New titanosauriform (Dinosauria: Sauropoda) specimens from the Upper Cretaceous Daijiaping Formation of southern China

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The two major clades of neosauropod dinosaurs, namely titanosauriforms and diplodocoids, differed greatly in their evolutionary fortunes during the Cretaceous. Titanosauriforms achieved a global distribution in the Early Cretaceous and continued to flourish until the end of the period. By contrast, the diversity of diplodocoids was lower in the Early Cretaceous than in the Late Jurassic, although rebbachisaurid diplodocoids radiated during the Early Cretaceous and survived in Africa, Europe, and South America until the early Late Cretaceous. A recent discovery from China demonstrates the presence of diplodocoids in Asia during the Middle Jurassic, but whether they survived into the Late Cretaceous on this continent remains unknown. Here, we give a detailed description of recently discovered sauropod specimens from the Upper Cretaceous Daijiaping Formation of Tianyuan County, Zhuzhou City, Hunan Province, southern China. Most of the material pertains to basal Titanosauriformes, and increases the diversity and geographic range of this group in eastern Asia. However, some specimens also display some features seen in basal sauropods and derived diplodocoids, suggesting complex patterns of character evolution in neosauropods during the Late Jurassic and Early Cretaceous. The Zhuzhou material likely represents one or more titanosauriforms with some primitive sauropod and diplodocoid character states, but the possibility that some individual bones are of diplodocoid origin cannot be ruled out entirely despite the lack of clear evidence for the presence of diplodocoids in Asia during the Late Cretaceous.

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Abstract

29 The two major clades of neosauropod dinosaurs, namely titanosauriforms and diplodocoids,
30 differed greatly in their evolutionary fortunes during the Cretaceous. Titanosauriforms achieved
31 a global distribution in the Early Cretaceous and continued to flourish until the end of the period.
32 By contrast, the diversity of diplodocoids was lower in the Early Cretaceous than in the Late
33 Jurassic, although rebbachisaurid diplodocoids radiated during the Early Cretaceous and
34 survived in Africa, Europe, and South America until the early Late Cretaceous. A recent
35 discovery from China demonstrates the presence of diplodocoids in Asia during the Middle
36 Jurassic, but whether they survived into the Late Cretaceous on this continent remains unknown.
37 Here, we give a detailed description of recently discovered sauropod specimens from the Upper
38 Cretaceous Daijiaping Formation of Tianyuan County, Zhuzhou City, Hunan Province, southern
39 China. Most of the material pertains to basal Titanosauriformes, and increases the diversity and
40 geographic range of this group in eastern Asia. However, some specimens also display some
41 features seen in basal sauropods and derived diplodocoids, suggesting complex patterns of
42 character evolution in neosauropods during the Late Jurassic and Early Cretaceous. The Zhuzhou
43 material likely represents one or more titanosauriforms with some primitive sauropod and
44 diplodocoid character states, but the possibility that some individual bones are of diplodocoid
45 origin cannot be ruled out entirely despite the lack of clear evidence for the presence of
46 diplodocoids in Asia during the Late Cretaceous.

47

Introduction

49 By the dawn of the Cretaceous, the diversity of sauropod dinosaurs had been reduced to the
50 major clades Diplodocoidea and Titanosauriformes, which differed greatly in their subsequent
51 evolutionary fortunes (Wilson 2005; Whitlock 2011; D'Emic 2012; Fanti et al. 2015).
52 Rebacchisaurid diplocoids underwent a modest radiation in the Early Cretaceous, and a few
53 persisted into the early Late Cretaceous in Africa, Europe and South America, but diplodocoids
54 were less diverse even in the Early Cretaceous than they had been in the Late Jurassic.
55 Titanosauriforms, by contrast, achieved a worldwide distribution and a high level of diversity
56 during the Early Cretaceous, and were among the most successful herbivorous dinosaur groups
57 of the Late Cretaceous. Although titanosauriforms were once thought to have been relatively rare
58 in China, it was eventually realized that all known Chinese Cretaceous sauropods were
59 titanosauriforms (e.g. Whitlock et al. 2011), and a series of discoveries have shown that the
60 diversity of this group in China was substantial. To date, nine titanosauriform genera have been

61   described from the Upper Cretaceous of China (Fig. 1), including *Sonidosaurus* from the Erlian

62   Formation of Inner Mongolia (Xu et al. 2006), *Borealosaurus* from the Sunjiawan Formation of

63   Liaoning Province (You et al. 2004), *Huabeisaurus* from the Huiquanpu Formation of Shanxi

64   Province (Pang & Cheng 2000), *Zhuchengtitan* from the Wangshi Group of Shandong Province

65   (Mo et al. 2017), *Gannansaurus* from the Nanxiong Formation of Jiangxi Province (Lü et al.

66   2013b), *Qingxiusaurus* from Upper Cretaceous red beds in Guangxi Province (Mo et al. 2008),

67   *Jiangshanosaurus* and *Dongyangosaurus* from the Jinhua Formation of Zhejiang Province (Tang

68   et al., 2001; Lü et al. 2008; Yu et al., 2010), and *Baotianmansaurus* from the Xiaguan Formation

69   of Henan Province (Zhang et al. 2009; Wang et al., 2013). The situation in China conforms to a

70   wider biogeographic pattern, in that Titanosauriformes is the only sauropod clade known to have

71   been present in the Cretaceous of Asia as a whole (Wilson, 2005; Wilson and Upchurch, 2009).

