacral vertebrae are in articulation with the pelvis. The neural arches of these elements are poorly preserved, although it is possible to determine that these elements were not fused. The first sacral rib is firmly attached to the anterior margin of the ilium (Fig. 4A). This rib is anteroposteriorly short and dorsoventrally tall. The second sacral rib is attached to the posterior half of the ilium and has an anteroposteriorly long distal articular facet (Fig. 4A). The three anteriormost caudals have been preserved in articulation with the sacrum. Their centra are somewhat constricted at their midpoint (i.e., “spool-shaped”) and are completely fused to the neural arch pedicels. The first two elements do not have posteroventral facets for the hemal arches. The posterior region of the third centrum is poorly preserved, and it is not possible to determine the presence or absence of such an articular facet.

Pelvis. The ilia are poorly preserved on their dorsal surface, and it is not possible to determine the development of the anterior iliac process and the supra-acetabular buttress. The preserved portion of the acetabulum seems to be deep, although the presence of a laterally expanded acetabular roof cannot be determined due to poor preservation. Both ischia and pubes are completely preserved close to their natural articulation with the iliac pedicels. The ischium is a rather short element with a markedly constricted shaft, the lateral surface of which is convex, smooth, and lacks ridges (Fig. 4D). The distal end of the ischium is only slightly expanded in comparison with other crocodyliforms. The pubis is notably elongated, being approximately 150% the length of the ischium (Fig. 4D), in contrast to the generalized condition of crocodyliforms where the pubis and ischium are approximately equal in length (e.g., *Orthosuchus* SAM-K 409; *Araripesuchus* AMNH 24450; *Steneosaurus* SMNS 17484a; *Goniopholis* AMNH 533; *Crocodylus* AMNH CA30). A similarly elongated pubis is present in *Protosuchus* (AMNH 3024) and some basal crocodylomorphs [e.g., *Terrestrisuchus* (Crush, 1984)]. The pubis is extremely narrow at its proximal head, which probably articulated exclusively with the anterior edge of the ischium (i.e., excluded from the acetabulum, a synapomorphic character of Crocodyliformes). The pubic shaft is an extremely elongated and thin, rod-like process (Fig. 4B, D). The distal end of this element is moderately expanded as in mesoeucrocodylians, although this expansion is reduced in GMPKU-P 200102 and occupies only the distal fourth of the pubic length. The distal end of both pubes is in articulation with two posterior elements of the gastralium (Fig. 4B).

Hindlimb. The left hindlimb is completely preserved in articulation with the pelvis, except for the distal end

of the metatarsals and the pedal phalanges. Only the proximal head of the left femur is preserved from the right hindlimb. The femur is extremely slender and elongate, as in most basal crocodyliforms (e.g., *Protosuchus* AMNH 3024; *Gobiosuchus* ZPAL MgR-II/67), in contrast to the proportionally short and stout femur of most derived mesoeucrocodylians. The proximal head of the femur is restricted to the proximal 10% of the preserved femoral length (Fig. 4A). No details on the morphology of the femoral trochanters can be observed. Distal to the femoral head, the medial margin of the femur is straight and smooth, lacking the prominent process for the insertion of the m. caudofemoralis present in most basal mesoeucrocodylians [e.g., *Notosuchus* MPCA #1; *Araripesuchus* AMNH 24450; *Mahajangasuchus* (Buckley and Brochu, 1999)]. The distal region of the femur has not been preserved. The left tibia is poorly exposed except for its poorly preserved proximal region and only the shaft and distal end of the fibula are preserved in GMPKU-P 200102. However, the proximal end of the tibia and the distal end of the fibula seem to be in natural articulation with the femur and tarsus, respectively. Based on the proximal and distal position of these elements, their proximodistal length would be approximately similar to that of the femur. The preserved portion of the fibula is markedly slender and elongate and in natural articulation with the rounded fibular condyle of the calcaneum.

The calcaneum has a well-defined, rounded, and extensive fibular condyle. The sustentaculum for the articulation with the astragalar trochlea extends posteromedially from the posterior edge of the fibular condyle. Posterior to the fibular condyle the calcaneum bears a robust calcaneal tuber (Fig. 4A–C), the posterior surface of which has a well-developed groove as in all crocodyliforms. In contrast to the condition of *Protosuchus* (AMNH 3024), the calcaneal tuber groove is oriented along a plane that is slightly deflected laterally with respect to the major axis of the fibular condyle, suggesting it had a more sprawling foot (Parrish, 1987). Distal to the fibular condyle, on its anteroventral surface, the calcaneum has an extensive, flat and obliquely oriented articular facet for the distal tarsal (Fig. 4C). The astragalus is not exposed except for its distal roller in articulation with the metatarsals I and II.

The proximal ends of the five left metatarsals are preserved in articulation with the tarsus. The proximal ends of metatarsals I–III overlap laterally the adjacent element (Fig. 4B), although the degree of overlapping seems to be less marked than that of *Protosuchus* (AMNH 3024). The proximal halves of metatarsals I–IV are subequal in their dimensions (Fig. 4B), in contrast to the condition of most neosuchians in which metatarsal I is notably more robust than metatarsals III and IV. Metatarsal IV is the only metatarsal completely preserved and has a weakly expanded distal articular

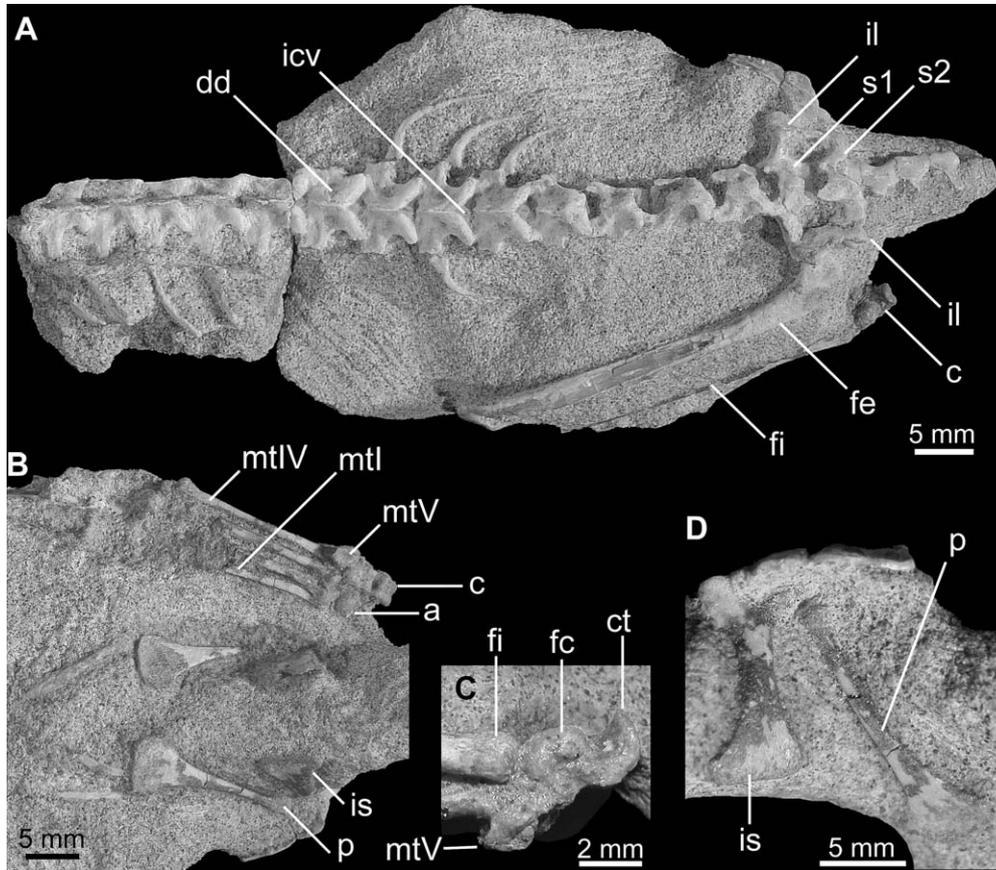


Fig. 4. Postcranial remains of GMPKU-P 200102 in A, dorsal view; B, ventral view; C, left calcaneum in lateral view; D, right ischium and pubis in lateral view: a, astragalus; c, calcaneum; ct, calcaneal tuber; dd, depression on dorsal surface of neural arch; fc, calcaneal fibular condyle; fe, femur; fi, fibula; il, ilium; icv, incisura vertebralis caudalis; is, ischium; mtI, metatarsal I; mtIV, metatarsal IV; mtV, metatarsal V; p, pubis; s1, first sacral vertebra; s2, second sacral vertebra.

end. Its proximodistal length is approximately half of the inferred fibular length. Only the most proximal region of the fifth metatarsal is preserved (Fig. 4B), and it is not possible to determine if it was reduced as in all crocodyliforms. This element is located ventral to the fourth metatarsal and articulates proximally with a large distal tarsal.

