



A late Permian archosauriform from Xinjiang shows evidence of parasagittal posture

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Received: 8 September 2021 / Revised: 1 October 2022 / Accepted: 24 October 2022 / Published online: 5 December 2022
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Abstract

Archosaurs diversified and became dominant during the Mesozoic Era, but their earliest relatives (non-archosaurian archosauromorphs) were already scarcely present in the late Permian. Here we describe a new species of non-archosaurian archosauriform from the upper Permian of Xinjiang, China. Preserved as a partial hindlimb, it possesses a few derived features shared with other archosauriforms, including a much stouter tibia than fibula, a longer metatarsal III than metatarsal IV, and a hooked metatarsal V. Phylogenetic analysis confirmed the new taxon to be a non-archosaurian archosauriform. The morphology of the knee, crus, and pes shows traits that are commonly related with a parasagittal posture, including an entirely proximo-distal articulation of the femur and fibula, the slender and closely spaced tibia and fibula, and a mesaxonic foot with a reduced fifth toe. The new taxon shows that the parasagittal posture evolved before the end-Permian Mass Extinction.

Keywords Archosauriformes · Late Permian · Semi-erect posture · Hindlimb

Introduction

The rise of the archosaurs (represented by birds and crocodiles today) is a major event in vertebrate evolution (Brusatte et al. 2008). Although major clades of archosaurs started to flourish and diversify in the Triassic, their earliest stem members (archosauromorphs) were already known before the end-Permian mass extinction (EPME) (Nesbitt 2011; Ezcurra et al. 2014; Bernardi et al. 2015; Ezcurra 2016; Pinheiro et al. 2016). The Permian archosauromorph fossil record is scarce. So far, only four definite taxa have been reported: *Protorosaurus speneri* from England and Germany, *Aenigmastropheus parringtoni* from Tanzania, and

Archosaurus rossicus and *Eorasaurus olsoni* from Russia (Ezcurra et al. 2014; Bernardi et al. 2015). *Prolacerta broomi* and *Proterosuchus* from South Africa could also be late Permian (Lopingian) in age following the work of Gastaldo et al. (2020) (but see Viglietti et al. 2021), so were some unnamed archosauromorph remains from the Buena Vista Formation of Uruguay (Ezcurra et al. 2015; Ernesto et al. 2020).

The late Permian archosauromorph record provides key information on the early morphological evolution of the clade, by filling in the gap between the more plesiomorphic body plan as seen in other diapsids and the highly specialized and diverse body forms of crown-group archosaurs. One of these gaps is how archosaurs transformed from sprawling to parasagittal posture. Bernardi et al. (2015) reported archosauriform trackways from the upper Permian of southern Alps. These trackways were characterized by a mesaxonic foot (toes digits III longer than IV), posterolaterally directed and reduced digit V, and a narrow trackway, all of which suggested a parasagittal posture. The late Permian skeletal record, however, with only *Protorosaurus speneri* preserving the hindlimb and clearly a sprawler, is not in accordance with the footprint record currently. Here we report a new late Permian archosauriform that provides key information on the hindlimb morphology and may fill this mismatch.

Communicated by: Robert R Reisz

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Geology of the fossil locality

The specimen was discovered from the Guodikeng Formation of the South Taodonggou locality, Turpan, Xinjiang (Fig. 1). South Taodonggou locality is a well-studied locality for Permo-Triassic terrestrial deposits, which are rich with vertebrate and plant fossils (Wan et al. 2020; Yang et al. 2021). The Guodikeng Formation is the upper-most part of the Wutonggou low-order cycle and is Changhsingian and Induan in age (Yang et al. 2021), containing the Permo-Triassic boundary (PTB) and bearing fossils such as dicynodonts *Turfanodon bogdaensis* and *Lystrosaurus* (Cheng et al. 1996; Lucas 2001; Angielczyk and Sullivan 2008; Kammerer et al. 2011; Liu and Abdala 2017). The new specimen was discovered ~26 m below the purported PTB of Yang et al. (2021) (Fig. 1 and Fig. 7C of Yang et al. 2021), and was Changhsingian in age. The Bayesian age model estimates the age to be around 252.2 Ma for the new specimen (Fig. 3 of Yang et al. 2021).

Institutional abbreviation

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

Method

The specimen was prepared under microscope, and CT-scanned at the high-resolution CT lab of IVPP at the resolution of 36.2 μm . The 3-D segmentation was reconstructed in the software VGstudio Max 3.5 using the region growing method and manual drawing in 2-D slices. The CT data is stored at IVPP and is available upon request to the authors.

Systematic paleontology

Diapsida Osborn 1903.

Archosauromorpha von Huene 1946 (sensu Gauthier et al. 1988).

Archosauriformes Gauthier 1986.

Vigilosaurus gaochangensis gen. et sp. nov.

Holotype

IVPP V22764, a partially left hindlimb, missing the proximal part of the femur and some toe digits.

