Cranial anatomy of a new crocodyliform (Archosauria: Crocodylomorpha) from the Lower Cretaceous of Song-Liao Plain, northeastern China

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Abstract: *Rugosuchus nonganensis*, a new genus and species of crocodyliform, is erected on the basis of its peculiar cranial features. This late Early Cretaceous species represents the second, and most complete, crocodyliform known from northeastern China. Its discovery is significant for our understanding of both the local vertebrate fauna and its stratigraphical correlations, and the paleobiogeography of the Crocodyliformes. The palatine contribution to the anterior border of the choana excludes the new form from the Eusuchia, and evidence from osteoderms (not detailed in the present paper) suggests that the new form appears to be phylogenetically closer to the Eusuchia than to the Goniopholididae. Therefore, comparisons are made primarily with those taxa which have a closer relationship to the former than the latter. The unsculpted, depressed, and lobe-like posterolateral process of the squamosal is further demonstrated to be ontogenetically variable and thus inappropriate for use as a character in phylogenetic analyses.

Résumé : *Rugosuchus nonganensis*, un nouveau genre et une nouvelle espèce de crocodyliforme, est défini à partir de ses caractéristiques crâniennes particulières. Cette espèce du Crétacé précoce représente le second, et le plus complet, crocodyliforme connu provenant du nord-est de la Chine. Sa découverte est importante pour notre compréhension de la faune vertébrée locale, de ses corrélations stratigraphiques et de la paléobiogéographie des Crocodyliformes. La contribution du palatin au bord antérieur de la choane exclut la nouvelle forme des Eusuchiens, alors que des évidences (non détaillées dans le présent article) provenant des ostéodermes suggèrent que la nouvelle forme soit phylogénétiquement plus près des Eusuchiens que des Goniopholididés. Les comparaisons sont donc faites surtout avec les taxons qui ont une relation plus proche aux premiers qu'aux derniers. Finalement, nous démontrons que le processus postéro-latéral du squamosal, non sculpté, déprimé et de type lobe varie de façon ontogénétique et qu'il est donc inapproprié pour servir de caractère dans les analyses phylogénétiques.

[Traduit par la Rédaction]

Introduction

Paralligator sungaricus Sun 1958 was heretofore the only crocodylomorph taxon known from the Early Cretaceous Nenjiang Formation of De-Hui (Tê-Hui) County, Jilin (Kirin) Province, on the Song-Liao (Sungarian) Plain, northeastern China (Li in Sun et al. 1992). *Paralligator* was first described by Konjukova (1954) on the basis of cranial material from the Upper Cretaceous of southern Mongolia and later synonymized by Efimov (1983) with *Shamosuchus* Mook 1924 from the Late Cretaceous Baruungoyot Formation of Bayan Zag, Mongolia (Storrs and Efimov 2000). This crocodyliform is a common member of the vertebrate fauna of the Upper Cretaceous of the Mongolian Gobi Desert, and,

so far, several species of this taxon have been described (see Efimov 1988).

In the vertebrate fossil collections of the Geological Institute (IG) of the Chinese Academy of Geological Sciences in Beijing, there are three crocodyliform specimens from the Song-Liao Basin. Of these, one (IGV 33) includes a fairly well-preserved cranium (the skull and mandible), another (IGV 31) consists of more than 40 vertebrae with an incomplete pelvic girdle and many osteoderms, and the last (IGV 32) is represented by only two sacral vertebrae and the first caudal vertebra and an incomplete pelvic girdle. These specimens were collected in 1958 by the Petroleum Geological Survey of the Song-Liao Basin, the Ministry of Geology, People's Republic of China, from the Lower Cretaceous of Nong'an County, about 44 km southwest of De-Hui County, the type

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Fig. 1. Schematic map of Jilin Province (the solid area in the insert) showing the locality of *Rugosuchus nonganensis*.
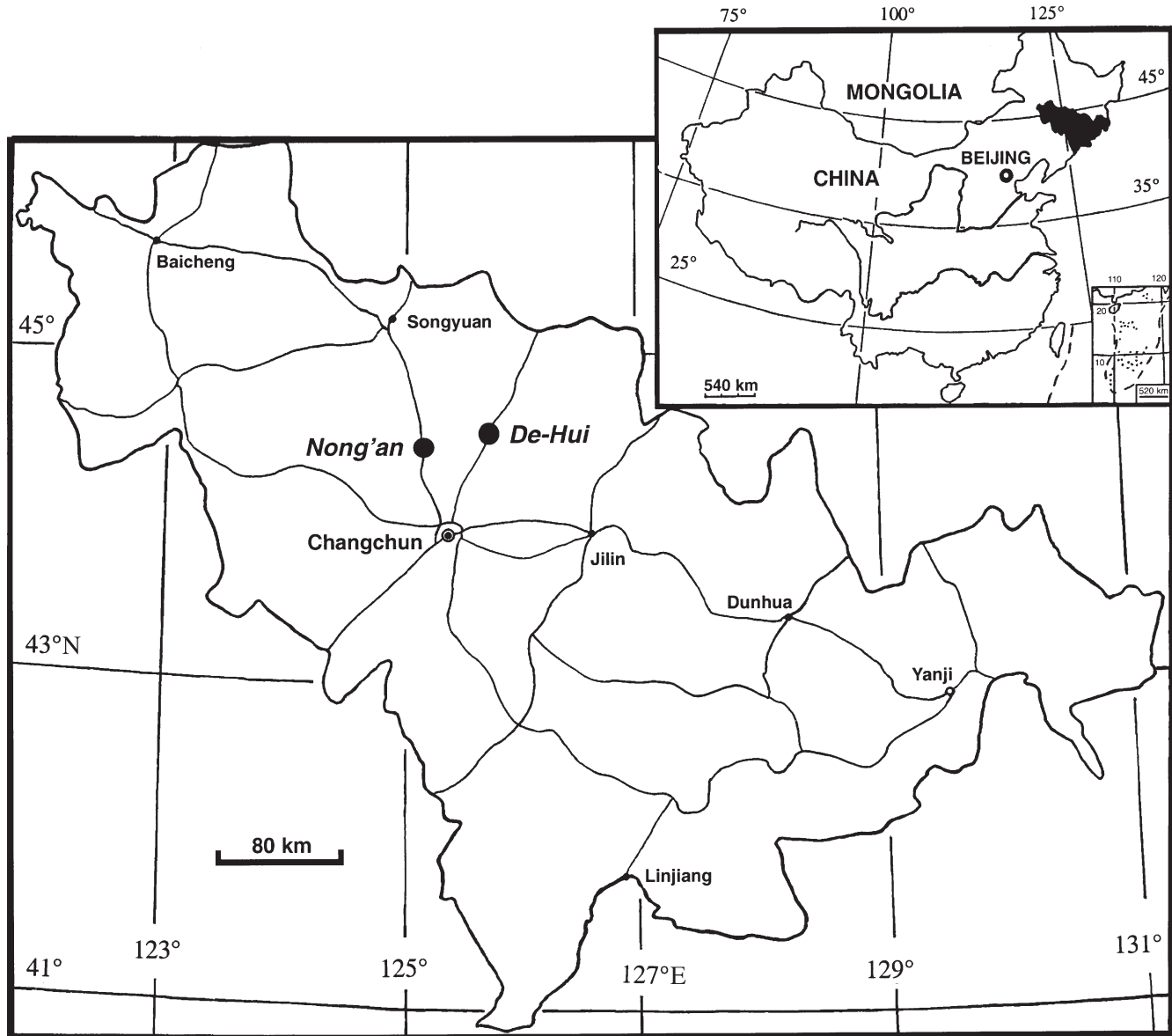

