

贵州中三叠世安顺龙(爬行纲:海龙目) 一新种¹⁾

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摘要: 中国的海龙类以前仅发现于法郎组瓦窑段,包括安顺龙和新铺龙两属。最近在法郎组竹杆坡段也发现了海龙化石(完整的骨架,中国科学院古脊椎动物与古人类研究所标本编号 V 13782),被归入安顺龙属。标本产自贵州兴义乌沙,时代是中三叠世拉丁期。

此标本小于黄果树安顺龙两个已知标本,但是根据以下特征判断应该是个成年个体:头骨相对较小,许多骨缝愈合,髓椎线(neurocentral suture)封闭,肱骨上各种结构已经显著分化,掌骨和跖骨骨化程度高。根据以下特征建立一新种,乌沙安顺龙(*Anshunsaurus wushaensis* sp. nov.):头骨相对较小(相对肩臼至髁臼长度);轭骨后突短,向后延伸不超过下颞孔之半;后背区的神经棘高度小于宽度,其背缘有垂向沟;脊;间锁骨十字形,前突基部宽;肱骨外髁沟明显,内髁很发育,在内腹侧有脊但无孔;第五掌骨比第四掌骨稍长;第四指失去一个指节;髌骨板向后背向展开;7个跖骨骨化。

关键词: 贵州兴义,拉丁期,法郎组竹杆坡段,海龙类

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A NEW SPECIES OF THE THALATTOSAUR GENUS ANSHUNSAURUS (REPTILIA:THALATTOSAURIA) FROM THE MIDDLE TRIASSIC OF GUIZHOU PROVINCE, SOUTHWESTERN CHINA

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Abstract A new species of the thalattosaur genus *Anshunsaurus* is described from the Zhuganpo Member of the Falang Formation, Ladinian. It differs from the geologically younger *Anshunsaurus huangguoshuensis* (from the Wayao Member of the Falang Formation, lower Carnian) in many morphological characteristics as well as in a smaller size at adult stage. Both occurrences are in the marine Triassic of southwestern Guizhou Province, China.

Key words Xingyi, Guizhou, Ladinian, Zhuganpo Member of Falang Formation, Thalattosauria

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Thalattosaurs are a group of Triassic marine reptiles that have been known from a variety of localities in western North America and Europe (Nicholls, 1999; Rieppel et al., 2000; Rieppel and Liu, 2006). Until recently, the only putative thalattosaur described from the Middle Triassic of southern China (Hubei Province) is *Hanosaurus hupehensis* Young, 1972, but this taxon was later identified as a pachypleurosaur sauropterygian (Rieppel, 1998). *Anshunsaurus huangguoshuensis* Liu, 1999, thus became the first thalattosaur to be reported from the Middle Triassic of southwestern China (Rieppel et al., 2000; Liu and Rieppel, 2005). Since then, a number of papers have been published describing and discussing two species of *Xinpusaurus*, a second Chinese thalattosaur (Cheng, 2003; Jiang et al., 2004; Liu and Rieppel, 2001; Luo and Yu, 2002; Yin et al., 2000). Here, we describe a second species of *Anshunsaurus* from the Middle Triassic of Guizhou Province, southwestern China. This complete skeleton was collected from the Zhuganpo Member of Falang Formation in 2003, together with an *Asialepidotus* sp.

Thalattosauria Merriam, 1904

Askeptosauridae Kuhn-Schwyder, 1952

Anshunsaurus Liu, 1999

Type species *Anshunsaurus huangguoshuensis* Liu, 1999.

Known distribution Middle to Late Triassic, southern China.

Anshunsaurus wushaensis sp. nov.

(Figs. 1~3)

Etymology “Wusha”, the name of fossil locality.

Holotype Institute of Vertebrate Paleontology and Paleoanthropology, IVPP V 13782; complete skeleton.

Locality and horizon Wusha of Xingyi, Guizhou Province, southwestern China; Zhuganpo Member of Falang Formation, Ladinian of Middle Triassic.

Diagnosis A new species of the thalattosaur genus *Anshunsaurus* that differs from *Anshunsaurus huangguoshuensis* in a relatively smaller skull (relative to glenoid-acetabulum length); a short and relatively massively built posterior process of the jugal not extending backwards beyond the midpoint of the lower temporal fossa; the neural spines in the posterior dorsal region not taller than their antero-posterior width, and with a distinct ornamentation of vertical grooves and ridges near their dorsal margin; cruciform interclavicle with a broad-based anterior process; ectepicondylar groove and notch on humerus distinct; entepicondyle well developed, with ridge on ventral side of medial margin but no foramen; 5th metacarpal slightly longer than 4th metacarpal; loss of one phalanx in 4th digit; iliac blade posterodorsally expanded; seven tarsal ossifications (two of problematic homology).

Comments The skeleton is almost complete, approximately 2.6 meters in length (as preserved) (Fig. 1). The skull has been removed from the matrix for inspection from both sides.

