Discovery of Omeisaurus (Dinosauria: Sauropoda) in the Middle Jurassic Shaximiao Formation of Yunyang, Chongqing, China: Postprint

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Abstract

A cervical vertebra recovered from the Middle Jurassic Lower Member of the Shaximiao Formation in Town of Puan, Yunyang County, Chongqing is assigned to an species undeterminata of the sauropod dinosaur Omeisaurus based on morphological and comparative study. The centrum of this mid-cervical is much hollower than solider with extremely developed fossa/foramen complex and has a high ratio (5.05) of its anteroposterior length excluding the articular ball divided by the mean value of the posterior articular surface mediolateral width and dorsoventral height. Additional features of this cervical include central length about twice the total vertebral height, a prominent midline keel on the central ventral surface, deep and long cavities bounded by centroprezygapophyseal lamina/ intraprezygapophyseal lamina and centropostzygapophyseal lamina/intrapostzygapophyseal lamina, respectively, a coel on the dorsal half of the postzygapophyseal centrodiapophyseal fossa, long prone epipophysis extending beyond the postzygapophysis facet, anteroposteriorly length of the neural spine about half the length of the centrum, and concavities on the anterior one third lateral surface of the neural spine. Therefore, this discovery reveals new morphological information on Omeisaurus, and this Omeisaurus-bearing Puan dinosaur quarry represents the easternmost occurrence of this genus.

Full Text

Discovery of *Omeisaurus* (Dinosauria: Sauropoda) in the Middle Jurassic Shaximiao Formation of Yunyang, Chongqing, China

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Abstract

A cervical vertebra recovered from the Middle Jurassic Lower Member of the Shaximiao Formation in the town of Puan, Yunyang County, Chongqing, is assigned to an *species undeterminata* of the sauropod dinosaur *Omeisaurus* based on morphological and comparative study. The centrum of this mid-cervical is much hollower than solid, with an extremely developed fossa/foramen complex and a high ratio (5.05) of its anteroposterior length (excluding the articular ball) divided by the mean value of the posterior articular surface' s mediolateral width and dorsoventral height. Additional features include: central length about twice the total vertebral height; a prominent midline keel on the ventral surface of the centrum; deep and long cavities bounded by centroprezygapophyseal lamina/intraprezygapophyseal lamina and centropostzygapophyseal lamina/intrapostzygapophyseal lamina, respectively; a coel on the dorsal half of the postzygapophyseal centrodiapophyseal fossa; long, prone epipophysis extending beyond the postzygapophysis facet; anteroposterior length of the neural spine about half the length of the centrum; and concavities on the anterior one-third lateral surface of the neural spine. This discovery reveals new morphological information on *Omeisaurus*, and the *Omeisaurus*-bearing Puan dinosaur quarry represents the easternmost occurrence of this genus.

Key words: Chongqing, Puan; Shaximiao Formation; Sauropoda; *Omeisaurus*

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1 Introduction

In 2016, a new dinosaur locality was discovered in the vicinity of the town of Puan, Yunyang County, Chongqing Municipality. After intensive fieldwork, a bonebed of approximately 1050 m^2 has been exposed, and partial bones have been excavated and prepared in the laboratory. Preliminary observations indicate that sauropod dinosaurs dominate this bonebed, with occasional theropod and stegosaur remains, and the fossils derive from the lower-middle portion of the Lower Member of the Shaximiao Formation. Unfortunately, the bones are all mixed together, with few confident associations, making identification of individual specimens difficult. Nevertheless, sauropod cervical vertebral morphology is highly diagnostic at the generic level, and here we provide a description of one well-preserved middle cervical vertebra. Comparative studies demonstrate that this cervical can be assigned to an *species undeterminata* of *Omeisaurus*, a common dinosaur taxon in the Jurassic red beds of the Sichuan Basin (He et al., 1988; Peng et al., 2005). This discovery therefore represents the easternmost occurrence of *Omeisaurus* and provides detailed information on its cervical anatomy.

