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ARTICLE

A NEW ARCHOSAUR (DIAPSIDA, ARCHOSAURIFORMES) FROM THE MARINE TRIASSIC OF CHINA

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ABSTRACT—A new Middle Triassic archosaur, *Diandongosuchus fuyuanensis*, gen. et sp. nov., is described on the basis of a skeleton from the Zhuganpo Member (Ladinian) of the Falang Formation, eastern Yunnan Province, China. It is primarily characterized by the nasal process of the premaxilla extending posteriorly well beyond the external naris, the super-sized coracoid foramen laterally bordered by the scapula, the ischium with a strongly expanded medial portion anteroposteriorly longer than the proximodistal height of the bone, and anteriorly notched cervical osteoderms. *D. fuyuanensis* is a pseudosuchian on the basis of the crocodile-normal tarsal joint and other features, such as the distal end of the ulna in posterolateral view squared off, osteoderms with a distinct anterior process, the presacral vertebrae dorsally covered by more than one osteoderm, dorsal osteoderm alignment dorsal to presacrals 10–24 staggered, the pubis-ischium contact reduced to a thin proximal contact, and the medial contact of the ischia extensive but the dorsal margins separate. It is from a marine deposit but shows few morphological adaptations of the postcranial skeleton for a semiaquatic way of life when compared with *Qianosuchus* from the Anisian limestone of the same area. A phylogenetic analysis derived from an existing data matrix suggests that the new archosaur occupies the basal-most position in Poposauroidea and further confirms the poposauroid status of *Qianosuchus*. On the basis of current information, the discovery of *Diandongosuchus* does not firmly underscore the affinity of the semiterrestrial vertebrate faunas between the eastern and western regions along the northern coastline of the Tethys.

INTRODUCTION

The Archosauria (sensu Gauthier, 1986), the crown group of the traditional ‘archosaur’ clade (Benton, 1990, 2004), originated in the Early to Middle Triassic and consists of dinosaurs, including birds, pterosaurs, and crocodylomorphs (Gauthier et al., 1988; Gower and Wilkinson, 1996). Its early members were long considered to live in terrestrial ecosystems (Charig and Sues, 1976; Chatterjee, 1978; Parrish, 1993; Juul, 1994; Wu and Russell, 2001) until the discovery of *Qianosuchus* from the Middle Triassic (Anisian) marine Guanling Formation of Guizhou, China, which is semiaquatic and clearly demonstrates adaptation to a marine ecosystem (Li et al., 2006).

Recently, another archosaur specimen was collected from the Middle Triassic Zhuganpo Member of the Falang Formation in Fuyuan County, eastern Yunnan Province, China, less than 50 km southwest of the *Qianosuchus* locality. The Falang Formation is thought to represent a sequence of sediments deposited in a shelf sea during the Ladinian on the basis of its lithology and invertebrate fossils (Guizhou Bureau of Geology and Mineralogy, 1997). In addition to the diverse fish fauna and the terrestrial protorosaur *Macrocnemus* (Li et al., 2007), various marine reptiles such as nothosaurs, placodonts, pachypleurosaur-like animals, pistosaurs, some protorosaurs, and thalattosaurs are known from the Zhuganpo Member (Li et al., 2002; Cheng et al., 2004, 2006; Li, 2007; Rieppel et al., 2006, 2010; Zhao et al., 2008a, 2008b, 2008c; Sato et al., 2010). The new archosaur had few postcranial anatomical modifications for an aquatic way of life, although its large external naris is relatively posteriorly positioned as in *Qianosuchus*, the proterochampsid *Chanaresuchus* from the Middle Triassic of Argentina (Romer, 1971), and the semiaquatic spinosaurid dinosaurs (Sereno et al., 1998; Amiot et al., 2010), and its skull roof bones are ornamented by pits, grooves, and ridges.

Here, we describe the osteology of the new archosaur and analyze its phylogenetic relationships within the Archosauria. As revealed by the following phylogenetic analysis, a set of skeletal features and the crocodile-normal pattern of the tarsals suggest that the new archosaur can be attributed to the Pseudosuchia (sensu Nesbitt, 2011) and, therefore, the anatomical comparisons in the following text will be made mainly with pseudosuchian archosaurs.

Institutional Abbreviations——**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **UFRGS**, Institute of Geosciences, Federal University of Rio Grande de sul, Porte Alegre, Brazil; **ZMNH,** Zhejiang Museum of Natural History, Hangzhou, China.

Anatomical Abbreviations——**ac**, acetabulum; **aic**, atlas intercentrum; **amp**, medial process of articular; **an**, angular; **aof**, antorbital fossa; **apcr**, anterior process of cervical ribs; **ar**, articular; **as**, astragalus; **atna**, atlas neural arch; **atr**, atlas rib; **ax**, axis; **axc**, axial centrum; **axna**, axial neural arch; **axnp**, axial neural spine; **axr**, axial rib; **bra**, braincase; **ca**, calcaneum; **cal**, carpal; **caos**, caudal osteoderm; **cav1**, **cav5**, caudal vertebrae 1, 5; **cgs**, central segment of gastralia; **chr**, chevron; **cl**, clavicle; **co**, coracoid; **cof**, coracoid foramen; **cos**, cervical osteoderm; **cr**, cervical rib; **cr4**, **cr7**, **cr8**, cervical ribs 4, 7, 8; **cv5**, **cv8**, cervical vertebrae 5, 8; **d**, dentary; **dip**, diapophysis; **dlp**, deltopectoral process; **dt3**, **dt4**, distal

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tarsals 3, 4; **dv3**, dorsal vertebra 3; **ec**, ectopterygoid; **en**, external naris; **eo**, exoccipital; **f**, frontal; **fi**, fibula; **fil**, facet for ilium; **fis**, facet for ischium; **fpu**, facet for pubis; **fqi**, facet for quadratojugal; **fsc**, facet for scapula; **fsr1+2**, facets for sacral ribs 1+2; **fsy**, symphysial facet of dentary; **gl**, glenoid; **h**, humerus; **hy**, hyoid; **icl**, interclavicle; **il**, ilium; **is**, ischium; **j**, jugal; **l**, lacrimal; **lf**, left femur; **los**, limb osteoderm; **m**, maxilla; **mfis**, medial facet for ischium; **n**, nasal; **ob**, orbit; **od**, odontoid process; **os**, osteoderm; **p**, parietal; **par**, prearticular; **pat**, proatlas; **pbp**, parabasisphenoid process; **pf**, prefrontal; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pop**, paroccipital process; **ptbs**, pit for M. triceps brachii; **prq**, pterygoid ramus of quadrate; **pt**, pterygoid; **pu**, pubis; **q**, quadrate; **qh**, quadrate head; **qj**, quadratojugal; **qrp**, quadrate ramus of pterygoid; **ran**, right angular; **ra**, radius; **rap**, retroarticular process; **rf**, right femur; **ro**, roller; **sa**, surangular; **sc**, scapula; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **sr1**, **sr2**, sacral ribs 1 and 2; **stc**, stomach content; **stf**, supratemporal fenestra; **sv1**, sacral vertebra 1; **ti**, tibia; **trf**, transverse flange; **trp**, transverse process; **vg**, ventral groove; **ul**, ulna; **I to V**, metacarpals or metatarsals I to V.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAUROMORPHA Huene, 1946 sensu Benton, 1985
ARCHOSAURIFORMES Gauthier, Kluge, and Rowe, 1988
ARCHOSAURIA Cope, 1869 sensu Gauthier, 1986
PSEUDOSUCHIA Zittel, 1887–1890 sensu Nesbitt, 2011
POPOSAUROIDEA Nopcsa, 1923, sensu Nesbitt, 2011
DIANDONGOSUCHUS, gen. nov.

Type and Only Species——*Diandongosuchus fuyuanensis*, sp. nov.

Diagnosis——As for the type and only species.

Distribution——As for the type and only species.

Etymology——The generic name is derived from 'Diandong,' indicating the easternmost part of Yunnan Province where the specimen was collected.

DIANDONGOSUCHUS FUYUANENSIS, sp. nov.
(Figs. 1–6)

Holotype——ZMNH M8770, a nearly complete skeleton with most of the caudal vertebrae missing.

Locality and Horizon——West of Huangnihe River, southeast Fuyuan County, Yunnan Province; Zhuganpo Member (Ladinian) of the Falang Formation, late Middle Triassic (Chen, 1985).

Etymology——The specific name refers to Fuyuan County, where the holotype specimen was excavated.

Diagnosis——A small- to medium-sized poposauroid, differing from other poposauroids in having the combination of the following derived character states: anterodorsal (nasal) process of premaxilla extending posteriorly well beyond external naris; presence of a fossa expanded in anteroventral corner of external naris; squamosal with supratemporal fossa in posterior portion and distinct ridge on dorsal surface along edge of supratemporal fossa; external naris neither terminal in position nor close to antorbital fossa; jugal with pronounced longitudinal ridge on lateral surface and anterior process much broader than the posterior process underlying anterior process of quadratojugal; supratemporal fossa present anterior to supratemporal fenestra; coracoid foramen super-sized and laterally bordered by scapula; ischium with a strongly expanded medial portion anteroposteriorly longer than the proximodistal height of the bone; metatarsal IV the longest; narrowed anterior margin of cervical osteoderms deeply concave; snout about 2.5 times longer than post-snout region along dorsal midline of skull; premaxilla with nine teeth (shared with *Qianosuchus*); and maxilla excluded from external naris (shared with *Poposaurus*).

DESCRIPTION

The skeleton is articulated from the skull to the eighth caudal vertebra or to the 21st pair of caudal osteoderms. It is embedded in a slab of clay-limestone and much of the right lateral side of the skeleton is available for examination, except for the trunk, which is exposed in ventrolateral view, showing the gastralia and stomach content (Fig. 1). The skull was taken out of the slab and prepared on both sides. The preserved length of the specimen is about 97 cm and the length of the body (from the last sacral vertebra to the snout tip of the skull) is about 77 cm. The specimen may have reached a total length of 155 cm in life if the tail length occupies 53% to 54% of the total length as in the extant *Alligator sinensis* (Cong et al., 1998).

Skull and Mandible

The skull is severely flattened towards the right side and practically two-dimensional (Figs. 2, 3). The left side is better preserved than the right. It is about 24 cm long from the tip of the snout to the quadrate condyle on the right side. The snout, the portion anterior to the orbit, is about 2.5 times longer than the rest of the skull along the dorsal midline, which is proportionally similar to *Qianosuchus* but still much shorter when compared with phytosaurs such as *Parasuchus* (Chatterjee, 1978) and *Mystriosuchus* (Hungerbühler, 2002). The mandible is about 25 cm long from the anterior tip to the end of the retroarticular process (right side), being 13 cm shorter than that of *Qianosuchus*. All openings or fossae are preserved on the left side of the skull, although many of them are slightly distorted. The external naris should have been an elongate oval in life, although it is distorted by the anterior thrust of the anteroventral process of the nasal. The naris is not terminal in position, but is placed at a level posterior to the sixth premaxillary tooth as in *Qianosuchus*, although it is smaller than that of the latter. The relatively posterior position of the naris is also comparable to the condition in the proterochampsian *Chanaresuchus* (MCZ 4039) and the pterosaur *Eudimorphodon* (Wild, 1978), but the premaxillary portion anterior to the naris bears fewer teeth in those taxa. The posterior margin of the naris is widely separated from the antorbital fossa as in many other archosauriforms such as *Proterosuchus* (Cruickshank, 1972), *Saurosuchus* (Alcober, 2000), *Postosuchus* (Chatterjee, 1985), *Sphenosuchus* (Walker, 1990), and *Dibothrosuchus* (Wu and Chatterjee, 1993); it differs from the condition in *Qianosuchus* and phytosaurs (Chatterjee, 1978; Hungerbühler, 2002; Stocker, 2010) where the posterior margin of the naris extends beyond the anterior edge of the antorbital fenestra. The antorbital fossa is roughly triangular in outline, unlike the elongate oval of *Qianosuchus*, and contains an elliptical antorbital fenestra near the anteroventral corner as in the basal archosauriforms *Proterosuchus*, *Erythrosuchus* (Gower, 2003), and *Euparkeria* (Ewer, 1965). The orbit is circular in outline and similar to that of *Aetosaurus* (Schoch, 2007) but larger than the antorbital fossa. Circumorbital bones form an elevated rim that extends anteriorly to the dorsal margin of the antorbital fossa and posteriorly to the dorsal margin of the infratemporal fenestra: a similar condition is known in *Saurosuchus*, *Chanaresuchus*, *Qianosuchus*, and *Turfanosuchus* (Wu et al., 2001). The supratemporal fossa is slightly distorted by the anteromedial displacement of the squamosal. It is smaller than the orbit, oval in shape, and diagonal in orientation with respect to the dorsal midline. The bones surrounding the supratemporal fossa form an elevated supratemporal rim as for the orbit mentioned earlier. The supratemporal fenestra occupies much of the lateral part of the supratemporal fossa. The infratemporal fenestra is distorted but may have been roughly