Morphological description The skull of *A. wushaensis* is complete but severely laterally compressed (Fig. 2). In many areas, the sutures remain indistinct. The skull measures 198 mm from the tip of the rostrum to the posterior tip of the left supratemporal, and 211.5 mm from the tip of the left dentary to the posterior tip of the left retroarticular process (See Table 1 for more measurements). As is typical for thalattosaurs, the rostrum is long and slender. The distance from the tip of the rostrum to the anterior margin of the (left) external naris is 74.7 mm, the distance from the tip of the rostrum to the anterior margin of the left orbit is 105.4 mm. The length of the rostrum (preorbital skull) thus exceeds the length of the postorbital skull. The rostrum is formed entirely by the premaxillaries. It shows nearly parallel margins before tapering to a blunt tip at its anterior end, and it shows no sign of a ventral deflection. However, the tooth-bearing (alveolar) margin of the premaxilla is slightly concave in lateral view,

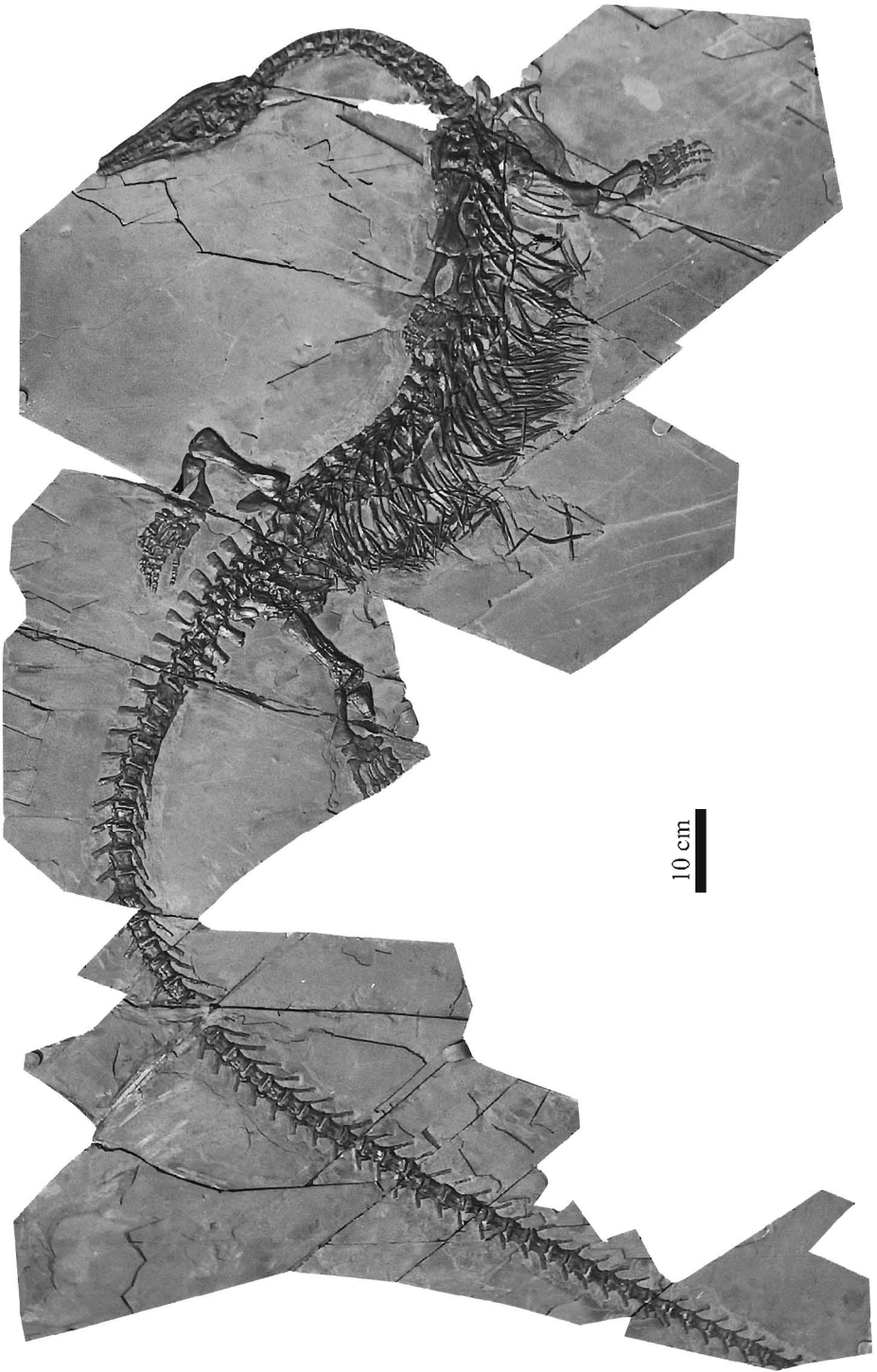


Fig. 1 The skeleton of *Anshunsaurus wushaensis* (holotype, IVPP V 13782)

which results in a curvature that is matched by a slightly convex alveolar margin of the dentary.