72   In the Jurassic, the sauropod fauna of China was overwhelmingly dominated by basal (non-

73   neosauropod) taxa, the only known Chinese diplodocoid being the recently described

74   *Lingwulong* from the Toarcian-Bajocian of Ningxia (Xu et al. 2018).

75

76   In 2008, a new fossil site containing numerous dinosaur bones was discovered in the Upper

77   Cretaceous Daijiaping Formation of Tianyuan County, Zhuzhou City, Hunan Province, southern

78   China (Fig. 1). The site is on the east side of Lianhua Road, in the northern part of Tianyuan

79   County, and was the intended location of a new middle school. Prior to construction of the

80   school, workers were using explosives to level an area of elevated terrain when a crew member

81   named Dangsheng Fang noticed fragments resembling animal bones among the shattered rock.

82   Some of these fossils were sent to experts from the Institute of Vertebrate Paleontology and

83   Paleoanthropology in Beijing, who identified them as dinosaur bones. The local government

84   protected the site immediately and arranged for all visible fossils to be collected. More than 200

85   bones were gathered and apportioned between the Zhuzhou Museum and the Bureau of Land and

86   Resources of Zhuzhou City. Most of the bones were fragmented and displaced by the explosives,

87   and are consequently difficult to identify (Han et al., 2017) or to assign to particular beds, but

88   some remained in place so that their stratigraphic positions could be documented as they were

89   collected (Fig. 2).

90

91   The dinosaur bones occurred within an area of about 6,000 m^2 and within strata of the Daijiaping

92   Formation, which includes a lower portion consisting of sandstone and an upper portion

93   consisting of siltstone and mudstone. On a regional scale, the total thickness of the formation is

94   about 1 km. However, the beds exposed at the site span only ~50 m of thickness and are believed

95   to represent a transitional region between the lower and upper parts of the formation. The

96   exposed beds can be divided into three parts: a lower part consisting of red calcareous siltstone,

97   interspersed with conglomerate layers; a middle part consisting of alternating siltstone and

98   conglomerate beds, and containing the dinosaur bones; and an upper part mainly consisting of

99   siltstone (Fig. 2). The dinosaur bones were recovered from six units in the middle part of the

100 section, within a stratigraphic interval ranging in thickness from 8.6 to 16.0 m across the width

101 of the outcrop (Fig. 2).

102

103 The Daijiaping Formation is generally considered to date from the early Late Cretaceous

104 (Coniacian to Santonian) (Han et al. 2017). However, analysis of a total of 22 pollen samples

105 from layers 4 and 9, situated in the middle part of the exposed section, instead suggests a latest

106 Cretaceous (Campanian to Maastrichtian) age (Zhu et al. 2019).

107

108 A preliminary study (Han et al., 2017) concluded that the sample of bones from this locality may

109 have two types of sauropod, and several species of theropod and hadrosaur. These bones are

110 disarticulated and appear to have been rapidly buried in the course of a flooding event following

111 transport over a short distance, as the clasts in the conglomerate are poorly rounded. Sauropod

112 bones are particularly abundant in the sample, and Han et al. (2017) identified derived features

113 suggesting that some of these bones were of titanosauriform whereas at least one, the left

114 ischium ZMW148, was from a diplodocoid. Relatively complete sauropod bones are known from

115 the third and eighth units in the middle part of the section. The third bed is composed of siltstone

116 and mainly contains cervical fragments, whereas the eighth is composed of conglomerate and is

117 even richer in sauropod fossils, having produced the complete fibula, humerus, and ischium

118 described here in addition to many unidentified fragments (Fig. 2).

119

120 Here, we present the first detailed study of the anatomically informative sauropod bones from the

121 Tianyuan site, and reconsider their probable affinities within Sauropoda. The bones in the sample

122 are not all proportionate in size to one another (see Tables 1-3), so multiple individuals are

123 clearly represented. These bones may represent either a single species or multiple species,

124 especially considering that they came from different stratigraphic levels.

125

126 **Institutional Abbreviations**: **AODF**, Australian Age of Dinosaurs, Winton, Queensland,

127 Australia; **BYU**, Brigham Young University, Earth Sciences Museum, Provo, Utah, USA; **HMN**,

128 Humboldt Museum für Naturkunde, Berlin, Germany; **ZGT**, Bureau of Land and Resources of

129 Zhuzhou City, Zhuzhou, Hunan, China; **ZMW**, Zhuzhou Museum, Zhuzhou, Hunan, China.

130

131 **Materials & Methods**

132 All specimens described here are postcranial bones, including the following elements: ZGT002,
133 a nearly complete cervical vertebra lacking only the posteriormost part; ZGT012, a partial
134 cervical with the left rib preserved in articulation; ZGT005, two articulated, very incomplete
135 cervical centra; ZGT044 and ZGT013, partial cervical ribs; ZGT003, a nearly complete caudal
136 vertebra lacking the neural spine; ZMW143, a partial scapula; ZGT056-060, the well-preserved
137 proximal half of a humerus; ZGT089, a midshaft fragment of a small humerus; ZMW148, a
138 complete left ischium; ZMW51-57, a nearly complete fibula; and ZMW013, an almost complete
139 pedal ungual. Some of these specimens are housed in the Bureau of Land and Resources of
140 Zhuzhou City (ZGT), while others are in the Zhuzhou Museum (ZMW). Measurements of all
141 these bones are presented in Tables 1-3. Comparisons with other taxa were mainly based on
142 published literature and photographs. A high-resolution 3D model of the cervical vertebra
143 ZGT002 is available in Figshare, https:// doi.org/10.6084/m9.figshare.9642785. It was scanned
144 using an Artec Space Spider hand-held 3D Scanner and the data of the model were edited to
145 make a 3D Image using the editing software Artec Studio.
146
147 Definitions of clades used in this study follow Mannion et al. (2013).
148