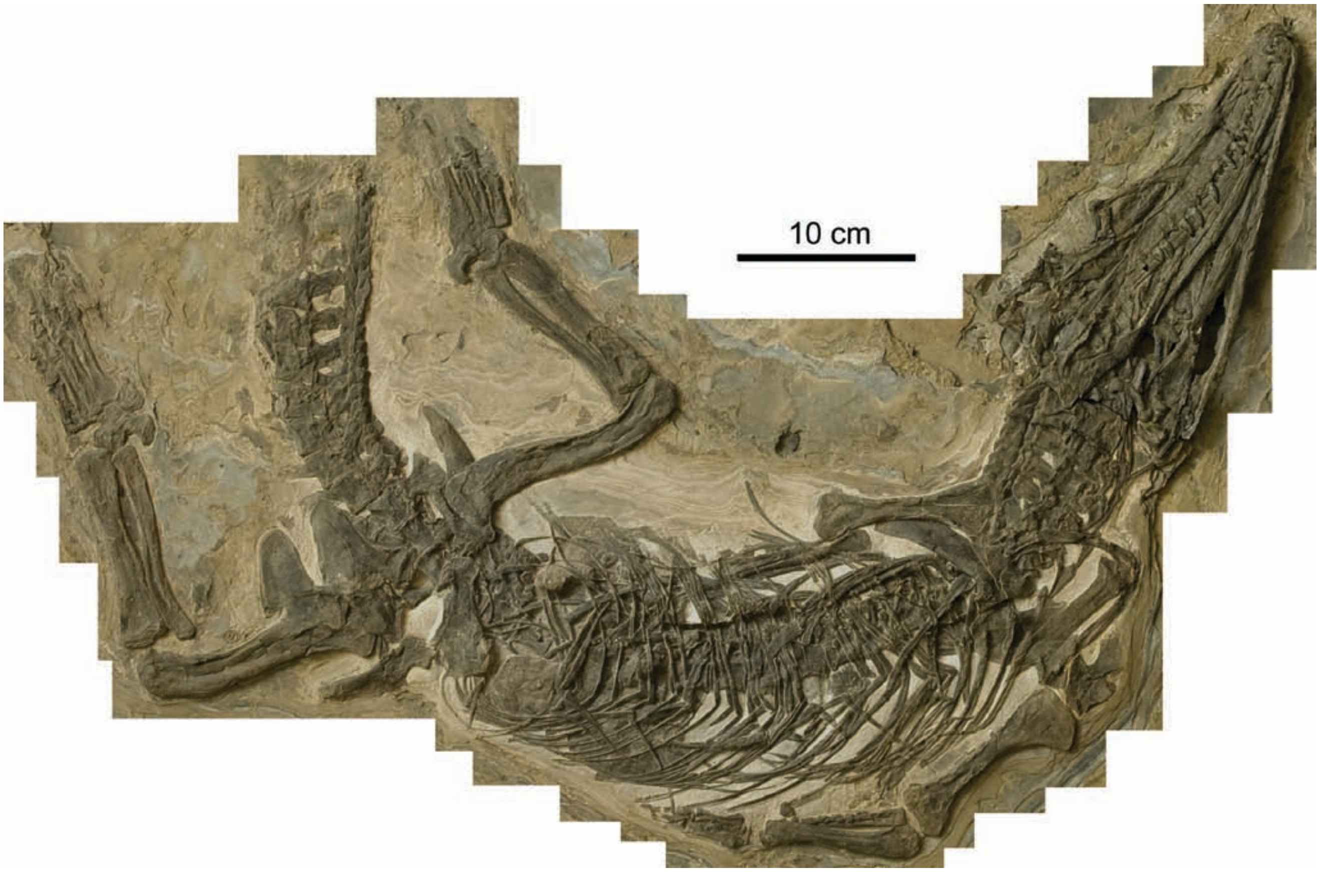

FIGURE 1. Skeleton of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770).

triangular in outline as in *Qianosuchus* and *Riojasuchus* (Sereno, 1991), with the anterior and ventral margins straight, the short dorsal margin slightly arched, and the posterior margin projecting strongly into the fenestra. The posttemporal fenestra is common in some archosauriforms such as phytosaurs (Hungerbühler, 2002) and aetosaurs (Schoch, 2007) but cannot be observed in this specimen because of the flattening of the skull. The outline of the external mandibular fenestra is obscured due to damage, but the remaining edges suggest an elongate shape, unlike the triangular shape of the fenestra in *Qianosuchus*.

The premaxilla is much larger than in other archosauriforms except for phytosaurs (Chatterjee, 1978; Hungerbühler, 2002) and the pterosauromorph *Eudimorphodon*. It is most similar to that of *Qianosuchus*, the proterochampsian *Chanaresuchus*, and the pseudosuchian *Effigia* (Nesbitt and Norell, 2006) in that the portion anterior to the external naris is much longer than the posteroventral process. Its anterodorsal (nasal) process is much larger than the posterodorsal (maxillary) process and extends posteriorly well beyond the external naris as in *Eudimorphodon*; this appears to be unique among the Pseudosuchia. The dental margin of the premaxilla is noticeably convex as in *Qianosuchus* and the phytosaur *Smilosuchus* (Nesbitt, 2011:fig. 7J). Posteriorly, the base of the elongate nasal process forms the anterodorsal margin of the external naris, whereas the short maxillary process forms the anterior half of the ventral margin of the naris. There is a shallow fossa anterior to the external naris on the lateral surface of the premaxilla, which is absent in *Qianosuchus* and other members of the Poposauroidea (sensu Nesbitt, 2011). The external surface is well ornamented by pit-grooves and short ridges. The palatal portion cannot be observed due to the occlusion of the mandible.

The nasal is the longest bone among the roof elements, extending posteriorly over the anterior border of the orbit. Its anterior end is forked and its posterior end tapers. Of the two rami of the anterior fork, the longer dorsal ramus forms the dorsalmost margin of the external naris. The shorter ventral ramus lines the posteroventral margin of the naris and meets the premaxilla to exclude the maxilla from the external naris: this condition is known in many archosaurs such as *Gracilisuchus* (Romer, 1972), *Saurosuchus*, and *Sphenosuchus* but not in other taxa such as *Qianosuchus*, *Xilousuchus* (Wu, 1981; IVPP V6068), *Batrachotomus* (Gower, 1999), and *Aetosaurus*. The nasals meet along the midline except for the anterior one-third; posteriorly, each nasal sends a projection that wedges between the frontal and prefrontal. The nasal has sutures with the premaxilla, maxilla, and lacrimal laterally to form a nearly straight line. The nasal-prefrontal suture has a weak convexity close to the nasal-lacrimal suture. There are short ridges and grooves on the external surface of the bone.

The frontals are about one-third the length of the nasal. They are widest in the interorbital region where the bones enter the orbits; they narrow anteriorly and posteriorly, and are truncated at both ends. The dorsal surface is extensively ornamented with short ridges and grooves. A weak but distinct ridge parallels the midline ridge on each frontal. Sutures with the nasal, prefrontal, postfrontal, and parietal are clearly marked. The ventral structures of the bone are not exposed.

The parietals are short but widen posterolaterally. In dorsal view, the parietal comprises a portion of the skull roof, a recessed

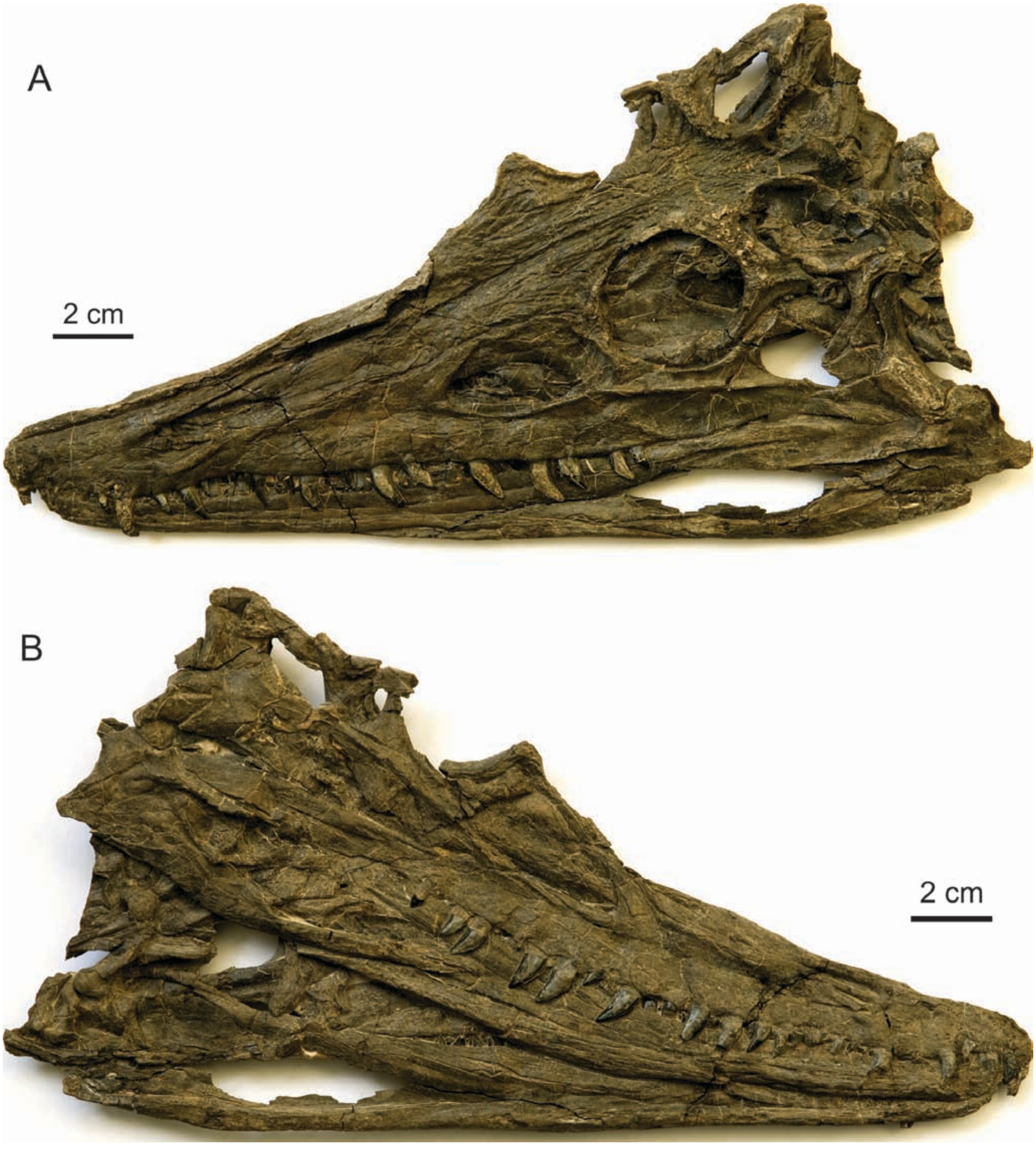

FIGURE 2. Skull and mandible of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770), in left dorsolateral (**A**) and right ventrolateral (**B**) views.

part within the supratemporal fossa, and a posterolateral process. The roof portion is anteriorly broad and constricted in the interfenestral region. The dorsal surface of the roof portion is extensively ornamented with short ridges and grooves, as on the frontal. The recessed part forms most of the supratemporal fossa. The posterolateral process is a thin layer of bone, nearly vertical in orientation; it forms the major part of the deeply incurved occipital edge and underlies the parietal process of the squamosal. Anterolaterally, the parietal meets the postorbital just anterior to the supratemporal fossa, excluding the postfrontal from the latter. Both the occipital and ventral surfaces of the parietal are not exposed.

