A Late Jurassic Protosuchian *Sichuanosuchus huidongensis* from Zigong, Sichuan Province

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Abstract

A more detailed description is provided to supplement diagnostic characters for the Upper Jurassic protosuchid crocodilian *Sichuanosuchus huidongensis* (Peng, 1995) which was collected from the Upper Shaximiao (Shangshaximiao) Fm., Zigong Municipality, Sichuan Province. *Sichuanosuchus* shares a close affinity to *Shantungosuchus,* both of which may represent the latest independent evolutionary lineage of the Protosuchidae. Cranial and postcranial characters indicate that *Sichuanosuchus* was adapted to a carnivorous diet in an aquatic habitat.

Introduction

In 1995 the author provided a short report on protosuchid material designated *Sichuanosuchus huidongensis* (Peng, 1995) (#ZDM3403) collected from purple-red mudstones of the upper portion of the Upper Jurassic Upper Shaximiao Fm. at the village of Daquekou, Hongzuxiang Township, neighboring the municipality of Zigong, Sichuan Province (Figure 1). This constituted the first discovery of the Protosuchidae from the Late Jurassic of the Sichuan Basin and represents the most complete specimen of the family in China to date. The specimen is extremely significant to the understanding of protosuchid phylogeny and evolutionary relationships and hence warrants a description in more detail.

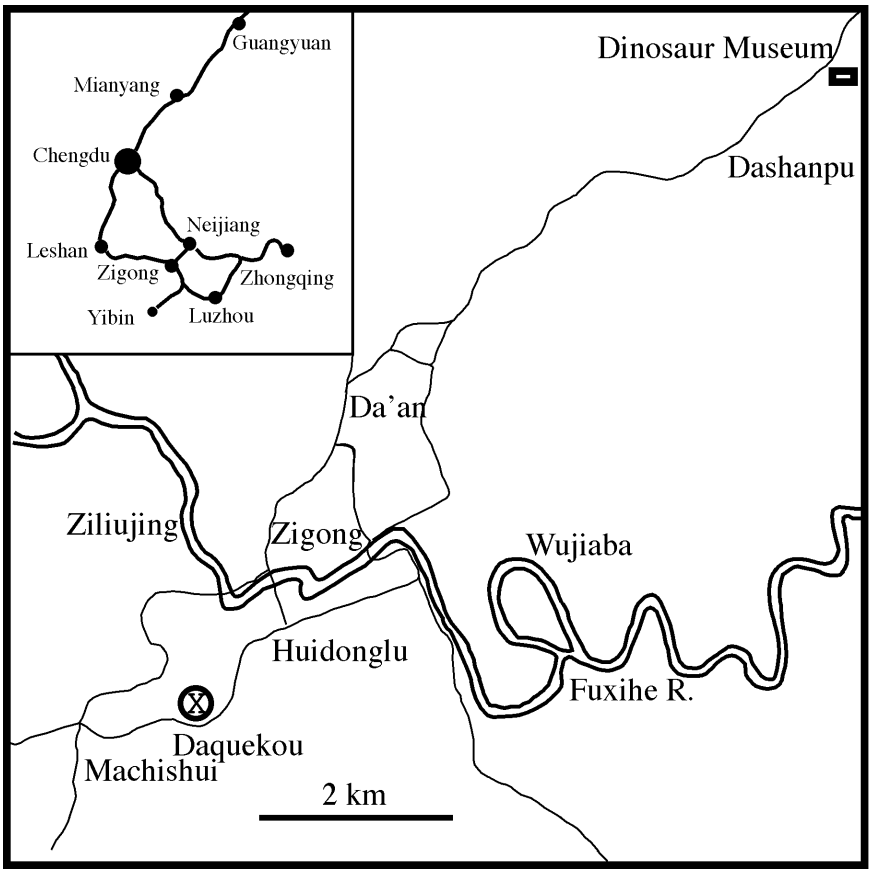

Figure 1. Locality map of *Sichuanosuchus huidongensis* in the Zigong region of Sichuan.

Description

Amended diagnosis: Internarial bar is composed of the premaxilla; orbital margin on the frontal is very slightly inflated to compose a thin crescentic brow ridge; postorbital has completely encroached over the subtemporal foramen; length of dentary symphysis is less than its breadth; ventral margin of angular is transversely expanded with long anteroposterior ridges traversing its the medial and lateral sides; apical dental serrations are larger than anterior and posterior serrations.

Specimen description: Specimen ZDM3403 is basically completely preserved with the exception of a damaged portion of the left oral region and basicranium. Compressional distortion has flattened the specimen slightly, altered the positions of postcranial elements, and compressed the mandible into tight occlusion.

The premaxilla is small, triangular in shape, not expanded anteriorly, slightly convex laterally, and slightly surficially ornamented. The ventral margin is slightly crescentic, but not anterodorsally curved to form a beak. Consequently, the anterior outline of the skull is rather smoothly rounded. The posterodorsal lamina of the premaxilla extends posteriorly to wedge between the nasal and maxilla.

The maxilla is large, broad, and constitutes the majority of the lateral oral region. It is dorsolaterally concave and relatively richly ornamented with abundant grooves but, ventrolaterally, as its surface becomes convex, the ornamentation decreases. Several small nutrient foramina lie above the dentition and the ventral margin of the maxilla lacks conspicuous curvature. The posteroventral process is acute and extends obliquely to the anteroventral portion of the orbit to contact the anterior process of the jugal. The antorbital foramen is located in the posterodorsal angle of the maxilla. Ventrally, the maxillary palatine process extends posteriorly nearly to the end of the dentition where it becomes isolated by the palatine and interpterygoid vacuity. This condition resembles that on *Shantungosuchus hangjinensis* (Wu et al. 1994), on which the ventral surface of the palatine process is slightly concave; there is a slight amount of ornamentation anteriorly; medially the process contacts the pterygoid and palatine; and the posterior margin resembles an inverted V that composes a thin attenuating lamina and forms the medial and lateral boundary of the suborbital foramen.

The nasal is narrow anteriorly, broad posteriorly, and fuses laterally to the maxilla and prefrontal. Posteriorly the nasal fuses to the frontal with a serrated suture pattern, and anteriorly it attenuates to an acute angle to wedge between the premaxillae, but does not form any of the margin of the external nares (Fig. 2B) which differs from all other species in the family. The nasal also differs from *Protosuchus richardsoni* (Colbert and Mook, 1951; Clark, 1986) and specimen #UCMP97638 (=?*Edentosuchus wellesi,* Clark, 1986) in which they are ventrally curved and form a portion of the facial region.

The lacrimal is small, gracile, slightly thickened dorsally, maintains a small foramen, and is sinuously curved into an S pattern in lateral perspective. Ventrally this element is wedged between the anterior jugal process and the posterior maxillary process.

The prefrontal is narrow, long, and thins gradually posteriorly. Its medial margin contacts the frontal and nasal, the anterolateral margin contacts the lachrymal, and the posterolateral margin composes the anterodorsal margin of the orbit. The ventral process of the postorbital is short, transversely broad, nearly perpendicular to the main body of the

postorbital, and resembles other crocodylomorphs by contacting the medial ascending jugal process to form the postorbital bar.

Table 1. Cranial and mandibular measurements for *Sichuanosuchus huidongensis* (mm)

Maximum length of skull	60.8
Maximum width of skull	36.0
Maximum height of skull	12.0
Length of oral region	21.6
Maximum diameter of orbit	16.0
Narrowest interorbital breadth	9.3
Maximum diameter of supratemporal fenestra	11.0
Minimum diameter of supratemporal fenestra	6.0
Minimum breadth of temporal region	7.8
Squamosal length	17.5
Maximum width of squamosal	12.6
Mandible length	57.0
Length of mandibular symphysis	10.7
Maximum width of mandibular symphysis	11.8

As in other protosuchids, *S. huidongensis* displays relatively large orbits with orbital margins that are inclined at approximately 40°. The dorsal surface of the two thin palpebrae are ornamented, anteriorly they are broad and overlap the prefrontal and lachrymal while posteriorly they are small and are fused to the anterodorsal postorbital (Figs. 2A, B). *P. richardsoni* and *Orthosuchus stormbergi* (Nash, 1968, 1975) also possess palpebrae, however those on *O. stormbergi* are situated on the antero- and posterodorsal angles of the orbits and are unconnected (Nash, 1968: figs. 1,2; 1975: figs. 1,3). On the UCMP specimen of *P. richardsoni* (Clark, 1986) the palprebrae are also unconnected. However, on specimen AMNH3024 (Colbert and Mook, 1951, pls. 11-1,12-1) these elements appear fused.

The long anterior process of the jugal gradually attenuates anteriorly which differs from the vertically expanded jugal of *Protosuchus* and UCMP97638. The posterior jugal is also elongated, but not to the extent of *P. richardsoni* on which it extends to the posterior cranium and approaches the articulation with the mandible. The margin of the posterodorsal process contacts the quadratojugal and surrounds the highly compressed subtemporal foramen. The quadratojugal is expanded and irregular in shape with an anterodorsal process that extends medially to make an expansive contact with the postorbital and another contact with the ascending process of the jugal, which causes the postorbital to occlude the subtemporal foramen.

The quadrate composes a large portion of the cranium ventral to the otic notch and is ventrally damaged exposing a large pneumaticised internal structure. The medial margin of the anteromedial branch is serrated and fused to the parietal; the lateral margin consists of a single smooth bar that contacts the squamosal; the anterior extremity constitutes the posterodorsolateral margin of the temporal canal and the posterior extremity. Together with the parietal they surround the temporo-orbito arterial foramen, the margin of which pierces the squamosal. This is a character observed in *Edentosuchus tienshanensis* (see Li, 1985).

The squamosal comprises the posterolateral angle of the cranial platform and is triradiate in morphology from a dorsal perspective. Dorsally, it is slightly convex with

conspicuous ornamentation and lies above the quadrate to form the dorsal plate of the external otic recess. Anteromedially it contacts the quadrate while posteriorly it contacts with the parietal. On the occipital surface it contacts the exoccipital with a suture line that runs slightly ventrolaterally.

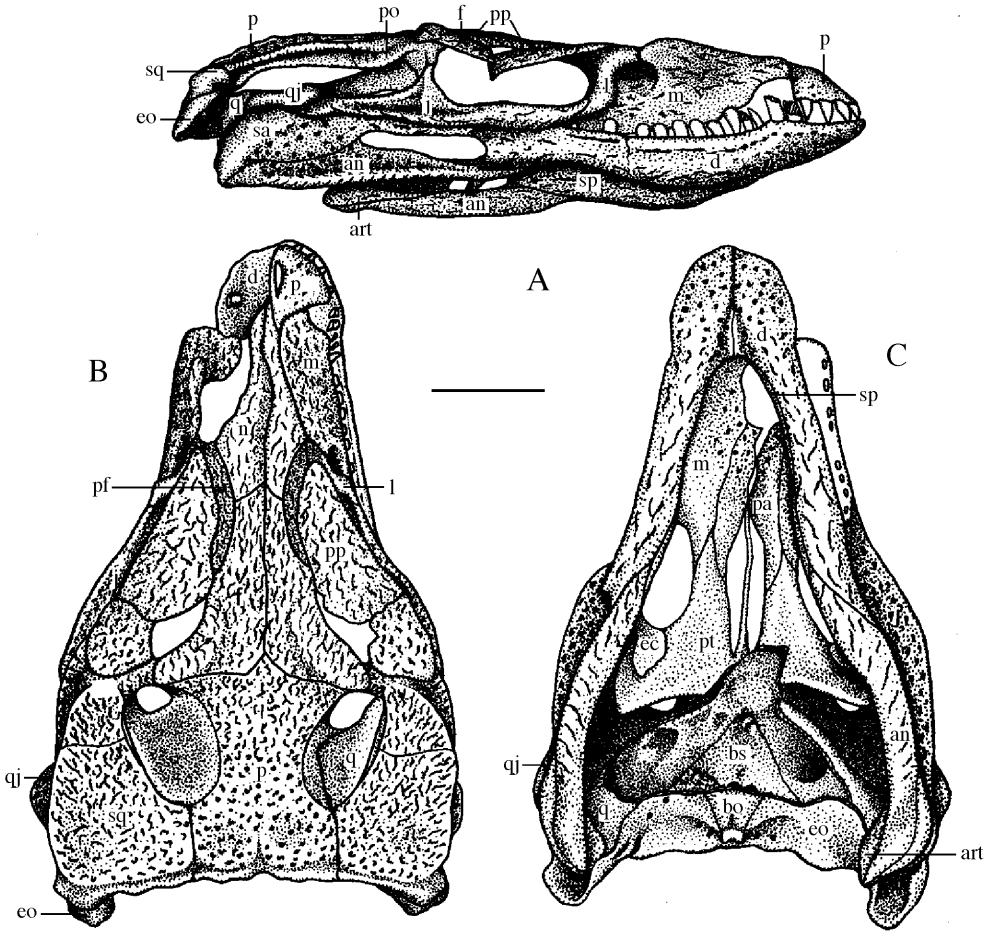

Figure 2. Skull and mandible of *Sichuanosuchus huidongensis* (scale bar = 1 cm). A. Lateral view; B. Dorsal view; C. Ventral view.

an, angular; art, articular; bo, basioccipital; bs, basisphenoid; d, dentary; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lachrymal; m, maxilla; n, nasal; p, parietal; pa, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pp, palpebral; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal.

The fused parietals constitute the largest element on the cranial platform. Anteriorly they contact the frontals with an anterior medial projection, while dorsally they are slightly convex. The anterior half is ornamented with short dispersed grooves, while the posterior half is ornamented with small densely packed pitting. Laterally, the supratemporal fossa is relatively small, elliptical in shape, and extends obliquely. This character resembles *Dianosuchus changchiawaensis* (Young, 1982; Wu and Sues, 1995), though the

intertemporal region is relatively narrow, and on *D. changchiawaensis* the intertemporal region is slightly broader than the interorbital region. The supratemporal fossa is unornamented, expands ventrolaterally, and bounds the quadrate with its lateral margin.

The supraoccipital has undergone damage which obscures its morphology and the relationships of the surrounding cranial elements. The exoccipital-opisthotic complex lies lateral to the supraoccipital and foramen magnum with a concave crescentically shaped posterior surface. Its dorsal margin contacts the squamosal and parietal, while medially it fuses with the basioccipital and composes the dorsal portion of the occipital condyle, which is a contrast to *P. richardsoni* in which the exoccipital is not a component of the occipital condyle. The paroccipital process extends posteroventrally and has a trough shaped anteroventral surface. Its dorsal surface compliments the posterior process of the squamosal. The ventromedial margin of the paroccipital process contacts the quadrate and surrounds the spacious lateral cranioquadrate canal. On the vast majority of mesosuchians and eusuchians this canal is sealed.

The basioccipital is relatively small and composes the majority of the posteroventral neurocranial wall and the occipital condyle. The condyle is small and semicircular in shape with a concave posterior surface. The cervical region is not completely exposed but appears to be reduced. There has been some slight damage to the anterior end of the basioccipital, but as in *P. richardsoni* there appears to be two small nodes at its anterior margin.

Like the pterygoid and the quadrate, the basisphenoid has attained the same degree of pneumatisation. It is broken ventrally, but what can be observed from the remaining dorsal plate, it is triangular in shape, larger than the basioccipital, and composes the ventral wall of the neurocranium. The pterygoid has also suffered some slight damage, but still displays a well developed pterygoid flange and it is also well pneumaticised. Ventrally it lacks sculpturing and is smooth and glossy. The posterior laterally extended lamina determines the posterior aperture for the internal nares. A thin and long lamina lies between the two pterygoids and extends anteriorly to displace the interpterygoid vacuity. The medioventral portion of the ectopterygoid is relatively large and broad and contacts the anteroventral pterygoid. Its medial portion is extremely narrow while dorsally it is anteroposteriorly expanded to contact the jugal.

The palatine differs from that on *S. hangjinensis* by being relatively narrow, long, and linear (Fig. 2C). However, like *S. hangjinensis*, it does not compose a boundary of the suborbital foramen. The ventral palatine is ornamented with a small amount of pitting ornamentation.

The dentary is long, exceeding two-thirds the length of the mandible, and is laterally heavily ornamented. The symphysis is extremely short and broad with its length less than its breadth, which is a character that is not shared with other members of the Protosuchia. Dorsally the symphysis is concave, ventrally it is convex, and is generally spade-shaped. Posteriorly the dentary becomes broadened, the bifurcated posterior margin encapsulates the anterior margin of the mandibular fenestra, and the splenial is fused to the medial dentary with its anterior terminus extending to the symphyseal region, which surficially appears to compose a portion of the symphyseal region.

The angular is anteroposteriorly elongated, triangular in lateral perspective, and slightly laterally curved in ventral perspective. Its ventral margin is transversely expanded creating anteroposteriorly directed laminar ridges on the ventromedial and ventrolateral sides (Figs. 2A, C). This character is unreported on other protosuchids. Anteriorly, the angular gradually descends to form the ventral boundary of the mandibular fenestra.

Posteriorly it also gradually descends and attenuates as it rotates ventrally to finally terminate at the posterior margin of the mandible. The angular/surangular suture line extends as an oblique line from the posterior end of the mandibular fenestra posteroventrally to ultimately terminate at the posteroventral surface of the ramus. The surangular is relatively large and long with a dorsal margin that is very slightly dorsally curved. Anteriorly it contacts the dentary while posteriorly it narrows slightly to eventually form the lateral side of the articular fossa.

The articular is fused to the posteromedial side of the angular and surangular. It is dorsally concave and together with the surangular composes a large and broad surface for articulation with the quadrate. It resembles *S. hangjinensis* in that it is medially expanded to form a laminar process (Fig. 2C). The dorsal side of this process contacts with the ventrolateral side of the neurocranium while the articular fossa is expanded to contact the dorsal surface of this process.

Premaxillary teeth are long and large with acute apices. Anterior margins are convex and lack serrations, while posterior margins are vertical and very slightly serrated. Because the maxilla and mandible have shifted in position the right maxilla is obscured by the opposing dentary. The left maxilla preserves nine teeth within eleven alveolae. The second maxillary tooth is large and caniniform with a smooth and convex anterior margin, while its posterior margin is vertical and slightly serrated. The posterior teeth are not reduced at their bases, are laterally compressed, and have flattened apical. Under magnification the apices margins are very slightly serrated anteriorly and posteriorly with serrations at the apices more well developed than anteroposteriorly. This feature differs from other protosuchids.

The left mandible displays only the base of a single large tooth as the remaining dentition is obscured by the maxilla and maxillary dentition. The right mandible preserves eleven teeth with three empty alveoli at its midpoint for a total of fourteen potential teeth in the dentition. Anteriorly there are two large caniniform teeth that have undergone varying degrees of damage and are anteriorly convex and posteriorly linear in cross-section. Posterior to the caninform teeth are two relatively small and thin teeth. The remaining posterior dentition resembles that on the maxilla in morphology and size.

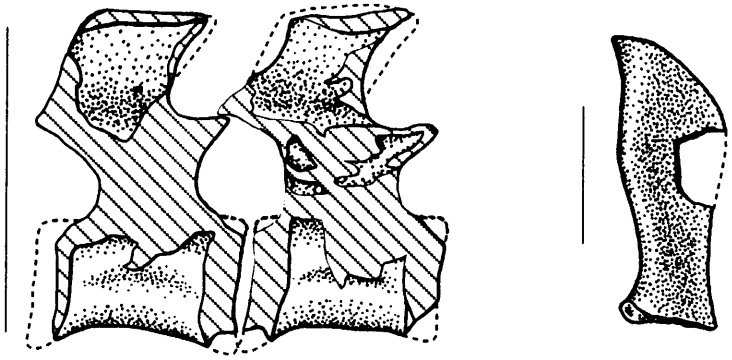

Figure 3. (A) Right lateral view of 22nd and 23rd presacral vertebrae and (B) medial view of left scapula of *Sichuanosuchus huidongensis* (scale bare = 1 cm).

Twenty three presacral vertebrae are preserved. Nine cervical vertebrae are identified based upon centrum and rib relationships. Cervical centra are approximately four mm in length 0with distinctly inflated anterior and posterior ends. There is a conspicuous

median ventral keel, transverse processes are extremely well developed, but lateral fossae are indistinct. Dorsal vertebrae 22 and 23 bound the sacral region with centra that are 6.5 mm in length, are amphicoelus with conspicuously inflated anterior and posterior ends, lack median keels, and lateral fossae are indistinct. Neural arches are high composing a spacious neural canal. Anterior and posterior zygopophyses are long, neural spines are low but relatively broad, extending obliquely anteriorly, and are slightly thickened at their termini to fuse with the ventral surface of the overlying osteoderms.

Specimen ZDM3403 preserves over ten articulated medial and posterior caudal vertebrae which have short centra of six to seven mm, lateral fossae are relatively distinct, and neural arches are extremely low, as are the neural spines which extend obliquely posterodorsally. Anterior zygopophyses are well developed but posterior zygopophyses are inconspicuous.

Cervical ribs are basically in the condition of the Eusuchia, being bicapitate with transversely broadened proximal ends that extend anteriorly into sharp processes. Shafts are short and gradually attenuate posteriorly with a distal end that contacts the anterior process of the succeeding rib. Dorsal ribs are more robust with slightly expanded proximal ends and relatively long shafts. Several relatively well preserved, approximately three mm long, haemal arches are preserved on the medial and posterior caudal vertebrae which in lateral perspective resemble ax blades. Dorsal ends are slightly inflated and shafts are small with distal ends that broaden abruptly before diminishing.

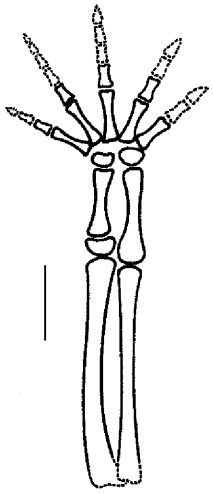

Figure 4. Reconstruction of the left forelimb and manus of *Sichuanosuchus huidongensis* (scale bar = 1 cm).

Anterior limbs represented on ZDM 3404 include a left scapula, humerus, ulna, the majority of a radius, and a manus. The scapula (Fig. 3B) resembles that on *O. stormbergi* in its simitar-shaped morphology. Its distal margin is thin, transversely expanded, elongated dorsoventrally, and attenuates to a sharp angle. Dorsally it narrows but thickens to an expanded terminus to compose the dorsal half of the glenoid fossa.

The humerus is represented only by eleven mm of its distal end, but the impression preserved within the matrix appears to exceed 30 mm. The shaft is slightly curved and the distal end is distinctly inflated with the medial condyle slightly smaller than the lateral condyle. The posterior intercondylar groove is spaciously broad, but an anterior groove is absent.

The most proximal end of the ulna is missing but there is a 31 mm impression in the matrix. The olecranon process is relatively well developed, the shaft is slightly curved and twisted, the distal end is very slightly expanded, and a posterior intercondylar groove is particularly conspicuous. The proximal end of the radius is also missing but the length of its matrix impression is 30 mm.

Five carpals are present as in *O. stormbergi* (Nash, 1975; fig. 14) (Fig. 4). The pisiform is a compressed spherule that lies between the ulna and ulnare. The radiale is 13 mm in length which is, relatively speaking, longer than in other protosuchids. Its proximal end is distinctly inflated and the distal end is kidney shaped to articulate with the radius and ulna. The ulnare is 10 mm in length with a shaft that is slightly more gracile than the radiale. Distal carpal 1+c is a relatively large compressed spherule. Distal carpal 3+4 is relatively small and elliptical.

Metacarpal I is short, robust, five mm in length, and has a proximal end that is distinctly more expanded that the distal end. Metacarpal IV is seven mm in length with a relatively gracile shaft. Metacarpals II and II are incompletely exposed, and metacarpal V is obscured beneath III and IV with only a portion of its shaft visible.

Preservation of the hind limbs includes 13 mm of the right distal femur, 18 mm of the right proximal tibia, 7.5 mm of the right proximal fibula and a portion of the left limb. The distal femur is distinctly laterally expanded with the lateral condyle slightly larger than the medial condyle and there are distinct anterior and posterior intercondylar grooves. The proximal tibia is distinctly expanded into a triangular morphology but a cnemial crest is indistinct. The proximal fibula is very weakly inflated and maintains an elliptical articulation surface. The fibular shaft is relatively gracile, the lateral surface is more convex than the medial surface, and in cross-section it is triangular.

The astragalus is irregular in shape, five mm broad, and three mm thick. An extended oblique ridge lies on the dorsomedial surface and at each side lies a sulcus for articulation with the tibia and calcaneum. The calcaneum is also irregular and slightly smaller than the astragalus with a dorsal sulcus for articulation with the fibula. The metatarsal region preserves Mt II, III, and IV, all of which are gracile and long. Mt III is the longest attaining 21 mm. Four digits are preserved: phalanx 1 of digit II is 7.7 mm in length, has distinctly inflated proximal and distal ends, the proximal articular surface is concave, and is generally triangular in shape. Phalanx 1 of digit three is slightly longer with a straight shaft. Digit 1 of phalanx four is 7.0 mm in length with a relatively gracile shaft. Phalanx 4 of digit 2 is slightly shorter than phalanx 1 of digit four.

Twenty-one continuous pairs of large quadratic presacral osteoderms are present on ZDM3403, but only the left side of presacral osteoderms 22 and 23 are preserved. Additionally, several fragmentary transversely expanded ventral osteoderms are present on the left side. The morphology of these osteoderms generally resembles those on *O. stormbergi* and *P. richardsoni*. The osteoderms overlap in configuration and each pair corresponds to a single vertebrae. Those corresponding to the cervical region are extremely small. Posteriorly they gradually increase in size with the largest being 7.5 mm in length and 12 mm in breadth. The dorsal surfaces are slightly convex and are ornamented with relatively regular pitting or short grooves.

Comparison and discussion: Peng (1995) conducted a brief discussion on the phylogenetic status of *Sichuanosuchus huidongensis* by comparing it to taxa outside of China. Detailed comparisons, however, were yet to be conducted upon the protosuchids found within China. Currently, *Sichuanosuchus* is known to share characters with *Shantungsuchus* from the Late Jurassic of Shandong and the Early Cretaceous of the Ordos region (Peng, 1995; Wu and Sues, 1995). Both appear to represent a late evolutionary independent lineage of the Protosuchidae and share the following characters: in lateral perspective, premaxillary and maxillary region are shorter than all other protosuchids; ventral jugal is expanded to compose a convex plate; there is a well developed interpterygoid vacuity; palatine does not compose a boundary of the suborbital foramen, and the posterior angular rotates ventrally. These two genera differ in that: *Sichuanosuchus* has a shorter oral region with a relatively long posterior maxillary process; the posterior process of the jugal is long and laterally expanded; the ventral squmosal lacks a supporting buttress or a ridged structure as in *Shantungosuchus;* the palatine is narrow and long as opposed to being foliate; the ventral palatine is unornamented as opposed to the well ornamented ventral palatine on *Shantungosuchus;* and the symphysis is short with a straight suture line, with both sides being basically symmetrical.

Specimen IVPP10594 is an undescribed protosuchid skull identified as *Sichuanosuchus* recovered from the Sichuan Basin and which is purportedly Early Cretaceous although precise locality data is absent (Wu and Sues 1995). Xiaochun Wu believes it to represent a distinct species (pers. com.). It is distinguished from *S. huidongensis* by the morphology of its first maxillary caniniform tooth; the presence of only a single mandibular caniniform tooth in the third alveolus; the dentary is distinctly reduced posterior to the caniniform tooth; the ventral symphysis suture line is a groove; and frontals are fused.

Several protosuchids have been recovered from the red beds of the Lower Jurassic Lower Lufeng Fm. in the Lufeng Basin of Yunnan Province. *Microchampsa scutata* (Young, 1951) was erected on the basis of a partial skeleton associated with dorsal scutes, but there is controversy regarding the legitimacy of this assignment due to the absence of precise diagnostic characters (Wu and Sues, 1995). *Platyognathus hsui* (Young, 1944) is represented by a skull and mandible and resembles *Sichuanosuchus* by the presence of two caninform teeth in the mandible but differs in the positions of these teeth which lie in the fifth and sixth alveoli. Also, in cross-section the sixth tooth is polygonal and not a anteriorly convex and posteriorly linear (Young, 1944; Wu and Sues, 1995). Simmons (1965) described another Lower Jurassic protosuchid (CUP2083) which he assigned to *P. hsui* but Wu and Sues (1995) regard this specimen as a separate taxon. Its symphysis is relatively long, dentition is acute and there is only a single caniniform tooth in the mandible, which also distinguishes it from *Sichuanosuchus.*

Dianosuchus changchiawaensis (Young, 1982) is yet another protosuchid derived from the Lower Lufeng Fm. at Lufeng that shares characters with *Sichuanosuchus* including a relatively short symphysis and eliptically extended supratemporal foramen. It differs distinctly, however, in its relatively broad intertemporal region, long post-temporal foramen region, and unserrated dentition.

ZDM3403 is a small form with a cranial length of six cm and a presacral vertebrae column length of approximately twelve cm. Body length estimations of *Protosuchus richardsoni* (Colbert and Mook, 1951) and *Orthosuchus stormbergi* (Nash, 1975) indicate an approximate 40 cm length. Although several characters indicate the Zigong specimen is an adult, such as the fused parietal and well developed cranial ornamentation, characters suggesting juvenile status include the frontals being incompletely fused, the relatively broad parietal platform, small and elliptically shaped supratemporal fossa, relatively large orbits, relatively short preorbital region, and distinct suture lines between the neural arches and centra on the presacral vertebrae.

A carnivorous diet of *Sichuanosuchus huidongensis* is demonstrated by the heterodont dentition with large upper and lower caniniform teeth and laterally compressed and serrated post caniniform dentition. Relatively long and gracile anterior limbs are reflected in the radius, ulna, and carpal sequence indicating quadrupedality. Characters indicating a predominantly aquatic habitat such as in the Eusuchia include the posterior positioned internal nares as displayed by the ventrally ridged pteryoid which indicates only the basal wall of the internal nares was a soft tissue complex.

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