Redescription of Turfanosuchus dabanensis (Archosauriformes) and new information on its phylogenetic relationships

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REDESCRIPTION OF *TURFANOSUCHUS DABANENSIS* (ARCHOSAURIFORMES) AND NEW INFORMATION ON ITS PHYLOGENETIC RELATIONSHIPS

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ABSTRACT—The skeleton of the archosauriform *Turfanosuchus dabanensis* Young, 1973 is redescribed on the basis of further preparation. For the first time a set of derived features is recognised for diagnosing this species. Re-examination of the specimen reveals the presence of palatal teeth in the pterygoid; the ventral entrance of the internal carotid arteries posterior to the basipterygoid processes; the calcaneal tuber shaft taller than broad; the absence of flaring of the distal end of the calcaneal tuber; the calcaneal tuber shaft convex laterally and concave medially; and the tibial facet on the astragalus simply concave. These features are strongly indicative that *T. dabanensis* is not a suchian and not even a crurotarsan, which sharply contrasts with its recently-proposed basal suchian status.

INTRODUCTION

Turfanosuchus dabanensis was initially described by Young (1973) on the basis of a partially complete disarticulated skeleton (IVPP V3237, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica) from the Middle Triassic of the Xinjiang Autonomous Region, northwestern China. Young considered it to be a euparkeriid, but to be more derived than *Euparkeria* from the Middle Triassic of South Africa (Ewer, 1965). Twenty years later, Parrish (1993) re-examined the specimen and concluded that it is a suchian, implying that *T. dabanensis* is phylogenetically much more derived than Young had originally suggested.

At the time of Young's (1973) description, the specimen had not been fully prepared, especially the skull region. This misled Young (1973) in his interpretation of its anatomy. For example, he erroneously stated that the premaxilla bore six or seven teeth; and he identified the palatal shelves of the premaxillae as the vomers. Parrish (1993) did not prepare the specimen any further and therefore about 42% of the characters upon which he based his phylogenetic analysis of the Crocodylotarsi (sensu Benton and Clark, 1988) were not known for *Turfanosuchus dabanensis*.

Young (1973:29) provided an extensive list of diagnostic features for defining *Turfanosuchus dabanensis*. Of these very few are really diagnostic among known archosauriforms; some are commonly present in many archosauriforms, such as the supratemporal fenestra being triangular in outline and the orbit being large, and others were the result of errors made in his original investigation, such as the prefrontal being "small," the medial border of the supratemporal fenestra being formed "entirely by the parietal," the antorbital fenestra being "nearly as large as the orbit," the presence of "two external mandibular fenestrae," the presence of a "third sacral vertebra," and "the absence" of osteoderms. In Parrish's paper (1993), Young's diagnosis of the taxon was not supported.

We herein redescribe *Turfanosuchus dabanensis*, based upon further preparation of the specimen, and present new figures of the skull, mandible, and some elements of the postcranial skeleton. Some of the elements in the figures provided by Young (1973) were not correctly identified, and this is also the case

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for the illustration provided by Parrish (1993:fig. 4D). In this redescription we concentrate on those structures that were unknown or incorrectly documented in the two previous studies. We then establish a diagnosis for this taxon and finally make comments on phylogenetic relationships on the basis of new information for *T. dabanensis* as revealed in the present study.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIFORMES Gauthier et al., 1988
TURFANOSUCHUS Young, 1973
TURFANOSUCHUS DABANENSIS Young, 1973

Emended Diagnosis—Although a thorough comparison with other archosauriforms is not possible at the present time, owing to the incomplete knowledge of many related taxa, the following set of cranial features may be used to diagnose this species: (1) narrow anterolateral process of nasal bifurcated for receipt of posterodorsal process of premaxilla; (2) maxilla with a posterodorsal process forming ventral portion of pre-orbital bar between antorbital fenestra and orbit; (3) anterior process of jugal very short, reaching only base of pre-orbital bar; (4) mediolaterally flat postorbital bar inset below surface of bones and with very broad ventral base; (5) angular excluded by surangular-dentary contact from margin of external mandibular fenestra; (6) dentary with elongate posteroventral process longer than posterodorsal process; (7) posterolateral surface of surangular highly concave.

Holotype—IVPP V3237, much of a disarticulated skeleton.

Locality and Horizon—Taoshuyuanzi, about 30 km northwest of Turfan Basin, Xinjiang; Vertebrate Fossil Bed IV (Kannemeyeriid Zone), lower Kelamayi Formation, Middle Triassic.

REDESCRIPTION

Skull Roof

Young's (1973) description implies that the posterodorsal process of the premaxilla is very short. In contrast, this process is depicted as being elongate in Parrish's (1993:fig. 4D) illustration, extending dorsally and exceeding the posterodorsal border of the external naris. Although Parrish's figure appears to illustrate the right side of the skull, this is actually a reversal of the left side of the specimen. This reversal may have been carried out to permit a more direct comparison with
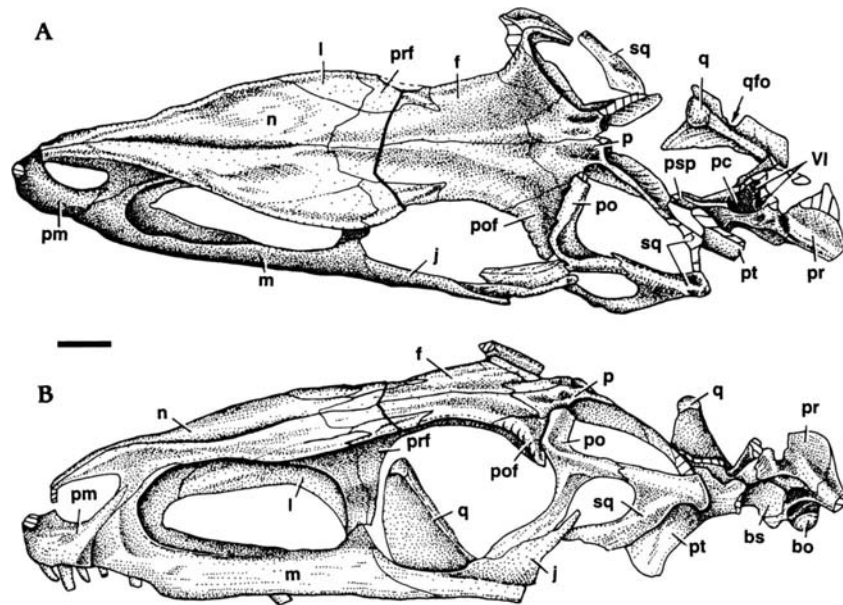
FIGURE 1. Skull of *Turfanosuchus dabanensis*. **A**, dorsal view; **B**, lateral view. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pc**, pituitary fossa; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pr**, prootic; **prf**, prefrontal; **psp**, parasphenoid process; **pt**, pterygoid; **q**, quadrate; **qfo**; quadrate foramen; **sq**, squamosal; **VI**, foramina for cranial nerve VI. Scale bar equals 1 cm.

skulls of the other taxa in the same figure, but it was not mentioned (see Parrish, 1993:fig. 4). Our re-examination reveals that the posterodorsal process of the premaxilla is tall, but that it does not reach the posterodorsal border of the external naris (Fig. 1). Its dorsal end does not extend along the posterior border of the naris, but rather is restricted to its posteroventral margin and then inserts into a groove on the dorsal surface of the nasal.

The right maxilla has been displaced posteriorly and has lost its contact with most of its neighbouring elements (Fig. 2), whereas the left maxilla is almost complete and is still in situ (Fig. 1). Anteriorly each maxilla is not firmly sutured with the premaxilla, and there is a fissure between these two bones. Dorsally the maxilla-lacrimal contact is extensive, rather than being restricted as described by Young (1973). The step-like

anteroventral profile of the maxilla is the result of erosion and is not an original feature. Posteriorly sutures with the jugal and lacrimal are clearly visible. The maxilla-jugal suture runs from anterodorsal to posteroventral, and not in an anteroventral-posterodorsal direction as illustrated by Parrish (1993:fig. 4D). The maxilla possesses a posterodorsal process, which forms the lower third of the pre-orbital bar between the antorbital fenestra and orbit, and excludes the jugal from the antorbital fenestra.