The maxilla is slightly shorter but broader than the nasal in dorsal view, and most similar to that of *Proterosuchus* in having

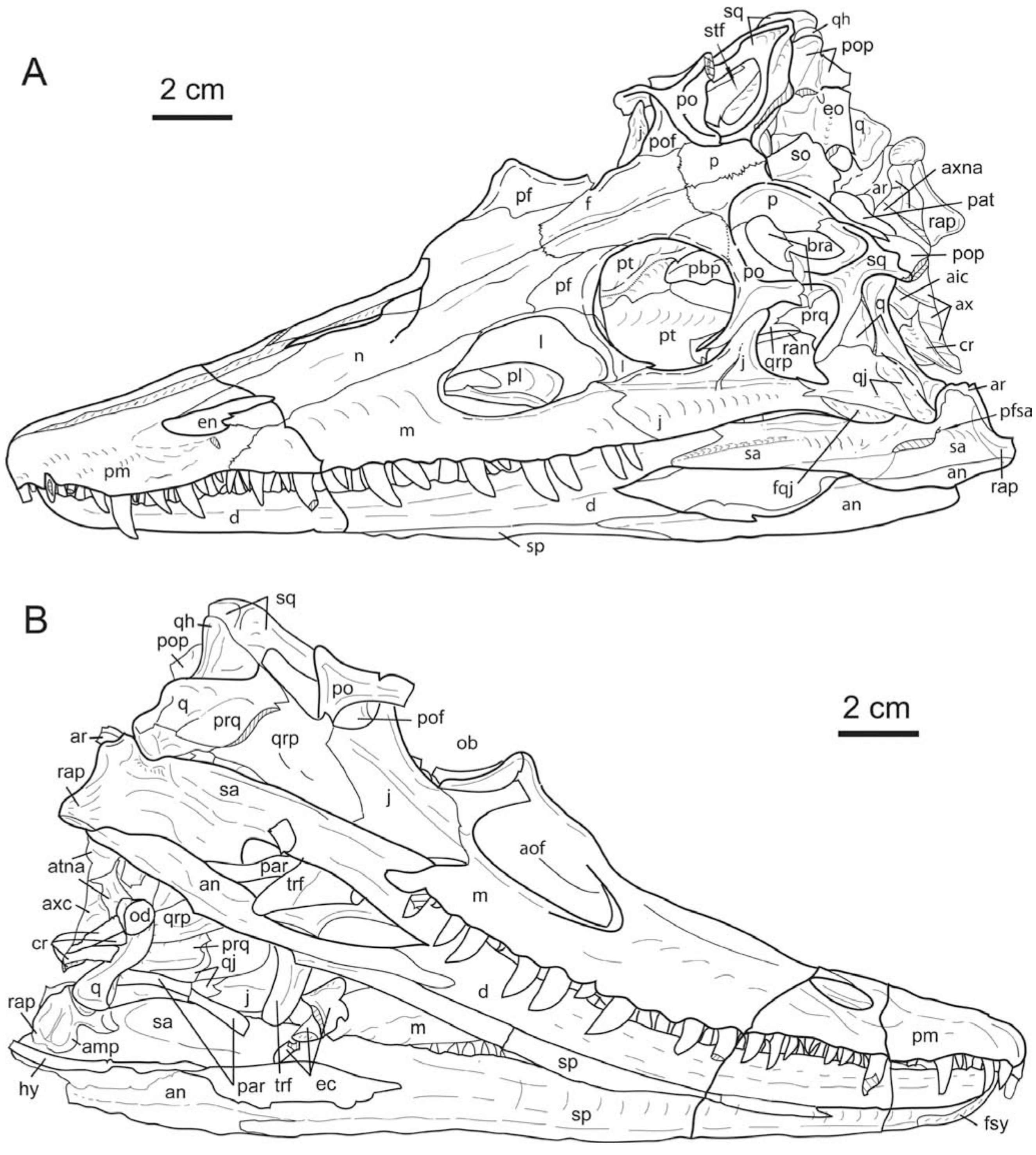

FIGURE 3. Outlines of the skull and mandible of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770), in left dorsolateral (**A**) and right ventrolateral (**B**) views. See text for abbreviations.

a large antorbital portion. Anteriorly, the maxilla narrows and meets the premaxilla posteroventral to the external naris. The dorsal process is triangular and posterodorsally directed; it forms the anterior border of the antorbital fossa, and the narrow tip inserts between the nasal and the lacrimal. The posteroventral process of the maxilla forms the anteroventral half of the margin of the antorbital fossa. There is a longitudinal ridge along the posteroventral margin of the antorbital fossa, which is the anterior continuation of a ridge on the jugal (see below). The lateral surface is uneven in the anterior portion, with pits, short grooves, and ridges scattered around, but it becomes concave and weakly ornamented posteriorly. The dental margin is slightly convex but distinctly concave near the suture with the premaxilla. The maxilla-jugal suture is zigzagged and extends posteroventrally. The palatal shelf of the maxilla is not exposed.

The triangular prefrontal most resembles that of *Qianosuchus*, with a stout anterior process between the nasal and lacrimal and forming the anterodorsal rim of the orbit. The dorsal surface is rugose, with distinct short ridges and grooves; among those ridges, the one forming the part of the orbital rim is the most pronounced. The prefrontal does not enter the antorbital fossa. Sutures with the nasal, lacrimal, and frontal are clearly marked. The ventral portion (the descending pillar) is observed through the orbit but cannot be detailed because of the flattening of the skull.

The lacrimal is a roughly crescent-shaped bone and much larger than the prefrontal. In lateral view, the bone is much broader than in *Qianosuchus*. The large anterior part of the bone is recessed in the antorbital fossa as in many archosauriforms such as *Euparkeria*, *Chanaresuchus*, *Gracilisuchus*, and aetosaurs. The posterior portion posterior to the fossa is anteroposteriorly narrow, with a strong ridge to form the anteroventral part of the orbital rim posteriorly and meet the elevated posteroventral margin of the antorbital fossa ventrally. The recessed anterior part forms the posterior and dorsal borders of the antorbital fenestra. The lacrimal foramen is situated at the lacrimal-prefrontal suture slightly medial to the orbital rim.

The postfrontal is well preserved on the right side, and its morphology is most similar to that of *Euparkeria* and *Gracilisuchus*. It is triangular in outline, occupying the posterodorsal corner of the orbital edge. Medially, the postfrontal meets the frontal and barely contacts the parietal. Posteriorly, the postfrontal meets the postorbital and is excluded from the supratemporal fossa by the parietal-postorbital contact. The observable surface bears ridges and grooves.

The triradiate postorbital is generally similar to that of non-crocodylomorph archosauriforms but distinct in that the posterior ramus is short and distally not sharply pointed. The dorsomedial ramus is distally pinched off and meets the parietal and the short posterior ramus meets the squamosal. In dorsal view, the postorbital is recessed posteromedially to form the anterolateral part of the supratemporal fossa and encloses the supratemporal fenestra. The descending ramus is the largest and tapers off distally along the orbit. The posterodorsal portion of this ramus is recessed as well to form the anterodorsal margin of the infratemporal fenestra. The external surface of the postorbital consists of grooves and ridges.

The squamosal consists of four processes. It differs from that of *Qianosuchus* and many other archosauriforms such as phytosaurs, *Gracilisuchus*, *Batrachotomus*, and *Turfanosuchus* in that its stout anterior (postorbital) process is distally truncated and receives the narrow overlap of the postorbital anteriorly. The anterior process forms the posterior portion of the upper temporal bar. The posteromedial (parietal) process is nearly vertical in orientation and distally thinned. These two processes are medially recessed to form the posterolateral part of the supratemporal fossa and enclose the supratemporal fenestra. The descending process is the longest and is larger than that of *Qianosuchus*; it tapers distally, projects anteroventrally into the infratemporal fenestra, and forms the majority of the posterior margin of the latter as in the ornithosuchid *Riojasuchus*. This process contacts the quadrate posteriorly and the quadratojugal ventrally. The posterolateral process is the smallest; it, together with the base of the descending process, caps the dorsal head of the quadrate anteriorly and meets the paroccipital process of the exoccipital posteriorly. The external surface of the squamosal is noticeably rugose, with pronounced ridges and grooves. No ventral structures of the squamosal are exposed.

The jugal is triradiate and shorter than the maxilla as in *Proterosuchus* and *Qianosuchus*. It differs from that of *Qianosuchus* and many other pseudosuchians such as *Gracilisuchus*, *Effigia*, and *Arizonasaurus* (Nesbitt, 2005) in having a very broad anterior process and a narrow posterior process. The anterior end of the anterior process forms a fork and meets the maxilla ventrally and the lacrimal dorsally. The dorsal edge of the anterior process forms the ventral part of the pronounced orbital rim. The posterior process is nearly as long as the anterior process but it is dorsoventrally about half the broadness of the latter, and its ventral edge is concave. Posteriorly, the process tapers and underlines the quadratojugal. The relatively short ascending process directs dorsally and slightly posteriorly; the pointed distal tip wraps the posterior side of the descending ramus of the postorbital. In lateral view, there is a robust ridge that extends anteriorly to meet the antorbital rim but diminishes posteriorly before the jugal-quadratojugal suture. The external surface of the jugal is smoothly concave ventral to this ridge.

The quadratojugal is a plate-like bone, most similar to that of many phytosaurs such as *Parasuchus* and *Mystriosuchus* (Hungerbühler, 2002). It lies decumbently at the posteroventral corner of the skull. It is distinct in that its small jugal process is anteriorly forked and overlaps the jugal to form the posterior third of the ventral margin of the infratemporal fenestra. The main body of the quadratojugal has a prominence near the posterior margin. The wide posterior edge of the bone abuts against the ventrolateral side of the quadrate. Posteroventrally, the quadratojugal appears to join the formation of the mandibular condyle. The external surface lacks ornamentations except for the prominence near the posterior margin.

Exposure of the quadrate is limited due to compression. The body is column-like, with a concave posterior margin and a triangular anterolateral process inserting between the descending process of the squamosal and the quadratojugal. The presence of the quadrate foramen is obscured by cracks along the boundary with the quadratojugal. The well-developed condyle is still articulated with the articular. The large dorsal cephalic head is capped by the squamosal but laterally exposed as in *Qianosuchus*. The pterygoid ramus of the left quadrate is visible in the infratemporal fenestra, showing the slightly convex lateral surface; the medial surface, seen through the other side, is concave.

The palatal elements are only partly observed in the antorbital fenestra, the orbit, and the infratemporal fenestra of the left side, and in ventral view on the right side. The anterolateral part of the palatine is exposed in dorsal view in the antorbital fenestra; this part shows an embayment in the anterior edge, which may represent the posterior margin of the internal choana. The pterygoid exposed in the orbit is mainly the palatal process of the bone in dorsal view; the exposed part is broad and thin. The left pterygoid partly overlaps the right pterygoid; the latter appears to be folded but this may have been caused by severe distortion. The quadrate ramus of the left pterygoid is partly visible in the infratemporal fenestra on the both sides. It is a sheet of bone nearly vertically oriented; its medial surface is concave and its posterior end is overlapped by the pterygoid ramus of the quadrate. The transverse flange of the pterygoid is exposed on the right side; it is a massive process directed ventrally and slightly posteriorly, and its lateral side is thickened. The ectopterygoid is completely exposed in ventral view, although it is broken into three pieces. It is a small bone that consists of a short but broad medial part to contact the pterygoid flange and a long and distally pointed posterolateral process that may have articulated with the maxilla and jugal. The ectopterygoid lacks an anterolateral process as in many other pseudosuchians such as *Postosuchus*. Its anterior edge and ventral surface are slightly concave.

