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An unusual archosaurian from the marine Triassic of China

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Abstract A new Triassic archosaurian from China shows a number of aquatic specializations, of which the most striking is the extreme lateral compression of the long tail. Others that may also reflect aquatic adaptations include platelike scapula and coracoid, elongate neck with extremely long and slender ribs, and reduction of osteoderms. In contrast, its pelvic girdle and hind limb have no aquatic modifications. Anatomic features, taphonomy, and local geological data suggest that it may have lived in a coastal–island environment. This lifestyle, convergent with some Jurassic marine crocodyliforms that lived at least 40 million years later and the saltwater species of extant *Crocodylus*, contradicts with the prevailing view that Triassic archosaurians were

restricted to nonmarine ecosystems. Its mosaic anatomy represents a previously unknown ecomorph within primitive archosaurians.

Introduction

The Archosauria [the Archosauriformes in some publications (Gauthier 1986; Sereno 1991)] originated in the Late Permian (about 250 million years ago) and later gave rise to dinosaurs (including birds), pterosaurs, and crocodylomorphs (including extant crocodylians) (Gower and Wilkinson 1996; Benton 2004). Its early members, traditionally called “thecodonts,” flourished worldwide during the Triassic, from 250 to 205 million years ago, and have been long considered terrestrial (Charig et al. 1976; Chatterjee 1978; Parrish 1993; Juul 1994; Wu and Russell 2001). Archosaurian remains have been reported from Triassic marine strata before (Wiman 1918; Huene 1939; Krebs 1965; Pinna and Arduini 1978), but none showed aquatic adaptation and are believed to be the remains of terrestrial animals washed out to sea (Nicholls et al. 1998). *Sikannisuchus* (Nicholls et al. 1998), recently collected from the marine Upper Triassic, is considered to be aquatic due to its flat and sculpted skull as in aquatic archosauromorphs such as *Doswellia*, proterochampsids, and advanced crocodylomorphs. However, most of the latter animals lived in terrestrial ecosystems and the habitat of *Sikannisuchus* is controversial because of its fragmentary nature. In this study, we report a new Triassic archosaurian, which has several specializations normally associated with aquatic reptiles. Together with fishes, nothosaurs, protosauroids and ichthyosaurs, it has been collected recently from the Middle Triassic marine limestone in west Guizhou, China. The new archosaurian is well-represented by articulated skeletons (Fig. 1), and shows the following archosaurian features: presence of antorbital fenestra, postfrontal reduced to less than half

