A re-evaluation of goniopholidid crocodylomorph material from Central Asia: Biogeographic and phylogenetic implications

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Central Asia is a key area for crocodylomorph evolution, lying midway between the highly documented deposits in Europe and North America, but crocodylomorph fossils from this part of the world are rare. Included among these are specimens collected in the 1970s and 1980s by the Soviet-Mongolian Expeditions in the Jurassic and Cretaceous of Mongolia, Tajikistan, and Kazakhstan. Three species, "*Sunosuchus*" *shartegensis*, *Kansajsuchus extensus*, and *Turanosuchus aralensis* are redescribed and subjected to phylogenetic analysis for the first time. "*Sunosuchus*" *shartegensis* and *Kansajsuchus* are relatively derived goniopholidids, and part of a pan-east-Laurasian radiation of goniopholidids from which the European goniopholidids subsequently radiated. No characters can be used to distinguish "*Sunosuchus*" *shartegensis* from "*S.*" *thailandicus*; the two species are therefore synonymized. *Turanosuchus aralensis* is here considered a nomen dubium. Cladistic analysis suggests that *Sunosuchus* is polyphyletic, indicating a higher degree of diversification than was previously thought, but also pointing to the need for further systematic revision.

Key words: Reptilia, Crocodylomorpha, Neosuchia, Goniopholididae, phylogeny, Mesozoic, Asia.

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Introduction

The interrelationships of crocodylomorphs, and the understanding of their biogeographic history have been substantially revised in the past 25 years (Benton and Clark 1988; Brochu 2001; Buscalioni et al. 2001; Salisbury et al. 2006). The stability of some subclades within Crocodylomorpha has improved considerably. For instance, Thalattosuchia has long been considered a monophyletic group (Clark 1994), recent work stabilising internal thalattosuchian relationships (e.g., Young et al. 2010), and there has been strong evidence to suggest that Notosuchia is also a clade (e.g., Pol and Powell 2011; Soto et al. 2011). Nonetheless, there are many parts of the tree that are less well resolved. Goniopholididae, a clade consistently placed within Neosuchia (Clark 1994; Buckley et al. 2000; Ortega et al. 2000; Karl et al. 2006) and traditionally regarded as a natural group (e.g., Buffetaut 1982; Lauprasert et al. 2007; Andrade et al. 2011), is considered by some not to be monophyletic (Clark 1994; Pol 2003). Furthermore, intrafamilial relationships remain unresolved (Turner and Buckley 2008), with some suggesting further

that *Goniopholis*, the type genus, may not be monophyletic (Wu et al. 1996; but see also Andrade et al. 2011). By applying cladistic methods to an increased sample of Goniopholididae (the majority of the analyses considered only two or three members see discussion in Andrade et al. 2011), as well as large numbers of representatives from other crocodylomorph taxa, these questions may be addressed.

Goniopholididae is an Early Jurassic to Late Cretaceous Laurasian group, with representatives from North America (Tykoski et al. 2002), Europe (Salisbury et al. 1999; Salisbury 2002; Schwarz 2002; Andrade et al. 2011; Salisbury and Naish 2011), Central Asia (Efimov 1975, 1988a, b; Maisch et al. 2003; Schellhorn et al. 2009), and south-east Asia (Buffetaut and Ingavat 1980). The Central Asian taxa occupy an intermediate position geographically, and work on dinosaurs (Upchurch et al. 2002) has already indicated the importance of this region in understanding the palaeobiogeographic history of terrestrial tetrapods.

The Central Asian taxa "*Sunosuchus*" *shartegensis* Efimov, 1988, *Kansajsuchus extensus* Efimov, 1975, and *Turanosuchus aralensis* Efimov, 1988 were collected by the Joint Soviet-Mongolian Palaeontological Expeditions, from Mongolia, Tajikistan, and Kazakhstan respectively. The existing published figures and English-language descriptions of these taxa are brief, such that they have received little attention beyond occasional passing mentions in the literature (Maisch et al. 2003; Wings et al. 2010). Further, the Russian-language descriptions (Efimov 1988a, b) are also brief. Since the discovery of these specimens, understanding of Mesozoic crocodylomorph distributions, as well as phylogenetic methods, has advanced substantially. It is therefore timely to redescribe the material and subject it to cladistic analysis for the first time.

Institutional abbreviations.—PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow.

Other abbreviations.—MPTs, most parsimonious trees.

Material

Specimens redescribed herein include PIN 4174-1, previously assigned to *Sunosuchus shartegensis*, from the Shar Teeg locality of the Tithonian (Upper Jurassic) of Mongolia; PIN 2399-301 to PIN 2399-426, assigned to *Kansajsuchus extensus*, from the Fergana Basin, in the Santonian (Upper Cretaceous) of Tajikistan; PIN 2229-501 to PIN 2229-510, previously assigned to *Turanosuchus aralensis*, from the Zhirkindek Formation of the Santonian (Upper Cretaceous) of Kazakhstan. All material was observed first-hand at PIN by TJDH, and photographs and drawings were made. Specimens include those described in earlier papers, as well as previously undescribed material. To avoid confusion between basal and derived taxonomic groups, the terms "Crocodylomorpha" and "Crocodyliformes" are used instead of Crocodylia Gmelin, 1789, and the word "crocodilian" is applied solely when referring to the crown-group containing extant branches of Crocodylomorpha (but see discussion in Martin and Benton 2008; Brochu et al. 2009).

Systematic palaeontology

Order Crocodylomorpha Hay, 1930

Suborder Neosuchia Clark, 1988

Family Goniopholididae Cope, 1875

Genus "*Sunosuchus*" Young, 1948

Type species: *Sunosuchus miaoi* Young, 1948. Holotype specimen from the Late Jurassic of Gansu, China.

"*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980

Figs. 1–3, 4A.

1988 *Sunosuchus shartegensis* sp. nov.; Efimov 1988: 54, fig. 8.

Holotype: PIN 4174-1. The holotype is a fragmented skull, comprising the rostrum, the preorbital region of the skull table, the quadrates and parts of the quadratojugal, the occipital condyle and near-complete mandibles (Fig. 1). The holotype is the only specimen known of this species. There has been some discrepancy in the museum number recorded in the literature, namely PIN 4174-1 (e.g., Efimov 1988a) and PIN 4171-1 (e.g., Efimov 1988b). The correct number on the specimen label is PIN 4174-1.

Type locality: The specimen was found in the Ulan Malgait beds, in the Shar Teeg locality, of the Gobi-Altai region of Outer Mongolia, embedded in grey clay. The Ulan Malgait Beds are situated 2200 m east-southeast from Ulan Malgait Mountain, and are described in Gubin and Sinitza (1996), who indicate that PIN 4174-1 was extracted from "Layer 2".

Type horizon: The age generally ascribed to this section is Upper Jurassic (Tithonian). Sedimentological profiles indicate that the Ulan Malgait beds were formed in a temporary lacustrine environment with seasonal outwashes of shore sediments and drying of lakes (Gubin and Sinitza 1996; Watabe et al. 2007). This gives the specimen a similar age to *Sunosuchus miaoi* from north-west China, geographically near to Shar Teeg, and well within the time during which the goniopholidids were most diverse. Shar Teeg has since yielded a diverse array of species, including insects such as lacewings (Khramov 2011), fishes, turtles, crocodyliforms, and temnospondyl amphibians (Gubin and Sinitza 1996).

Emended diagnosis.—"*Sunosuchus*" *thailandicus* differs from all other goniopholidids except *Kansajsuchus* in lacking neurovascular foramina on the dorsal surface of the rostrum and in possessing a relatively broad quadrate with an expanded medial hemicondyle. The ventral margin of the neurovascular foramina is very close to the teeth, along the alveolar margin, compared with other goniopholidids, but the maxillary depression is elevated from the tooth row higher than in other goniopholidids. Unlike other goniopholidids, the mandibular symphysis is inclined dorsally. Differs from all goniopholidids except *Calsoyasuchus* in the presence of an anteroposteriorly elongate antorbital cavity. The extent to which the premaxillo-maxillary notch surrounds the tooth is limited, and the lat-

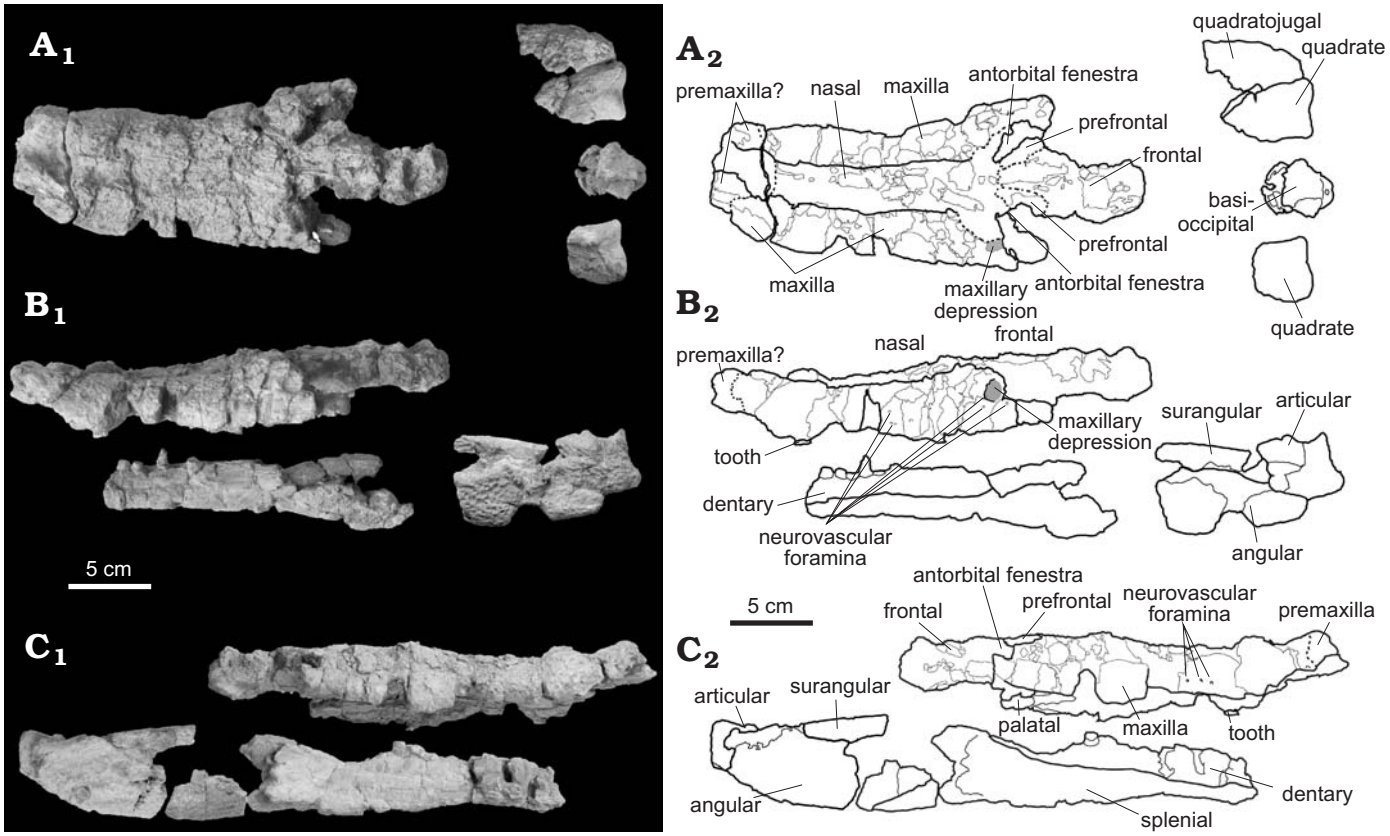


Fig. 1. Adult crocodylomorph "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980, PIN 4174-1, from the Tithonian (Upper Jurassic) of Shar Teeg, Mongolia. **A**. Rostrum, quadrates, and occipital condyle in dorsal aspect. **B**, **C**. Rostrum and mandible in left (**B**) and right (**C**) views. Photographs (A_1–C_1) and explanatory drawings (A_2–C_2).

eral margins of the nasal are convex, as in other Asian goniopholidids, but unlike the European forms. Differs from *S. miaoi* in having a tooth row lower than the quadrate condyle. Differs from *S. junggarensis* in the festooning of the jaw, which has a double rather than single sinusoid. Differs from both *S. miaoi* and *S. junggarensis* in lacking a maxillo-palatine fenestra and dental ornamentation.

Description.—*General features*: The holotype comprises a highly fragmented and slightly distorted skull (Figs. 1–3). Several sutures cannot be discerned reliably because the material is incomplete and fractured.

The largest preserved part is composed mostly of maxillae and nasals, clearly distinguishable from one another in dorsal view (Fig. 1). The premaxillae are present, though the tip is missing, and the nares cannot be fully delineated. It appears that the anterior portions of the frontals, as well as all of the prefrontals, are preserved towards the rear of this portion. The teeth extend laterally along the entire length of this fragment (Figs. 1, 2), and no maxillojugal suture can be seen. The skull is reconstructed as being between 40 and 50 cm long in total, and about 20 cm wide at the quadrates, which agrees broadly with the conclusions of Efimov (1988a), whose estimate of length was slightly shorter, perhaps following his interpretation of the antorbital fenestra-like structures as orbits (see below). The increase in width at the orbital region of the skull is dramatic, and the skull has an overall medium-length, but narrow rostrum. The rostrum is nonetheless broader than it is high, and has a slightly concave appearance when viewed laterally (Fig. 1B). It seems to make up a significant proportion of the length of the skull—PIN 4174-1 is therefore considered meso- to longirostrine, as is "*S.*" *thailandicus*. The dermal bones of the skull are ornamented with a pitted pattern for the majority of their length (Fig. 1A), though the more posterior parts of the maxilla do not have preserved ornamentation. When the mandible is reconstructed from the several fragments, the quadrate condyle is clearly not level with the tooth row.