Small portions of the braincase can be observed through the orbit and the temporal fenestrae of the left side, and on the occipital surface. The exposed parts in the supratemporal and the infratemporal fenestrae are barely visible owing to compression. The tongue-like process exposed in the posterodorsal corner of the orbit may be the anterior part of the parabasisphenoid process in lateral view; it bears a midline groove on the dorsal surface. A flat bone posterior to the parietal may represent the supraoccipital. This bone bears a ridge along the dorsal midline, which disappears before reaching the ventral edge of the bone; sutures with the parietal and exoccipital are ridged. The lateral sides of the midline ridge are shallowly concave. The only part of the exoccipital available for examination is the right paroccipital process, which contacts the cephalic head of the quadrate at its lateral end.

The dentary is large and occupies over two-thirds of the total mandibular length. It is anteriorly shallow and posteriorly deep. It appears that the posterior edge of the bone had three processes: one meeting the surangular and two binding the angular. The dorsal two processes form the anterior border of the external mandibular fenestra. In lateral view, the bone surface is uneven, especially in the anterior half, and extensively ornamented by longitudinal pit-grooves and ridges. The occlusal margin is mostly covered by the upper jaw and teeth; the ventral edge of the bone is nearly straight. The symphysis is displaced and the left facet is exposed. The dentary is tightly articulated with the splenial on the medial side, and their sutures are hardly recognizable.

The left surangular is better preserved than the right. It is forked anteriorly and the ventral process of the fork may have joined in the anterodorsal border of the external mandibular fenestra. The dorsal process of the anterior fork is more slender than the ventral process but not completely exposed, which obscures the presence or the absence of the anterior foramen seen in *Proterosuchus* and *Euparkeria*. Posteriorly, the surangular broadens and extends to the end of the retroarticular process, as in many pseudosuchians such as aetosaurs (Schoch, 2007), *Effigia*, and *Sphenosuchus*. The lateral surface of the bone is ornamented with ridges, including a short ridge along the posterodorsal margin, a relatively long ridge dorsal to the suture with the angular, and a short and curved ridge around the articular fossa. The posterior surangular foramen seen in the aforementioned two archosauriforms (Nesbitt, 2011) is present but the presence of the foramen is obscured on the right surangular owing to surface damage. The dorsal margin of the bone is slightly convex. Medially, the adductor chamber is broad but shallow, which may have been exaggerated by the flattening.

The angular is incomplete on both sides. Anteriorly, it pinches off into a sharp process to underlie the posteroventral process of the dentary laterally and meet the splenial medially, as in *Qianosuchus* and other archosauriforms such as *Proterosuchus*, *Gracilisuchus*, and *Batrachotomus*. Posteriorly, the bone narrows and extends posteriorly close to the end of the retroarticular process. Posteromedially, the angular forms the ventral border of the adductor chamber.

The left articular is well exposed in medial view. It is a stout bone, barely visible in lateral view owing to the surangular and the angular. In medial view, the articular fossa broadens medially, and there is a ridge just ventral to the fossa. In posterior view, the retroarticular process is short but robust, with a short medial process broadening the dorsal surface of the process. The retroarticular process faces posteriorly and slightly dorsally and bears a fossa that is further divided longitudinally by a weak septum. The distal end of the retroarticular process tilts downward and is much lower than the articular fossa in position.

The splenial is a large bone and more extensively exposed on the left side than the right. It is tightly articulated with the dentary on the medial surface of the mandible. Relationships with the neighboring elements are obscured by poor preservation and it is uncertain whether it joined the mandibular symphysis.

The left prearticular was displaced from the ventral margin of the mandible to the posterodorsal edge on the medial surface. It is a strap of bone, with both ends slightly broadened. It is slightly convex dorsally and concave ventrally. Its relationships with other elements remain unknown.

The rod-like bone just dorsal to the surangular-angular suture on the medial surface of the mandible on the left side is identified as a segment of the left hyoid. It is structurally simple and somewhat curved posteriorly.

The dentition of the upper jaw bears nine premaxillary teeth, as in *Qianosuchus*, but only 15 maxillary teeth, three fewer than in *Qianosuchus*. Most archosauriforms have five or fewer premaxillary teeth, although *Proterosuchus* and *Archosaurus* (Tatarinov, 1960) have six and phytosaurs have more than 10 (Nesbitt, 2011). The teeth are similar to those of *Qianosuchus* and many other archosauriforms such as *Proterosuchus*, *Shansisuchus* (Young, 1964), *Fugusuchus* (Cheng, 1980), *Saurosuchus*, and *Postosuchus*, exhibiting typical carnivorous archosauriform tooth morphology. They are homodont in morphology but heterodont in size. All of the upper teeth are dagger-like and curve posteriorly. They are serrated along the anterior and posterior carinae; the serrations extend along the entire posterior carina, but only the apical portion of the anterior carina, especially in functional teeth. Both the lingual and the labial surfaces of the teeth are slightly convex. Among the nine premaxillary teeth of the right side, the fifth tooth is the largest and located at the peak of the convex dental edge, and the ninth tooth is the smallest. Dentary teeth are similar to those of the upper jaw in both shape and size variation. The exact number of the dentary teeth remains unknown because of the occlusion of the jaws.

Vertebral Column

The vertebral column is articulated with the skull (Fig. 1). The anterior end is overlapped by the occiput so that the elements of the atlas and the proatlas are poorly exposed. The vertebral centra are severely flattened, exaggerating vertebral height. The preserved vertebral column consists of 25 presacral, two sacral, and the first seven caudal vertebrae (Fig. 4B).

The plate-like proatlas is displaced towards the left side. It is largely covered by the skull and its entire outline cannot be determined (Figs. 2, 3). Elements of the atlas are disarticulated and represented by the intercentrum and the left atlantal neural arch. The intercentrum exposed with the skull on the left side is preserved in ventral view, but detailed morphology is not available because of the overlying quadrate. The partly exposed medial surface of the preserved right neural arch is significantly concave and its dorsal spine is longitudinally broad, with a tip bending medially (Fig. 3B).

The axis is characterized by a high and broad neural spine, of which the dorsal margin is nearly straight (Fig. 4A); the axial neural arch is posterodorsally expanded, arched, or concave in other archosauriforms such as *Chanaresuchus*, *Arizonasaurus*, *Batrachotomus* (Gower, 2009), *Gracilisuchus*, or *Postosuchus*. The anterior portion of the spine is not observable (Figs. 2–4). The posterior margin of the axial spine is notably concave. The odontoid process is disarticulated from the axial centrum; the latter is relatively short and laterally concave. The postzygapophysis is much more pronounced than the prezygapophysis. Much of the neurocentral suture is untraceable, indicating that the specimen is at least a young adult (Brochu, 1996).

Cervical vertebrae 3–7 are well exposed in right lateral view (Fig. 4A), and differ from those of *Qianosuchus* in their shorter centra and taller neural spines, as indicated by the following ratios. In *Qianosuchus*, the centrum of cervical 5 is about 2.9 times longer than that of dorsal 13 and the neural spine height of cervical 5 (dorsal to the prezygapophysis) reaches about 0.46 of the total vertebral length (IVPP V143000). However, these ratios are 0.93 and 1.0, respectively, in *Diandongosuchus*. All of

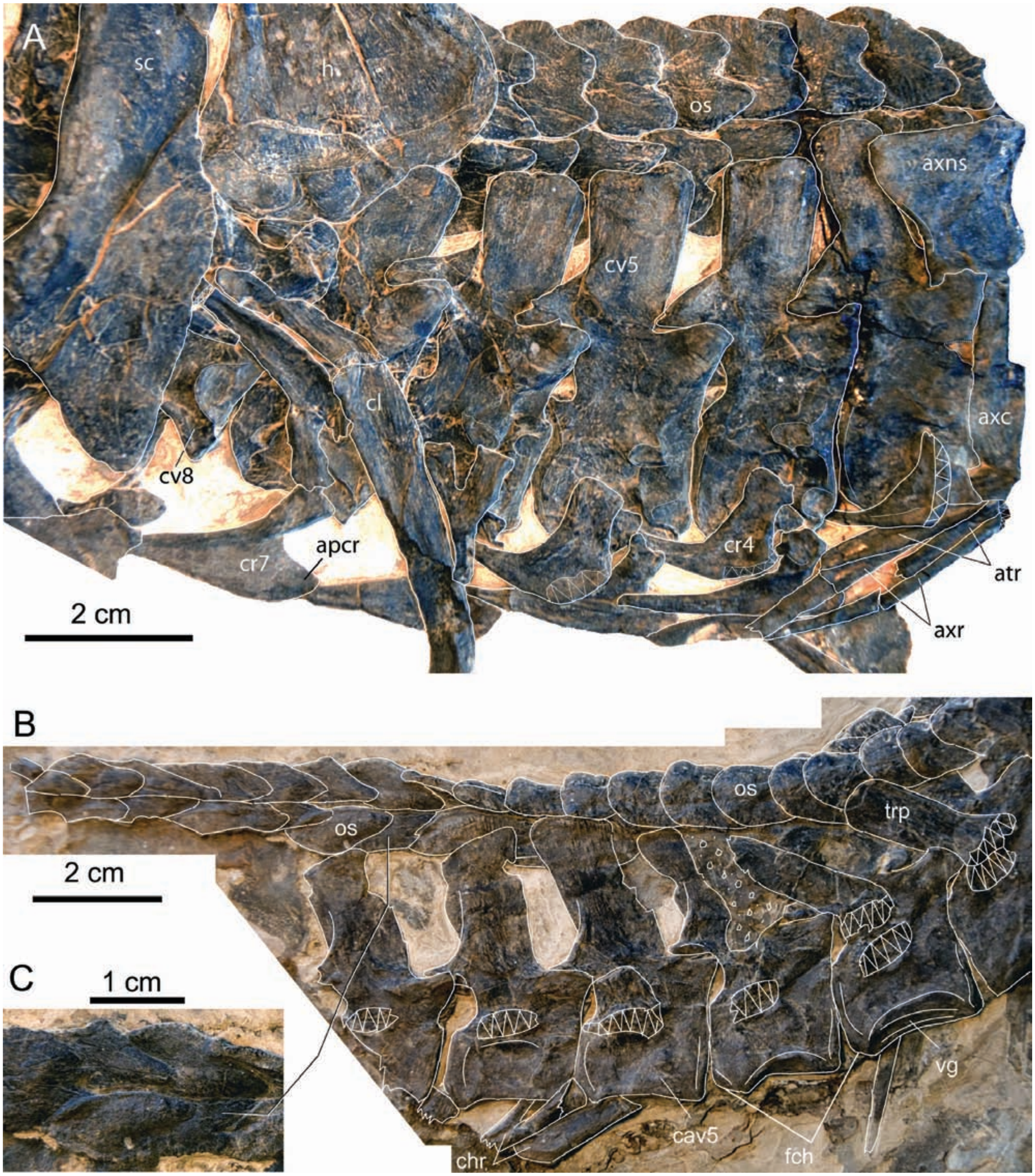

FIGURE 4. Cervical and first seven caudal vertebrae, and the related osteoderms of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770), in lateral views. Note that the cervical (**A**) and the posterior six caudal (**B**) pairs of osteoderms are preserved in ventral view but that the first 15 pairs of the caudal osteoderms (**B**) are in dorsal view. **C**, a close-up of the 16th to 18th caudal osteoderms in ventral view. See the text for abbreviations.

the cervicals of *Diandongosuchus* are similar in morphology but differ in the details of the neural spine. The spine is distinctly narrower in cervical 3 than in the others. The distal surface of the neural spine in cervicals 4–7 is transversely broad to receive osteoderms. The lateral surface of the centrum is concave but lacks the dorsally positioned fossa seen in *Turfanosuchus* (Wu et al., 2001). The diapophysis and the parapophysis of each vertebra gradually move dorsally and posteriorly between cervicals 3–7. The total length of cervical centra 3–5 reaches 53 mm. Most of the last two cervicals and the first dorsal is covered by the

TABLE 1. Selected measurements (in mm) of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770).

Measurements	
Length of skull (to quadrate condyle)	240
Length of mandible (to retroarticular process)	250
Vertebral length	
3 to 5	53
10	17
13	18
17	20.5
21 + 22	42
Two sacrals	43
Caudal 1	21
Interclavicle	
Length	91
Anterior width	32
Length of left humerus	104
Length of left radius	82
Length of left ulna	86
Length of right femur	140
Length of fibula	112 (R), 112 (L)
Length of tibia	110 (R), 113 (L)
Length of metatarsals (left)	I: 29 II: 41 III: 44 IV: 52 V: ?