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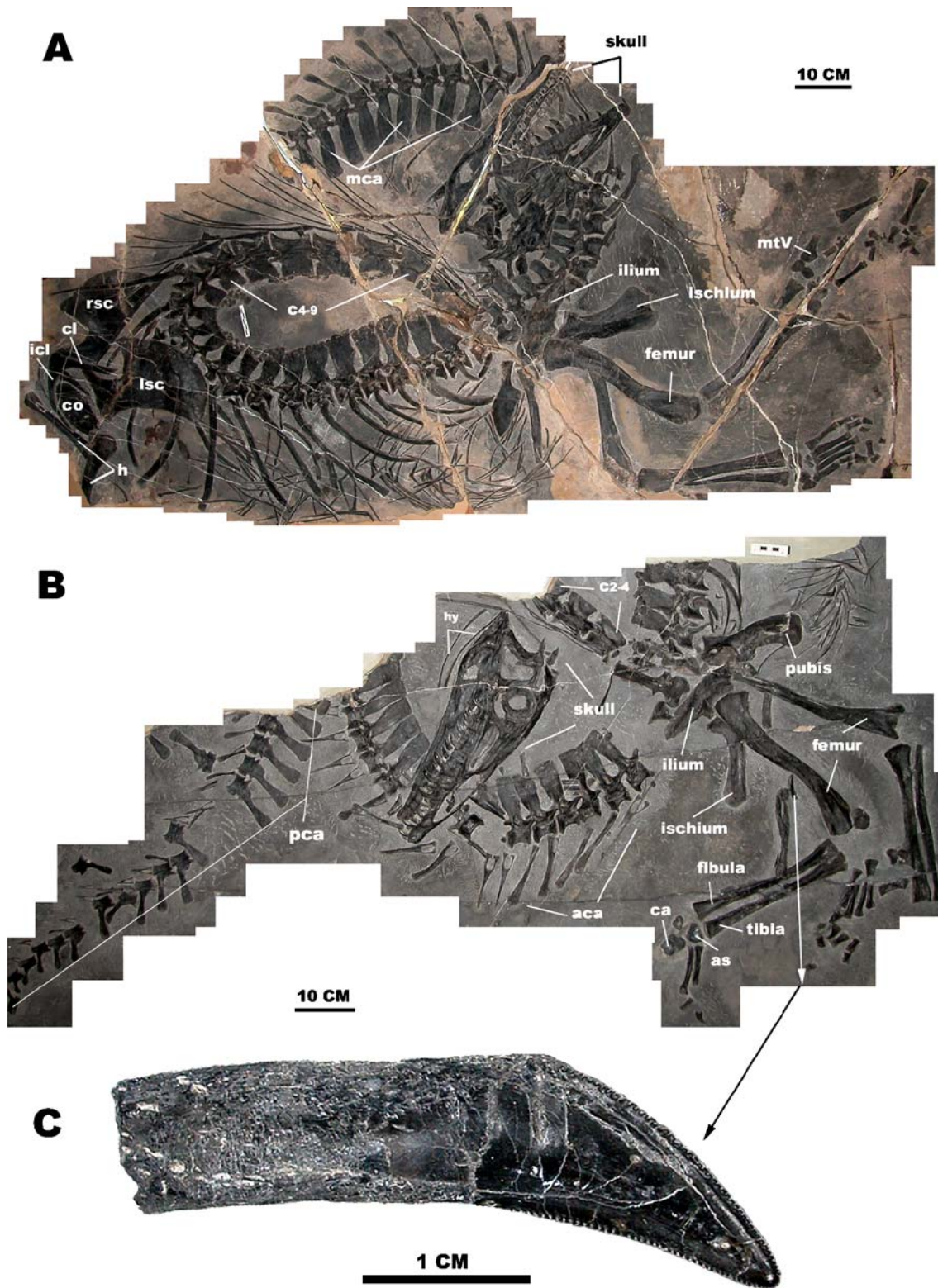


Fig. 1 *Qianosuchus mixtus* gen. et sp. nov. **a** Holotype (IVPP V13899). **b** Paratype (IVPP V14300). **c** An isolated tooth. *aca* anterior caudal vertebrae, *as* astragalus, *ca* calcaneum, *cl* clavicle, *co* coracoid, *c2-4* and *c4-9* cervical vertebrae 2 to 4 and 4 to 9, *h*

humerus, *hy* hyoid, *icl* interclavicle, *lsc* left scapula, *rsc* right scapula, *mca* midcaudal vertebrae, *mtV* metatarsal V, *pca* posterior caudal vertebrae with no transverse process

dimensions of postorbital, teeth with serrated margins, and presence of external mandibular fenestra (Benton 2004).

Description of specimens

Taxonomy

Archosauria Cope, 1869

- Crurotarsi Sereno & Arcucci, 1990
- *Qianosuchus mixtus* gen. et sp. nov.

Etymology

Generic name is derived from “Qian,” the Chinese abbreviation of Guizhou Province. The specific name is referred to the combination of aquatic and terrestrial features in the archosaurian.

Holotype

Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), *Academia Sinica*, V13899, a skeleton with distal part of forelimbs and posterior end of the tail missing.

Paratype

IVPP V14300, an incomplete skeleton with nearly complete skull and mandible.