Discussion. The postcranial remains of GMPKU-P 200102 show several characters that are exclusively found either in basal mesoeucrocodylians or in basal crocodyliforms but generally absent in neosuchian crocodyliforms (e.g., anteroposteriorly long transverse processes in dorsal vertebrae, depression on dorsal surface of neural arches of dorsal vertebrae, elongated pubis with slightly expanded distal end, elongated and slender hindlimb, subequal metatarsi). These similarities suggest that GMPKU-P 200102 belongs to a non-neosuchian crocodyliform. Unfortunately, the inadequate knowledge of postcranial remains of most fossil crocodyliforms precludes, at the moment, a more precise taxonomic identification within a phylogenetic context. Thus, the identification of this specimen as *Edentosuchus*

cannot be rejected or corroborated at present, although both this taxon and GMPKU-P 200102 are interpreted to be small terrestrial non-neosuchian crocodyliforms from the same levels of the Tugulu Group.

4. Phylogenetic relationships of *Edentosuchus*

Previous considerations of *Edentosuchus* regarded this taxon either as a basal crocodyliform (i.e., “protosuchian”; Young, 1973) or as a basal mesoeucrocodylian (Li, 1985). However, in these studies the phylogenetic relationships of this taxon were not tested within a cladistic framework. Additionally, recent phylogenetic analyses of Crocodyliformes did not include *Edentosuchus* among the sampled taxa, probably because of the incompleteness of the type specimen. The novel information available through the study of this new specimen allows the previously proposed phylogenetic hypotheses of *Edentosuchus* to be tested within a cladistic analysis.

A dataset was constructed with the addition of new characters to a revised list of characters used in previous

studies of crocodyliform phylogeny (Clark, 1994; Wu et al., 1997; Buckley et al., 2000; Ortega et al., 2000; Pol, 2003). A total of 183 characters were used in this analysis scored across 45 taxa. Due to the putative relationships of *Edentosuchus*, our taxon sampling scheme focused on both basal crocodyliforms and basal mesoeucrocodylians (comprising 25 out of 45 taxa). The phylogenetic analysis was analyzed under equal weighted parsimony using Nona (Goloboff, 1993). A heuristic tree search was performed consisting of 1000 replicates of RAS + TBR with a final round of TBR (mult*1000; max*); holding 20 trees per replication (hold/20;). Zero-length branches were collapsed with the strictest criterion (i.e., when any possible states are shared between the ancestor and descendant node; amb-). Two most parsimonious trees of 627 steps ($CI = 0.36$, $CI_{inf} = 0.35$, $RI = 0.67$) were found in 817 out of 1000

replications. Further searches conducting 10,000 iterations of the Parsimony Ratchet (Nixon, 1999) resulted in the same set of topologies (hitting the best length 6884 times).

In all most parsimonious hypotheses, *Edentosuchus* is depicted as the sister taxon of an unnamed taxon from the Lower Jurassic Kayenta Formation of Arizona (Fig. 5). This form has been discussed by Clark and Fastovsky (1986, pp. 298, 299), Clark (in Benton and Clark, 1988), and Clark (1994), and illustrated by Sues et al. (1994, fig. 16.3). The group comprising *Edentosuchus* and the Kayenta taxon is diagnosed by five unambiguous synapomorphies (choana opens posteriorly into a choanal groove [character 39; paralleled in most mesoeucrocodylians]; cheek teeth constricted at their crown base [character 156; paralleled in some mesoeucrocodylians]; posterior teeth with multiple cusps

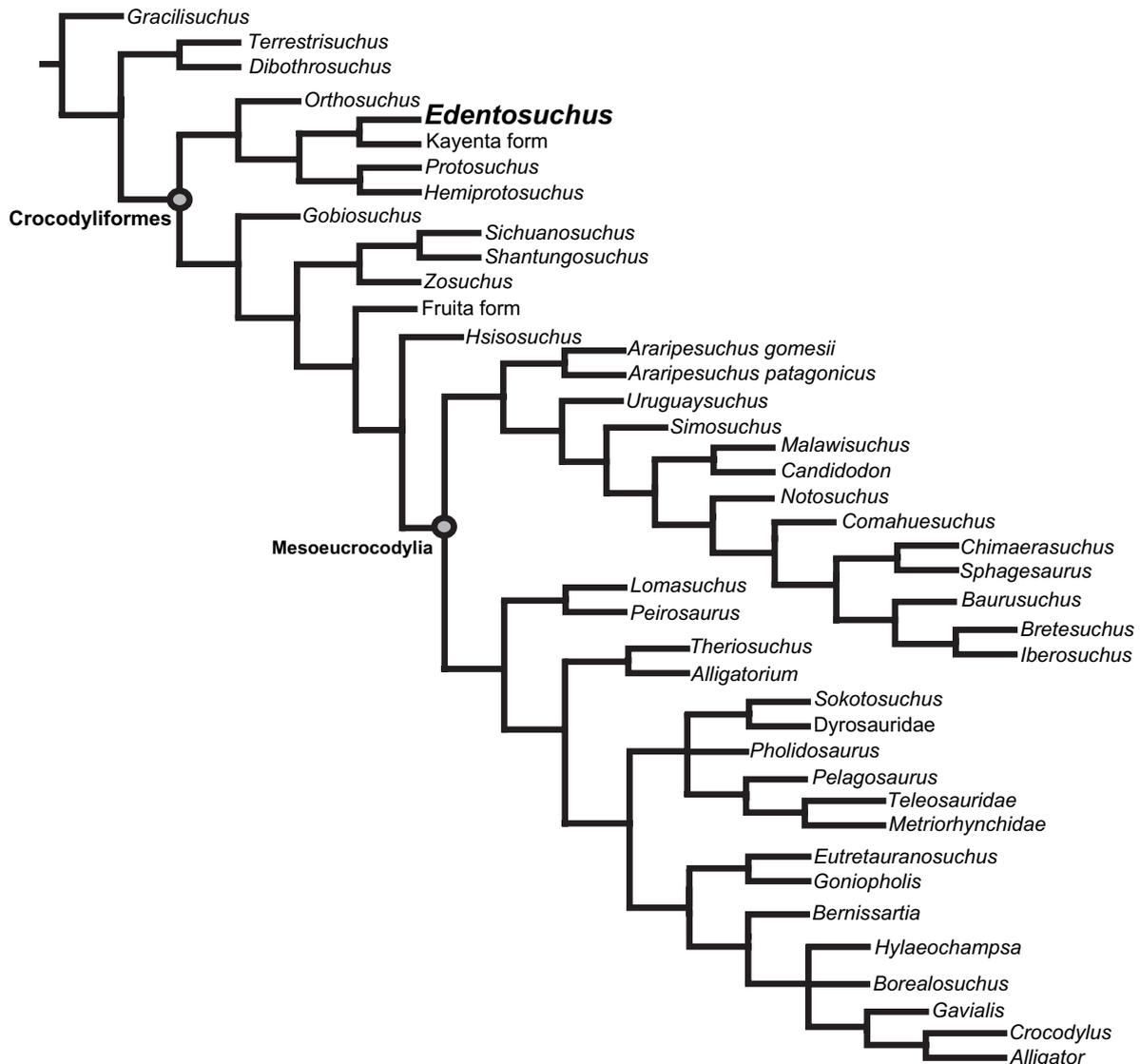


Fig. 5. Strict consensus of the most parsimonious hypotheses obtained in the phylogenetic analysis.

located on the edges of the occlusal surface [character 161]; major axis of ectopterygoid body directed anteriorly [character 164]; dorsally arched jugal below infratemporal fenestra [character 179]). This clade is the sister group of a clade formed by *Hemiprotosuchus leali* and *Protosuchus richardsoni* from the Late Triassic and Early Jurassic, respectively. The results of this cladistic analysis also support the monophyly of Protosuchidae, as defined by Clark (1986). Protosuchidae is here diagnosed in this dataset by four synapomorphies (narrow ventrolateral contact between otoccipial and quadrate [character 48]; pterygoid ramus of quadrate with deep groove along ventral edge [character 50]; arched dorsal edge of surangular [character 74; paralleled in some mesoeucrocodylians]; lateral eustachian openings and foramen intertympanicum anteroposteriorly aligned [character 132]), of which only one could be scored in the new specimen.