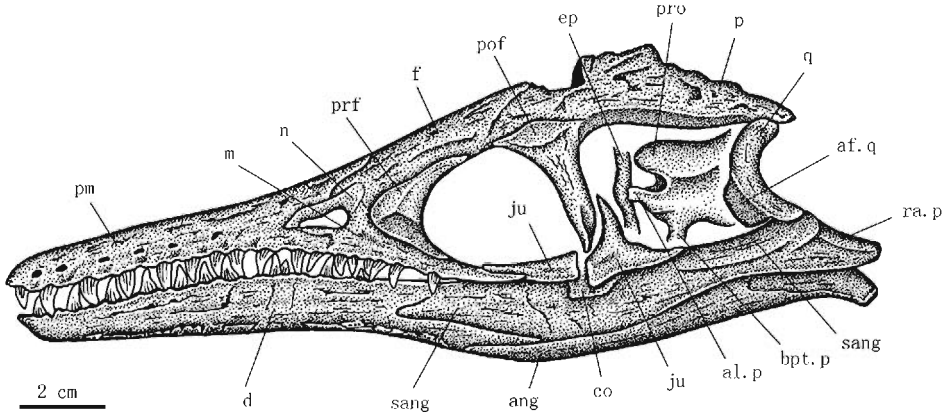


Fig. 2 The skull of *Anshunsaurus wushaensis* (holotype, IVPP V 13782) in left lateral view. Abbreviations: af. q. anterior flange of quadrate; al. p. alar process of basisphenoid; ang. angular; bpt. p. basipterygoid process; co. coronoid; d. dentary; ep. epipterygoid; f. frontal; ju. jugal; m. maxilla; n. nasal; p. parietal; pm. premaxilla; pof. postorbitofrontal; prf. prefrontal; pro. prootic; q. quadrate; ra. p. retroarticular process; sang. surangular

The external naris is retracted. It is a relatively small (longitudinal diameter of the left external naris; 11.2 mm), keyhole shaped opening, narrow anteriorly but widening posteriorly. The premaxillaries form a combined posterior process that is embraced by the anteromedial processes of the frontal(s). It extends posteriorly to the level behind the posterior margin of the external naris.

The anterior dorsal margin of the left nasal is unequivocally identifiable. It shows that the nasal forms most of the dorsal margin of the external naris, and that the nasal forms an anteriorly pointed process that projects somewhat beyond the anterior margin of the external naris. The posterior delineation of the nasal remains unclear, as does its relation to the anterolateral process of the frontal, prefrontal, and maxilla.

The relation of the premaxilla and maxilla lateral and ventral to the external naris remains unclear as well. There is certainly no identifiable suture line, but the topology of the bone surface suggests an anteriorly concave premaxilla-maxilla contact below the posterior third of the length of the external naris, with a slender maxillary process extending anteriorly, forming the ventral margin of the external naris and narrowly approaching the nasal at the anteroventral corner of the external naris. If this interpretation is correct, the premaxilla would remain excluded from most of the ventral margin of the external naris, but again, suture lines are not identifiable.

The prefrontal is a prominent element that defines the anteroventral, anterior, and anterodorsal margin of the orbit. The lateral surface of the prefrontal is characterized by a tri-radiate ridge that separates a somewhat recessed ventral part of the prefrontal from its laterally convex dorsal part. This surface topology of the prefrontal, which is also characteristic of other thalattosaurs (e. g., *Thalattosaurus*; Nicholls, 1999), is suggestive of the presence of a somewhat recessed lacrimal, which in fact is absent, however. At the ventral margin of the orbit, the jugal remains separate from the posteroventral process of the prefrontal. The posterodorsal process of the prefrontal that extends for some distance along the dorsal margin of the orbit remains separate from the anterior process of the postorbitofrontal, such that the frontal gains a relatively narrow entry into the dorsal margin of the orbit.

The postfrontal and postorbital are fused into a massive postorbitofrontal. The ventral

process of the postorbitofrontal reaches far down into the posteroventral corner of the orbit, thus forming the entire posterior margin of the orbit. The relatively short dorsal process of the jugal was received in a facet that lines the posterolateral aspect of the ventral process of the postorbitofrontal. Behind the postorbital arch, the left lateral margin of the skull table is lined by what looks like a well-defined facet along its entire length. It is unclear whether this facet received the elongate posterior process of the postorbitofrontal now broken off, or whether the posterior process of the postorbitofrontal has been pushed inwards, slipping under the lateral margin of the skull table. The elongate posterior process of the postorbitofrontal is in an undisturbed contact with the lateral margin of the skull table on the right side of the skull, confirming the absence of an upper temporal fossa.

The skull roof, comprising the frontal(s) and parietal(s) is, in general, poorly preserved, and sutures remain indistinct. It is impossible to delineate the participation of the frontal, supratemporal and squamosal in the formation of the lateral margin of the skull table. As in all thalattosaurs, the occiput is deeply excavated, and the large pineal foramen is located in a forward position within the parietal skull table.

The jugal is a distinct, tri-radiate bone. Its anterior process lines the posterior ventral margin of the orbit, tapering out somewhat in front of the midpoint of the longitudinal diameter (33.8 mm on the left side) of the orbit. The dorsal process of the jugal is relatively short, barely reaching the midpoint of the height of the orbit. The posterior process of the jugal is relatively massively built, terminating in a pointed tip just about below the midpoint of the longitudinal diameter of the lower temporal fossa. This results in an incomplete lower temporal arch, with a significant gap between the posterior tip of the jugal and the quadrate. There is no evidence for the presence of a quadratojugal.