Results

Systematic Paleontology

151
152 Saurischia Seeley, 1887
153 Sauropoda Marsh, 1878
154 Neosauropoda Bonaparte, 1996
155 Macronaria Wilson & Sereno, 1998
156 Titanosauriformes Salgado, Coria and Calvo, 1997
157
158 **Description and comparisons.**
159 **Cervical vertebrae and ribs.** All of the cervical vertebrae described here were excavated from
160 layer 3, in the middle part of the exposed section (Fig. 2). Two partial cervical vertebrae
161 (ZGT002 and ZGT012), both with associated ribs, were identified (Fig. 3). ZGT002 is the better-
162 preserved of the two and also exhibits some distinctive features. A detailed description of
163 ZGT002, supplemented in places by information from the much less complete ZGT012, follows
164 below. A 3D version of ZGT002 is shown in Figshare. Measurements of ZGT002 are given in
165 Table 1.

166

167   The anterior part of the centrum is well-preserved but has undergone strong diagenetic

168   compression in the dorsoventral direction. On the less distorted left side, both an anterior and a

169   posterior pleurocoel are completely preserved, suggesting that only a small portion of the

170   centrum is missing posteriorly. The anterior articular surface is strongly convex, with a

171   subcircular outline. The position of this partial vertebra within the cervical series is hard to assess

172   with certainty. However, the relatively anteroposteriorly short and dorsoventrally tall centrum

173   suggests that the vertebra may be an anterior or a posterior cervical (Upchurch, Barrett &

174   Dodson 2004). The most prominent part of the anterior condyle is displaced dorsally from the

175   center of the articular surface as in the anterior and middle cervicals of the non-titanosaurian

176   titanosauriform *Euhelopus* (Wilson & Upchurch 2009), although in the anterior cervicals of

177   *Erketu* and *Yunmenglong* the convexity of the anterior condyle is more uniform (Ksepka &

178   Norell 2006; Lü et al. 2013a). The relatively shallow fossae and weakly developed laminae are

179   more consistent with attribution to the anterior part of the cervical column, as posterior cervicals

180   tend to bear more elaborate laminae and pneumatic cavities than anterior ones (Gomani 2005).

181   The low and transversely narrow neural spine is another indication that the vertebra is an anterior

182   cervical, as in *Euhelopus* the neural spines become transversely wide and bifurcated posterior to

183   cervical 11 (Wilson & Upchurch 2009). Finally, a prominent ventral keel is usually present on

184   the anterior portion of the ventral surface in anterior cervical vertebrae of basal titanosauriforms

185   in general (see below for detailed discussion).

186

187   The lateral surface of the centrum is excavated by two shallow pleurocoels, one anterior and one

188   posterior, which are separated by a prominent, posterodorsally oriented ridge (ppr, Fig. 3A) as in

189   *Omeisaurus* and neosauropods (Upchurch, Barrett & Dodson 2004). This ridge is more robust in

190   ZGT012 than in ZGT002 (Fig. 3H). In ZGT012, a small, deep fossa penetrates the widened

191   posterodorsal end of the lamina (fo, Fig. 3H). The anterior pleurocoel is subtriangular in lateral

192   view, whereas the posterior one is elongate and shallow dorsoventrally. In ZGT002, a weak,

193   vertically oriented secondary ridge separates the posterior pleurocoel into an anterior

194   subrectangular fossa and a posterior shallow triangular fossa (Fig. 3A). In contrast to the shallow

195   pleurocoels seen in ZGT012 and ZGT002, more than two pairs small deep pleurocoels occur in

196   the anterior cervicals of *Yunmenlong* (Lü et al. 2013a) and *Qiaowanlong* (You & Li 2009),

197   whereas in the preserved posterior cervical vertebrae of the titanosauriforms *Daxiatitan* and

198   *Yongjinglong* only a single large and deep fossa is present on the lateral surface of the centrum

199   (You et al. 2008; Li et al. 2014).