2 Systematic Paleontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995
Omeisaurus Young, 1939
***Omeisaurus* sp.** (Figs. 1–2)

Specimen: The specimen is temporarily deposited at the Chongqing Laboratory of Geological Heritage Protection and Research (CLGPR): v00001; field number: 17YP3304-S66(5) (abbreviated as S66 hereafter). It consists of a mid-cervical vertebra, missing a large portion of the anterior articular ball, both

parapophyses, the left diapophysis, and prezygapophysis. The specimen was broken into two parts along the parapophysis-diapophysis cross-section, providing an opportunity to examine the internal structure of the centrum.

Locality and horizon: Town of Puan, Yunyang County, Chongqing Municipality. The specimen was recovered from purplish-red muddy siltstone and silty mudstone interbedded with siltstone and mudstone in the lower-middle portion of the Lower Member of the Shaximiao Formation. The Shaximiao Formation is divided into Lower and Upper members, equivalent to the Lower and Upper Shaximiao formations, respectively (Peng et al., 2005). The age of the Shaximiao Formation is generally accepted as Middle Jurassic (Sha et al., 2010; Li et al., 2011; Li et al., 2018), though some have argued for a Late Jurassic age for its Upper Member (the Upper Shaximiao Formation) (Peng et al., 2005).

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3 Description

Terminology of vertebral laminae and fossae follows Wilson (1999) and Wilson et al. (2011).

The centrum is long and opisthocoelous (Fig. 1 [Figure 1: see original paper]). Both anterior and posterior articular surfaces are taller than wide (Fig. 2 [Figure 2: see original paper]), with heights and widths of 133 by 88 mm and 152 by 133 mm, respectively; thus, the centrum increases in dimension posteriorly. The articular ball is not completely preserved, and the centrum length without the ball is 720 mm. Therefore, the elongation index (EI) value, defined as the centrum' s anteroposterior length excluding the articular ball divided by the mean value of the posterior articular surface' s mediolateral width and dorsoventral height (Mannion et al., 2013), is 5.05 in S66.

The ventrolateral ridges of the centrum curve slightly dorsally, with the portion anterior to the parapophysis-diapophysis bending more ventrally than the remainder. The ventral surface is highly concave transversely along its entire length except at both ends, featuring a prominent midline keel that gives the impression of two long, well-developed coels dominating this area. A mediolateral septum separates the posterior portion of each coel.

The lateral surface of the centrum is highly excavated with complex fossa/foramen structures (Fig. 1). The entire lateral surface is concave, and within this concavity (fossa), a large foramen and an additional posterior foramen occupy almost the posterior three-fourths. The large foramen originates between the parapophysis and diapophysis, tapers posteriorly, and terminates ventral to the postzygapophysis. An anteroventrally oblique lamina further divides this foramen into two sub-foramina. The anterior sub-foramen is extremely large and deep, consisting of an extremely large coel and two small coels anteroventral to it and posterodorsal to the parapophysis. This sub-foramen is separated from its counterpart on the opposite side by a very

thin midline septum of bone. The posterior sub-foramen is further divided by laminae into several coels, but these are not symmetric on each side: two are clearly visible on the left lateral side, while this sub-foramen extends more posteriorly on the right lateral side than on the left. The additional foramen is located in the posteroventral corner of the lateral surface and separated from the large foramen by a prominent oblique ridge that is anteroposteriorly long and expands posteriorly to the level of the posterior end of the postzygapophysis. This foramen is also subdivided into at least two coels.

The internal structure of the centrum can be observed along the broken surfaces across the parapophysis-diapophysis cross-section (Fig. 2A, B) and on the left lateral side of the centrum because the left parapophysis and diapophysis, as well as the left surface anterior to them, are not preserved. Large cavities separated by irregular, thin bony septa occupy much of the anterior portion of the centrum, including the articular ball. Therefore, the entire centrum is much more hollow than solid.