The anterior process of the jugal is shorter than its posterior process (Fig. 2A), the former simply tapering anteriorly to form the lower border of the orbit. The posterior process extends posteriorly to the posteroventral end of the infratemporal fenestra. It is evident that the lateral face of the dorsal process of the jugal is inset relative to the main body of the jugal, as in
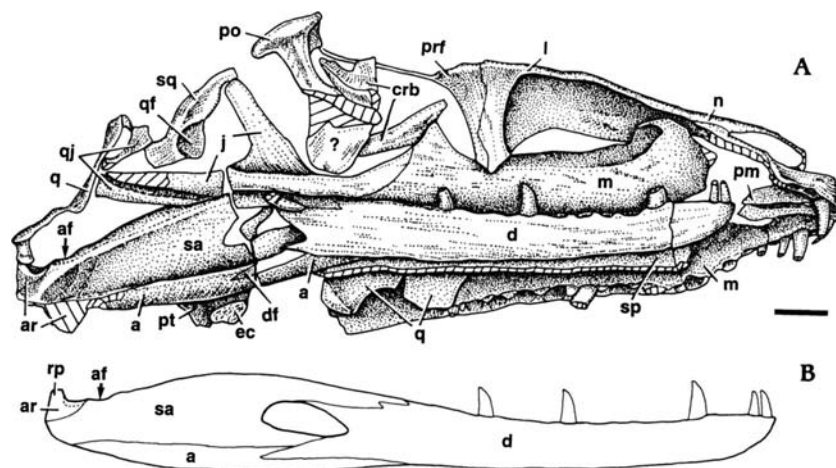

FIGURE 2. **A**, skull and right ramus of mandible of *Turfanosuchus dabanensis* in lateral and slightly ventral view; **B**, reconstruction of right ramus of mandible in lateral view. **Abbreviations as figure 1 plus**: **a**, angular; **af**, articular fossa for quadrate; **ar**, articular; **crb**, cervical rib; **d**, dentary; **df**, facet for dentary; **ec**, ectopterygoid; **qf**, fossa for cephalic head of quadrate; **qj**, quadratojugal; **rp**, dorsal process at end of retroarticular process; **sa**, surangular; **sp**, splenial; **?**, unidentifiable bony fragment. Scale bar equals 1 cm.

most mesocrocodylians (Wu et al., 1996). The base of this process is very broad when compared to that of other archosauriforms.

The anterolateral process of the nasal is narrow and is bifurcated at its junction with the premaxilla to receive the posterodorsal process of the latter. The anterior ramus of the fork is shorter than the posterior, and forms the dorsal third of the posterior border of the external naris (Fig. 1). In dorsal view the nasals form most of the dorsal surface of the rostrum, which is table-like in outline, as it is in some archosauriforms such as *Euparkeria*. Posteriorly the nasals are laterally expanded and, together with the lacrimals, form a laterally protruding margin of the posterodorsal border' of the table-like structure of the snout, which overhangs the antorbital fenestra, as it does in *Euparkeria* (Ewer, 1965:fig. 1a), *Gracilisuchus* (Romer, 1972a: fig. 1) and *Postosuchus* (Chatterjee, 1985:fig. 5a). In these taxa the maxilla is excluded from the flattened dorsal surface of the snout.

The frontal does not border the supratemporal fenestra (Fig. 1), contrary to the situation depicted in Parrish's illustration (1993: fig. 4D). Anteriorly the frontals do not taper to a point, but broadly wedge between the two nasals. The suture of the frontal with the prefrontal is "L"-shaped when viewed from the right side. The frontal barely contacts the lacrimal. Each frontal has a longitudinal depression on the dorsal surface and forms, with its opposite, a table-like structure along the midline, which is continued posteriorly by the parietals. Posteriorly sutures of the frontals with the postorbitals and parietals form a "W"-like pattern.

The posterolateral process of the parietal is not as elongate as indicated by Young (1973). It forms approximately the anterior two thirds of the medial border of the triangular supratemporal fenestra (Fig. 1). A flange of the parietal extends ventrally to form the medial wall of the supratemporal fenestra. Posteromedially a flange of the posterolateral process of the parietal turns ventrally to form part of the occiput. In dorsal view each parietal bears a depression on its posterior surface near the midline. We cannot confirm the presence of the interparietal because the relevant region is poorly preserved.

The lacrimal is much larger than indicated by Young's (1973) description or Parrish's (1993) figure. Laterally it has a large, concave anterior portion that forms the dorsal part of the antorbital fossa (Fig. 1B). The anterior part of the descending process of the lacrimal is also concave, and forms the posterior part of the antorbital fossa. Thus the perforated area of the antorbital fenestra is of roughly triangular outline, and is much smaller than was depicted by Young and Parrish, where it was shown to be large and rectangular, with only its anterior and anteroventral margins bordered by the fossa. Dorsally the lacrimal is flat and is situated at the broadest part of the table-like dorsal surface of the snout.

The dorsal part of the prefrontal is irregular in outline (Fig. 1) and gives rise posteromedially to an acute process that wedges into the frontal. An antero-posteriorly extended shallow groove is present on the posterodorsal surface of the prefrontal. Anteriorly its dorsal suture with the lacrimal curves posteriorly. Laterally the descending process of the prefrontal is much deeper than was described by Young (1973) or illustrated by Parrish (1993). Ventrally it apparently contacts the posterodorsal process of the maxilla, but it does not reach the jugal along the anterior edge of the orbit (Fig. 2A).

The posterior border of the left postfrontal is overlapped by the anterior displacement of the postorbital, which has resulted in a step-like configuration (Fig. 1) that Young (1973) considered to be a real feature. Along the posterodorsal edge of the orbit the postfrontal is roughened. Its contact with the parietal excludes the frontal from the margin of the supratemporal fenestra.
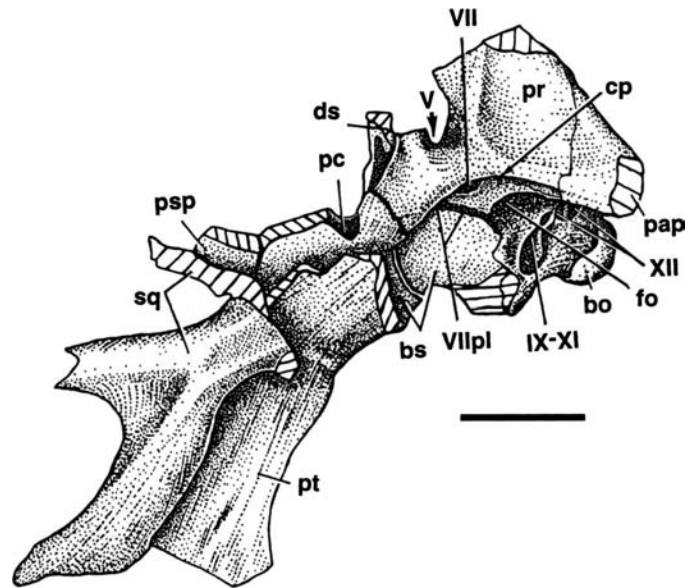

FIGURE 3.   Braincase of *Turfanosuchus dabanensis* in lateral view. **Abbreviations as in figure 1 plus: cp,** crista prootica of prootic; **ds,** dorsum sellae; **fo,** fenestra ovalis; **pap,** paroccipital process; **VIIpl,** a groove probably for palatal ramus of facial nerve; **V, VII, IX–XI, XII,** foramina for cranial nerves V, VII, IX–XI, XII. Scale bar equals 1 cm.

The left postorbital is nearly complete, and its anteromedial and posterolateral processes are of equal length. In dorsal view the supratemporal fossa expands anteriorly on to the postorbital. The suture of the postorbital with the squamosal is clearly evident on the left side. The postorbital forms the anterior half of the supratemporal bar. The descending process of the postorbital is very elongate and may, in life, have reached ventrally as far as the base of the postorbital bar. The posterodorsal half of the descending process is concave posteriorly, which may have been an area of attachment of the jaw adductor muscles in life.

The left squamosal is well preserved except for its small medial process (Figs. 1, 3). The medial process is damaged, but it is clear that this process formed the posterior third of the medial border of the supratemporal fenestra. The descending process of the squamosal is large, forming the dorsal half of the posterior border of the infratemporal fenestra, and its ventral end is broad, and lacks any fragment of the quadratojugal still attaching to it. This contrasts with the condition described by Young (1973) and illustrated by Parrish (1993). The lower half of the posterior border of the infratemporal fenestra is formed by the quadratojugal (see below).