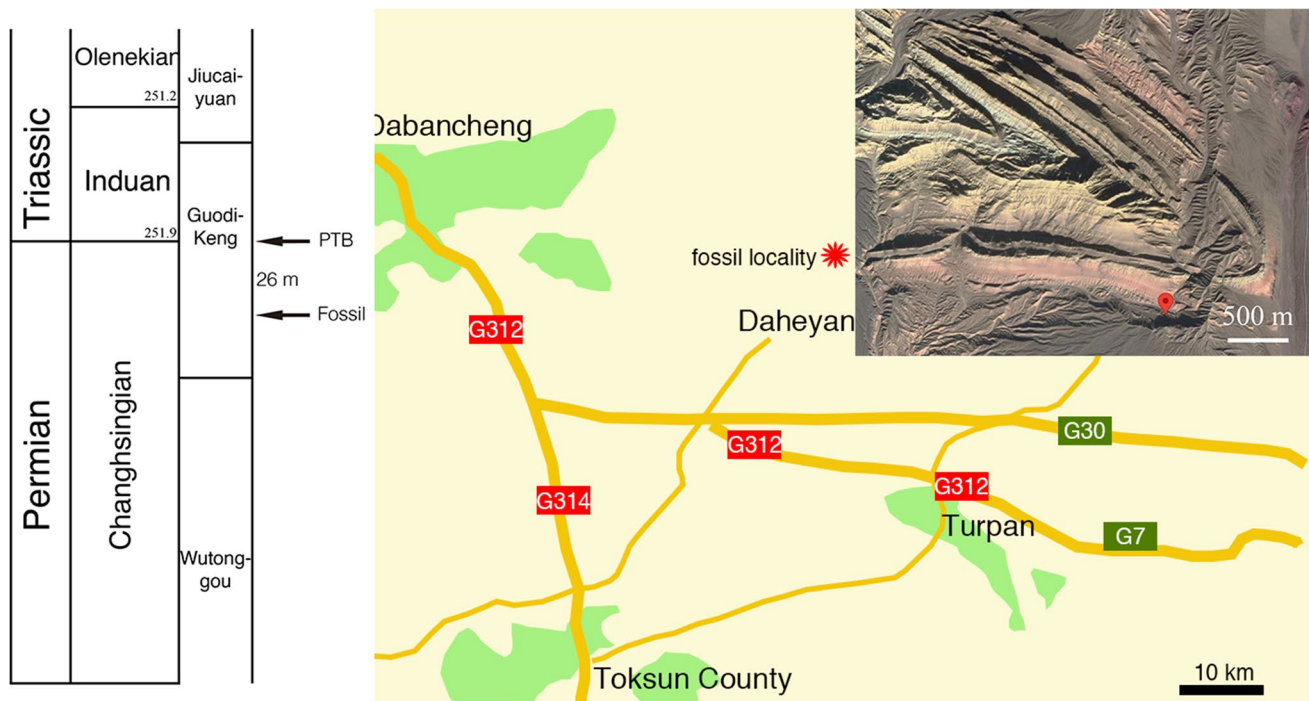


Fig. 1 Map and age of the fossil locality of *Vigilosaurus gaochangensis*. The map and satellite photo were modified from Google Maps. The horizon of the specimen was modified based on Fig. 7 of Yang et al. (2021)

Etymology

Vigil- means “to stay awake”; *-saurus* means reptiles; *-gaochang* is the name of an ancient kingdom where the fossil was discovered.

Locality and horizon

South Taodonggou, Daheyan, Turpan, Xinjiang, China; Guodikeng Formation, late Permian (Changhsingian).

Diagnosis

An archosauriform that differs from all other non-archosaurian archosauriforms by the combination of the following character states: a medial crest on the distal end of the fibula, the calcaneum overlapping the astragalus proximo-medially, the absence of an anterior hollow on the astragalus; a greatly expanded distal end of the metatarsal II, and an L-shaped metatarsal V with a tapering distal end.

Description

The holotype preserves a partial left hindlimb on red fine sandstone (Fig. 2). It is easily identified as a hindlimb rather than a forelimb based on the distinct morphology of the astragalus-calcaneum, and an L-shaped metatarsal V. For an explanation of the orientation of the hindlimb morphology, see Fig. 2c.

Femur

Only the distal portion of the shaft and the distal end are preserved. The shaft is slightly bowed towards the dorsal side. The adductor crest is inconspicuous on the ventral surface. The distal end gradually expands from the shaft without forming an abrupt bulbous end (Fig. 3). The medial (tibial) and lateral (fibular) condyles are separated by a shallow intercondylar fossa ventrally, and are roughly at the same proximo-distal level, without the latter projecting distally beyond the former. From the distal view, the lateral condyle is similar in size to the medial condyle (Fig. 3b). The distal articulation surface of the femur with the crus is generally rounded and restricted to the distal side. There is no obvious articulation surface with the fibula on the lateral side.

Fig. 2 Holotype (IVPP V22764) of *Vigilosaurus gaochangensis*. **a**—Photo of IVPP V22764; **b**—3-D reconstruction of the specimen; **c**. demonstration of orientation. The scale bar equals 10 mm. Abbreviations: **as**, astragalus; **ca**, calcaneum; **dt4**, distal tarsal 4; **fe**, femur; **fib**, fibula; **mt2**, metatarsal II; **mt3**, metatarsal III; **mt4**, metatarsal IV; **mt5**, metatarsal V; **phl**, phalanges; **tib**, tibia

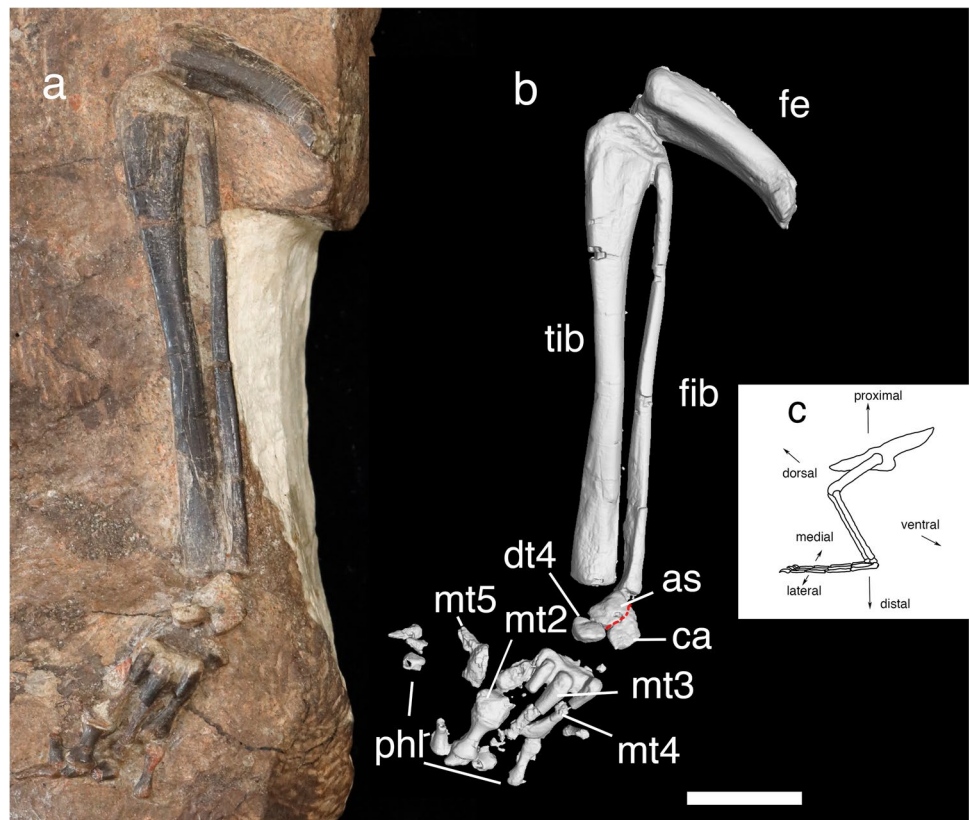
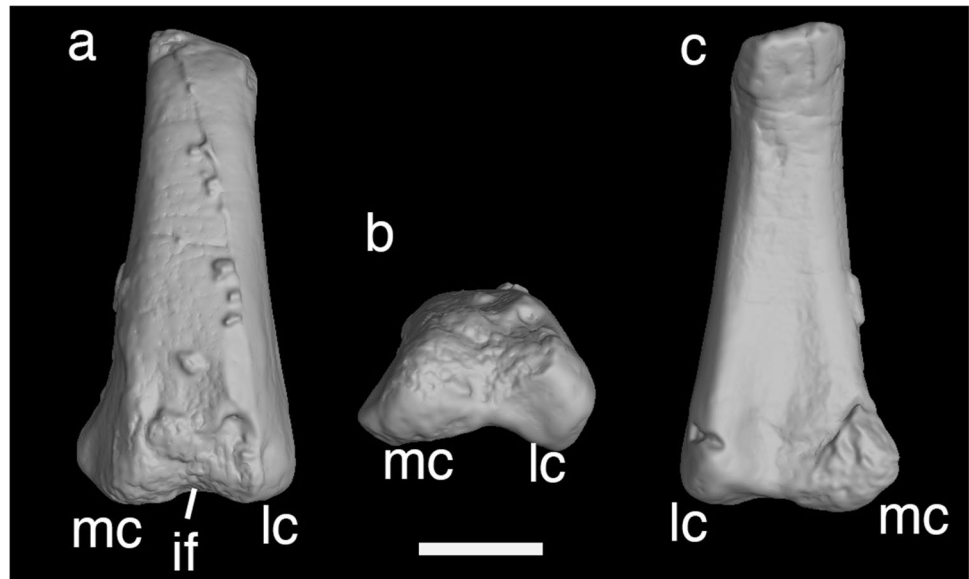