Premaxilla: The rostrum is broken at the premaxillo-maxillary suture, where there is a constriction and the skull is narrower. The suture is just present on the anteriormost end of the specimen (Fig. 1B). Because of this, the shape of the premaxillae is not clear, but given that there appears to be a strong constriction, as in *Goniopholis*, *Eutretauranosuchus*, and other goniopholidids, it is highly probable that there is a lateral expansion anterior to the constriction. The nares do not appear to be preserved in this specimen; there is an area lacking bone in the centre of the rostrum (Fig. 1A), but this is too far from the expected end of the snout, and seems to represent taphonomic loss. The nasals do not extend to the end of the specimen, and are therefore certainly excluded from the narial cavity, as in other *Sunosuchus* species, *Goniopholis*, and *Eutretauranosuchus*.

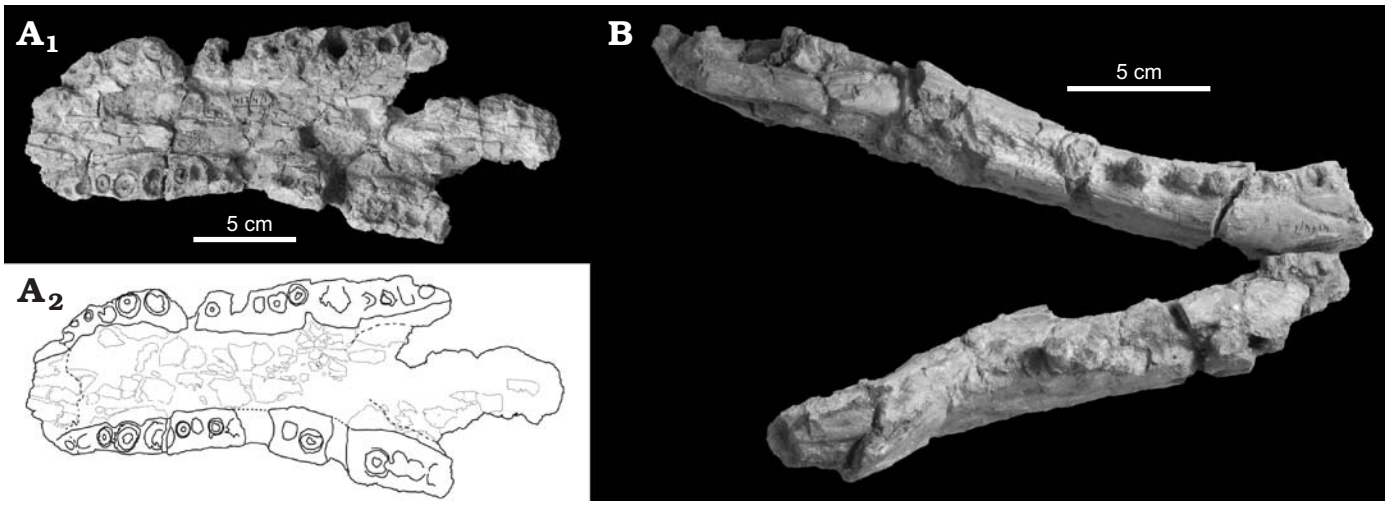


Fig. 2. Crocodylomorph "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980 dentition, PIN 4174-1, from the Tithonian (Upper Jurassic) of Shar Teeg, Mongolia. **A**. Rostrum in palatal aspect. Photograph (A_1) and explanatory drawing (A_2). **B**. Anterior mandible in dorsal view, from symphysis to the anterior edge of the external mandibular fenestra.

Only the posterior end of the palatal region of the premaxilla is preserved (Fig. 2); this part is unornamented and not perforated by any fenestrae. The palatal rami meet in the middle of the palate and contribute significantly to the region. The suture with the maxillary region of the palate is straight rather than concave or convex.

Maxilla: The maxillae are festooned in a sinusoidal pattern both in dorsal and lateral view (Fig. 1), with the lateral expansions coinciding with ventral expansions and increases in tooth size (Fig. 2). The entire dorsal surfaces of the maxillae are ornamented with a series of pits, except for a small, smooth depression towards the posteriormost end of the specimen (maxillary depression in Fig. 1B), which contains two neurovascular foramina, the larger of which is large enough and positioned in such a way that it could have housed the maxillary branch of the trigeminal nerve. This oval depression appears to be entirely enclosed by the maxilla, though its posterior end is missing, and there are no sutures apparent between any of the lacrimal, maxillary or jugal bones. As the posterior section is missing, the proportions of the depression are unknown. The depression has a raised anterior rim through which the largest of the neurovascular foramina passes. Although maxillary depressions are synapomorphic for goniopholidids, this specimen possesses notable differences from the standard goniopholidid pattern. Primarily, the position of the depression is considerably dorsally displaced relative to the alveolar margin and the main lines of the neurovascular openings. Goniopholidid maxillary depressions are thought to derive from the neurovascular foramina (Andrade 2009), and hence this displacement indicates a lack of homology, despite the structural similarity to that of *Eutretauranosuchus* (Smith et al. 2010) and other goniopholidids.

There is a possible antorbital fenestra between the maxilla and the prefrontal, taking the form of an elliptical opening, with the main axis oriented roughly anteroposteriorly, as in *Calsoyasuchus* (Fig. 1A). This feature is unreported in all other specimens of *Sunosuchus*, and indeed is unique among goniopholidids in *Calsoyasuchus*. The maxillary depression is positioned near to the anterolateral edge of this antorbital fenestra, which penetrates through the skull to the palate.

There is a wide and relatively shallow constriction at the premaxillo-maxillary suture (Fig. 1). This broadly agrees with Efimov (1988a), who stated that "the festooning at the premaxilla is located for the insertion of the mandibular tooth". Although the "festooning" is present, no large caniniform mandibular tooth is preserved, and the constriction is shallower and wider than would be expected for such a tooth. Only the posterior end of the constriction is preserved, leading to an impression of simple narrowing. The constriction can be distinguished from an anterior narrowing of the jaw, as the rapid decrease in tooth size would suggest a diastema rather than the end of the jaw, where no significant reduction in tooth size would be expected.

The maxilla forms a large proportion of the preserved secondary palate (Fig. 2), though many of the sutures are fused or destroyed. The maxillary portion is entirely unornamented, and extends as far back as the antorbital fenestra, where is appears to meet the palatine bone. Because of the high fragmentation of the palate, the identification of any fenestrae is next to impossible, but from what is preserved, the "anterior palatal openings" previously described (Efimov 1988a) are not evident. The presence of anterior fenestrae in the maxillary palate is one of the supposed synapomorphies of *Sunosuchus*, and the absence of such a feature here is notable. Even though it is fragmented, the palate seems to form a continuous surface in the area in which such fenestrae would be expected (Fig. 2). The edges of the secondary palate, as mentioned by Efimov (1988a), are bounded by a groove, and his interpretation that this held the palatine artery is followed here.

Nasal: The nasal bones are incomplete along their length. The sutures with the maxillae are nonetheless clear, as the

maxillae are well preserved. The nasals are rectangular, with no lateral concavity or convexity along their length (Fig. 1A). They are of constant width along the rostrum, and they do not taper towards either end. No midline suture between the nasals has been preserved. The nasals are slightly concave when viewed in lateral aspect, curving with the whole rostrum (Fig. 1B, C). The anterior limit of the nasal bones is not clear, but it appears that they are excluded from the nares by the premaxillae. The nasals are ornamented with the same pattern of pits as the other dermal bones of the skull.

Posteriorly, the nasals are limited by the nasofrontal suture, which occurs at the same level as the large elliptical antorbital fenestra (Fig. 1A). This suture is narrow and straight, unlike other specimens of *Sunosuchus*. The morphology of this suture is used to distinguish *Sunosuchus* from other goniopholidids such as *Calsoyasuchus* and *Eutretauranosuchus*, which possess a W-shaped naso-frontal suture, although *Anteophthalmosuchus* also possesses a V-shaped suture. The lack of a nasal process between the frontal and prefrontals relates this specimen to *Sunosuchus*, although the area is heavily damaged, and interpretations of the positions of sutures are tentative.

Frontal: The unpaired frontal is partially preserved, with the anterior portion that contacts the prefrontal and nasal bones relatively well preserved. In PIN 4174-1, the frontal and prefrontal bones are very closely associated (Fig. 1A), and distinction between these elements is difficult. This region, where the frontal meets the prefrontal and nasal, lies directly between the antorbital fenestrae, and is flat to slightly concave (Fig. 1B, C). The bone is covered in pitted ornamentation. The frontal tapers significantly anteriorly and extends far further forward than the orbital region, which contrasts with Efimov's (1988b) interpretation, which suggested that previous interpretations of the forward position of the frontal, such as Young's (1948) description of *S. miaoi*, were wrong. This interpretation possibly arose from misinterpretation of the antorbital fenestra as an orbit. In *Calsoyasuchus* and in *S. miaoi* (see Young 1948; Tykoski et al. 2002), the frontals extend anterior to the orbits, and in *Calsoyasuchus* the former are level with the antorbital fenestra (the latter taxon does not possess an antorbital fenestra). There is neither a transverse nor a longitudinal ridge on the frontal bone (Fig. 1A), though the level of the frontal is slightly below the surrounding bones, giving the appearance of ridges surrounding the frontal.

Prefrontal: The paired prefrontals are both preserved in their entirety, and are positioned on the medial edge of the antorbital fenestra. They are wedge-shaped, tapering to a point anteriorly and probably contacting the nasals, though the bone is broken here, and they may have been excluded from contact by a nasofrontal suture. They are covered in heavy pitted ornamentation (Fig. 1A).

Lacrimal: The lacrimals do not appear to be preserved. They are expected to bound the rim of the antorbital fenestra on the lateral edge, but they cannot be located because they have either been destroyed or the sutures are not preserved.

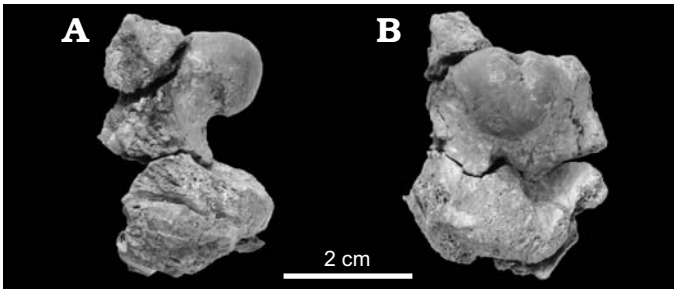


Fig. 3. Crocodylomorph "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980, PIN 4174-1, from the Tithonian (Upper Jurassic) of Shar Teeg, Mongolia. Occipital condyle in lateral (**A**) and posterior (**B**) views.

Palate: The secondary palate of "*S.*" *thailandicus* is preserved nearly complete (Fig. 2A), except under the premaxilla, and it extends back to the limit of the internal nares. The maxillae comprise the majority of the palate; the medial suture is not visible. The palatine bones are just visible at the posterior end, also perforated by several neurovascular foramina of varying size. The largest of these is on a region of the palate that could be the right palatine wing (Fig. 2A). The suture between maxillae and premaxillae is not obvious, since this area is damaged.

The palate was originally described as possessing two distinctive openings at the posterior end of the maxilla, but no evidence of palatal openings warranting the description "distinctive" was found. These are understood to refer to the anterior palatal openings, which in *Sunosuchus miaoi* are positioned between the maxilla and palatine. Among neosuchians, such openings are only known in *Sunosuchus* and *Eutretauranosuchus* (Buffetaut 1986).

Quadrate: The articular heads of both quadrates are well preserved (Fig. 1A), and the right quadrate retains its connection to the quadratojugal. The condylar heads of the quadrate are not equal in size, with the medial head being considerably smaller but more ventrally directed than the lateral head. The heads are separated by a well-defined groove on the ventral surface. The quadrates are held horizontally, as in all other goniopholidids and pholidosaurids. There are no identifiable large foramina on the preserved surface of the quadrate, and Efimov's (1988a) claim that the air cavity connecting the middle ear to the maxillary sinuses can be seen opening in the quadrate cannot be substantiated. The bone is not complete, however. The quadrate is an entirely unornamented bone, in contrast to those that surround it (Fig. 1A), and is non-pneumatic. The posterior edge of the quadrate expands laterally and shows a weaker concavity than that of *S. junggarensis* or *S. miaoi*.

Basioccipital: The basioccipital is almost complete, with everything ventral to the occipital condyle present (Fig. 3). The bone is extremely spongy, and is perforated by a variety of foramina for nerves, blood vessels, and also sinusal channels. Efimov (1988a) devoted considerable space to identifying the paths of the different sinuses, but little can be seen of the sinuses on the exterior surface. It is possible that the specimen has degraded since 1988, but the detail in Efimov's de-

scription cannot now be confirmed; only a tomographic scan could reveal the pneumatic structure. The occipital condyle is subcircular, with two wing-like structures on the lateral edges, which give it an overall heart shape in posterior view.

When viewed laterally (Fig. 3B), the hypoglossal nerve (cranial nerve XII) canal can be seen clearly, passing through the occipital bone, surrounded as it is by the highly perforated and spongy structure. The path of the hypoglossal nerve was interpreted by Efimov (1988a) to be a primitive feature in an otherwise highly derived occipital region. As described by Efimov (1988a), the braincase floor is verticalised (Fig. 3A), a trait characteristic of more derived members of Eusuchia, which would suggest, in conjunction with the overall body size and single frontal that this is a mature and derived crocodylomorph.

Dentary: The mandible is shallow and straight throughout its length (Fig. 1B, C), and Y-shaped in dorsal view (Fig. 2B), as it has an extensive mandibular symphysis, similar to that in *Sunosuchus miaoi* and "*S.*" *junggarensis*. The tooth rows run parallel along the entire length of the preserved symphyseal region, of which the anterior section is missing. The bone of the symphyseal region is highly pneumatic and spongy, and the section is inclined dorsally by approximately 5° (Fig. 1B, C). The dorsal surface of the symphysis is flat, with no depressions or ridges, and is estimated to have been about twice as long as it is wide. As in the maxilla, the teeth are isolated in their own alveoli, at least in the symphyseal region, where the bases of the teeth are preserved in greatest detail.

Splenial: The splenial contributes substantially to the mandibular symphysis, entering as a wedge-shaped projection into the dentary portion of the symphysis (Fig. 2B). In most other *Sunosuchus* species the splenial plays a small part in the mandibular symphysis, but none as strongly as in "*S.*" *thailandicus*. The splenial peg in the symphysis is present on both dorsal and ventral surfaces, and the splenial bone is large and robust throughout.