Referred specimen

National Museum of Natural Science (NMNS) 000408/F003877, an incomplete skull.

Locality and horizon

Near Xinmin, Panxian County, southwest Guizhou Province, China; Guanling Formation, Middle Triassic (Anisian).

Diagnosis

A medium-sized archosaurian, over 3 m in length, differing from all other archosaurians in having the following combination of derived features: low premaxilla bearing nine daggerlike teeth; posteriorly positioned external naris longer than any other skull opening and mainly enclosed by nasal dorsally and maxilla ventrally; external mandibular

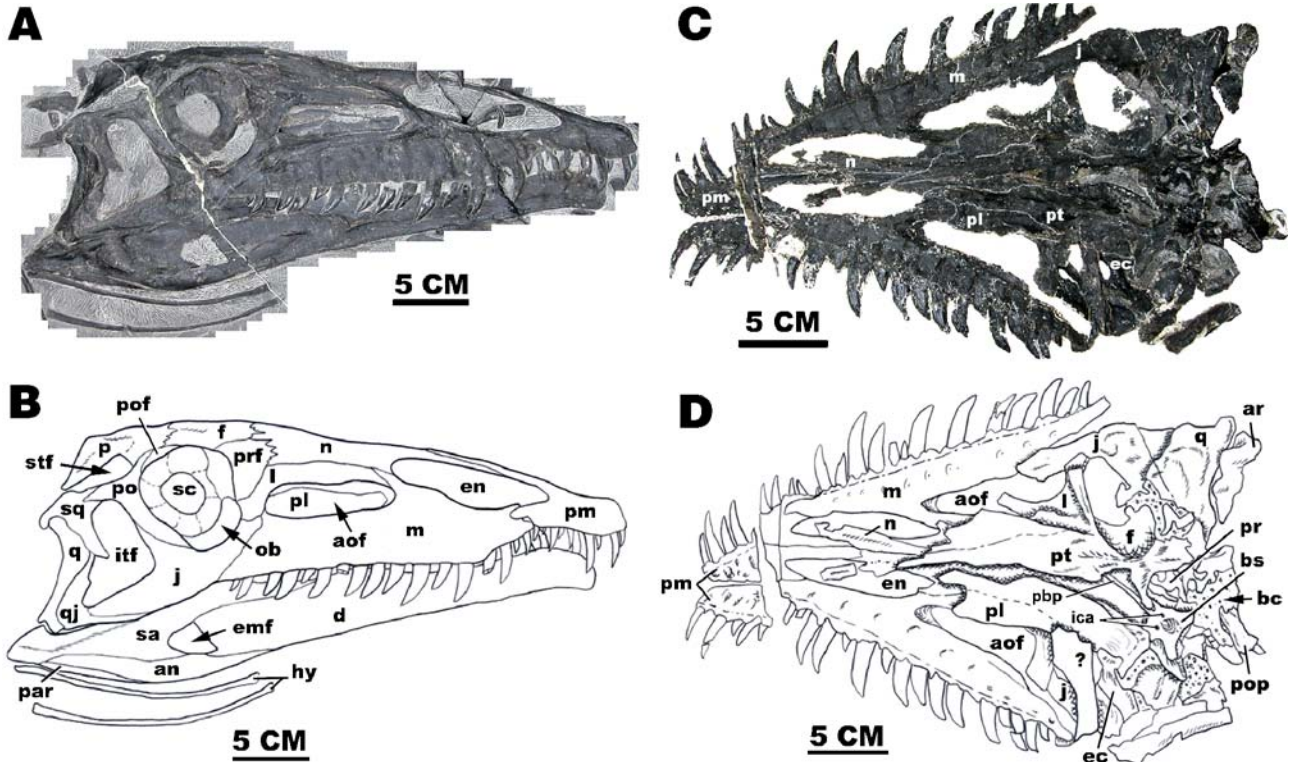


Fig. 2 Skulls of *Qianosuchus mixtus* gen. et sp. nov. **a, b** Skull of paratype (IVPP V14300) in lateral views. **c, d** Skull of referred specimen (NMNS 000408/F003877) in ventral view. *an* Angular, *aof* antorbital fenestra, *ar* articular, *bc* braincase, *bs* basisphenoid, *d* dentary, *ec* ectopterygoid, *emf* external mandibular fenestra, *en* external naris, *f* frontal, *hy* hyoid, *j* jugal, *ica* foramen for internal