The left quadrate is prominently exposed in lateral view. As preserved, the quadrate slants somewhat posteroventrally, with the mandibular condyle located behind (rather than below) the cephalic condyle. The posterior margin of the quadrate is deeply concave, and a distinct anterior flange projects from the anteromedial margin of the shaft of the quadrate into the lower temporal fossa.

In the area of the lower temporal fossa, the contours of the epipterygoid and of parts of the braincase can be identified. The middle part of the epipterygoid is exposed on the left side of the skull, indicating a slender, rod-shaped but laterally flattened element. On the right side of the skull, the epipterygoid shows a moderate antero-posterior expansion at its ventral end. The trigeminal incisure (notch) is well delineated behind the epipterygoid on the left side of the skull. It is defined ventrally by the crista alaris of the basiptyergoid (sensu Oelrich, 1956), dorsally by the prootic (cupola anterior of the otic capsule). The base of the left basiptyergoid process is likewise identifiable; its distal end obscured by the lower jaw, however.

The lower jaw is relatively heavily built, as is typical for thalattosaurs in general. The coronoid process is obscured by the jugal. The surangular carries a distinct horizontally projecting shelf that served as insertion site for superficial jaws adductor muscle fibers. The sutural pattern is not entirely clear, but the following points can be ascertained. The surangular tapers to a blunt tip anteriorly, terminating at a level in front of the anterior margin of the orbit. The anterior end of the surangular is embraced by the posteriorly bifurcated dentary. The exact posterior extent of the dorsal posterior process of the dentary cannot be delineated, although it appears to remain much shorter than the posterior ventral process of the dentary. The latter overlaps with the anterior tip of the angular at a level below the posterior half of the orbit. Breakage along the ventral margin of the anterior part of the mandible renders the identification of the splenial impossible.

The teeth of *A. wushaensis* are all of similarly robust shape with a conical (monocuspid) and slightly recurved crown, and a somewhat expanded base showing a weak striation of the en-

amel surface. There are no enlarged, fang-like teeth present on premaxilla, maxilla, and dentary, and there is no diastema between the premaxillary and maxillary teeth. A precise tooth count is difficult to obtain because of the preservation of the lower jaw in articulation, and because the delineation of the premaxillary-maxillary contact is uncertain. But assuming the presence of an anteriorly truncated maxilla that terminates below the posterior third of the longitudinal diameter of the external naris, the premaxilla appears to have carried 11 (perhaps 12) teeth, of which at least the anterior five or six were interlocking with the opposing dentary teeth. The maxilla may have carried eight tooth positions, with six teeth preserved *in situ*. The posteriormost maxillary tooth is located at the level of the anterior margin of the orbit. On the left dentary, 12 teeth are preserved *in situ*, but the total dentary tooth count may be as high as (maximally) 18.

The exact presacral vertebral count is difficult to establish, in part because the atlas-axis complex is buried in the deeply excavated occiput, in part because elements of the pectoral girdle obscure part of the presacral vertebral column, and in part because elements of the pelvic girdle obscure the sacral vertebrae. Nevertheless, a reasonable estimate is the presence of 39 presacral vertebrae in *A. wushaensis*, of which 16 (17) are cervicals, 23 (22) dorsals.

A vertebral element exposed in the deeply excavated occiput is somewhat sturdier and has a somewhat taller neural spine than the succeeding cervical vertebrae, and for this reason is here interpreted as the axis. The atlas cannot be identified at the back end of the skull, in front of the axis. All cervical vertebrae are articulated, but the occasional partial exposure of the anterior or posterior aspect of the centra indicates their amphicoelous structure. The lateral margins of the centra appear distinctly concave. In some vertebrae, the neurocentral suture is identifiable as a ridge, and it appears generally to be fused, indicating an adult status for the specimen. The plane of articulation between pre- and postzygapophyses is somewhat inclined relative to the horizontal (by approximately 30° to 35°), and the degree of inclination appears to slightly increase from front to back within the cervical vertebral column. The neural spine forms a low sagittal crest on the anterior cervical vertebrae, but gains in height more posteriorly.

The third cervical vertebra carries a distinct partially fused synapophysis for the articulation of a cervical rib, which is not preserved, however. The first preserved cervical rib is associated with the fifth cervical vertebra (the first cervical rib articulates on the atlas in *A. huangguoshuensis*; Rieppel et al., 2000). The partially fused synapophyses are located high up on the lateral aspect of the cervical vertebrae, closer to the anterior than to the posterior end. They straddle the ridge that represents the fused neurocentral suture, and provide a partially subdivided articular surface for the dichocoelous cervical ribs. The cervical ribs are relatively short and robust, yet gaining in length in the posterior cervical region, and they carry a free-ending anterior process.