The Early Jurassic *Orthosuchus stormbergi* of South Africa is depicted as the sister taxon of the protosuchid clade, forming a group diagnosed by four synapomorphies: large ventrolateral part of otoccipital ventral to paroccipital process [character 60]; transverse process of dorsal vertebrae dorsoventrally high [character 114]; lateral margins of nasals laterally concave posterior to external nares [character 127]; postorbital process of jugal located anteriorly [character 143; secondarily modified in *Edentosuchus*]. In all most parsimonious hypotheses *Gobiosuchus*, *Sichuanosuchus*, and *Shantungosuchus* were depicted as more closely related to mesoeucrocodylians than to Protosuchidae (i.e., rejecting the monophyly of the group traditionally named “Protosuchia”, contra Wu and Sues, 1996, and Wu et al., 1997).

Bremer support values for most nodes are low and most basal nodes of the crocodyliform clade have a value of 1, denoting that addition of new evidence can easily overturn the relationships proposed here (although the most parsimonious hypotheses presented above are those that best explain the data at hand). Interestingly, among the suboptimal trees found during the Bremer analysis, two different alternative topologies were consistently retrieved. One of these topologies depicted a monophyletic Protosuchia (a group supported by characters such as multiple fenestra in the quadrate, broad ascending process of the quadratojugal, inflated basisphenoid, hypertrophied posterior premaxillary tooth, fourth dentary tooth caniniform, jugal anterior end not exceeding the anterior orbital margin). In contrast, the other topology placed the clade of *Edentosuchus* and the Kayenta form closer to mesoeucrocodylians than to protosuchids (supported by characters such as fused frontals, reduced number of maxillary teeth, bulbous teeth lacking denticulate carinae, ornamented

quadratojugal base, and pterygoid flanges dorsoventrally thick and pneumatic).

5. Conclusions

The specimens reported here add significant information to the poorly known crocodyliform fauna of the Lower Cretaceous beds of the Junggar Basin (Xinjiang Uygur Autonomous Region, China). Although it is unknown if GMPKU-P 200102 also belongs to *Edentosuchus*, this specimen is also interpreted to be a basal Crocodyliformes.

In particular, the new specimen of *Edentosuchus* (GMPKU-P 200101) provides key information for testing the phylogenetic relationships of this taxon within a cladistic framework. The preliminary phylogenetic analysis conducted here depicted this Early Cretaceous taxon as a member of the most basal clade of Crocodyliformes, Protosuchidae, extending the stratigraphic record of this clade for, approximately, 75 my.

Furthermore, the remarkable degree of heterodonty of GMPKU-P 200101 provides another case of unique multicusped tooth morphology among basal crocodyliforms. Previously known multicusped-tooth crocodyliforms are restricted to a clade of basal mesoeucrocodylians (e.g., *Malawisuchus*, *Simosuchus*, *Candidodon*, *Chimaerasuchus*). Therefore, the specimen reported here demonstrates that multicusped dentition evolved independently in at least two groups of basal crocodyliforms: in basal mesoeucrocodylians and in Protosuchidae.

Of particular interest is the presence of a suite of characters shared by *Edentosuchus* and the poorly known *Chimaerasuchus paradoxus* (Wu et al., 1995; Wu and Sues, 1996), also from the Lower Cretaceous of China (e.g., multicusped teeth, smooth lateral surface on maxilla, well developed jugal ridge, arched surangular). Although the most parsimonious topologies depict *Chimaerasuchus* as deeply nested with notosuchians within Mesoeucrocodylia and unrelated to *Edentosuchus*, further remains of the fragmentary *Chimaerasuchus paradoxus* are needed in order to conduct a more stringent test of its phylogenetic affinities.

Finally, considering the outcome of the present phylogenetic analysis, it is significant that the Cretaceous crocodyliform *Edentosuchus* is depicted as closely related to Late Triassic and Jurassic taxa from other continents. Moreover, other lineages of Cretaceous basal crocodyliforms from Central Asia (e.g., *Gobiosuchus*, and the *Zosuchus* + *Sichuanosuchus* + *Shantungosuchus* clade) also appear to have diverged from the earliest radiation of crocodyliforms during the Late Triassic and Early Jurassic. Thus, these results support the hypothesis that basal crocodyliform lineages

survived much longer in Central Asia than in the rest of the world.

Acknowledgements

We are grateful to the LACM-NGM crew for their dedication during the field season and to C. Coy, who skillfully prepared the specimens. Field work was supported by grants from the National Geographic Society, the Infoquest Foundation, and the Eppley Foundation to LMC. Part of this project was supported by National Natural Science Foundation of China (grant no. 40272008 to SAJ). Financial support to DP was provided by the Department of Earth and Environmental Sciences of Columbia University and the American Museum of Natural History. Access to specimens was made possible thanks to: J. Maisey (AMNH), M. Moser (BSP), M. Maisch (GPIT), X. Xing (IVPP), J.F. Bonaparte (MACN), E. Gomani (MAL), D. Unwin (MB), L.E. Ruigomez and R. Cuneo (MEF), Z.B. Gasparini and M. Reguero (MLP), F.L. de Broin (MNHN), A. Kellner (MNUFRJ), S. Cocca (MOZ), J.O. Calvo and L. Salgado (MUC-PV), J. Powell (PVL), C. Cartelle (RCL), A. Chinsamy (SAM), R. Wild (SMNS), D. Krause and G. Buckley (UA), A. Buscalioni and F. Ortega (UAM), I.S. Carvalho (UFRJ), and H. Olsomska (ZPAL).

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- 7 [Clark, 1994; ch 7]. Palatal parts of premaxillae: do not meet posterior to incisive foramen (0), or meet posteriorly along contact with maxillae (1).
- 8 [Clark (1994); ch 8]. Premaxilla-maxilla contact: premaxilla loosely overlies maxilla (0), or sutured together along a butt joint (1).
- 9 [modified from Clark (1994); ch 9]. Ventrally opened notch on ventral edge of rostrum at premaxilla-maxilla contact: absent (0), or present as a notch (1), or present as a large fenestra (2).
- 10 [Clark (1994); ch 10]. Posterior ends of palatal branches of maxillae anterior to palatines: do not meet (0), or meet (1).
- 11 [Clark (1994); ch 11]. Nasal-lacrimal contact: (0), or do not contact (1).
- 12 [Clark (1994); ch 12]. Lacrimal contacts nasal along: medial edge only (0), or medial and anterior edges (1).
- 13 [Clark (1994); ch 13]. Nasal contribution to narial border: yes (0), or no (1).
- 14 [Clark (1994); ch 14]. Nasal-premaxilla contact: present (0), or absent (1).
- 15 [modified from Clark (1994); ch 15]. Descending process of prefrontal: does not contact palate (0), or contacts palate (1).
- 16 [Clark (1994); ch 16]. Postorbital-jugal contact: postorbital anterior to jugal, or postorbital medial to jugal (1), or postorbital lateral to jugal (2).
- 17 [Clark (1994); ch 17]. Anterior part of the jugal with respect to posterior part: as broad (0), or twice as broad (1).
- 18 [Clark (1994); ch 18]. Jugal bar beneath infratemporal fenestra: flattened (0), or rod-shaped (1).
- 19 [Clark (1994); ch 19]. Quadratojugal dorsal process: narrow, contacting only a small part of postorbital (0), or broad, extensively contacting the postorbital (1).
- 20 [Clark (1994); ch 20]. Frontal width between orbits: narrow, as broad as nasals (0), or broad, twice as broad as nasals (1).
- 21 [Clark (1994); ch 21]. Frontals: paired (0), unpaired (1).
- 22 [Clark (1994); ch 22]. Dorsal surface of frontal and parietal: flat (0), or with midline ridge (1).
- 23 [modified from Clark (1994); ch 23, by Buckley and Brochu (1999); ch 81]. + Parieto-postorbital suture: absent from dorsal surface of skull roof and supratemporal fossa (0), or 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).
- 24 [Clark (1994); ch 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).
- 25 [modified from Clark (1994); ch 25]. Postorbital bar: sculptured (if skull sculptured) (0), or unsculptured (1).
- 26 [modified from Clark (1994); ch 26]. Postorbital bar: transversely flattened (0) or cylindrical (1).
- 27 [Clark (1994); ch 27]. Vascular opening in dorsal surface of postorbital bar: absent (0), present (1).
- 28 [modified from Clark (1994); ch 28]. Postorbital anterolateral process: absent or poorly developed (0), or well developed, long and acute (1).
- 29 [Clark (1994); ch 29]. Dorsal part of the postorbital: with anterior and lateral edges only (0), or with anterolaterally facing edge (1).
- 30 [Clark (1994); ch 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).
- 31 [Clark (1994); ch 31]. Bar between orbit and supratemporal fossa broad and solid, with broadly sculptured dorsal surface (0), or bar narrow, sculpturing restricted to anterior surface (1).
- 32 [modified from Clark (1994); ch 32]. Parietal: with broad occipital portion (0), or without broad occipital portion (1).