200

201   In ZGT002 the diapophysis arises from the dorsal portion of the centrum and has been deflected
202   upward as a result of distortion (Fig. 3C, G). A narrow process extends ventrolaterally from near
203   the anterior end of the anteroposteriorly elongate base of the diapophysis, so that the diapophysis
204   as a whole has a rotated "L" shape in lateral view. On the left side of the vertebra, the base of the
205   diapophysis is embayed by small notches both anteriorly and posteriorly (Fig. 3C). On the right
206   side, however, only a posterior notch is present, suggesting that the anterior notch on the left
207   diapophysis is a result of damage (Fig. 3G). The ventral process of the diapophysis overlaps the
208   dorsolateral surface of the tuberculum. The long, shallow parapophysis extends laterally from the
209   anteroventral corner of the centrum and is fused with the capitulum of the cervical rib. In other
210   titanosauriforms such as *Euhelopus*, *Erketu*, *Huabeisaurus* (Ksepka and Norell 2006; Wilson &
211   Upchurch 2009; D'Emic et al. 2013), the parapophysis has a strong ventrolateral inclination, and
212   the lateral orientation of the parapophysis of ZGT002 may be a result of taphonomic
213   deformation. The dorsal surface of the parapophysis is excavated by a large pneumatic fossa
214   (Fig. 3G), as in many other neosauropods including *Haplocanthosaurus* (Upchurch, Barrett &
215   Dodson 2004).
216
217   The anterior part of the ventral surface of the centrum bears three adjacent large fossae, whereas
218   the posterior part bears a prominent midline keel (Fig. 3A, B). In many titanosauriforms (e.g.
219   *Qiaowanlong* You & Li 2009; *Euhelopus* Wilson & Upchurch 2009), the ventral surface is
220   concave and a keel is lacking. The right fossa is semicircular in outline and is relatively small
221   and shallow, whereas the midline fossa has an oblong outline and is longer, narrower and deeper.
222   The left fossa is similar in length to the midline fossa but is much wider, and semicircular in
223   outline. The three fossae are separated by long, sharp ridges. A shallow depression is situated on
224   the ventral surface of the midline keel, just posterior to the medial part of the left fossa, and is
225   separated from the left fossa by a short but prominent transverse ridge. The shapes and sizes of
226   the three fossae may be affected by the overall distortion of the vertebra. Other taxa have paired
227   fossae in the same position as the three fossae seen in ZGT002, including the basal titanosaurs
228   *Rukwatitan* (posterior cervical, Gorscak et al., 2014) and *Overosaurus* (posterior cervical, Coria
229   et al., 2013). Paired fossae have also been reported in the cervicals of *Lingwulong* (Xu et al.
230   2018) and some other dicraeosaurids (Whitlock 2011), but are separated by a keel (Tschopp et
231   al., 2015: Fig. 38), whereas in ZGT002 the ventral keel begins posterior to the fossae. In
232   titanosaurs with paired fossae, the presence of a keel separating the fossae is variable (Gorscak et
233   al. 2014).
234
235   The presence of a trio of fossae at the anterior end of the ventral surface of the centrum of
236   ZGT002 is unusual, having never been reported in another sauropod cervical vertebra, and may

237 potentially represent an autapomorphy indicating that at least some of the Zhuzhou sauropod
238 material can be referred to a new species. However, we refrain from erecting a new species
239 pending recovery of more complete material, particularly given the paucity of other clear
240 potential autapomorphies in the material and the fact that pneumatic features such as fossae can
241 be highly variable.
242

243 The keel occupying the posterior part of the ventral surface of the centrum is transversely wide
244 anteriorly and narrows posteriorly, taking on a wedge-like shape. The keel essentially divides the
245 posterior part of the ventral surface into two large, shallow depressions (Fig. 3B). A ventral keel
246 is a primitive character that appears in the cervicals of some non-neosauropods (e.g.
247 *Shunosaurus*) and some diplodocoids, occurring in most cervicals of *Dicraeosaurus* (Harris
248 2006, Fig. 2), the middle and posterior cervicals of *Kaatedocus* (Tschopp & Mateus 2013) and
249 the only known reasonably intact anterior cervical of *Katepensaurus* (Ibiricu et al. 2013, Fig.
250 3C). A ventral keel is also seen in some titanosauriform cervicals, such as the axis of *Erketu*
251 (Ksepka & Norell 2006, Fig. 3), the axis and anterior cervicals of *Mongolosaurus* (Mannion,
252 2011, Fig. 6), the axis of *Futalognkosaurus* (Mannion, 2011), the only known (posterior) cervical
253 of *Savannasaurus* (Poropat et al., 2016), and the cervicals of *Rapetosaurus* (Curry Rogers 2009).
254 A weak midline ridge on the anterior part of the ventral surface of the centrum in cervicals 3 and
255 17 of *Euhelopus* (Wilson & Upchurch, 2009). Therefore, it seems that ventral keels can occur
256 throughout the cervical series in non-neosauropods, diplodocoids and titanosauriforms. The
257 ventral keel seen in ZGT002 resembles those on the axial vertebrae of *Erketu* and
258 *Mongolosaurus* (Ksepka & Norell 2006; Mannion 2011) in being transversely thickened
259 anteriorly and becoming narrower and shallower posteriorly, providing more evidence that
260 ZGT002 may represent an axis or anterior postaxial cervical.
261

262 The posterior end of the centrum is broken away, resulting in the exposure of internal cavities. In
263 posterior view, the interior of the centrum can be seen to be divided into two large chambers
264 (camerae) by a longitudinal lamina (Fig. 3F), as in basal sauropods such as *Camarasaurus*
265 (Wedel, Cifelli & Sanders 2000). However, the interior of the neural arch region has a porous
266 appearance, being divided irregularly into smaller chambers (camellae) as in titanosauriforms
267 such as *Euhelopus* (Wilson & Upchurch, 2009). The combination of a largely camerate centrum
268 and an at least partly camellate neural arch is evident in basal titanosauriforms, such as
269 *Brachiosaurus* (Wedel, Cifelli & Sanders 2000, BYU12866, Fig. 12C), but differs from the fully
270 camellate condition typically seen in derived titanosaurians, such as *Saltasaurus* (Wedel 2003).
271