In the dorsal region, the lateral and ventral margins of the centra again are distinctly concave. The occasional partial exposure of their articular surface again reveals their amphicoelous nature. The synapophysis for the rib articulation is again located rather high on the vertebrae, straddling the (fused) neurocentral suture (well exposed on the 26th through 28th presacral), and located more closely to the anterior than to the posterior end of the centrum. The zygapophyseal articulations are mostly obscured by the dorsal ribs, but where exposed they indicate some inclination of the plane of articulation relative to the horizontal, the prezygapophysis facing upwards and inwards, the postzygapophysis facing downwards and outwards. The neural spines are generally taller in the dorsal than in the cervical region, and again increase in height towards the posterior dorsal region. As they get taller, the neural spines develop a distinct pattern of vertical grooves and ridges on their lateral surface near their dorsal margin. The dorsal ribs are single-headed, more pronouncedly curved proximally than distally, and they show a moderate expansion of their distal ends.

The sacral vertebrae are completely buried under elements of the pelvic girdle. Most prob-

ably no more than two sacral vertebrae were present. Only the distal end of one right sacral rib is exposed, showing a marked distal expansion.

With its tip missing, the preserved part of the tail comprises 55 caudal vertebrae (a gap between the 23rd and 24th caudal vertebrae is estimated to have accommodated two caudals). The centra continue to show concave lateral margins. The plane of articulation between the pre- and postzygapophyses appears to be more nearly horizontally oriented than in the trunk, but the tight articulation of the vertebrae renders an exact assessment of the degree of inclination difficult. The neural spines are most prominently developed in the proximal part of the tail. They are taller but more slender than the neural spines in the posterior dorsal region. Their dorsal end is slightly expanded and without grooves and ridges near the dorsal margin. Behind the tenth preserved caudal vertebra, the neural spines become progressively more slender and posterodorsally inclined.

Free (i. e., unfused) caudal ribs are preserved up to the 13th exposed caudal vertebra. The anterior caudal ribs are short but massive structures which articulate in well-developed facets set low on the lateral side of the centrum located entirely below the (fused) neurocentral suture. Behind the sixth exposed caudal vertebra, the caudal ribs gradually decrease in size.

The chevrons articulate in an intervertebral position, the first located between the sixth and the seventh exposed caudal vertebrae. There is no indication of more anteriorly placed chevrons. They slant in a posteroventral direction, their proximal end abutting against the posteroventral margin of the preceding centrum. The length and orientation of the chevrons approximately mirror the length and orientation of the neural spines.

The gastral rib cage is well developed. Each gastral rib is composed of three elements, a slightly angulated medioventral one that may or may not bear a short anteromedial projection, and a collateral element on either side of the medioventral one. The gastral ribs are more massively developed in the posterior than in the anterior trunk region.

Of the elements of the pectoral girdle, the interclavicle is well exposed but only partly preserved. Nevertheless, it clearly indicates a cruciform morphology with a broadly developed central portion. The posterior stem is long and massively built. The transverse processes are relatively short (the left one is broken at its tip, the tip of the right one is partially concealed) and slightly deflected backwards, pointing in a posterolateral direction. The anterior process is broken, such that its extent cannot be established. Its presence is indicated, however, by the intact lateral margins of its broad base.

Parts of both clavicles are preserved. The more completely preserved right clavicle indicates an evenly curved, massive bar of bone with a distinct facet at its distal (dorsal) end for the articulation with the scapula. No morphological detail is available for both scapulae, which are crushed across the anterior dorsal vertebrae. The ventral (medial) portion of the left coracoid is well exposed along the posterior stem of the interclavicle, indicating a distinctly elongated shape that matches the length of the posterior stem of the interclavicle.

Both humeri are well preserved and exposed. They show distinctly expanded proximal and distal ends, and a biconcave shaft. Beyond its expansion and rugosities for muscle attachment, the proximal end of the humerus shows little morphological differentiation. Distally, the entepicondyle is prominently developed, with a ridge running along the ventral surface of its medial margin, but an entepicondylar foramen is absent. The ectepicondylar groove is distinct, forming a shallow notch at the distal end of the humerus. The radius and ulna are elements showing little morphological differentiation. The ulna appears more robust than the radius, an effect of its more pronounced proximal expansion. Both elements show a biconcave shaft, and a comparable distal expansion. A distinct spatium interosseum separates the radius from the ulna.

A total of seven carpal ossifications can be identified, of which the ulnare is the largest (Fig. 3A). All of these ossifications are polygonal or rounded, except for the intermedium,

which has a distinctly concave proximal margin indicating the passage of the perforating artery between the distal ends of radius and ulna. A centrale is located distal to the intermedium, but proximal to the distal carpals 3 and 2; three distal carpals lie proximal to the metacarpals 4, 3, and 2. The last carpal element to ossify lies distal to the radius, between it and the first metacarpal. It is somewhat larger than the distal carpals 2 and 3, and about equal in size as distal carpal 4 and the centrale. It is here interpreted as a radiale, rather than as a first distal carpal (see the discussion of *Anshunsaurus huangguoshuensis* below).

