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 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 centrodiaipophyseal 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.

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

**Citation** Tan C, Dai H, He J J et al., 2019. Discovery of *Omeisaurus* (Dinosauria: Sauropoda) in the Middle Jurassic Shaximiao Formation of Yunyang, Chongqing, China. Vertebrata PalAsiatica, 57(2): 105–116

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中国科学院战略性先导科技专项(B类) (编号：XDB26000000)、国家自然科学基金(批准号：41688103, 41872021, 41472020)、重庆市国土资源和房屋管理局《重庆市云阳县普安乡恐龙化石保护与研究》和重庆市博士后科研项目特别资助(编号：Xm2017069)资助。

收稿日期：2018-09-10
1 Introduction

In 2016, a new dinosaur locality was discovered in the vicinity of Town of Puan, Yunyang County, Chongqing Municipality. After intense field efforts, a bonebed of about 1050 m² has been exposed, and partial bones have been excavated and prepared in lab. Preliminary observation shows that sauropod dinosaurs dominate this bonebed with occasionally recovered theropods and stegosaurs, and the fossils are from the lower-middle portion of the Lower Member of the Shaximiao Formation. Unfortunately, the bones are all mixed together, rarely with confidence on their associations, making identification of each individual difficult. Nevertheless, sauropod cervical vertebral morphology is very diagnostic at generic level, and here we provide description of one well preserved middle cervical vertebra. Comparative studies show that this cervical can be assigned to an species undeterminata of *Omeisaurus*, a common dinosaur taxon in the Jurassic red beds in the Sichuan Basin (He et al., 1988; Peng et al., 2005). Therefore, this discovery 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 Chongqing Laboratory of Geological Heritage Protection and Research (CLGPR): v00001; field number: 17YP3304-S66 (5) (Abbreviated as S66 hereafter). 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-diaphophysis cross section, and this provides an opportunity to see the internal structure of the centrum.

**Locality and horizon** Town of Puan, Yunyang County, Chongqing Municipality. The specimen was recovered from the 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), but with different opinion for a Late Jurassic age for its Upper Member (the Upper Shaximiao Formation) (Peng et al., 2005).
3 Description


The centrum is long and opisthocoelous (Fig. 1). Both the anterior and posterior articular surfaces are taller than wide (Fig. 2), and their heights and widths are 133 by 88 mm and 152 by 133 mm, respectively; therefore, the centrum increases its dimension posteriorly. The articular ball is not completely preserved, and the length of centrum without the ball is 720 mm; therefore, the elongation index (EI) value, defined as the centrum anteroposterior length excluding the articular ball divided by the mean value of the posterior articular surface mediolateral width and dorsoventral height (Mannion et al., 2013), is 5.05 in S66. The ventrolateral ridges of the centrum curve slightly dorsally, and the portion anterior to the parapophysis-diapophysis bends more ventrally than the rest. The ventral surface is highly concave transversely through its whole length except at both ends, with a prominent midline keel in between, giving the impression that two long well-developed coels dominate this area.

Fig. 1 The middle cervical vertebra of *Omeisaurus* sp. (17YP3304-S66) in right lateral (A), left lateral (B) and ventral (C) views based on 3D surface scanning
Note the specimen was broken into two parts along the parapophysis-diapophysis cross section
Mediolateral septum separates the posterior portion of each coels.

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 one posterior to it occupy almost the posterior three fourths. The large foramen starts between the parapophysis and diapophysis, tapers posteriorly, and terminates ventrally to the postzygapophysis. An anteroventrally oblique lamina further divides this foramen into two sub-foramens. The anterior sub-foramen is extremely large and deep, and consists of an extremely large coel and two small coels anteroventral to it and posterodorsal to the parapophysis. This sub-foramen is separated by a very thin midline septum of bone from its counterpart on the other side. The posterior sub-foramen is further divided by laminae into several coels, but they 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 other side. The additional foramen is located on the posteroverentral corner of the lateral surface and separated from the large foramen by a prominent oblique ridge, which is anteroposteriorly long and expands posteriorly until 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). It can also be seen on the left lateral side of the centrum because the left parapophysis and diapophysis as well as the left surface anterior to it are not preserved. Large cavities separated by irregular and thin bony septa occupy large space of the anterior portion of the centrum, including the articular ball. Therefore, the whole centrum is much more hollow than solid.