272   There is no visible suture at the neurocentral junction, and the neural arch is damaged, although

273   the neural canal is large. The pre- and postzygapophyses are missing. The PRDL

274   (prezygodiapophyseal lamina) is robust and extends posteroventrally from the lateral side of the

275   prezygapophysis to the base of the diapophysis (Fig. 3C). Most of the neural spine is missing,

276   but the preserved basal part is transversely thin, suggesting that this structure was non-bifid. In

277   contrast, bifurcated neural spines are present in some of the presacral vertebrae of many

278   sauropods (Wedel & Taylor 2013), including *Euhelopus* (Wilson & Upchurch 2009) and *Erketu*

279   (Ksepka & Norell 2006). The paired spinoprezygapophyseal laminae are well-preserved, and are

280   thin and deep with sharp edges. These laminae diverge anterolaterally from the spine, forming

281   between them an angle of 45°, and merge into the prezygapophyses. There is no prespinal lamina

282   or fossa.

283

284   In posterior view, it is evident that the centrum and neural arch are both distorted. The neural

285   canal is subrectangular, being dorsoventrally elongate and transversely narrow. The left

286   infrapostzygapophyseal fossa (ipozf, Fig. 3F) is well preserved, and flanked by the PCDL and

287   PODL. This fossa is subtriangular in outline and bounded dorsolaterally by a horizontal lamina,

288   ventrolaterally by a laterally curved lamina, and medially by a vertical lamina that separates the

289   fossa from the neural canal. A second shallow fossa (fo, Fig. 3F) is situated just lateral to the

290   large infrapostzygopophyseal fossa. The small fossa is dorsoventrally elongate but transversely

291   narrow.

292

293   The proximal part of the left cervical rib belonging to ZGT002 is well-preserved, but the distal

294   part is broken away. The rib shaft is robust and straight, and narrows dorsoventrally towards the

295   missing distal end. The lateral surface is strongly dorsoventrally convex whereas the medial

296   surface is flatter, producing a semi-circular cross-section, as in the anterior to mid cervical ribs of

297   *Kaatedocus* (Tschopp and Mateus, 2013). The proximal end is divided into a slender dorsal

298   tuberculum and a deep, short ventral capitulum. The capitulum is fused to the parapophysis of

299   ZGT002 as described above, but the tuberculum is not fused to the diapophysis (Fig. 3A). Three

300   other cervical ribs are also well-preserved. In ZGT012, the tuberculum is fused with the

301   diapophysis, and the parapophysis and capitulum are broken away. The angle between the

302   tuberculum and capitulum is about 90°, as in basal sauropods such as *Shunosaurus* (Dong, Zhou

303   & Zhang 1983), but may have been altered by preservational distortion. The cervical rib bears a

304   long anterior process, which is transversely narrow, tapers gradually to a point, and has a convex

305   lateral surface and a concave medial one. On the medial surface of the rib (Fig. 3I), a ridge

306   extends upwards from the base of the capitulum along the anterior margin of the tuberculum.

307   Most of the shaft is missing, but the base of the shaft is dorsoventrally deep and transversely

308 narrow. The capitulum is broken through near its medial end, and the cross-section shows several
309 small cavities.
310
311 Cervical ribs ZGT044 and ZGT013 are similar to each other but differ in size (Fig. 3J-O). The
312 positions of these ribs within the cervical series are unknown. ZGT044 is double-headed, and
313 fused at the capitulum and tuberculum to a fragment of the corresponding vertebra. In ZGT013,
314 the tuberculum is mostly broken away, whereas the capitulum is fused to a fragment of the
315 elongate parapophysis of the corresponding vertebra. A moderately well-developed ridge extends
316 posteromedially across the dorsal surface of the base of the posterior process (Fig. 3M). In both
317 these ribs, the angle between the capitulum and the tuberculum is about 45°, as in *Omeisaurus*
318 and neosauropods (Wilson & Sereno 1998). The tuberculum is anteroposteriorly narrow, and has
319 a thin anterior margin but a thick posterior one. The capitulum is wide anteroposteriorly and thin
320 dorsoventrally. The dorsal surface of the capitulum bears a large, shallow fossa (Fig.3J, O), as in
321 some basal sauropods (Upchurch, Barrett & Dodson 2004). The medial surface of the
322 tuberculum is visible in ZGT012, ZGT013, ZGT044. A robust vertical ridge extends from the
323 midpoint of the base of the tuberculum and extends dorsally across the entire medial face,
324 curving posteriorly near its dorsal end (Fig. 3I, K, O).
325
326 The anterior and posterior processes of both ZGT044 and ZGT013 are well-developed. In both
327 cases the anterior process is slightly damaged at the tapering, anterodorsally curving tip, whereas
328 the posterior process is only partially preserved.
329
330 **Caudal vertebra (ZGT003).** A single, almost complete caudal vertebra (ZGT003) is present
331 (Fig. 4). This specimen appears to represent a middle caudal vertebra, based on its large size and
332 lack of transverse processes. The centrum is elongate, with a length of 143 mm, a width of 100
333 mm, and a height of 109 mm (Table 1). By contrast, most sauropod anterior caudal centra,
334 including those of the the first eleven caudals of *Tambatitanis* (Saegusa & Ikeda 2014) and the
335 anterior 10 caudals of *Huanghetitan ruyangensis* (Lü et al. 2007), are wider than long. The
336 length of the centra tends to increase posteriorly along the caudal series (Upchurch et al. 2004).
337 Centrum length and centrum width are usually equal in length among caudals 10 to 15 (You,
338 Tang & Luo 2003). Therefore, ZGT003 is probably from the part of the tail posterior to caudal
339 10.
340
341 The centrum is slightly amphicoelous and subcylindrical, as in the middle caudals of basal
342 titanosauriforms such as *Gobititan* (You, Tang & Luo 2003) and *Phuwiangosaurus* (Martin
343 1999, Fig. 25, 26). In *Huanghetitan ruyangensis*, the anteriormost five caudal centra are