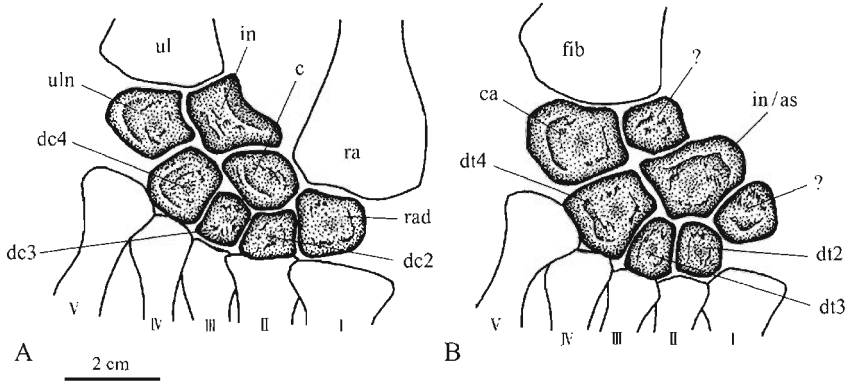


Fig. 3 The left carpus (A) and left tarsus (B) in *Anshunsaurus wushaensis* (holotype, IVPP V 13782; semidiagrammatic), dorsal view

Abbreviations: c. centrale; ca. calcaneum; dc2 ~ 4. distal carpals 2 through 4; dt2 ~ 4. distal tarsals 2 through 4; fib. fibula; in. intermedium; in / as. intermedium / astragalus; ra. radius; rad. radiale; ul. ulna; uln. ulnare; I ~ V. metacarpals and metatarsals I through V; ? see discussion in text

The metacarpals are relatively short and broad. The first metacarpal is much broader than the remaining four. The length of the metacarpals increases gradually from the first through the fifth, the latter being the longest in the series. The longest digit, including the phalanges, is the third. The phalangeal formula for the manus is 2 - 3 - 4 - 4 - 3, indicating a slight phalangeal reduction in the fourth digit.

The right pelvic girdle is well exposed in medial view. The ventral (acetabular) part of the ilium is of a triangular outline, and separated from the iliac blade by a distinct constriction. The posteroventral margin of the ilium that articulates with the ischium is shorter than the anteroventral margin that contacts the pubis.

The pubis shows a broad dorsal margin that meets the ilium (not preserved in articulation), and concave anterior and posterior margins. The obturator foramen is fully enclosed by bone. The ventral part of the pubis is broken and obscured by overlapping ribs and gastralia.

The relatively narrow dorsal part of the ischium is preserved in articulation with the pubis. The ischium expands ventrally, but its ventral part is again difficult to analyze due to overlapping ribs and gastralia. The ventral expansion of the ischium occurs mainly in a posterior direction, resulting in a deeply concave posterior margin. The anterior margin of the ischium is obscured by a gastral rib fragment, but it is certainly not deeply concave. Indeed, the anterior margin of the ischium was probably slightly convex, matching the posterior margin of the pubis such that the thyroid fenestra was either severely reduced or, more probably, obliterated.

The femur is somewhat longer and more lightly built than the humerus. The right femur is well exposed in ventral view. The bone is slightly sigmoidally curved, and expanded both proximally and distally, which results in a biconcave shaft. The internal trochanter is prominently

developed, well set off from the shaft.

Neither the tibia, nor the fibula, is fully preserved and/or exposed in either limb. In general, the fibula is more lightly built but more distinctly expanded distally than the tibia. In contrast, the tibia is proximally more distinctly expanded than the fibula. The proximal head of the fibula is not expanded, but instead forms a preaxially facing cup that articulates with the postaxial aspect of the distal end of the femur.

The interpretation of the tarsus is somewhat difficult, because of a broad crack that passes through the proximal tarsus in the right limb. In the left limb, a crack passes through the distal zeugopodium, leaving the distal end of the tibia missing. There are seven tarsal ossifications to account for (Fig. 3B). Of those, the largest one is located directly distal to the fibula, between the distal end of the fibula, the fourth distal tarsal and the proximal end of the fifth metatarsal. This element unquestionably represents the calcaneum. The third (not second) largest element lies immediately proximal to the fourth metatarsal, and is accordingly interpreted as the fourth distal tarsal. In both limbs, but particularly well shown in the left tarsus, there are two elements of successively smaller size that are located preaxially to the fourth distal tarsal and proximal to the third and second metatarsal respectively. These ossifications are accordingly interpreted as the third and second distal tarsal.

On the above interpretations, there remain three tarsal ossifications to account for, two small ones plus one larger one that is smaller than the calcaneum but larger than the fourth distal tarsal. The alignment of these three ossifications, particularly in the left foot, suggests that all of them belong to the proximal tarsus. The largest of the three ossifications is located distal to the spatium interosseum between tibia and fibula. It is flanked on either side by one of the smaller ossifications, the three elements thus forming an arc in the proximal tarsus that nicely parallels the fourth, third and second distal tarsals. The larger of the three elements, located distal to the spatium interosseum, must be interpreted as the intermedium or astragalus, an interpretation that does not account for the other two smaller elements, one intercalated between the intermedium and the calcaneum, the other lying in front of the intermedium and distal to the tibia. It might be argued that they represent a proximal centrale and a tibiale respectively, which would imply the absence of a true astragalus, possibly due to pedomorphosis. By comparison to *A. huangguoshuensis* (IVPP V 11834; see discussion below), it might also be argued that the putative tibiale, located preaxial to the intermedium (astragalus) and distal to the tibia, represents a proximally dislocated first distal tarsal. But whatever the correct interpretation is of the tarsus of *A. wushaensis*, it is certainly autapomorphic with respect to other thalattosaurs.