locality of "*Paralligator*" *sungaricus* (Fig. 1). Both De-Hui and Nong'an counties belong to the Nong'an geological subdivision, which forms the eastern part of the Song-Liao Plain.

The Nong'an specimens were all derived from the same locality in Fulongquan Township and collectively sent to the Geological Institute. They most probably belong to a single taxon, based on the identical pattern of the dorsal sculpturing of the osteoderms. The sculpturing pattern of dorsal osteoderms in crocodyliform species is, to our knowledge, quite constant for both living forms (such as *Alligator sinensis* (see Cong et al. 1998) and *Caiman crocodilus* (see Canadian Museum of Nature, CMN 25542)) and fossil forms (such as *Sunosuchus junggarensis* (see Wu et al. 1996a) and *Stangerochampsa mccabei* (see Wu et al. 1996b)). Additionally, the corresponding vertebrae of these Nong'an specimens show very similar anatomies. The cranium and one of the two postcranial skeletons are possibly from

the same individual, but evidence to establish this is lacking due to inadequate documentation of the specimens. The individuals from which the two postcranial skeletons are derived were of similar size, as suggested by the size of their sacral vertebrae and pelvic girdle elements.

At the fossil locality and in the neighbouring area, outcrops are mainly of the Nenjiang Formation, which forms the highest of the six formations of the Lower Cretaceous in the Song-Liao Basin (Bureau of Geology and Mineral Resources of Jilin Province 1988). Lithologically, the Nenjiang Formation is derived from lake deposits. It has a general thickness of 200–400 m, with the lower part dominated by black mudstones (interbedded with oil shales) and the upper part composed of an alternation of blackish-grey, greenish-grey, and reddish-brown mudstones with sandstones. It is most likely that the Nong'an specimens were collected from this formation, although the original labels associated with them state only the Cretaceous as their stratigraphical provenance.

Fig. 2. (A) Two incomplete dorsal osteoderms (from the right side of the sacral region) of *Shamosuchus* (= *Paralligator*) *sungaricus* (IVPP V2302) in dorsal view. (B) One dorsal osteoderm (from the right side of the last presacral vertebra) of *Rugosuchus nonganensis* (from referred specimen IGV 31) in dorsal view, showing much smaller and more concentrated dorsal pits than in *S. sungaricus* (see A). (C) The 19th caudal vertebra and associated dorsolateral osteoderms of *R. nonganensis* (from referred specimen IGV 31) in lateral view, showing more than two longitudinal rows of dorsal osteoderms in the tail region. poz, postzygapophyses; rsf, articular facet on the right side of the osteoderm, indicating the presence of more than one longitudinal row of dorsal osteoderms on each side of the trunk region in life.
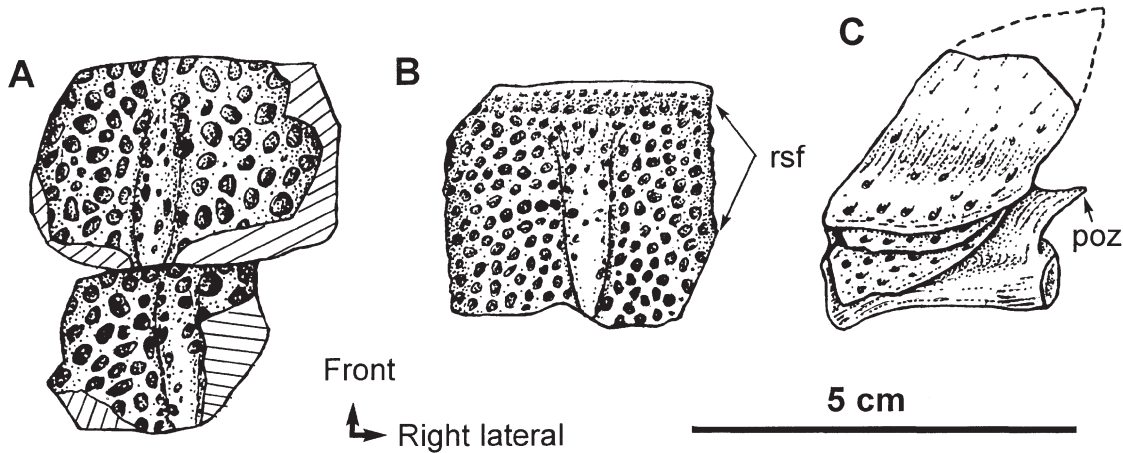
The greenish-grey nature of the matrix attached to these specimens, however, indicates that they were probably excavated from the upper part of the Nenjiang Formation. Our re-examination of the type specimens of "*P.*" *sungaricus* (Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V2302) reveals that the attached matrix is also of greenish-grey mudstone, suggesting that "*P.*" *sungaricus* was also probably retrieved from the same stratum. The assignment of geological age to the Nenjiang Formation has varied (either Late or Early Cretaceous), but has most recently been considered to be provisionally representative of the latest Early Cretaceous. This is based on the coexistence in these deposits of Early and Late Cretaceous ostracods and bivalves and the presence of the fish *Sungarichthys*, which is more derived than *Manchurichthys* of the Dalazi Formation of the Yanbian Division (Bureau of Geology and Mineral Resources of Jilin Province 1988, p. 233).