The parapophyses are not preserved. Judging from the ventrolateral extension of the diapophysis-tuberculum region, which extends beyond the ventral level of the centrum, the parapophysis-capitulum region probably extends ventrolaterally well below the ventral level of the centrum. Furthermore, based on the anteroposterior extension of the diapophysis-tuberculum region, the parapophysis is probably elongated anteroposteriorly but within the anterior half of the centrum. Posteriorly, the parapophysis merges smoothly with the ventrolateral ridge of the centrum.

The neural arch is lower than the height of the neural spine or the centrum. It is long, sitting along the centrum except for the portion ventral to the postzygapophyseal articular facets. In posterior view, the neural canal is small and wider than high.

Only the right prezygapophysis is preserved, but it is missing its anterior end including the articular facet. Because the central articular ball is not completely preserved, it is unknown whether the prezygapophysis extends beyond the ball. Ventrally, the prezygapophysis is supported by the transversely thin centroprezygapophyseal lamina (CPRL), which appears to merge with the prezygadiapophyseal lamina (PRDL) posteriorly. The CPRL is not divided. The ventromedially directing intraprezygapophyseal lamina (TPRL) extends along the dorsal edge of the CPRL and meets its counterpart dorsal to the neural canal. A deep and long cavity is bounded by the CPRL and TPRL.

The diapophysis is situated at the neurocentral junction at the vertical level along the anterior edge of the neural spine. It is fused with the tuberculum and forms a broad ventrolateral extension. The posterior centrodiapophyseal lamina (PCDL) projects posteroventrally and ends around the midlength on the dorsolateral edge of the centrum. The postzygadiapophyseal lamina (PODL) is prominent and surrounds the postzygapophyseal centrodiapophyseal fossa (POCDF) ventrally. The POCDF is better preserved on the right side than on

the left. The anterior half of the POCDF is more deeply excavated than the posterior half and shows a rugose surface texture, while on the posterior half, a coel exists in the middle of its dorsal half.

The postzygapophysis does not extend beyond the centrum. Its articular facet is concave and faces ventrolaterally and posteriorly. The centropostzygapophyseal lamina (CPOL) is not divided. Similar to the condition in the prezygapophysis, the ventromedially directing intrapostzygapophyseal lamina (TPOL) extends along the dorsal edge of the CPOL. The left and right TPOLs meet at the midline of the dorsal surface of the neural arch and form a deep V-shaped cavity between them. On either side, a deep and long cavity is bounded by the CPOL and TPOL. The epipophysis is long, prone, and extends parallel to the posterior one-third of the postzygadiapophyseal lamina, with its tip beyond the posterior margin of the postzygapophysis facet.

The neural spine is very long anteroposteriorly, about half the length of the centrum. It is dorsoventrally low and transversely narrow, maintaining this depth and narrowness along its entire length. The spinoprezygapophyseal lamina is not well preserved and appears to start from the base of the neural spine. The anterior margin of the neural spine is slightly concave. The spinopostzygapophyseal lamina starts from the slightly expanded posterodorsal corner of the neural spine and projects posterolaterally, with its dorsal edge meeting its counterpart along almost the entire length of the postzygapophysis. The anterior one-third of the lateral surface of the neural spine is concave, while the remainder is relatively flat.

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4 Phylogenetic Analysis

To explore the phylogenetic position of S66, we performed a cladistic analysis based on the data matrix of Carballido et al. (2017). This matrix comprises 405 characters and 88 operational taxonomic units (OTUs) (including S66). Among the 36 cervical vertebra characters (9% of total characters), 25 can be scored for S66 (6% of total characters and 69% of cervical characters). During the scoring process, we noticed many problematic scorings for the cervical vertebrae of *Mamenchisaurus* and *Omeisaurus* in the original matrix and revised these based on personal observation and published references of *Mamenchisaurus youngi* (Ouyang and Ye, 2002) and *Omeisaurus tianfuensis* (He et al., 1988) (Table 1).