Within the metatarsus, the first metatarsal is distinctly more robust than all the others. There is no indication of any 'hooking' of the fifth metatarsal. The length of the metatarsals gradually increases from the first through the fourth, the latter being of equal length as the fifth metatarsal (unlike in the manus, where the fifth metacarpal is the longest). Including the phalanges, the fourth digit is the longest. The phalangeal formula in the pes is 2 - 3 - 4 - 5 - 4. There is thus no indication of any loss of phalanges as there is in the fourth digit of the manus.

Discussion The description of *A. wushaensis* (IVPP V 13782) as a separate species distinct from *A. huangguoshuensis* (IVPP V 11835 [holotype], V 11834 [referred specimen]) requires careful comparison to establish the relatively smaller *A. wushaensis* known from a single specimen as an adult individual, not a juvenile of *A. huangguoshuensis*. There are a number of features indicating that *A. wushaensis* (IVPP V 13782) is an adult individual. These include the relatively smaller skull (Table 1), the closure (fusion) of many sutures in the skull, the closed (fused) neurocentral suture throughout the vertebral column, the greater degree of morphological differentiation of the humerus (by comparison to *A. huangguoshuensis*), and the well-ossified carpus and tarsus in *A. wushaensis*.

Table 1 Measurements of *Anshunsaurus wushaensis* (mm)

head length =length of lower jaw	211.5		metacarpal length					metatarsal length				
			mc1	mc2	mc3	mc4	mc5	mt1	mt2	mt3	mt4	mt5
neck length (approx.)	340		20	23.2	24.4	25.2	25.9	25.5	28.2	31.3	33	33.7
trunk length (approx.)	560		20.9	24	25.5	25.8	27.2	25.6	29.1	30.5	32.8	32.5
tail length (as preserved)	1495											

	humerus		radius		ulna		femur		tibia		fibula	
	R	L	R	L	R	L	R	L	R	L	R	L
length	108.5	-	58	-	57	-	127.6	120	-	-	-	-
proximal width	41.5	-	~19	-	23.5	24	35.1	33.8	~27.7	~32.2	-	15
minimal width	25.5	16	9.5	10.2	7.7	8.4	16.7	-	11.9	13.9	8	10.4
distal width	44.7	36.8	16.8	19	21	19	39.5	-	-	-	31.8	29.6

diameter	radiale	Intermedium (hand)	ulnare	4 th distal carpal	calcaneum	Intermedium (foot)	4 th distal tarsal
right	9.2	13.5	13	11.5	20.6	20	-
left	10.7	14.7	14.8	12	19.5	19.1	16

In tetrapod vertebrates, the skull generally grows negatively allometric. In *A. huangguoshuensis*, the trunk (glenoid-acetabulum) is approximately 1.91 (IVPP V 11835, lower jaw: 397 mm; trunk: approx. 759) to 1.95 (IVPP V 11834, lower jaw: 375 mm; trunk: approx. 730) times the skull length, whereas in *A. wushaensis* the trunk is 2.65 (IVPP V 13872, lower jaw: 211.5 mm; trunk: approx. 560) times the skull length. This is due, in part, to a somewhat shorter rostrum in *A. wushaensis*, where the lower jaw length is about twice as long as the rostrum (IVPP V 13782, lower jaw: 211.5 mm; distance from tip of rostrum to anterior margin of orbit: 105.4 mm). In *A. huangguoshuensis*, the lower jaw is about 1.73 times as long as the rostrum (IVPP V 11835, lower jaw: 397 mm; distance from tip of rostrum to anterior margin of orbit: 230 mm). In most respects, the two species are closely similar in skull structure, as they share the parallel-sided rostrum, the retracted and rather slit-like external nares, the absence of a lacrimal and a corresponding depression of the lower part of the prefrontal, the large pineal foramen that lies anteriorly in the skull table, at the level of the postorbital arch, the fusion of the postfrontal and postorbital, the absence of an upper temporal fossa, the presence of an anterior quadrate flange, and a similar differentiation of tooth morphology with the absence of a diastema between premaxillary and maxillary teeth. There is, however, an important difference in the morphology of the jugal between the two species. The posterior process of the jugal is relatively short and massively built in *A. wushaensis*, terminating at about the midpoint of the longitudinal diameter of the lower temporal fossa. This is a stark contrast to *A. huangguoshuensis* (IVPP V 11835), where the posterior process of the jugal is long and slender, narrowly approaching (perhaps even contacting) the ventral tip of the descending process of the squamosal (Rieppel et al., 2000; Liu and Rieppel, 2005).

The vertebral count is similar in both species, with 39 (*A. wushaensis*) or 38 (*A. huangguoshuensis* (IVPP V 11835)) presacrals respectively, of which 16 (17) are cervicals. The neural spines tend to be somewhat higher in *A. huangguoshuensis* (IVPP V 11835), where their height exceeds their antero-posterior width in the posterior dorsal region, which is not the case in *A. wushaensis*. There is no indication of an incomplete development of the neural spines in the latter species, however, given their finished margins and the ornamentation of grooves and ridges present near their dorsal margin.