The parapophyses are not preserved. Judging from the ventrolateral extension of the diapophysis-tuberculum region, which is 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 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 or not. Ventrally, the prezygapophysis is supported by the transversely thin centroprezygapophyseal lamina (CPRL), which seems 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.
Fig. 2   The middle cervical vertebra of *Omeisaurus* sp. (17YP3304-S66)

Anterior views (A, B) of the broken main part of the cervical, and B (sketch) shows the internal camerate structure with large cavities bounded by thin bony septa. Anterior (C) and posterior (D) views of the cervical

Abbreviations: CPOL. centropostzygapophyseal lamina; CPRL. centroprezygapophyseal lamina; TPOL. intrapostzygapophyseal lamina; TPRL. intraprezygapophyseal lamina

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 ventrolaterally extension. The posterior centrodiaapophyseal 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 centrodiaapophyseal 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 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 in between. On either side, a deep and long cavity is bounded by the CPOL and TPOL. The epipophysis is long, prone and extending 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 and about half the length of the centrum. It is dorsoventrally low and transversely narrow, and keeps this depth and narrowness along its whole length. The spinoprezygapophyseal lamina is not well preserved, and it seems to start from the base of the neural spine. The anterior margin of the neural spine is concave slightly. 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 rest is relative flat.
4 Phylogenetic analysis

In order to explore the phylogenetic position of S66 a cladistic analysis is performed 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 vertebrae 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).

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→ indicates character scoring changes in this study.

Phylogenetic analysis was performed under TNT (ver. 1.1) (Goloboff et al., 2008), applying a heuristic search by 1000 replicates of Wagner trees and tree bisection-reconnection (TBR) with 10 trees saved per replication. All characters are equally weighted. Our phylogenetic analysis generated 8760 most parsimonious trees (MPTs) with 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). 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 prongs 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 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).
5 Comparison and discussion

Besides of *Mamenchisaurus* and *Omeisaurus*, three other mamenchisaurid genera (*Chuanjiesaurus*, *Qijianglong*, and *Yuanmousaurus*) have been reported from the Jurassic in 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 length of centrum / height of posterior surface of the centrum can be calculated for cervicals 7, 9 and 11, and they are 3.69 (554/150 in mm), 3.94 (631/160 in mm), and 3.08 (677/220 in mm), respectively, no more than 4 as in *Omeisaurus*; this ratio is 4.74 (720/152 in mm) in S66. Furthermore, the
lateral surface of *Chuanjiesaurus*’ centra is occupied by a relative shallow and large fossa without complicated ridges further separated it into several foramen, different from the extremely developed fossa/foramen complex in S66.

A partial cervical vertebra is reported in *Yuanmousaurus jiangyiensis* (Lü et al., 2006). This is described as an anterior portion of one 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 the existence of the parapophysis. Here we interpreter it as the posterior portion of one posterior cervical. If so, the excavation on the lateral surface of the centrum is well bounded until the posterior end of the centrum. Also, as noticed 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 judge 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* is from the Late Jurassic in Qijiang, Chongqing, and preserves a complete cervical vertebrate series (Xing et al., 2015). Among the 17 cervicals, cervicals 5 and 6 bear high ratios (more than 4) of length of centrum / height of posterior surface of the centrum, which are 5.11 (310/60.7 in mm) and 4.25 (350/82.4 in mm), respectively. However, the lateral surface of its centrum is not excavated by the 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 the early evolution of sauropods (Upchurch et al., 2004; Mannion et al., 2013; Carballido et al., 2017). All the reported seven 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 either preserve only a few cervicals (*O. junghsiensis* Young, 1939, *O. changshouensis* Young, 1958, *O. luquanensis* Li, 1988, and *O. maoianus* Tang et al., 2001) or do not preserve cervicals (*O. fuxiensis* Dong et al., 1983 and *O. jiaoi* Jiang et al., 2011).