Fig. 3 Left femur (IVPP V22764) of *Vigilosaurus gaochangensis*. a—dorsal view; b—distal view; c—ventral view. The scale bar equals 5 mm. Abbreviations: **mc**, medial condyle; **if**, intercondylar fossa; **lc**, lateral condyle

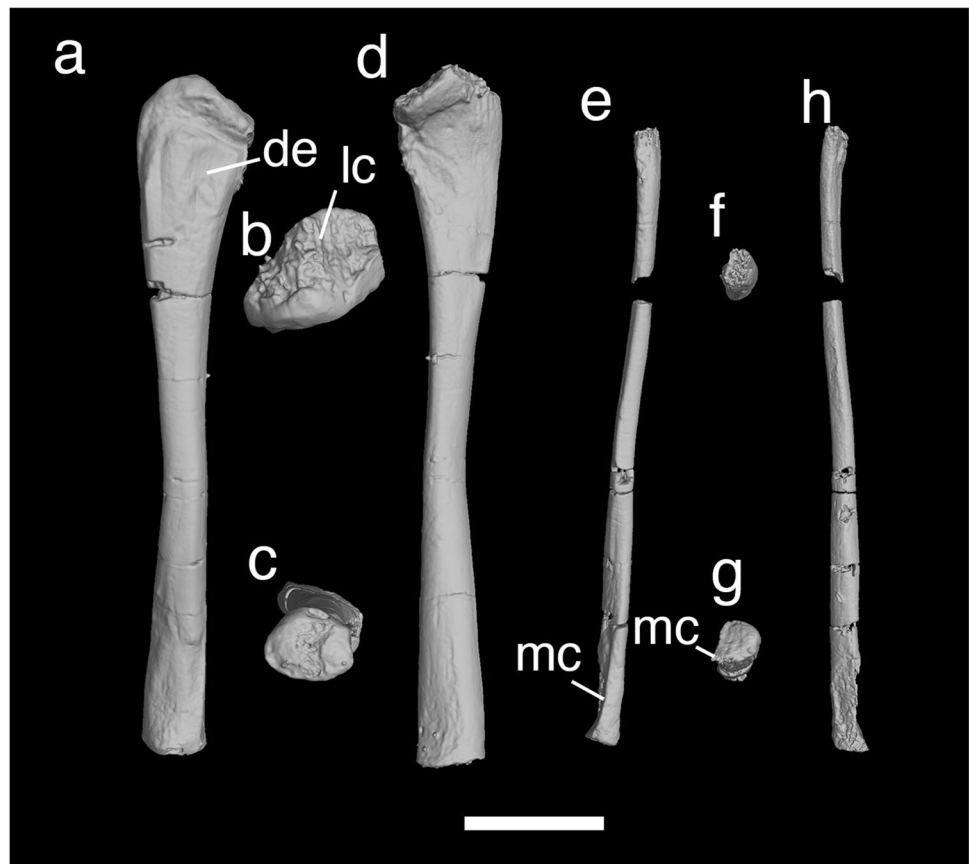


Tibia and fibula

Both the tibia and fibula are long and slender. The tibia is slightly longer than the fibula (tibia: 44 mm, fibula: 41 mm), and much stouter. From the middle shaft region, the tibia is proximally twice the width of the fibula (Fig. 4). Most of the weight bearing must fall on the tibia, rather than the fibula.

The derived condition of a much narrower fibula compared with the tibia strongly suggests its archosauromorph affinity (Ezcurra 2016), in contrast to the plesiomorphic condition as seen in non-saurian diapsids (e.g. *Youngina capensis*), in which the fibula and tibia have similar width. The proximal head of the tibia is broad with well ossified epiphysis. The cnemial crest is absent, and the lateral condyle forms a

Fig. 4 Left crus (IVPP V22764) of *Vigilosaurus gaochangensis*. a to d—Tibia in dorsal, proximal, distal, and ventral view, respectively; c to h—fibula in dorsal, proximal, distal, and ventral view, respectively. The scale bar equals 10 mm. Abbreviations: **de**, depression; **lc**, lateral condyle, **mc**, medial crest



single convex articulation with the distal surface of both the medial and lateral condyles of the femur (Fig. 4). A shallow depression is present from the dorsal view near the proximal head (Fig. 4a). The shaft of the tibia is slightly sigmoid in dorsal view and dorso-ventrally flattened. The distal surface is essentially flat and not much laterally expanded, articulating with the astragalus.

Both the proximal and distal ends of the fibula are unexpanded. The fibula is closely adjacent with the tibia for the most length of the element, with only a narrow space on the proximal part and little space on the distal part (Fig. 2). The proximal end does not extend beyond the tibia nor does it articulate with the lateral part of the femur. Instead, it is confluent with the tibial epiphysis to form a single proximo-distal articulation with the femur (Fig. 2). The shaft of the fibula is straight and cylindrical in cross-section. It lacks an obvious attachment site for the iliofibularis muscle. The distal end of the fibula bears a small medial crest towards the tibia, resulting in a pointed medial edge from the distal view (Fig. 4e, g). The distal surface is flat, articulating with both the astragalus and calcaneum.