Abbreviations: **R**, right; **L**, left.

pectoral girdle; the exposed anteroventral part of the eighth centrum shows that the parapophysis is still quite low in position.

All dorsal vertebrae are exposed in ventrolateral view with their neural spines buried in the matrix and ribs and gastralia covering most of them (Figs. 1, 5). From dorsal 2, the diapophysis becomes more pronounced than the parapophysis. These two rib facets are separated in the first four dorsals, but they shift upward onto the neural arch. As in *Qianosuchus*, the centra of these dorsals are laterally concave but do not form a rimmed fossa such as that seen in *Koilamasuchus* from the Lower Triassic of Argentina (Ezcurra et al., 2010). The centra become longer towards the sacrum (see Table 1).

There are two sacral vertebrae as in *Qianosuchus* and many other pseudosuchians such as *Gracilisuchus*, *Postosuchus*, and *Sphenosuchus*. The sacrals are exposed only in ventrolateral view and the neural spines are hidden in the slab. The two sacrals reach a total length of 43 mm, of which the second is slightly longer than the first. Their centra are slightly concave, with a smooth ventral surface.

Of the preserved caudal vertebrae, the first six are nearly complete but the seventh is missing the posterior half of the centrum. The caudals are very different from those of *Qianosuchus* in having much shorter neural spines, which (dorsal to the prezygapophysis) are about 0.56 of the total height of the vertebra in caudal 5 of *Diandongosuchus*, but this ratio is about 0.66 in *Qianosuchus* (IVPP V143000). The lateral surface of the centrum in the first six caudals is concave. The exposed ventral surface of the third centrum shows a longitudinal trough along the midline (Fig. 4B). The transverse process is bar-shaped and complete in caudals 2–4. The neural spine is totally exposed in caudals 5–7 and is moderately broad (about half the length of centrum) and directed dorsally and slightly posteriorly. There is a vertical ridge, derived from the dorsal surface of the postzygapophysis, on the lateral surface of the spine, which becomes indistinct before reaching the distal margin of the spine. Whether or not this ridge is present in all caudal vertebrae is uncertain because the majority of the tail is missing.

Ribs, Gastralia, and Chevrons

Single-headed ribs of the atlas and axis are elongate and rodlike but still much thicker and shorter than those in *Qianosuchus* (Figs. 3, 4A). From the third cervical vertebra, the ribs are short and dichocephalous. Both the capitulum and the tuberculum curve strongly inward from the shaft. There is an anterior (middle) process between the capitulum and the tuberculum, which is pointed and free distally. It is possible that cervical rib 9 still has this process. Whether or not the anterior process is retained in the first dorsal rib cannot be confirmed due to the overlying pectoral girdle. The dorsal ribs are slender and curved when complete. The last dorsal rib is short; it appears incomplete and its expanded distal end might be the result of preservation. Judging from the proximal width, the second sacral rib is the most massive, with a strongly expanded distal end (Fig. 6A). The first sacral rib is not completely exposed but its proximal width suggests that this rib is slightly less massive than the second. On the medial surface of the left ilium, facets for the two sacral ribs are exposed near the base of the iliac blade. The sacral ribs are more or less displaced from their centra, indicating a loose connection between the sacral ribs and the vertebral column.

Gastralia are loosely articulated and displaced from their original position (Figs. 1, 5). A complete set of gastralia consists of an angled central segment and two pairs of the lateral segments. The interior angle of the central segment is smaller than 80 degrees in the first two or three sets but exceeds 90 degrees in the posterior sets.

There are three chevrons preserved posterior to the fifth caudal vertebra but none of them is complete (Fig. 4B). That between the fourth and fifth caudals is the most complete but is missing its distal symphysis, and its forked proximal part is lightly built. The chevrons are articulated with the preceding centrum, as in *Qianosuchus*. Morphology of the posteroventral edges of the second and the third centra indicates that the first chevron should have been attached to the third caudal vertebra.

Pectoral Girdle and Forelimbs

Elements of the pectoral girdle are partly articulated or closely associated with one another (Figs. 1, 5A). The right scapula is nearly completely exposed in external view. It bears a tall but narrow dorsal blade, in contrast to the low and broad blade in *Qianosuchus*. The blade also differs from those of many other archosauriforms, such as *Ticinosuchus* (Krebs, 1965), *Postosuchus*, and *Batrachotomus*, but is similar to that of the phytosaur *Smilosuchus* (Long and Murry, 1995; Nesbitt, 2011:fig. 30A) in that the thinned anterior margin is not evenly concave but concavoconvex, with the anteroventral margin strongly projecting out. The acromion process is not as pronounced as in *Smilosuchus*. The distal end of the blade is moderately expanded, but it is unclear whether it is broader than the proximal portion due to the overlying humerus. A pit rather than a tuber for the M. triceps brachii is evident just dorsal to the glenoid facet. Proximally, the scapula partly articulates with the coracoid, with a concave articular facet. The lateral surface of the scapula is slightly convex in the dorsal blade but concave in the proximal portion, the latter situation is exaggerated by a vertical crack.

The right coracoid is nearly complete and exposed in external view, with its medial portion covered by the interclavicle and the anterolateral edge slightly damaged. It does not have the postglenoid process seen in *Qianosuchus* and many other archosaurs such as the ornithosuchid *Ornithosuchus* (Walker, 1964) and basal crocodylomorphs (*Dibothrosuchus*, *Sphenosuchus*), but is characterized by an embayment-shaped anterior notch facing the scapula. As shown by the dashed line in Figure 5A, the coracoid may have had an arched or convex medial margin. The coracoidal glenoid facet is larger than its counterpart in the scapula. The external surface of the right coracoid is concavoconvex, whereas its

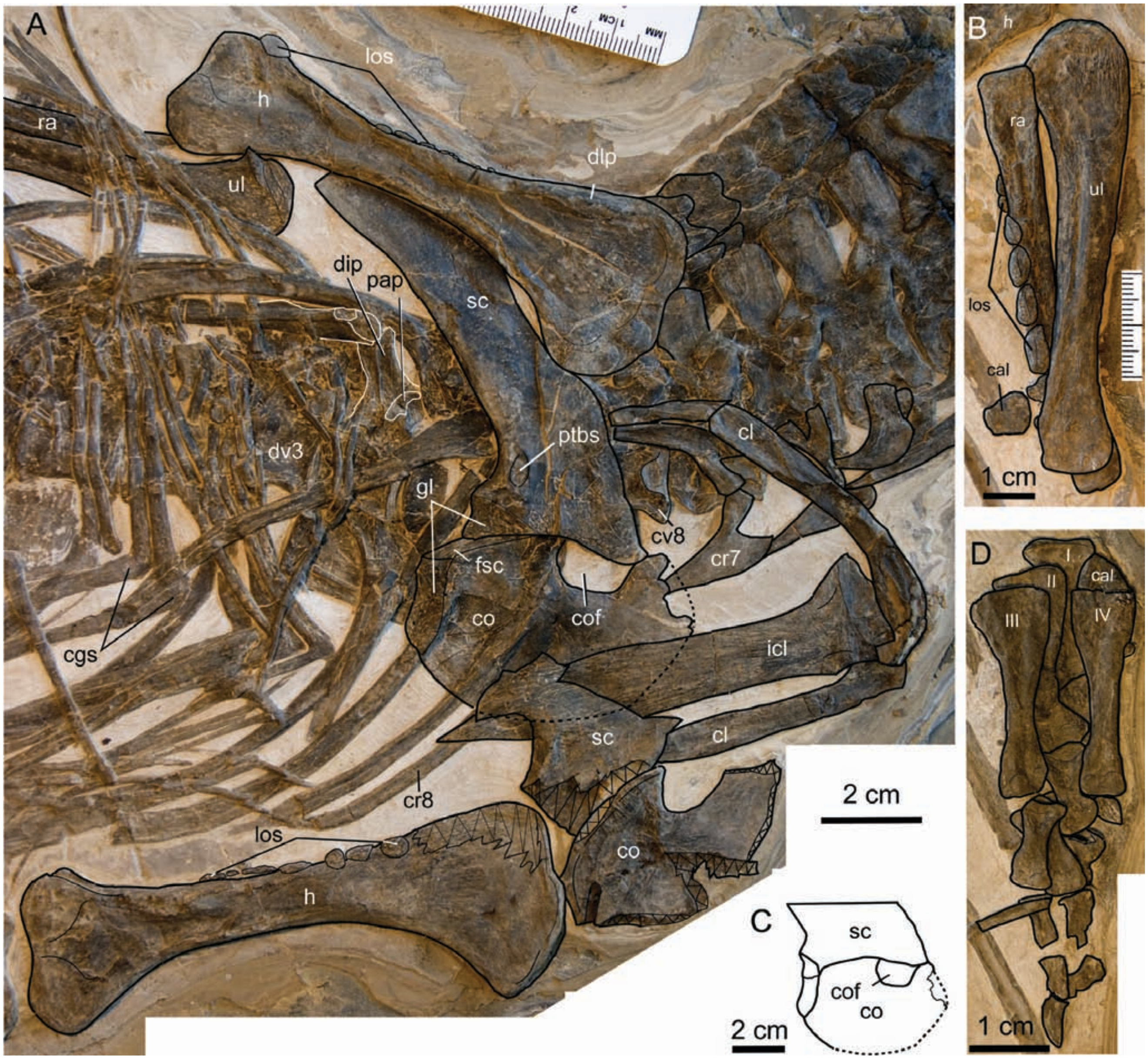

FIGURE 5. Pectoral girdle and the forelimbs of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770). **A**, pectoral girdle and humeri (see text for the orientation of each element); **B**, left ulna and the radius in lateral view; **C**, reconstruction of the right coracoid and the proximal portion of the right scapula, showing the super-sized coracoid foramen; **D**, left hand in ventral view. See text for abbreviations.

internal surface is concave (seen in the left bone), although extensively flattened during preservation.

As indicated by the right scapula and coracoid, the adjoined articular portions of the two bones are not anteroposteriorly equally wide, but are narrower in the former and broader in the latter. It is clear that the scapula width was reduced owing to a fold caused by the vertical crack and the coracoid was broadened slightly due to dorsoventral flattening. Therefore, as reconstructed, the proximal portions of both bones should have been similar in width and the large anterior notch of the coracoid should have been bordered by the scapula (Fig. 5C). The enclosed coracoid notch may have included or even just represented an enlarged coracoid foramen. Such a super-sized coracoid foramen appears to be unique within the Archosauria.

The right clavicle is exposed in posteromedial view. Facets for the scapula and the interclavicle are clearly marked. The interclavicle is exposed in dorsal view; it is slightly damaged at its right anterolateral corner. It is sword-shaped, with a weakly developed anterolateral process and a short anterior process as seen in phytosaurs such as *Smilosuchus* (Nesbitt, 2011) and *Parasuchus*, and some other archosaurs such as *Revueltosaurus* (Parker et al., 2005), *Ornithosuchus*, and *Sphenosuchus*. The body is slightly bilaterally constricted, with a sharply pointed posterior end. Articular facets on the anteromedial surface of the interclavicle suggest that two clavicles approached midline but did not meet each other medially.