The Cretaceous deposits of the Song-Liao Basin are very fossiliferous, but fossil vertebrates are rare. Up until now, all known fossil vertebrates are of fish, except for the aforementioned "*P.*" *sungaricus*. The new Nong'an crocodyliforms are, therefore, important to our understanding of the nature and correlations of the vertebrate fauna of the Nenjiang Formation, the evolution and biogeography of the Crocodyliformes, and the stratigraphical correlations of the area with others. It is evident that the Nong'an specimens described herein represent a previously unknown crocodyliform, based on a set of peculiar features of the cranium. This new form also differs from "*P.*" *sungaricus* in that the dorsal osteoderms of the trunk region have a sculpturing pattern consisting of much smaller and more concentrated pits and a weaker dorsal ridge (Fig. 2), and the proximal shaft of the femur is rounder in cross section. Although the cranial morphology of "*P.*" *sungaricus* is unknown, the abovementioned differentiating features appear to be sufficient to distinguish it from the new form. However, we must await further evidence to determine whether or not they are congeneric. A new genus is necessary for the Nong'an specimens because, even if it transpires that they represent a taxon congeneric with "*P.*" *sungaricus*, the cranial morphology differs markedly from that of *Shamosuchus* (= *Paralligator*). It is difficult to appraise the taxonomic validity of "*P.*" *sungaricus* in terms of current evidence, although the taxon is distinguishable from the Nong'an specimens. This problem will be resolved when better specimens are discovered.

In the present paper, we focus on skull anatomy and the reasons for the erection of a new taxon for the Nong'an specimens. The description of the postcranial material and the phylogenetic relationships of this taxon cannot be completed until the specimens are fully prepared.

Systematic paleontology

Crocodyliformes Clark in Benton and Clark, 1988
Mesoeucrocodylia Whetstone and Whybrow, 1983
Neosuchia Clark in Benton and Clark, 1988
Rugosuchus, gen.nov.

Etymology
Rugæ (Latin), uneven, wrinkled; referring to the presence of a series of fossae on the dorsal surface of each maxilla.

Type and only known species
Rugosuchus nonganensis, sp.nov.

Diagnosis
As for the type and only known species

Rugosuchus nonganensis, sp.nov.

Etymology
Named for Nong'an County, from which the specimens were collected.

Fig. 3. Skull and mandible of *Rugosuchus nonganensis*, holotype, IGV 33, in dorsal (A) and ventral (B) views. a, angular; afo, articular fossa; ar, articular; bo, basioccipital; bs, basisphenoid; ca, crest A; cb, crest B; ch, anterior border of choana; d, dentary; da, area damaged by breakage; ec, ectopterygoid; eo, exoccipital; eu, foramina for eustachian tube; f, frontal; ffo, fossa on dorsal surface of frontal; ic, internal carotid artery; j, jugal; l, lacrimal; m, maxilla; mf, fossae on dorsal surface of maxilla; n, nasal; p, parietal; pbr, rostrum or parasphenoid process of basisphenoid; pf, prefrontal; pfo, fossa on the dorsal surface of the parietal; pl, palatine; pm, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; qf, foramen for siphonal tube; qj, quadratojugal; rap, retroarticular process; rf, median ridge of frontal; rp, median ridge of parietal; sa, surangular; sd, area damaged by surface erosion; sp, splenial; sq, squamosal; tf, transverse flange of pterygoid; th, tooth; th.5, fifth maxillary tooth; to, orbito-temporal foramen; V, IX–XI, and XII, foramina for cranial nerves V and IX–XII.

Holotype

IGV 33, majority of skull with mandible in tight occlusion.

Referred specimens

IGV 31, 13 presacral vertebrae, two sacral vertebrae, 27 caudal vertebrae, many dorsal osteoderms and some ventral osteoderms, incomplete pelvic girdle, and some limb fragments; IGV 32, two sacral vertebrae attached to the first caudal vertebra, left ilium with proximal head of left femur, and some dorsal osteoderms.

Horizon and type locality

Upper part of Nenjiang Formation, latest Early Cretaceous; Fulongquan Township, Nong'an County, Song-Liao Basin, Jilin Province, northeastern China.

Diagnosis

A medium-sized crocodyliform differing from other neosuchians in having the following apomorphies: a series of nine or ten fossae on the dorsal surface of each maxilla; dorsal surfaces of both frontal and parietal deeply concave and concavities on these bones continuous; median ridge of frontal not continuing towards posterior end of bone; median ridge of parietal not extending to anterior end of bone; 16 or 17 maxillary teeth with broad spaces between them.

Description

Skull

The skull and mandible are tightly occluded. The left side of the skull is nearly complete, but the right side is missing the anteriormost end and the posterolateral part posterior to the snout (Fig. 3). The post-rostral portion of the skull is displaced towards the right side anteriorly. All openings (such as the external nares, orbits, supratemporal fenestrae, and infratemporal fenestrae) are incomplete. However, the skull in dorsal view can be reconstructed reasonably accurately, although sutures between some of the bones remain indistinct (Fig. 4). The skull is elongate, its maximal width (13 cm across the quadrate condyles) being about 0.46 times its length (28 cm from the anterior tip of the snout to the posterior margin of the skull table). The snout is 2.65 times as long as the post-snout region. The nares were most probably paired, as suggested by the pronounced narial processes of the nasals. Each naris is egg-shaped, as is the supratemporal fenestra. The latter is about 1.5 times the size of the former. The triangular infratemporal fenestra is of about the same length as the supratemporal fenestra. The orbits are more or less triangular in outline and are similar in length to the two pairs of temporal fenestrae, but are much broader than the supratemporal fenestrae. The suborbital fenestrae on the