carotid artery, *itf* infratemporal fenestra, *l* lacrimal, *m* maxilla, *n* nasal, *ob* orbit, *p* parietal, *par* prearticular, *pbp* parabasisphenoid process, *pl* palatine, *pm* premaxilla, *po* postorbital, *pof* postfrontal, *pop* paroccipital process, *pr* prootic, *prf* prefrontal, *pt* pterygoid, *q* quadrate, *qj* quadratojugal, *sa* surangular, *sc* sclerotic ring, *sq* squamosal, *stf* supratemporal fenestra

fenestra half-oval in outline; neural spines in cervical vertebrae 2 to 9 longitudinally very broad, each with five pairs of small osteoderms on its top; neural spines of caudal vertebrae very tall, at least four times height of centra and longer than chevrons in midtail region; cervical ribs elongate, most of them over four times length of corresponding centra; scapula platelike, hatchet-shaped in outline.

Description

The skull of *Qianosuchus mixtus* is about 33 cm long (to the occipital edge of the skull roof). The long snout is very shallow anteriorly but becomes dorsoventrally deeper posterior to the premaxillary/maxillary suture (Fig. 2). The elongate external naris extends posteriorly over the anterior end of the antorbital fenestra, resulting in a very narrow interfenestral septum. The jugal does not enter the