Both forelimbs are fairly well preserved, only missing the carpals and some phalanges of the right manus (Fig. 5). The right humerus is exposed in anteromedial view and the left in

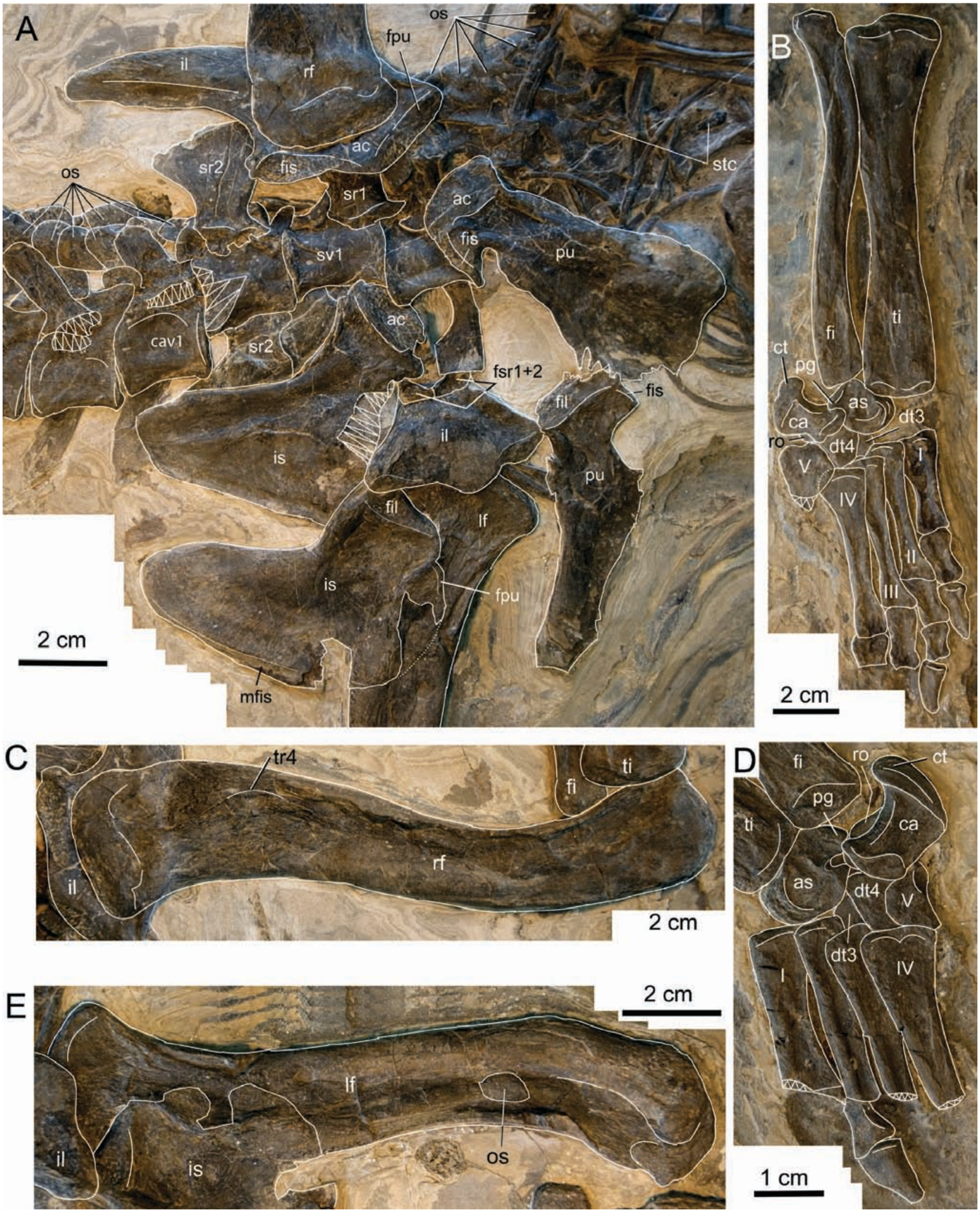

FIGURE 6. Pelvic region and hind limbs of *Diandongosuchus fuyuanensis*, gen. et sp. nov. (ZMNH M8770). **A**, pelvic region (see text for the orientation of each sacral element); **B**, left tibia, fibula, and pes in posteroventral view; **C**, right femur in posteromedial view; **D**, right pes in posteroventral view; **E**, right femur in posteromedial view. See text for abbreviations.

posterolateral view. Both ends of the humerus are strongly expanded; it differs from that of *Batrachotomus* and *Turfanosuchus shageduensis* (Wu, 1982) in that the proximal end is wider than the distal end. The shaft is straight and constricted asymmetrically so that the proximal head of the bone directs posteromedially. Distally, the medial articular condyle is larger than the lateral one. The posterolateral surface of the humerus is slightly convex. Medially, the deltopectoral process is moderately developed along the anterolateral edge, at the proximal quarter of the total length of the bone. The medial surface is distinctly concave, especially in the proximal quarter. The left ulna and radius are well exposed in medial view (Fig. 5B). They are similar to those of extant crocodylians such as *Alligator sinensis* (Cong et al., 1998) in that the olecranon process of the ulna is not well developed and the ulna is slightly longer and much thicker than the radius. The ulnar shaft is slightly sigmoidal, with the proximal end much wider than the distal end. The radius is essentially bar-like, with its ulnar margin weakly concave. As with the ulna, the medial surface of the radius is slightly concave. The carpus is represented by two carpals (Fig. 5B, D); the one displaced proximally is probably the radiale, which is asymmetrically rectangular in outline, and the other still articulated with metacarpal IV is probably the fused distal carpals 3+4. Metacarpals I to IV are preserved. The first and the second are partly exposed and their exact lengths remain unclear, and the third and fourth are fully exposed (Fig. 5D). The first metatarsal appears the shortest but thickest among the preserved four. The second is longer than the first but shorter than the third and the fourth, the latter two are similar in length and thickness. There are 10 or 11 phalanges preserved, of which one is a laterally compressed claw with a pointed distal end. The phalanges are disarticulated and the phalangeal formula is unknown.

Pelvic Girdle and Hind Limbs

The preserved elements of the pelvic girdle are disarticulated, and some are partly covered by other bones (Fig. 6A). The right ilium in lateral view is better exposed than the left (in medial view), and the acetabular fossa is largely overlapped by the femoral head. The iliac blade is spike-like, dorsoventrally narrow, and anteroposteriorly long; it is more posterodorsally directed than in *Qianosuchus* and many other archosaurs such as *Batrachotomus*. The presence of a preacetabular process seen in many other archosaurs remains unclear. The articular facets for the pubis and the ischium are similar in size, and their long axes form a wide angle of about 130 degrees in lateral view. The proximal portion of the left ilium shows a convex medial surface on which rib facets are clearly marked. The right pubis is exposed in medial view and is more complete than the left. It differs from those of many other archosaurs, except for *Qianosuchus*, in that the distal portion is wider than the proximal portion, and that the ischial facet is smaller than the iliac facet and is hook-like in lateral view. The better-preserved left ischium is slightly damaged along the anterior margin. The bone is characterized by a distal/medial portion that is much more expanded than the proximal portion and anteroposteriorly longer than the proximodistal height of the bone (Fig. 6A). It differs from that of *Qianosuchus* and other archosaurs such as *Arizonasaurus* (Nesbitt, 2011:fig. 33D) and *Poposaurus* (Schachner et al., 2011:fig. 6C, D) in which the distal portion of the bone is not so expanded and the posterior margin is not so strongly concave. The ischium of phytosaurs appears expanded in both dorsal and distal portions, but to a lesser degree (especially the distal portion), and its posterior margin is weakly concave (Chatterjee, 1978:fig. 12a). The facet for the ilium is clear, but that for the pubis is incomplete. The ischium is shorter but distally broader than the pubis.

Many elements of both hind limbs are complete except for the metatarsals and the phalanges (Fig. 6). The right femur is exposed in posteromedial view and resembles that of *Qianosuchus* and some Triassic archosaurs such as *Turfanosuchus*, *Ticinosuchus*, and *Batrachotomus*, with a slightly sigmoid and twisted shaft so that the proximal head and the distal condyle are not in the same plane. The femoral head is not ball-shaped and does not strongly bend anteriorly to form a fold. The fourth trochanter, located near the proximal third of the total length, is pronounced but was compressed during fossilization. The moderately developed distal condyle does not project markedly beyond the shaft. The medial surface of the shaft is concave. Both the tibia and the fibula are exposed in posteroventral view (Fig. 6B) and are proportionally shorter (about 80% the length of the femur) than in *Qianosuchus* (about 84% the length of the femur), but much longer than in phytosaurs such as *Parasuchus* (where this ratio is about 64%; Chatterjee, 1978). The tibia is massive and the proximal end is more expanded than the distal end. The tibial shaft is straight and symmetrically constricted. The facets for the femur and the astragalus are concave. The fibula is relatively much thinner and more sigmoid than in *Qianosuchus*, and is slightly longer than the tibia (see Table 1). The posteroventral surface of the fibula is concave.

There are four tarsals in each foot; they are the calcaneum, astragalus, and separate distal tarsals 3 and 4, all exposed in posterior view (Fig. 6B, D). The calcaneum and the astragalus form a ball-and-socket articulation as in many other pseudosuchians (see below). The dorsolaterally directed calcaneal tuber is pronounced and the calcaneal condyle is well developed and roller-shaped; the facets for the third and fourth distal tarsals and the fibula are continuous. The facet for the astragalus on the anteromedial side, as well as its relationships with the hemicylindrical condyle, cannot be observed. Posteriorly, the calcaneum is strongly concave, and its large tuber is distally expanded and faces posterolaterally.

The astragalus is characterized by a well-developed peg, which suggests that a socket was present in the calcaneum to form a crocodile-normal tarsal joint. In posterior view, the dorsal facet for the fibula is small and separated by a sharp ridge from the tibial facet that is large and slightly concave and flexed. The posterior surface of the astragalus is concave but divided by a weak ridge. The ventral facets for metatarsals I and II appear convex (see the right pes). Distal tarsals 3 and 4 are sutured, instead of being separated from each other as in *Postosuchus*; and the third is smaller than the fourth.

All metatarsals are preserved and the first four are complete in the left foot. These four are similar in thickness and are successively longer from the first to the fourth; in other words, metatarsal IV is the longest, which differs from *Qianosuchus* and many other archosaurs such as *Ticinosuchus* and *Batrachotomus* in which metatarsal III is the longest. The new taxon also differs from *Qianosuchus* in that metatarsals II and IV are similar in length in the latter. In *Diandongosuchus*, the fifth metatarsal is more expanded proximally than the others; it is incomplete distally and its total length is unknown. The medial side of the proximal end of the fifth metatarsal articulates with the lateral side of distal tarsal 4 as shown in the left foot, which indicates that the fifth may have been hooked in life. There are seven phalanges preserved in the left pes, and the first and the second digits bear two and three phalanges, respectively, as in *Qianosuchus*. The phalangeal count is unknown for the other digits.

Osteoderms

From the axis to the sixth cervical vertebra, two rows of seven and a half osteoderms are exposed in ventral view. They are associated with the neural spines of the five vertebrae, indicating one and a half pairs of osteoderms per vertebra (Fig. 4A). Each osteoderm overlaps the anterior margin of the succeeding one, and the first set of the osteoderms is smaller than the rest.

All osteoderms are asymmetrically oval in outline, with a narrow anterior portion that is evidently notched from the third. As preserved, most of the dorsal osteoderms of the trunk are covered by the body, but the last five of the right row are exposed in dorsal view, covering the posterior-most two dorsal vertebrae and the anterior portion of the first sacral vertebra. This indicates that there are two pairs of osteoderms per dorsal vertebra. These osteoderms are connected with one another in a pattern as seen in the cervical series. They have a slightly narrowed posterior portion, a longitudinal dorsal thickening, and an anterolateral process. Their dorsal surface is ornamented by numerous pits. The exposed portion of the dorsal osteoderms is roughly rectangular in outline.

Caudal osteoderms are well preserved along the dorsal side of the caudal neural spines, and similarly connected to each other as in the more anterior series (Figs. 4B, 6A). There are about 21 pairs of caudal osteoderms preserved from the last sacral vertebra, of which the anterior 15 and a half pairs are exposed in dorsal view and cover the first seven caudal vertebrae; the remaining posterior seven pairs are preserved in ventral view. Again, each caudal vertebra is at least covered by two pairs of osteoderms. The anterior 15 pairs appear similar to the posterior dorsal osteoderms in morphology. The osteoderms in the posterior seven pairs have a pointed anterior portion and a smooth ventral surface (Fig. 4C). As in extant crocodilians and some basal archosaurs such as aetosaurs (Schoch, 2007), osteoderms cover both the forelimbs and the hind limbs. The preserved limb osteoderms are associated with the humerus, radius, and femur (Figs. 5, 6). They are small and oval in outline, and have a convex dorsal surface.