ventral surface were most probably elliptical, and they are slightly larger than the orbits. It is difficult to determine the form of the incisive foramina because of poor preservation. The skull surface is well sculptured, mainly by small pits and ridges. We consider that the skull is from a fully adult individual, this being supported by the following evidence: absence of any sutures in the frontal, and the orbito-temporal foramen is posteriorly positioned and is partly roofed by the squamosal and parietal (see Wu et al. 1996*a* for details).
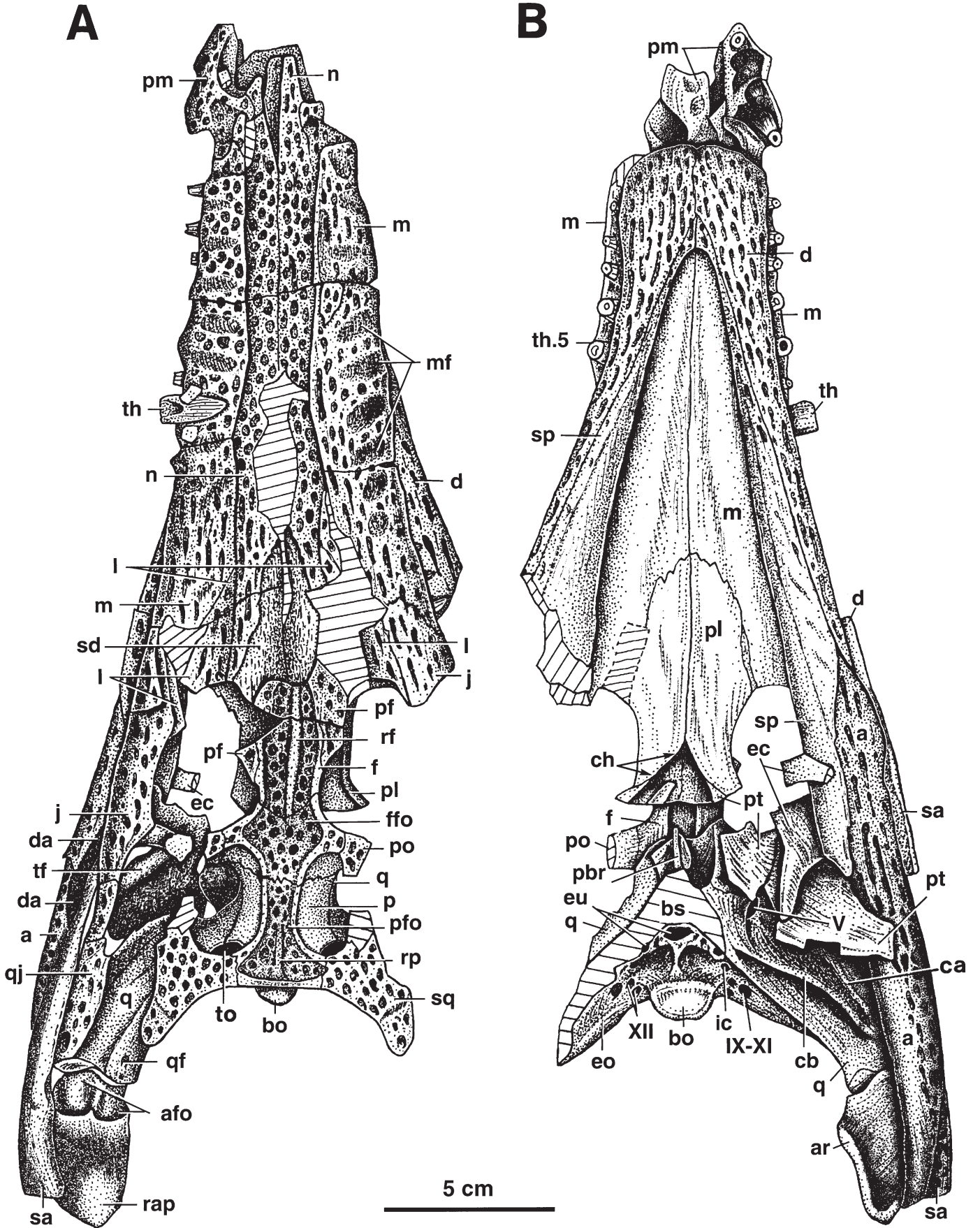
Much of the right premaxilla is preserved, except for its anterior end (Fig. 3). It may have formed the anterior portion of the narial septum in life. Due to damage to the snout, it is uncertain whether the portion anterior to the naris was very narrow or expanded. The premaxillary–maxillary suture is clear, but the area is obscured by damage such that the lateral notch between these two bones has been greatly exaggerated. The posterodorsal process of the premaxilla is short and broad and forms a ridge around the posterolateral border of the naris. No details are available for the palatal region of the premaxilla due to incompleteness.

The left nasal is better preserved than the right nasal (Fig. 3). The nasal clearly extends anteriorly into the nares and contributes to the formation of the internarial septum. Posteriorly the nasal broadens slightly. Its sutures to the maxilla, lacrimal, prefrontal, and frontal are not determinable because of damage.
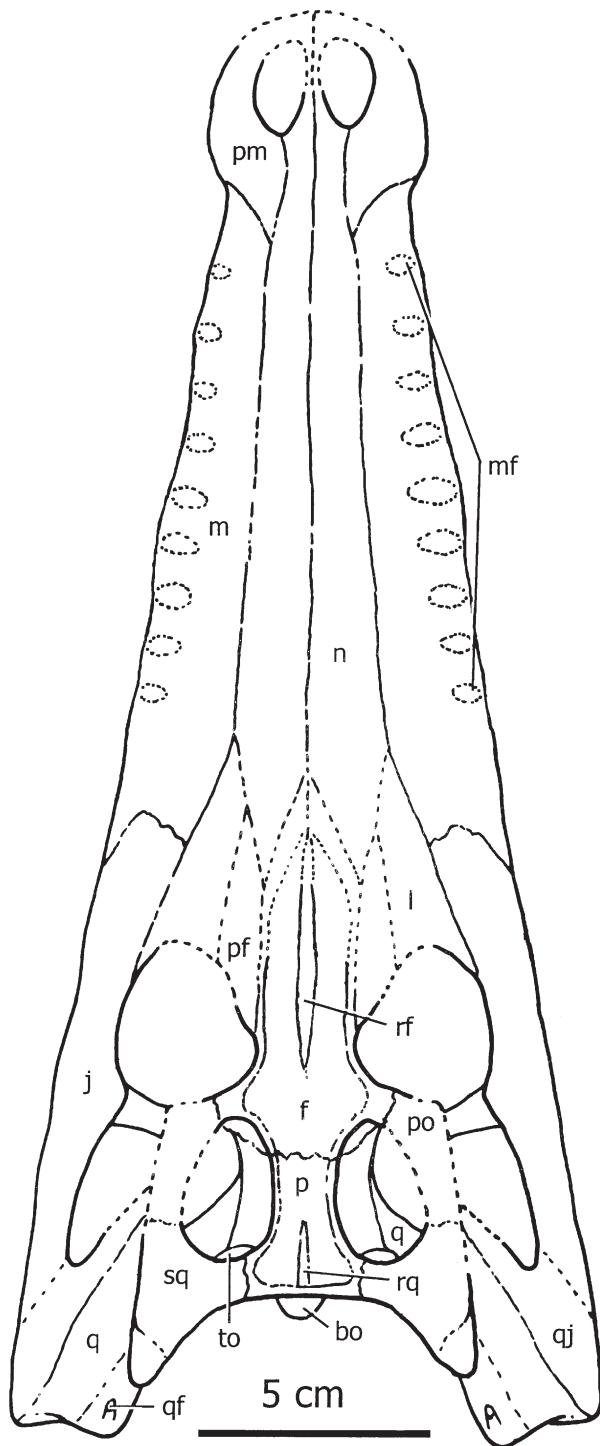
The maxillae are nearly complete and each bears a distinctive set of fossae on the lateral portion of the flattened dorsal surface (Fig. 3). The fossae are located between maxillary teeth from the second to the ninth or tenth (on the right side). There is no evidence to indicate that these fossae are receptacles for the dentary teeth; each fossa does not reach the dental margin of the maxilla laterally. The surface of each fossa is smooth, with no ornamentation. This excludes the possibility that these fossae may have been artifacts of preservation because the zones between teeth have a lesser resistance than do those corresponding to teeth. The lateral border of the maxilla is festooned in two weak waves. In ventral view, the maxillary–premaxillary suture is not visible due to the occlusion of the mandible. Posteriorly the maxilla forms the anterolateral border of the suborbital fenestra, and the maxillary–palatine suture is well demarcated.