Phylogenetic analysis was performed under TNT (ver. 1.1) (Goloboff et al., 2008), applying a heuristic search with 1000 replicates of Wagner trees and tree bisection-reconnection (TBR), with 10 trees saved per replication. All characters were equally weighted. Our phylogenetic analysis generated 8760 most parsimonious trees (MPTs) with the following values: tree length = 1404, consistency index (CI) = 0.348, and retention index (RI) = 0.724. The strict consensus tree is relatively well-resolved (Fig. 3 [Figure 3: see original paper]).

S66 and *Omeisaurus* are recovered as sister OTUs, and this (*Omeisaurus* + S66) clade and *Mamenchisaurus* form the Mamenchisauridae clade.

S66 shows three of the 12 synapomorphies of the Mamenchisauridae clade: ventral surface of cervical centra is transversely concave (ch. 124, state 1), epipophyses in cervical vertebrae prong posteriorly beyond postzygapophyses (ch. 129, state 1), and height of the neural arch in middle cervical vertebrae is less than the height of the posterior articular surface (ch. 141, state 0). The (*Omeisaurus* + S66) clade is supported by three synapomorphies: anteroposterior length divided by the height of the posterior articular surface in middle cervical centrum is more than 4 (ch. 142, state 1), prominent triangular flange on posterior edge of the diapophyseal process in middle and posterior cervical vertebrae (ch. 146, state 1), and parapophysis in middle and posterior cervical vertebrae is anteroposteriorly elongate (ch. 148, state 1).

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5 Comparison and Discussion

Besides *Mamenchisaurus* and *Omeisaurus*, three other mamenchisaurid genera (*Chuanjiesaurus*, *Qijianglong*, and *Yuanmousaurus*) have been reported from the Jurassic of southwestern China (Fang et al., 2000; Lü et al., 2006; Xing et al., 2015). *Chuanjiesaurus anaensis* was reported from the Middle Jurassic Chuanjie Formation in Lufeng, Yunnan Province (Fang et al., 2000) and received a detailed description by Sekiya (2011). Its referred specimen preserves a series of 11 cervicals (Axis–cervical 11). The ratio of centrum length to posterior surface height can be calculated for cervicals 7, 9, and 11, yielding values of 3.69 (554/150 mm), 3.94 (631/160 mm), and 3.08 (677/220 mm), respectively —no more than 4 as in *Omeisaurus*; this ratio is 4.74 (720/152 mm) in S66. Furthermore, the lateral surface of *Chuanjiesaurus*' centra is occupied by a relatively shallow, large fossa without complicated ridges further separating it into several foramina, unlike the extremely developed fossa/foramen complex in S66.

A partial cervical vertebra was reported in *Yuanmousaurus jiangyiensis* (Lü et al., 2006). This was described as an anterior portion of a posterior cervical, with the articular surface 14 cm wide and 26 cm high. However, this articular surface is concave and the central lateral surface does not show evidence of parapophysis. We interpret this as the posterior portion of a posterior cervical. If so, the excavation on the lateral surface of the centrum is well-bounded to the posterior end of the centrum. Also, as noted by the authors, the broken surface shows the internal structure of the centrum is occupied by large cavities. Based on this limited information, it is difficult to assess the relationship between *Yuanmousaurus* and S66. However, cladistic analyses including this taxon show that *Yuanmousaurus* is more closely related to *Mamenchisaurus* than to *Omeisaurus* (Sekiya, 2011; Xing et al., 2015).

Qijianglong from the Late Jurassic of Qijiang, Chongqing, preserves a complete

cervical vertebral series (Xing et al., 2015). Among its 17 cervicals, cervicals 5 and 6 bear high ratios (more than 4) of centrum length to posterior surface height: 5.11 (310/60.7 mm) and 4.25 (350/82.4 mm), respectively. However, the lateral surface of its centrum is not excavated by a well-developed fossa/foramen complex, and the parapophysis does not elongate anteroposteriorly as in S66.