Stomach Contents

Within the rib cage, there are bone fragments of small vertebrates concentrated just anterior to the pelvis (Figs. 1, 5A). These are considered as stomach contents. None of the elements are identifiable, with the exception of a fish vertebra. There is no doubt that *Diandongosuchus* included fishes in its diet, although it is uncertain to which fish taxon the vertebra belongs and it is not clear if the fish was freshwater or marine at present.

PHYLOGENETIC RELATIONSHIPS

Phylogenetic relationships within the Archosauria and Archosauriformes have been analyzed in many papers, with particular emphasis on the Avemetatarsalia and Pseudosuchia/Crurotarsi (see Brusatte et al., 2010; Nesbitt, 2011). A number of recent studies (Gower and Nesbitt, 2006; Nesbitt, 2007; Weinbaum and Hungerbühler, 2007; Dilkes and Sues, 2009; Nesbitt et al., 2009; Desojo et al., 2011; Ezcurra et al., 2010) dealt with relationships within specific archosaur or archosauriform groups, but Brusatte et al. (2010) and Nesbitt (2011) are the only two recent studies in which the Archosauria as a whole was subjected to analysis. In the following phylogenetic study of *Diandongosuchus*, our data matrix was derived from that of Nesbitt (2011), which is much larger than that of Brusatte et al. (2010) and the most complete data matrix among existing phylogenetic studies of the Archosauriformes.

In this study, we ran four analyses of two data sets to evaluate the effect of *Diandongosuchus*, four other operational taxonomic units (OTUs) (*Archosaurus*, UFRGS 156T, UFRGS 152T, and *Pseudolagosuchus*) that were originally listed by Nesbitt in his 2011 data matrix), and the ordering of character states in multistate characters on the resulting tree topologies. With the addition of *Diandongosuchus*, the data matrix comprises 82 taxa and 412 characters. Compared with the original data matrix of Nesbitt (2011), two new character states (5, 6) and one new character state (2) were introduced for characters 6 and 218, respectively. The scoring of some characters was altered for several taxa: for *Vancleavea*, *Chanaresuchus*, and *Eudimorphodon*, the scoring of character 139 was changed from state 0 to 1; for the three phytosaurs included, character 6 was emended from state 3 to 6; and five characters were rescored for *Qianosuchus*, namely character 6 (changed from state 2 to 5), character 139 (changed from state 0 to 2), character 207 (changed from state 1 to 0), character 218 (changed from state 0 to 2), and character 273 (changed from state 2 to ?). For full details of the modifications made to the data matrix, see Supplementary Data (available online at www.tandfonline.com/UJVP).

Nesbitt (2011:appendix 3) originally scored 412 characters for 83 taxa, but the phylogenetic analysis he presented was based on a data matrix including only 77 taxa, with 6 taxa excluded (the proterosuchid *Archosaurus*, three representatives of *Prestosuchus* [UFRGS 156T, UFRGS 152T, and a combined *Prestosuchus* OTU], and two dinosauriforms [*Pseudolagosuchus* and combined *Lewisuchus*/*Pseudolagosuchus*]). Following Nesbitt (2011), the six above-mentioned OTUs were excluded from an analysis of his pruned data set that was expanded to include *Diandongosuchus* (thus comprising 78 taxa and 412 characters): this analysis was run with 18 ordered multistate characters (32, 52, 121, 137, 139, 156, 168, 188, 223, 243, 258, 269, 271, 291, 297, 328, 356, and 399) and was performed using a heuristic search in PAUP* 4.0b10 (Swofford, 2002). It yielded 14,040 most parsimonious trees (MPTs) with tree lengths (TL) of 1345 steps, consistency index (CI) of 0.3636, and retention index (RI) of 0.7615. As shown in the strict consensus of the 14,040 MPTs (Fig. 7A), the interrelationships of *Diandongosuchus* are well established: it is a pseudosuchian, the basal-most member of Poposauroidea, and its position is supported by 17 synapomorphies (ACCTRAN), including five unequivocal character states. As for the other taxa in this analysis, their interrelationships are largely comparable to those recovered by Nesbitt (2011) except for those of Ornithosuchidae, *Ticinosuchus*, and some taxa within Paracrocodylomorpha and Ornithodira. In the new analysis, the Ornithosuchidae was not recovered as the basal-most group of the Pseudosuchia or the sister group of Suchia (sensu Nesbitt, 2011), but formed unresolved interrelationships with four basal pseudosuchians (*Gracilisuchus*, *Turfanosuchus*, Aetosauria [sensu Nesbitt, 2011], and the Paracrocodylomorpha [sensu Nesbitt, 2011]); *Ticinosuchus* was not resolved as the sister group of the Paracrocodylomorpha, but moved to become the basal-most member of Loricata (sensu Nesbitt, 2011). With the alternative position of the Ornithosuchidae, the contents of the clades Suchia (node-based) and the Pseudosuchia (stem-based) remained the same in this analysis as defined by Nesbitt (2011). The interrelationships of the paracrocodylomorph *Saurosuchus* and the crocodyliforms *Orthosuchus*, *Protosuchus*, and *Alligator* are not exactly same as in Nesbitt (2011). Within the Ornithodira, only the interrelationships of the ornithischians *Pisanasaurus* and *Heterodontosaurus* and the theropod *Staurikosaurus* are slightly different in this analysis (see Fig. S1A in Supplementary Data). For comparison, we re-ran this data matrix a second time with all multistate characters unordered. The results of this second analysis were almost identical to those from the first analysis, with minor differences in the tree indexes (14,040 MPTs with TL of 1338 steps, CI of 0.3655, and RI of 0.7581): the poposauroid status of *Diandongosuchus* is supported by 18 synapomorphies, including five unequivocal character states.

To test the effect of the four single-specimen OTUs excluded by Nesbitt (2011), we included these in a second expanded data set (now with 82 taxa and 412 characters, including *Diandongosuchus*). An analysis was carried out using a heuristic search in PAUP* 4.0b10, with the aforementioned 18 multistate characters ordered. This yielded 105,300 MPTs, with TL of 1355 steps, CI of 0.3616, and RI of 0.7637. As shown in Figure 7B, the topology of the strict consensus tree of the 105,300 MPTs is more similar to that of Nesbitt (2011:figs. 51, 52) than to that recovered by

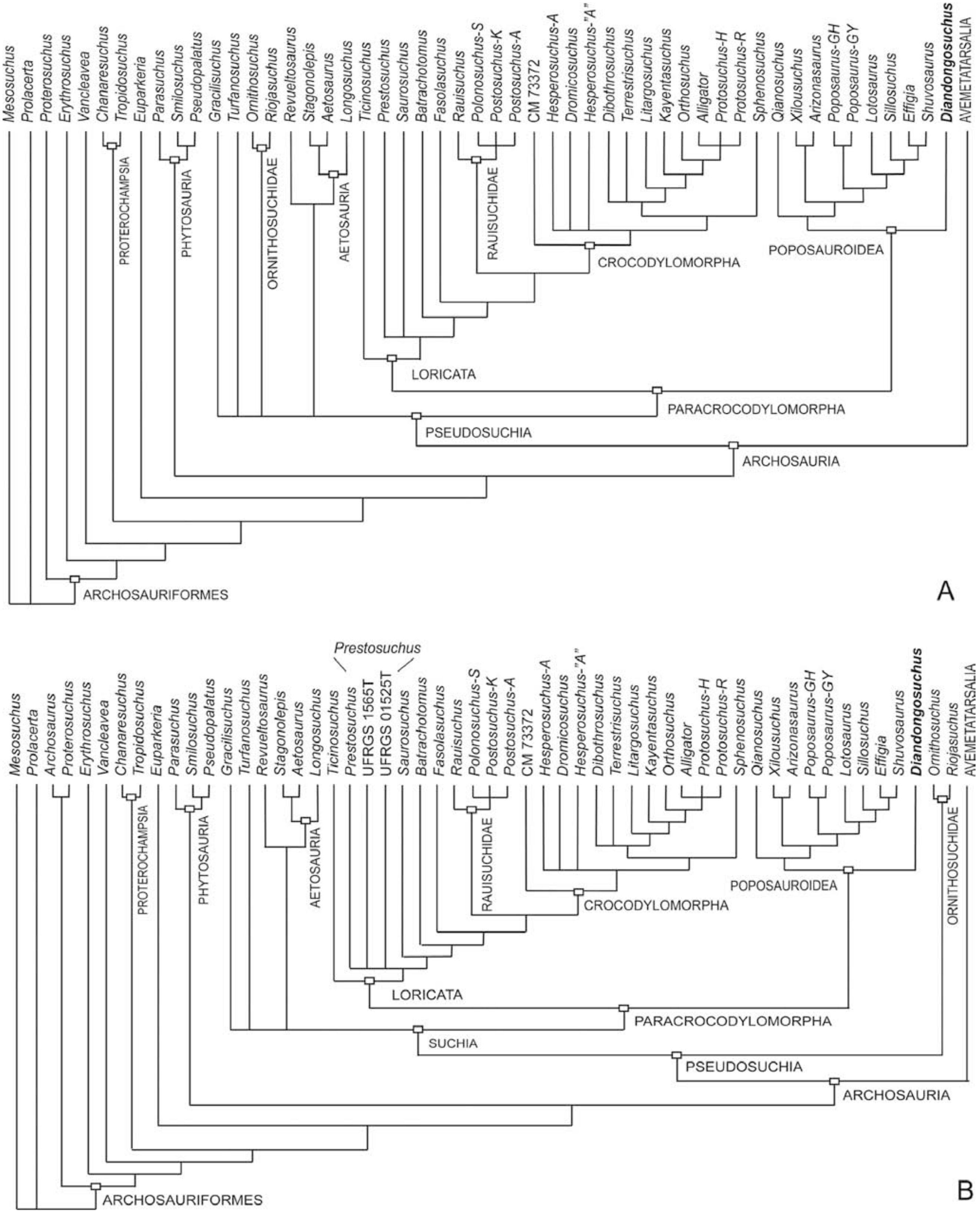

FIGURE 7. Cladograms depicting archosaur relationships (with no avian-line forms) based on the data matrix derived from Nesbitt (2011). **A**, the strict consensus tree of 14,040 MPTs obtained by the analyses of 78 taxa and 412 characters (see text for details); **B**, the strict consensus tree of 105,300 MPTs yielded by the analyses of 82 taxa and 412 characters (see the text for details). **Key**: ***Hesperosuchus-A*** and ***Hesperosuchus-”A”***, *Heperosuchus agilis* and *Hesperosuchus* “*agilis*”; ***Polonosuchus-*****S**, *Polonosuchus silesiacus*; ***Postosuchus-K*** and ***Postosuchus-A***, *Postosuchus kirkpatricki* and *Postsuchus alisonae*; ***Poposaurus-GH*** and ***Poposaurus-GY***, *Poposaurus gracilis* (holotype) and *Poposaurus gracilis* (Yale specimen); ***Protosuchus-H*** and ***Protosuchus-R***, *Protosuchus haughtoni* and *Protosuchus richardsoni*. Synapomorphies, as optimized under accelerated (ACCTRAN) transformation assumptions in tree 1 of the 105,300 MPTs, are listed for Proterochampsia, Phytosauria, and the other major archosaur clades (see Appendix 1).

the above-mentioned analyses excluding these taxa; i.e., Ornithosuchidae was identified as the basal-most group within Pseudosuchia or the sister group of Suchia. As for *Diandongosuchus*, its interrelationships with other pseudosuchians did not change and its poposauroid status was supported by 18 synapomorphies, including five unequivocal character states. The loricatan status of *Ticinosuchus* within Paracrocodylomorpha is very stable in this analysis, still differing from its position in the study of Nesbitt (2011). Within Ornithodira, *Lewisuchus* was not recovered as a member of Silesauridae (contra Nesbitt, 2011), but formed a polytomy with a less inclusive Silesauridae, *Pseudolagosuchus*, and Dinosauria (see Fig. S1B in Supplementary Data). A second analysis of this data set, with the 18 multistate characters run unordered, also produced 105,300 MPTs and their consensus tree showed the same interrelationships as derived from the first analysis of this data set, differing only in some of tree indexes, with TL of 1349 steps (six steps shorter), CI of 0.3632 (higher), and RI of 0.7601 (lower). The poposauroid status of *Diandongosuchus* is supported by 17 synapomorphies, including five unequivocal character states.