344 amphicoelous, whereas those of caudals 6 to 10 are amphiplatyan (Lü et al. 2007). In contrast,
345 the anterior and middle caudals are procoelous in *Mamenchisaurus* and some titanosauriforms,
346 including *Daxiatitan* (You et al. 2008) and *Tambatitanis* (Saegusa & Ikeda 2014). In
347 *Mamenchisaurus*, the 15 anteriormost caudal centra are procoelous, whereas the centra are
348 amphiplatyan from caudal 16 onward (Young & Zhao 1972). In *Borealosaurus* (You et al. 2004)
349 and *Fukuititan* (Azuma & Shibata 2010), the only preserved caudal centra are middle or distal in
350 position, and are opisthocoelous.
351
352 The lateral surface of the centrum has no pneumatic fossae, is strongly dorsoventrally convex,
353 and bears a weak longitudinal ridge at about two-thirds of its height (Fig. 4B). The presence of
354 the ridge gives the cross-section of the centrum a hexagonal outline, as in the eighth and ninth
355 caudal vertebrae of *Huanghetitan* (Lü et al. 2007). Several nutrient foramina are present on the
356 lateral surfaces of the centrum, as in *Ganannosaurus* (Lü et al. 2013b).
357
358 The anterior and posterior articular surfaces are both well-preserved and expanded
359 dorsoventrally, the anterior surface being the larger of the two. In anterior or posterior view the
360 outline of the centrum resembles a hexagon with slightly convex sides, and a slightly concave
361 top and bottom with the widest region bellow the midline vertically. The ventral surface of the
362 centrum is smoothly concave, which is closed anteriorly and opened posteriorly (Fig. 4C, D).
363 The apex of the concavity lying just below the posterior part of the neural arch, and bears weak
364 longitudinal ridges near its lateral margins (Fig. 4A). However, the ventral surface lacks a
365 midline groove, a feature present in many forms (Upchurch, Barrett & Dodson 2004) including
366 *Huanghetitan* (caudals 8 and 9, Lü et al. 2007). The ventral surface also lacks the anteroposterior
367 row of distinct ventral fossae that occur in the anterior caudals of derived diplodocids and
368 lithostrotians (Upchurch, Barrett & Dodson 2004).
369
370 Both the anterior and posterior chevron facets are well-developed. The anterior facets are
371 convex, directed ventrally, and subcircular in outline. The posterior facets are relatively
372 flattened, directed more posteriorly than ventrally, and subtriangular in outline.
373
374 The neural canal is very small compared to the centrum, being only about 1/5 as high as the
375 latter. The width and height of the anterior opening are approximately equal, whereas the
376 posterior opening is only two thirds as wide as high. The neural arch is restricted to the anterior
377 half of the centrum as in the middle caudal vertebrae of *Phuwiangosaurus* (Martin et al. 1999,
378 Fig. 26) and most other titanosauriforms (Upchurch 1998). In *Gobititan* the neural arch is placed
379 near the mid-length of the centrum in the mid-caudals, but is entirely restricted to the anterior