External mandibular fenestra: The mandibular fenestra is preserved on both rami (Fig. 1B, C), each across multiple fragments. The fenestra is long and thin, with angular ends, and is oriented horizontally. Each fenestra occurs at the point where the articular rises to the condyle. It is in line with the tooth row, and slightly below the level of the quadrate-articular joint, and is bounded by the articular ventrally and surangular dorsally.

Angular: The angulars are heavily pitted on their external surfaces, like the dermal bones of the skull, but unlike the mandible itself (Fig. 1B, C). The posterior portion of the jaw shows no increase in depth or curvature.

Surangular: The surangular is in two sections on both sides, and the morphology of each end differs slightly. The posterior end, which extends onto the retroarticular process, and forms the posteriormost part of the preserved specimen, is more strongly pitted, while the region above the external mandibular fenestra is smooth and unornamented, contacting the angular smoothly (Fig. 1B, C).

Articular: Both articulars are complete. The condyle is extremely robust relative to the rest of the bone, which is entirely unornamented. The articular ventrally contacts the angular and laterally the surangular with simple sutures. The descending process of the articular on the medial side of the mandible is strongly grooved down the centre (Fig. 1B, C). The quadrate condyle is oriented horizontally, and has a deeper rim on the posterior than on the anterior edge. It is directly beneath the articular, on the posteroventral surface, where the ventral surface of the mandible is most curved. This feature of greatest curvature on the posteroventral surface rather than directly below the external mandibular fenestra is a character common to all goniopholidids.

Teeth: The teeth are similar in morphology throughout, being unornamented and cone-shaped (Figs. 2, 4A). Along the maxilla, the tooth size changes (Table 1), with the greatest diameter at the points of greatest lateral and ventral expansion (Fig. 2A), and least where the snout is narrowest. The teeth are circular in cross-section, and are conical to caniniform in morphology. This differs strongly from other *Sunosuchus* specimens, which possess ornamented, ridged posterior teeth that are slightly laterally compressed, and

Table 1. Measurements (in cm) of tooth alveoli. Ordinal numbers refer to the order of preserved alveoli, not to the actual order of the alveoli, as preservation of the anterior portions is not always complete. In *Kansajsuchus*, PIN 2399-301, the first preserved alveolus is the first premaxillary tooth. In "*Sunosuchus*" *thailandicus*, attempts have been made to correlate the two sides of the jaw to one another. The gaps are due to missing portions of the maxillary edge or mandible: –, not applicable as outside the specimen; ×, gap in specimen.

Species	Specimen	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th	15th	16th
"*Sunosuchus*" *thailandicus*	PIN 4174-1 left mandible	0.7	0.8	0.8	0.8	0.8	1.0	1.3	–	-	–	–	–	–	–	–	–
	PIN 4174-1 right mandible	×	×	×	×	×	×	1.1	–	–	–	–	–	–	–	–	–
	PIN 4174-1 left maxillary	0.3	0.5	0.6	1.1	1.2	1.0	×	1.0	0.8	1.0	1.2	1.6	1.4	1.0	1.1	0.8
	PIN 4174-1 right maxillary	0.5	0.6	0.9	1.4	1.4	0.8	0.7	0.7	×	1.0	1.0	×	1.2	1.1	1.0	1.0
Kansajsuchus extensus	PIN 2399-301 right premaxilla	1.2	1.0	1.4	1.8	1.0	–	–	–	–	–	–	–	–	–	–	–
	PIN 2399-307 left maxilla	1.5	2.7	2.1	2.0	1.3	1.5	–	–	–	–	–	–	–	–	–	–
	PIN 2399-313 caniniform tooth	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	PIN 2399-314 molariform tooth	2.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
"*Sunosuchus*" *thailandicus*	PIN 2229-502 right maxilla	1.3	1.4	1.5	1.2	1.0	1.0	–	–	–	–	–	–	–	–	–	–
	PIN 2229-507 left mandibular symphysis	1.6	0.9	1.4	1.5	0.7	0.8	0.8	0.7	–	–	–	–	–	–	–	–
	PIN 2229-507 right mandibular symphysis	1.3	1.1	×	×	0.7	0.8	×	×	–	–	–	–	–	–	–	–

possess a clear keel (Buffetaut and Ingavat 1984; Wu et al. 1996; Averianov 2000; Maisch et al. 2002). Though in PIN 4174-1 the teeth are not preserved save in cross section and for one relatively anterior dentary tooth (Fig. 4A), the teeth are clearly not compressed in cross section rather than subcircular, as in other *Sunosuchus* specimens.

Each tooth is vertical and set in a separate alveolus (Fig. 2), isolated from other teeth and from both lateral and medial walls of the alveolar margin. Most previously described specimens of *Sunosuchus* also possess separate alveoli, though some had apparent grooves (Maisch et al. 2002). The preserved mandibular teeth are 10 mm in length, and 6 mm in diameter at the base (Fig. 4A), similar in size to the teeth of the fragment described by Maisch et al. (2002). They are slender, and taper to a point. All teeth are approximately the same size in the mandible, unlike in the maxilla.

The tooth rows are continuous in both upper and lower jaws (Fig. 2), with no diastemata. Teeth are neither cusped nor faceted. Because few teeth are preserved in full, occlusion is difficult to determine, but it appears that the upper and lower dentitions interlocked—there is some suggestion of pits between the lower teeth, although these are not well preserved—and there is no overbite, as in *Goniopholis*. The maxillary tooth row extends far further back than the dentary tooth row, to almost the same level as the mandibular external fenestra.

Remarks.—The antorbital fenestra of PIN 4174-1 is seen among Goniopholididae otherwise only in the American Jurassic *Calsoyasuchus* (Tykoski et al. 2002), though it is known in more basal crocodylomorphs (Osmólska et al. 2007) and many notosuchians (Andrade and Bertini 2008; Kley et al. 2010). An antorbital fenestra is absent in other species of *Sunosuchus.* Since PIN 4174-1 and *Calsoyasuchus* do not form a monophyletic group in this study, the presence of the antorbital fenestra in these taxa is optimized as a convergence rather than a synapomorphy. Many outgroups to Goniopholididae possess antorbital fenestrae, and the loss of the trait may be a general neosuchian feature.

PIN 4174-1 exhibits several features consistent with placement in the Goniopholididae, including a highly festooned rostrum, a strong constriction at the premaxilla-maxilla suture, and the pattern of ornamentation (Fig. 1). The maxillary depression is present in a highly unusual form. This structure is traditionally a key synapomorphy of Goniopholididae, but Martin and Buffetaut (2012) consider it homologous to that in some pholidosaurs. This structure is ontogenetically related to the line of neurovascular foramina that runs along the alveolar margin (Andrade 2009), and in all goniopholidids possessing the maxillary depression, the structure is situated in this region (e.g., Schwarz 2002; Andrade 2009, Andrade et al. 2011).

The maxillary depression in *S. miaoi*, as described by Buffetaut (1986) is a "deep elongated depression subdivided by faint transversal ridges", and is a feature unique to Goniopholididae, in which it is most usually bordered by the maxilla, close to the lacrimal and jugal sutures. There is a depression of sorts in PIN 4174-1; it lacks the posterior end, but appears not to be elongated, and possesses no transverse ridges. There is also no evidence that the lacrimal was involved in this depression; no sutures are seen

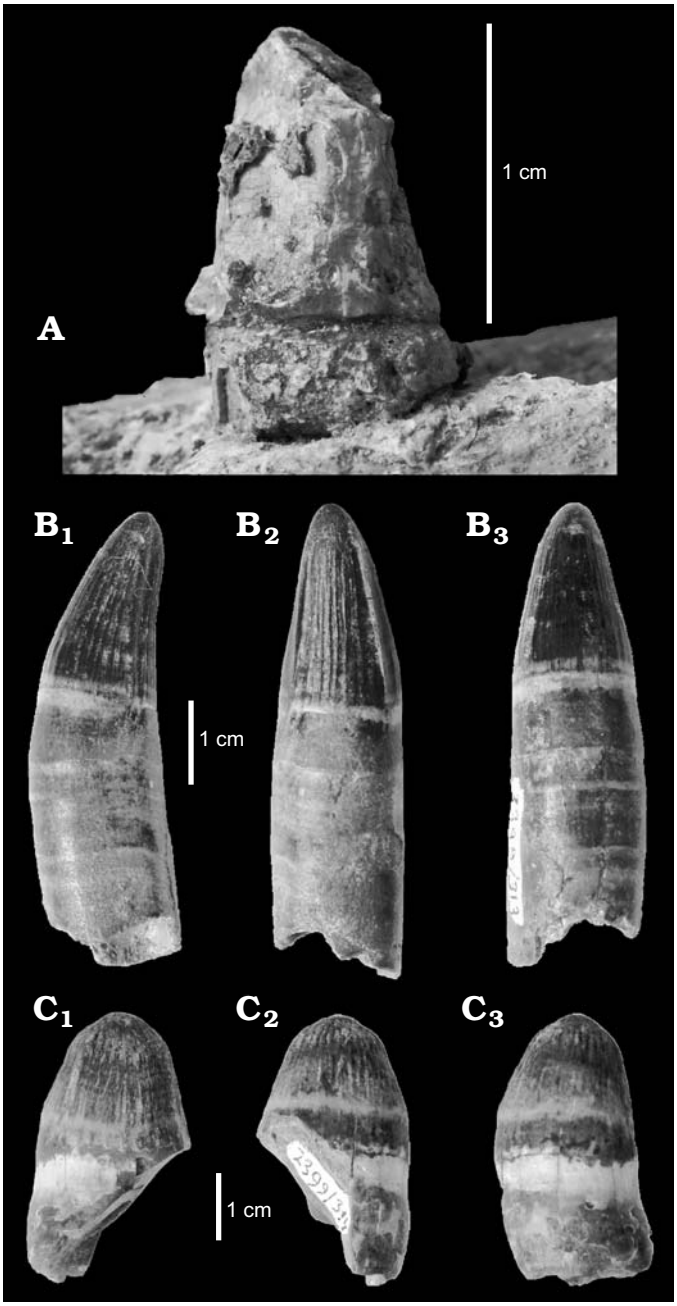


Fig. 4. Teeth of crocodylomorphs from the Cretaceous of Central Asia. **A**. "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980, left mandibular tooth of PIN 4174-1. Tooth is from mid-mandible and is similar in size to all of the other mandibular teeth, which show little size variation. **B**, **C**. *Kansajsuchus extensus* Efimov, 1975. **B**. Caniniform tooth of PIN 2399-313 in anterior (B_1), posterior (B_2), and lateral (B_3) views. The tooth is characterized by prominent ridges, including a distinctive "double keel" on the posterior side of the tooth. The tooth is from the anterior part of the jaw. **C**. Molariform tooth of PIN 2399-314 in posterior (C_1), anterior (C_2), and lateral (C_3) views. The tooth shares the ridges characteristic of *Kansajsuchus*, including a less prominent version of the double keel, but is blunter, and derived from the posterior part of the jaw.

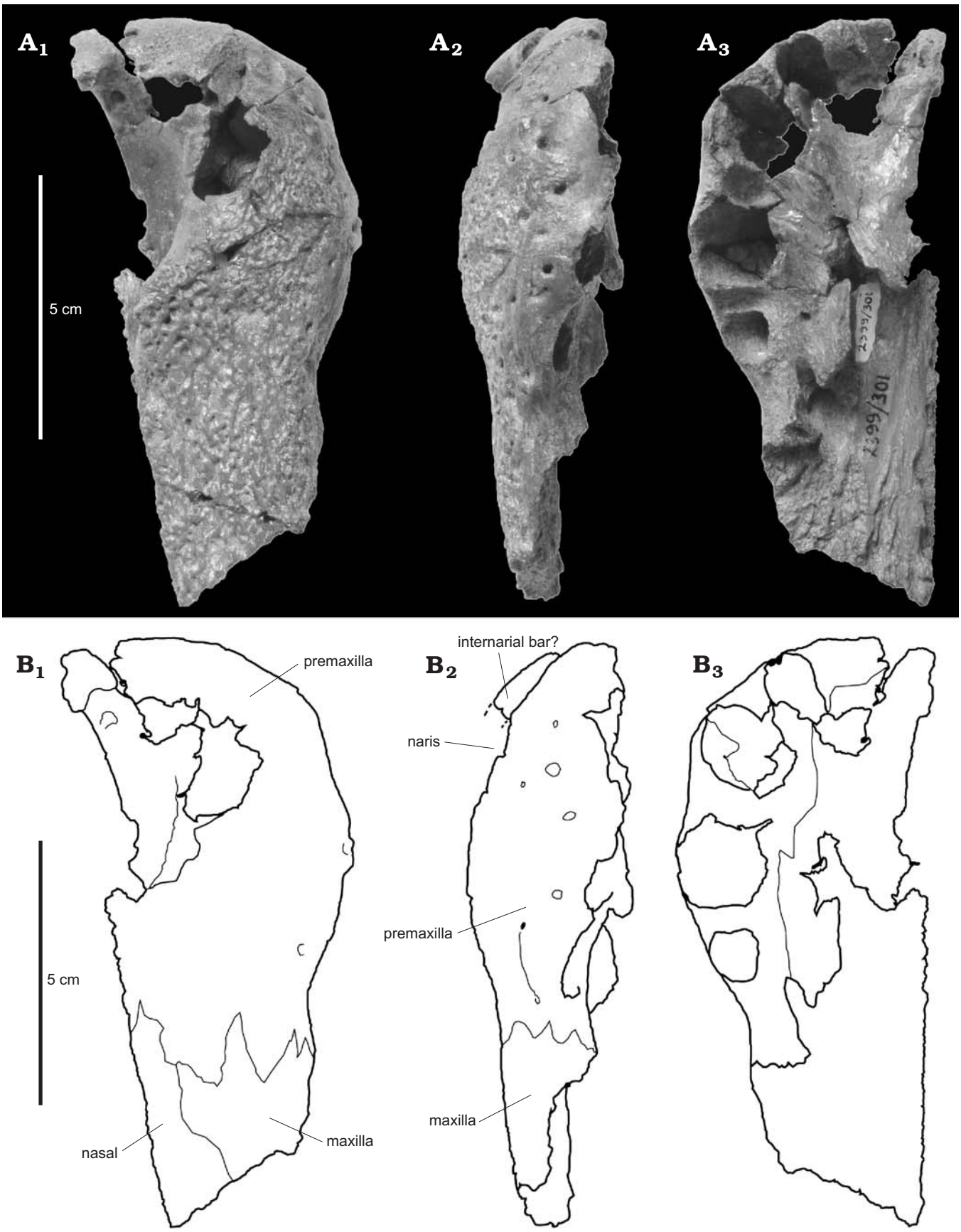


Fig. 5. Crocodylomorph *Kansajsuchus extensus* Efimov, 1975, holotype, PIN 2399-301 from the Santonian (Upper Cretaceous) of Fergana, Tajikistan. Right premaxilla of an adult crocodilian in dorsal (**A**), lateral (**B**), and ventral (**C**) views. Photographs (A_1–C_1) and explanatory drawings (A_2–C_2).