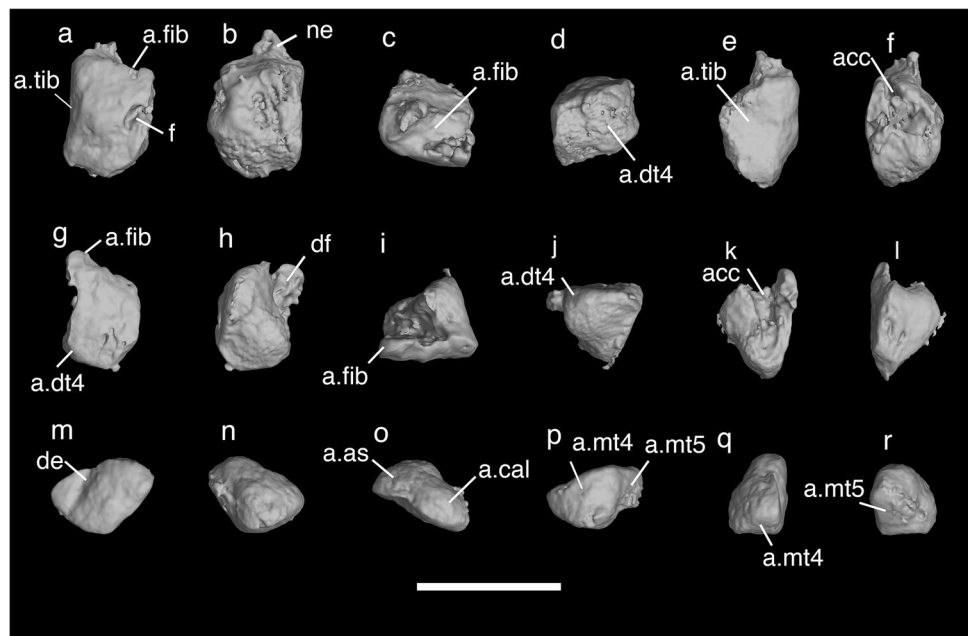
Tarsus

Three tarsal elements are preserved: the astragalus, calcaneum, and distal tarsal 4. Another element appears lateral to the distal tarsal 4 and superficially resembles a distal tarsal 5 on the holotype. However, CT reconstruction reveals that the density of this element is distinctively lower than that of bones but is close to the rock matrix, so we interpret this as a very thin slice of bone surface broken off, instead of representing an actual tarsal element.

The two proximal tarsals are compact in size, not much laterally expanded over the metatarsal and phalanges. Both the astragalus and calcaneum are trapezoid in dorsal view. The astragalus is slightly larger than the calcaneum. It bears two articulation surfaces proximally, one with the tibia and one with the fibula, separated by a non-articulation “neck” (Fig. 5a, b). The two articulation surfaces form an angle of about 90°. The tibial articulation surface is larger and slightly concave, and the fibular articulation is smaller and flat. The dorsal surface of the astragalus is essentially flat, lacking an obvious “anterior hollow” (sensu Cruikshank 1979) as seen in some non-archosaurian archosauriforms (e.g. *Proterosuchus fergusi*, *Erythrosuchus africanus*, and *Euparkeria capensis*). The articulation between the astragalus and calcaneum is obscure under the microscope but easily distinguishable from the 3-D reconstruction. It is of the simple flat articulation type, similar with other non-archosaurian archosauriforms (e.g. *Proterosuchus fergusi* and *Euparkeria capensis*) but unlike the “crocodile normal” or the “crocodile reversed” types as seen in crown archosaurs. The perforating foramen is present and is almost entirely enclosed by the astragalus (Fig. 5a). From the lateral view (Fig. 5f), the astragalo-calcaneal canal can be seen, and it extends continually onto the calcaneum (Fig. 5k).

The calcaneum is specialized in bearing a distinct dorsal flange that overlaps the astragalus proximodorsally near the articulation surface (Fig. 5g). The articulation facet for the fibula is on the flange, in continuation with the fibular facet of the astragalus. Neither a laterally nor posteriorly directed calcaneal tuber is present (Fig. 5g–i). The distal margin of the astragalus and calcaneum are both rounded for the articulation with the distal tarsal 4.

Fig. 5 Tarsals (IVPP V22764) of *Vigilosaurus gaochangensis*. a to f—astragalus in dorsal, ventral, proximal, distal, medial, and lateral view, respectively; g to l—calcaneum in dorsal, ventral, proximal, distal, medial, and lateral view, respectively; m to r—distal tarsal 4 in dorsal, ventral, proximal, distal, medial, and lateral view, respectively. The scale bar equals 5 mm. Abbreviations: **acc**, astragalus-calcaneum canal; **a.as**, articulation for astragalus; **a.cal**, articulation for calcaneum; **a.dt4**, articulation for distal tarsal 4; **a.fib**, articulation for fibula; **a.mt4**, articulation for metatarsal IV; **a.mt5**, articulation for metatarsal V; **a.tib**, articulation for tibia; **de**, depression; **df**, dorsal flange; **f**, perforating foramen; **ne**, neck



Distal tarsal 4 is of triangular shape from the dorsal view, with a depression on the dorsal surface (Fig. 5m). Proximally, it articulates with both the astragalus and calcaneum, fitting into the concave area embraced by the latter two bones. Distally, it bears two articulation surfaces, separated by an angle. The medial one articulates with the metatarsals III and IV and the lateral one with the hooked metatarsal V.

Pes

All five metatarsals are preserved in IVPP V22764; metatarsals I–IV are more or less in situ and are exposed on the specimen, whereas metatarsal V is disarticulated and buried in the rock matrix, only discovered with the help of the CT scanning (Fig. 2b; Fig. 6b–e).

Metatarsals I–IV are straight rod-like. The relative length from the longest to the shortest is: III (10.14 mm) > IV (9.16 mm) > II (8.84 mm) > I (6.38 mm) (Fig. 2; Fig. 6a). A longer metatarsal III than IV in IVPP V22764 is a derived condition as seen in crown-group archosaurs and some non-archosaurian archosauriforms close to the Archosauria (Nesbitt 2011; Bernardi et al. 2015). In contrast, non-saurian diapsids (e.g. *Youngina capensis*, *Kenyasaurus mariakaniensis*), non-archosauriform archosauromorphs (e.g. *Protorosaurus speneri*, *Prolacerta broomi*), and proterosuchids all have the plesiomorphic condition of metatarsal IV longer than the III. The proximal heads of the metatarsals I–IV are expanded medio-laterally and overlap each other. Metatarsal II is specialized in having a strongly expanded distal end, articulating with a proximally wide pedal phalanx (Fig. 2). Metatarsal V is distinctly L-shaped in dorsal view (Fig. 6b), with a long proximomedial process that articulates with the distal tarsal 4 and possibly the calcaneum too. The medial articular surface is concave (Fig. 6d). The lateral edge bears

an outer process near the proximal end (Fig. 6b, e). The shaft is somewhat broken, and the medullary cavity is exposed (Fig. 6c). Towards the distal end it tapers, and no associated phalanges was found near the bone, indicating that the fifth digit lacks phalanges.