Appendix

1. Character list corresponding to the data matrix used in the phylogenetic analysis

Character (ch) definitions 1–101 were taken from Clark (1994) and have the same numeration as in the original publication. Ch 5 was excluded from the analysis (due to dependence with the modified definition of ch 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 source is cited along with the character number of the original publication. Characters 1, 3, 6, 23, 37, 45, 49, 65, 67, 69, 73, 77, 79, 90, 91, 96, 97, 103, 104, 105, 107, 126, 143, 149, and 166 were set as ordered characters (also marked with a + in this list).

- 1 [modified from Clark (1994); ch 1]. + External surface of dorsal cranial bones: smooth (0), slightly grooved (1), and heavily ornamented with deep pits and grooves (2).
- 2 [modified from Clark (1994); ch 2]. Skull expansion at orbits: gradual (0), or abrupt (1).
- 3 [modified from Clark (1994); ch 3]. + Rostrum proportions: narrow oreinrostral (0), or broad oreinrostral (1), or nearly tubular (2), or platyrostral (3).
- 4 [Clark (1994); ch 4]. Premaxilla participation in internarial bar: forming at least the ventral half (0), or with little participation (1).
- 5 [Clark (1994); ch 5]. Premaxilla anterior to nares: narrow (0), or broad (1).
- 6 [modified from Clark (1994); ch 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).

- 33 [Clark (1994); ch 33] Parietal: with broad sculptured region separating fossae (0), or with sagittal crest between supratemporal fossae (1).
- 34 [Clark (1994); ch 34]. Postparietal (dermosupraoccipital): a distinct element (0), or not distinct (fused with parietal?) (1).
- 35 [Clark (1994); ch 35]. Posterodorsal corner of the squamosal: squared off, lacking extra “lobe” (0), or with unsculptured “lobe” (1).
- 36 [modified from Clark (1994); ch 36]. Posterolateral process of squamosal: poorly developed and projected horizontally at the same level of the skull (0), or elongated, thin, and posteriorly directed, not ventrally deflected (1), or elongated, posterolaterally directed, and ventrally deflected (2).
- 37 [Clark (1994); ch 37]. + Palatines: do not meet on palate below the narial passage (0), or form palatal shelves that do not meet (1), or meet ventrally to the narial passage, forming part of secondary palate (2).
- 38 [Clark (1994); ch 38]. Pterygoid: restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0), or pterygoid extends dorsally to contact laterosphenoid and forms ventrolateral edge of the trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1).
- 39 [modified from Clark (1994); ch 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).
- 40 [Clark (1994); ch 40]. Palatal surface of pterygoids: smooth (0), or sculpted (1).
- 41 [Clark (1994); ch 41]. Pterygoids posterior to choanae: separated (0), or fused (1).
- 42 [modified from Clark (1994); ch 42, by Ortega et al. (2000); ch 139]. Depression on primary pterygoidean palate posterior to choana: absent or moderate in size being narrower than palatine bar (0), or wider than palatine bar (1).
- 43 [Clark (1994); ch 43]. Pterygoids: do not enclose choana (0), or enclose choana (1).
- 44 [modified from Clark (1994); ch 44]. Anterior edge of choanae situated near posterior edge of suborbital fenestra (or anteriorly) (0), or near posterior edge of pterygoid flanges (1).
- 45 [Clark (1994); ch 45]. + Quadrate: without fenestrae (0), or with single fenestrae (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2).
- 46 [Clark (1994); ch 46]. Posterior edge of quadrate: broad medial to tympanum, gently concave (0), or posterior edge narrow dorsal to otoccipital contact, strongly concave (1).
- 47 [Clark (1994); ch 47]. Dorsal, primary head of quadrate articulates with: squamosal, otoccipital and prootic (0), or with prootic and laterosphenoid (1).
- 48 [Clark (1994); ch 48]. Ventrolateral contact of otoccipital with quadrate: very narrow (0), or broad (1).
- 49 [Clark (1994); ch 49]. + Quadrate, squamosal, and otoccipital: do not meet to enclose cranioquadrate passage (0), or enclose passage near lateral edge of skull (1), or meet broadly lateral to the passage (2).
- 50 [Clark (1994); ch 50]. Pterygoid ramus of quadrate: with flat ventral edge (0), or with deep groove along ventral edge (1).
- 51 [Clark (1994); ch 51]. Ventromedial part of quadrate: does not contact otoccipital (0), or contacts otoccipital to enclose carotid artery and forms passage for cranial nerves IX–XI (1).
- 52 [Clark (1994); ch 52]. Eustachian tubes: not enclosed between basioccipital and basisphenoid (0), or entirely enclosed (1).
- 53 [Clark (1994); ch 53]. Basisphenoid rostrum (cultriform process): slender (0), or dorsoventrally expanded (1).
- 54 [Clark (1994); ch 54]. Basispterygoid process: prominent, forming movable joint with pterygoid (0), or basispterygoid process small or absent, with basisphenoid joint suturally closed (1).
- 55 [modified from Clark (1994); ch 55, by Ortega et al. (2000); ch 68]. Basisphenoid ventral surface: shorter than the basioccipital (0) or wide and similar to, or longer in length than basioccipital (1).
- 56 [Clark (1994); ch 56]. Basisphenoid: exposed on ventral surface of braincase (0), or virtually excluded from ventral surface by pterygoid and basioccipital (1).
- 57 [Clark (1994); ch 57]. Basioccipital: without well-developed bilateral tuberosities (0), or with large pendulous tubera (1).
- 58 [Clark (1994); ch 58]. Otoccipital: without laterally concave descending flange ventral to subcapsular process (0), or with flange (1).
- 59 [Clark (1994); ch 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).
- 60 [Clark (1994); ch 60]. Otoccipital: without large ventrolateral part ventral to paroccipital process (0), or with large ventrolateral part (1).
- 61 [Clark (1994); ch 61]. Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0), or horizontal (1).
- 62 [Clark (1994); ch 62]. Supraoccipital: forms dorsal edge of the foramen magnum (0), or otoccipitals broadly meet dorsal to the foramen magnum, separating supraoccipital from foramen (1).
- 63 [Clark (1994); ch 63]. Mastoid antrum: does not extend into supraoccipital (0), or extends through transverse canal in supraoccipital to connect middle ear regions (1).
- 64 [Clark (1994); ch 64]. Posterior surface of supraoccipital: nearly flat (0), or with bilateral posterior prominences (1).
- 65 [modified from Clark (1994); ch 65]. + One small palpebral present in orbit (0), or one large palpebral (1), or two large palpebrals (2).
- 66 [Clark (1994); ch 66]. External nares: divided by a septum (0), or confluent (1).
- 67 [Clark (1994); ch 67]. + Antorbital fenestra: as large as orbit (0), or about half the diameter of the orbit (1), or much smaller than the orbit (2), or absent (3).
- 68 [modified from Clark (1994); ch 68 by Ortega et al. (2000); ch 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).
- 69 [modified from Clark (1994); ch 69]. + Choanal groove: undivided (0), or partially septated (1), or completely septated (2).
- 70 [Clark, 1994; ch 70]. Dentary: extends posteriorly beneath mandibular fenestra (0), or does not extend beneath fenestra (1).
- 71 [modified from Clark (1994); ch 71]. Retroarticular process: absent or extremely reduced (0), or very short, broad, and robust (1), or with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally and facing dorsomedially (2), or posteriorly elongated, triangular shaped and facing dorsally (3), or posteroventrally projecting and paddle-shaped (4).
- 72 [Clark (1994); ch 72]. Prearticular: present (0), or absent (1).
- 73 [modified from Clark (1994); ch 73]. + Articular without medial process (0), or with short process not contacting braincase (1), or with process articulating with otoccipital and basisphenoid (2).
- 74 [Clark, 1994; ch 74]. Dorsal edge of surangular: flat (0), or arched dorsally (1).
- 75 [Clark (1994); ch 75]. Mandibular fenestra: present (0), or absent (1).
- 76 [Clark (1994); ch 76]. Insertion area for M. pterygoideus posterior: does not extend onto lateral surface of angular (0), or extends onto lateral surface of angular (1).
- 77 [modified from Clark (1994); ch 77]. + Splenial involvement in symphysis in ventral view: not involved (0), or involved slightly in symphysis (1), or extensively involved (2).
- 78 [Clark, 1994; ch 78]. Posterior premaxillary teeth: similar in size to anterior teeth (0), or much longer (1).
- 79 [modified from Clark (1994); ch 79]. + Maxillary teeth waves: absent, no tooth size variation (0), or one wave of teeth enlarged (1), or enlarged maxillary teeth curved in two waves (“festooned”) (2).