Although the numbers of the synapomorphies supporting the poposauroid status of *Diandongosuchus* within Pseudosuchia vary between the four analyses, the five unequivocal synapomorphies are consistently the same in all of them. They are (1) the length of the anterodorsal (nasal) process of the premaxilla greater than the anteroposterior length of the premaxilla, character 1(1); (2) the posterior (maxillary or subnarial) process of the premaxilla restricted to the ventral border of the external naris, character 5(1); (3) the centrum of cervical 3 is longer than the axis centrum, character 183(1); (4) the presence of a thickened process on the proximal portion of the pubic apron, character 288(1); and (5) the bone wall thickness to the shaft diameter of the femur at the midshaft >0.2 but <0.3, character 323(1). These five synapomorphies were also identified among the 12 unequivocal synapomorphies used by Nesbitt (2011) in his diagnosis of Poposauroidea. Although the interrelationships of *Diandongosuchus* did not change between the four analyses carried out herein, the results derived from the analysis of the total data matrix (82 taxa and 412 characters) with all multistate characters unordered are preferred in interpreting the phylogeny of the other taxa in this study (Fig. 7B; Fig. S1B in Supplementary Data) and the synapomorphies of Proterochampsia, Phytosauria, and other major archosaur clades are listed in Appendix 1.

DISCUSSION

Our analysis establishes the poposauroid status of *Diandongosuchus* and also supports previous studies that proposed *Qianosuchus* as a basal poposauroid (Brusatte et al., 2010; Nesbitt, 2011). It needs to be emphasized, however, that the poposauroid status of the two Chinese archosaurs obtained in our study is strongly supported by at least 17 synapomorphies, including five unequivocal character states, for the former taxon and more for the latter, although neither bootstrap values nor Bremer support values were obtained owing to the difficulty of analyzing the large data matrix. Our study hypothesizes that *Diandongosuchus* is the basal-most taxon within Poposauroidea, being even more basally positioned than *Qianosuchus* because it is plesiomorphic in 16 character states, mainly in those: (1) the maxilla is excluded from the external naris, character 24(0); (2) the anterodorsal margin of the maxilla at the base of the dorsal process is convex or straight, character 25(0); (3) the distal end of the neural spines in the cervical vertebrae are expanded, character 191(1); (4) the cervical ribs are short and stout, character196(1); and (5) metatarsal IV is longer than metatarsal II, character 395(0). With the inclusion of *Diandongosuchus*, the phylogenetic relationships of *Qianosuchus* conflict with those recovered by Dilkes and Sues (2009), Ezcurra et al. (2010), and Desojo et al. (2011) in which *Qianosuchus* was hypothesized to be more basal than the Phytosauria (represented by *Parasuchus*) within Crurotarsi. In addition, our inclusion of *Diandongosuchus* did not alter the non-archosaurian status of the Phytosauria, which was hypothesized by Nesbitt (2011).

Diandongosuchus appears to be unique within Pseudosuchia in the following features: a nasal process of the premaxilla that extends posteriorly well beyond the external naris, a super-sized coracoid foramen laterally bordered by the scapula, a broadly expanded medial portion of the ischium, and the cervical osteoderms that are anteriorly notched. Besides the aforementioned character states, our study also suggests that *Diandongosuchus* is apomorphic in more than 15 character states within Poposauroidea. Of those character states, the following nine are the most convincing and form part of the diagnosis of the new taxon because their alternative states are known in all or most of the taxa within the clade: characters 9(1), 49(1), 55(1), 71(1), 75(1), 139(1), 144(1), 337(0), and 393(0).

Diandongosuchus is the second archosaur from the marine deposits of southwest China. As mentioned earlier, it shows no obvious specializations to an aquatic way of life. However, (1) the relatively posterior positioned external naris, (2) the ornamented skull roof elements, and (3) the large number of the premaxillary teeth are not common in fully terrestrial archosaurs, but are seen in *Qianosuchus* (1, 3), *Chanaresuchus* (1), and the spinosaurid dinosaurs (3), which were considered to be semiaquatic (Romer, 1971; Sereno et al., 1998; Li et al., 2006; Amiot et al., 2010). As to the skull ornamentation, the pattern of pits, short grooves, and ridges does not resemble the fine elongate ridges and grooves seen in *Qianosuchus* and other Triassic marine reptiles such as thalattosaurs (Wu et al., 2009) and nothosaurs (Rieppel, 1996), but is more comparable to that of marine crocodyliforms (especially with respect to the ornamentation of the mandible) such as *Terminonaris* (Wu et al., 2001) and the Tomistominae (Shan et al., 2009). These skull features suggest that *Diandongosuchus* might have had a lifestyle similar to phytosaurs or recent saltwater crocodiles, living near the water and adapted for an amphibious way of life. In addition, such a way of life for *Diandongosuchus* may be further inferred from its stomach content that includes fish remains. However, this assumption can only be verified by a detailed comparative phylogenetic and functional analysis of the taxon (Padian, 1987).

It has been documented that the Middle Triassic marine vertebrate fauna of Guizhou and Yunnan, China resembles those of Europe (Li, 2006; Rieppel et al., 2010). Discovery of the terrestrial protorosaur *Macrocnemus* from Yunnan also suggested a close affinity between the semiterrestrial faunas of the eastern and western coastal regions along the northern shore of Tethys (Li et al., 2007). This similarity receives no additional support from the discovery of *Diandongosuchus*. *Ticinosuchus* from the Middle Triassic (near to the Anisian–Ladinian boundary) of Monte San Giorgio, Switzerland, is the only archosaur found in the Middle Triassic marine vertebrate faunas of Europe. Nesbitt (2011) stated that the skeletal morphology of *Qianosuchus* resembled that of *Ticinosuchus*. Compared with *Qianosuchus*, *Diandongosuchus* is morphologically more similar to *Ticinosuchus*, especially in the postcranial skeleton, sharing features such as short cervical vertebrae with short ribs, the low neural spines of the caudal vertebrae, and the tall dorsal blade of the scapula. Surprisingly, *Ticinosuchus* and *Qianosuchus* did not form a sister-taxon relationship, as also suggested by previous studies (Li et al., 2006; Brusatte et al., 2010; Nesbitt, 2011). Our analysis also failed to recover a sister-taxon relationship between *Diandongosuchus* and *Ticinosuchus*, although they are both grouped within Paracrocodylomorpha as separately formed basal-most members of the two subgroups Poposauroidea (the former) and Loricata (the latter). Therefore, the archosaurs provide no evidence for a close affinity between the Triassic reptilian faunas of the eastern and western coastal regions along the northern shore of Tethys, although evidence from the protorosaurs and marine reptiles does support such affinities.

North America also produces Triassic marine vertebrate faunas, including the archosaur *Sikannisuchus* Nicholls, Brinkman, and Wu, 1998. It was collected along with shastasaurid ichthyosaurs from the Norian (Late Triassic) limestone of western Canada and hypothesized to live in either a local river system or the coastal region like the recent saltwater crocodile *Crocodylus porosus* (Nicholls et al., 1998). *Sikannisuchus* is too fragmentary to be included in any phylogenetic analysis and its affinities with other archosaurs or archosauriforms are currently unknown. *Ticinosuchus* from Europe has long been considered as a terrestrial animal although from a marine deposit (e.g., Nicholls et al., 1998), but recent study of its stomach contents (Nesbitt, 2009) suggests that it consumed fish as part of its diet. Therefore, the lifestyle of *Ticinosuchus* might be similar to *Diandongosuchus* or *Sikannisuchus*, living near coastal regions, although no evidence for aquatic adaptations is available from the current specimens.

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APPENDIX 1. Scores for the new archosaur and the list of synapomorphies for major clades. Character scores for *Diandongosuchus* added to the analysis of Nesbitt (2011).

<matrix>					
1	2	3	4	5	6
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
1000150010	0001000000	0000001000	0?00000000	0000000110	1000110000
7	8	9	10	11	12
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
0010000011	1000100?0	0000?00???	??????????	???????000	??????????
13	14	15	16	17	18
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
??????????	???0012110	?001110??0	0??00010?0	0001?00100	0001?11?0?
19	20	21	22	23	24
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
0010000000	1000?1?000	0?1000000?	?000100001	10?0?00?00	000000?1??
25	26	27	28	29	30
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
10001????0	????01?01	0????????0	0000000000	0010101100	100000000?
31	32	33	34	35	36
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
?000?00000	000?100100	001000?00?	?0000000?0	??1??10000	?0?00??0??
37	38	39	40	41	
1234567890	1234567890	1234567890	1234567890	1234567890	12
?0001??110	1101?221?1	10000?0000	00000?00?2	1110100001	00

List of Synapomorphies for Archosaur Clades (Unequivocal Character States Labeled by an Asterisk)

Proterochampsia, 47*(1), 55*(1), 75*(1), 338*(1), 388*(1), 394*(1), and 399*(2); Phytosauria, 6*(6), 10*(1), 14*(1), 19*(1), 27*(2), 46*(1), 77*(1), 139(1), 140(1), 150*(1), 160*(1), 167*(1), 210(1), 226*(1), 234*(0), 305(0), 339*(1), 352(1), 378*(1), and 405(1); Archosauria, 32*(1), 95(2), 118*(1), 122*(1), 137*(2), 220(1), 222(1), 225(1), 237*(1), 245*(1), 300*(1), 320(1), 353(1), 366*(1), 377*(2), and 398(1); Pseudosuchia, 15(0), 100*(1), 117(1), 238*(1), 278(1), 282(1), 292(1), 330*(1), and 337*(1); Suchia, 27*(1), 75*(2), 114(2), 234(0), 240(1), 320(0), 372*(1), 376*(2), 378*(1), 403*(1), and 410*(1); Ornithosuchidae, 8*(1), 13*(10, 29(1), 33*(1), 62*(1) 85*(1)142*(1) 160*(1), 190*(1), 199*(1), 205(1), 210(1), 308*(1), 339*(1), 340(1), 368*(2), and 407(1); Paracrocodylomorpha, 51(1), 132(1), 157*(1), 195*(1), 265(1), 283(1), 287*(1), 291*(1), 294*(1), 298(1), 314*(1), and 411*(1); Poposauroidea (including *Diandongosuchus*), 1*(1), 5*(1), 6(5), 14(1), 90(1), 95(0), 114(0), 141(1), 183*(1), 197(0), 202(1), 240(0), 288*(1), 301(0), 323*(1), 341(1), and 345(1); “Poposauroidea” (without *Diandongosuchus*),12(1), 20(1), 24*(1), 25*(1), 51(0), 156(1), 181(1), 191*(0), 196*(0), 200(1), 212(1), 273(2), 319(1), 349(1), 352(1), and 395*(1); Loricata (including *Ticinosuchus*), 2(1), 30*(1), 52(1), 108(1), 133(1), 142(1), 191(2), 210*(1), 219(1), 239(1), 270(1), 293*(1), 367(1), and 397(1); “Loricata” (without *Ticinosuchus*), 278*(1), 282*(1), 339(1), 340*(1), 371*(2), and 395*(1); Rauisuchidae, 14(1) 26(2), 29(1) 35*(1), 52(2), 75*(3), 83(1), 125(1), 149(1), 180*(1), 191(2), and 249(0); Crocodylomorpha, 2(0), 4(1), 6(2), 11(1), 22(0), 32(2), 37(0), 39(1), 44(1), 55(1), 65(0), 76(1), 79(1), 112(1), 114(1), 115(1), 116(1), 119(1), 120(1), 124(1), 128(1), 142(0), 156(2), 195(0), 213(2), 223(1), 233(1), 234(1), 269*(1), 274(1), 294*(0), and 297(2); Avemetatarsalia, 6(1), 44(1), 84(1), 87(1), 93(0), 111(1), 114(1), 141(1), 152(1), 159(0), 179(1), 183(1), 191*(0), 197*(0), 218(1), 233(1), 255*(1), 257*(1), 274(1), 299*(1), 301(0), 232(1), 341(1), 345(1), 347*(1), 348*(1), 357*(1), 361*(1), 363(1), 370(1), 373(1), 374(0), 382*(1), 400(0), 401*(0), and 412*(1).