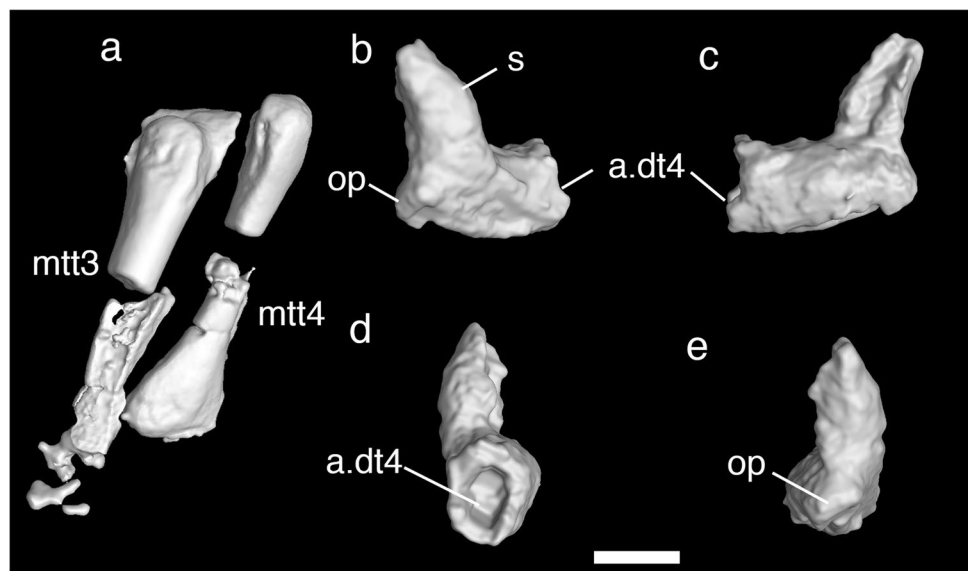
The pedal digits are incompletely preserved, and the exact phalangeal formula is uncertain. The third toe is probably the longest. A few phalanges not exposed on the specimen were found underneath the surface with the help of the CT reconstruction (Fig. 2b).

Phylogenetic position of IVPP V 22,764

We performed two phylogenetic analyses to determine the phylogenetic position of IVPP V 22,764. In the first analysis, we coded 14 hindlimb characters of *Vigilosaurus gaochangensis* in the early amniote phylogeny of Ford and Benson (2020). The data matrix contains a total of 294 morphological characters coded for 71 taxa (suppl. S1). We analyzed the data in TNT (Goloboff et al. 2008) using Wagner building (1000 replications), ratchet (10 iterations), drifting (10 cycles), and tree fusing (3 rounds), until 20 hits of minimum tree length. It resulted in 49 most parsimonious trees (MPTs) with a tree length of 1559 steps, and recovered the new species at the base of the Neoreptilia (including Parareptilia) in an unresolved polytomy, together with other early diapsids, lepidosauromorphs, and archosauromorphs (suppl Fig. 1).

In the second analysis, we used the data matrix of Ezcurra and Sues (2021), which is the newest version of the ongoing Complete Archosauromorph Tree Project, first introduced in Ezcurra (2016). This matrix has an extensive sampling of archosauromorphs and samplings of several early diapsids and lepidosauromorphs, which is suitable for determining the

Fig. 6 Metatarsals of *Vigilosaurus gaochangensis*. a. metatarsals III and IV in dorsal view; b–e. metatarsal V in dorsal, ventral, medial, and lateral views, respectively. The scale bar equals 2 mm. Abbreviations: **a.dt4**, articulation for distal tarsal 4; **mtt3**, metatarsal III; **mtt4**, metatarsal IV; **op**, outer process; **s**, shaft



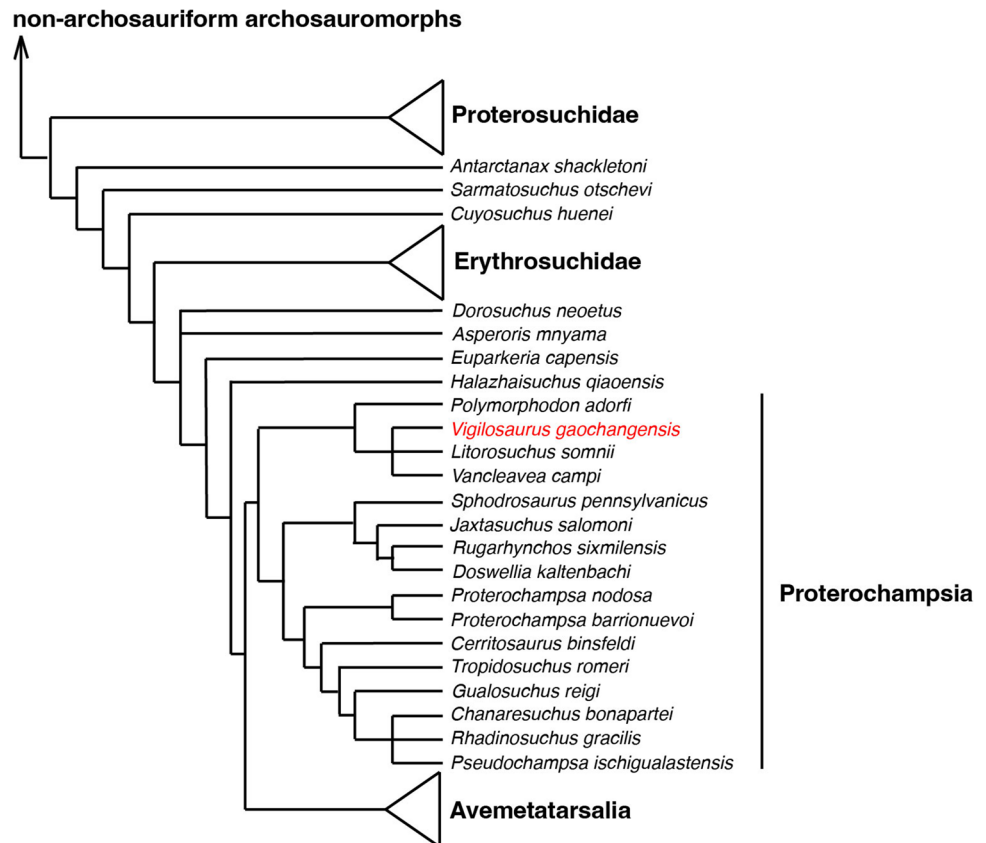
position of the new species. We coded 85 hindlimb characters for the new species. The data matrix contains 191 terminals and 887 morphological characters (suppl. S2). We analyzed the data in TNT (Goloboff et al. 2008) using Wagner building (1000 replications), ratchet (50 iterations), drifting (50 cycles), and tree fusing (5 rounds). It resulted in 91 most parsimonious trees (MPTs) with a tree length of 6293 steps. The simplified diagram of the strict consensus tree was shown in Fig. 7, and the complete strict consensus tree can be found in supplementary Fig. 2. It is fairly well resolved, and the tree topology largely agrees with Fig. 9 of Ezcurra and Sues (2021, Fig. 9). *V. gaochangensis* is weakly supported (bootstrap: 5/Bremer support:1) as clustered with *Vancleavea campi* and *Litorosuchus somnii* in an unresolved polytomy within the Proterochampsia. Nevertheless, the archosauriform affinity of the new species is confirmed.

As the first late Permian archosauriform fossil reported from Xinjiang, China, *Vigilosaurus gaochangensis*, despite only preserved as a partial hindlimb, shows a few diagnostic features that can indicate its relationships.