The right quadratojugal provides details of the basic structure of this element, although it has been broken into a dorsal (ascending) and a horizontal (anterior) process (Figs. 2, 4). The identification of the former is based on its shape and position. It is medio-laterally broad and inclines anterodorsally along the posterior border of the infratemporal fenestra, as in *Euparkeria* (Ewer, 1965:pl. 32, fig. 23). Its expanded dorsal margin may have made broad contact with the descending process of the squamosal, while its medial margin contacts the quadrate. The anterior process of the quadratojugal is elongate and extends anteriorly along the ventral side of the posterior process of the jugal, also as in *Euparkeria*. It is clear that the quadratojugal was excluded from the ventral margin of the infratemporal fenestra, although it has an elongate anterior process.
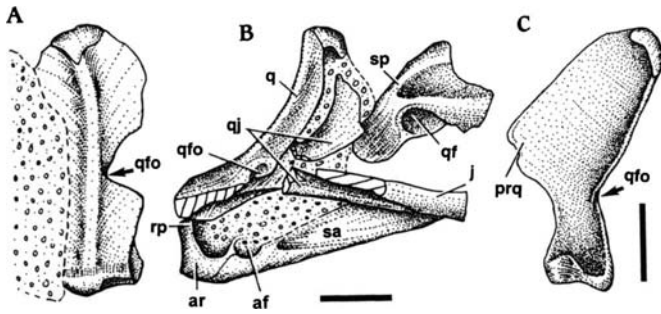
FIGURE 4. Quadrates and related portions of skull of *Turfanosuchus dabanensis*. **A**, right quadrate in posterior view; **B**, right quadrate and posterior portion of skull and mandible on right side in dorsolateral view; **C**, left quadrate in anteromedial view. **Abbreviations as in figures 1 and 2 plus**: **prq**, pterygoid process of quadrate. Scale bars equal 1 cm.

FIGURE 5. Braincase of *Turfanosuchus dabanensis* in ventral view. **Abbreviations as in figures 1, 2, and 3 plus**: **bobt**, basal tuber of basioccipital; **bsbt**, basal tuber of basisphenoid; **bpt**, basipterygoid process; **eo**, exoccipital; **ic**, foramen for internal carotid artery; **opo**, opisthotic; **pl**, palatine; **prp**, palatal ramus of pterygoid; **ptf**, transverse flange of pterygoid; **qrp**, quadrate ramus of pterygoid. Scale bar equals 1 cm.

Quadrate and Palate

The left quadrate is more complete than the right, although it is partially covered by the jugal (Fig. 1B). As in many other archosauriforms, the quadrate has a well-developed pterygoid ramus and a less well-developed anterolateral wing (Fig. 4). The latter meets the descending process of the squamosal dorsally and the dorsal process of the quadratojugal ventrally. A notch is present near the mid-point of the anterolateral wing—this marks the position of the quadrate foramen. The cephalic (dorsal) head is hemispheric and may have fitted into the fossa on the ventral surface of the squamosal (Fig. 4A, B). Between the pterygoid ramus and anterolateral wing, the quadrate forms a curved ridge, which may have served for the anterior attachment of the tympanum.

Most of the palate remained unexposed before our further preparation. No vomer is preserved. The bones that lie below the external naris were considered by Young (1973) to be the vomers, but are actually the palatal shelves of the premaxillae that form the anterior borders of the choanae (Fig. 2A). The remaining part of the palate has been displaced posteriorly, along with the braincase. The left palatine, as identified by Young (1973), is actually the left quadrate, which has been displaced anteriorly. The true left palatine has been partially exposed by our further preparation (Fig. 5). It does not bear any teeth or denticles on the exposed part of its ventral surface. No further comments can be made about this bone at present.

Most of the left pterygoid is now exposed (Fig. 5). Its palatal ramus is very long, and may have excluded the palatine from the interpterygoid vacuity, as it does in *Euparkeria* (Ewer, 1965:fig. 1b). Its suture with the palatine is partially obscured posteriorly. A row of teeth of variable size is present along the ventromedial edge of the pterygoid, and each tooth is clearly separate from its neighbours. The posterior three turn medially towards the anterior edge of a fossa. The transverse flange of the pterygoid has been disarticulated from the ectopterygoid, and its configuration seems to have been distorted. No teeth or denticles are present on the ventral surface of this flange. The quadrate ramus is dorso-ventrally oriented, as it is in most other archosauriforms, but in this specimen its posterior portion is missing.

The left ectopterygoid has been dislocated from its original position, with its articular facet for the maxilla and jugal facing medially.

Braincase

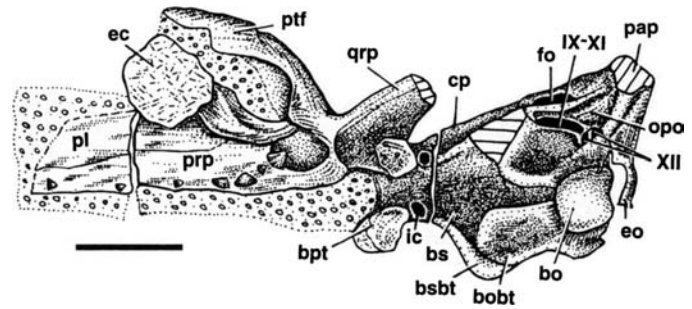The braincase has been displaced towards the left side (Fig. 1). Our further preparation reveals that the laterosphenoid and supraoccipital are not preserved, and most of the right side of the braincase and the large dorsal portion of the exoccipital have been damaged. The description of each braincase element is based mainly on that of the left side.

The basioccipital makes up most of the occipital condyle (Fig. 5). The basal tuber of each side of the bone is relatively large, ventrally and slightly anteriorly oriented, and with a concave ventral surface. Between the basal tubera the basioccipital is deeply excavated on its ventral surface. The basioccipital-basisphenoid suture is clearly evident, but sutures with the exoccipital (and opisthotic) are obscured, possibly, due to fusion.

The bone identified by Young (1973) as the basisphenoid is, in fact, an incomplete cervical rib. The basisphenoid itself was entirely embedded in matrix prior to our further preparation. In ventral view the posterior part of the basisphenoid is broader than its anterior part (Fig. 5). The basal tubera are relatively small when compared with those of *Xilosuchus* from the Middle Triassic of northern China (Wu, 1981; Gower and Sennikov, 1996), but the basipterygoid processes are prominent. The ventral surface of the basisphenoid is highly concave. Anteroventrally a pair of foramina for the entry of the internal carotid arteries are located posteroventral to the basipterygoid processes, as in *Euparkeria* (Gower, 1998:fig. 4), rather than as in *Dorosuchus*, an euparkeriid-like animal (Sennikov, 1989) in which the foramina enter the basisphenoid lateral to the basipterygoid processes. The ventral position of the foramina is a common pattern in early archosauriforms (see Gower and Sennikov, 1996), and is also true of *Chanaresuchus* from the Upper Triassic of Argentina (see Romer, 1971:fig. 3). In lateral view the basisphenoid is deep (Fig. 3). Its posterior part meets the prootic along a groove that is probably for the palatine ramus of the facial nerve (cranial nerve VII). Posterodorsally its suture with the prootic is not recognisable. Posteroventrally the semilunar depression (sensu Gower and Sennikov, 1996) seen in *Euparkeria* and other early archosauriforms is absent. Anterodorsally the basisphenoid is covered by the quadrate ramus of the pterygoid. In dorsal view the pituitary (hypophyseal) fossa is deep. The anterior exits of the internal carotid arteries are located within this fossa. The parasphenoid process is incomplete anteriorly, but appears to be elongate and rod-like (Fig. 3). Posteriorly the basisphenoid forms a vertical, upturned anterior surface, anterior and ventral to the dorsum sellae. This anterior surface is highly concave and continues ventrally as the deep pituitary fossa. There is a foramen at each dorsolateral corner of the anterior surface (Fig. 1A), which probably represents the exit of the external abducens nerve (cranial nerve

VI). The concavity of the anterior surface may have been the site of origin of the retractor bulbi eye muscles.

The left prootic is nearly complete. Its large posterior portion forms the anterior surface of the proximal base of the paroccipital process (Fig. 3). Its suture with the exoccipital (plus opisthotic) is evident. Dorsolaterally a deep notch represents the ventral part of the foramen of the trigeminal nerve (cranial nerve V). Anterior to the trigeminal foramen the prootic pillar appears to be incomplete at its distal end; thus, it is not clear whether the laterosphenoid contributed to the formation of the trigeminal foramen in life. Ventrolaterally the crista prootica is well-developed and gently curved, and the foramen for the facial nerve (cranial nerve VII) is located just ventral to this. Anterior to the facial nerve foramen and ventral to the crista prootica is a small pit from which a groove, probably for the palatal ramus of the facial nerve, leads away posteroventrally along the prootic-basisphenoid suture to the edge of a fossa that contains the fenestra ovalis. It cannot be determined whether or not this pit-like structure penetrates the bone. Anteroventrally the crista prootica extends onto the lateral surface of the basisphenoid.