The lacrimal is fragmentary, but its anterior portion and lateral face can be fairly accurately restored on the basis of a combination of the preserved parts on both sides. As restored, it appears sharply triangular in configuration. Its sutures with the maxilla, jugal, and nasal are clearly marked on the left side.

The posteromedial portion of the prefrontal is preserved on both sides, forming the anterodorsal borders of the orbits

Fig. 4. Reconstruction of the skull of *Rugosuchus nonganensis* in dorsal view. Abbreviations as in Fig. 3.

the concavity broadens as the bone widens and becomes shallower, but remains distinct. There is no transverse ridge crossing the anterior portion of the frontal, but a pronounced median ridge extends along the midline. The latter may have reached to the anterior end of the bone, but it fades out posteriorly well before the frontal–parietal suture. The frontal enters into the supratemporal fossa and forms the anterior third of the intertemporal region. The suture with the prefrontal extends along the ridge-like lateral border of the concavity. In ventral view the deep olfactory groove is visible.

Each postorbital is preserved only in its anteromedial portion, which forms the lateral component of the narrow bar between the orbit and supratemporal fenestra (Fig. 3A). The relationships of this element with the jugal and squamosal are not known.

The single parietal is complete (Fig. 3A) and is very distinctive in that its dorsal surface is deeply concave (in a fashion similar to that of the frontal) and bears a median ridge that extends along only the posterior half of the midline. The fossa-like concavity broadens posteriorly as the bone widens, and becomes shallower anteriorly and insensibly merges with that of the frontal to form a single, large fossa of distinctive pattern on the skull roof. Sutures with the squamosal and frontal are clearly recognizable. Within the supratemporal fossa, the parietal forms the majority of the fossa floor, meets the quadrate laterally, and, together with the latter, forms the ventral border of the orbito-temporal foramen.

The squamosal lacks much of the anterolateral process on each side (Fig. 3A). The bone bears a pronounced posterolateral process, the posterior half of which is depressed as a lobe-like structure that is sculpted by weakly developed pits. The squamosal, together with the parietal, forms the dorsal border of, and partly overhangs, the orbito-temporal foramen. The lateral groove for the earflap is very shallow. In occipital view the squamosal contributes a small dorsolateral portion of the occiput (Fig. 5). The squamosal–exoccipital suture is slightly curved dorsally. There is a concavity near (at) the suture with the supraoccipital, which may be the remnant of the posttemporal fenestra.

The left jugal is nearly complete (Fig. 3A). Its sutural surface with the maxilla is convex. Along the ventral border of the orbit the jugal is concave and does not form a rim-like ridge. The narrow posterior ramus of the jugal is straight and tapers off posteriorly, but its suture with the quadratojugal is obscured because of poor preservation. This ramus seems to be shorter than the broad anterior ramus. The ascending process of the jugal, which forms the lower portion of the postorbital bar, is nearly round in cross section, has an inset surface, and is not sculpted.

The left quadratojugal is incomplete along its anterior border, and it is uncertain whether the bone contacted the postorbital anterodorsally and bore a pronounced spine projecting into the infratemporal fenestra (Fig. 3A). Its horizontal portion is sculpted and reaches as far posteriorly as the lateral end of the articular condyle of the quadrate. The quadratojugal may form the posteroventral border of the infratemporal fenestra, but it is not known how far its anterior process extended along the ventral margin of the fenestra because of inadequate preservation.

(Fig. 3). There is no trace of a ridge on the dorsal surface of the preserved portion of the prefrontal. The sutural pattern with the nasal and lacrimal may have been configured as depicted in the restored skull (Fig. 3).

The single frontal, with its heavily eroded anterior portion, is characterized by its deeply concave dorsal surface (Fig. 3A). The fossa-like concavity clearly extends anteriorly, possibly to the anteriormost extremity of the bone. Posteriorly

Fig. 5. Occipital view of the skull of *Rugosuchus nonganensis*, holotype, IGV 33. qc, cranio-quadrate canal; so, supraoccipital. Other abbreviations as in Fig. 3.

5 cm
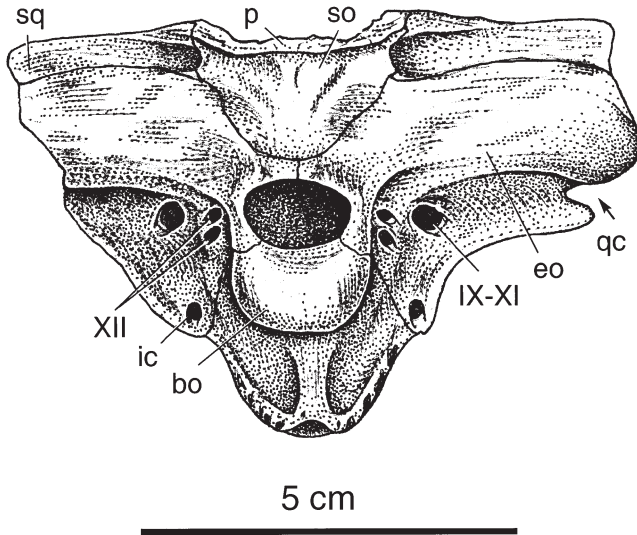
The left quadrate is nearly complete (Fig. 3). The dorsal surface of its body is distinctively divided by a pronounced ridge passing anterodorsally close to the external otic chamber. Its anterodorsal process clearly forms the lateroventral border of the orbito-temporal foramen. Its articular condyle is well divided into a larger lateral part and a smaller medial part. In ventral view, crest B (Iordansky 1973) is very strong and curved anterolaterally. Crest A (Iordansky 1973) is also pronounced, although it is not as strong as crest B. Anteriorly, crests A and B are widely separate, but posteriorly they converge and almost meet. Anteroventrally, the quadrate forms the posterior half of the lateral aperture for cranial nerve V (trigeminal). Sutures with the pterygoid, laterosphenoid, and basisphenoid are obscured by damage, but the suture with the exoccipital is clearly marked.