IVPP V22764 differs from the non-saurian diapsids or lepidosauromorphs and resembles the archosauromorphs in two derived characters: a much stouter mid shaft of the tibia than fibula, and a L-shaped metatarsal V in dorsal view. In non-saurian diapsids (e.g. *Araeoscelis*, *Youngina*, *Kenyasaurus*,

and *Petrolacosaurus*), the tibia and fibula are of similar width in the mid shaft (Peabody 1952; Harris and Carroll 1977; Reisz et al. 1984; Smith and Evans 1996; Ezcurra 2016). All archosauromorphs have the tibia much stouter than the fibula (Romer 1956; Nesbitt 2011; Ezcurra 2016), and Ezcurra (2016) recognized it as a synapomorphy of the Archosauromorpha. Basal lepidosauromorphs such as *Gephyrosaurus bridensis* have the tibia and fibula similar in width in the mid shaft (Evans 1981), but some lepidosauromorphs close to the crown group (e.g., *Huehuecuetzpalli mixtecus*, *Clevosaurus hudsoni*) and modern *Sphenodon punctatus* have a stouter tibia than fibula (Frazer 1988; Reynoso 1998). The evolution of this character in lepidosauromorphs is not well understood and deserves further study. The shape of the metatarsal V has been a “classic” character in diapsid phylogeny (Goodrich 1916; Romer 1956; Robinson 1975; Gauthier 1984; Sereno 1991; Lee 1997; Dilkes 1998; Nesbitt 2011; Ezcurra 2016; Borsuk-Bialynicka 2018; Spiekman et al. 2021). A simple rod-like metatarsal is the plesiomorphic condition as it appeared in the outgroup of the diapsids and stem diapsids such as *Araeoscelidia* and *Younginiformes*, whereas a hook-shaped metatarsal V is the derived condition as seen in most lepidosauromorphs, archosauromorphs, and turtles (if it is a diapsid), either homologous at the base of Sauria or convergent in each clade (Nesbitt 2011; Ezcurra 2016). Metatarsal V is further derived in certain archosauromorph taxa (e.g.

Fig. 7 Simplified strict consensus of the phylogenetic analysis to show the relationships of *Vigilosaurus gaochangensis* (labeled in red). Several clades (Aveimetatarsalia, Erythrosuchidae, and Proterosuchidae) are merged into a single terminal. The complete strict consensus tree is in supplementary Fig. 2



in *Macronemus bassanii*, *Boreopricea funerea*, *Prolacerta broomi*, proterosuchids and erythrosuchids), in which the medial process is elongated and the proximolateral corner is squared, making it distinctly L-shaped (Ezcurra 2016). This is also the case in IVPP V22764. Metatarsal V is L-shaped (Fig. 6), the long medial process of which forms an angle of 120° with the shaft and articulates with distal tarsal 4.

IVPP V22764 differs from all non-archosauriform archosauriforms (e.g., *Protorosaurus speneri*, *Procalerta broomi*, tanystropheids, and rhynchosaurs) and Proterosuchidae (e.g. *Proterosuchus fergusi*) in that the metatarsal III is longer than metatarsal IV (Colbert 1987; Sereno 1991; Gottmann-Quesada and Sander 2009; Bernardi et al. 2015; Spiekman 2018; De-Oliveira et al. 2020). Nesbitt (2011) recognized this as a synapomorphy of the clade comprising *Erythrosuchus* + Archosauria. The earliest occurrence of a longer metatarsal III was documented in the late Permian footprints from northeastern Italy (Bernardi et al. 2015), without skeletal evidence. This character was used as evidence of the earliest footprints produced by archosauriforms. IVPP V22764 corroborates the ichnologic evidence that a longer metatarsal III than IV was indeed present in the skeletal record prior to the Triassic and indicates that the phylogenetic position of IVPP V22764 was within the Archosauriformes.

Within the Archosauriformes, IVPP V22764 possesses a few character states, especially in the ankle bones, which are unusual (Ewer 1965; Cruickshank 1978; Sereno 1991; Gower 1996; Dilkes 1998; Wu and Russell 2001; Dilkes and Sues 2009; Nesbitt 2011; Li et al. 2008, 2012; Trotteyn et al. 2012; Ezcurra et al. 2013; Trotteyn and Ezcurra 2014; Bernardi et al. 2015; Ezcurra 2016; Li et al. 2016; Sookias 2016; Maidment et al. 2020; Trotteyn and Ezcurra 2020). Most notably are the absence of either a lateral or a posterior calcaneal tuber on the calcaneum in IVPP V22764. In Contrast, in other archosauriforms, a calcaneal tuber is present either laterally (e.g. *Proterosuchus fergusi*, *Erythrosuchus africanus*, and *Euparkeria capensis*) or posteriorly (bird and crocodile-line archosaurs) (Ewer 1965; Gower 1996; Sereno 1991; Nesbitt 2011). Furthermore, the astragalus-calcaneum articulation is flat but not of a ball-and-socket type as seen in the Archosauria. IVPP V22764 further differs from the Euparkeriidae and Archosauria in two plesiomorphic conditions: the presence of a perforating foramen on the astragalus and an astragalo-calcaneal canal (char. 365, Nesbitt 2011), and the presence of a non-articulation neck between the tibial and fibular articulation surface of the astragalus (char. 369, Nesbitt 2011).

Posture of *Vigilosaurus gaochangensis*.

The posture shift from a sprawling to the parasagittal position is a major evolutionary transition in archosaurs (Bakker 1971; Charig 1972; Cruickshank 1978, 1979; Parrish 1986, 1987; Brinkman 1980; Gatesy 1991; Sereno 1991; Hutchinson and Gatesy, 2000; Kubo and Benton,

2009; Hutchinson 2006; Demuth et al. 2020). Crown-group archosaurs (birds, dinosaurs, crocodiles, pterosaurs, and their relatives) are able to stand and move in a parasagittal position, whereas early archosauriforms (e.g. *Protorosaurus speneri*, *Proterosuchus fergusi*) were assumed to be sprawlers. When the first parasagittal posture occurred and whether it is plesiomorphic or convergently derived in different archosauriform clades are still not well understood. Evidence showed that the Middle Triassic *Euparkeria capensis* possessed a semi-erect posture based on hip morphology, but the ankle joint was plesiomorphic relative to the Archosauria (Demuth et al. 2020). Some studies assume that the parasagittal position occurred in archosaurs and therapsids independently during the Triassic as an adaptive response to the drastic climate change (Kemp et al. 1982; Bonaparte 1984; Parrish 1987; Kubo and Benton 2009). But in recent years, late Permian trackways from Italy indicates that parasagittal posture might have already occurred prior to the EPME (Bernardi et al. 2015; Marchetti et al. 2020), but no skeletal evidence was yet available.

To achieve a parasagittal posture, a suit of girdle and limb modifications are necessary, some of which can be seen in *V. gaochangensis*. The knee joint of *V. gaochangensis*, especially the articulation between the femur and fibula, is entirely dorsoventral, unlike the cases seen in typical sprawlers, in which the fibula articulates with both the ventral and lateral facets of the femur. Two distal condyles of the femur are almost symmetrical. The proximal ends of the tibia and fibula form a confluent single articulation distal to the femur. The shaft of the tibia and fibula are closely spaced with little gap in between, and the tibia, with a much larger diameter, is the major weight-bearing bone of the crus. The overall build of the knee and crus closely resembles other parasagittal archosauriforms (e.g., *Euparkeria capensis*), in which the rotation of the knee is much limited; it is in contrast with sprawling diapsids (e.g., *Youngina capensis*), in which the shafts of the tibia and fibula are usually of similar width and are separated by a gap, allowing a greater degree of rotation.