- 80 [Clark, 1994; ch 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).
- 81 [modified from Clark (1994); ch 81]. Dentary teeth posterior to tooth opposite premaxilla-maxilla contact: equal in size (0), or enlarged dentary teeth opposite smaller teeth in maxillary tooth row (1).
- 82 [modified from Clark (1994); ch 82, by Ortega et al. (2000); ch 120]. Anterior and posterior scapular edges: symmetrical in lateral view (0), or anterior edge more strongly concave than posterior edge (1), or dorsally narrow with straight edges (2).
- 83 [modified from Clark (1994); ch 83, by Ortega et al. (2000); ch 121]. Coracoid length: up to two-thirds of the scapular length (0), or subequal in length to scapula (1).
- 84 [Clark (1994); ch 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).
- 85 [Clark (1994); ch 85]. Pubis: rod-like without expanded distal end (0), or with expanded distal end (1).
- 86 [Clark (1994); ch 86]. Pubis: forms anterior half of ventral edge of acetabulum (0), or pubis at least partially excluded from the acetabulum by the anterior process of the ischium (1).
- 87 [Clark (1994); ch 87]. Distal end of femur: with large lateral facet for the fibula (0), or with very small facet (1).
- 88 [Clark (1994); ch 88]. Fifth pedal digit: with phalanges (0), or without phalanges (1).
- 89 [Clark (1994); ch 89]. Atlas intercentrum: broader than long (0), or as long as broad (1).
- 90 [modified from Clark (1994); ch 90]. + Cervical neural spines: all anteroposteriorly large (0), only posterior ones rod-like (1), or all spines rod-like (2).
- 91 [modified from Clark (1994); ch 91, by Buscalioni and Sanz (1988) and Brochu (1997a); characters 37 and 7, respectively]. + Hypapophyses in cervicodorsal vertebrae: absent (0), or present only in cervical vertebrae (1), or present in cervical and the first two dorsal vertebrae (2), or present up to the third dorsal vertebra (3), or up to the fourth dorsal vertebrae (4).
- 92 [Clark (1994); ch 92]. Cervical vertebrae: amphicoelous or amphiplatian (0), or procoelous (1).
- 93 [Clark (1994); ch 93]. Trunk vertebrae: amphicoelous or amphiplatian (0), or procoelous (1).
- 94 [Clark (1994); ch 94]. All caudal vertebrae: amphicoelous or amphiplatian (0), or first caudal biconvex with other procoelous (1), or procoelous (2).
- 95 [Clark (1994); ch 95]. Dorsal osteoderms: rounded or ovate (0), or rectangular, broader than long (1), or square (2).
- 96 [modified from Clark (1994); ch 96, and Brochu (1997); ch 40]. + Dorsal osteoderms without articular anterior process (0), or with a discrete convexity on anterior margin (1), or with a well-developed process located anterolaterally in dorsal parasagittal osteoderms (2).
- 97 [modified from Clark (1994); ch 97, by Ortega et al. (2000); characters 107 and 108]. + Rows of dorsal osteoderms: two parallel rows (0), or more than two (1), more than four with "accessory ranges of osteoderms" [sensu Frey, 1988] (2).
- 98 [Clark (1994); ch 98]. Osteoderms: some or all imbricated (0), or sutured to one another (1).
- 99 [Clark (1994); ch 99]. Tail osteoderms: dorsal only (0), or completely surrounded by osteoderms (1).
- 100 [Clark (1994); ch 100]. Trunk osteoderms: absent from ventral part of the trunk (0), or present (1).
- 101 [Clark (1994); ch 101]. Osteoderms: with longitudinal keels on dorsal surfaces (0), or without longitudinal keels (1).
- 102 [Wu and Sues (1996); ch 14]. Jugal: participating in margin of antorbital fossa (0), or separated from it (1).
- 103 [modified from Wu and Sues (1996); ch 23]. + Articular facet for quadrate condyle: equal in length to the quadrate condyles (0), or slightly longer (1), or close to three times the length of the quadrate condyles (2).
- 104 [modified from Wu and Sues (1996) and Wu et al. (1997); characters 24 and 124, respectively]. + Jaw joint: placed at level with basioccipital condyle (0), or below basioccipital condyle about above level of lower tooth row (1), or below level of tooth row (2).
- 105 [modified from Wu and Sues (1996) and Ortega et al. (2000); characters 27 and 133, respectively]. + Premaxillary teeth: five (0), four (1), three (2), or two (3).
- 106 [modified from Wu and Sues (1996); ch 29]. Unsculptured region along alveolar margin on lateral surface of maxilla: absent (0), or present (1).
- 107 [modified from Wu and Sues (1996); ch 30]. + Maxilla: with eight or more teeth (0), or seven (1), or six (2), or five (3), or four (4) teeth.
- 108 [Wu and Sues (1996); ch 33]. Coracoid: without posteromedial or ventromedial process (0), or with elongate posteromedial process (1), or distally expanded ventromedial process (2).
- 109 [Wu and Sues (1996); ch 40]. Radiale and ulnare: short and massive (0), or elongate (1).
- 110 [Wu and Sues (1996); ch 41]. Postacetabular process: directed posteroventrally or posteriorly (0), or directed posterodorsally and much higher in position than preacetabular process (1).
- 111 [modified from Gomani (1997); ch 4]. Prefrontals anterior to orbits: elongated, oriented parallel to anteroposterior axis of the skull (0), or short and broad, oriented posteromedially–anterolaterally (1).
- 112 [modified from Gomani (1997); ch 32]. Basioccipital and ventral part of otoccipital: facing posteriorly (0), or posteroventrally (1).
- 113 [Buscalioni and Sanz (1988); ch 35]. Vertebral centra: cylindrical (0), or spool shaped (1).
- 114 [modified from Buscalioni and Sanz (1988); ch 39]. Transverse process of posterior dorsal vertebrae dorsoventrally low and laminar (0), or dorsoventrally high (1).
- 115 [Buscalioni and Sanz (1988); ch 44]. Number of sacral vertebrae: two (0), or more than two (1).
- 116 [Buscalioni and Sanz (1988); ch 49]. Supra-acetabular crest: present (0), or absent (1).
- 117 [Buscalioni and Sanz (1988); ch 54]. Proximal end of radiale expanded symmetrically, similar to the distal end (0), or more expanded proximomedially than proximolaterally (1).
- 118 [Ortega et al. (1996); ch 5]. Lateral surface of the dentary: without a longitudinal depression (0), or with a longitudinal depression (1).
- 119 [Ortega et al. (1996); ch 9]. Ventral exposure of splenials: absent (0), or present (1).
- 120 [Ortega et al. (1996, 2000); characters 11 and 100, respectively]. Tooth margins: with denticulate carinae (0), or without carinae or with smooth or crenulated carinae (1).
- 121 [modified from Pol (1999a) and Ortega et al. (2000); characters 133 and 145, respectively]. Lateral surface of anterior process of jugal: flat or convex (0), or with broad shelf below the orbit with triangular depression underneath it (1).
- 122 [Pol (1999a); ch 134]. Jugal: does not exceed the anterior margin of orbit (0), or exceeds (1).
- 123 [Pol (1999a); ch 135]. Notch in premaxilla on lateral edge of external nares: absent (0), or present on the dorsal half of the lateral margin of external nares (1).
- 124 [Pol (1999a); ch 136]. Dorsal border of external nares: formed mostly by the nasals (0), or by both the nasals and premaxilla (1).
- 125 [Pol (1999a); ch 138]. Posterodorsal process of premaxilla: absent (0), or present, extending posteriorly, wedging between maxilla and nasals (1).
- 126 [Pol (1999a) and Ortega et al. (2000); characters 139 and 9, respectively]. + Premaxilla-maxilla suture in palatal view, medial to alveolar region: anteromedially directed (0), or sinusoidal, posteromedially directed on its lateral half and anteromedially directed along its medial region (1), or posteromedially directed (2).
- 127 [Pol (1999a); ch 140]. Nasal lateral border posterior to external nares: laterally concave (0), or straight (1).