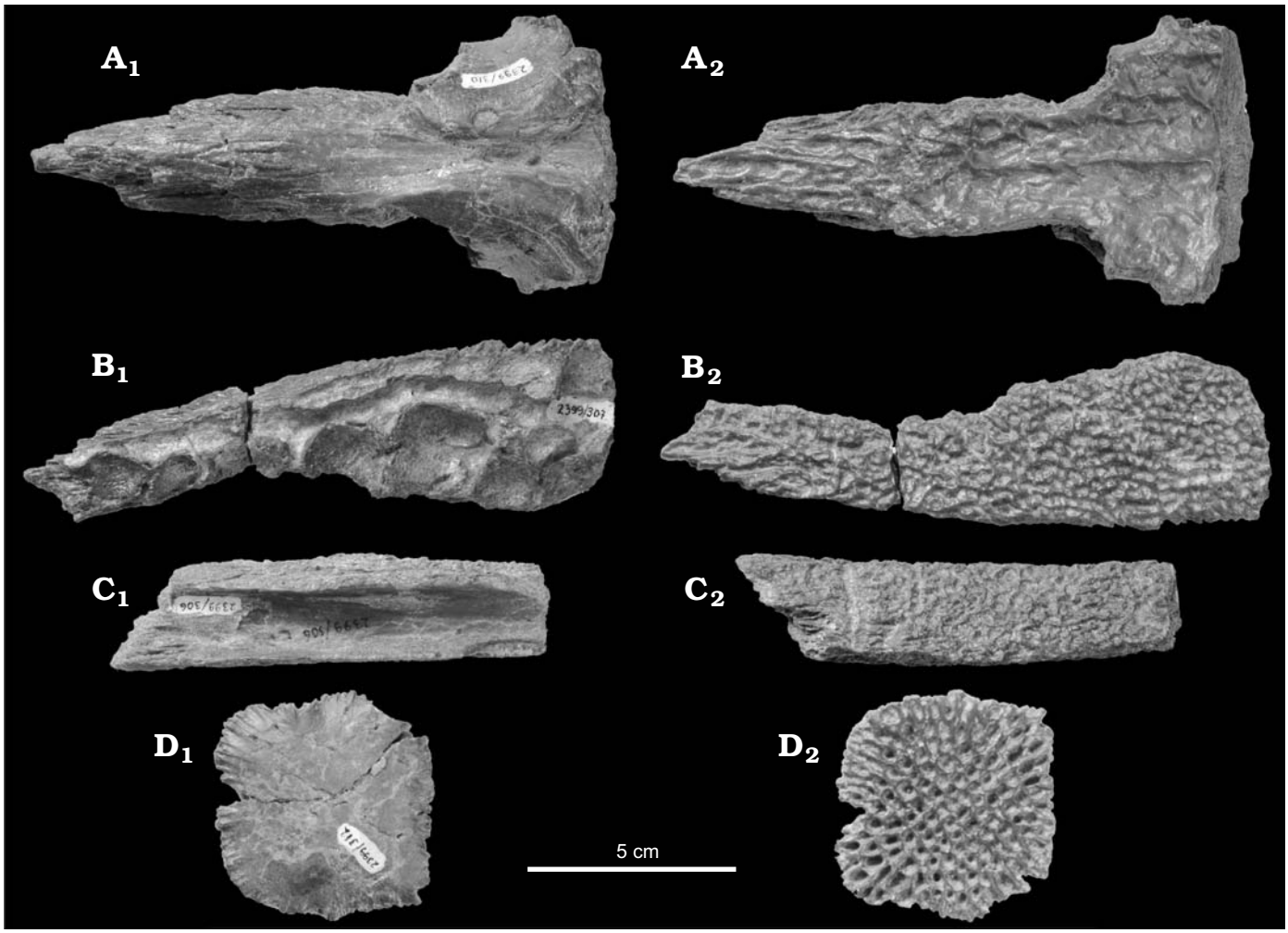


Fig. 6. Crocodylomorph *Kansajsuchus extensus* Efimov, 1975 specimens from the Santonian (Upper Cretaceous) of Fergana, Tajikistan. **A**. Portion of frontal bone and posterior end of nasal, PIN 2399-310. **B**. Broken portion of a left maxilla, PIN 2399-307. **C**. Anterior section of right nasal bone, PIN 2399-306. **D**. Example of dorsal dermal osteoderm, PIN 2399-312. In ventral (A_1–D_1) and dorsal (A_2–D_2) views.

in close proximity to the bone, and the position is far too dorsal with respect to the alveolar neurovascular network to be considered homologous to a true goniopholidid maxillary depression.

In summary, PIN 4174-1 possesses many goniopholidid synapomorphies, and it shares some features with other species of *Sunosuchus*, and yet the lack of other definitive synapomorphies suggests it might belong to a different genus, or, if the derivation of the maxillary depression from the alveolar neurovascular region is considered a universally held goniopholidid synapomorphy, it might even lie outside that clade. There is no diagnostic feature that separates it from the extremely fragmentary *S. thailandicus*, suggesting that PIN 4174-1 could be considered a synonym of *S. thailandicus*. These ideas are tested further in the cladistic analysis.

Genus *Kansajsuchus* Efimov, 1975

Type species: *Kansajsuchus extensus* Efimov, 1975. Holotype specimen from the Santonian (Upper Cretaceous), of the Fergana Basin, Tajikistan.

Kansajsuchus extensus Efimov, 1975

Holotype: PIN 2399-301, a right premaxilla (Fig. 5), approximately 11.5 cm in length and 5 cm wide at the widest point, though this only extends to the midline of the rostrum. The maxilla and nasal bones are also partially represented, with the sutures obviously present. It is broken along the midline.

Type locality: The Kansaj part of the Yalovachskaya Svita in the Fergana Basin, a region of northern Tajikistan. Coordinates are 40.5N, 69.7E. The depositional setting was a river delta of one of the major rivers flowing into the Tethys Ocean. The exact location within this general locality of any individual specimen is unrecorded either in publication, or, as far as can be ascertained, in any field notebooks at PIN.

Type horizon: This locality was referred to the Upper Cretaceous (lower Santonian) by Rozhdestvensky (1977) and everyone since (Nessov 1995).

Material.—PIN 2399-301 (holotype) to PIN 2399-426. There is a great deal of other material assigned to *K. extensus*, some 300 identifiable elements and fragments, all collected from the same locality on the same expedition. This additional material includes a large left premaxilla/maxilla complex, a right nasal bone, a right maxilla, a frontal (Fig. 6), a right

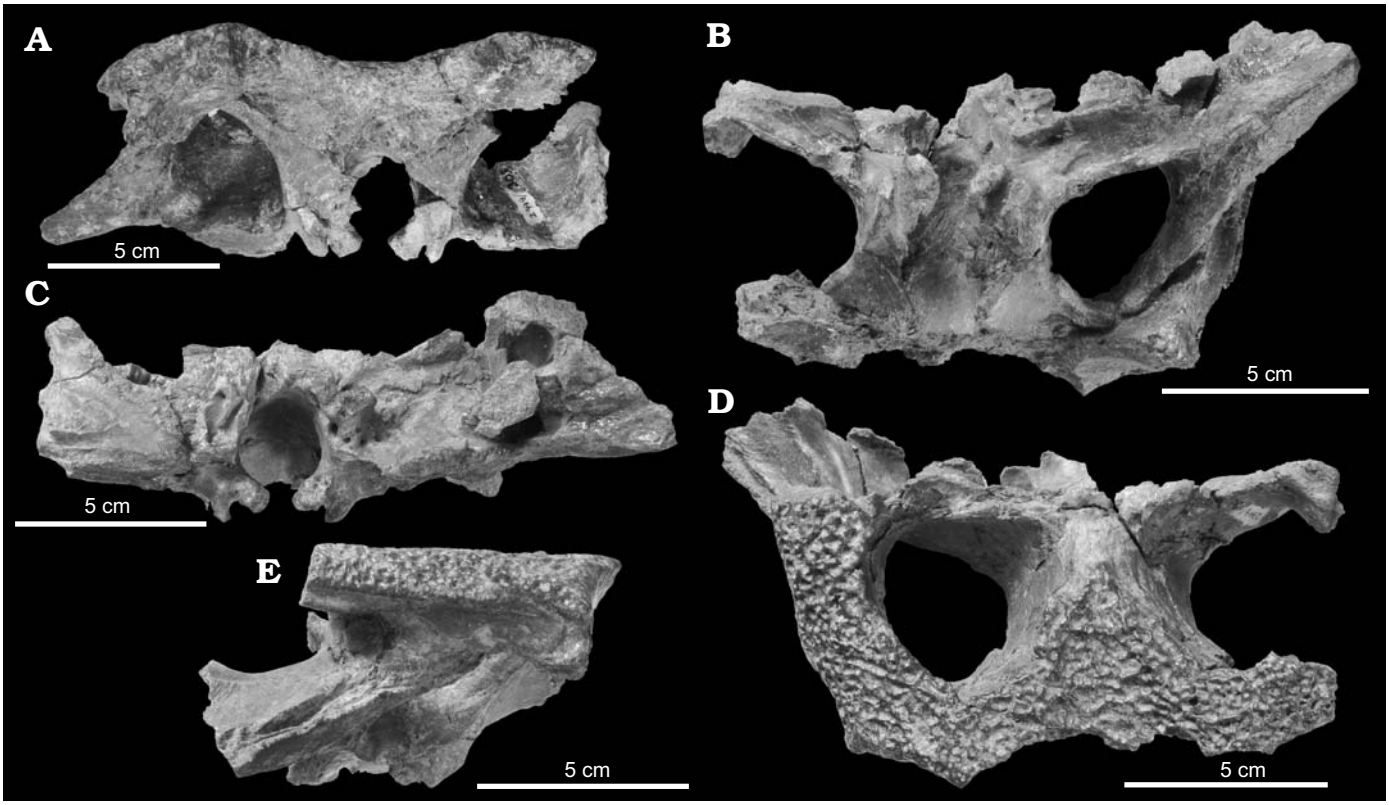


Fig. 7. Crocodylomorph *Kansajsuchus extensus* Efimov, 1975 frontoparietal region from the Santonian (Upper Cretaceous) of Fergana, Tajikistan, PIN 2399-308, in posterior (**A**), ventral (**B**), anterior (**C**), dorsal (**D**), and lateral (**E**) views, clearly demonstrating the trapezoidal shape of the skull roof, and the near-circular fenestrae.

quadrate, a large complex of the skull roof and occipital region (Figs. 7, 8; this specimen was also figured in Efimov 1988b), a separate occipital condyle, parts of the lower jaw (Fig. 9), a femur, vertebrae (Fig. 10), several osteoderms, and over 100 teeth, all well preserved.

It is hard to determine how much of the supplementary material should be assigned to *K. extensus*. Several fragments are clearly not from the same individual because of size differences, but the collection data, bone preservation, and overall size range do not exclude the possibility that all specimens belong to the same species. This has been the assumption made by previous workers, who accepted that the numbering by PIN shows that all specimens with the primary number 2399 were collected from the same formation and locality at the same time, and presumably close together. Here, we describe the holotype, and then add comments on additional elements as appropriate.

Emended diagnosis.—Although largely possessing goniopholidid features, *Kansajsuchus* differs from all other goniopholidids in the following: (i) possessing an ornamentation in which grooves are present alongside the pits; (ii) lacking neurovascular foramina on the dorsal surface of the rostrum; (iii) possessing a frontal with concave, ridged margins; and (iv) the skull roof forming a trapezoidal shape. The postorbital bar is slender, and the quadrate is relatively broad compared with other goniopholidids. The retroarticular process is more posteroventrally directed, and more strongly concave. Unlike all goniopholidids except *Eutretauranosuchus*, *Kansajsuchus* possesses a highly serrated premaxillo-maxillary suture. *Kansajsuchus* differs from *Siamosuchus, Goniopholis*, *Nannosuchus*, *Anteophthalmosuchus*, and other European goniopholidids in the extent to which the premaxillo-maxillary notch contacts the alveoli, and in the convexity of the margins of the nasal bone. *Kansajsuchus* resembles European goniopholidids in the morphology of the frontal, which is narrow with a narrow anterior projection, with the anterior and posterior surfaces at different heights, unlike *Siamosuchus*, *Sunosuchus*, *Eutretauranosuchus*, or *Calsoyasuchus*. The lateral processes of the frontal are arched, similarly to *Goniopholis willetti*, Dollo's goniopholidid, and *Anteopthalmosuchus hooleyi*. There is a small sagittal crest on the frontal, like that of *Sunosuchus junggarensis* and *Siamosuchus*. The specific diagnosis is as that of the genus.