Omeisaurus represents one of the best-known non-neosauropodan eusauropod dinosaurs and plays an important role in understanding early sauropod evolution (Upchurch et al., 2004; Mannion et al., 2013; Carballido et al., 2017). All seven reported species of *Omeisaurus* are recovered from the Jurassic Shaximiao Formation in the Sichuan Basin of southwestern China (Young, 1939, 1958; Dong et al., 1983; He et al., 1984; Li, 1988; Tang et al., 2001; Jiang et al., 2011). However, among these, only *O. tianfuensis* is represented by well-preserved cervical series, while others preserve only a few cervicals (*O. junghsiensis* Young, 1939; *O. changshouensis* Young, 1958; *O. luoquanensis* Li, 1988; *O. maoianus* Tang et al., 2001) or lack cervicals entirely (*O. fuxiensis* Dong et al., 1983; *O. jiaoi* Jiang et al., 2011).

Omeisaurus junghsiensis, the type species of *Omeisaurus* from the Lower Member of the Shaximiao Formation in Rongxian, Sichuan Province, was established by Young (1939). It preserves four partial cervical vertebrae, with the best-preserved one probably from the seventh or eighth cervical based on comparison to *Euhelopus* (Young, 1939). Based on the original description and figure 2, the lateral surface of this centrum is depressed with an oblique ridge inside (Young, 1939). However, the posterior portion of this depression is not excavated by additional coels, indicating the lack of an extremely developed fossa/foramen complex on its central lateral surface, unlike the condition in S66.

Omeisaurus changshouensis from the Upper Member of the Shaximiao Formation in Changshou, Chongqing, preserves three partial cervicals (Young, 1958). The best-preserved cervical shows a "quite simply smooth" central lateral surface without a developed fossa/foramen complex (Young, 1958:fig. 10 [Figure 10: see original paper]). He et al. (1988) considered this species to have a closer relationship to *Mamenchisaurus* than to *Omeisaurus* based on its proximal caudal vertebral features. Based on its cervical features, we agree with He et al. (1988).

Omeisaurus luoquanensis from the Lower Member of the Shaximiao Formation in Luoquan, Sichuan, preserves the posterior portion of one cervical centrum and two cervical neural spines (Li, 1988). The centrum is considered to be from the fifth cervical and bears several coels on its lateral surface, similar to the condition in S66. However, no ventral keel is developed in this centrum, unlike the condition in S66.

Omeisaurus maoianus from the Upper Member of the Shaximiao Formation in Jingyan, Sichuan, preserves three cervicals (Tang et al., 2001). These three cervicals are identified as C5, C9, and C10. Based on figure 19 [Figure 19: see original paper] and plate VI of Tang et al. (2001), the prezygapophyses extend craniodorsally but not beyond the centra in C9 and C10, unlike the condition

in S66. In C5, the centrum is elongate and bears pleurocoels as in S66, but its postzygapophysis is elevated much higher than the level of the prezygapophysis, and the neural spine is located within the posterior half of the vertebra with a slightly sloping dorsal edge, different from the condition in S66.

Omeisaurus tianfuensis was named by He et al. (1984) and received a monographic description by He et al. (1988). Tens of individuals of this species have been recovered from the Lower Member of the Shaximiao Formation in the Dashanpu Quarry of Zigong, about 425 km west-southwest of the current specimen site. The cervical count of *O. tianfuensis* is estimated to be 17, and descriptions and illustrations of the cervicals are based on three specimens housed in the Zigong Dinosaur Museum: T 5701 (C1–8 and C11–17), T 5703 (C1–12), and T 5704 (C3, C11–17). The middle cervicals of T 5703 are preserved in relatively good condition and are most suitable for comparison to our specimen (Table 2).