The paired palatines, the posterolateral ends of which are missing, form a tongue-shaped anterior portion (Fig. 3B) that unites in a zig-zag suture with the maxillae. The interfenestral (suborbital fenestrae) portion is slightly narrower than the base of the tongue-like portion and slightly broadens posteriorly. It is evident that the palatine does not reach to the posteriormost end of the suborbital fenestra because of the intrusion of the pterygoid. The palatines form the reversed V-shaped anterior border of the choana. The latter is preserved only in its anterior portion (possibly the anterior third), and its transversely broad appearance may have been exaggerated by distortion.

The very fragmentary pterygoid, mainly represented by the left transverse flange (Fig. 3), forms the posterior border of the suborbital fenestra. Its palatal process is sharply pointed and extends anteriorly along the medial side of the palatine to reach the V-shaped portion of the choana.

Much of the left ectopterygoid is preserved, but its lateral portion is obscured by the occlusion of the mandible (Fig. 3B). Its posteromedial process, which overlaps the lateral side of the transverse flange of the pterygoid, is narrow. Anteriorly, it lacks contact with the palatine along the border of the suborbital fenestra. It cannot be determined whether the ectopterygoid meets the descending process of the postorbital or bears an additional posterolateral process inserting into the jugal (Norell et al. 1994), or closely abuts the posterior tooth sockets of the maxilla.

The basisphenoid is ventrally exposed because of damage to the pterygoid (Fig. 3B). Its short rostrum is dorsoventrally broad. Dorsolateral to the rostrum is a concavity, here identified as the fossa for attachment of the extrinsic eye muscles. Posteriorly, the basisphenoid borders the three Eustachian foramina along with the basioccipital. Dorsolaterally, its sutures with the prootic, quadrate, and laterosphenoid cannot be determined because of poor preservation.

The complete basioccipital forms the entire occipital condyle (Figs. 3B, 5). The fan-shaped vertical portion of the bone bears a strong, W-shaped ridge on its posterior surface.

The complete right exoccipital is clearly divided into a large dorsal portion, which forms most of the occiput, and a small ventral portion, which faces anteroventrally (Figs. 3B, 5). The lateral end of the dorsal portion narrows abruptly and turns slightly forwards. Medially, the bone narrows medioventrally into a process that meets its counterpart dorsal to the foramen magnum. The small lower portion is highly concave and bears three foramina: the two smaller ones closer to the foramen magnum are identified as exits for cranial nerve XII, and the other, larger one positioned farther laterally as the exit for cranial nerves IX–XI. An additional foramen located at the ventromedial end of this portion is for the passage of the internal carotid artery. The lateral margin of the lower portion is strongly curved into a deep embayment that forms the medial border of the posterior exit of the cranio-quadrate canal.

The well-preserved supraoccipital, with a nearly round ventral margin, is more or less triangular in appearance in occipital view (Fig. 5). The bone is deep and its ventral border closely approaches the foramen magnum. There is a weakly developed median ridge that does not extend ventral to the lower half of the bone. Sutures with neighbouring bones are clearly marked.

Mandible

The left ramus of the mandible is nearly complete, although some of its elements have been somewhat displaced (Figs. 3, 6). The mandible does not bear an external mandibular fenestra, and much of its lateral surface is sculpted by round or elongate pits (mainly on the anteroventral surface) and ridges. In lateral view, the sculpturing covers the entire lateral surface of the posterior portion of the mandible and there is no smooth area near the posterior margin for the attachment of the *M. pterygoideus posterior*.

The left dentary is slightly damaged. It forms the anterior two thirds of the dorsoventrally shallow symphysis. The broadened appearance of its anterior end has been exaggerated by erosion (Fig. 3B). The dentary is slightly constricted at a level just posterior to the symphysis. The dorsal border of the dentary is covered by the upper jaw. Posteriorly, the dentary may have been forked, with a broad posteroventral process and probably a short and narrow posterodorsal process. The posteroventral process overlaps the angular posteriorly and contacts the surangular dorsally, but the latter is displaced dorsoventrally, leading to the dorsoventrally shallow appearance of the mandible in this region. The posterodorsal process is

Fig. 6. Skull and mandible of *Rugosuchus nonganensis*, holotype, IGV 33, in lateral view. df, facet for dentary; ra, ridge-like structure on lateral surface of angular. Other abbreviations as in Fig. 3.
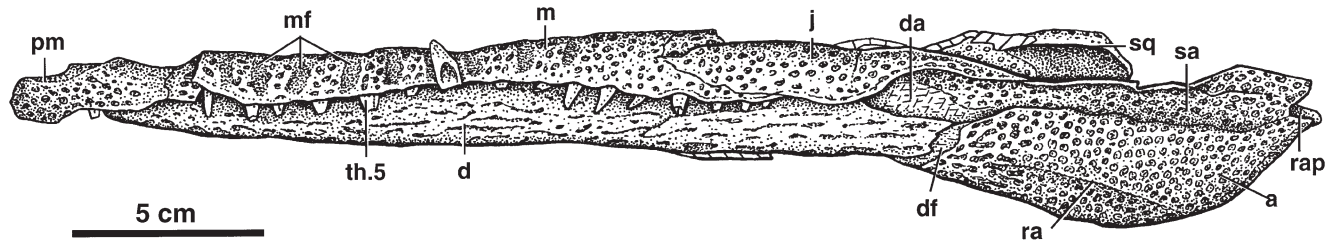
not visible due to its occlusion with the skull, but it probably overlapped the surangular.

The left splenial, with its ventral surface exposed, is nearly complete (Fig. 3). It forms the posterior third of the symphysis. Its symphysial portion is broadened. Posteroventrally the splenial widens and forms the medial half of the ventral surface of the mandible and extends farther posteriorly than the dentary. Details of the medial surface are not visible due to occlusion with the skull, but a foramen for the *intermandibularis oralis* of the trigeminal nerve (cranial nerve V) is present on the anterolateral surface of the bone.

The surangular is obscured anteriorly by occlusion with the skull and was damaged by breakage anterolaterally. It forms the narrow dorsal part of the posterior portion of the mandible, which is further exaggerated by the dorsoventral displacement of its anterior portion (Fig. 6). The surangular has a nearly straight dorsal margin and extends caudally almost to the posterior end of the retroarticular process. Its lateral surface is moderately concave, and dorsomedially it contributes, in small part, to the articular fossa (Fig. 3A). Medially no details can be observed because of occlusion with the skull.

The left angular is complete. It forms the major part of the posterior portion of the mandible (Figs. 3, 6). Posterolaterally, it bears a ridge-like structure that extends to the posterior margin of the bone. Posteriorly, the angular reaches to the posterior end of the retroarticular process and is strongly arched posteroventrally. Anterolaterally, its facet for the overlap of the dentary is exposed because of the displacement of the bone. Posterodorsally, its suture with the surangular is slightly curved. In ventral view, the angular extends much farther anteriorly and wedges between the dentary and splenial (Fig. 3B).