The pes of *V. gaochangensis* is characterized by a mesaxonic foot with the reduction of the digit V. A mesaxonic foot is commonly seen in crown-group archosaurs and is often associated with parasagittal locomotion. Metatarsals I-IV of *V. gaochangensis* are compact and proximally overlapped, with metatarsal III the longest. Metatarsal V is hooked-shaped and loosely detached from the other metatarsals. The distal end of metatarsal V tapers and no phalanges of digit V are associated with it as preserved.

The advanced conditions of the knee and pes suggests that *V. gaochangensis* was probably parasagittal. It shows that in the Archosauriformes, the transition from a sprawling to the parasagittal posture probably took off before the EPME, corroborated the evidence from ichnology (Bernardi et al. 2015; Marchetti et al. 2020).

Conclusions

Vigilosaurus gaochangensis documents the first late Permian archosauriform from Xinjiang, China. Its morphology of the knee and pes suggests that a parasagittal posture is possible in *V. gaochangensis*. The presence of *V. gaochangensis* as a small, parasagittal archosauriform in the latest Permian indicates that this group already underwent considerable taxonomic diversification and acquired some key morphological innovations before the Triassic, paving the road for them to become the dominant clade in the upcoming Mesozoic.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00114-022-01823-8>.

Acknowledgements We thank Lu Li, Yufeng Liu, Xingwen Li, and Xu Xu for the fieldwork, Fu Hualin and Yong Wu for preparing the specimen, and Jingsong Shi and Yemao Hou for CT-scanning the specimen.

Funding This work is funded by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), and the International Partnership Program of Chinese Academy of Sciences (132311KYSB20190010).

References

- Angielczyk KD, Sullivan C (2008) *Diictodon feliceps* (Owen, 1876), a dicynodont (Therapsida, Anomodontia) species with a Pangaeian distribution. *J Vertebr Paleontol* 28(3):788–802
- Bakker RT (1971) Dinosaur physiology and the origin of mammals. *Evolution* 636–658
- Bernardi M, Klein H et al (2015) The origin and early radiation of archosauriforms: integrating the skeletal and footprint record. *PLoS ONE* 10(6):e0128449
- Bonaparte JF (1984) Locomotion in rauisuchid thecodonts. *J Vertebr Paleontol* 3(4):210–218
- Borsuk-Bialynicka M (2018). Diversity of diapsid fifth metatarsals from the Lower Triassic karst deposits of Czatkowice, southern Poland—functional and phylogenetic implications. *Acta Palaeontologica Polonica* 63(3)
- Brinkman D (1980) The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. *Can J Zool* 58(12):2187–2200
- Brusatte SL, Benton MJ et al (2008) Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* 321(5895):1485–1488
- Charig AJ (1972) The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. *Stud Vertebrate Evol* 121–155
- Cheng Z, Wu S, et al (1996) The Permian–Triassic sequences in the southern margin of the Junggar basin and the Turpan basin, Xinjiang, China 30th International Geologic Congress, Field Trip Guidebook
- Colbert EH (1987) The Triassic reptile *Prolacerta* in Antarctica. *American Museum novitates*; no. 2882
- Cruikshank A (1978) The pes of *Erythrosuchus africanus* Broom. *Zool J Linn Soc* 62(2):161–177
- Cruikshank A (1979) The ankle joint in some early archosaurs. *S Afr J Sci* 75(4):168
- Demuth OE, Rayfield EJ, et al (2020) 3D hindlimb joint mobility of the stem-archosaur *Euparkeria capensis* with implications for postural evolution within Archosauria. *Scientific reports* 10(1). <https://doi.org/10.1038/s41598-020-70175-y>
- De-Oliveira TM, Pinheiro FL et al (2020) A new archosauromorph from South America provides insights on the early diversification of tanystropheids. *PLoS ONE* 15(4):e0230890
- Dilkes DW (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philos Trans R Soc Lond B Biol Sci* 353(1368):501–541
- Dilkes D, Sues H-D (2009) Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. *J Vertebr Paleontol* 29(1):58–79
- Ernesto M, Demarco PN et al (2020) Age constraints on the Paleozoic Yaguari-Buena Vista succession from Uruguay: paleomagnetic and paleontologic information. *J S Am Earth Sci* 98:102489. <https://doi.org/10.1016/j.jsames.2019.102489>
- Evans SE (1981) The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. *Zool J Linn Soc* 73(1):81–116
- Ewer RF (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Philos Trans R Soc Lond B Biol Sci* 248(751):379–435
- Ezcurra MD (2016) The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* 4:e1778. <https://doi.org/10.7717/peerj.1778>
- Ezcurra MD, Sues H-D (2021) A re-assessment of the osteology and phylogenetic relationships of the enigmatic, large-headed reptile *Sphodrosaurus pennsylvanicus* (Late Triassic, Pennsylvania, USA) indicates archosauriform affinities. *J Syst Paleontol* 19(24):1643–1677
- Ezcurra MD, Butler RJ et al (2013) ‘Proterosuchia’: the origin and early history of Archosauriformes. *Geol Soc, London, Special Publ* 379(1):9–33. <https://doi.org/10.1144/sp379.11>
- Ezcurra MD, Scheyer TM et al (2014) The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. *PLoS ONE* 9(2):e89165. <https://doi.org/10.1371/journal.pone.0089165>
- Ezcurra MD, Velozo P et al (2015) Early archosauromorph remains from the Permo-Triassic Buena Vista Formation of north-eastern Uruguay. *PeerJ* 3:e776. <https://doi.org/10.7717/peerj.776>
- Ford DP, Benson RB (2020) The phylogeny of early amniotes and the affinities of Parareptilia and Varanopidae. *Nat Ecol Evol* 4(1):57–65
- Fraser NC (1988) The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philos Trans Royal Soc London b, Biol Sci* 321(1204):125–178
- Gastaldo RA, Kamo SL, et al (2020) The base of the *Lystrosaurus* Assemblage Zone, Karoo Basin, predates the end-Permian marine extinction. *Nat Commun* 11(1). <https://doi.org/10.1038/s41467-020-15243-7>
- Gatesy SM (1991) Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *J Zool* 224(4):577–588
- Gauthier J (1984) A cladistic analysis of the higher taxonomic categories of the Diapsida. Ph. D. dissertation, University of California, Berkeley
- Gauthier J (1986) Saurischian monophyly and the origin of birds. *Mem Calif Acad Sci* 8:1–55
- Gauthier J, Kluge AG et al (1988) Amniote phylogeny and the importance of fossils. *Cladistics* 4(2):105–209
- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24(5):774–786. <https://doi.org/10.1111/j.1096-0031.2008.00217.x>
- Goodrich ES (1916) On the classification of the Reptilia. *Proc Royal Soc London Series b, Containing Papers Biol Character* 89(615):261–276