In T 5703, C5 has the closest EI value to that of S66 (5.21 versus 5.05). These two cervicals also share very similar ratios of neural spine length to centrum length (0.51 versus 0.50) and posterior articular surface height to width (1.16 versus 1.14). However, S66 is longer (1.5 times the central length of C5) and higher (total height about half central length in S66 versus one-third in C5) than C5. On the other hand, the longest centrum without articular ball in T 5703 is C9 (770 mm), 50 mm longer than that of S66, but this cervical is still very low, with its total height only about one-fourth of its central length. C9 and S66 also differ in other features: the posterior articular surface of C9 is wider than high, opposite to the condition in S66; its EI value is 3.54, in contrast to 5.05 in S66; and its neural spine length is about one-third the central length, while in S66 the neural spine length is half the central length. Therefore, these two cervicals are distinct.

The EI value generally reaches its maximum at mid-cervicals and decreases progressively posteriorly, with the highest EI value of T 5703 being 6.06 in C7. Therefore, S66 is very likely from a vertebra in the anterior portion of the mid-cervicals and probably anterior to C9 based on comparison to T 5703. On the other hand, given that EI values increase progressively in anterior cervicals and the lengths of these cervicals increase rapidly, S66 is probably not from C3 or C4 (EI values are 3.30 and 3.87, and central lengths are 241 mm and 368 mm in T 5703, respectively) and may represent a cervical from C5–8. The average EI value for C5–7 in T 5703 (C8 is not available) is around 5, and the length of their neural spines remains relatively long, about 40%–55% of their corresponding central length, comparable to those of S66. Because the details of the middle cervicals of other specimens of *O. tianfuensis* are not adequately documented and illustrated—such as the degree of development of the lateral pneumatic fossa/foramen complex—it is difficult to determine whether S66 could be assigned to any specific cervical, and furthermore, to this species.

Interestingly, the central length to total vertebral height value for C5–9 of T5703 increases from around 3.0 (C5 and C6) to 3.5 (C8) to 3.85 (C9), until a sudden

decrease to 2.65 in C10, with its highest value coincident with the longest cervical in C9. However, although S66 shares a similar central length with C9, this length is only about twice the total vertebral height, implying a rapid increase in neural arch and spine heights of the middle cervicals in S66, though whether this increase occurred suddenly or gradually is unknown. S66 also possesses other notable features: a centrum that is much more hollow than solid with an extremely developed fossa/foramen complex; a prominent midline keel on the ventral surface of the centrum; deep and long cavities bounded by CPRL/TPRL and CPOL/TPOL, respectively; a coel existing on the dorsal half of the POCDF; a long, prone epipophysis extending beyond the postzygapophysis facet; and concavity on the anterior one-third lateral surface of the neural spine. The distribution of these features in *Omeisaurus* and other related sauropods needs to be explored in future studies.

Based on the above analysis, comparison, and discussion, S66 can be assigned as a member of *Omeisaurus*. It also shows various differences from all known species of *Omeisaurus* with relevant cervical material and probably has a closer relationship to *O. tianfuensis* and *O. luoquanensis* than to others. However, it is difficult to name a new species based on a single mid-cervical, although it does bear a unique combination of features. Therefore, S66 is assigned to an *species undeterminata* of *Omeisaurus*, pending discovery of more material and study.

This study demonstrates the existence of *Omeisaurus* at the newly discovered Puan site in Yunyang, Chongqing, representing the easternmost occurrence of this genus. Detailed anatomy of a middle cervical of *Omeisaurus* is provided, which will help elucidate the phylogeny of *Omeisaurus* because we realize that scorings for this genus in various matrices of previous cladistic analyses need to be reevaluated (Mannion et al., 2013; Carballido et al., 2017). Finally, the horizon of this *Omeisaurus*-bearing quarry in Puan can be generally correlated to that of the Dashanpu Quarry in Zigong, although the radiometric age of the Shaximiao Formation remains controversial (Wang et al., 2018).

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Note: Figure translations are in progress. See original paper for figures.