

# An atoposaurid neosuchian (Archosauria: Crocodyliformes) from the Lower Cretaceous of Inner Mongolia (People's Republic of China)

X.-C. Wu, H.-D. Sues, and D.B. Brinkman

**Abstract:** Cranial and postcranial remains from the Laolonghuoze locality in the Ordos Basin, Inner Mongolia (China), represent a previously unrecorded taxon of crocodyliform archosaurs from the Lower Cretaceous Luohandong Formation (Zhidan Group). Several cranial features indicate that this form is referable to the Atoposauridae, which were previously definitely known only from the Upper Jurassic and Lower Cretaceous of Europe. Certain derived characters further indicate that the Ordos material is closely related to, if not actually referable to, *Theriosuchus*. The Ordos atoposaurid differs from the species of *Theriosuchus* in only a few features. In view of its fragmentary nature, the new material is identified as cf. *Theriosuchus* sp. at present.

**Résumé :** Les vestiges crâniens et postcrâniens collectés au site de Laolonghuoze, dans le bassin d'Ordos, en Mongolie intérieure (Chine), représentent un taxon non décrit auparavant des archosauriens crocodyliformes, de la Formation de Luohandong (Groupe de Zhidan), du Crétacé inférieur. Plusieurs particularités crâniennes indiquent que cette forme peut être assignée aux Atoposauridés, qui n'avaient été rapportés auparavant que dans les strates du Jurassique supérieur et du Crétacé inférieur en Europe. En plus, certains caractères dérivés indiquent que le matériel d'Ordos est très similaire à, et même attribuable actuellement à, *Theriosuchus*. C'est seulement par quelques particularités que l'atoposauride d'Ordos diffère d'avec les espèces de *Theriosuchus*. Pour le moment, à cause de son état fragmentaire, ce nouveau matériel est identifié comme cf. *Theriosuchus* sp.  
[Traduit par la rédaction]

## 内容提要

产自中国内蒙鄂尔多斯盆地老龙豁子地点下白垩统志丹群罗汉洞组的头颅及躯干化石代表了一迄今尚未报导过的鳄形类初龙动物。头颅部分的几个特征表明这个种类可归入 Atoposauridae 科; 在此以前, 本科成员的确切发现只限于欧洲的上侏罗和下白垩统地层中。标本的某些进步性征进一步表明, 鄂尔多斯的材料既使不属于 *Theriosuchus*, 也与此属关系密切。鄂尔多斯的 atoposaurid 标本与 *Theriosuchus* 诸种相比只在少数几个特征上有别。鉴于材料的破碎状态, 目前谨将这些标本定为 cf. *Theriosuchus* sp.

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## Реферат

Кранидийные и посткранидийные останки из Лаолонгуоз в бассейне Ордос, Внутренняя Монголия (Китай) представляют ранее не зарегистрированный таксон крокодилообразных архозаврусов из формации Луохандонг нижнего мела (группа Жидан). Несколько

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X.-C. Wu,<sup>1</sup> Department of Vertebrate Palaeontology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada, and Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, P.O. Box 643, Beijing 100044, People's Republic of China.

H.-D. Sues,<sup>2</sup> Department of Vertebrate Palaeontology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada, and Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada.

D.B. Brinkman, Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, AB T0J 0Y0, Canada.

<sup>1</sup> Present address: Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, AB T0J 0Y0, Canada.

<sup>2</sup> Corresponding author (e-mail: hdsues@rom.on.ca).

кранидийных характеристик указывают на родство этой формы с Atoposauridae, которые ранее с определенностью были известны только из верхней юры и нижнего мела Европы. Некоторые унаследованные характеристики дополнительно указывают на тесную близость, если не прямое родство, с *Theriosuchus*. Атопозаурид бассейна Ордос отличается от видов *Theriosuchus* только несколькими чертами. В силу фрагментарной природы останков, новый материал идентифицирован в настоящее время как cf. *Theriosuchus* sp.

[Перевод выполнен для редакции Научно-Исследовательские Журналы]

## Introduction

The Dinosaur Project (China – Canada – Alberta – Ex Terra) has demonstrated the presence of a diverse assemblage of vertebrates in the Lower Cretaceous Luohandong Formation of the Ordos Basin, Inner Mongolia, China (Brinkman and Peng 1993; Dong 1993; Russell and Dong 1993). Two taxa of crocodyliform archosaurs have previously been described from the Luohandong Formation. *Eotomistoma multidentatum* Young, 1964 is now represented only by the anterior portion of a snout and is best considered a nomen dubium. The posterior portion of the holotypic snout of *E. multidentatum* was subsequently designated the holotype of the champsosaur *Ikechosaurus sunailinae* Sigogneau-Russell, 1981. *Shantungosuchus hangjinensis* Wu et al., 1994 is a protosuchian. Young (1961) initially considered *Shantungosuchus* an atoposaurid, but Wu et al. (1994) have demonstrated that this taxon is a protosuchian closely related to the Protosuchidae (sensu Clark 1986).

In the present paper, we describe fragmentary skeletal remains of a third crocodyliform taxon from the Luohandong Formation. It represents the first definite record of the Atoposauridae from China. We consider the new material closely related to, if not referable to, *Theriosuchus*. The material comprises fragments of the skull and mandible and some postcranial bones, which were collected during the 1988 field season of the Dinosaur Project at the Laolonghuoze locality, approximately 35 km southwest of the quarry from which the holotype of *S. hangjinensis* was recovered. All skeletal remains described here were recovered from the same layer at the locality within a range of less than 500 m. Most bones are compatible in size and appear referable to the same taxon. The material will be housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Academia Sinica, Beijing.

## Systematic paleontology

Crocodyliformes Clark in Benton and Clark, 1988  
Neosuchia Clark in Benton and Clark, 1988  
Atoposauridae Gervais, 1871

cf. *Theriosuchus* sp.

## Material

IVPP V10613, left jugal, left frontal, fused parietals, right

exoccipital, incomplete left and right angulars, six vertebrae, both ilia, and several osteoderms. One dorsal vertebra appears to represent a different individual (see below).

## Locality and horizon

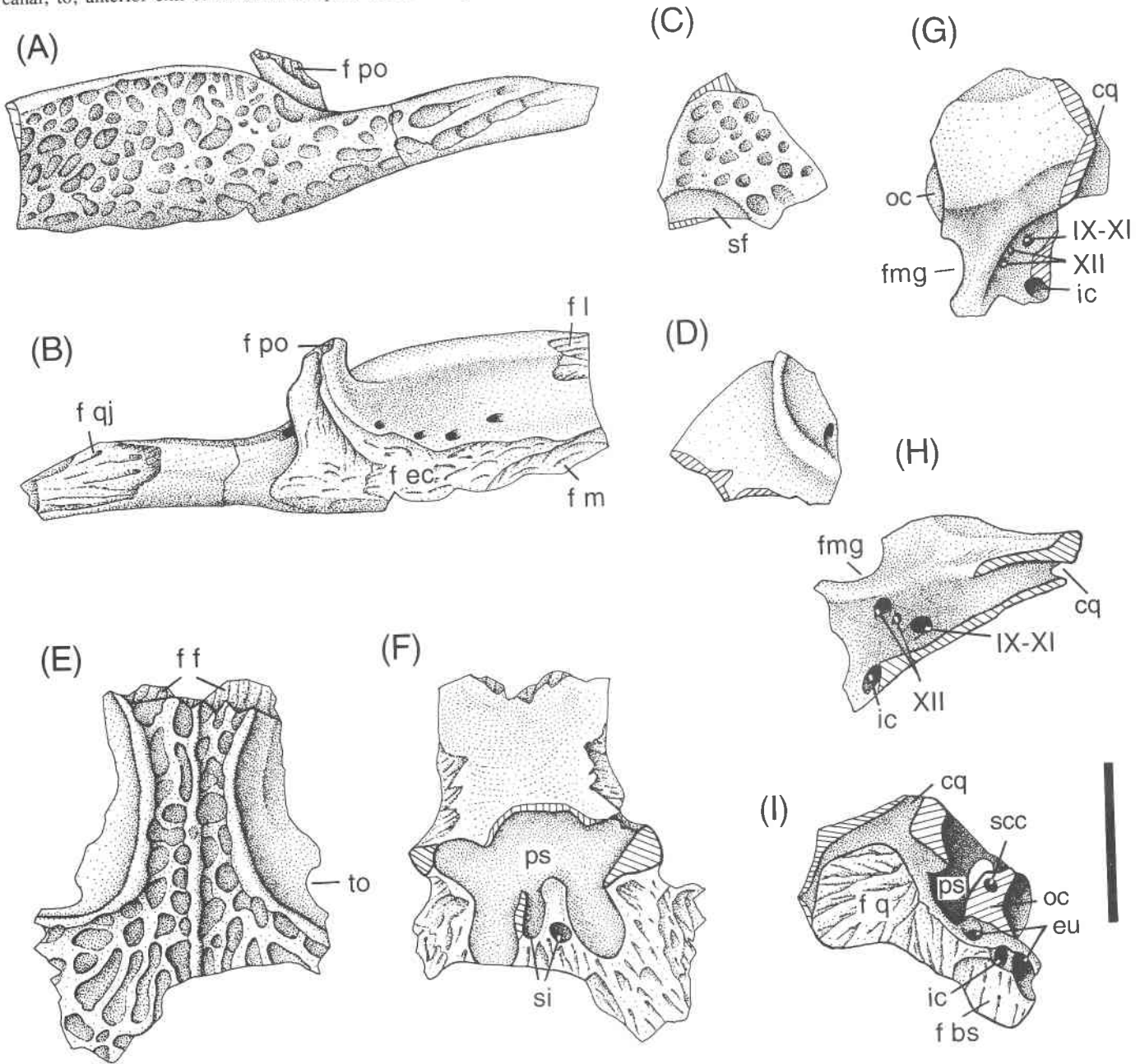
Laolonghuoze, about 53 km west of Hangjin Qi, Inner Mongolia, China; geographic coordinates: 38°55'N, 108°5'E. Luohandong Formation, Zhidan Group. Age: Early Cretaceous (Dong 1993).

## Description

### Cranial bones

The left jugal (preserved length 40 mm) only lacks the anterior edge and closely resembles the jugal of *Theriosuchus ibericus* (Brinkmann 1992). The anterior or infraorbital process is plate-like and twice as deep dorsoventrally as the slender posterior or infratemporal process (Figs. 1A, 1B). It is separated from the latter by a distinct step along the dorsal margin. The lateral surface of the jugal is slightly convex dorsoventrally and sculptured with deep, round pits. Several pits near the sutural contact with the quadratojugal are connected with one another to form two short grooves. The rather short ascending or postorbital process of the jugal is columnar and deeply inset. It is relatively massive compared with that in other neosuchians. The jugal reaches its greatest transverse width across the base of the postorbital process. The facet for the descending process of the postorbital extends along the dorsolateral margin of the ascending process. The posterior or infratemporal process of the jugal is slender and has more or less parallel dorsal and ventral edges. On the medial surface, the jugal is not thickened to form a strong prominence ventral to the base of the ascending process. Anteriorly, there are facets for sutural contact with the maxilla and lacrimal, respectively. Posteriorly, there is an extensive facet for the quadratojugal. The facet for the ectopterygoid extends dorsally along the entire medial surface of the ascending process, as in *Theriosuchus* (Clark 1986; Brinkmann 1992). This indicates that there was a postorbital–ectopterygoid contact, as in many other neosuchians. Posteriorly, the facet for the ectopterygoid also indicates the presence of a posterior process of the ectopterygoid, as described by Norell (1989) for *Bernissartia* and some extant crocodylians. A small foramen is present posterior to the base of the ascending process, and four smaller foramina are situated anterior to the process along the dorsal margin of the articular facet for the maxilla, simi-

**Fig. 1.** Cranial bones of cf. *Theriosuchus* sp. (IVPP V10613). (A, B) Left jugal in (A) lateral and (B) medial views. (C, D) Fragment of left frontal in (C) dorsal and (D) ventral views. (E, F) Fused parietals in (E) dorsal and (F) ventral views. (G–I) Left exoccipital in (G) occipital, (H) posteroventral, and (I) anterior views. cq, cranio-quadrato canal; eu, passage for eustachian tube; f bs, facet for basisphenoid; f ec, facet for ectopterygoid; f f, facet for frontal; f l, facet for lacrimal; f m, facet for maxilla; fmg, foramen magnum; f po, facet for postorbital; f q, facet for quadrate; f qj, facet for quadratojugal; ic, canal for internal carotid artery; oc, otic capsule; ps, pneumatic space; sf, supratemporal fossa; si, paired sinuses on parietal; scc, semicircular canal; to, anterior exit of canal for temporo-orbital artery. Roman numerals denote cranial nerves. Scale bar = 1 cm.



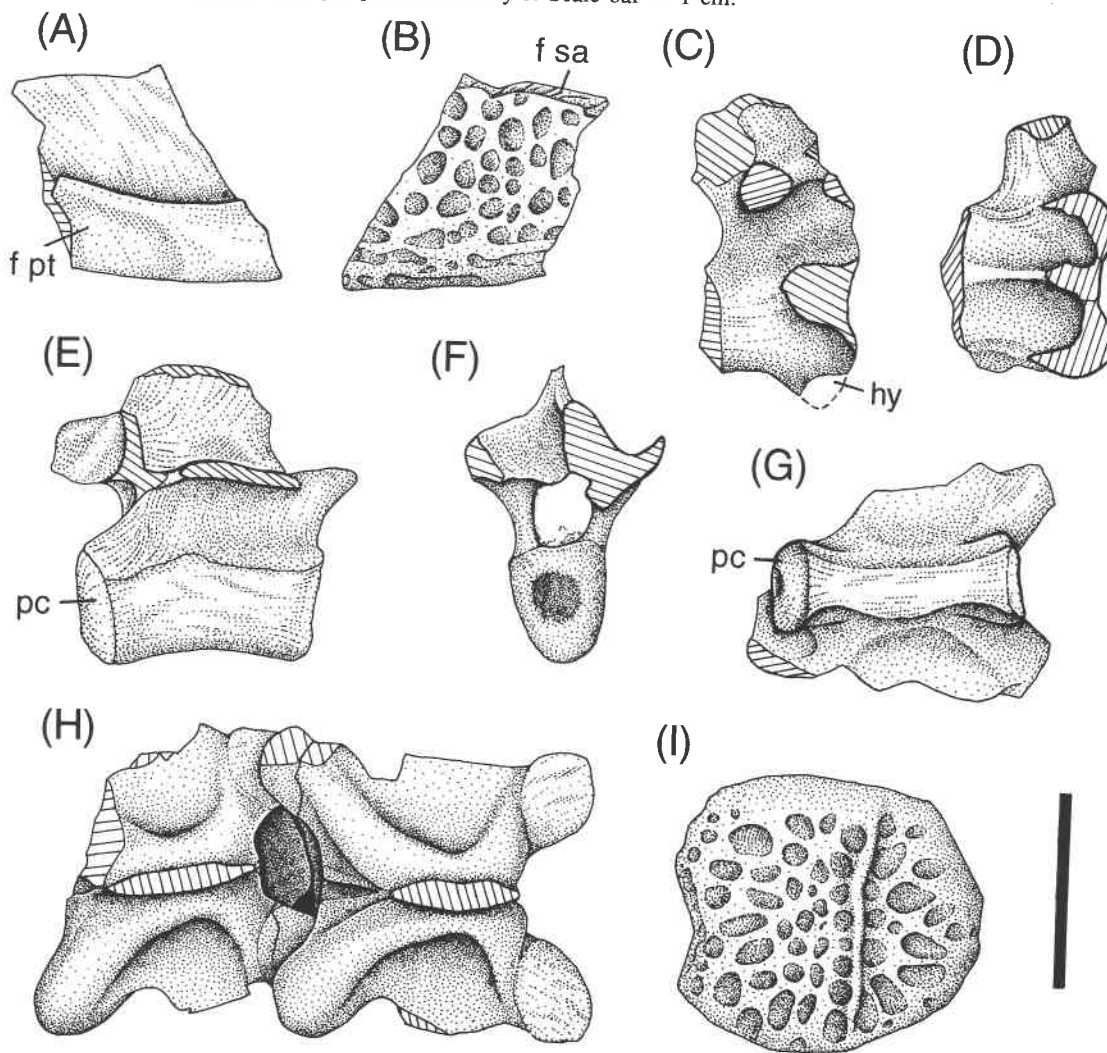
lar to the condition in *T. ibericus* (Brinkmann 1992).

The left frontal is documented only by a small piece of the posterolateral portion (Figs. 1C, 1D). A concave, smooth area situated posterolaterally on its dorsal surface represents the anterior portion of the supratemporal fossa. Laterally, the concave area almost reaches the orbit, indicating a very narrow region between the orbit and supratemporal fossa, much as in other atoposaurids (Wellnhofer 1971; Clark

1986). The dorsomedial rim of the orbit is elevated and the interorbital region is concave as in *Theriosuchus pusillus*. It cannot be ascertained whether the frontals were fused and whether the median ridge on the parietals continued anteriorly onto the frontal(s). The smooth lateral surface forming the dorsomedial roof of the orbit is ventromedially delimited by a low crista frontalis.

The fused parietals are nearly complete, except in the

**Fig. 2.** Bones of cf. *Theriosuchus* sp. (IVPP V10613). (A, B) Fragment of right angular in (A) medial and (B) lateral views. (C, D) Last cervical vertebra in (C) lateral and (D) ventral views. (E–G) Dorsal vertebra in (E) lateral, (F) posterior, and (G) ventral views. (H) Two articulated dorsal vertebrae in dorsal view. (I) Osteoderm in dorsal view. f pt, facet for contact with transverse flange of pterygoid flange; f sa, facet for surangular; hy, hypapophysis; pc, posterior condyle. Scale bar = 1 cm.



region along the posterior margin (Figs. 1E, 1F). The compound bone is about 24 mm long and is very similar to that of *T. pusillus*. The dorsally sculptured intertemporal region is narrow and bears a median ridge for much of its length. The supratemporal fossa is delimited medially by a raised rim. Lateral to that rim, the parietal is smooth and depressed and forms a partial floor to the supratemporal fossa. The thin lateral edge of the depressed portion was damaged by erosion. A notch anteroventral to the posterior border of the fossa forms the medial margin of the foramen for the anterior exit of the canal for the temporo-orbital artery. The transverse suture with the fused frontals is straight but interdigitating. It is placed farther forward than in *T. pusillus*, as is indicated by the medial margin of the supratemporal fenestra that starts to curve anterolaterally. The interdigitating suture with the squamosal extends posteriorly and slightly medially. Posteriorly, the dorsal ornamentation on the fused parietals consists of three or four large, elongate pits on either side. The ventral surface of the parietals is

divided into anterior and posterior portions. The former is concave and roofs the endocranial cavity. The latter is deeply hollowed out by a large pneumatic space associated with the middle ear chamber. On the roof of that space, a pair of small sinuses (the right one lacking its ventral floor) is situated parallel to the midline just anterior to the sutural facet for the supraoccipital; similar sinuses are present in some extant alligatorids, such as *Paleosuchus* (M.A. Norell, personal communication, 1994).

The right exoccipital is missing the medial portion dorsal to the foramen magnum and the lateral extremity of the paroccipital process (Figs. 1G–1I). The bone does not differ appreciably from that in other neosuchians. The dorsoventrally narrow ventral portion of the exoccipital is incomplete ventrally, but all the major foramina for blood vessels and cranial nerves in this region of the braincase are preserved. Two foramina for N. hypoglossus (XII) and one (foramen vagi) for cranial nerves IX–XI are closely grouped together. The foramen for internal carotid artery is situated

ventrally near the suture with the basioccipital. In anterior view, the lateral surface of the exoccipital is grooved by the cranio-quadrate canal, indicating a broad contact between the paroccipital process, quadrate, and squamosal lateral to the canal. Anteromedially, the bone is highly pneumatized. Anterior to the otic capsule (oc), two foramina are connected by a canal, through which the eustachian tube passed dorsally into the middle ear region, as in extant crocodylians. Located between these foramina is the anterior exit of the canal for the internal carotid artery. Two facets on the anterior surface represent the articular contacts for the quadrate (lateral) and basisphenoid, respectively.

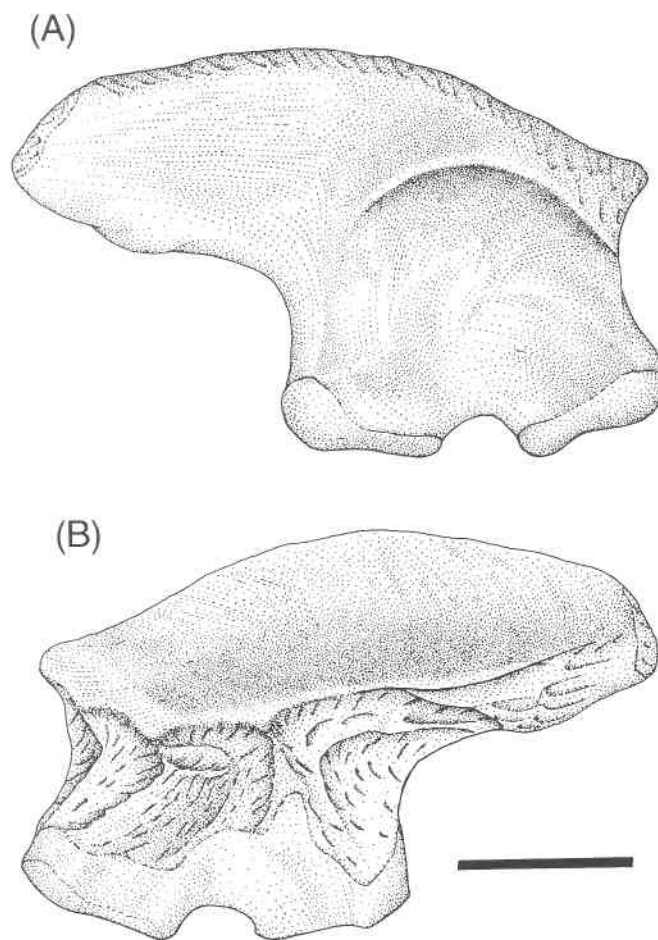
The fragment of the right angular represents the portion adjacent to the pterygoid flange (Figs. 2A, 2B). A concave area for contact with the pterygoid flange is developed on the medial surface of this piece. The angular is dorsoventrally very deep in this region, and its dorsolateral edge bears a facet, presumably for contact with the surangular. Thus it appears that the external mandibular fenestra was completely closed in IVPP V10613. The fragment of the left angular represents a portion of that bone more posterior in position than the piece of the right angular. It is also dorsoventrally deep in lateral view and dorsoventrally shallow in medial view. Posteriorly, the facet for contact with the surangular extends along the dorsomedial margin. The lateral surface of the two fragments is densely sculptured with deep pits and, more ventrally, short grooves, but the convex ventral surface is smooth.

#### Postcranial bones

The six preserved vertebrae comprise one cervical and five dorsals. All are incomplete. The cervical is probably the last one, as indicated by the high position of the parapophyses and by the short centrum (Figs. 2C, 2D). Its neural arch has lost most of the neural spine and all zygapophyses. The right diapophysis is nearly horizontal. The centrum is fused to the neural arch. The parapophyses along anterodorsal edges of the centrum are for the most part worn off. A slightly abraded hypapophysis is developed anteromedially on the ventral surface of the centrum. A similar process is also present in *T. pusillus* (Clark 1986). The anterior surface of the cervical centrum is concave, and the mostly eroded posterior surface was apparently convex.

The positions of the five dorsals were determined by the position of the transverse processes, which are entirely situated on the neural arch (Figs. 2E–2H). Two of the vertebrae are still in articulation. One isolated vertebra retains open sutures between the neural arch and centrum. Its centrum (12.5 mm long) is distinctly more slender (but not shorter) than those of the other four. This vertebra appears to belong to a different individual, although it closely resembles the other four in overall structure. It is the most complete dorsal preserved, with both ends of its centrum intact. As on the other dorsal vertebrae, the zygapophyses are nearly horizontally oriented. The neural spine is moderately long antero-posteriorly. The ventral surface of the centrum is gently concave and smooth, the posterior condyle of the centrum being convex but bearing a distinct depression at its centre ("semi-procoelous" condition). This condition is similar to the truncated vertebrae in *Bernissartia* (Buscalioni and Sanz 1990a). Buffetaut (1982) interpreted an anterior caudal

Fig. 3. Right ilium of cf. *Theriosuchus* sp. (IVPP V10613) in (A) lateral and (B) medial views. Scale bar = 1 cm.



vertebra of *T. pusillus* as being of the "semi-procoelous" type, but this was not confirmed for that taxon (Clark 1986; Norell and Clark 1990). The other four dorsals each show a trace of a central depression on the posterior condyle.

The well-preserved right ilium (Fig. 3) resembles that of *Alligatorium franconicum* (Wellnhofer 1971) in the reduction of the preacetabular process to a knob-like projection. The postacetabular process is unusually well developed. When compared with the homologous bone in the Eusuchia, the ilium differs in that the postacetabular process is relatively longer, is dorsoventrally narrow, and lacks a pronounced ventral expansion for the attachment of *M. coccygeofemoralis brevis*. The posterior end of the postacetabular process is at the same level as the anterior end of the very short preacetabular process. The supraacetabular rim of the acetabulum is moderately well developed. The facets for the pubis and ischium are separated by a notch. The lateral surface of the iliac blade is slightly everted laterally. Two facets for sacral ribs are developed on the medial surface of the ilium.

#### Osteoderms

One complete osteoderm and pieces of seven others are preserved. The complete osteoderm (Fig. 2I) is slightly wider than long and bears a low dorsolateral keel. A narrow

smooth area along the anterodorsal margin indicates that this osteoderm was overlapped by the preceding one. These features are shared by the dorsal osteoderms of other atoposaurid taxa (Wellnhofer 1971). The lateral and posterior margins of the osteoderm are gently rounded. The osteoderm is most likely derived from the posterior region of the trunk or from the first transverse row of the tail because it is only slightly wider (17 mm) than long (15 mm).

### Comparisons and discussion

Although the validity of various described atoposaurid taxa remains contentious, most recent authors have restricted the Atoposauridae to taxa from the Upper Jurassic and Lower Cretaceous of Europe. Clark (1986 and in Benton and Clark 1988) recognized only two valid taxa: *Theriosuchus pusillus* Owen, 1879 and *Alligatorium meyeri* Gervais, 1871. Buscalioni and Sanz (1988) accepted four taxa as valid, adding *Alligatorellus beaumonti* Gervais, 1871 and *Montsecosuchus depereti* (for "*Alligatorium*" *depereti* Vidal, 1915) to Clark's list. We mainly compared IVPP V10613 with *Alligatorium* and *Theriosuchus*. In addition, we compared it to the recently described *T. ibericus* Brinkmann, 1992 from the Lower Cretaceous of Spain and the following non-atoposaurid neosuchian crocodyliforms: *Sunosuchus* spp. (Upper Jurassic and Lower Cretaceous of China; Wu et al. 1996), *Bernissartia fagesii* (Lower Cretaceous of Europe; Norell and Clark 1990; Buscalioni and Sanz 1990a), and *Shamosuchus* spp. (Upper Cretaceous of Mongolia and China; Efimov 1988).

Although the skeletal material catalogued as IVPP V10613 is rather fragmentary, the following 13 features are identifiable and relevant for assessing the phylogenetic position of the Ordos taxon: (1) The supratemporal fossa extends almost to the orbital margin on the dorsal surface of the frontal. (2) The external mandibular fenestra is absent. (3) The post-orbital bar is columnar and supported by the ectopterygoid. (4) The dorsal surface of the fused parietals bears a median ridge. (5) The supratemporal fossa is delimited medially by a raised rim. (6) The dorsomedial margin of the orbit is elevated. (7) The intertemporal region of the parietals is narrow. (8) The anterior process of the jugal is twice as wide as the posterior process. (9) The frontoparietal suture is placed relatively far forward. (10) There are three or four large pits present on the posterodorsal surface of the parietals lateral to the midline. (11) A knob-like hypapophysis is present on the cervical vertebrae. (12) The "semi-procoelous" vertebrae are characterized by the presence of a central depression on the posterior condyle of the centra. (13) The ilium has a knob-like preacetabular process and an elongate, posterodorsally directed postacetabular process. These characters, especially the structure of the jugal and vertebrae and the closure of the external mandibular fenestra, preclude reference of IVPP V10613 to *S. hangjinensis* from the same horizon and same general provenance. This assessment is further supported by the open cranio-quadrangle canal in the latter taxon. IVPP V10613 cannot be compared to *E. multi-dentatum* from the same horizon, because it does not include the corresponding portion of the snout. Most of the characters listed above also preclude the reference of the Ordos material to *Sunosuchus* from the Upper Jurassic and Lower Cretaceous of Mongolia and northwestern China. Characters

1, 4, 5, 7, 8, 10, and 13 distinguish IVPP V10613 from both *Shamosuchus* and *Bernissartia*.

Characters 1 and 2 support reference of IVPP V10613 to the Atoposauridae. Character 1 was hypothesized by Clark (1986) as an apomorphy of the latter taxon, and character 2 was regarded by both Buscalioni and Sanz (1988) and Clark (1994) as one of the diagnostic features for that group. Character 13 appears to support reference to the Atoposauridae as well. Although a relatively well developed preacetabular process is present in *Alligatorellus* (Wellnhofer 1971), this process is absent in *Alligatorium franconicum* (Wellnhofer 1971) and *M. depereti* (Buscalioni and Sanz 1990b). The ilium of *T. pusillus* is unknown (Clark 1986) and thus the presence or absence of the process cannot be verified. Character 3 is a derived feature shared by the Atoposauridae and other derived crocodyliform archosaurs (Clark 1994).

We consider IVPP V10613 most similar to *T. pusillus* based on the shared possession of the derived states for characters 4–7 (determined by outgroup comparison with Goniopholididae and *Bernissartia*). Characters 4–6 were described by Clark (1986) for *T. pusillus*, but they are absent in the other atoposaurid taxa (Clark 1986; Buscalioni and Sanz 1990b). The available evidence indicates that the narrow intertemporal region of the parietals (character 7) is shared only by IVPP V10613 and *T. pusillus*. In other atoposaurid taxa, the intertemporal region of the parietals is relatively much broader than the posterior portion of the parietals. Character 11 probably also indicates a close relationship between the Ordos material and *T. pusillus*. It was hypothesized by Buscalioni and Sanz (1988) as an apomorphy of *Theriosuchus*. However, according to Norell and Clark (1990), this feature is also present in *Bernissartia*. A central depression on the posterior condyle of the vertebrae (character 12) is present on the dorsal vertebrae of *Bernissartia* (Buscalioni and Sanz 1990a; Brinkmann 1992). This type of vertebra has also been reported in a small, as yet unnamed neosuchian from the Lower Cretaceous of Texas (Joffe 1967; Langston 1974) and apparently had a wide distribution among Cretaceous neosuchians.

There are two differences (characters 8 and 9) between IVPP V10613 and *T. pusillus*. Although the anterior process of the jugal was distorted during fossilization in the holotype of *T. pusillus* (Clark 1986), it was not twice as deep as the posterior process. In this feature, the Ordos material more closely resembles *T. ibericus* (Brinkmann 1992). The frontal forms a considerable portion of the supratemporal fossa in *T. pusillus*. As noted earlier, the sutural contact between frontal and parietal is placed relatively farther forward in IVPP V10613 than in *T. pusillus*. This character is unknown in *T. ibericus*. Character 10 is definitely absent in most other atoposaurid taxa and is equivocal in the holotype of *T. pusillus* where the critical area is incompletely preserved. Although IVPP V10613 may represent a new species of *Theriosuchus*, the material is too incomplete for adequate diagnosis, and it is more appropriate to refer to it as cf. *Theriosuchus* sp. at present.

According to Clark (1986) and Buscalioni and Sanz (1988), valid taxa referable to the Atoposauridae (including *T. ibericus* Brinkmann, 1992) are known only from the Upper Jurassic and Lower Cretaceous (Tithonian–Barremian) of Europe. Three taxa of small crocodyliform archosaurs from

correlative strata outside Europe have previously been referred to that group (see Clark 1986). One of them, *Shantungosuchus* Young, 1961 from the Upper Jurassic and Lower Cretaceous of China, has already been reassigned to the *Protosuchia* by Wu et al. (1994). *Karatausuchus sharovi* Efimov, 1976 from the Upper Jurassic Karabastau Formation of Kazakhstan shows no features to indicate atoposaurid affinities (Clark 1986). *Hoplosuchus kayi* Gilmore, 1926 from the Upper Jurassic Morrison Formation of Utah appears to be a basal crocodyliform (Clark 1986). Thus the discovery of cf. *Theriosuchus* sp. in the Ordos Basin of China represents the first definite record of the Atoposauridae outside Europe.

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