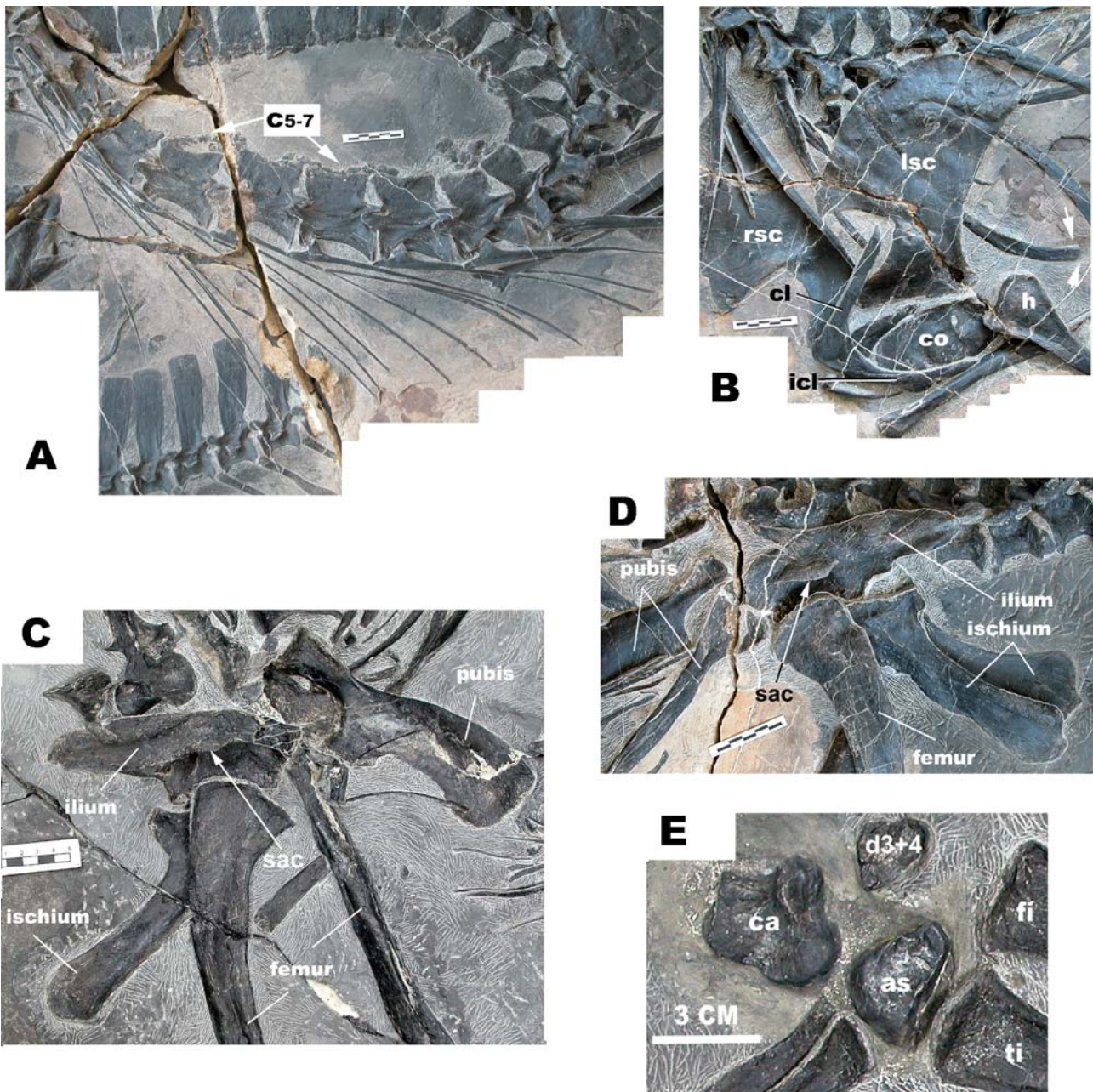


Fig. 3 *Qianosuchus mixtus* gen. et sp. nov. **a, b, d** Holotype (IVPP V13899) showing neck vertebrae with long and slender ribs, long centrum, and broad neural spine that bear five small osteoderms in **a**; shoulder girdle with short, platelike scapular and coracoid in **b**; and pelvic girdle in **d**. **c, e** Paratype (IVPP V14300) showing pelvic

girdle in **c** and ankle elements in **e**. Arrows in **b** pointing pachyostotic end of dorsal rib. Abbreviations as in Fig. 1, plus: *c5–7* cervical vertebrae 5 to 7, *d3+4* fused distal tarsals 3 and 4, *fi* fibula, *ti* tibia, *sac* supra-acetabular crest

antorbital fenestra. The orbit is filled with the sclerotic ring. In dorsal view, each frontal has a deep fossa that extends posteriorly over its suture with the parietal. A similar-sized fossa is present at the midline suture of the parietals close to the posterior edge of the skull roof. None of the palatal elements bear teeth. The mandible bears a shallow and slightly downward deflecting symphyseal region and a posteroventrally directed retroarticular process. The half oval-shaped external mandibular fenestra is relatively small. The nine premaxillary and 18 maxillary teeth are all daggerlike, being laterally compressed, posteriorly curved, and bearing a serrated crown (Fig. 1c), as in most other Triassic carnivorous archosaurians. The dentary teeth are not fully exposed because of occlusion. A pair of long rodlike hyoids, each with slightly expanded ends, is preserved.