- 128 [Pol (1999a); ch 141]. Nasal lateral edges posterior to external nares: nearly parallel (0), or entirely oblique to each other converging anteriorly (1), or oblique to each other diverging anteriorly (2).
- 129 [Pol (1999a); ch 143]. Palatine anteromedial margin: exceeding the anterior margin of the palatal fenestrae wedging between the maxillae (0), or not exceeding the anterior margin of palatal fenestrae (1).
- 130 [Pol (1999a); ch 144]. Dorsoventral height of jugal antorbital region with respect to infraorbital region: equal or lower (0), or antorbital region more expanded than infraorbital region of jugal (1).
- 131 [Pol (1999a); ch 145]. Maxilla-lacrimal contact: partially included in antorbital fossa (0), or completely included (1).
- 132 [Pol (1999a); ch 146]. Lateral eustachian tube openings: located posteriorly to the medial opening (0), or aligned anteroposteriorly and dorsoventrally (1).
- 133 [Pol (1999a); ch 147]. Anterior process of ectopterygoid: developed (0), or reduced—absent (1).
- 134 [Pol (1999a); ch 148]. Posterior process of ectopterygoid: developed (0), or reduced—absent (1).
- 135 [Pol (1999a) and Ortega et al. (2000); characters 149 and 13, respectively]. Small foramen located in the premaxillo-maxillary suture in lateral surface (not for big mandibular teeth): absent (0), or present (1).
- 136 [Pol (1999a); ch 150]. Jugal posterior process: exceeding posteriorly the infratemporal fenestrae (0), or not (1).
- 137 [Pol (1999a); ch 151]. Compressed crown of maxillary teeth: oriented parallel to the longitudinal axis of skull (0), or obliquely disposed (1).
- 138 [Pol (1999a); ch 152]. Large and aligned neurovascular foramina on lateral maxillary surface: absent (0), or present (1).
- 139 [modified from Pol (1999a); ch 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).
- 140 [Pol (1999a) and Ortega et al. (2000); characters 154 and 104, respectively]. Maxillary teeth: not compressed laterally (0), or compressed laterally (1).
- 141 [Pol (1999a); ch 155]. Posteroventral corner of quadratojugal: reaching the quadrate condyles (0), or not reaching the quadrate condyles (1).
- 142 [Pol (1999a); ch 156]. Base of postorbital process of jugal: directed posterodorsally (0), or dorsally (1).
- 143 [Pol (1999a); ch 157]. + Postorbital process of jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2).
- 144 [Pol (1999a) and Ortega et al. (2000); characters 158 and 36, respectively]. Postorbital-ectopterygoid contact: present (0), absent (1).
- 145 [Pol (1999a); ch 161]. Quadratojugal: not ornamented (0), or ornamented in the base (1).
- 146 [Pol (1999a); ch 162]. Prefrontal-maxillary contact in the inner anteromedial region of orbit: absent (0), or present (1).
- 147 [Pol (1999a); ch 163]. Basisphenoid: without lateral exposure (0), or with lateral exposure on the braincase (1).
- 148 [Pol (1999a); ch 165]. Quadrate process of pterygoids: well developed (0), or poorly developed (1).
- 149 [modified from Pol (1999a) and Ortega et al. (2000); characters 166 and 44, respectively]. + Quadrate major axis directed: posteroventrally (0), or ventrally (1), or anteroventrally (2).
- 150 [Pol (1999a); ch 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).
- 151 [Pol (1999a); ch 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).
- 152 [Pol (1999a); ch 169]. Prezygapophyses of axis: not exceeding anterior edge of neural arch (0), or exceeding the anterior margin of neural arch (1).
- 153 [Pol (1999a); ch 170]. Postzygapophyses of axis: well developed, curved laterally (0), or poorly developed (1).
- 154 [modified from Pol (1999b); ch 212]. Shape of dentary symphysis in ventral view: tapering anteriorly forming an angle (0), or U-shaped, smoothly curving anteriorly (1), or lateral edges longitudinally oriented, convex anterolateral corner, and extensive transversally oriented anterior edge (2).
- 155 [Pol (1999b); ch 213]. Unsculptured region in the dentary below the tooth row: absent (0), or present (1).
- 156 [Ortega et al. (1996) and Buckley et al. (2000); ch 13]. Cheek teeth: not constricted at base of crown (0), or constricted (1).
- 157 [Ortega et al. (2000); ch 42]. Outer surface of squamosal laterodorsally oriented: extensive (0), or reduced and sculptured (1), or reduced and unsculptured (2).
- 158 [Ortega et al. (2000); ch 74]. Length/height proportion of infratemporal fenestra: higher than wide or equal (0), or very antero-posteriorly elongated (1).
- 159 [Ortega et al. (2000); ch 90]. Foramen intramandibularis oralis: small or absent (0), or big and slot-like (1).
- 160 [Ortega et al. (2000); ch 146]. Ectopterygoid medial process: single (0) or forked (1).
- 161 [modified from Gomani (1997) and Buckley et al. (2000); characters 46 and 113, respectively]. Cusps of teeth: unique cusp (0), one main cusp with smaller cusps arranged in one row (1), or one main cusp with smaller cusps arranged in more than one row (2), or several cusps of equal size arranged in more than one row (3), or multiple small cusps along edges of occlusal surface (4).
- 162 [Pol and Norell, 2004; ch 164]. Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).
- 163 [Pol and Norell, 2004; ch 165]. Palatine-ptyergoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).
- 164 Major axis of ectopterygoid body oriented: anterolaterally (0), or anteriorly (1).
- 165 [Wu et al. (1997); ch 103]. Squamosal descending process: absent (0), or present (1).
- 166 [modified from Wu et al. (1997); ch 105]. + Development of distal quadrate body ventral to otoccipital-quadrate contact: distinct (0), or incipiently distinct (1), or indistinct (2).
- 167 [Wu et al. (1997); ch 106]. Pterygoid flanges: thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).
- 168 [Wu et al. (1997); ch 108]. Postorbital participation in infratemporal fenestra: almost or entirely excluded (0), or bordering infratemporal fenestra (1).
- 169 [Wu et al. (1997); ch 109]. Palatines: form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).
- 170 [Wu et al. (1997); ch 110]. Angular posterior to mandibular fenestra: widely exposed on lateral surface of mandible (0), or shifted to the ventral surface of mandible (1).
- 171 [Wu et al. (1997); ch 112]. Posteroventral edge of mandibular ramus: straight or convex (0), or markedly deflected (1).
- 172 [modified from Wu et al. (1997); ch 119]. Quadrate ramus of pterygoid in ventral view: narrow (0), or broad (1).
- 173 [Wu et al. (1997); ch 121]. Pterygoids: not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).
- 174 [Wu et al. (1997); ch 122]. Olecranon: well developed (0), or absent (1).
- 175 [Wu et al. (1997); ch 123]. Cranial table width with respect to ventral portion of skull: as wide as ventral portion (0), or narrower than ventral portion of skull (1).
- 176 [Wu et al. (1997); ch 127]. Depression on posterolateral surface of maxilla: absent (0), or present (1).
- 177 [Wu et al. (1997); ch 128]. Anterior palatal fenestra: absent (0), or present (1).
- 178 [Pol and Norell, 2004; ch 179]. Paired ridges located medially on ventral surface of basisphenoid: absent (0), or present (1).

- 179 Ventral margin of infratemporal bar of jugal: straight (0), or dorsally arched (1).
- 180 [Pol and Norell, 2004; ch 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).
- 181 [Pol and Norell, 2004; ch 181]. Orientation of quadrate body distal to otoccipital-quadrata contact in posterior view: ventrally (0), or ventrolaterally (1).
- 182 [Gasparini et al. (1991); ch 3]. Wedge-like process of the maxilla in lateral surface of premaxilla-maxilla suture: absent (0), or present (1).
- 183 Choanal opening: opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1).