The large dorsal part of the exoccipitals is missing, and the foramen magnum is thus dorsally incomplete (Fig. 1A). Medially each exoccipital overlaps the dorsolateral corner of the occipital condyle. It cannot be determined whether or not the two exoccipitals met along the midline of the braincase floor, dorsal to the basioccipital, in life. Laterally the distal end of the paroccipital process has been damaged (Fig. 3). Two foramina for the hypoglossal nerve (cranial nerve XII) are clearly evident. Anteroventral to the hypoglossal foramina is the metotic fissure, which is large and houses the exits for cranial nerves IX–XI. A lamina-like septum is present between the fenestra ovalis and metotic fissure. Further anteromedially the opisthotic part of the exoccipital forms the posterior border of the fenestra ovalis. No suture between the opisthotic and exoccipital is recognizable.

Mandible

The right ramus of the mandible is almost complete, although there is a crack across the bones that border the external mandibular fenestra (Fig. 2). The posterior end of the dentary is bifurcated into a dorsal and a ventral process. The latter is incomplete distally owing to the aforementioned crack, but in life may have been of greater length than the dorsal process. This is indicated by the facet for its receipt on the lateral surface of the angular. The second external mandibular fenestra identified by Young (1973) is an artifact of preservation. The bone fragment posterior to the posterior border of the dentary is the anteroventral portion of the surangular. The ventral process of the dentary may have, in life, formed approximately the anterior quarter of the ventral border of the fenestra (Fig. 2B).

The angular is not as large as Young (1973) described (Fig. 2). It is dorsoventrally narrow and strap-like, and forms the posteroventral part of the mandible. Anteriorly it is forked for the receipt of the posteroventral process of the dentary. Posteriorly the angular tapers and may have terminated anterior to the end of the mandible. This cannot be determined, however, as its posterior end is incomplete. Its suture with the surangular is nearly straight, running along a ridge, rather than being convex at its mid-point, as Young (1973) described.

The surangular is a large bone, and larger than Young (1973) described it. It forms most of the posterior part of the mandible (Fig. 2). Dorsolaterally a ridge is present, which runs parallel to the dorsal border of the bone and ends anteriorly above the external mandibular fenestra. The lateral surface of the bone is highly concave, especially in the region between the ridge just described and that along the suture with the angular. The an-

teroventral portion of the surangular forms most of the anteroventral border of the external mandibular fenestra and excludes the angular from the latter. Posteriorly the surangular narrows, exposing the articular on the lateral surface of the mandible.

The articular fossa identified by Young is actually the concave dorsal surface of the retroarticular process. Thus, the latter is large, with a pronounced dorsal eminence at the end of the process (Figs. 2, 4), as is the case in *Euparkeria* (Ewer, 1965: fig. 2a), *Xilosuchus* (Wu, 1981:fig. 5), and *Proterosuchus* (Cruickshank, 1972:fig. 2c). The true articular fossa for the quadrate is located anterior to this (Fig. 4B). The suture of the articular with the surangular is clearly evident on the lateral surface of the mandible.

The splenial is partially disarticulated from the dentary, such that its ventral border is exposed (Fig. 2A). No further comments can be made about this bone. The entire medial face of the mandible is not visible due to its occlusion with the skull.

Dentition

Preserved teeth and tooth sockets (Fig. 2A) suggest that the premaxilla bore five teeth, not six or seven as was described by Young (1973). The premaxillary teeth are compressed, especially the more posterior teeth. Their crowns bear fine serrations on both anterior and posterior edges and their tips recurve posteriorly. The third tooth is the largest and the fifth is the smallest, much smaller than the third.

There were at least thirteen maxillary teeth, as indicated by tooth sockets. Young (1973) believed that the maxilla bore eleven or twelve teeth, because he erroneously referred the first two maxillary teeth to the premaxillary series. The maxillary teeth may have generally resembled the morphology of the more posterior premaxillary teeth, except for size-related differences, but no single complete maxillary tooth is preserved. Interdental plates are present along the medial side of the maxillary alveoli, and most of them appear to be ankylosed to the medial walls of the tooth sockets.

The exact number of dentary teeth is unknown because of the occlusion of the mandible with the skull. The dentary definitely bore at least sixteen teeth (Young [1973] believed there may have been twelve or thirteen) in life, as is evident from the number of preserved tooth sockets. The preserved dentary teeth reveal no significant differences from the premaxillary teeth.

Vertebrae

Fifty-four vertebrae are preserved. Four closely associated vertebrae near the left pelvic girdle are the most complete (Fig. 6). The first of these four vertebrae is inverted in orientation and is a cervical, on the basis of the ventral location of its tubercular facet for its rib. The next two vertebrae most probably represent the last two cervicals because their tubercular facets do not reach the suture with the neural arch. In this case the first three of these four vertebrae are cervicals seven to nine, and the last of the series is the first dorsal, if the neck consisted of nine vertebrae in *Turfanosuchus dabanensis,* as in most archosaurians (sensu Gauthier, 1986). Young (1973) considered only the first two of these four to be cervicals. These four vertebrae are generally similar to one another, although the last two are shorter in length than the first two. The lateral surfaces of the centrum of each of these four vertebrae is concave, with a fossa situated dorsally. The neural spine of each vertebra is not very tall, and has a well-developed spine table at its top, as is also seen in *Euparkeria* (Ewer, 1965:fig. 19). There is no median ridge on the ventral surface of each centrum, but such is present in the more anterior cervicals, as was described by Young (1973).
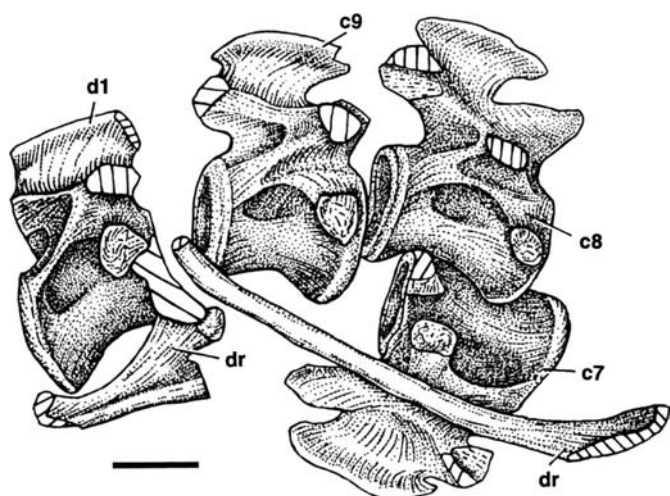
FIGURE 6. Posterior three cervical and the first dorsal vertebrae of *Turfanosuchus dabanensis* in lateral view. **Abbreviations:** **dr**, dorsal rib; **d1, c7–c9**; dorsal vertebra 1, cervical vertebrae 7–9. Scale bar equals 1 cm.

FIGURE 7. Sacral and anterior caudal vertebrae of *Turfanosuchus dabanensis*. **Abbreviations:** **ca1, ca2, ca4**, caudal vertebrae 1, 2, and 4; **s1, s2**, sacral vertebrae 1, 2; **sr**, sacral rib. Scale bar equals 1 cm.

The presence or absence of the intercentrum in the presacral vertebrae is obscured owing to the disarticulation of these vertebrae. The ventral edge of both anterior and posterior sides of each centrum is not bevelled, in contrast to those seen in *Proterosuchus* (*Chasmatosaurus* [Charig, and Sues, 1976:fig.5A, B]), in which the wedge-shaped intercentrum is present in the presacral section of the vertebral column. However, in *Halazhaisuchus* (an euparkeriid-like form from the Lower Ermaying Formation of China [Wu, 1982], which was mistakenly identified by Parrish [1993] as *Turfanosuchus shageduensis* Wu, 1982) and *Euparkeria* the ventral edge of both sides of the presacral centra is not clearly bevelled, but the intercentra are present in the presacral vertebrae. The intercentra of these two taxa are, in contrast to those of *Proterosuchus,* small, oval in ventral view, and dorsoventrally very thin (see Ewer, 1965:406; Wu, 1982:fig. 1). On the basis of this comparative data, there is no assurance of the absence of intercentra in the presacral vertebrae of *Turfanosuchus dabanensis.*

There are two, rather than three (as Young described in 1973), sacral vertebrae. The vertebra attached to the acetabulum of the left ilium is not a sacral (although Young considered it to be the third sacral) but instead a posterior dorsal, showing no distinct features of a sacral. The first sacral is missing its neural spine (Fig. 7). Its sacral rib or transverse process is very strong and massive, with a nearly round distal surface for articulation with the ilium. The second sacral is exposed on its right ventrolateral surface (Fig. 7). Its transverse process is flat, with a very broad and fan-shaped distal end for articulation with the ilium. The lateral surface of the two sacrals is concave. The first appears to have a shallow depression ventral to the transverse process. Following the second sacral are what are interpreted as the transverse processes of the first two caudal vertebrae. The first of these is distally broad. Between this transverse process and the centrum of the second sacral is a bony fragment, which may be a piece of a rib. The vertebra posterior to the transverse process of the second caudal is probably the fourth caudal, with the spine missing. It is much shorter than the sacrals and its lateral surface is concave. Its transverse process is situated along the dorsal edge of the centrum.