Description.—*General features*: Little can be elucidated about the general shape of the skull, since all fragments are of different sizes. However, some broad patterns are clear. The snout is relatively long, with a broadening of the premaxillae at the anterior end. The skull table is raised above the rostrum, but in general the skull is wider than high, and relatively flat. The whole surface posterior to the narial opening is covered in a series of pits and wrinkles. Though pits dominate, there are occasional ornamentations that would be

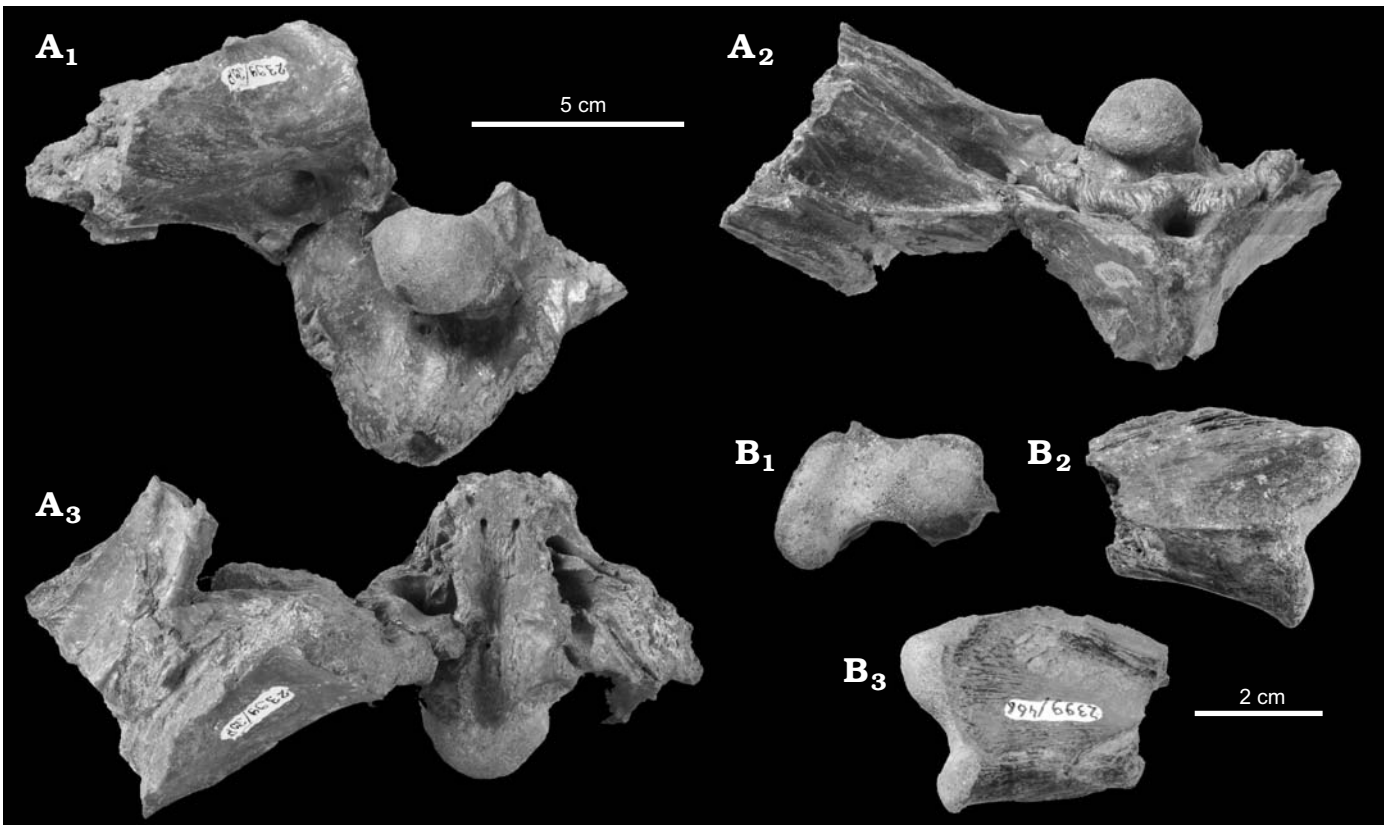


Fig. 8. Crocodylomorph *Kansajsuchus extensus* Efimov, 1975 basioccipital region and quadrate, preserving several nerve and vascular foramina. Specimens from the Santonian (Upper Cretaceous) of Fergana, Tajikistan. **A**. PIN 2399-308 (second part) in posterior (A_1), ventral (A_2), and dorsal (A_3) views. **B**. PIN 2399-468, a quadrate in posterior (B_1), dorsal (B_2), and ventral (B_3) views.

better described as wrinkles or ridges; these are, however, rare. There is an expansion just anterior to the premaxillo-maxillary suture, giving the anterior edge of the snout a keyhole-shaped appearance. There are no teeth in the holotype, and the region surrounding the narial opening is slightly damaged, but otherwise preservation is good.

Premaxilla: Three fragments of premaxillae are preserved from three different individuals. They vary in quality of preservation, with most detail preserved in the holotype. In PIN 2399-301 half of the naris is seen (Fig. 5), and its shape is somewhere between subtriangular and heart-shaped. There is a dorsally oriented projection resulting from an extension of the anterior rami of the premaxillae. This projection extends vertically to a point where the bone is broken off, and could be an intranarial bar or a completely vertical projection (Fig. 5B). As the bone is broken, the length of this projection cannot be established, or the extent to which it projects over the narial cavity.

The suture with the maxilla occurs at the same point as the lateral constriction of the snout, meaning that there is a shallow notch here. While it is far shallower than in other species, the constriction is clearly present (Fig. 5A, B). All goniopholidids possess this feature, and in many it houses an enlarged mandibular caniniform tooth. As the mandible is not preserved, this cannot be confirmed in *Kansajsuchus*. The premaxillo-maxillary suture is very roughly serrated, with a wedge of the premaxilla penetrating between the maxilla and nasal bones, giving a clear posterior process to the premaxilla.

The premaxillary section of the palate is only partially preserved, but what has survived is unornamented and raised with respect to the alveoli (Fig. 5C). Each tooth in the premaxilla is in its own separate alveolus, and there is a great disparity in size of teeth, with the third and fourth alveolus significantly larger than the others. There is a small diastema beyond the fifth alveolus, with the maxillary and premaxillary teeth separated from each other. There is a notch medially between the third and fourth alveolus that might have housed an enlarged mandibular tooth. The palate at the level of the premaxilla is entirely composed of premaxilla, with the two sides fully extending into the middle.

Maxilla: The anterior part of the maxilla is preserved in the holotype (PIN 2399-301), as well as separately in PIN 2399-307, which is composed of a right maxilla, now fractured into two pieces, unconnected to any other portion of the specimen (Fig. 6B). It is extremely damaged and thin, but the remains of six alveoli are visible in ventral view, with obvious festooning with an increase in size of the teeth. No sutures are apparent on either fragment.

Nasal: The nasal is incompletely preserved in the posteriormost part of the holotype, PIN 2399-301, as well as more completely in PIN 2399-306, which is just a nasal

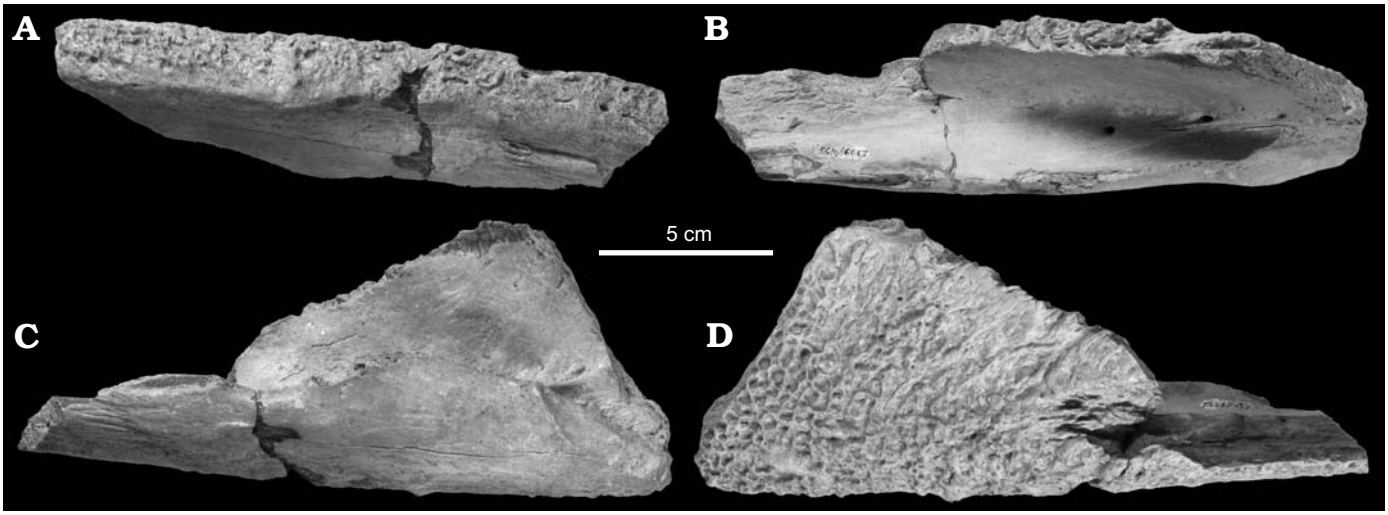


Fig. 9. Crocodylomorph *Kansajsuchus extensus* Efimov, 1975 left angular region of the mandible. Specimens from the Santonian (Upper Cretaceous) of Fergana, Tajikistan, PIN 2399-453, in ventral (**A**), dorsal (**B**), medial (**C**), and lateral (**D**) views.

bone (Fig. 6C). The nasal is ornamented like other skull bones. In dorsal view, the nasal is rectangular and does not taper at either end; although one end is broken to suggest tapering, this is a break rather than a suture. At the anterior end, the nasal is separated from the maxilla by a posteriorly directed process. The angle at which the two unfused nasals contact each other is strongly convex (Fig. $6C_1$), implying that the snout itself was very steep-sided. The bone at the maxillary suture is much thicker than it is at the midline. Here it has a laminar appearance when the internal structure is visible—a direct result of several layers of interdigitating bone.

Frontal: One specimen (PIN 2399-310) is a T-shaped piece of the skull including the dorsal and ventral surfaces of the frontal, with part of the palate and the external rim of the orbit (Fig. 6A). This bone has ornamentation unlike other specimens, comprising wrinkles and ridges rather than pits. This suggests that the frontal is possibly from another species, though it may simply be that this skull region showed different patterning. There is a major anteroposterior ridge down the midline (Fig. $6A_2$). The frontal is at a lower level than the orbits, the medial extremities of which are preserved. The suture with the nasal bones is extremely clear, and takes the form of a V, with frontal penetration into the nasal region. The frontal does not project strongly in front of the orbit, unlike the condition observed in *Sunosuchus*, which has an extremely anteriorly placed naso-frontal suture. There is only a single, fused frontal bone, which appears to comprise only a small proportion of skull width.

Parietal: The parietal is preserved as part of PIN 2399-308, which includes all of the area surrounding the supratemporal fenestrae, as well as the occipital region (Fig. 7). The parietal is a single fused element, as in other derived crocodyliforms, and is flat in lateral view, and relatively broad. The part of the parietal between the supratemporal fenestrae is covered in the same pitted ornamentation as the other dermal skull bones (Fig. 7D).

Orbit: The medial edges of the orbits are preserved on the ventral surface of PIN 2399-310 (Fig. 6A). The shape is unknown, but the size is reconstructed as larger than the supratemporal fenestrae, based on the curvature present in the preserved fragments. Having orbits larger than the supratemporal fenestrae is often seen in goniopholidids, although this feature is not exclusive of this group.

Postorbital: The right postorbital is complete in PIN 2399-308, and the anterior half of the left postorbital is preserved in the same specimen (Fig. 7), with the border of the left supratemporal fenestra missing. The jugal process of the postorbital bar is extremely short, being barely present. The bone surface is, as with the other skull roof bones, ornamented, and the postorbital fenestra is present at the anterolateral corner.

Squamosal: The right squamosal is visible in PIN 2399-308, and like all other skull bones, is ornamented with a series of strong pits (Fig. 7). The left squamosal has been lost through damage to that side of the skull. However, the squamosal does not extend back far enough to reach the ventrally directed squamosal prong (Fig. 7E). The region dorsal to the external auditory meatus, which is well preserved, shows the fossa for the muscles involved in the movement of the external ear flap, as in modern alligatorids.

The external auditory meatus is, as in most other crocodyliforms, subcircular in shape, and relatively large and obvious. The suture between the quadrate and the squamosal is deflected anterodorsally (Fig. 7E), with the quadrate making up a large part of the distal edge of the external auditory meatus.

Quadrate: The right head of the quadrate is preserved in PIN 2399-468 (Fig. 8B). As in *Sunosuchus*, the medial condylar head is slightly ventrally directed, though the quadrate as a whole is horizontally oriented, and, like the condition in *Sunosuchus*, the medial condylar head is smaller than the lateral (Fig. $8B_1$). The groove on the ventral surface in "*Sunosuchus*" *thailandicus* is not present in *Kansajsuchus*, but there is a strongly angled ridge on the lateral edge of the ventral surface (Fig. $8B_2$), which may represent the same

structure. The dorsal surface is, in comparison, convex, with an antero-posteriorly oriented ridge lying between the condylar heads. In lateral view, it is possible to see the internal structure of the bone, which contains the paths of several sinuses, some of which open onto the dorsal surface of the bone. The largest of these is the cranioquadrate canal, which has its opening near the posterior end of the quadrate, and curves along the length of the preserved specimen.

The anterior ends of the quadrate are also preserved in PIN 2399-308. The otic joint and the external auditory meatus are visible, though this region is slightly damaged around the foramen for cranial nerve VII. The quadrate is sutured simply to the quadratojugal, overlying it for the majority of its face.

Exoccipital: The entire occipital region is preserved in PIN 2399-308. In the exoccipital, all major foramina for the cranial nerves are extremely well preserved (Fig. 8A), and the bone damage reveals the spongy nature of the bone and the pattern of sinuses. As with *Sunosuchus*, Efimov (1975) dealt extensively with the paths of all the sinuses and air channels. The cranial nerves IX, X, and XII, as well as the jugular vein, pass through the largest of the preserved foramina (Fig. $8A_1$), and the smaller foramen for the path of a branch of cranial nerve XII is also present. A derived feature is the separate and very small foramen through which the carotid artery passes (Fig. $8A_2$), positioned between the foramen magnum and the other foramina. The area for the attachment of the epaxial musculature is large and more vertically oriented than in other forms. This is noted by Efimov (1975) who reports the "bold lateral ridges" on and around the basioccipital for muscle attachment.

Basioccipital: The occipital condyle, which is not dorsoventrally compressed, is subcircular in caudal view (Fig. $8A_1$), and has a rim running around the posterior end. There are no basal tubera. The basioccipital surface entirely obscures the underlying basisphenoid, and in this way the basioccipital resembles that of all neosuchians, including all goniopholidids and modern crocodyliforms.