2. Data matrix used in the phylogenetic analysis

Gracilisuchus stipanicorum
000000?0?000000000000?0?00000000?0?0?00000?000?00000?-
0??00000?100000?00000000?0??0000?0?000001012?00?00??0?1?0
1000?1?01??000001002?0??0000?0??0?0??0000?00000?0?000000
Terrestriusuchus gracilis
000?00?0?0?000000?000?0?00?000?110?00000?00000?000?0?000?00
0??00?0?0?10?0?000000?010?0000?0200000101??01100?00000?00
100??10?00?110?0?0?01]110??00000?0?00?0?00?0?00?0?0?0?0?0?0?0
Dibothrosuchus elaphros
0 0 0 ? 0 0 ? 0 2 0 ? ? 0 0 1 ? ? ? 0 0 0 0 0 0 ? ? ? ? ? ? 0 0
110000000?00000?00000?00000?0?0101000?010100?0010?000?0???
2000?0?0??0?010?0?01100?0?00000001001?10?00?1?0001010
11100?000001??000000100001000100?0?000000
Protosuchus richardsoni
2100000120?000011010002100000100010001010?002010011111100
10101102011?110210001010100011100[1234]00?1200110101110210010
10000[01]000000?01??01??10010[01]0101000000??01000000000
120000011110?00100
Hemiprotosuchus leali
?00?00?10?0??0?10010?0?00?0010?11?0?01??0020?00?11?110010
1??12?11??121??011??0??0??0??0??1200?1?01??0??0??0??000?000?
?10?00?00000?10??00?0000?12??001??10?00?000
Orthosuchus stormbergi
21100001201?0001001000[01]10000010001000?000?00201100
111100??1?1?02011?0?0?001000100011100000?120010010211421001?
10010?100000001?01010000000000?0??00001??000000?012?0000
11110?000100
Kayenta form
[12]01110?1200000?10010?0?00??0?0??11110?00201001111110000
1011?2011?0102100?1010?0??00?0?0?1200101101112??0?0??0?
1100?00?01000111?101001?01?10000000011?0??400112??00011?0?0?
10??0
Edentosuchus tienshanensis
201????[12]????0?01]0?0?10100?0?0??02?110?00?????????????????
[12]2311????10?01010????????[234]????????????[23]????????00110?1?
01?1??1000110?11?1????0011??4?01??1????11?0?1?00
Gobiosuchus kielanae
101000?110000011001?01]01]1?00001?10?0201000?00201120
11111000?0??0201??1?20100[01]010?0?1?????0?010110[01]01200
2??0000??0010[01]00001000000?00001001211?0000??110000000?0
121000011?00?00?000
Sichuanosuchus shuhanensis
[12]01??0?1200[01]00?10010[01]1?110??1?00?021?10?00020?1?011?
1100??????2?11??1?000011?1?1??0000??????1?11?0?1??0?0?100
100?1?1?0?0??00110[01]1210?00?0??1????010?11101111100?10
1000

Shantungosuchus hangjinensis
2?1????1?0??0?1?1????11?????????21?1[01]100020?1?011?1100?
10??????101?1?000??10??????0?????????????1??????1?????00
100????00?10?00?011211?001????0?00?0?0101111?0?1[01]10?0
Zosuchus davidsoni
201??0?1200000??001010[01]110?001110?02211010012?1??011?
11000?0?1?0211110????0?0111?????????????????1?23????1????00
10001101?0001?0?0010112?[01]?0001????00?0?0100111?1011?10110
1000
Hsisosuchus chungkingensis
211????1?000000100001100011000?0221101000[12]?12?11?
10000?0?1?0??111?4?00[01]02?1??10????000?1000??101?0021??
1????01001????0000?000?1?1?1?000??????0?0??0[0]00?0?011[0
1]2000?1
Fruita form
201??001200100010000100100000110010221?1?0020112?
1??0?0??0?1?2?31????1?0111101011?1?0001112?0??1??[0]00??
1?1001?001?0?0100100??101?0011?01110?0?0?00?10?0000?
10??000?0?101?0?0?
Notosuchus terrestris
101?00110101001110001111100110001022110110021112011?
1000010?110211112?0101110001[01]111?1?200001000?0122011??
1100101[01]1101[01]01001000000111111111?00011100100001011010
110000111011?0001
Comahuesuchus brachybuccalis
103?0?101??00??0112????00102??0?1?1?1?????????????????
131?????0?10101????????????????????[01]13??1?????0?10?101201?
01????011?0?1????1??11?00100?10?0?000??100??0??
Uruguaysuchus aznarezi
201?001101?00?10?1??1????1??01022?101?0011????1????0?0??0
1111[12]??000110100?1?1????0000?0?01?21002100?00?000[01]??0
1?1?00??1?0111?11????11????1?0001????????0??10?0?0??1
Chimaerasuchus paradoxus
101?0001111?00????????????????????????????????????????12??
0110?01010?0?1?1?????2100?00??0?11[12]?314210?0?00?
010011111011?????0?010?????????10?11????3?????????1?00?????
Malawisuchus mwakayasyunguti
101?00?1110000?01]10001[01][01]1100?110001?22110100011??20??
1000?10?1?02?111[01]2?0101110001????1??210000010?01[12]2111??0
1?0??01100101?11000??110110101?0?0001??0?100?211010?10000
11100000001
Candidodon itapecurensis
????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????
0?????????????1??2????????????????????
Simosuchus clarki
1030101100000010001011110?0110001021?10100011?11011?10000
10?1?020112121010110000?????02100?2010?10002010??01?????110
11012120000101001110021100120??211[12]00011101011001[01]1?
100010001
Sphagesaurus huenei
101?000101?00??100?????110?????????21101?00?????011?
1000??????132??????100??????1?????????????312????0?????
1111101111111111111110011101111?0?1?0?0110?0?10?0?
1?00000001
Bretesuchus bonapartei
1[01]0?0?121?00?????????0?????????2??10011??????01011?
1????13?1?1?00?10110????????????????????100??1??????01?0????
1??0??0?1?0????????[01]0[01]1?10?1????1?001?00?0??1
Baurusuchus pachecoi
100?0?121??00?1101????111?0110?????2?10110011112011?1000?
10??10??311121010111111????????????????????12103????1????110
1110101011100110011110110?0111??[01]0[01]1110110101?0000
1?000100001
Iberosuchus macrodon
1?0?00012?0?011100011111?01?000?02??10100111?12??1?01??
10?1????11??10?0?1011011????[12][1234]00?00?000?[12][01]0?

2?0000??11001101010?1?0??100?11001?0??101??[0]??0111?001010
1?0?01?1000?0101

Araripesuchus gomesii

20100011010000111000101111011[0]001022110100011112011?
10000?0?110201121210001101[0]1[0]11111?1[234]0001000100
11110021001001010100100100100000010011000210000110?0011[0
1]00001101101000011100?00001

Araripesuchus patagonicus

201000?1010000?1[0]1000101111?0111001022?10100011?12?11?
1000?0?1?02?11212?0?011[0]1?1?1?1?1?1?1?1?1?1?1?1?1?1?1?1?
1?01101?010000??100110102?0?01?1?1?0?0?[0]10001101?010000
1110?000001

Lomasuchus palpebrosus

201????1211?00?1100010111??110001022?1010001??12??1?
100??1??1??2?21??2??00?0[12]11??2??2??2??2??2??2??
1??00??00??00??00??1?110?00??00011?0?1?0?0??010??0?1?
1??10??01?10000??11

Petrosaurus tormini

201?011??1?00????10?1??????0??2?10?????????????????????
1????????[12]1????????????????????000????????0????1??0??????0?
1????????????[0]1?????0????????????00??1?

Theriosuchus pusillus

201101111010011000011011100110011?211010001?11?0
1111000?0??1?20211?4100101010110111100011112001001010002?00?
10?110110[0]1001?1100?00?0?00100?01?0?00??1010000?01?010?0?
1?1000?0?1

Alligatorium

?0????1?0000?1000010?111??0?100?1??0?00??11?1??1000?????
20?1??200101?101?011111000??1?00100??2??2??2??10??
1????????????????0????????????????0????????????????0?