Forelimbs

In contrast to Young's description, the humerus is more similar to that of non-crocodylomorph and non-ornithodiran archo-
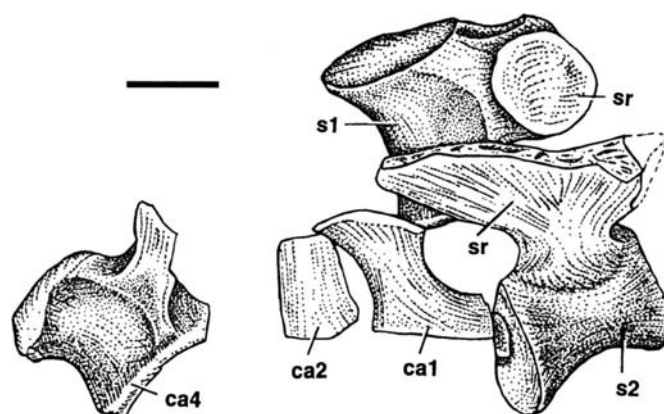
sauriforms such as *Ticinosuchus* (Krebs, 1965:figs. 37, 38) and *Euparkeria* (Ewer, 1965:fig. 10a–c) than it is to that of *Hesperosuchus* (Colbert, 1952), on the basis of the morphology of the deltopectoral crest (Fig. 8). The humerus of the latter is crocodylian-like, with a well-developed deltopectoral crest, which is more or less independent of the proximal head of the bone, and is set off at almost a right angle from the long axis of the head (see Colbert, 1952:fig. 22). The deltopectoral crest of the humerus of *Turfanosuchus dabanensis* is closely associated with the proximal head, and is more appropriately regarded as a continuation of the latter. Additionally the deltopectoral crest makes only a small angle with the long axis of the proximal head, so that the latter appears to be very broad and has a large, basin-like fossa on its anteromedial surface. These features also occur in two late Early to early Middle Triassic euparkeriids from northern China, *Turfanosuchus shageduensis* (Wu, 1982:fig. 5) and *Halazhaisuchus* (Wu, 1982:fig. 3).

Pelvic Girdle

In further preparing the specimen we cleaned the left pelvic girdle of its surrounding matrix (Fig. 9). As illustrated in Young
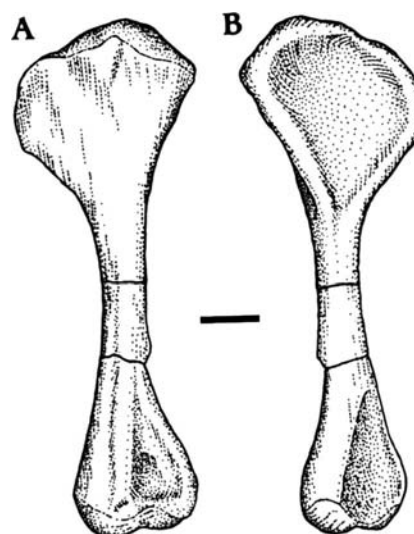

FIGURE 8. Left humerus of *Turfanosuchus dabanensis* in posterolateral (**A**) and anteromedial (**B**) views. Scale bar equals 1 cm.
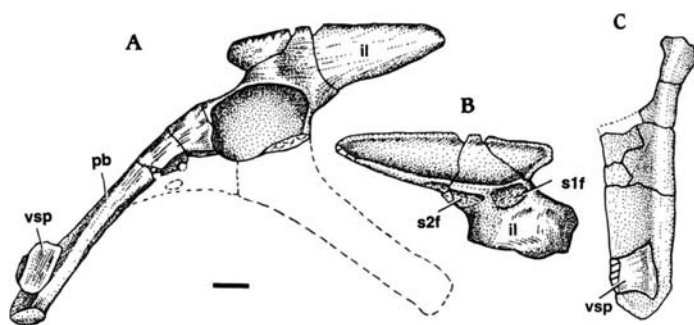
FIGURE 9.   Left pelvic girdle of *Turfanosuchus dabanensis*. **A**, articulated ilium and pubis in lateral view; **B**, ilium in medial view; **C**, pubis in anterior view. **Abbreviations: il**, ilium; **pb**, pubis; **s1f**, **s2f**, facets for sacral ribs 1, 2; **vsp**, spine of a vertebra. Scale bar equals 1 cm.

FIGURE 10.   Left femur of *Turfanosuchus dabanensis* in anterolateral (**A**), posterior (**B**), posteromedial (**C**), and anterior (**D**) views. **Abbreviation: 4th**, fourth trochanter. Scale bar equals 1 cm.

(1973:fig. 2), this pelvic girdle is inverted and anteroposteriorly reversed. The ilium resembles that of *Ticinosuchus* (Krebs 1965:fig. 49d) in features of the iliac blade. The anterior process of the iliac blade is more definitive in outline, and the posterior process is more massive when compared to the same features of *Euparkeria*. It is similar to that of *Euparkeria* (Ewer, 1965: fig. 11) in features of the acetabulum, with a larger anteroventral portion towards the pubis and a smaller portion towards the ischium. The suture of the ilium with the pubis is visible, and extends ventrally into the acetabulum. This indicates that the acetabulum expands on to the pubis, as it does in other archosauriforms. The supraacetabular crest is well-developed, and projects laterally. The ventral border of the acetabulum is convex, suggesting that the acetabulum is not penetrated by a fenestra. Medially the dorsal blade is highly concave, such that the ventral margin of the blade forms a prominent ridge. Two articular facets for the sacral ribs are clear ventral to the ridge, this being further indicative that no third sacral vertebra was present in *Turfanosuchus dabanensis*. Ventral to the sacral facets, the medial surface of the ilium is highly convex.

The proximoventral portion of the pubis is damaged. In the preserved portion only one pubic foramen can be recognized (Young described the presence of two pubic foramina). As a whole, the pubis is also similar to that of *Ticinosuchus* (Krebs, 1965:figs. 46, 49d) or that of *Ornithosuchus* (Walker, 1964:fig. 11b, h). It has a relatively short proximal portion in anterior view, and a triangular distal end (Fig. 9C). The pubis is less than three times the width of the acetabulum as it is in non-ornithodirans (Juul, 1994). In the left pelvic girdle no proximal base of the ischium remains in articulation with the ilium.

Hindlimbs

Like the humerus, the femur resembles that of *Ticinosuchus* (Krebs, 1965:figs. 50, 51) or *Euparkeria* (Ewer, 1965:pl. 34; fig. 31). Young (1973) considered the femur to be very similar to that of *Hesperosuchus,* but we feel that such similarities are only superficial. The femur of *Hesperosuchus* is crocodylian-like, its proximal head having a distinct anteromedial process or turn (Colbert, 1952:fig. 27). In contrast, this anteromedial process is not clear-cut in the femur of *Turfanosuchus dabanensis* (Fig. 10), *Ticinosuchus, Euparkeria* and other non-crocodylomorph and non-ornithodiran archosauriforms. The broad proximal head of the femur, as a whole, turns anteromedially in these taxa. Additionally the fourth trochanter is relatively more distal in location when compared with that of *Hesperosuchus.* These features are also evident in *T. shageduensis* (Wu, 1982:fig. 6).