- Gottmann-Quesada A, Sander PM (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. *Palaeontogr Abt A* 287(4–6):123–220. <https://doi.org/10.1127/pala/287/2009/123>
- Gower DJ (1996) The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. *Zool J Linn Soc* 116(4):347–375
- Harris JM and Carroll RL (1977). *Kenyasaurus*, a new eosuchian reptile from the Early Triassic of Kenya. *J Paleontol* 139–149
- Hutchinson JR (2006) The evolution of locomotion in archosaurs. *CR Palevol* 5(3–4):519–530
- Hutchinson JR, Gatesy SM (2000) Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology* 26(4):734–751
- Kammerer CF, Angielczyk KD et al (2011) A comprehensive taxonomic revision of *Dicynodon* (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. *J Vertebr Paleontol* 31(sup1):1–158
- Kemp DF, Kemp TS et al (1982) Mammal-like reptiles and the origin of mammals. Academic Press
- Kubo TAI, Benton MJ (2009) Tetrapod postural shift estimated from Permian and Triassic trackways. *Palaeontology* 52(5):1029–1037. <https://doi.org/10.1111/j.1475-4983.2009.00897.x>
- Lee M (1997) The evolution of the reptilian hindfoot and the homology of the hooked fifth metatarsal. *J Evol Biol* 10(2):253–263
- Li C, Wu X-C et al (2012) A new archosaur (Diapsida, Archosauriformes) from the marine Triassic of China. *J Vertebr Paleontol* 32(5):1064–1081. <https://doi.org/10.1080/02724634.2012.694383>
- Li C, Wu X-C et al (2016) A new armored archosauriform (Diapsida: Archosauromorpha) from the marine Middle Triassic of China, with implications for the diverse life styles of archosauriforms prior to the diversification of Archosauria. *Sci Nat* 103(11–12). <https://doi.org/10.1007/s00114-016-1418-4>
- Li J, Wu X et al (2008) The Chinese fossil reptiles and their kin. Science Press Beijing
- Liu J, Abdala F (2017) Therocephalian and chroniosuchian (Reptiliomorpha) from the Permo-Triassic transitional Guodikeng Formation of the Dalongkou Section, Jimsar, Xinjiang, China. *Vertebrata Palasiatica* 55:24–40
- Lucas S (2001) Chinese fossil vertebrates. Columbia University Press, New York, p 375
- Maidment SC, Sennikov AG et al (2020) The postcranial skeleton of the erythrosuchid archosauriform *Garjainia prima* from the Early Triassic of European Russia. *R Soc Open Sci* 7(12):201089
- Marchetti L, Ceoloni P et al (2020) The Lopingian tetrapod ichnoassociation from Italy, a key for the understanding of low-latitude faunas before the end-Permian crisis. *Tetrapod Ichnol Italy: the State of the Art Journal of Mediterranean Earth Sciences* 12:61–81
- Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. *Bull Am Mus Nat Hist* 352:1–292. <https://doi.org/10.1206/352.1>
- Osborn HF (1903) The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Mem Am Mus Nat Hist* 1:449–507
- Parrish JM (1986) Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. University of Col, Museum
- Parrish JM (1987) The origin of crocodylian locomotion. *Paleobiology* 13(4):396–414
- Peabody FE (1952). *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas
- Pinheiro FL, França MAG, et al (2016) An exceptional fossil skull from South America and the origins of the archosauriform radiation. *Scientific reports* 6(1). <https://doi.org/10.1038/srep22817>
- Reisz RR, Berman DS et al (1984) The anatomy and relationships of the Lower Permian reptile *Araucoscelis*. *J Vertebr Paleontol* 4(1):57–67
- Reynoso V-H (1998) *Huehucuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México. *Phil Trans R Soc Lond B* 353(1367):477–500
- Robinson P (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. *Colloq Int C N R S* 218:461–483
- Romer AS (1956) Osteology of the reptiles. The University of Chicago Press, Chicago & London
- Sereno PC (1991) Basal archosaurs: phylogenetic relationships and functional implications. *J Vertebr Paleontol* 11(S4):1–53
- Smith RM, Evans SE (1996) New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles. *Palaeontology* 39(2):289–304
- Sookias RB (2016) The relationships of the Euparkeriidae and the rise of Archosauria. *R Soc Open Sci* 3(3):150674. <https://doi.org/10.1098/rsos.150674>
- Spiekman SN, Fraser NC et al (2021) A new phylogenetic hypothesis of Tanystropheidae (Diapsida, Archosauromorpha) and other “protorosaurs”, and its implications for the early evolution of stem archosaurs. *PeerJ* 9:e11143
- Spiekman SNF (2018) A new specimen of *Prolacerta broomi* from the lower Fremouw Formation (Early Triassic) of Antarctica, its biogeographical implications and a taxonomic revision. *Scientific reports* 8(1). <https://doi.org/10.1038/s41598-018-36499-6>
- Trotteyn MJ, Ezcurra MD (2014) Osteology of *Pseudochampsia ischigualastensis* gen et comb nov (Archosauriformes: Proterochampsidae) from the early Late Triassic Ischigualasto Formation of northwestern Argentina. *PLoS one* 9(11):e111388
- Trotteyn MJ, Ezcurra MD (2020) Redescription of the holotype of *Chanaresuchus bonapartei* Romer, 1971 (Archosauriformes: Proterochampsidae) from the Upper Triassic rocks of the Chañares Formation of north-western Argentina. *J Syst Paleontol* 18(17):1415–1443. <https://doi.org/10.1080/14772019.2020.1768167>
- Trotteyn MJ, Martínez RN et al (2012) A new proterochampsid *Chanaresuchus ischigualastensis* (Diapsida, Archosauriformes) in the early Late Triassic Ischigualasto Formation. *Argentina Journal of Vertebrate Paleontology* 32(2):485–489. <https://doi.org/10.1080/02724634.2012.645975>
- Viglietti PA, Benson RB, et al (2021) Evidence from South Africa for a protracted end-Permian extinction on land. *Proc Natl Acad Sci* 118(17)
- von Huene FRF (1946) Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biol Zent Bl* 65:268–275
- Wan M-L, Yang W et al (2020) Palaeocupressinoxylon uniseriale n. gen. n. sp., a gymnospermous wood from the upper Permian of Central Taodonggou, southern Bogda Mountains, northwestern China. *Palaeoworld* 29(1):117–125. <https://doi.org/10.1016/j.palwor.2019.06.002>
- Wu X-C, Russell AP (2001) Redescription of *Turfanosuchus dabanensis* (Archosauriformes) and new information on its phylogenetic relationships. *J Vertebr Paleontol* 21(1):40–50
- Yang W, Wan M, et al (2021) Paleoenvironmental and paleoclimatic evolution and cyclo- and chrono-stratigraphy of upper Permian-Lower Triassic fluvial-lacustrine deposits in Bogda Mountains, NW China—implications for diachronous plant evolution across the Permian-Triassic boundary. *Earth-Sci Rev* 103741

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