Pelagosaurus typus

202?11111001102010100000000000[0]10021101000000110
1111001001?10001200?3000002000011011?0000001200011101?00??
10?????1?1?????0000?010010?0010??00??000100001012010000
110000001?1

Teleosauridae

[0]2?11111001102010010000000000110021?01000?0011011100
101?1?00120003?000?20000210111?0000?12000101011?0??10?0100
1101??1011000011000010100?0?0000??100010000101?010?0111000100
101

Metriorhynchidae

[0]2?12110100111201011000?0000000110021?0?000?00110
1111001011?1?001200?300010200002101?11?0000?????0??012?0??
100?01001101??101?0000?000010102?0??000??0010000101?01000?
11000000101

Sokotosuchus ianwilsoni

2?2??1101??10??001001??101001?012?1?????1112?11?1?1??0??
1?1?0?2??2??2?01??2??2??2??2??2??2??2??2??2??2??2??2??
1????????????0?0????????????????0????????????????

Dyrosauridae

002??1?101?010?1?0010001?1010011012?10101001112011?1011?
10?10101302?3?00??2?000?0?????0?00?????1?????????????????
1????????????0?0?????????????021?00010????0????00??1?1

Pholidosaurus decipiens

212?111101??11?110110011?00100010?211?100001112111?101??
10?100?1311?300??2?0??11?1??0?0?2?0????????????????????1????1?
110????0?0010?????????????0?1?00010??10?001?100?0101

Goniopholis

203?1211110010111000100111?0010001002?101000?1112011?1010?
10?1?021312?4100[0]10[12]02011?1?1??0?0?1200?1?000002100010?
1101101??101100?000010010001?1??000011002000001010010000
11110?00101

Eutretauranosuchus delfsi

203????1?10010111000100111?00?0001001110?000?1112011?
1010?0?0?1?0?121204?00001020111??1??0??0?0?
1????????000??00?0??0?01????110??????0?00??1?1??0??10?
2??0010?0?000?1?110??01?1

Bernissartia fagesii

203??21111?00111000?00111?001000?002????0001112?11?1?10
100?0?1??1?1??410010102011?1?11??020021110110
100000?00??????1????1??????0?0?10??01??0??1?1200000
1????0????00??101

Hylaeochampsia vectiana

00?????11??11??1?01??0??0?002?1?1011??????101??1??1????
10????????????????????????????????????????0?????10??????????0??
0?????0??????????2?00????????????????????1

Borealosuchus formidabilis

203?1211110010111000100111?0010001002110101111112111110
10010?110?1310031000110?0111111113111?110?00?000002110?100
100?101??11110?000000010001?1??0000110?20?0001010010000
11100000101

Gavialis gangeticus

212?12111100111110110111110010001002110101101112011110
110101110[0]1310031000120000011111013111211100?000002110?
100100?101??121100?00000001000101?1?00001?0?20?0001010010000
111000001?1

Crocodylus niloticus

203012111100[0]011100010211110010001002110?0111112011110
100101110[0]13100310001001012111110131112021100?0000021100
100100?101??121100?0000000100110101100001?0?2000001010010000
11100000101

Alligator mississippiensis

203112?101?0001110001021111001000?00211010111112011110
100101110[0]031203100010020121111111311120211?0?0000021100
1001001101??111000?00000001001[12]0101000011[0]120000010100
1000011100000101

3. List of the fossil taxa used in the phylogenetic analysis

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

- Gracilisuchus stipanicorum* (Romer, 1972)
- Terrestriusuchus gracilis* (Crush, 1984)
- Dibothrosuchus elaphros* (Wu and Chatterjee, 1993; IVPP V 7907)
- Protosuchus richardsoni* (Colbert and Mook, 1951; AMNH 3024; MCZ 6727; UCMP 130860, 131827)
- Hemiprotosuchus leali* (Bonaparte, 1971; PVL 3829)
- Kayenta form (Clark, 1986; UCMP 97638, 125359, 125871)
- Edentosuchus tienshanensis* (Young, 1973; IVPP V 3236; GMPKU-P 200101)
- Orthosuchus stormbergi* (Nash, 1975; SAM-K 409)
- Gobiosuchus kielanae* (Osmolska, 1972; Osmolska et al., 1997; ZPAL MgR-II/67–II/71)
- Shantungosuchus hangjinensis* (Wu et al., 1994a)
- Sichuanosuchus shuhanensis* (Wu et al., 1997; IVPP V 10594)
- Zosuchus davidsoni* (Pol and Norell, 2004; IGM 100/1304–1308)
- Fruita form (Clark, 1985, 1994; LACM 120455a)
- Hsisosuchus chungkingensis* (Young and Chow, 1953; Li et al., 1994; Wu et al., 1994b; cast of CNM V 1090)
- Notosuchus terrestris* (Gasparini, 1971; MACN-RN 1037)
- Comahuesuchus brachybuccalis* (Bonaparte, 1991; MUC-PV 202; MACN-N 30, 31; MOZ P 6131)
- Uruguaysuchus aznarezi* (Rusconi, 1933)
- Chimaerasuchus paradoxus* (Wu and Sues, 1996; IVPP V8274)
- Malawisuchus mwakasyunguti* (Clark et al., 1989; Gomani, 1997; MAL 45, 49)
- Candidodon itapecurensis* (Carvalho, 1994)
- Simosuchus clarki* (Buckley et al., 2000; UA 8679)
- Sphagesaurus huenei* (Price, 1950; Pol, 2003; RCL 100)

Araripesuchus gomesii (Price, 1959; AMNH 24450)
Araripesuchus patagonicus (Ortega et al., 2000; MUC-PV 269, 270)
Baurusuchus pachecoi (Price, 1945; DGM 299-R)
Bretesuchus bonapartei (Gasparini et al., 1993; PVL 4735)
Iberosuchus macrondon (Antunes, 1975; Ortega et al., 2000)
Theriosuchus pusillus (Owen, 1879; Clark, 1986, 1994; Ortega et al., 2000)
Alligatorium (Wellnhofer, 1971; Clark, 1986, 1994)
Eutretauranosuchus delfsi (Mook, 1967; Clark, 1986, 1994; AMNH 570)
Gontopholis (Mook, 1942; Clark, 1986, 1994; Salisbury et al., 1999; AMNH 5782)
Pholidosaurus decipiens (Owen, 1878; Clark, 1986, 1994)
Sokotosuchus ianwilsoni (Buffetaut, 1979; Clark, 1986, 1994)
Dyrosauridae (Buffetaut, 1976, 1978; Clark, 1986, 1994; CNRST-SUNY 190)
Pelagosaurus typus (EudesDeslongchamps, 1863; BSP 1890.I.5)
Teleosauridae (Buffetaut, 1982; Clark 1986, 1994; AMNH 5138; BSP 1945.XV.1; GPIT Auer-1909-f.22; MB 1921.12)
Metriorhynchidae (Kälin, 1955; Gasparini and Diaz, 1977; AMNH 997; BSP AS.I.504; MACN-N 95; SMNS 10116)
Hylaeochampsia vectiana (Clark and Norell, 1992; Ortega et al., 2000)
Bernissartia fageessi (Buscalioni and Sanz, 1990; Norell and Clark, 1990)
Borealosuchus formidabilis (Erickson, 1976; Brochu, 1997b)
Gavialis gangeticus (Clark, 1994; Brochu, 1997a)
Crocodylus niloticus (Clark, 1994; Brochu, 1997a)
Alligator mississippiensis (Clark, 1994; Brochu, 1997a)

4. List of institutional acronyms used throughout this paper

AMNH	American Museum of Natural History, New York, USA	CNM	Chongqing Natural Museum, Sichuan, People's Republic of China
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany	DGM	Departamento de Produção Mineral, Rio de Janeiro, Brazil
		GMPKU	Geological Museum, 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
		IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China
		LACM	Los Angeles County Museum, Los Angeles, USA
		MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
		MAL	Malawi Department of Antiquities, Malawi
		MB	Institut für Palaontologie, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany
		MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
		MLP	Museo de La Plata, La Plata, Argentina
		MOZ	Museo Profesor J. Olsacher, Zapala, Argentina
		MUC-PV	Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina
		PVL	Instituto Miguel Lillo, Tucumán, Argentina
		RCL	Museo de Ciencias Naturales, Pontificia Universidade Católica de Minas Gerais, Brazil
		SAM-K	South African Museum, Cape Town, South Africa
		SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
		UA	University of Antananarivo, Madagascar
		UCMP	Museum of Paleontology, University of California, Berkeley, USA
		ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland