

# 中国陆相上三叠统第一个初龙形类动物<sup>1)</sup>

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**摘要** 初步研究了山西省永和县桑壁镇铜川组二段产出的两件初龙形类化石标本(IVPP V 12378, V 12379),在此基础上建立了一新属新种——桑壁永和鳄(*Yonghesuchus sangbiensis* gen. et sp. nov.)。

它以下列共存的衍生特征区别于其他初龙形类(archosauriforms): 1) 吻部前端尖削; 2) 眶前窝前部具一凹陷; 3) 眶前窝与外鼻孔间宽; 4) 眶后骨下降突的后 2/3 宽且深凹; 5) 基蝶骨腹面有两个凹陷; 6) 齿骨后背突相当长; 7) 关节骨的反关节区有明显的背脊, 有穿孔的翼状的内侧突, 以及指向前内侧向和背向的十分显著的后内侧突。

由于缺乏附骨的形态信息, 目前很难通过支序分析建立永和鳄的系统发育关系。但可以通过头骨形态来推测永和鳄在初龙形类中的系统位置。永和鳄有翼骨齿, 这表明它不属于狭义的初龙类(archosaurians)。其通过内颈动脉脑支的孔位于基蝶骨的前侧面而不是腹面, 在这点上永和鳄比原鳄龙科(Proterochampsidae)更进步, 这表明与后者相比永和鳄和狭义的初龙类的关系可能更近。在中国早期的初龙形类中, 达坂吐鲁番鳄(*Turfanosuchus dabanensis*)与桑壁永和鳄最接近, 但前者由于内颈动脉脑支的孔腹位而比后者更为原始。

根据以上头骨特征以及枢后椎椎体之间间椎体的存在与否, 推测派克鳄(*Euparkeria*)、达坂吐鲁番鳄(如果存在间椎体)、原鳄龙科和永和鳄与初龙类的关系逐渐接近。而且这与这些初龙形类的生存时代基本一致。

永和鳄比产于上三叠统下部的原鳄龙(*Proterochampsia*)进步, 它的发现支持含化石的铜川组时代为晚三叠世的观点。

**关键词** 山西永和, 晚三叠世, 铜川组, 初龙形类, 解剖学

**中图法分类号** Q915.864

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# THE ANATOMY OF THE FIRST ARCHOSAURIFORM (DIAPSIDA) FROM THE TERRESTRIAL UPPER TRIASSIC OF CHINA

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**Abstract** *Yonghesuchus sangbiensis*, a new genus and species of the Archosauriformes, is erected on the basis of its peculiar cranial features. This taxon represents the first record of tetrapods from the Late Triassic terrestrial deposits of China. Its discovery is significant not only to our study on the phylogeny of the Archosauriformes but also to our understanding of the evolution of the Triassic terrestrial vertebrate faunae in China. The presence of pterygoid teeth may exclude the new form from the Archosauria, and the apomorphic position of the foramen for the internal carotid artery indicates that the new form appears to be phylogenetically closer to the Archosauria than are *Turfanosuchus* and the Proterochampsidae. Comparisons with these taxa suggest that the *Y. sangbiensis*-bearing Tongchuan Formation is probably of early Late Triassic age.

**Key words** Yonghe, Shanxi, Late Triassic, Tongchuan Formation, Archosauriform, Anatomy

## 1 Introduction

Archosauriforms (sensu Gauthier et al., 1988) were dominant carnivores of terrestrial tetrapod faunae throughout the Triassic. Their early representatives (to which the term “thecodont” traditionally has been applied) have been known from nearly all continents (Romer, 1966; Carroll, 1988; Parrish, 1992, 1993). China has the greatest variety of early archosauriforms in the World, including a number of very well represented taxa (Young, 1964, 1973a, 1973b; Cheng, 1980; Wu, 1981, 1982; Peng, 1991; Wu and Russell, 2001). However, in China unlike most of other localities, these archosauriforms are restricted to the Early and Middle Triassic terrestrial redbeds. Terrestrial Triassic redbeds of China are distributed throughout the northern and northwestern parts of the country, primarily in the Ordos (Shaan-Gan-Ning) Basin (covering parts of Shaanxi, Gansu and Shanxi provinces and parts of Ningxia and Nei Mongol autonomous regions) and in several basins with variety of sizes in Xinjiang Autonomous Region. The Ermaying Formation of the Ordos Basin and the Kelamayi Formation in Xinjiang Autonomous Region are generally considered to be of late Early-Middle Triassic or the Middle Triassic age, respectively and previously represented the highest redbeds of the Triassic that yield tetrapod vertebrate faunae in China (Zhao, 1980; Sun, 1980; Cheng, 1986; Li and Cheng, 1995; Lucas, 1996). The Late Triassic terrestrial deposits also have a broad distribution in northern and northwestern China, but produce few vertebrate fossils, except for some fishes.

There are two terrestrial faunae that have previously been considered by some to be the Late Triassic in age. One is the “Lufeng Saurischian Fauna” from Yunnan Province, southern China, which has been recently demonstrated to be of Early Jurassic age (Luo and Wu, 1994, 1995). The other is the “Fukang Fauna” from the top of the Kelamayi Formation or the base of the Huangshanjie Formation of the Junggar Basin in Xinjiang Autonomous Region. According to Lucas and Hunt (1993a, b), two of the three known vertebrates of this fauna were mistakenly identified. They believe that the specimen referred to an aetosaur (an archosaurian of the Late Triassic) is actually a fragment of the squamosal of a dicynodont (a mammal-like reptile) while the specimen referred to metoposaurid

(labyrinthodont amphibians of the Late Triassic) is a fragment of capitosauroid amphibians of the Early-Late Triassic). The third vertebrate of the “Fukang Fauna” is a palaeoniscid fish that is more primitive than *Tanaocrossus* of Carnian (early Late Triassic) from western United States (Lucas, 1996). Thus, the presence of these vertebrates suggests an age older than Late Triassic for the “Fukang Fauna”, nor is there evidence of any archosauriform in this fauna. The absence of a Late Triassic terrestrial fauna, especially archosauriforms that were commonly present during this age in other continents, is one of the most important gaps in the Mesozoic vertebrate record of China. It is obvious that any finding of archosauriforms and other tetrapods from strata stratigraphically higher than the Kelamayi Formation in Xinjiang Autonomous Region or the Ermaying Formation in the Ordos Basin would be significant to our understanding of the local faunal evolution and to establishing the international faunal and stratigraphical correlations.

In 1992, a field team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences at Beijing, collected several individuals of a new archosauriform from the southwestern region of Shanxi province (southeastern Ordos Basin). The fossil locality is close to Sangbi township, Yonghe county. The new material actually consists of several individuals that are mixed together in the very hard, fine sandstone. The fossil spot, lying on the northern side of the river course of the Sangbi Creek, is seasonally submerged by floods, which decemented the superficial layers of the fossil block but also heavily damaged the specimens. The sandstone block that contains the specimens was broken into several pieces to make the collection of the specimens possible before a flood came. Each piece shows different sections of the individual specimens. After our detailed stratigraphical correlation around the fossil locality in the fall of 1999, it is clear that the new archosauriform is from Member II of the Tongchuan Formation (see Liu et al. 2001), above the Ermaying Formation, and underlies the Yanchang Formation (sensu Institute of Geology, Chinese Academy of Geological Sciences, 1980). Thus, the new archosauriform bearing beds represents the uppermost stratigraphical record of the tetrapod fauna so far known from the terrestrial Triassic deposits of China.

In this paper, we present a preliminary study of the new archosauriform based on two specimens. A full and detailed investigation of the taxon has to wait until all the specimens are fully prepared. Regarding the definition of the Archosauria in this study, we follow the crown-group concept of Gauthier et al. (1988) rather than the traditional meaning. In other words, the Archosauriformes used here is taxonomically equivalent to the “Archosauria” of Benton (1985) or of Benton and Clark (1988), and the Archosauria used here is exclusively restricted to two living lineages (the two crown-groups: the crocodylian-line and bird-line) and their common ancestors.

## 2 Systematic Paleontology

### **Diapsida Gauthier et al., 1988**

#### **Archosauromorpha Gauthier et al., 1988**

#### **Archosauriformes Gauthier et al., 1988**

#### ***Yonghesuchus* gen. nov.**

**Type and only known species** *Yonghesuchus sangbiensis* sp. nov.

**Etymology** Referring to Yonghe County in which the fossil locality is situated.

**Diagnosis** As for the type and only known species.

*Yonghesuchus sangbiensis* sp. nov.

(figs. 1~4; pl. I)

**Holotype** IVPP V 12378, incomplete skull with the mandible occluded.**Paratype** IVPP V 12379, incomplete skull in articulation with the first 7 cervical vertebrae and several cervical ribs.**Etymology** Referring to the Sangbi Creek from the bank of which the specimens were collected.**Type locality and horizon** On the north bank of the Sangbi Creek, about 1.5 km southwest of the Sangbi township; the upper part of Member II of the Tongchuan Formation, early Late Triassic.**Diagnosis** Small to medium-sized archosauriform differing from other known taxa in having the following combination of apomorphies: 1) anterior end of snout sharply pointed; 2) a concavity in antorbital fossa; 3) region between antorbital fossa and external naris broad; 4) posterior two thirds of descending process of postorbital broadly and deeply concave; 5) two fossae on ventral surface of basisphenoid; 6) dentary with a posterodorsal process remarkably long relative to those of other archosauriforms; and 7) retroarticular region of articular having a pronounced dorsal ridge, a penetrated wing-like medial process, and a sharply pointed posteromedial process directed anteromedially and dorsally.

### 3 Description and Comparison

**Skull** The outline of the skull of the holotype (V 12378) in both dorsal and ventral views was distorted by dorsoventral compression, exaggerating its width, as suggested by the unusually large size of the interpterygoid vacuity (see below). Both dorsal and ventral surfaces of the holotypic skull were heavily eroded (figs. 1, 2). Most of the skull roof elements were badly eroded, the palate has lost the vomers, palatines, and ectopterygoids, and the braincase is represented by only the incomplete basisphenoid. The skull of the paratype is preserved in ventral view, but a transverse break has resulted in the loss of much of its ventral surface, especially in the braincase region (fig. 3). The paratypic skull has a narrower profile in ventral view than the holotype. This is considered to be an artifact of preservation, caused by the medial shift of the postorbital region of the skull, as suggested by the nearly closed interpterygoid vacuity. The following description of each skull element is based on the holotype unless indicated otherwise. The reconstruction of the skull and mandible is based on both the holotype and paratype (fig. 4).The premaxilla is dorsoventrally shallow relative to that of *Turfanosuchus dabanensis* (Young, 1973a; Wu and Russell, 2001). Its maxillary process is directed more posteroventrally than in the latter, with the pointed end inserting between the maxilla and nasal as in many other archosauriforms (fig. 2C). The anterior end of each premaxilla is incomplete, missing the nasal (anterodorsal) process. The ventral outline of the premaxilla is clear in the paratype, although incomplete. In ventral view, the premaxilla, preserved partly as impression, extends anteriorly to form a pointed end anterior to the dental rim of the bone. This produces a pointed anterior tip of the snout distinct from the round end of the snout commonly seen in other archosauriforms (fig. 3). The palatal shelf of the premaxilla is incomplete posteriorly. The preserved part suggests that a foramen similar to the incisive foramen normally seen in crocodylomorphs (see Wu and Chatterjee, 1993) might have been present.The maxilla is characterized by a shallow concavity located within the antorbital fossa (figs. 1A, 2C). In lateral view, the portion of the maxilla anterior to the antorbital fossa is anteroposteriorly broader than in *Turfanosuchus dabanensis* and most other non-

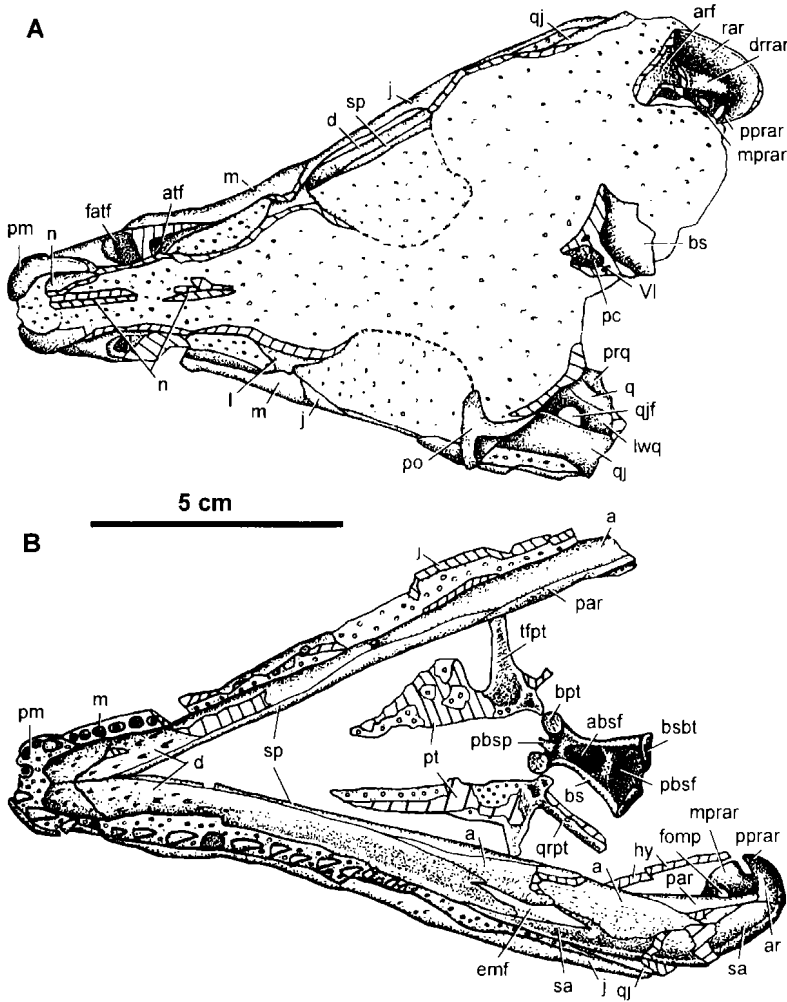


Fig. 1 Skull and mandible of *Yonghesuchus sangbiensis* gen. et sp. nov. (holotype: IVPP V 12378) in dorsal (A) and ventral (B) views

Abbreviations 简字说明: a, angular 隅骨; absf, anterior fossa on ventral surface of basisphenoid 基蝶骨腹面的前凹; ar, articular 关节骨; arf, articular fossa for quadrate 下颌与方骨的关节窝; atf, antorbital fossa 眶前窝; bpt, basiptyergoid process 基翼突; bs, basisphenoid 基蝶骨; bsbt, basal tuber of basisphenoid 基蝶骨的基突; d, dentary 齿骨; drrar, dorsal ridge of retroarticular region 反关节区背脊; emf, external mandibular fenestra 下颌外窗; eo, exoccipital 外枕骨; fatf, fossa within antorbital fossa 眶前窝中的凹陷; fomp, foramen piecing medial process of retroarticular region 反关节区内侧突上的穿孔; hy, a piece of hyoid 舌骨一部分; j, jugal 轭骨; l, lacrimal 泪骨; lwq, posterolateral wing of quadrate 方骨的后外侧翼; m, maxilla 上颌骨; mprar, medial process of retroarticular region 反关节区内侧突; n, nasal 鼻骨; par, prearticular 前关节骨; pbsf, posterior fossa on ventral surface of basisphenoid 基蝶骨腹面的后凹; pbsp, parabasisphenoid process 基蝶骨的副蝶骨突; pc, pituitary concavity 垂体窝; pm, premaxilla 前颌骨; po, postorbital 眶后骨; pprar, posterior process of retroarticular region 反关节区后突; prq, pterygoid ramus of quadrate 方骨的翼骨支; pt, pterygoid 翼骨; q, quadrate 方骨; qj, quadratojugal 方轭骨; qjf, quadratojugal foramen 方轭孔; qrpt, quadrate ramus of pterygoid 翼骨的方骨支; rar, retroarticular region 关节骨的反关节区; sa, surangular 上隅骨; sp, splenial 夹板骨; tfpt, transverse flange of pterygoid 翼骨翼; VI, foramina for cranial nerve VI 第VI脑神经孔。

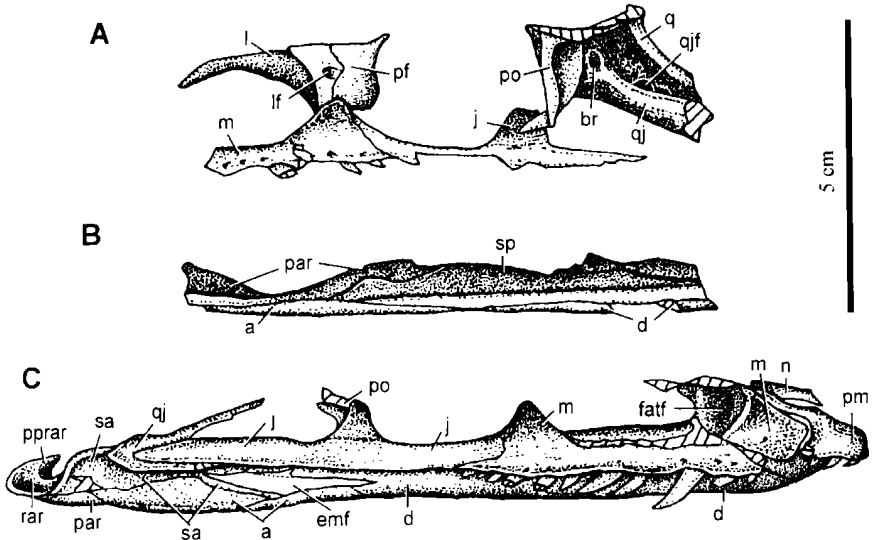


Fig. 2 Skull and mandible of *Yonghesuchus sangbiensis* gen. et sp. nov. (holotype: IVPP V 12378)

A, antorbital, orbital, and infratemporal regions in right lateral view; B, posterior portion of left ramus of mandible in medial view; C, skull and mandible in left lateral view

Abbreviations as fig. 1 plus: br, breakage on lateral surface of quadratojugal 方轭骨外侧面的破损; lf, lacrimal foramen 泪孔; pf, prefrontal 前额骨

crocodylomorph archosauriforms (see Parrish, 1992, 1993). The anterior tip of the maxilla narrows but does not become sharply pointed as in *Euparkeria* (Ewer, 1965) and *Chanaresuchus* (Romer, 1971). Its ventrolateral margin bears a series of small nutritional foramina. Its ventral edge is almost straight. The maxillary teeth are different in size. As in *Turfanosuchus dabanensis* (see Wu and Russell, 2001; fig. 1B), the maxilla is distinct in having a pronounced posterodorsal process forming, with the ventral processes of the lacrimal and prefrontal, a broad septum between the antorbital fenestra and orbit, which excludes the jugal from the antorbital fenestra (fig. 2A, C). As indicated by the preserved parts on both sides, the antorbital fossa, especially its anterior part, is most probably larger relative to that seen in most other non-crocodylomorph archosauriforms. Other aspects of the maxilla are obscured by the occlusion of the mandible in the holotype or by the breakage in the paratype.

The nasals are very fragmentary but appear to be in original position (fig. 1A). The anteroventral portion of each nasal is clearly not forked (fig. 2C), being different from those seen in *Turfanosuchus dabanensis*.

The lacrimal has only its vertical part preserved on both sides (figs. 1A, 2A). This process contributes to the dorsal part of the antorbital fossa and the anterodorsal part of the antorbital septum. The lacrimal foramen is laterally exposed, which can be observed on the left side.

The prefrontal preserves only its ventral process on both sides, which forms the anterodorsal margin of the orbit (fig. 2A). This process is relatively broader longitudinally than in *Turfanosuchus dabanensis* and larger than in most other non-crocodylomorph archosauriforms. The ventral extremity of the process on both sides may have been damaged by the dorsoventral distortion. The suture between the process and the lacrimal is curved posteriorly. Neither frontals nor parietals are preserved.

The left postorbital is preserved, but its dorsal part was somewhat damaged (figs. 1A, 2A). This bone is distinct in that the posterior part of its descending process is broadly and

deeply depressed, clearly inset below the bone surface. A comparable condition is seen in *Turfanosuchus dabanensis* and a proterochampsid *Chanaresuchus* (see below) among known archosauriforms. The broad anterior process of the postorbital is short and the long posterior process is narrow. The sharply pointed end of the posterior process is largely exaggerated by breakage.

The right jugal is nearly complete except for the dorsal extremity of its ascending process (figs. 1, 2). It resembles that of *Turfanosuchus dabanensis* in that its anterior process tapers off along the orbital margin and does not reach the antorbital fossa and its posterior process is slightly longer than the anterior process. Unlike in the latter, the ascending process of the jugal is not depressed below the lateral surface and appears to be shorter in size.

The quadratojugal preserves its ventral part on the right side and a portion of its dorsal part on the left side (fig. 1A). It is comparable to that of *Turfanosuchus dabanensis* in that its anteroventral process is slender and extends anteriorly along the ventromedial side of the posterior process of the jugal to the mid-point of the latter (fig. 2C). The quadratojugal is evidently excluded from the ventral border of the infratemporal fenestra as it is in *T. dabanensis*, *Euparkeria*, *Erythrosuchus* (see Parrish, 1992), and *Proterosuchus* (Cruikshank, 1972; fig. 2B). The preserved dorsal part is massive and broad, and missing its articular surface with the squamosal. The dorsal part of the quadrate is strongly anterodorsally oriented, which must have resulted from distortion (fig. 1A). It is evident that the quadratojugal forms the posteroventral border of the infratemporal fenestra. This fenestra is large, as suggested by its broad ventral border formed by the jugal (fig. 2C).

The squamosal is not preserved. The left quadrate is preserved, with its ventral mandibular condyle and dorsal cephalic head missing (figs. 1A, 2A). The shaft of the quadrate is most similar to that of *Turfanosuchus dabanensis*. It has a broad anterolateral wing that is posteriorly concave. This posterior surface is pierced by a large quadratojugal foramen that is laterally enclosed by the quadratojugal as in most other non-crocodylomorph archosauriforms. The pterygoid ramus of the quadrate is dorsoventrally broad and its narrowed distal end is incomplete. The quadrate forms a curved ridge between the anterolateral wing and pterygoid ramus (fig. 1A), which presumably have served for the attachment of the tympanum in life.

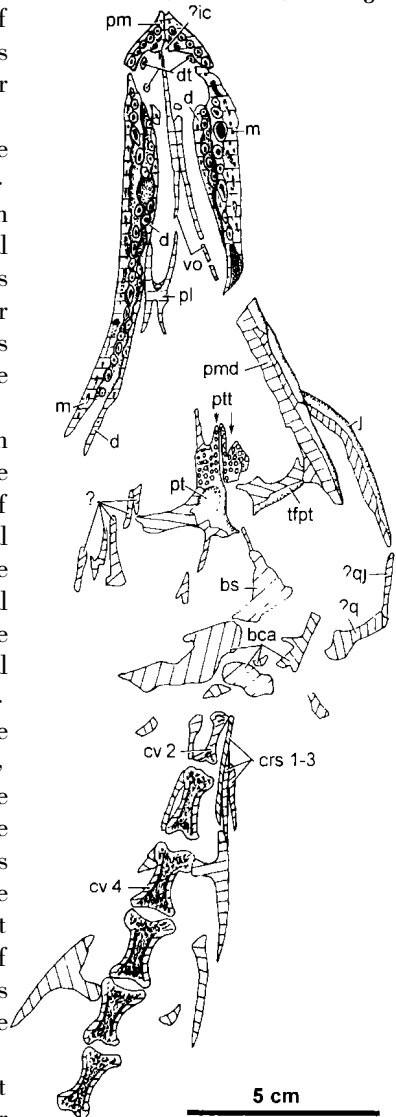


Fig. 3 Paratype of *Yonghesuchus sang-biensis* gen. et sp. nov. (IVPP V 12379) in ventral view

Abbreviations as in fig. 1 plus: bca, brain-case 脑颅; cv. 2, 4, cervical vertebrae 2, 4 第2, 第4颈椎; crs 1-3, cervical ribs 1-3 第1~3颈肋; dt, dentary teeth 齿骨齿; pl, palatine 腭骨; pmd, posterior portion of left mandible 左颌的后部; ptt, pterygoid teeth 翼骨上的腭齿; vo, vomer 犁骨; ic, incisive foramen 门齿孔

The vomers are preserved in the paratype but very fragmentary (fig. 3). They appear to be very slender in ventral view. The right palatine is preserved in the paratype although incomplete. Its U-shaped anterior margin forms the posterior border of the choana (fig. 3). Its lateral contact with the maxilla is obscured by the occlusion of the mandible. The narrowly forked posterior margin of the preserved part of the palatine is the artifact of preservation. The true posterior margin of the bone which forms the anterior border of the suborbital fenestra is completely missing. Relationships with other palatal elements and the presence or absence of teeth on the palatine cannot be determined owing to the poor preservation.

Both pterygoids are preserved in the holotype (fig. 1B). The elongate palatal ramus is missing the anterior end and its ventral surface is not complete but clearly bears many denticles (fine teeth) as in *Turfanosuchus dabanensis* (see Wu and Russell, 2001), *Euparkeria* (Ewer, 1965), and other early non-eurythrosuchid archosauriforms (see Parrish, 1992, 1993). The presence of the pterygoid teeth in the palatal ramus of the pterygoid is confirmed by the paratype (fig. 3). The transverse flange bears no denticles and is narrow, which may have been exaggerated by crushing. The incomplete quadrate ramus preserved on the right pterygoid shows that it is a thin, nearly vertical plate. The junction area of the three parts of the pterygoid is broadly concave. A small posteromedial process marks the articulation with the basiptyergoid process of the basisphenoid. The interptyergoid vacuity was largely broadened by the lateral displacement of each pterygoid in the holotype while it is nearly closed by the medial dislocation of each pterygoid in the paratype.

The basisphenoid of the holotypic skull is the only preserved braincase element with anatomical features that can be observed. It is incomplete dorsally (fig. 1). In ventral view, the basisphenoid is characterized by an anterior fossa and a posterior fossa (fig. 1B). It is longer and anteriorly much narrower than in *Turfanosuchus dabanensis* (see Wu and Russell, 2001; fig. 5), *Xilousuchus* (an early archosauriform from the upper Lower Triassic of the eastern Ordos Basin, China [Wu, 1981; fig. 2]), and other early archosauriforms (see Gower and Sennikov, 1996). Its nearly round basiptyergoid process bears a short neck as in *T. dabanensis* and its basal tuber is moderately developed. There is no foramen for the entrance of the cerebral branches of the internal carotid artery on the ventral surface posterior to the basiptyergoid process. This foramen must have been located on the dorsal side as in *Dorosuchus* (an euparkeriid-like animal [Sennikov, 1989; fig. 1a]) and more derived archosauriforms (see Parrish, 1993). The preserved base of the parabasisphenoid process suggests that the process may have been very slender. In dorsal view, the *dorsum sellae* and anterior part of the braincase concavity are preserved but incomplete (fig. 1A). The foramen for cranial nerve VI is clearly visible posterodorsal to the pituitary concavity. Other anatomical features of the dorsal part are largely obscured by poor preservation.

**Mandible** The right ramus of the mandible of the holotype is almost complete but its dorsal surface is covered by the occlusion with the skull (fig. 1B). The fragmentary mandible of the paratype is also occluded with the skull (fig. 3). The description of each mandibular element is exclusively based on the holotype.

The right dentary is nearly complete except for its anteriormost and posterodorsal ends. It is about two-thirds of the mandibular length. It is distinct among early archosauriforms in that its posterodorsal process, although incomplete, is clearly much longer than its very short posteroventral process. The elongate posterodorsal process of the dentary may have formed two-thirds of the dorsal border of the external mandibular fenestra, which is both dorsoventrally much narrower and much longer than those seen in *Turfanosuchus dabanensis* (see Wu and Russell, 2001; fig. 2), *Euparkeria*, *Ornithosuchus* (see Sereno, 1991; fig. 11), and other early archosauriforms (see Parrish, 1992, 1993). In lateral view, much of



the lateral surface of the dentary is slightly concave. There are some fine pits on the anteroventral surface of the dentary. The dentaries form the most of the mandibular symphysis and slightly bulge laterally just anterior to the posterior end of their symphysis, as in some crocodyliforms (see Clark, 1994, Wu et al., 1996).

The right surangular, although superficially damaged in its posterior region, is almost complete. Its main body is dorsoventrally narrow relative to those seen in *Turfanosuchus dabanensis*, *Euparkeria*, and most early archosauriforms where its anatomy is known (figs. 1B, 2C). Its slender anterodorsal process extends along the dorsal surface of the dentary to level of the last preserved maxillary tooth. Posteriorly, the surangular extends nearly to the end of the retroarticular region. The lateral surface of the surangular is concave, and along its posterodorsal edge of the bone bears a crest that subsides in the region dorsal to the external mandibular fenestra. This crest is present in *T. dabanensis* but is more pronounced and elongate (Wu and Russell, 2001; fig. 2). The anteroventral process of the surangular is narrowly exposed and forms the posteroventral border of the external mandibular fenestra. Medial structures of the surangular cannot be observed owing to the occlusion of the mandible with the skull.

The right angular is complete but there is a crack at its mid-portion (figs. 1B, 2C). In lateral view, the major body of the angular is dorsoventrally much broader than in *Turfanosuchus dabanensis*, *Euparkeria*, *Ornithosuchus*, and most other early archosauriforms. The angular is also broad in *Chanaresuchus* but unlike in the new taxon, its lateral surface is strongly concave (Romer, 1971; fig. 4). As in *Chanaresuchus*, the angular/surangular suture curves dorsally towards the surangular. Anteriorly, the angular forms the anteroventral border of the external mandibular fenestra and its sharp anterior process deeply wedges between the dentary and splenial. Posteriorly, the angular narrows as it wedges between the surangular and prearticular before reaching the articular.

The preserved right articular is missing most of the articular fossa and the portion anterior to it, but the retroarticular region is well-preserved (figs. 1, 2C). The latter is unique in that its posterior end is dorsoventrally thin and gives rise a sharply pointed posteromedial process directing mediodorsally and anteriorly, and bears a dorsoventrally compressed, wing-like medial process on the mid-portion of its medial margin between the articular fossa and the posteromedial process. The wing-like medial process is posteriorly much thicker than anteriorly and is pieced by a foramen. The posteromedial process is present in sphenosuchian crocodylomorphs where the retroarticular region is known but in the latter it is very massive and pillar-like (see Wu and Chatterjee, 1993; fig. 19). A wing-like process, penetrated by a foramen, is commonly present in a number of rauisuchiforms (sensu Parrish, 1993), such as *Batrachotomus kupferzellensis* (Gower, 1999; fig. 20), *Fasolasuchus tenax* (Bonaparte, 1981; fig. 6), *Rauisuchus tiradentes* (Huene, 1942; pl. 25, fig. 3b), and *Postosuchus kirkepatroeki* (Chatterjee, 1985; figs. 8, 9b). The dorsal surface of the retroarticular region is very concave and partly divided by a pronounced ridge that runs from the posterior edge of the articular fossa but subsides well before the posterior end of the region. This ridge is not known in other archosauriforms in which the relevant part is preserved. The ventral surface of the retroarticular region is strongly convex.

Both splenials are largely obscured because of the skull/mandible occlusion. In ventral view, they clearly meet each other anteriorly and form the posteriormost one fifth of the mandibular symphysis (fig. 1B). The splenial is narrowly exposed anteriorly but contributes more to the ventral surface of the mandible posteriorly. Other features of the bone cannot be observed.

The right prearticular is complete but its medial portion is covered by the displacement of the mandible (fig. 1B). However, this aspect is observable on the left side (fig. 2B).

The bone is elongate and exposed on the lateral surface of the mandible as in *Ornithosuchus longidens* (see Sereno, 1991; fig. 11A) and two crocodylomorphs (*Dibothrosuchus elaphros* [Wu and Chatterjee, 1993; fig. 8A] and *Sphenosuchus acutus* [Walker, 1990; fig. 31a]), and possibly *Turfanosuchus dabanensis* (Pers. Obs.). The prearticular extends further posteriorly than the angular does and even more posteriorly than the posterior edge of the winglike medial process of the retroarticular region of the articular. In medial view the posterior part of the prearticular, as shown on the left side (fig. 2B), is ventrally thick and dorsoventrally broader than the anterior part, the latter is mediolaterally thin and curves upwards along the posterior edge of the splenial. It is unknown if this part met the surangular and coronoid anterodorsally in life as in many other archosauriforms due to the incompleteness of the relevant region.

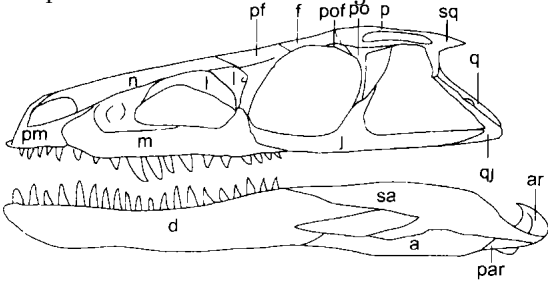


Fig. 4 The reconstruction of the skull and mandible of *Yonghesuchus sangbiensis* in lateral view. Abbreviations as in figs. 1, 2 plus: f, frontal 额骨; p, parietal 顶骨; pof, postfrontal 后额骨; sq, squamosal 鳞骨

A segment of the hyoid is preserved medial to the right prearticular. It is rod-like, showing no specific features (fig. 1B).

**Dentition** Both premaxillaries of the paratype bear the roots of five teeth. In contrast to the premaxillary dentition of *Turfanosuchus dabanensis*, it is the fifth rather than the third tooth, as the preserved tooth roots indicated, that is the largest, although the other four are not much smaller (fig. 4). Complete premaxillary teeth preserved in the holotype lack serrations along both anterior and posterior edges of their

crowns. Fine preparation reveals that the premaxillary teeth of *T. dabanensis* also lack anterior or posterior serrations, in contrast to the description of Wu and Russell (2001). The premaxillary teeth are slightly compressed, with their crown tips recurving posteriorly.

The right maxilla of the holotype has a complete row of 12 preserved teeth and two alveoli for the first and the fifth teeth (fig. 1B). The maxillary teeth are more laterally compressed and bear serrations on both anterior and posterior edges of their crowns. The maxillary teeth vary in size. The fourth and fifth teeth (as indicated by the alveoli) are similar in size and are much larger than the others. The maxillary teeth become smaller from the fourth tooth forward and from the fifth tooth backward. Further preparation shows that the alveoli of the fourth and fifth teeth are of similar size and distinctly larger than the remainders in *Turfanosuchus dabanensis* as well.

The dentary dentition is entirely invisible because of the skull/mandible occlusion in the holotype. Dentary teeth in the paratype are preserved in transverse sections (fig. 3). No distinct features can be observed in these dentary teeth.

**Postcranial skeleton** The first seven cervical vertebrae and some ribs associated with in the paratype are only elements of the postcranial skeleton preserved. As with the skull and mandible, these vertebrae and ribs are preserved in ventral view and their ventral portions were shared off (fig. 3). The dorsal portions of these elements are still in the hard matrix and thus, cannot provide much information.

The atlas has been almost eroded away but except possibly for small fragments located anterior to the axis. The ventral parts of the centra of the axis and the remaining five cervical vertebrae were largely lost. The centrum of the axis is anteriorly convex, because of the fusion of the intercentrum of the atlas with it, and posteriorly concave. The centra of the

remaining vertebrae are amphicoelous and bilaterally strongly concave, as suggested by the outlines of their broken surfaces. There is no way to determine if an intercentrum was present between these vertebrae in life. The preserved anterior two cervical ribs (left side) are of simple structure, and elongate. These two ribs resemble the first two cervical ribs seen in other archosauriforms, such as crocodyliforms (see Wu et al., 1996; fig. 11Q, R). The other preserved cervical ribs are stouter than the anterior two, although incomplete. They are short and should have had two articular heads and an anterior process in life, as commonly seen in other archosauriforms.

#### 4 Discussion

1) *Yonghesuchus sangbiensis* is a new archosauriform, exhibiting a number of distinct features in the snout, temporal region, braincase, and retroarticular region of the mandible. The abruptly and sharply pointed anterior end of the snout, as shown in the paratype (fig. 3), has not been reported in other known archosauriforms. The snout is anteriorly very narrow and sharp in *Riojasuchus tenuiceps*, an ornithosuchid, but it does not form an abrupt and pointed extremity just anterior to the dentition (see Sereno, 1991; fig. 12). In the temporal region of *Y. sangbiensis*, the posterior two thirds of the descending process of the postorbital is strongly depressed, which may have provided an extra area for the attachment of jaw adductor muscles. Among early, non-archosaurian archosauriforms, a similar depression of the postorbital is present in *Turfanosuchus* (*T. dabanensis*) and *Chanaresuchus* but it is much shallower and faded out within the dorsal third of the descending process in *T. dabanensis* (Wu and Russell, 2001; fig. 1B) or the narrow depression extends downward on to the posterolateral surface of the ascending process of the jugal in *Chanaresuchus* (Romer, 1971; fig. 2). The basisphenoid of the braincase generally bears only one fossa or concavity on its ventral surface in early archosauriforms (see Gower and Sennikov, 1996), while it clearly has two fossae in *Y. sangbiensis* (fig. 1B). The retroarticular region of the mandible is very complex in *Y. sangbiensis*, being unique in the combination of three structures: a pronounced ridge running on the dorsal surface, a wing-like medial process pierced by a foramen, and a sharp terminal process pointing mediadorsally and anteriorly (figs. 1, 4). It is true that all of these three have been reported in some of other archosauriforms; for instance, the retroarticular region in many rauisuchiforms has, as mentioned above, a penetrated wing-like medial process although it does not bear a dorsal ridge. Furthermore, in some of rauisuchians (see Gower, 1999), the retroarticular region bears a posteromedial process that is superficially similar to the sharp terminal process of *Y. sangbiensis* and posteromedial process of sphenosuchians (Wu and Chatterjee, 1993). Actually, this process is different in the latter taxa, being dorsoventrally vertical in orientation in the rauisuchians and is very thick and massive in the sphenosuchians. In addition, the retroarticular region bears one or two fossae on its dorsal surface in rauisuchians (see Gower, 1999; fig. 20C) and does not have a wing-like medial process and a dorsal ridge in sphenosuchians. In any case, all three features have never been recorded together in any archosauriform.

2) As with other groups, phylogenetic relationships within archosauriforms have been increasingly investigated using cladistic methodology (Benton, 1985; Gauthier, 1986; Benton and Clark, 1988; Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994; Gower and Wilkinson, 1996; Gower and Weber, 1998). Most recent studies agree that characters from the two proximal tarsals (astragalus and calcaneum) have played an important role in establishing phylogenetic relationships within archosauriforms (see Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994; Gower, 1996). Therefore, without information on the two proximal tarsals, it is difficult for us to conduct a cladistic

analysis for establishing the phylogenetic relationships of *Yonghesuchus sangbiensis*. However, many of the aforementioned studies have also recognized some skull characters that bear significant implications for phylogenetic relationships between early archosauriforms and crown-taxa (archosaurians). In the following text we focus on those skull characters that may imply the phylogenetic position of *Y. sangbiensis* within the Archosauriformes.

Recent phylogenetic studies of the Archosauriformes have almost unambiguously considered that the palatal dentition is entirely absent, an apomorphic character state, in all archosaurians. The synapomorphies used by Gauthier (1986) to define the Archosauria do not include the absence of the palatal teeth because he considered *Euparkeria* (with palatal teeth) to be an archosaurian. However, most other recent cladistic studies have hypothesized that *Euparkeria* is not an archosaurian and the absence of the palatal teeth represents a strong evidence in support of the monophyly of the Archosauria (see Benton and Clark, 1988, Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994). *Yonghesuchus* has pterygoid teeth, which indicates that, as with *Euparkeria* and the Proterochampsidae, it may not be referable to the Archosauria.

An additional skull character that was considered by Parrish (1993) to be important in establishing phylogenetic relationships among early archosauriforms is the position of the foramen for the entrance of the cerebral branch of the internal carotid artery. In its plesiomorphic state, the foramen is located on the anteroventral surface of the basisphenoid posterior to the basiptyergoid process and in its apomorphic state, the foramen is positioned on the anterolateral surface of the basisphenoid posterodorsal to the parabasisphenoid process. All archosaurians have the apomorphic state of this character. Parrish (1993) considered the apomorphic state of this character for the Proterochampsidae despite the plesiomorphic state did occur within the family, and with the support of the absence of the vertebral intercentrum between the post-axial vertebrae, he believes that the Proterochampsidae is more closely related to the Archosauria than is *Euparkeria*. However, in a proterochampsid, *Chanaresuchus*, the foramen for the internal carotid artery is plesiomorphically located on the anteroventral surface of the basisphenoid. As Parrish (1993) pointed out that this plesiomorphic state is also present in some specimens of *Proterochampsia*, the type genus of the Proterochampsidae. On the basis of the common, although not exclusive, presence of the foramen for the internal carotid artery on the ventral surface of the basisphenoid we believe that the Proterochampsidae should have been scored the plesiomorphic state of this character unless the plesiomorphic state can be demonstrated to be secondarily evolved within the family. With the absence of the vertebral intercentrum between the post-axial vertebrae, the Proterochampsidae still can be considered to be more closely related to the Archosauria than is *Euparkeria*.

As described above, it can be confirmed that the foramen for the internal carotid artery had an apomorphic position on the anterolateral surface of the basisphenoid in *Yonghesuchus*, this being strongly indicated by the absence of any foramen on the well-preserved ventral surface of the basisphenoid of the holotype (fig. 1B). In this point *Yonghesuchus* is more apomorphic than the Proterochampsidae, suggesting a closer relationship to the Archosauria than the latter although we cannot determine whether it did not have the intercentrum between the post-axial vertebrae and whether its two proximal tarsals were morphologically as apomorphic as those of the latter.

*Yonghesuchus* is most comparable with *Turfanosuchus* (*T. dabanensis*) among the Chinese early archosauriforms that are fairly represented. *T. dabanensis* has been recently considered as a suchian within one of the two archosaurian lineages, leading to the Crocodylomorpha (Parrish, 1993; fig. 1). In contrast, the latest restudy (Wu and Russell, 2001) has demonstrated that *T. dabanensis* is phylogenetically much more plesiomorphic

than what Parrish (1993) considered. It is not a suchian, nor can it be referred to the Crurotasi (crocodylan-line). The presence of pterygoid teeth and the ventral position of the foramen for the cerebral branch of the internal carotid artery on the anteroventral surface of the basisphenoid strongly indicate that *T. dabanensis* is furthermore not referable to the Archosauria. However, the relatively derived morphology of the calcaneum reveals that *T. dabanensis* is phylogenetically closer to the Archosauria than is *Euparkeria* (Wu and Russell, 2001). It is difficult to assess whether *T. dabanensis* is more remotely related to the Archosauria than is the Proterochampsidae because the absence of the intercentrum between the post-axial vertebrae cannot be confirmed, but it is obvious that *T. dabanensis* is not as derived as *Yonghesuchus* on the basis of the plesiomorphic position of its foramen for the internal carotid artery.

3) From the above discussion, *Euparkeria*, *Turfanosuchus dabanensis* (if the intercentrum was present between the post-axial vertebrae), the Proterochampsidae, and *Yonghesuchus* appear to be successively closer in relationship to the Archosauria. This pattern of relationships among these early archosauriforms seems to match their geological occurrences: *Euparkeria* from the middle subzone of the *Cynognathus* Zone of South Africa may be the earliest, being of late Early Triassic-early Middle Triassic in age (see Charig and Sues, 1976; Anderson and Cruickshank, 1978; Shubin and Sues, 1991; Shishkin et al., 1995; Gower and Weber, 1998); *T. dabanensis* from the lower Kelamayi Formation of Xinjiang Autonomous Region is of early Middle Triassic (see Sun, 1980; Li and Cheng, 1995); and the geological range of the South American Proterochampsidae spans from the early Middle (*Chanaresuchus* from Chanâres Formation of Argentina [see Romer, 1971]) to early Late Triassic (*Proterochampsa* from the Ischigualasto Formation of Argentina [see Sill, 1967; Shubin and Sues, 1991]).

Regarding *Yonghesuchus*, its host Tongchuan Formation discomfortably overlies the Ermaying Formation. The upper part of the latter formation is equivalent to the Kelamayi Formation that yields *Turfanosuchus dabanensis* (see Sun, 1980; Li and Cheng, 1995). The age of the Tongchuan Formation has long been controversial; some considering it to be of late Middle Triassic and some others believing that it is of early Late Triassic (see Liu et al., 2001). The discovery of *Yonghesuchus* seems to support the view of the early Late Triassic age for the Tongchuan Formation on the basis of its more derived skull morphology relative to that of *Proterochampsa* from the lower Upper Triassic. As mentioned by Parrish (1993), in *Proterochampsa* the foramen for the internal carotid artery shows both the plesiomorphic and apomorphic character states. Although we do not know whether *Yonghesuchus* consistently exhibits the apomorphic condition relative to the foramen for the internal carotid artery, the evidence available at least suggests that this new taxon cannot be more plesiomorphic in morphology than *Proterochampsa*. This is consistent with the early Late Triassic age of the *Yonghesuchus*-bearing Tongchuan Formation, a date which is supported by the presence of *Triassodus*, a derived palaeoniscid fish, morphologically most similar to *Turseodus* restricted to the Late Triassic Newark Group and Chinle Formation of North America. It also resembles the palaeoniscid fish, *Shuniscus* from the Late Triassic Xujiahe Formation of Sichuan Province (Su, 1984).

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### 图版 I 说明(Explanations of Plate I)

Skull and mandible (holotype, IVPP V 12378) of *Yonghesuchus sangbiensis* gen. et sp. nov. in dorsal (A), ventral (B), and lateral (C) views. ×0.8

**A**



**B**



**C**

