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ARTICLE

A LONG-SNOUTED PROTOROSAUR FROM THE MIDDLE TRIASSIC OF SOUTHERN CHINA

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ABSTRACT—A new protorosaur is described on the basis of a single specimen from the Ladinian of southern China. Although it has been greatly crushed, it still preserves clear details of the skull and axial skeleton. It possesses a neck that is longer than the trunk and is similar to tanystropheids in having 12 or 13 cervicals. Unusual among protorosaurs, the new form has an elongate snout. It also lacks a clear thyroid fenestra, although there is a slight separation of the pubis and ischium close to the pubic symphysis. The new form adds to the growing diversity and disparity of protorosaur taxa from the Middle Triassic of southern China.

INTRODUCTION

In recent years, an abundance of marine Middle Triassic (Ladinian, perhaps earliest Carnian) vertebrate fossils have come to light at several localities in southwestern Guizhou and eastern Yunnan provinces, collectively referred to as the 'Xingyi Fauna,' including fishes and reptiles (Jiang et al., 2009). The layers yielding the Xingyi Fauna correspond to the Zhuganpo Member of the Falang Formation. A new species of the protorosaur genus *Macrocnemus*, *M. fuyuanensis* Li, Zhao, and Wang, 2007, has recently been described from outcrops at Jiyangshan near Huabi, Fuyuan County, Yunnan Province; a second, more complete specimen from the same taxon and locality was recently described by Jiang et al. (2011). The second, related protorosaur genus that forms part of the Xingyi Fauna is *Tanystropheus* from outcrops of equivalent age in the Wusha District, Xingyi City, Guizhou Province (Li, 2007; Rieppel et al., 2010; undescribed material is known from the Fuyuan locality). Li et al. (2007) noted the close affinities of the Xingyi Fauna with the Middle Triassic marine vertebrate fauna from Monte San Giorgio (Switzerland) and Besano (Italy) in the western Tethys, which yielded fossils of the same two protorosaur genera, *Macrocnemus* and *Tanystropheus*. The only other protorosaur currently known (exclusively) from southwestern China is *Dinocephalosaurus orientalis* Li, 2003, from Anisian (Middle Triassic) localities in Panxian County, Guizhou Province.

Here we describe a completely new protorosaur based on a single specimen that preserves the back two-thirds of the skull, part of the cervical and dorsal axial skeleton, and the majority of both the pectoral and pelvic girdles (Fig. 1). However, practically all the limbs and tail are missing. The relatively large orbit and lack of complete fusion between the neural arches and centra of the dorsal vertebrae indicate that this may be an immature individual. The new form represents one more protorosaur within the Xingyi Fauna that exhibits some quite unexpected departures from the typical suite of protorosaurian characters.

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Geologic Background

The new protorosaur was found in the Zhuganpo Member of the Falang Formation. These beds comprise thin- to medium-bedded, gray to dark-gray laminated marl and limestone. Based both on lithology and its invertebrate fossils, particularly the ammonite *Anolcites*, this unit is considered to represent a sequence of sediments that were deposited on the sea shelf during Ladinian times (Mineral Bureau of Guizhou Province, 1982; Dong et al., 1997). However, the occurrence of the conodont *Paragondolella polygnathiformis* is suggestive of an earliest Carnian age (Jiang et al., 2009). Other protorosaurs occurring in the Zhuganpo Member include *Tanystropheus* (Rieppel et al., 2010) and the terrestrial form *Macrocnemus* (Li et al., 2007), along with a wide variety of additional marine reptiles and a very diverse fish fauna. Other marine reptiles that are known from the Zhuganpo Member include nothosaurids (*Nothosaurus*, *Lariosaurus*), placodonts (*Glyphoderma*), pachypleurosaurids (*Keichousaurus*), pistosaurids (*Yunguisaurus*), and thalattosaurs (*Anshunsaurus*) (Li et al., 2002; Cheng et al., 2004, 2006; Rieppel et al., 2006, 2010; Li, 2007; Zhao et al., 2008a, 2008b; Sato et al., 2010).

Institutional Abbreviations—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **ZMNH**—Zhejiang Museum of Natural History, Hangzhou, China.

SYSTEMATIC PALEONTOLOGY

ARCHOSAUROMORPHA von Huene, 1946
PROTOROSAURIA Huxley, 1871
FUYUANSAURUS ACUTIROSTRIS, gen. et sp. nov.
(Figs. 1–5)

Diagnosis—Small protorosaur with a pronounced elongate rostrum compared with all other protorosaurs; teeth small and needle-like similar to *Macrocnemus* and *Tanytrachelos*; 13 elongate cervical vertebrae shared with *Tanytrachelos* and *Tanystropheus*; cervical vertebrae 8 and 9 approximately three times as long as high; cervical ribs associated with cervicals 3–9 extend

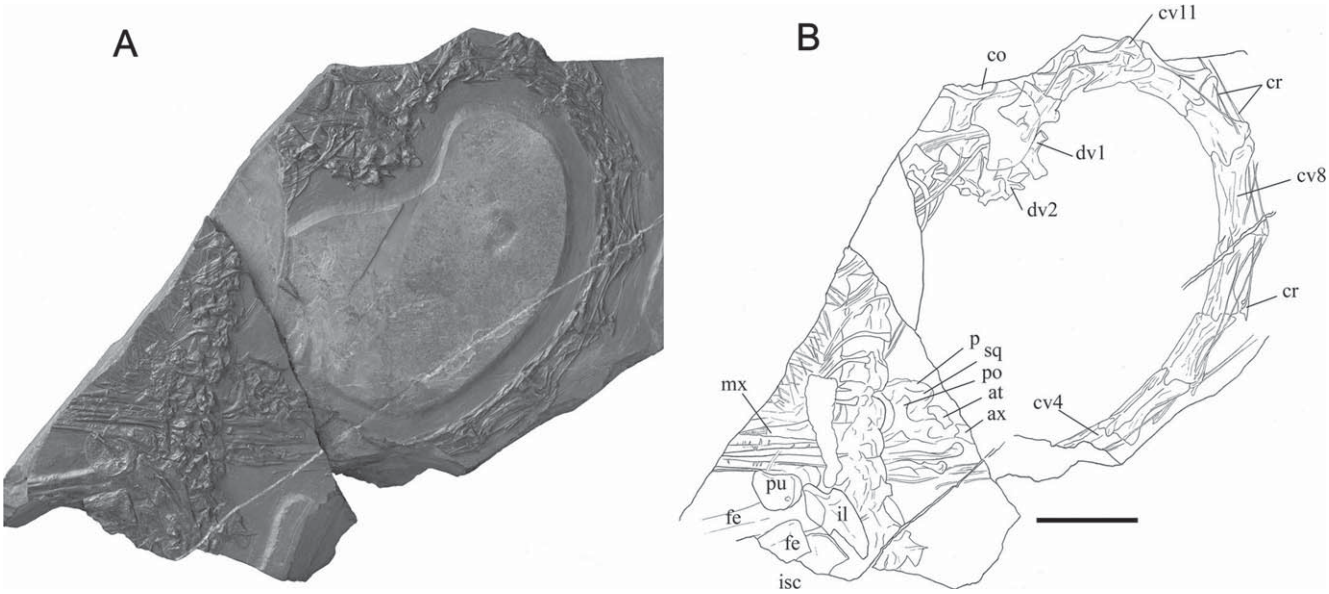

FIGURE 1. *Fuyuansaurus acutirostris*, gen. et sp. nov. Holotype IVPP V17983. **A**, complete specimen as preserved; **B**, line drawing of the skeleton. **Abbreviations**: **at**, atlas; **ax**, axis; **co**, coracoid; **cr**, cervical rib; **cv**, cervical vertebra; **dv**; dorsal vertebra; **fe**, femur; **hu**, humerus; **il**, ilium; **isc**; ischium; **mx**, maxilla; **p**; parietal; **po**, postorbital; **pu**; pubis; **sc**, scapula; **sq**, squamosal; Scale bar equals 20 mm.

across two intervertebral joints; pelvis lacking a thyroid fenestra is unique among protorosaurs other than *Dinocephalosaurus*.

Type Locality—Jiyangshan near Huabi, Fuyuan County, Yunnan Province.

Holotype—IVPP V17983.

Etymology—Generic name after the locality where it was discovered; specific name for the elongate preorbital region of the skull.

DESCRIPTION

Skull

The premaxillae have been completely lost along with the anterior parts of both maxillae, although on the left side only the anterior-most tip of the maxilla is missing. Based on the very low inclination of the dorsal margin of the maxillae and the absence of external nares, it seems likely that up to a third of the rostrum is missing. Consequently, it is clear that the rostrum was slender and elongate and tapered to a pointed tip (Fig. 2). The posterior portion of the left maxilla exhibits a surface ornamentation of longitudinal striae. Its dorsal margin forms the boundary between the skull roof and the lateral facial region and slopes gently posterodorsally. The bone deepens as it extends towards the orbit and there is some suggestion of a depression in this region—perhaps an expression of the lachrymal duct or even a posterior extension of a gutter associated with the external naris. Such a postnarial groove has been observed in two other protorosaurs: *Dinocephalosaurus* (Rieppel et al., 2008) and *Macrocnemus* (Jiang et al., 2011). Unfortunately, this area is partly obscured by gastralia and also contents of the hindgut, making it impossible to identify further detail. A few teeth are preserved on the exposed portions of both maxillae (and also the dentaries) and these are small and acutely conical, exhibiting no variation in size along the preserved parts of the rami.

The posterior dorsal region of the vertebral column and the pelvic girdle obscure details of the preorbital region. Nevertheless, the posterior margin of the orbit is preserved and there is a relatively short temporal region (Fig. 2). Parts of the slender jugal can be seen together with a relatively large postorbital still in natural articulation. It cannot be determined if the lower temporal arcade was complete. Parts of the left parietal and squamosal are preserved, although they have been somewhat displaced ventrally. The parietal appears to be developed into

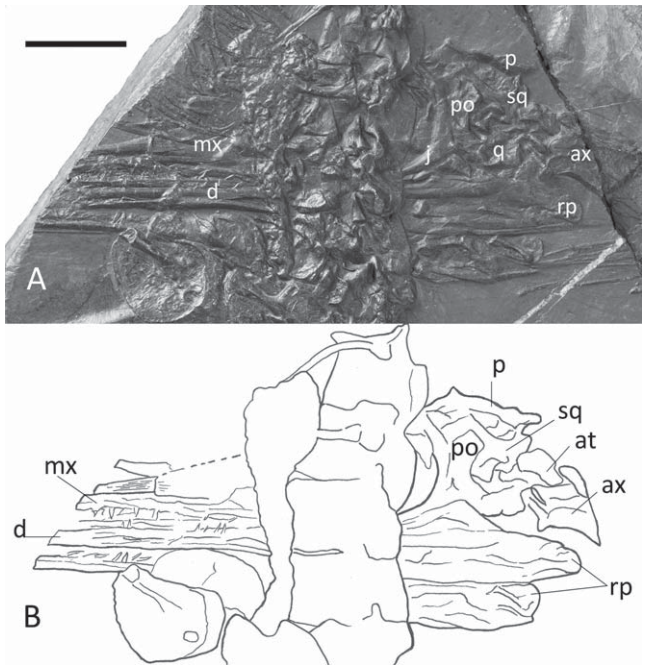

FIGURE 2. *Fuyuansaurus acutirostris*, gen. et sp. nov. Holotype IVPP V17983. **A**, skull overlain by the pelvis as preserved; **B**, line drawing of the skull. **Abbreviations**: **at**, atlas; **ax**, axis; **cop**, coprolite; **d**, dentary; **dv**, dorsal vertebra; **mx**, maxilla; **p**, parietal; **po**, postorbital; **q**, quadrate; **rp**, retroarticular process; **so**, supraoccipital; **sq**, squamosal; **sv**, sacral vertebra; Scale bar equals 10 mm.

a raised ridge above the supratemporal arcade, but this may be an artifact of preservation. Nevertheless, it should be noted that there is a weakly developed median ridge on the parietals of some other protorosaurs, including *Protorosaurus* (Gottmann-Quesada and Sander, 2009). A strap-like bone is here identified as the left squamosal: it is angled anterodorsally, but this is almost certainly the result of crushing. The left quadrate is approximately in its life position, although it has been pushed forward. Other details of the temporal region are unclear, although behind the quadrate and below the squamosal scattered elements of the braincase are preserved. These include a probable supraoccipital. The ventral part of the right quadrate appears to be lodged between the atlas and the supposed supraoccipital.

The posterior parts of both mandibles are complete and they are developed into very pronounced and clearly rounded retroarticular processes. These appear to have been displaced posteriorly so that they lie somewhat out of position underneath the axis. The retroarticular process is developed into a distinctive rounded termination. The right mandible is exposed in medial view, somewhat displaced ventrally, whereas the left is exposed in lateral view slightly displaced posteriorly.

TABLE 1. Length and height of the cervical vertebrae in *Fuyuansaurus acutirostris* IVPP V17983.

Element	Length (mm)	Height (mm)
Atlas	—	—
Axis	—	—
Cervical 3	—	—
Cervical 4	—	—
Cervical 5	15.25	4.7
Cervical 6	16.45	5.0
Cervical 7	17.2	5.0
Cervical 8	15.75	5.5
Cervical 9	15.35	6.1
Cervical 10	14.0	6.8
Cervical 11	12.1	6.8
Cervical 12	10.25	5.8
?Cervical 13	8.75	5.9
Dorsal 1	8.35	—
Dorsal 2	—	—
Dorsal 3	8.5	—
Skull as preserved	50 mm*	
Estimated total cervical series	172 mm	
Estimated total dorsal series	100 mm	

The height is measured at the midpoint of each vertebra from the ventral edge of the centrum to the dorsal edge of the neural spine. The length is taken from the anterior to the posterior edge of the centrum. *The skull may have extended at least another 15–20 mm.

Axial Skeleton

The left side of the axis neural arch is preserved just behind the posterior margin of the squamosal (Fig. 2). The axis lies at the edge of the block and is incomplete posteriorly and the neural spine is not preserved. It is therefore not possible to say whether the axis possessed the low but prominent neural spine that is typical of protorosaurs generally (e.g., Wild, 1973; Fraser and Rieppel, 2006; Jiang et al., 2011). The extreme dorsal edge of the neural spine is all that remains of the third cervical vertebra, but it is clearly long and low. The anterior part of the fourth cervical is also missing, but much of the neural spine is preserved, extending as a low ridge to a point level with the anterior edge of the prezygapophysis of the succeeding vertebra. Part of the shaft of the cervical rib runs parallel with the centrum and extends across the next two intervertebral joints. The fifth cervical is the first completely preserved (Fig. 3). The long and low neural spine extends anteriorly as a spine that terminates at a point level with the intervertebral joint. The prominent prezygapophysis has a depression towards the base that also appears to house a small foramen. A similar depression is also present in the succeeding cervical vertebrae. The facets for the double-headed ribs (diapophysis and parapophysis) lie one above the other low down on the anterior edge of the centrum, and are separated by a longitudinal groove that extends posterodorsally onto the body of the centrum.

The next two cervicals have a very similar shape to the fifth, but they are successively a little more elongate, with the seventh being the longest at 17.2 mm (Table 1). Cervicals 8 and 9 are also of a very similar form, although slightly shorter. In addition, they are slightly deeper, with the neural spine becoming a little taller. The neural spine of cervicals 10, 11, and 12 is slightly further pronounced and reduced in length. At first glance, the 13th vertebra in the series appears to lie on top of the anterior edge of the left scapula (but see below). At 8.75 mm long (and only 5.9 mm high at the midpoint), it too is relatively elongate. The neural spine is rather shorter than in preceding vertebrae and is restricted to the posterior half of the element. In other protorosaurs, the most posterior two or three cervicals have assumed 'dorsal-like' proportions so that the only distinguishing feature is the nature of the associated ribs. A single articulation facet for the rib is preserved on the anterodorsal edge of the centrum. Immediately behind this facet is a small foramen. Unfortunately, the rib is missing, and it is therefore not possible to say whether it had the form of a typical cervical rib with an anterior process. Nevertheless, we consider this most likely to represent the posterior-most cervical.

The vertebral column has clearly broken in the region of the cervical-dorsal transition. At first glance, the left scapula appears to underlie vertebra 13 while overlying vertebra 14. This would suggest that the pectoral girdle has shifted forwards and become lodged between the break in the column. However, on closer examination, a very faint rugose pattern can be discerned over the

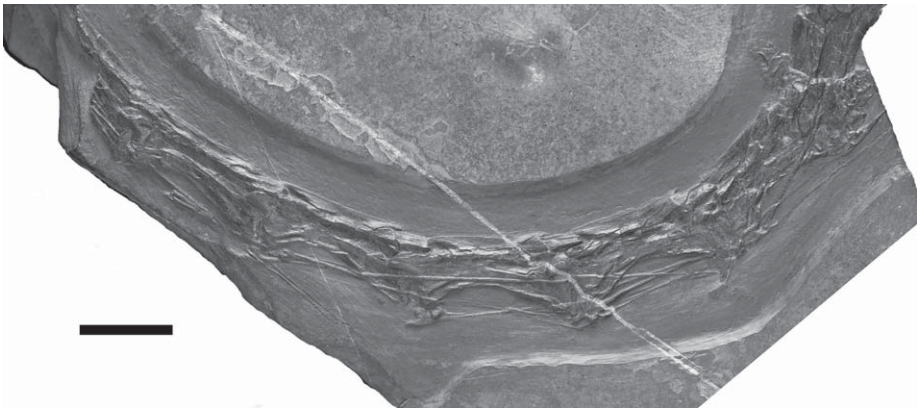

FIGURE 3. *Fuyuansaurus acutirostris*, gen. et sp. nov. Holotype IVPP V17983, cervical series. Scale bar equals 10 mm.

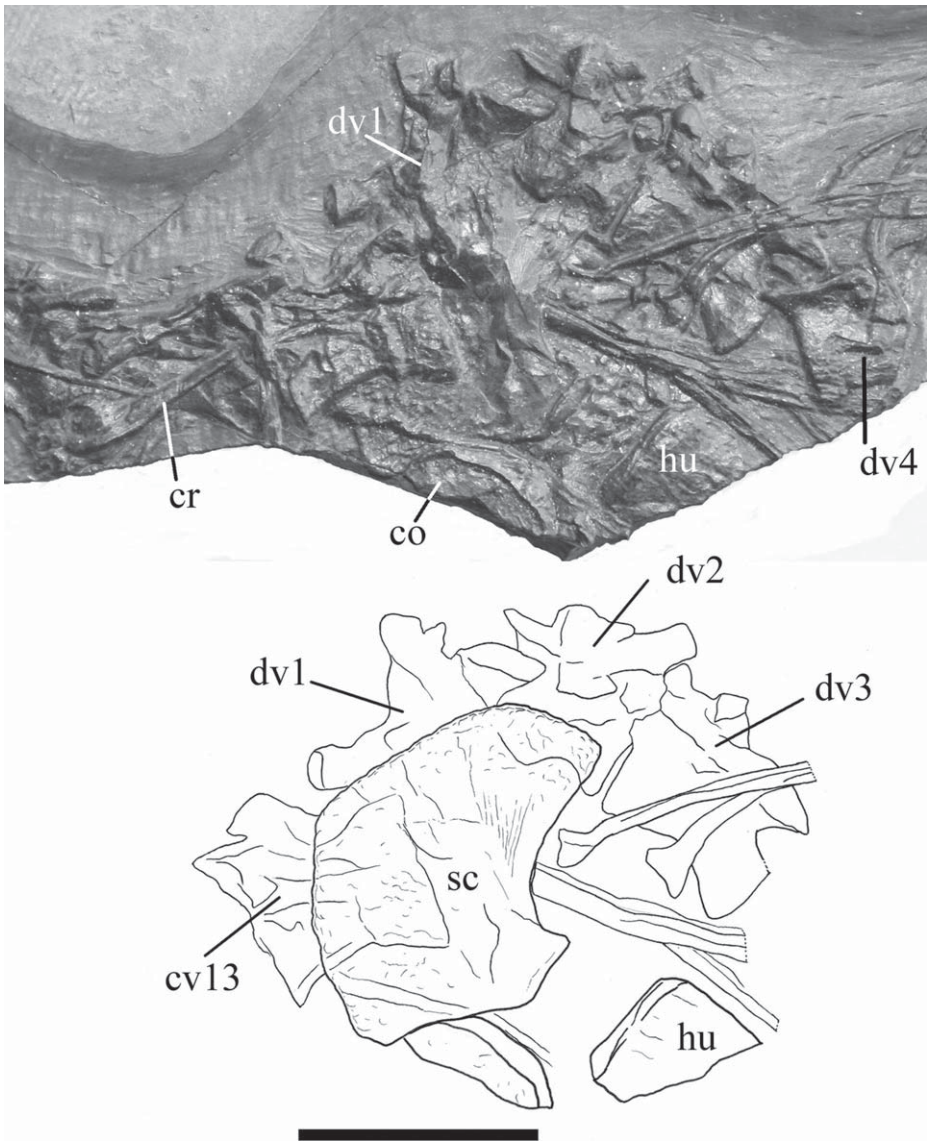

FIGURE 4. *Fuyuansaurus acutirostris*, gen. et sp. nov. Holotype IVPP V17983. Pectoral region and associated vertebrae as preserved together with an interpretative line drawing. **Abbreviations**: **co**, coracoid; **cr**, cervical rib; **cv**, cervical vertebra; **dv**; dorsal vertebra; **hu**, humerus; **sc**, scapula. Scale bar equals 10 mm.

posterior half of vertebra 13 that continues onto the scapula. It would seem that the extreme compression of the fossil has resulted in the scapula being plastically deformed over the vertebrae beneath it so that the structural details of the underlying vertebrae can be clearly seen.

Ribs associated with the cervicals have pronounced approximately circular tubercula and capitula and a small, but pronounced anterior process between the two. The ribs associated with cervicals 3–9 are relatively elongate and extend across two intervertebral joints. By contrast, the ribs associated with cervicals 10–12 are relatively short, extending posteriorly little more than half way along the length of the succeeding centrum in cervicals 10 and 11, and in cervical 12 extending only to the end of its centrum. These last three ribs are also a little more robust. The rib associated with cervical 12 tapers from a particularly deep anterior region with a pronounced tuberculum.

Remains of 11 dorsal vertebrae are preserved and a break in the block probably accounts for a further two missing, making a likely total of 13 dorsals. The neural arch and centrum of the posterior dorsals remain unfused. This is particularly well seen in dorsal 10.

The first vertebra that we confidently assign to the dorsal series is the fourteenth (Fig. 4). As noted above, it, together with the 15th, has popped out of alignment with the rest of the axial skeleton, and is displaced upwards over the left scapula so that it lies almost perpendicular to the long axis of the vertebral column. The anterior part of the centrum is covered by the scapula, yet once again the extreme compression of the fossil has resulted in the outline of the centrum appearing as a detailed impression on the scapula. It has a prominent, yet narrow, prezygapophysis, and there is a quite prominent trapezoidal neural spine occupying the posterior third of the neural arch.

The 15th dorsal appears to have been partly crushed and it is a little difficult to decipher the region surrounding the prezygapophyses. The narrow, square-ended neural spine is relatively low. The articulation facet for the rib is situated on a

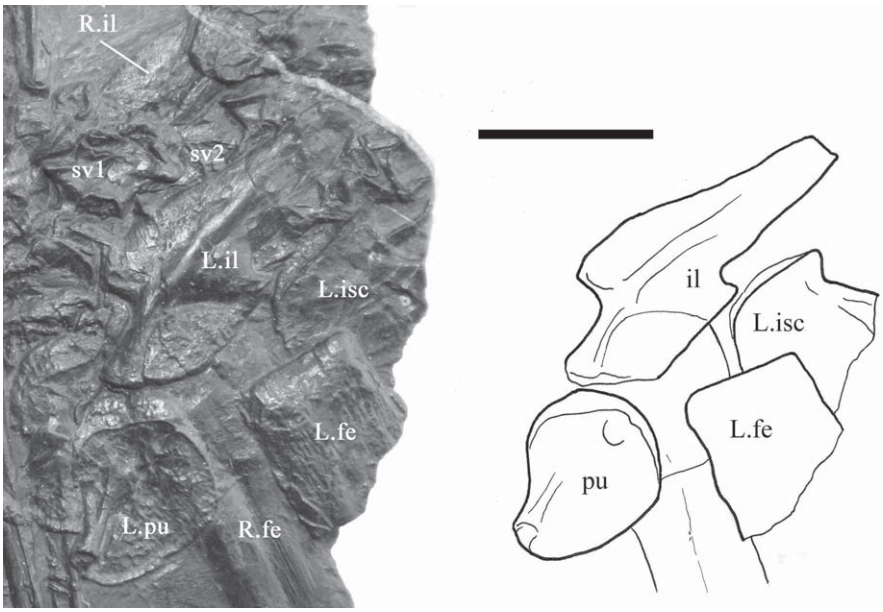

FIGURE 5. *Fuyuansaurus acutirostris*, gen. et sp. nov. Holotype IVPP V17983. Pelvic region as preserved overlying the skull together with an interpretative line drawing. **Abbreviations**: **L.il**, left ilium; **L.isc**, left ischium; **L.fe**, left femur; **L.pu**, left pubis; **sv1**, first sacral vertebra; **sv2**, second sacral vertebra. Scale bar equals 10 mm.

prominent transverse process that takes the form of a ridge or buttress that expands dorsally into a prominent swelling. Vertebra 16 also exhibits this characteristic buttress. Posteriorly, it is overlain by two rib shafts that cover much of the neural spine, although the spine appears to have been quite narrow and low. Only the anterior part of the 17th vertebra is present—the rest having been lost where the block has been fractured. In this element, the buttress or transverse process supporting the rib appears to be slightly less pronounced than the two preceding vertebrae. A lamina of bone extends from the prezygapophysis onto the transverse process. A holocephalous rib lies just below the transverse process—having been displaced so that the shaft passes upwards and across the neural spine.

Based on the size of the broken section of matrix, only one dorsal (the eighteenth) is completely missing, although only the very posterior end of the centrum of vertebra 19 is preserved.

Vertebrae 20–25 are very similar. Each is characterized by a broad neural spine extending the full length of the neural arch. The transverse processes are crushed but still prominent, and with vertebrae 21–23 the ribs are still intimately associated with them, but they do not appear to be fused. Running just ventral to the centra of vertebrae 23–25 is an elongate mass that tapers posteriorly. This mass has a textured surface and is assumed to represent either gut remains or an isolated coprolite.

Details of vertebrae 26 and 27 are difficult to interpret because of crushing, but they are in close proximity to the ilium and we take them to represent sacrals. Sacral 1 (vertebra 26) is shorter than the preceding dorsal vertebrae and has a noticeably shorter neural spine. Sacral 2 (vertebra 27) appears to have dropped out of line with the rest of the axial skeleton and is largely obscured by the left ilium. Behind it part of the iliac blade of the right ilium is visible. Due to the extreme compression of the specimen, it is not possible to comment on the nature of the sacral ribs. Remains of the first and possibly even the second caudal are preserved, but it is not possible to comment any further.

Appendicular Skeleton

The pectoral girdle preserves the left scapula, but only part of the coracoid on the edge of the block (Fig. 4). Part of the right scapula is also displayed beneath the glenoid of the left side. The clavicles have not been identified. The scapular blade is only slightly longer anteroposteriorly than it is deep, and is reminiscent of the same element in *Macrocnemus* and *Tanystropheus*. The extreme proximal tip of the left humerus is also preserved along with a small part of the right humerus in medial view. It appears to have very little expansion of the proximal head, although given the limited preservation of this bone this is difficult to confirm.

The pelvis preserves the entire left ilium and pubis and the major portion of the left ischium (Fig. 5). They have only become separated slightly from their natural articulation. The dorsal part of the right iliac blade is also exposed along with the anterior edge of the right pubis. The iliac blade is rather elongate and directed posterodorsally and with no development of an anterior portion. The impression of the right femoral head is clearly visible underneath the ilium. There is no indication of the right ischium. It is very clear that there is no true thyroid fenestra, although a slight divergence between the distal end of the pubis and ischium along the symphyseal margin indicates a small gap in this region. This is an unusual configuration for most protorosaurs. For example, the tanystropheids *Tanystropheus* and *Tanytrachelos* possess a prominent thyroid fenestra perforating the pubosichiadic plate, as too does *Amotosaurus* (Fraser and Rieppel, 2006), but in basal protorosaurs the condition is less clear and a thyroid fenestra is sometimes absent (see below for discussion).

The pubis is subcircular in outline and is perforated by an obturator foramen positioned in the posterodorsal quadrant of the element. A short, but prominent strut of bone extends anteroventrally down the anterior portion of the element, and terminates in a rounded buttress. This could simply be the impression of another bone underneath because there is considerable evidence of plastic deformation of the bones where they drape over other elements. Alternatively, it represents the pubic tubercle. The ischium is missing the posteroventral edge and the anteroventral corner is covered by the proximal head of the left femur, but it appears to have been approximately square in outline, although with a gentle embayment within the posterior margin.

The proximal ends of both femora are preserved. They are square-headed, lacking any swelling of the proximal head and

without any offset of the terminal articulation facet (Fig. 5). There is also no indication of any tuberosities or prominent muscle insertion points. The right femur as preserved is approximately 25 mm long, but less than 10 mm of the left femur remains.

DISCUSSION

Fuyuansaurus acutirostris is a small aquatic reptile that shows some similarities with tanystropheids, but also has its own very distinct specializations. The presence of elongate cervicals bearing ribs that extend posteriorly across at least two intervertebral articulations confirms its protorosaurian affinities (e.g., Rieppel et al., 2003). The neck is longer than the trunk, a feature that is shared by both *Tanystropheus* (and other tanystropheids) and *Dinocephalosaurus* (Rieppel et al., 2008). Furthermore, the low neural spines of the cervicals and the likely count of 13 cervicals and 12 dorsals are features also shared with tanystropheids (Rieppel et al., 2010). However, the cervical vertebrae and associated ribs are certainly not as elongate as in *Tanystropheus* (either absolutely or relatively). Indeed, in *Fuyuansaurus*, the cervical ribs do not form an overlapping bundle that sheathes the ventral edge of the vertebrae, but each one only extends across, at most, two intervertebral joints, resembling *Macrocnemus* more closely in this respect (Li et al., 2007). In *Tanystropheus*, the longest cervical is either cervical 8 or 9 (Wild, 1973; Rieppel et al., 2010), whereas in *Fuyuansaurus* cervicals 6 and 7 are the longest of the series. Unfortunately, in the absence of complete limbs, it is not possible to comment on the arrangement of the tarsus and whether it exhibited the characteristic elongate proximal phalanx on digit 5 that is so characteristic of tanystropheids.

The pelvic girdle of *Fuyuansaurus* is unusual among derived protorosaurs, such as the tanystropheids, in lacking a thyroid fenestra. Although we do note that Wild (1973:113) figured *Macrocnemus* with a rather narrow thyroid fenestra, our observations on other specimens of *Macrocnemus* from both Europe and China indicate that it was well developed. Nevertheless, within aquatic reptiles there is a tendency for elements of the pelvis to become more rounded and less well ossified such that the thyroid fenestra does tend to lose its identity (e.g., placodonts). Yet in *Fuyuansaurus* there is still a broad contact between the pubis and ischium ventral to the acetabulum, although they do diverge from each other towards the pubic and ischiadic symphyses. The condition within basal members of the group is less clear. Gottmann-Quesada and Sander (2009:166) were unable to determine whether a thyroid fenestra was present or not in *Protorosaurus*, although a thyroid fenestra is absent in *Prolacerta* (Gow, 1975). In addition, the authors have observed a very similar arrangement to *Fuyuansaurus* in an undescribed specimen of *Dinocephalosaurus* (ZMNH M8752), where the pubis and ischium meet along much of their length.

The markedly elongate rostrum that is more reminiscent of an ichthyosaur or certain thalattosaurs is also unique for a protorosaur. The numerous needle-like teeth might be indicative of a diet of crustaceans and fish.

There is some evidence to suggest that this is a juvenile individual. Most notably the apparent lack of complete fusion of the neural arch and centra within the dorsal series, but the relatively large orbit might also be indicative of a juvenile.

The constitution of the protorosaurs is very unclear. Currently there are only three characters uniting an assortment of different taxa: (1) the markedly elongate cervical vertebrae; (2) cervical ribs with a characteristic anterior process and; (3) cervical rib shafts that extend posteriorly across at least two intervertebral joints. The new taxon further complicates the picture, but a new phylogenetic analysis must wait until detailed studies have been completed on a number of new specimens of various protorosaurian taxa.

SUMMARY

Fuyuansaurus acutirostris is a further addition to a host of unusual tetrapods that populated the Middle Triassic seas of the eastern Tethys. Elongate cervical vertebrae bearing cervical ribs that extend across at least two intervertebral joints is a hallmark of all protorosaurs, but the likely presence of 13 cervical vertebrae is a character shared with tanystropheids in particular. The elongate and tapered rostrum of *Fuyuansaurus acutirostris* is unknown in any other protorosaur, and the absence of a typical thyroid fenestra is also notable.

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