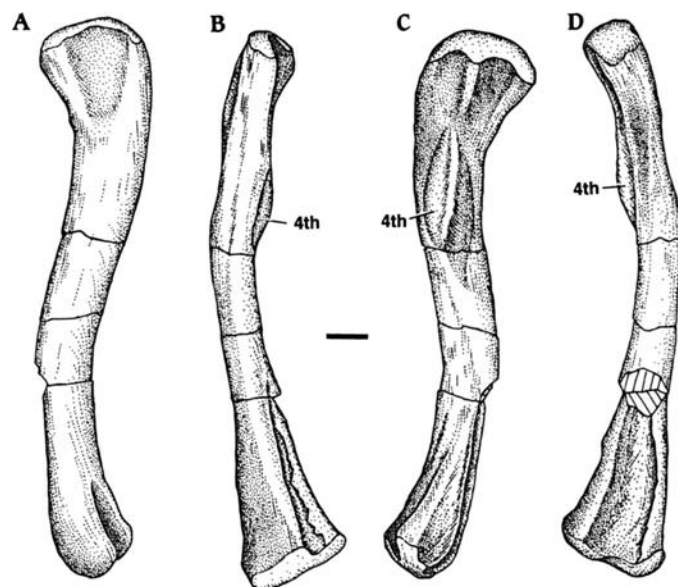The left calcaneum and astragalus have been cleaned of ma-

trix. The calcaneum is nearly complete (Fig. 11). It superficially resembles that of *Saurosuchus* (Sill, 1974:pl. 3; figs. A, C and pl.4; fig. A), in having a proximally or dorsally directed calcaneal tuber. The calcaneal condyle is well-developed and wheel-like, showing that facets for distal tarsal 4 and the fibula are continuous with one another as they are in crurotarsans. Anteromedially there is only a broad, curved facet for the astragalus. This facet continues the hemicylindrical condyle anterolaterally and expands posteromedially as a wing-like structure lying in the same plane as the calcaneal tuber (Fig. 11A). The geometry of this facet may have limited the mobility between the two proximal tarsals. Morphologically this facet differs from the condition seen in the calcaneum of those taxa with a crocodile-normal tarsus, such as *Rutiodon, Prestosuchus,* and living crocodylians. In the latter this facet for the astragalus is nearly anteroposteriorly vertical in orientation, or almost perpendicular to the long axis of the calcaneal tuber (see Sereno, 1991:figs. 6, 8; Parrish, 1993:fig. 3). The large calcaneal tuber is different from that of other archosauriforms. Its mediolateral dimension is slightly greater than its dorsoventral (proximodistal) dimension. Anteroposteriorly (dorsoventrally sensu Gower, 1996) the calcaneal tuber is thin or narrow (see Fig. 11C); in other words, the tuber is much taller than broad, in terms of the definition of character 9 of Sereno (1991), as it is in non-archosaurians such as *Euparkeria* (Sereno, 1991; Gower, 1996) and *Chanaresuchus* (Cruickshank, 1979; Gower, 1996). The lateral side of the calcaneal body is concave. The lateral side of the calcaneal tuber is convex but its medial side is concave. This is similar to the situation seen in *Saurosuchus, Rutiodon* (Sereno, 1991:fig. 6), *Riojasuchus* (Sereno, 1991:fig. 7G), and *Prestosuchus* (Parrish, 1993:fig. 3B). There is no median groove or depression spanning the anteroposterior depth (or length) of the dorsal surface of the calcaneal tuber. The end of the calcaneal tuber does not flare or form a pronounced rim around it, which is commonly seen in suchians such as *Saurosuchus* and *Ticinosuchus* (Krebs, 1965:fig. 57). In posterior view (Fig. 11B) a small depression is present near the end. There may have been an additional depression present on the posterior surface of the calcaneal tuber, but this region has been disrupted by a crack.
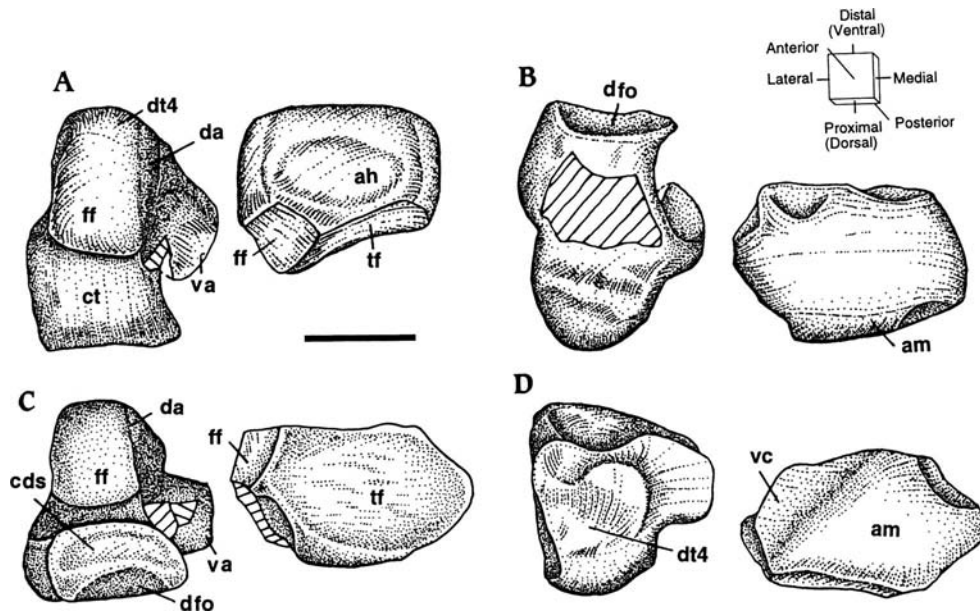
FIGURE 11. Left calcaneum and astragalus of *Turfanosuchus dabanensis* in anterior (**A**), posterior (**B**), dorsal or proximal (**C**), and ventral or distal (**D**) views. Icon indicates orientation of proximal tarsals in illustration A. **Abbreviations: ah**, anterior hollow; **am**, facet for metatarsals 1, 2; **cds**, dorsal surface of calcaneal tuber; **ct**, calcaneal tuber; **da**, anterior portion of facet for astragalus; **dfo**, fossa near end of calcaneal tuber on posterior surface; **dt4**, facet for distal tarsal 4; **ff**, facet for fibula; **tf**, facet for tibia; **va**, posterior portion of facet for astragalus; **vc**, facet for calcaneum. Scale bar equals 1 cm.

The astragalus is damaged on its ventrolateral side (Fig. 11C). In anterior view (Fig. 11A) the anterior hollow seen in living taxa is represented by a shallow depression. The facet for the fibula is small and square in outline, and is separated by a sharp ridge from the tibial facet on the dorsomedial surface. The latter is large and slightly concave (Fig. 11A, C). The posterior surface of the astragalus is convex, with small depressions near its proximal margin (Fig. 11B). There are two facets on the ventral surface (Fig. 11D). The large ventral one is slightly convex, being for the articulation of metatarsals I and II, while the small lateral one, with its lateral margin damaged, is dorsal in position, and is for the articulation of the concave facet of the calcaneum. As a whole, articular facets or surfaces of the astragalus are simple structures, in contrast with those of many members of the Crocodylotarsi.

Osteoderms

Young (1973) considered the lack of osteoderms to be a diagnostic feature. During our further preparation of the specimen
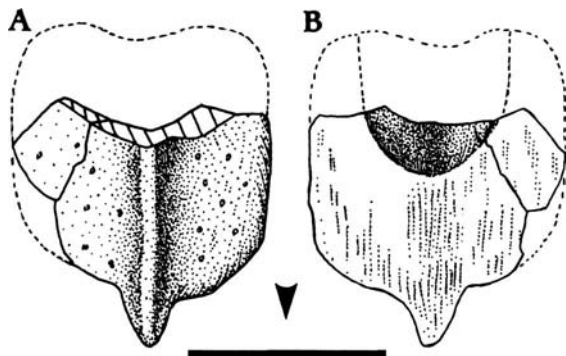
we found an osteoderm located near the left pelvic girdle, but its posterior part is missing (Fig. 12). This osteoderm may resemble (as reconstructed in Fig. 12) that of *Ticinosuchus* (Krebs, 1965:fig. 61), *Saurosuchus* (Sill, 1974:fig. 10), or *Halazhaisuchus* (Wu, 1982:fig. 1E, F) although it appears relatively broad and short. In dorsal view it bears a ridge running along the median line. Its anterior border is nearly round, with an anterior process which is the anterior continuation of the median ridge. On each side of the median ridge are small, irregularly-scattered pits. The osteoderm thins towards its margins. In ventral view the surface is smooth and slightly concave, and the anterior part of a median groove or depression is clearly marked in the posterior end of the preserved part. This groove probably received the anterior process of the osteoderm lying immediately posterior to it.

DISCUSSION

Young (1973) believed that among early archosauriforms (his pseudosuchians [or thecodonts in the more common parlance of that time]) *Turfanosuchus dabanensis* was morphologically most similar to *Euparkeria*, and classified both within the family Euparkeriidae. Employing the methods of traditional evolutionary systematics, Young also proposed relationships among major groups of archosauriforms (1973). In his hypothesis of archosauriform relationships Young proposed that *T. dabanensis*, after its split from *Euparkeria*, represented an evolutionary stage from which two lineages of dinosaurs, the Saurischia and Ornithischia, separately diverged.

In recent phylogenetic studies the proposed patterns of interrelationships within the Archosauriformes (=the Archosauria of Benton and Clark, 1988) differ greatly from those of Young's time (see Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Parrish, 1992, 1993; Juul, 1994). However, the phylogenetic position of *Turfanosuchus dabanensis* has been dealt with only by Parrish (1993). He considered *T. dabanensis* to be an archosaurian and one of the basal members of the Suchia,

FIGURE 12. An osteoderm of *Turfanosuchus dabanensis* in dorsal (**A**) and ventral (**B**) views. Arrow directed anteriorly. Scale bar equals 1 cm.

phylogenetically much more closely aligned to the lineage leading towards the Crocodylomorpha.