The left articular has its dorsal articular fossa and retroarticular process exposed (Fig. 3). The articular fossa is deep and divided by a ridge into a larger lateral and a smaller medial part. The retroarticular process is moderately elongate and tongue-like in outline. Its dorsal surface is slightly concave but is not segregated by a longitudinal ridge. Posterior to the articular fossa, there is no foramen for the passage of the siphonium to the internal cavity of the articular. The ventral surface of the retroarticular process is deeply concave. In lateral view, this process is directed posteriorly and slightly dorsally.

It is uncertain whether or not a prearticular is present because of occlusion with the skull.

Dentition

The premaxillary bears five teeth, of which the first, third, and fourth are present but incomplete. According to the

dimensions of the tooth sockets, the second tooth is the largest and the fifth is the next largest. A complete premaxillary tooth appears to be subconical, with its tip slightly recurved. The left maxilla bears 16 subconical teeth (there may be an additional one at the posterior end of the bone). They are widely spaced from one another and their crowns bear coarse striae. Maxillary teeth vary in size in accordance with the marginal waves of the maxilla. The fourth and fifth maxillary teeth are subequal in size and are the largest, but are not much larger in size than their immediate neighbours (Figs. 3B, 6). The posterior maxillary teeth are relatively more massive and shorter than the anterior ones, and they are very slightly constricted at their bases. No dentary teeth are exposed.

Comparison and discussion

Although a full phylogenetic analysis of *Rugosuchus* is not presented in this study, the basic position of the genus can be proposed on the basis of recent phylogenetic studies of the Crocodyliformes. It is evident that *Rugosuchus* is not a eusuchian because its choana is not entirely located within the pterygoids (Clark in Benton and Clark 1988; Clark 1994; Wu et al. 1997; Ortega et al. 2000). On the other hand, *Rugosuchus* is possibly more closely related to the clade including some derived neosuchians and the Eusuchia than it is to the Goniopholididae (sensu Wu et al. 1997), based on the presence of more than two longitudinal rows of dorsal osteoderms (Figs. 2B, 2C) and the absence of the anterolateral process of the dorsal osteoderms (Clark in Benton and Clark 1988; Clark 1994; Wu et al. 1997; Ortega et al. 2000). Therefore, the following comparison between *Rugosuchus* and other crocodyliforms is restricted mainly to those taxa phylogenetically closer to the Eusuchia than to the Goniopholididae. These taxa are all of Cretaceous age and are best represented by *Bernissartia fagesii* Dollo 1883 (also see Norell and Clark 1990; Buscalioni and Sanz 1990) from the Lower Cretaceous of Europe; *Shamosuchus* spp. (Mook 1924; Clark in Benton and Clark 1988; Efimov 1988) from the Upper Cretaceous of Mongolia; and a briefly described, but unnamed, taxon (= "Glen Rose Form" of Clark in Benton and Clark 1988) represented by two skulls from the Lower Cretaceous of North America (Langston 1973). There is one additional taxon (Las Hoyas Neosuchian) represented by a fragmentary skeleton from the Lower Cretaceous of Spain (Ortega and Buscalioni 1995), but this is excluded from our comparison because it has not been described or illustrated, although it was included in a

phylogenetic analysis of the Crocodyliformes by Ortega et al. (2000).

We erect the new taxon *Rugosuchus nonganensis* for the Nong'an crocodyliforms primarily on the basis of the following cranial features. (1) There is a set of nine or ten fossae on the dorsal surface of each maxilla. This is unique among known crocodyliforms. (2) The skull roof (the frontal-parietal region) bears a complex pattern of ridges and concavities. This feature is also unique to the new taxon. The frontal is very concave but lacks a median ridge, whereas the parietal has a flat dorsal surface in *B. fagesii* (Norell and Clark 1990). In *Shamosuchus* spp., the frontal and parietal are often partially ridged along the dorsal midline, but their dorsal surfaces are mostly, if not entirely, flat (see figs. 14–20 in Efimov 1988). In addition, there is a transverse ridge crossing the frontal and prefrontals just anterior to the orbits in *Shamosuchus* spp. (3) The maxillary teeth are widely separated. The snout of *R. nonganensis* (more than 2.5 times as long as the remainder of the skull) is relatively longer than those of *B. fagesii* (about 1.4 times as long as the rest of the skull; see fig. 3A in Norell and Clark 1990) and *Shamosuchus* spp. (about 1.7 times (*S. gradilifrons*, with a skull length of about 27 cm) or about 2.3 times (*S. ulgicus*, with a skull length of about 31 cm); see figs. 16 and 17 in Efimov 1988). However, in *R. nonganensis* the maxilla bears only 16 or 17 teeth, as is the case in *B. fagesii* and *S. gradilifrons*, but fewer than the 19 maxillary teeth of *S. ulgicus*. As for the "Glen Rose Form" of Langston (1973), two of these three features cannot be compared because no dorsal view of its skull is illustrated, but the maxillary teeth in this taxon are as closely spaced as they are in *B. fagesii* and *Shamosuchus* spp., and the maxilla definitely bears many more teeth than are present in *R. nonganensis*, as suggested by the presence of a large number of teeth posterior to the second tooth wave indicated by the position of a large tooth (see fig. 6E in Langston 1973). *Rugosuchus nonganensis* also differs from all of the aforementioned three taxa in that the choana is primitively anterior in position, with its anterior border far from the posterior border of the suborbital fenestra. This is the case commonly seen in more basal neosuchians, such as atoposaurids (*Theriosuchus* (fig. 16 in Clark 1986)) and goniopholidids (*Goniopholis* (= *Amphicotylus*, fig. 1C in Mook 1942) and *Sunosuchus* (figs. 3B and 4B in Wu et al. 1996*a*)). In *B. fagesii*, *Shamosuchus* spp., and the "Glen Rose Form," the choana is almost entirely formed by the pterygoids, with its anterior border located almost at the level of the posterior border of the suborbital fenestra (see fig. 2 in Buscalioni and Sanz 1990 for *B. fagesii*; figs. 17 and 19 in Efimov 1988 for *Shamosuchus* spp.; fig. 6E in Langston 1973 for the "Glen Rose Form").

Rugosuchus nonganensis is further differentiated from *B. fagesii* in the following cranial features: (*i*) the lateral borders of the maxillae are not strongly festooned in two waves; (*ii*) the external nares are separate; (*iii*) the ventral border of the orbit is clearly concave and not raised into a rim-like edge; (*iv*) the interorbital region of the skull roof is broader than the interfenestral region; (*v*) the supraoccipital has no strong vertical ridge on its occipital surface along the midline; (*vi*) the suborbital fenestra is much smaller and the interfenestral region of the palatines is much broader; (*vii*) crest A on the ventral surface of the quadrate is very strong; (*viii*) the posterolateral surface of the angular bears a longitudinal ridge-like structure; (*ix*) posterior maxillary teeth are not bulbous and carinate; and (*x*) the splenials form the posterior third of the symphysis.