380   part of the centrum in caudal 33 (You, Tang & Luo 2003). The neural spine and zygapophyses
381   are broken away, although the base of the left prezygapophysis is partially preserved. The
382   prezygapophysis appears to have originally extended anterodorsally, and has a transversely
383   convex ventral surface. The damaged surfaces of the neural arch are honeycombed with
384   pneumatic chambers in a camellate pattern, as in an anterior caudal of the titanosaurian
385   *Malawisaurus* (Wedel 2009).
386
387   **Humerus.** Two well-preserved partial humeri of different sizes (ZGT56-60 and ZGT089) are
388   present in the sample (Fig. 5). ZGT56-60 is the larger and more completely preserved of the two.
389   Measurements for these two humeri are given in Table 2.
390
391   ZGT56-60 is the proximal half of a right humerus, and is slightly compressed anteroposteriorly.
392   The long axis of this partial humerus appears straight in lateral view, and the proximal end is
393   transversely wide. Although the distal end is absent, the preserved portion of the humerus
394   extends more or less to the midshaft region, and indicates that the humerus as a whole was
395   robust.
396
397   The proximal end of the humerus is extremely expanded transversely, its width of 40 cm being
398   about double that of the distalmost preserved part of the humeral shaft. The head of the humerus
399   is proximally convex and forms a strong medial prominence as in other sauropods (Upchurch,
400   Barrett & Dodson 2004). The proximolateral corner is relatively rounded, and subdued relative
401   to the proximal apex of the humeral head, as in the basal titanosauriform *Qingxiusaurus* (Mo et
402   al., 2008, Fig. 1). By contrast, the proximolateral corner has a well-defined square outline in
403   most somphospondylans (Upchurch, Barrett & Dodson 2004). The medial part of the proximal
404   articular surface is slightly convex in anterior view, and the articular surface as a whole does not
405   show the sigmoid curvature that is present in some titanosaurs, such as *Diamantinasaurus*
406   (Poropat et al. 2015) and *Opisthocoelicaudia* (Borsuk-Białynicka 1977). The proximal articular
407   surface is rugose, crescent-shaped, and unevenly expanded anteroposteriorly to form the humeral
408   head, the greatest expansion occurring around the mediolateral midpoint of the proximal surface.
409   This is unlike the anteroposteriorly narrow humeral head in *Euhelopus* (Young 1935; Wilson &
410   Unchurch 2009). The medial end of the proximal articular surface tapers gradually to a point,
411   whereas approximately the lateralmost third of the proximal surface has a subrectangular outline,
412   is distinctly narrower than the expanded humeral head, and slopes down gently towards the
413   deltopectoral crest. No fossae or tubercles interrupt the proximal articular surface. The convex
414   humeral head is only moderately well-developed and merges gradually into the rest of the
415   proximal end of the humerus. In some macronarian taxa, such as *Haestasaurus* (Upchurch,

416 Mannion & Taylor 2015), the humeral head is more prominent and sharply defined. Well distal
417 to the proximal articular surface, a bulge is present on the lateral side of the humerus posterior to
418 the deltopectoral crest. A scar or eminence in this area occurs in a variety of titanosauriforms and
419 is conventionally identified as marking the insertion of M. scapulohumeralis anterior (Borsuk-
420 Białynicka 1977; Upchurch et al. 2015). The bulge is prominent and clearly visible in anterior
421 view, as in taxa such as *Qingxiusaurus* (Mo et al. 2008) and *Neuquensaurus* (Otero 2010).
422
423 The deltopectoral crest is situated along the anterolateral margin of the humerus and extends to
424 the distal part of the preserved portion. The crest is low, straight, and thickened mediolaterally in
425 its midlength portion. This is unlike the strongly medially directed deltopectoral crest seen in the
426 titanosaurs *Opisthocoelicaudia* (Borsuk-Białynicka 1977) and *Zhuchengtitan* (Mo et al. 2018).
427 The deltopectoral crest is a subdued structure with a flattened anterior surface, unlike the more
428 prominent and ridge-like deltopectoral crest of *Qingxiusaurus* (Mo et al. 2008, Fig. 1). In
429 anterior or posterior view the lateral margin of the shaft appears relatively straight in ZGT56-60
430 concave in the small humerus ZGT089, a variation that may reflect ontogenetic change. A
431 straight lateral humeral margin has been regarded as a derived feature only seen in some
432 titanosauriforms, such as *Malawisaurus* (Gomani 2005).
433
434 The proximal part of the cranial surface is mediolaterally concave, and is cracked due to poor
435 preservation. No rugosities are apparent on this part of the humeral surface. The posterior surface
436 is convex, giving the cross-section of this part of the humerus a thin, crescentic shape. In
437 ZGT56-60, the cross-section of the middle part of the shaft is three times as mediolaterally wide
438 as anteroposteriorly thick, but in ZGT089 the cross-section is oval and only slightly wider than
439 thick (Fig. 5). The extreme midshaft thinness of ZGT56-60 may be a result of the compression
440 that caused the cracks on the anterior surface.
441
442 **Ischium.** The left ischium ZMW148 is well-preserved and nearly complete (Fig. 6), and is
443 flattened, anteroposteriorly wide, and dorsoventrally elongate. It has a dorsoventral length of
444 59.5 cm (Table 3). The ischium has a short, robust iliac peduncle, a wide, elongate pubic
445 peduncle, and a slender, rod-like posteroventral shaft. The maximum width of the middle portion
446 of the ischium is more than twice that of the iliac peduncle or the distal shaft.
447
448 The iliac peduncle accounts for about one-fourth of the proximodistal length of the ischium, and
449 contributes a large portion to the margin of the acetabulum. The articular surface for the ilium
450 faces anterolaterally, while the iliac peduncle as a whole thickens posteriorly and therefore has a
451 subtriangular cross-section. The anterior margin of the iliac peduncle is continuous with the

452 dorsal margin of the pubic peduncle. The iliac peduncle has a relatively thin stalk but is

453 transversely expanded at the dorsal end for the articulation with the ilium. An acetabular surface

454 that is narrowest in its central portion. This condition occurs in most rebbachisaurids (Mannion

455 et al. 2012) but has also been reported in the titanosauriform *Huabeisaurus* from the Upper

456 Cretaceous of Shanxi Province, China (D'Emic et al. 2013, Fig. 20).

457

458 The concave posterior margin of the ischium is thickened, forming a prominent ridge that

459 extends from the base of the iliac peduncle to the posteroventral end of the ischial shaft. This

460 ridge is weakly developed distal to the iliac peduncle and near the distal end of the ischial shaft,

461 but sharper in the mid-region of the posterior margin. There is no ischial tuberosity on the lateral

462 surface of the ischium, unlike the condition in *Neuquensaurus australis* (see Otero 2010, Fig.