Angular: The angular is preserved in PIN 2399-453, which consists of the rear portion of the right lower jaw (Fig. 9). A suture with one of the neighbouring bones is apparent, and this appears to be the surangular, confirming that this is the rear part of the jaw behind the external mandibular fenestra. The angular is ornamented on the anterior edge with a pattern of pits just as in the bones of the skull, becoming less ornamented posteriorly. What is preserved of the surangular is unornamented. The whole of the preserved section of the mandible is 17 cm long and 8 cm high, which is a relatively large jaw. On the interior surface, there are large neurovascular foramina that housed the inferior alveolar branches of the mandibular nerve and associated blood vessels.

Teeth: The teeth of *Kansajsuchus* are distinctive and represent the majority of the preserved material from the Yalovachskaya Svita. There are two broad tooth morphologies. The anterior teeth are elongate, slender and pointed, and have extremely pronounced proximodistal ridges on all sides

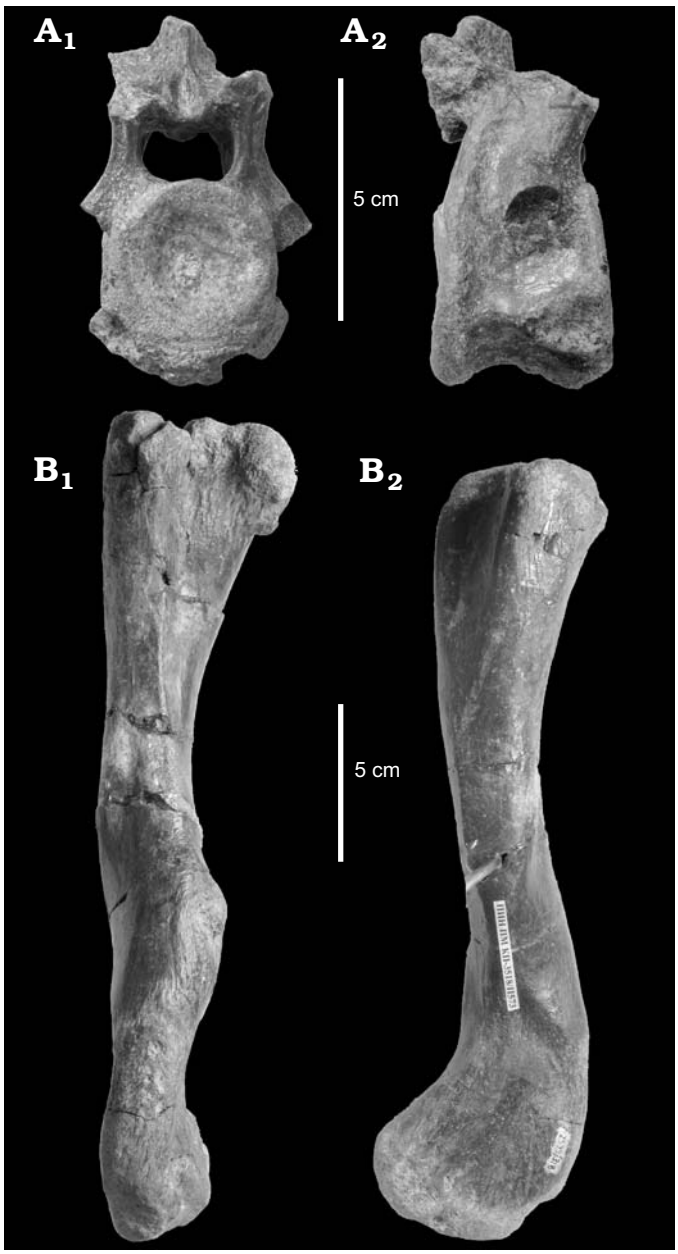


Fig. 10. Crocodylomorph *Kansajsuchus extensus* Efimov, 1975 postcranial material from the Santonian (Upper Cretaceous) of Fergana, Tajikistan. **A**. Cervical vertebra, PIN 2399-304, in anterior (A_1) and lateral (A_2) views. **B**. Left femur, PIN 2399-318, in posterior (B_1) and lateral (B_2) views.

(Fig. 4B). These teeth are recurved slightly, and on the medial (concave) surface, there are two ridges that are thicker and larger than the others, making the shape of the tooth almost triangular in distal view. This double-ridged pattern (i.e., "bicarinate" in Storrs and Efimov 2000) constitutes a very distinctive morphology, so far unparalleled within Crocodylomorpha. The second tooth morphology is seen in the distal end of the dental series; these are shorter, thicker and blunter (Fig. 4C), and appear to be better adapted for crushing than the other teeth. The pattern of ridges in the anterior teeth is also present in this morphotype, which suggests that the two tooth morphotypes come from a single heterodont species

rather than from two species, with the two tooth morphologies smoothly grading from one end of the dental series to the other. In the more posterior teeth, however, the largest ridges are not as pronounced as on the anterior teeth; they are nonetheless clearly present. The teeth are deep-rooted, descending well into the tooth-bearing bones, with the roots comprising about 60% of the length of the tooth. From the other bones preserved, including a mandibular fragment, the premaxillae and a maxillary fragment, it is clear that each tooth is situated apart from its neighbours in an individual alveolus, and not in a single groove. There is no constriction between the root and crown.

The teeth vary considerably in size, the largest being about 3 cm from the tip of the tooth to the base of the crown in caniniform teeth, and 2 cm in the blunter, slightly molariform teeth. The smallest of the teeth are slightly more than 1 cm long, and the average length seems to be about 2 cm. Local variation in tooth size is seen in PIN 2399-301, the holotype, where neighbouring alveoli vary substantially in size.

Cervical vertebrae: The neural spine of the cervical vertebrae has a robust base, expanding ventrally to fit onto the neural arch. It is oriented only slightly posteriorly. The centrum is cylindrical, and the zygapophyses are robust, forming a rigid structure (Fig. 10A).

Femur: The right femur (PIN 2399-318) has been damaged in mounting, being split by a metal spike. It is slightly sigmoid in shape, and twisted such that the heads are at 90° to one another (Fig. $10B_1$). A large process three-quarters of the way down the bone appears to be an attachment site for the lower leg musculature, apparently extremely enlarged. The bones are slender, being far longer than wide, although the femur is short with respect to the length of *Kansajsuchus*, which was estimated as 8 metres long by Efimov (1975). As previously discussed, however, this length may be an overestimate. Only one other Asian goniopholidid, "*Sunosuchus*" *junggarensis*, is in a complete enough state to include the femur, and it had relatively robust limb bones (Wu et al. 1996), in contrast to *Kansajsuchus*. It may well be, then, that the femur attributed to *Kansajsuchus* belongs to a different species, and should not be included in the generic definition.

Osteoderms: Several dermal osteoderms are preserved, mostly from the dorsal shield, though others are possibly from the belly. The dorsal osteoderms are square, with a strongly pitted ornament. On the anterior edge of the osteoderm is a region that is unornamented, the overlap flange for the neighbouring osteoderm. An anteroventrally directed keel is present along the centre of the osteoderm, and its slope is gentlest at the anterior end. Some osteoderms lack a keel, and these also lack the region of overlap (e.g., Fig. 6D), but have jagged edges and indications of a complexly arranged suture.

Remarks.—The presence of such a large number of isolated and identical teeth and osteoderms. The teeth in particular are distinctive, with their strongly ridged surface (Fig. 4B), which indicates that, while there are a large number of fragments, none of which can definitively be assigned to the same individual, the material is almost certainly from the same species. If there had been several crocodylomorphs in this deposits, other types of teeth and osteoderms should have been discovered. While crocodylomorphs are known from the northern part of the large Fergana Basin, including *Peipehsuchus* (Nessov 1995), which has been attributed to both Pholidosauridae (Carroll 1988) and Teleosauridae (Li 1993), none besides *Kansajsuchus extensus* is known from the south, indicating that *Kansajsuchus extensus* should be considered a valid taxon.

Suborder Neosuchia Clark, 1988

Family ?Goniopholididae Cope, 1875

Gen. et sp. indet.

Figs. 11, 12.

1988 *Turanosuchus aralensis* sp. nov.; Efimov 1988: 55, fig. 9 [nomen dubium].

Material.—PIN 2229-501–510. Isolated fragments of bone, including a mandible fragment (PIN 2229-501) and a putative dentary element (PIN 2229-506). The specimen described as holotype of *T. aralensis* is PIN 2229-507, a mandibular symphyseal region approximately 10 cm long and 5 cm wide (Fig. 11). It lacks a portion of the tooth row on the right-hand side, and is damaged by erosion. The symphysis itself extends along the whole length of the specimen, implying that the whole animal was of a similar size to *Kansajsuchus*. PIN 2229 was found on Tyul'kili Hill, an "isolated hill about 80 km north of Dzhusaly" (Averianov and Sues 2009: 553) in the north-eastern Aral Sea region, Kazakhstan. The beds of Tyul'kili are part of the Upper Cretaceous (Santonian) Zhirkindek Formation, a unit consisting primarily of sandstone, interspersed with grey and yellow clays. The Tyul'kili beds are 45 m thick; the material was discovered 18 m above the base (Kordikova et al. 2001) in a "gravelly sandstone".

Description.—*General features*: The scrappy nature of PIN 2229 (Figs. 11, 12) means that no diagnostic features can be interpreted about the general shape of the skull. Based on the length and flatness of the mandibular symphyseal region, the skull was probably extremely long-snouted, unlike European goniopholidids, but like *Sunosuchus thailandicus*.

Maxilla: The maxilla is poorly preserved in part in PIN 2229-502 (Fig. 12C). It is rather flat, and the medial suture with the nasal bones can be seen, indicating that the snout was extremely narrow. Ornamentation is not very clear, but it appears to show the same sort of pitted pattern as in other goniopholidids. The maxillary teeth are circular in cross section and sit in individual alveoli. There is also some festooning, as in both *Sunosuchus* and *Kansajsuchus*, where the larger alveoli are present at expansions in both the lateral and ventral directions.

Nasals: The nasal bones are thin, meeting the maxilla extensively with a concave border. The nasal passage is also preserved in part, though it is highly damaged.

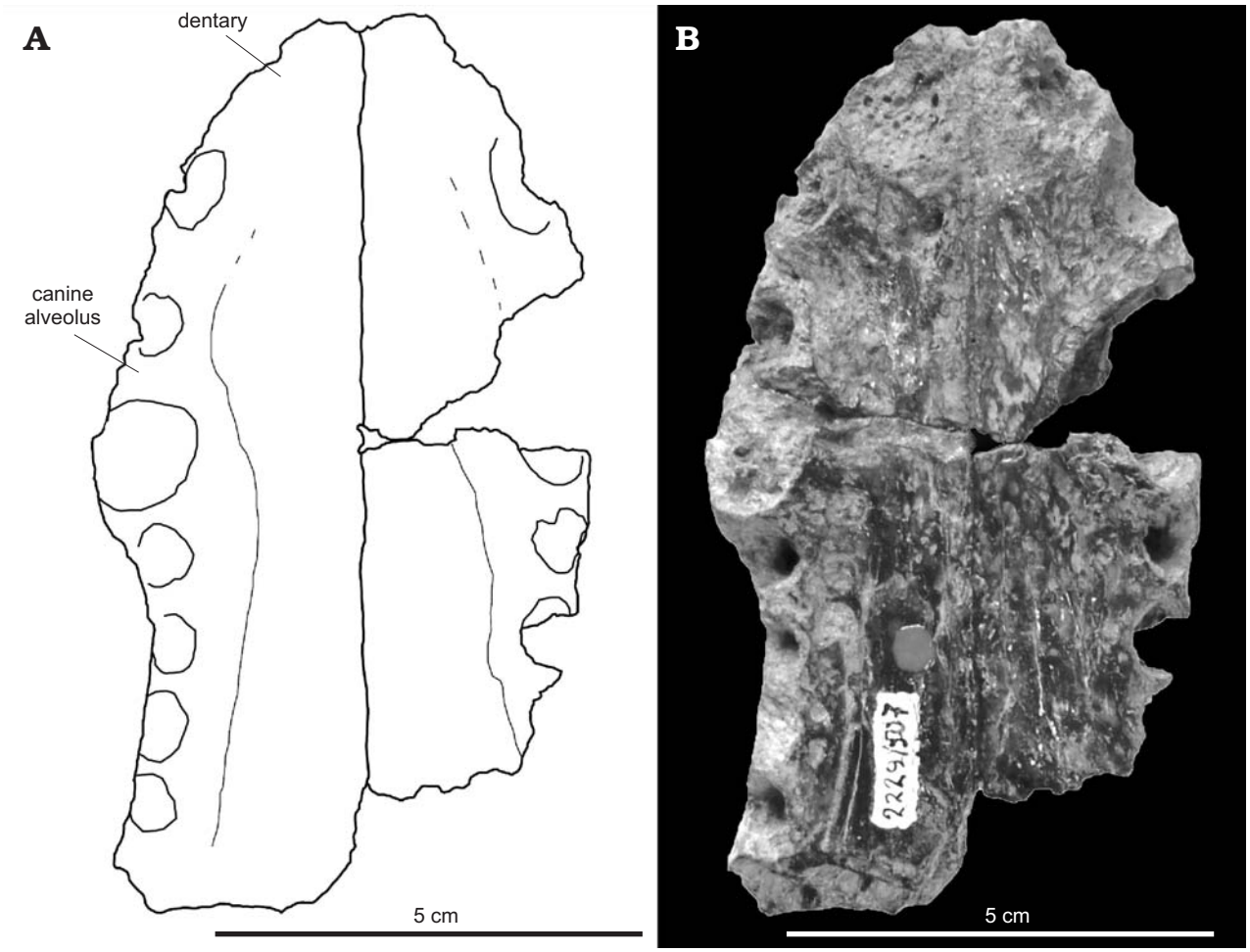


Fig. 11. Poorly preserved mandibular symphysis of ?Goniopholididae gen. et sp. indet. (previously *Turanosuchus aralensis* Efimov, 1988) from the Upper Cretaceous of Kazakhstan, PIN 2229-507, in dorsal view, with majority of tooth alveoli present but damaged. For full explanation see text.