The two species also differ in the morphology of the interclavicle. The transverse processes trend posterolaterally in both species, but their distal end tapers to a lesser degree in *A. wushaensis* than in *A. huangguoshuensis* (IVPP V 11834). In addition, the interclavicle in *A. wushaensis* preserves the broad base of a prominent anterior process, which is absent in *A. huangguoshuensis* (IVPP V 11834). In the latter specimen, the right clavicle is preserved in articulation with the interclavicle, which shows that the clavicle extends further medially along the anterior margin of the interclavicle than would have been possible in *A. wushaensis*, given the outline of the broad base of an anterior process, mapped out by finished margins along the unbroken anterior end of the interclavicle. The interclavicle of *A. huangguoshuensis* (IVPP V 11834) must therefore have been T-shaped rather than cruciform, or if there was an anterior process, it was certainly more narrow based and hence smaller than in *A. wushaensis*.

The humerus is somewhat shorter than the femur in both species, and both are characterized by a well-developed delto-pectoral crest and the absence of the entepicondylar foramen. However, the ectepicondular groove and notch are more distinctly differentiated in *A. wushaensis* than in *A. huangguoshuensis*. Similarly, the entepicondyle is more prominently developed in the first species, where it also carries a distinct ridge on the ventral side of its medial margin. With respect to the degree of development of the entepicondyle, the humerus of IVPP V 11834 is intermediate between the holotype of *A. huangguoshuensis* (IVPP V 11835) and *A. wushaensis*, again indicating that the latter specimen is not a juvenile. Seven carpal ossifications are present in the holotype of *A. huangguoshuensis* (IVPP V 11835) and in *A. wushaensis*, but only six carpal ossifications are preserved in IVPP V 11834 where the centrale is absent (not ossified), again indicating that the holotype of *A. wushaensis* is not a juvenile. In *A. wushaensis*, the intermedium shows a distinctly concave proximal margin, indicating the passage of the perforating artery. In contrast, the intermedium of *A. huangguoshuensis* is of more regularly rounded contours. In the metacarpus of *A. wushaensis*, the fifth metacarpal is the longest, whereas in *A. huangguoshuensis*, it is the fourth metacarpal which is the longest, or subequal in length to the third, but always longer than the fifth metacarpal. A loss of a phalanx in the fourth digit, as in *A. wushaensis*, is not known to occur in *A. huangguoshuensis*. In contrast, the phalangeal formula for the manus is 2-3-4-?-4 in IVPP V 11834, indicating the addition of a phalanx to the fifth digit, a condition not known for *A. wushaensis*.

The ilium is again different in the two species. The ilium carries a well-developed, posterodorsally ascending iliac blade in both species, but whereas its dorsal and ventral margins are more or less parallel in *A. huangguoshuensis*, the iliac blade expands in a posterodorsal direction in *A. wushaensis* due to divergent dorsal and ventral margins.

As discussed above, the tarsus of *A. wushaensis* comprises seven ossifications, some of questionable homology. This contrasts with *A. huangguoshuensis* (IVPP V 11834), with six tarsal ossifications, viz. an astragalus of complex shape, a calcaneum, and four distal tarsals (one through four). If, by comparison, *A. wushaensis* is interpreted as also having four distal tarsals (one through four), this still leaves three ossifications in the proximal tarsal row, as opposed to two ossifications in *A. huangguoshuensis* (IVPP V 11834). In fact, if it were assumed that the small element seen to be intercalated between the intermedium and the calcaneum in *A. wushaensis* were to fuse with the intermedium, an element of similarly complex shape would result as is the astragalus in *A. huangguoshuensis* (IVPP V 11834). In the metatarsus of *A. huangguoshuensis* (IVPP V 11834), the fifth metatarsal is distinctly shorter than the fourth, in contrast to *A. wushaensis*, where that difference is less prominent. The phalangeal formula for the pes is primitive (2-3-4-5-4) in both species.

Conclusions In accordance with the discussion above, it is concluded that specimen IVPP V 13782 is not a juvenile individual of *A. huangguoshuensis*, but instead represents a different species of the same genus. This does not entirely rule out the possibility of sexual dimorphism in

the genus *Anshunsaurus*, expressed in size and other morphological characteristics. Given the scarcity of the material, however, a case for sexual dimorphism can also not be substantiated. In addition, sauropterygian taxa known to be sexually dimorphic, such as pachypleurosaurs, show the female, not only to be of smaller size, but also to retain juvenile features in the skeleton by comparison to the male, such as a lesser morphological differentiation of the humerus (Cheng et al., 2004; Sander, 1989). Such is not the case in comparing the skeletal anatomy of *A. wushaensis* to that of *A. huangguoshuensis*, however.

On the basis of the currently available material, the genus *Anshunsaurus* seems therefore to have been represented by two different species of different adult size (and of different geological age) in the Middle and Early Late Triassic of Guizhou Province, southwestern China.

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