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

*Omeisaurus changshouensis* is from the Upper member of the Shaximiao Formation in Changshou of Chongqing, and preserves three partial cervicals (Young, 1958). The best preserved cervical shows a “quite simply smooth” central lateral surface without developed fossa/foramen complex (Young, 1958:fig. 10). He et al. (1988) considered this species to have a closer relationship to *Mamenchisaurus* than to *Omeisaurus* based on its proximal caudal
vertebral features. Here, based on its cervical features, we agree with He et al. (1988)’s opinion.

*Omeisaurus luquanensis* is from Lower member of the Shaximiao Formation in Luoquan of Sichuan, and 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, different from the condition in S66.

*Omeisaurus maoianus* is from Upper member of Shaximiao Formation in Jingyan of Sichuan, and preserves three cervicals (Tang et al., 2001). These three cervicals are identified as C5, C9 and C10. Based on fig. 19 and plate VI of Tang et al. (2001), the prezygapophyses extend craniodorsally and not beyond the centra in C9 and C10, different from the condition in S66. In C5, its 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* is 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 to the current specimen site. The cervical numbers of *O. tianfuensis* are estimated to be 17, and the description 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 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 the very close ratios of length of the neural spine / length of the centrum (0.51 versus 0.50) and height / width of the posterior articular surface (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

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Notes: measurements of T 5703 C2–12 based on He et al., 1988. EI, elongation index, the centrum anteroposterior length excluding the articular ball divided by the mean value of the posterior articular surface mediolateral width and dorsoventral height; H, height of vertebra; HPF, height of central posterior articular surface; L, central length without articular ball; LNS, anteroposterior length of neural spine; WPF, width of central posterior articular surface.
this cervical is still very low with its total height only about one fourth of its central length. C9 and S66 also possess other differences: the posterior articular surface of C9 is wider than high, which is the opposite condition to S66; its EI value is 3.54, in contrast to 5.05 in S66; the length of its neural spine is about one third the central length, while in S66 the length of the neural spine is half the central length. Therefore, these two cervicals are different.

The EI value generally reaches its highest at mid-cervicals and decreases progressively posteriorly, and the highest EI value of T 5703 is 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 its comparison to T 5703. On the other hand, given that the EI values increase progressively in anterior cervicals and the length of these cervicals increases 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 possibly represents 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 spine keeps 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 hard to determine whether S66 could be assigned to any specific cervical, and furthermore, to this species.

Interestingly, the central length/total vertebral height value for C5–9 of T 5703 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 the 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, although whether this increase happened suddenly or gradually is unknown. S66 also possesses some other noticeable features, such as much hollower than solider centrum with extremely developed fossa/foramen complex, a prominent midline keel on the central ventral surface, deep and long cavities bounded by CPRL/TPRL and CPOL/TPOL, respectively, a coel existing on the dorsal half of the pocdf, 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.

Based on 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 hard to name a new species based on one mid-cervical although it does bear a unique combination of features, and here S66 is assigned to an species undeterminata of *Omeisaurus*, pending on discovery of more material and study.

This study shows the existence of *Omeisaurus* in the newly discovered Puan site of Yunyang, Chongqing, representing the easternmost occurrence of this genus. Detailed anatomy of one middle cervical of *Omeisaurus* is provided, and this will help elucidate the phylogeny of *Omeisaurus* because we realize the scorings for this genus in various matrixes 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 is still controversial (Wang et al., 2018).

**Acknowledgments** We are grateful to the personnel of the Yunyang Dinosaur Administration for various help during the field works, to ZHANG Yu-Qing and others for preparing the specimen, to JIANG Shan and HAO Bao-Qiao for providing information on *Omeisaurus tianfuensis* of Zigong Dinosaur Museum, and to the editor and reviewers for constructive suggestions.

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