The holotype includes nine cervical, 15 dorsal, two sacral, and 23 anterior caudal vertebrae. All caudal vertebrae bear transverse processes. The paratype includes 22 (two of which are incomplete) more distal caudal vertebrae, all of which lack transverse processes (Fig. 1b). The size of the last vertebra in this series suggests that at least ten posterior caudals are missing. Therefore, *Q. mixtus* would have had a fairly long tail of more than 50 (23+20+10) vertebrae. Centra are longer and neural spines are lower in the cervical section than in other regions. The height of longitudinally broad neural spines increases caudally, becoming two and half times that of centra in posterior dorsal and anterior tail regions, and more than four times that of centra from the 12th tail vertebra of the type to the 12th of the 22 more distal caudal vertebrae of the paratype. In the midtail region, the chevrons are as long as the neural spines, but gradually become shorter posteriorly. Small, semioval, nonsculptured osteoderms cover the top of each neural spine (five pairs in the neck and three pairs in the trunk regions) of the presacral vertebrae. They are absent in the tail region in both type and paratype. Cervical ribs are extremely long and slender, over four times the length of the correspondent centrum (Fig. 3a). The dorsal ribs are slightly pachyostotic at their distal ends (Fig. 3b).

The hatchet-shaped scapula is unusually short and thin, with a deep embayment along the anterior margin ventral to its extremely broad dorsal blade (Fig. 3b). The thin, platelike coracoid is oval in outline. The articulated clavicle and interclavicle is L-shaped in lateral view. The low dorsal blade of the ilium bears a small anterior process and large posterior process (Fig. 3c,d). A buttresslike crest is evident along the dorsal margin of the acetabulum. The pubis, longer and broader than the ischium, bears an oval obturator foramen on its expanded proximal portion. The ischium is slightly expanded at the distal end.

The humerus is lightly built and its medial margin under the inner tuberosity is not strongly arched (Fig. 3b). The femur, typical of early archosaurians, is weakly S-shaped (Fig. 1). The fibula and tibia are nearly the same in length. The anterior trochanter of the fibula is weak. The astragalus and calcaneum are crocodile-like, with a hemicylindrical calcaneal condyle, broad calcaneal tuber shaft, and convex

astragalar tibial facet (Fig. 3e). There are two distal tarsals and five metatarsals. Metatarsal V is weakly hooked proximally (Fig. 1a). Measurable length ratios between limb elements are: humerus/femur=0.721, tibia/femur=0.869, metatarsal III/femur=0.303, which are very similar to those of *Aëtosaurus* (Krebs 1965).

Discussion

Q. mixtus is unique among Triassic archosaurians in having a mosaic of specializations for both aquatic and terrestrial ways of life. The most striking feature reflecting adaptation to aquatic locomotion is the conspicuous lateral compression of the long tail. As Mazin (2001) has documented, the lateral undulation of the body is a fundamental mechanism used by reptiles for swimming, and all known early representatives of marine reptiles (e.g., primitive ichthyosaurs, nothosaurs, pachypleurosaurs, thalattosaurs, mosasaurs, some marine crocodyliforms, etc) displayed body designs consistent with propulsion by undulation, largely, of the tail. The tail is dorsoventrally expanded by high neural spines but the limbs are, in most cases, little modified (Mazin 2001). The neural spines of *Q. mixtus* are broad and high (especially in the tail region) and tail chevrons are elongate. Both are relatively higher or longer than in other marine reptiles including *Hupehsuchus nanchangensis* that is fully marine, with a laterally compressed body outline (Carroll and Dong 1991), and certainly so in the extant saltwater crocodylian, *Crocodylus porosus* (Webb et al. 1987) and marine iguana, *Amblyrhynchus cristatus* (UNMN 165832 of Smithsonian Institution). Both of the latter taxa are effective undulating swimmers, yet show less extreme adaptation of the tail skeleton and no obvious adaptive modifications of the girdles and limbs at all. This suggests that *Q. mixtus* was at least as competent, if not more competent, a swimmer.