Dentary: The mandibular symphysis is extended at least as far as the seventh mandibular tooth (Fig. 11). The first and second mandibular teeth are present on the converging edges of the mandible, after which the tooth rows become parallel with the third tooth. The symphysis has a clear groove running down the midline, as the fusion of the bones is weak. The whole symphysis is only 15 mm deep, and it is very compressed dorsoventrally compared to other mandibular symphyseal regions such as that of *Sunosuchus*. There are remnants of a pitted ornamentation on the underside of the symphysis.

A second part of the dentary, PIN 2229-506, has also been assigned to *T. aralensis* (Fig. 12A). It is, however, far deeper, though the teeth are approximately the same size. It is almost certainly not from the same individual, and probably represents an unknown neosuchian crocodylomorph.

Splenial: The splenial is present as a thin wedge at the rear of the mandibular symphysis, but little more can be said because of its incompleteness.

Angular: In PIN 2229-501, the angular of the left mandible is preserved (Fig. 12D). It strongly resembles the mandible of *Kansajsuchus* in both the honeycomb-pitted ornamentation, and the shape and size of the foramina situated in the internal groove. The whole fragment is over 20 cm in length.

Osteoderms: The available dermal osteoderms are also ornamented with pits (Fig. 12B). They possess anteroposterior keels, and have an area of unornamented bone that is overlapped by the neighbouring scute on the anterior edge.

Comparisons.—The material attributed to *Turanosuchus aralensis* is so incomplete that there are no diagnostic characters. Coding for cladistic analysis results in a highly unstable position, being unresolved across many eusuchian lineages. PIN 2229 is certainly crocodylomorph, and most likely neosuchian, but beyond that it is impossible to place phylogenetically. For these reasons, *Turanosuchus aralensis* is here considered a nomen dubium.

Remarks.—*Turanosuchus aralensis* was originally assigned to *Kansajsuchus borealis* (Efimov 1988a), before Efimov (1988b) decided that the two species could not be combined within a single genus. *Turanosuchus* is a monospecific genus, it has been found at only one site in Kazakhstan, and the holotype comprises only the mandibular symphyseal region. In his monograph on crocodiles and champsosaurs of Mongolia and Central Asia, Efimov (1988b) admits that "the phylogenetic position of *Turanosuchus* may cause some debate". We propose that the material attributed to *T. aralensis*

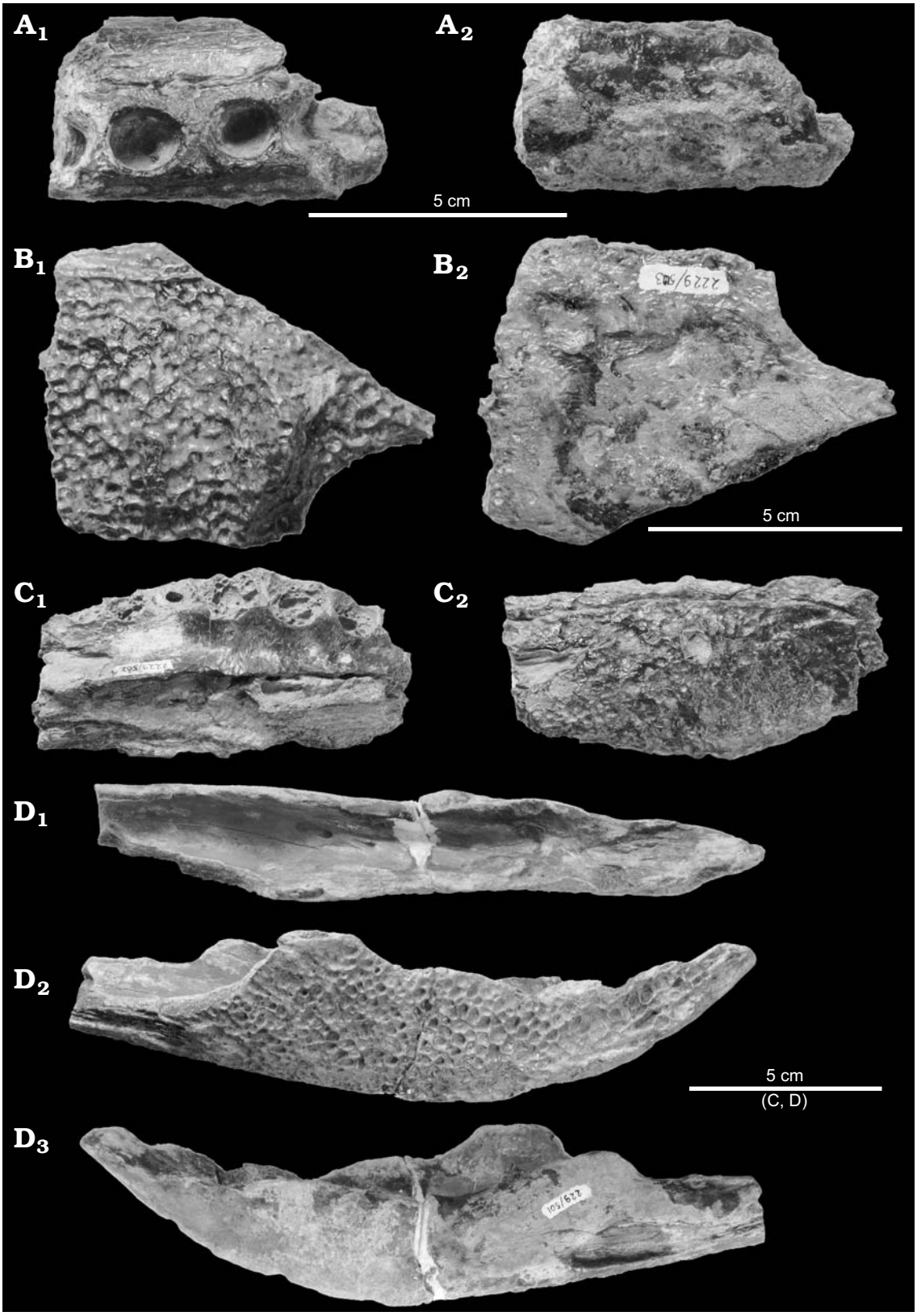


Fig. 12. ?Goniopholididae gen. et sp. indet. (previously *Turanosuchus aralensis* Efimov, 1988) from the Santonian (Upper Cretaceous) of the Zhirkindek Formation, Kazakhstan, material formerly attributed to *Turanosuchus aralensis* Efimov, 1988. **A**. Section of left dentary, PIN 2229-506, including two complete and two incomplete alveoli in dorsal (A_1) and lateral (A_2) views. **B**. Dermal osteoderm, PIN 2229-503, in dorsal (B_1) and ventral (B_2) views. **C**. Fragmented right maxilla, PIN 2229-502 (demonstrating the sinusoidal condition also seen in PIN 4174-1), in ventral (C_1) and dorsal (C_2) views. **D**. Posterior portion of left mandible, PIN 2229-501, in dorsal (D_1), lateral (D_2), and medial (D_3) views.

is non-diagnostic, and as such the genus be reduced to a nomen dubium. A description of those few fragments formerly attributed to the genus is presented here.

Phylogenetic analysis

Methods.—The cladistic analysis was founded on the taxon-character matrix of Andrade et al. (2011), modified to account for new information on *Eutretauranosuchus* in Smith et al. (2010). Details of the character states assigned to the study specimens and of modifications to the coding of *Eutretauranosuchus* are presented in Supplementary Online Material, SOM 1 available at http://app.pan.pl/SOM/app60-Halliday_etal_SOM.pdf. The data matrix comprises 112 taxa, of which ten were too fragmentary to be included in the final analysis, and a further two—PIN 2229 and *Sunosuchus thailandicus*—were included only because they had been identified as goniopholidids. As in Andrade et al. (2011), the putative goniopholidid *Denazinosuchus* was left out of the analysis as it is an unstable taxon, and is incomplete and poorly understood. Cladistic analyses were conducted in PAUP* version 4.0b10 (Swofford 2003), using a heuristic search, employing the TBR method, and in TNT version 1.1 (Goloboff et al. 2008), using sectorial search methods; 5000 replicates were produced for each program, saving a single most parsimonious tree from each search. Analyses were run with and without PIN 2229, in order to attempt to constrain its phylogenetic position, and then to refine the affinities of the other two taxa.

Results.—In the first analysis, with all 102 taxa retained, PAUP* produced 324 most parsimonious trees (MPTs) of length 2305 (Fig. 13), while TNT produced 28 MPTs of length 2225. The high number of trees arises from the fact that PIN 2229 and "*Sunosuchus*" *thailandicus* have very few codable characters, so that PIN 2229 is highly unstable, being resolved most specifically as part of Eusuchia. These two taxa were then excluded from a second analysis that yielded 36 MPTs of length 2219 in PAUP* (Fig. 14), and 4 MPTs, also of length 2219, in TNT. The strict consensus of each set of trees is identical between the two programs. The overall topology is similar to that in Andrade et al. (2011). Both strict consensus and majority rule consensus trees place *Kansajsuchus* and PIN 4174-1 well within Goniopholididae, as sister taxa to one another, nested within the genus *Sunosuchus*. Species currently assigned to *Sunosuchus* are allocated to three clades: (i) *S. junggarensis* resolves as sister taxon

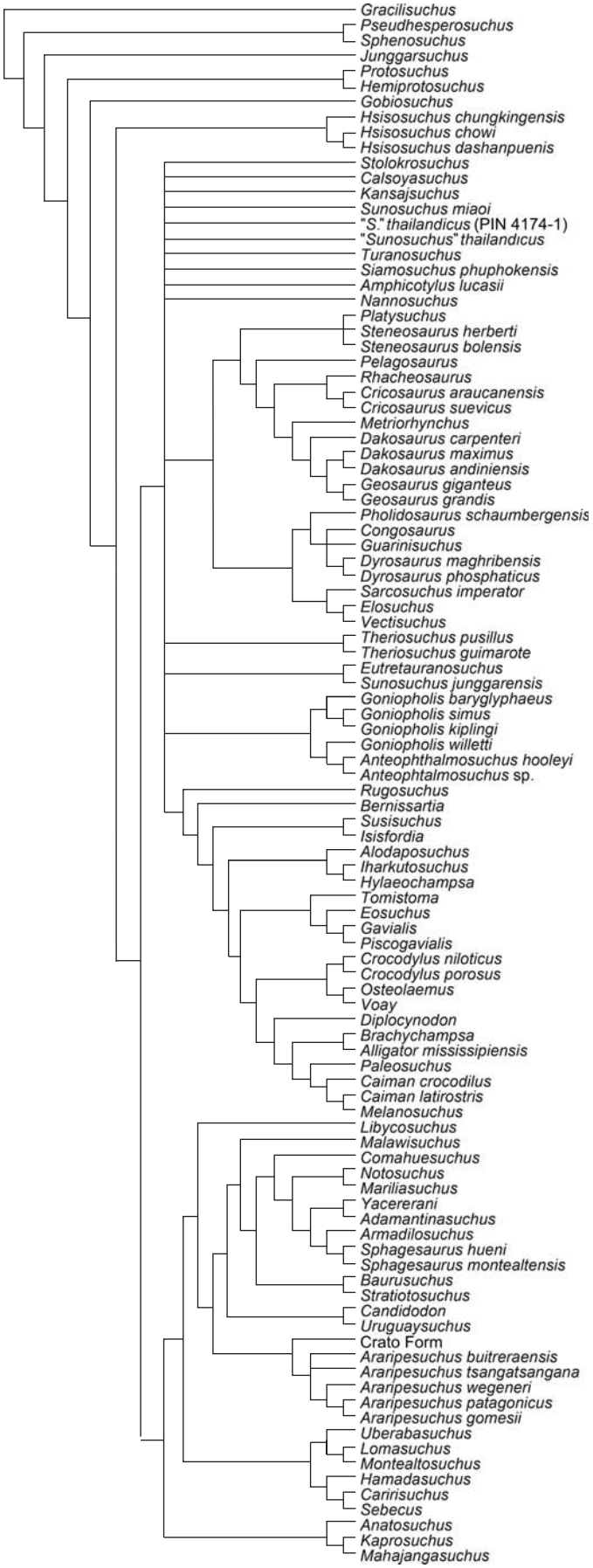
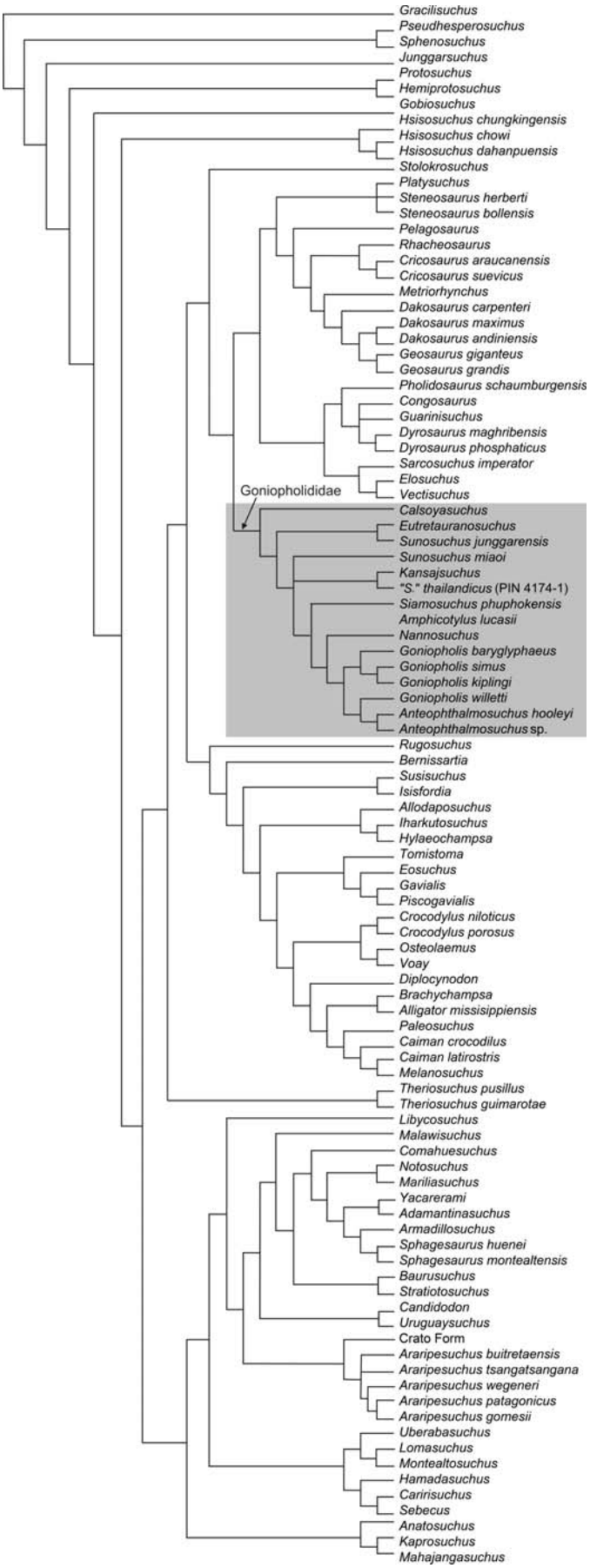


Fig. 13. Strict consensus of 324 trees. Length = 2305, CI = 0.2872, RI = 0.7497. 102 crocodilomorph taxa are included. The inclusion of "*Sunosuchus*" *thailandicus* and material formerly ascribed to *Turanosuchus aralensis* results in a large polytomy including Eusuchia, Goniopholididae, Pholidosauridae, and Metriorhynchidae. Relationships within Goniopholididae for the most part collapse. A notable exception is the association of *Eutretauranosuchus* and "*Sunosuchus*" *junggarensis*, which suggests that this is a very strongly supported relationship.



to *Eutretauranosuchus*, (ii) PIN 4174-1 and *S. thailandicus* as sister to *Kansajsuchus*, and (iii) *S. miaoi* in a three-way polytomy with the *Sunosuchus–Kansajsuchus* clade and the clade bounded by *Amphicotylus* and *Goniopholis* (Figs. 13, 14). As "*Sunosuchus*" *junggarensis* resolves as more closely related to *Eutretauranosuchus* than to any other member of the Goniopholididae, *Sunosuchus* is considered polyphyletic, as in Andrade et al. (2011).