Rugosuchus nonganensis is further distinguishable from *Shamosuchus* spp. on the basis of the following cranial features: (*i*) the skull is much more slender; (*ii*) the jugal lacks a longitudinal ridge on its lateral side; (*iii*) the second rather than the fourth premaxillary tooth is the largest; (*iv*) the supraoccipital is relatively large; (*v*) the dorsal border of the surangular is straight rather than convex; and (*vi*) the posteroventral margin of the angular is strongly arched.

Although only the posteroventral view of the skull of the "Glen Rose Form" is available for comparison (see fig. 6E in Langston 1973), differences, besides those discussed earlier, in the palatal region are evident between it and *R. nonganensis*. For example, the suborbital fenestra is smaller and rounder, and the interfenestral region of the palatines is broader in the latter than in the former.

It is evident from the above comparison that *Rugosuchus* is a new crocodyliform and cannot be referred to any previously known taxon. It may represent a clade phylogenetically further from the Eusuchia than *Bernissartia*, *Shamosuchus*, and the "Glen Rose Form" on the basis of the anterior position of the choana. Resolution of this awaits a full phylogenetic analysis of data from both the cranium and postcranial skeleton. Although *Rugosuchus* is more primitive in the placement of the choana, it resembles both *Shamosuchus* and *Bernissartia* in different aspects of cranial anatomy.

Rugosuchus shares with *Shamosuchus* a longitudinal ridge-like structure on the posteroventral surface of the angular, although the ridge-like structure is positioned more anteroventrally in *Shamosuchus* and its presence can only be currently confirmed for *S. gradilifrons* (fig. 16*b* in Efimov 1988), as the relevant region is not preserved in the other species of the genus. Furthermore, in *Rugosuchus* and *Shamosuchus*, crest A on the ventral surface of the quadrate is very strong and posteriorly almost meets the end of the more robust crest B and forms, together with the latter, a ridge system that is very similar to that seen in the goniopholidid, *S. junggarensis* (fig. 7B in Wu et al. 1996*a*), and a living alligator, *A. sinensis* (fig. 10H in Iordansky 1973). Crest A, however, is very weakly developed in the latter two taxa. Again, the presence of this feature among the species of *Shamosuchus* is currently known only for *S. ulgricus* and *S. tersus* (figs. 17*a* and 21*a* in Efimov 1988). As for the small suborbital fenestra and the broad interfenestral region of the palatine, *Rugosuchus* is more similar to *Shamosuchus* (see *S. major* and *S. ulgricus* (figs. 15 and 17 in Efimov 1988)) than to either *Bernissartia* or the "Glen Rose Form." The anterior end of the snout is complete only in *S. ulgricus* within *Shamosuchus*, indicating that the external nares are separated by a narial septum (see fig. 17*b* in Efimov). In this feature, *Rugosuchus* resembles *Shamosuchus* as well. The above features, except for those mentioned, are unknown for the "Glen Rose Form."

The most evident feature shared by *Rugosuchus* and *Bernissartia* is the strongly arched posteroventral margin of the angular (not known for the "Glen Rose Form"). In other words, the angle between the "ventral" margin and "posterior"

margin of the angular is small, being about 120° in *R. nonganensis* (Fig. 7) and the Spanish specimen of *B. fagesii* (fig. 3 in Buscalioni and Sanz 1990), and about 110° in the Belgian specimen of *B. fagesii* (figs. 2C and 2D in Norell and Clark 1990). In no other crocodyliforms is the angular, to our knowledge, so arched posteroventrally. Additionally, the surangular has a straight dorsal border in *Rugosuchus* and *Bernissartia* (not known for the "Glen Rose Form"), although this feature is also present in other crocodyliforms (see Clark 1994; Wu et al. 1997).

Rugosuchus shares with both *Shamosuchus* and *Bernissartia* the absence of the external mandibular fenestra and the presence of a longitudinal ridge dividing the dorsal surface of the quadrate (these two features are unknown in the "Glen Rose Form"). In most specimens of *Shamosuchus* spp., the dorsal surface of the quadrate is incomplete, but in one the right quadrate exhibits such a longitudinal ridge on its dorsal surface (*S. tersus* (fig. 21*a* in Efimov 1988)). However, the aforementioned two features have a more widespread occurrence in the Crocodyliformes (see the character-state distribution of characters 80 and 55 in Ortega et al. 2000).

Lastly, the morphology of the posterolateral process of the squamosal is worthy of mention. In several taxa (such as species of *Shamosuchus* (Efimov 1988), *Theriosuchus* (Clark 1986), *Sunosuchus* (Wu et al. 1996*a*), and *Goniopholis* (Ortega et al. 2000)), the posterolateral process of the squamosal is lobe-like, depressed, and not sculpted, and therefore the presence of an unsculpted posterolateral lobe of the squamosal has often been considered as a discrete character state in recent phylogenetic analyses of the Crocodyliformes (Clark in Benton and Clark 1988; Clark 1994; Ortega et al. 2000). Wu et al. (1996*a*) demonstrated that the unsculpted posterolateral lobe of the squamosal is an ontogenetic feature of young (small) individuals of *S. junggarensis* and suggested caution when considering this feature to be constant within a taxon. The posterolateral process of the squamosal in *Rugosuchus* is lightly sculpted, although it is still slightly depressed and separable by a weak ridge from the rest of the bone (Fig. 3A). This situation appears to be intermediate between the unsculpted and strongly depressed stage seen in young individuals of *S. junggarensis* and the strongly sculpted and superficially positioned stage seen in old (large) individuals of *S. junggarensis*. Actually, among the eight illustrated specimens of the species of *Shamosuchus*, the only one that does not have such an unsculpted posterolateral lobe is the largest specimen of *S. major*, with a skull length of about 51 cm (fig. 15*c* in Efimov 1998). The others, with skull lengths ranging from about 11 cm to about 31 cm, all possess such a lobe that is clearly distinguishable from the rest of the bone, although it is somewhat sculpted, as indicated by the illustrations, in relatively larger specimens, as in *R. nonganensis*. Therefore, the unsculpted posterolateral lobe of the squamosal is most probably an early ontogenetic feature commonly present in crocodyliforms and cannot be reliably used as a character in phylogenetic analyses.

Acknowledgments

Fig. 7. Posterior portion of the skull and mandible of *Rugosuchus nonganensis*, holotype, IGV 33, in lateral view, showing the strongly arched posteroventral margin of the angular. Size proportion as in Fig. 6.

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