Other potentially aquatic modifications of *Q. mixtus* include (1) a thinned platelike scapula and coracoid, (2) an elongate neck (the nine cervical vertebrae reaching 75% of the trunk length and, together with the skull, over 120% of the latter) with long and slender cervical ribs, and (3) small-sized dorsal osteoderms in the neck and trunk regions but absent in the tail region. Feature 1 is very common in marine reptiles, such as sauropterygians (Rieppel 2000), ichthyosaurs (McGowan and Motani 2002), and mosasaurs (Caldwell 1996). Feature 2 is only seen in marine protorosaurs such as *Tanystropheus* (Wild 1973) and *Dinocephalosaurus* (Li et al. 2004) among the Triassic reptiles. Feature 3, a reduction of dermal armor, is often seen in marine crocodyliforms, such as Jurassic metriorhynchids that lacked osteoderms and in extant *C. porosus* in which dorsal osteoderms are reduced in size while postoccipital and ventral osteoderms are lost. In contrast, all known Triassic terrestrial archosaurians had a well-developed scapula with a high dorsal blade and a thick coracoid with an irregular shape, a short neck with short and stout cervical ribs, and one or two pairs of large dorsal

osteoderms corresponding to each vertebra in all regions (Charig et al. 1976).

However, some features indicate that *Q. mixtus* was not obligatorily aquatic. Its pelvic girdle and hind limb differ little in morphology from those of terrestrial archosaurians, indicating that it was capable of terrestrial locomotion. The presence of the supra-acetabular crest of the ilium and well-developed ankle elements suggests that *Q. mixtus* may have had an erect posture as some of rauisuchians did (Serenio 1991). The tectonic history of the South China Block indicates that southwest Guizhou Province was entirely covered in marine water before the Jurassic, and the regional geology suggests that the limestone that yields the fossil was deposited in a near shore platform or lagoon during the Middle Triassic (Mineral Bureau of Guizhou Province 1982). This, combined with the mosaic anatomy and specimen taphonomy, suggests that *Q. mixtus* may have lived in a coastal–island environment, a situation similar to the recent saltwater *C. porosus*. *Q. mixtus* probably used the strong hind limbs to walk in land or shallow water and the long and laterally compressed tail to swim in deeper water as *C. porosus*. With daggerlike teeth and a large size, *Q. mixtus* may have dominated the fauna and preyed whatever it could reach, such as near shore nothosaurian sauropterygians and protorosaurs, and even mixosaurid ichthyosaurs and fishes (semionotids and parasemionotids), most of which commonly occur in the same beds of the new archosaurian (Wan 2002; Li et al. 2004).

The relatively long neck and elongate neck ribs may have served as an adaptation of prey capture in water. The long, slender ribs would have supported the long neck without compromising flexibility. The contraction of the *M. transversocostales cervicales* between cervical ribs (in association with the *M. iliocostalis cervicis*) on one side would have produced rapid lateral bending of the neck (Cong et al. 1988) during prey-catching in water. Bilateral contraction of these muscles would have rapidly straightened the neck and caused the ribs to simultaneously splay outward, increasing the esophageal volume. The suction created would have neutralized the pressure waves generated as its head lunged forward (Li et al. 2004). This would have resulted in a forceful strike at prey in the water, permitting large preys to be subdued.

Our phylogenetic analysis, based on an existing data matrix (see S1 and S2 for details in Electronic Supplementary Information), suggests that *Q. mixtus* is grouped within the lineage (the Crurotarsi) toward the *Crocodylomorpha* and shares with other members of this lineage at least seven unequivocal synapomorphies (see S3 for details in Electronic Supplementary Information). Relationships of *Q. mixtus* within the lineage are uncertain. More extensive preparation of the pelvic girdle may provide further information on its phylogenetic relationships at a lower level. Although *Q. mixtus* was not fully aquatic, it was unquestionably the first known archosaurian to have explored and adapted to a marine environment in the Triassic, which was independently exploited by Jurassic marine crocodyliforms more than 40 million

years later and the saltwater species of extant *Crocodylus*. Its mosaic anatomy indicates a more complicated evolutionary history of the Archosauria than previously thought.

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