Biogeography of goniopholidids.—Goniopholidids are exclusively Laurasian, with the apparent exception of one putative Gondwanan form from Africa, "similar to *Sunosuchus*" (Sereno 2009). The best-known goniopholidids are those of Europe (e.g., *Nannosuchus, Goniopholis*) and North America (e.g., *Calsoyasuchus, Eutretauranosuchus*). Goniopholididae has never been subjected to biogeographic analysis. By integrating the Central Asian forms into a biogeographic discussion, the radiation of the goniopholidids can be investigated.

In order to explore palaeobiogeographical patterns, the species in the data matrix were divided into 14 geographical regions and 10 time bins, the latter as in Andrade et al.

Table 2. Areas used for S-DIVA analysis.

Area code	Area	Definition of area
A	Europe	all area north of the Mediterranean Sea, west of the Black Sea and west of Russia
B	Western Asia	Russia west of the Urals, the Caucasus, the Middle East
C	Central Asia	the steppic nations between the Urals and 105°E
D	Eastern Asia	all Asia east of 105° E, as well as SE Asia from Myanmar eastwards, Indonesia
E	India	the Indian Subcontinent
F	Madagascar	Madagascar
G	Australasia	Australia, the Pacific Islands
H	Western Africa	all area west of and including Libya, Chad and Cameroon
I	Eastern Africa	all area east of Egypt, Sudan, Uganda, Kenya inclusive
J	Southern Arica	Gabon, CAR, DRC, Rep Congo, Zambia, Tanzania, and all area south
K	Antarctica	Antarctica
L	Southern America	Chile, Bolivia, Brazil south of the Amazon, and all area south
M	Central America	Mexico, Isthmus of Panama, Peru, Brazil north of the Amazon
N	Northern America	USA and Canada, the Caribbean

Fig. 14. Strict consensus of 34 trees. Length = 2219, CI = 0.2881, RI – 0.7500. 100 taxa are included. Goniopholididae are monophyletic, with *Calsoyasuchus* the most basal form. *Goniopholis* forms a paraphyletic group with respect to *Anteophthalmosuchus*. *Sunosuchus* is polyphyletic, spread among several groups including *Eutretauranosuchus*, *Kansajsuchus,* and the European goniopholidids. All European goniopholidids form a monophyletic group to the exclusion of the Asian and North American forms. *Tomistoma* and *Gavialis* cluster together to the exclusion of *Alligator*.

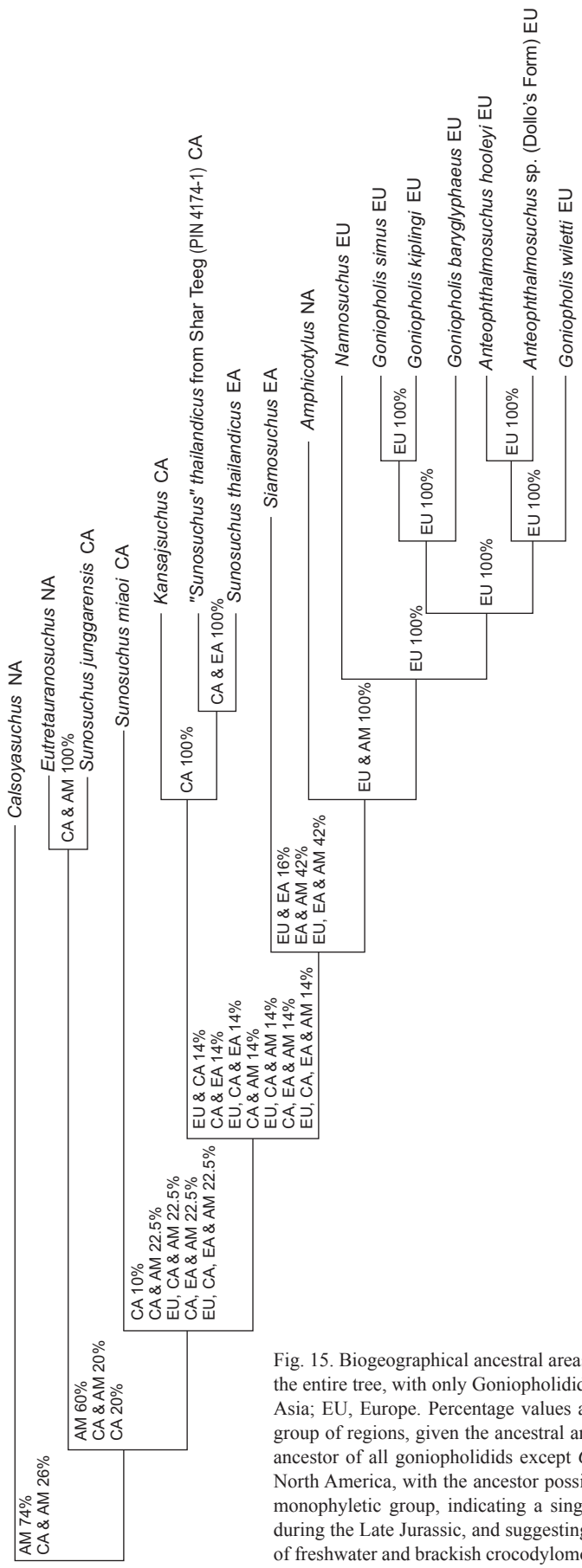


Fig. 15. Biogeographical ancestral areas for nodes in goniopholidid phylogeny. Analysis performed by S-DIVA across the entire tree, with only Goniopholididae presented here for clarity. AM, North America; CA, Central Asia; EA, East Asia; EU, Europe. Percentage values at nodes indicate the probability that the ancestor at that node occupied each group of regions, given the ancestral and descendant node distributions. For example, there is a 60% chance that the ancestor of all goniopholidids except *Calsoyasuchus* lived exclusively in North America. Goniopholididae arose in North America, with the ancestor possibly also residing in Central Asia. The European goniopholidids form a single monophyletic group, indicating a single dispersal event from an eastern Laurasian clade across the Turgai Straits during the Late Jurassic, and suggesting that the epicontinental seas played a vital role in controlling the distributions of freshwater and brackish crocodylomorphs, with only those more adapted to saline conditions being able to disperse.

(2011). The areas used (Table 2) have been defined on rough equality of area and tectonic history rather than on ecological domains, and also to ensure that Central, Eastern and Western Asia could be distinguished. Statistical Dispersal/Vicariance software (S-DIVA; Yu et al. 2010) was used to determine ancestral areas for nodes, and to inform on the patterns of speciation and extinction that occurred in Mesoeucrocodylia, particularly goniopholidid, evolution.

The S-DIVA analysis recreated the ancestral range of Goniopholididae as defined by tree topology, taking into account the outgroup of Metriorhynchidae and Pholidosauridae, as either in North America and Central Asia, or North America alone (Fig. 15). The Early Jurassic *Calsoyasuchus* is from North America, and it was not until the Late Jurassic that the main radiation took place. By this time, there are representatives across the majority of Laurasia, with Asian and American forms scattered in the cladogram. The American *Eutretauranosuchus* is next to the Mongolian "*Sunosuchus*" *junggarensis,* for instance. *Kansajsuchus,* "*Sunosuchus*" *thailandicus* and presumably also PIN 2229 can be considered part of this eastern Laurasian radiation of goniopholidids.

Discussion

Phylogeny and nomenclature.—Traditionally, the name *Sunosuchus* was generally given to goniopholidid remains from Central Asia. Five species have been established, *S. miaoi* Young, 1948, "*S.*" *thailandicus* Buffetaut and Ingavat, 1980, "*S.*" *shartegensis* Efimov, 1988, "*S.*" *junggarensis* Wu, Brinkman, and Russell, 1996, and "*S.*" *shunanensis* Fu, Ming, and Peng, 2005, coming variously from Mongolia, China, and Thailand. Further specimens from Kyrgyzstan and the Junggar Basin were attributed to *Sunosuchus* sp. (Averianov 2000; Schellhorn et al. 2009). If the relationships posited in the cladistic analysis are correct, then *Sunosuchus miaoi* is the only taxon to retain the generic name, as the type species of the genus.

On the basis of this redescription, there is no morphological characteristic that would allow a distinction to be drawn between PIN 4174-1 and "*S.*" *thailandicus*. Although the latter is composed of material limited to the lower jaw (Buffetaut and Ingavat 1980, 1984), the proportions of the jaw and position of key features are similar enough to warrant the tentative reference of PIN 4174-1 to "*S.*" *thailandicus*.

Despite its apparent close relationships with "*S.*" *thailandicus*, *K. extensus* is considerably younger, being Late

Cretaceous rather than Late Jurassic in age; known goniopholidids are mostly Early Cretaceous or earlier, with the exception of *Kansajsuchus* and the Campanian *Denazinosuchus kirtlandicus* (Wiman, 1932), from North America (see Lucas and Sullivan 2003). Although excluded from the analysis here due to phylogenetic instability, if *Denazinosuchus* is indeed a goniopholidid, as suggested by previous works (Andrade et al. 2011), this placement of *K. extensus* results in the persistence of two long ghost lineages in Goniopholididae, suggesting a long existence of both the Central Asian and the North American branches of Goniopholididae, to about the same age (Santonian–Campanian).

The phylogenetic placement of *Kansajsuchus* next to PIN 4174-1, "*S.*" *thailandicus* and *S. miaoi* may mean that, in later revisions, the name *Kansajsuchus* will be abandoned. It shows some clear similarities to "*S.*" *thailandicus*, such as the very long snout: *Sunosuchus* proper has been diagnosed as having a relatively short snout, which could exclude the long-snouted PIN 4174-1 from the genus, alongside *S. thailandicus*, which is also longirostrine.

There is one major phylogenetic point of interest outwith Goniopholididae. The relationships between *Gavialis gangeticus* and *Tomistoma schlegelii* have been a source of extensive discussion (see Brochu 1996). Molecular studies placed the two species as sister groups (e.g., Gatesy et al. 2003; Zhang et al. 2011), countering the morphological data, which suggest a grouping of *Tomistoma* with *Crocodylus* (Tarsitano et al. 1989). Here, *Tomistoma* and *Gavialis* are grouped solely by morphological data, supporting the molecular clade, and also supporting the conclusions of Trueman (1998) in providing cladistic morphological support for a *Gavialis–Tomistoma* link, although fossil taxa were not included in his analysis.

Palaeobiogeography.—During the Jurassic goniopholidid radiation, Laurasia was partially flooded, and the epicontinental Turgai Sea possibly acted as a biological barrier to freshwater neosuchians, preventing them from dispersing easily to Europe. *Eutretauranosuchus*, *Calsoyasuchus*, *Siamosuchus*, *Sunosuchus junggarensis*, and *Sunosuchus miaoi* are all found primarily in lacustrine, fluvial, floodplain or terrestrial palaeoenvironments, while *Kansajsuchus*, "*Sunosuchus*" *thailandicus*, and the European taxa are found in sediments interpreted as representing brackish or salt water palaeoenvironments. The monophyly of the European forms adds credence to this idea; any dispersal over the seas would have involved only a few forms, and so the radiation of *Goniopholis* and its kin in Europe may be viewed as determined by geographical factors, and an adaptation to greater tolerance of brackish water. Revision of the poorly understood North American taxon *Denazinosuchus* is important so that its status as a goniopholidid, and therefore its importance in palaeobiogeographic terms, can be proved or disproved with proper support. Similar patterns of biogeography are found in ceratopsian dinosaurs from the Late Cretaceous, which are also restricted to Asia and North America, though with isolated forms present in Europe, attributed to a later episode of island hopping (Ősi et al. 2010). S-DIVA analyses confirm that this scenario is at least possible in goniopholidid crocodylomorphs, in which Central Asian forms an important geographic, phylogenetic and ecological intermediary. Although island hopping is expected to be more likely to have happened in freshwater swimming groups than in terrestrial digitigrade dinosaurs, the similarity of pattern between both events is noticeable, with both events occurring through a similar route, in different epochs.

Note added in proof

Since submission of this manuscript, *Goniopholis willetti* has been reassigned to *Hulkepholis willetti* (Buscalioni et al. 2013), with the result that *Goniopholis* is no longer paraphyletic with respect to *Anteopthalmosuchus* in this study.

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