In Parrish's (1993) study, however, the suchian status of *Turfanosuchus dabanensis* was established on the basis of a data matrix in which only about 57% (24) of the total (42) characters were known for that taxon. Our restudy reveals that among the characters employed in Parrish's data matrix, 88% (37) can now be scored directly for *T. dabanensis*. Ideally, it should be reasonable for us to use Parrish's data matrix, together with our new information, for testing his hypothesis concerning the relationships of *T. dabanensis*. This is, however, not possible because Parrish's character state matrix (his table 2) for the phylogenetic analysis of the Crocodylotarsi is unfortunately replete with problems, not only those probably caused by an accident of transposition, but also those due to errors and inadequacy of the definition of certain character states (also see Gower, 1996; Gower and Wilkinson, 1996). For example, Parrish's character 7, describing the position of the exit of the internal carotid artery in his table 1 (character definition), does not match the state distribution of "character 7" in his table 2 (Character state matrix) in terms of his discussion of this character in the text. Characters 11 and 22 show two apomorphic states (1 and 2) in his table 2, but only one apomorphic state is described for these characters in his table 1. In addition, Parrish's data matrix also does not yield the tree, nor the tree statistics, that he reports. Because of these problems we are confined to a consideration of the characters that were previously unknown or incorrectly explained for this taxon, and that have been hypothesised in more recent studies to be significant in establishing the phylogenetic relationships among *Euparkeria,* the Proterochampsidae, and basal archosaurians.

1. Calcaneal Facets for Fibula and Distal Tarsal 4 Continuous—an apomorphic character state hypothesized in recent studies (Sereno, 1991; Parrish, 1993; Juul, 1994) to be confined within the Archosauriformes. It is present in *Turfanosuchus dabanensis*. The calcaneal facets for the fibula and distal tarsal 4 are separate in *Euparkeria* as described by Sereno (1991), but were considered by Parrish (1993) to be continuous. Gower (1996) supports Sereno's (1991) plesiomorphy of this character for *Euparkeria*. Therefore, the continuity of calcaneal facets for the fibula and distal tarsal 4 can be used to define the group including those archosauriforms with a phylogenetic position above *Euparkeria*.

2. Vertebral Intercentrum Absent between Postaxial Vertebrae—a derived character state commonly believed to be one of the synapomorphies of a group including all archosauriforms phylogenetically higher than *Euparkeria*. Unfortunately, the presence or absence of the postaxial intercentra cannot be determined for *Turfanosuchus dabanensis* owing to poor preservation. This character state would play a similar role in the above character state if *T. dabanensis* lacks intercentra in the postaxial vertebrae.

3. Calcaneal Tuber Projects More than 45 Degrees Posteriorly—a derived character state for the Archosauria (sensu Gauthier, 1986). Parrish (1993) further divided this character into two derived states versus the plesiomorphic state, without any posterior division (but see Gower's comments [1996]). Sereno (1991) and Gower (1996) argued that the calcaneal tuber is mainly laterally directed in *Euparkeria* and the Proterochampsidae, and that this represents the plesiomorphic state of this character. In *Turfanosuchus dabanensis* the tuber is nearly perpendicular to the long axis of the articulation between the tibia/fibula and astragalus/calcaneum, and thus shows the apomorphic state. This character state has been suggested by Sereno (1991), Parrish (1993), and Juul (1994) to be one of the synapomorphies of the Archosauria, which also suggests that *T. dabanensis* is possibly phylogenetically closer to the Archosauria than is *Euparkeria* or the Proterochampsidae.

4. Palatal Teeth Absent—an apomorphic character state within the Archosauriformes that has been commonly hypothesised in recent studies to be one of the synapomorphies of the Archosauria. Palatal teeth are present in *Turfanosuchus dabanensis,* as they are in *Euparkeria* and the Proterochampsidae.

5. Foramina for Internal Carotid Arteries Enter the Body of the Basisphenoid Lateral to the Basipterygoid Processes—an apomorphic character state within the Archosauriformes that was hypothesised by Parrish (1993) to be one of the synapomorphies of the group including the Proterochampsidae and Archosauria (including *Turfanosuchus dabanensis*). However, The plesiomorphic condition of this character is present in *T. dabanensis* and also in some specimens of the Proterochampsidae (Parrish, 1993). In this case the apomorphic state of this character only occurs in the Archosauria exclusive of *T. dabanensis*. The plesiomorphic condition of this character and character 4 (above) strongly suggest that *T. dabanensis* is not phylogenetically referable to the Archosauria.

6. A Rotary, Crurotarsal Proximal Ankle Joint (the Major Morphological Feature Characteristic of This Structure is an Extended, Wheel-like Process on the Calcaneum that Rotates on the Fibula)—an apomorphic character state commonly hypothesised in recent studies to be one of the synapomorphies of the Crurotarsi (Sereno and Arcucci, 1990). *Turfanosuchus dabanensis* possesses this apomorphic state.

7. Calcaneal Tuber Shaft Broader (Anteroposterior Length) than Tall (Dorsoventral Length) = the Dorsoventral Length Greater than the Proximodistal Length (Gower, 1996)—an apomorphic character state recognised by Sereno (1991) and Juul (1994) as one of the synapomorphies of the Crurotarsi. The polarity of the character states was altered by Parrish (1993), without providing a reason. The plesiomorphic state of this character is present in *Turfanosuchus dabanensis* as it is in early archosauriforms. In *T. dabanensis* the end of the calcaneal tuber has an anteroposterior length much smaller than the dorsoventral (proximodistal) length (see Fig. 11A, C). The plesiomorphic state of this character is also considered by Sereno (1991) and Gower (1996) to be present in *Euparkeria* and the Proterochampsidae.

8. Calcaneal Tuber Flared Distally—an apomorphic state hypothesised in recent studies (Sereno, 1991; Juul, 1994) to be one of the synapomorphies of the Crurotarsi. The end of the calcaneum is not flared in *Turfanosuchus dabanensis* (see Fig. 11), showing a plesiomorphic character state equivalent to that seen in all non-archosaurians plus ornithodirans.

9. Tibial Facet on Astragalus Flexed—an apomorphic character state determined by Sereno (1991) and Juul (1994) to be one of the synapomorphies of the Crurotarsi (but Parrish [1993] considers the apomorphic state of this character to be present in two less inclusive groups: the Suchia and Dinosauria). As in many early archosauriforms, *Turfanosuchus dabanensis* has the plesiomorphic state of this character: the facet is simply concave. Characters 7–9 mentioned here apparently call into question the conclusion that *T. dabanensis* is a crurotarsan. The presence of a rotary, crurotarsal ankle joint (character 6) in *T. dabanensis* and the Crurotarsi suggests a possible convergence within the Archosauriformes.

10. Crocodile-normal Tarsus, with a Ball on Astragalus and a Socket on Calcaneum—an apomorphic character state hypothesised by Parrish (1993) to be one of the synapomorphies of the Crocodylotarsi. *Turfanosuchus dabanensis* possesses a crocodile-normal tarsus. This may again be due to convergence within the Archosauriformes.

11. Heterodonty, with Caniniform Anterior Teeth and Mediolaterally Compressed and Recurved Posterior Teeth—an apomorphic character state considered by Parrish (1993) to be one of the synapomorphies of the Crocodylotarsi. It is apparent that *Turfanosuchus dabanensis* possesses the plesiomorphic

state of this character: lacking the anterior caniniform teeth (see Fig. 2).

12. Calcaneum with Distinct Socket Ventral to Anterior Part of Bone Medial and Ventral to Fibular Facet—an apomorphic character state considered by Parrish (1993) to be one of the four synapomorphies of the Suchia (including *Turfanosuchus dabanensis*). Our examination reveals that in *T. dabanensis* the calcaneum does not bear a socket on the facet for the astragalus, and thus exhibits the plesiomorphic state of this character (see Fig. 11A, C).

13. Calcaneal Tuber with a Dorsoventrally (Anteroposteriorly) Aligned Median Depression on its Distal End—an apomorphic state used by Parrish (1993) to define the Suchia. In *Turfanosuchus dabanensis* there is a shallow depression on the end of the calcaneal tuber, which is lateromedially elongate rather than anteroposteriorly aligned (see "cds," Fig. 11C). In addition, there is a depression on the ventral posterior surface of the calcaneal tuber near the distal end ("dfo", Fig. 11B, C). We consider the condition of this character to be plesiomorphic for *T. dabanensis*.

14. Anterior Parts of the Lateral Sides of the Dorsal Centra Constricted—an apomorphic character state hypothesised by Parrish (1993) to be one of the synapomorphies of the Suchia. It is true that this apomorphic character state is present in *Turfanosuchus dabanensis*, but this state is also present in *Euparkeria* according to figure 20 of plate 31 of Ewer (1965). The presence of this character state in *Euparkeria* certainly influences the branching pattern of the Archosauriformes as proposed by Parrish (1993).

15. Quadratojugal Making up over 50 Percent of Ventral Margin of Infratemporal Fenestra—an apomorphic character state recognised by Parrish (1993) as one of the synapomorphies of the Suchia. This character is very vague and it is hard to determine the states based on the original definition of the character (quadratojugal makes less than [0] or 50% or more [1] of the ventral margin of the lateral temporal fenestra) because the anterior process of the quadratojugal extends along the ventral side of the posterior process of the jugal in many included taxa, but along its dorsal side in a few included taxa (see Parrish, 1993:figs. 4, 6, 9). The derived state was apparently scored by Parrish for *Turfanosuchus dabanensis* as well as for *Lotosaurus* and *Prestosuchus*. It is true that the anterior process of the quadratojugal in these taxa is elongate, longer than the 50% of the ventral margin of the lateral temporal fenestra, but the part that enters the ventral border of the fenestra is very short. If one uses the proportion of the total length of the anterior process of the quadratojugal to the ventral length of the infratemporal fenestra as a criterion, then the derived state of the character should be scored for *Chanaresuchus* (see Romer, 1971:fig. 2), *Rutiodon* and *Prestosuchus* as well. Additionally in some of the taxa included by Parrish (1993), such as *T. dabanensis*, *Proterosuchus* (Cruickshank, 1972:fig. 2b), *Erythrosuchus* (Parrish, 1992:fig. 6), *Desmatosuchus* (Parrish, 1993:fig. 6B), and *Postosuchus* (Parrish, 1993:fig. 9B), the posterior process of the jugal extends posteriorly to the end of the infratemporal fenestra and separates the quadratojugal from the ventral border of the fenestra (see Figs. 2, 4). Therefore, this character must be redefined before it can be treated as being informative.

Among the four synapomorphies employed by Parrish (1993) to define the Suchia, two (characters 12 and 13) definitely are present in the plesiomorphic state for *Turfanosuchus dabanensis*, and one (character 15) is uninformative. The other (character 14) has a broader distribution within the Archosauriformes. Therefore, the suchian status of *T. dabanensis*, as proposed by Parrish (1993), is questionable, and this is made more so when taking characters 4, 5, 7–9, and 11 into consideration.

16. Quadratojugal Forms Entire Posterior Border of Infratem-

poral Fenestra—an apomorphic state considered by Parrish (1993) to be one of three synapomorphies of the group including *Turfanosuchus dabanensis*, *Lewisuchus*, and his Rauisuchiformes (see Fig. 12). In contrast, our study shows that *T. dabanensis* possesses the plesiomorphic state of this character: the quadratojugal forms only part of the posterior border of the infratemporal fenestra (see Figs. 2B and 4B).

17. Calcaneal Tuber Flares Such that Both its Medial and Lateral Sides are Concave—an apomorphic character state shared by *Turfanosuchus dabanensis* and the Rauisuchiformes according to Parrish (1993). This is not true for *T. dabanensis*, however. As discussed above, the end of the calcaneal tuber is anteroposteriorly narrow and is not flared at all, and the shaft of the tuber is laterally convex and medially concave in this taxon (see Fig. 11).

In summary, most of the characters that have been used to establish phylogenetic relationships among the archosauriforms (early archosauriforms and basal archosaurians in particular) are now known for *Turfanosuchus dabanensis*. Our study reveals that most of the previously undetermined characters of *T. dabanensis* show the plesiomorphic character state, which casts doubt upon the phylogenetic position of this taxon as proposed by Parrish (1993). Additionally, Parrish (1993), mistakenly assigned the apomorphic state to a number of the characters of *T. dabanensis*, which makes his phylogenetic conclusions yet more questionable. Although we have not conducted a new phylogenetic analysis, the new information resulting from our restudy strongly indicates that *T. dabanensis* is not a suchian and is not even a member of the Crurotarsi. Whether it is an archosaurian requires a detailed phylogenetic study of relevant taxa, but the apomorphic state of some characters regarding the ankle elements rules out its close relationship with *Euparkeria*.

ACKNOWLEDGMENTS

LITERATURE CITED

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylomorpha; pp. 295–338 *in* M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Vol. 1. Amphibians, Reptiles, Birds. Systematic Association Special Volume 35A. Clarendon Press, Oxford.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. W. H. Freeman Company, 689 pp.

Charig, A. J., and H.-D. Sues. 1976. Suborder Proterosuchia Broom

1906; pp. 11–39 *in* O. Kuhn (ed.) Encyclopedia of Paleoherpetology Part 13 (Thecodontia). Gustav Fischer Verlag, Stuttgart, New York.

Chatterjee, S. 1985. *Postosuchus,* a new thecodontian reptile from the Upper Triassic of Texas and the origin of tyrannosaurs. Philosophical Transactions of the Royal Society of London, Series B 309: 395–460.

Cruickshank, A. R. I. 1972. The proterosuchian thecodonts; pp. 89–119 *in* K. A. Joysey and T. S. Kemp (eds.), Studies In Vertebrate Evolution. Oliver and Boyd, Edinburgh.

————— 1979. The ankle joint in some early archosaurs. South African Journal of Science 75:168–178.

Colbert, E. H. 1952. A pseudosuchian reptile from Arizona. Bulletin of the American Museum of Natural History 99:561–592.

Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Philosophical Transactions of the Royal Society of London, B 248:379–435.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. Memoirs of the California Academy of Science 8:1–55.

—————, A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Gower, D. J. 1996. The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. Zoological Journal of the Linnean Society 116:347–375.

————— 1998. The braincase of *Euparkeria,* and the evolutionary relationships of birds and crocodilians. Biological Reviews 73:367–411.

—————, and A. G. Sennikov. 1996. Morphology and phylogenetic informativeness of early archosaur braincases. Palaeontology 39:883–906.

—————, and M. Wilkinson. 1996. Is there any consensus on basal archosaur phylogeny? Proceeding of Royal Society of London, B 263:1399–1406.

Juul, L. 1994. The phylogeny of basal archosaurs. Palaeontologia Africana 31:1–38.

Krebs, B. 1965. Die Triasfauna der tessiner Kalkalpen. XIX. *Ticinosuchus ferox,* nov. gen. nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. Schweizerische Paläeontologische Abhandlungen 81:1–140.

Parrish, M. J. 1992. Phylogeny of the Erythrosuchidae (Reptilia: Archosauriformes). Journal of Vertebrate Paleontology 12:93–102.

————— 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crutotarsan monophyly. Journal of Vertebrate Paleontology 13:287–308.

Romer, A. S. 1968. The Osteology of the Reptiles. 2nd ed. University of Chicago Press, Chicago, London, 772 pp.

————— 1971. The Chañares (Argentina) Triassic reptile fauna XI. Two new long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus.* Breviora 379:1–21.

————— 1972a. The Chañares (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipanicicorum,* gen. et sp. nov. Breviora 389:1–24.

————— 1972b. The Chañares (Argentina) Triassic reptile fauna. XVI. Thecodont classification. Breviora 395:1–24.

Sennikov, A. G. 1989. Novyy euparkeriid (Thecodontia) iz srednego triasa Yuzhnogo Priural'ya. Paleontologicheskii Zhurnal 1989:71–78. [Russian]

Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Society of Vertebrate Paleontology Memoir 2:1–53.

—————, and A. B. Arcucci. 1990. The monophyly of crutotarsal archosaurs and the origin of bird and crocodile ankle joints. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 180:21–52.

Sill, W. D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecondonts. Bulletin of the Museum of Comparative Zoology. Harvard University 146:317–362.

Walker, A. D. 1964. Triassic reptiles from the Elgin Area:*Ornithosuchus* and the origin of carnosaurs. Philosophical Transactions of the Royal Society of London, B 248:53–134.

Wu, X.-C. 1981. [The discovery of a new thecodont from northeast Shanxi.] Vertebrata PalAsiatica 19:122–132. [Chinese with English summary].

————— 1982. [Two pseudosuchian reptiles from Sha-Gan-Ning-Basin.] Vertebrata PalAsiatica 20:289–301. [Chinese with English summary]

Young, C. C. 1973. [On a new pseudosuchian from Turfan, Sinking (Xinjiang).] Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology of the Academia Sinica, Series B 10:15–37. [Chinese]