463 8A-B). The pubic peduncle is mediolaterally thin and has a flat lateral surface. Its anterior

464 margin has an irregular appearance resulting from damage. The dorsoventral height of the pubic

465 peduncle is about triple its anteroposterior length, as in the titanosauriforms *Sonidosaurus* (Xu et

466 al. 2006) and *Qiaowanlong* (You & Li 2009, Fig. 3). The ventral margin of the ischium is

467 sharply embayed between the pubic peduncle and the posteroventral shaft.

468

469 The length of the posteroventral shaft is slightly less than the dorsoventral height of the ischial

470 peduncle. The posterior edge of the shaft is transversely expanded and rounded whereas the

471 anterior edge is thin and sheet-like, so that the shaft has a subtriangular cross-section. The shaft

472 is extremely narrow anteroposteriorly, in contrast to the wide shaft seen in most titanosauriforms,

473 such as *Huabeisaurus* (D'Emic et al. 2013), *Qiaowanlong* (You & Li 2009, Fig. 3), *Sonidosaurus*

474 (Xu et al. 2006) and *Rapetosaurus* (Curry Rogers 2009, Fig. 41). However, an ischium with a

475 narrow distal shaft also occurs in some titanosauriforms, such as *Dongyangsaurus* (Lü et al.

476 2008, Plate II), *Opisthocoelicaudia* and an unnamed Brazilian taxon (Lehman & Coulson 2002),

477 as well as in such rebbachisaurids as *Comahuesaurus* (Carballido et al. 2012, Fig. 10) and

478 *Rebbachisaurus* (Wilson & Allain 2015, Fig. 15). The distal end of the shaft is just slightly

479 expanded. The anteroposterior length of the distal end is only twice the mediolateral width,

480 compared to three times the width in *Sonidosaurus* (Xu et al. 2006).

481

482 **Fibula.** The long and slender right fibula ZMW 51-57 is well-preserved, except that part of the

483 midshaft region is missing (Fig. 7). Measurements of the fibula are provided in Table 3. In lateral

484 view, the anterior margin of the fibula is relatively straight, whereas the posterior margin is

485 strongly concave. The proximal end is transversely compressed and flares asymmetrically in

486 lateral view, being expanded posteriorly but not anteriorly. The proximal end has a crescentic

487 outline, being convex laterally and concave medially, and the posterior part of the proximal end

488   is thicker than the anterior part. Additionally, the proximal end lacks the anteromedial crest,

489   which fits into a notch on the tibia, seen such titanosauriforms as *Gobititan* (You et al. 2003, Fig.

490   2), *Erketu* (Ksepka and Norell 2006, Fig. 10) and *Euhelopus* (Wilson et al. 2009, Fig.25)

491

492   The anteroproximal portion of the fibula appears rounded in lateral view. The strong posterior

493   expansion of the proximalmost part of the fibula has a subtriangular outline in lateral view,

494   although the posterior apex is truncated (Fig. 7A). The lateral surface of the shaft remains

495   strongly convex over the entire length of the fibula, whereas the medial surface is concave over

496   the proximal half of the bone but slightly convex over the distal half.

497

498   A lateral trochanter is present near the midpoint of the shaft. The trochanter is slightly curved

499   and anterodorsally oriented, and takes the form of two elongate, narrow parallel ridges as

500   observed in many titanosauriforms, such as *Huabeisaurus* (D'Emic et al. 2013, Fig. 23). Deep

501   fossae are present both anterior and posterior to the posterior ridge. The distal end of the fibula is

502   expanded relative to the midshaft, strongly convex both anteroposteriorly and transversely, and

503   lenticular in outline.

504

505   **Ungual.** A well-preserved, nearly complete large pedal ungual (ZMW013), with a length of

506   about 10 cm, is present. This element is strongly compressed laterally, with slightly

507   dorsoventrally convex lateral and medial sides, as in other Eusauropoda (Wilson & Sereno

508   1998). The proximal end of the ungual is dorsoventrally deep, transversely narrow, and

509   symmetrical in outline. The dorsal margin of the ungual is sharp and curved anteroventrally,

510   whereas the ventral surface is transversely expanded and flattened (Fig. 7I). Which pedal digit

511   the ungual belongs to is uncertain.

512

513   **Discussion**

514   Sauropods are relatively diverse and abundant in the Cretaceous of eastern Asia, at least 20

515   species having been erected (D'Emic et al. 2013; Mo et al., 2016; Averianov & Skutschas 2017;

516   Averianov et al. 2018). The Zhuzhou sauropod specimens add to this wealth of fossil evidence,

517   and collectively display an interesting and complex combination of morphological characters.

518   Most of the bones (e.g. the humerus and the fibula) can be at least tentatively referred to

519   Titanosauriformes on the basis of derived features, an interpretation consistent with the

520   prevalence of titanosauriforms in the Cretaceous of Asia. Others, however, combine

521   titanosauriform characteristics with features that are more typical of diplodocoids or basal

522   sauropods. For example, pneumatic fossae and a sharp keel are present on the ventral surface of

523   the probable anterior cervical ZGT002, and similar features occur in the anterior cervical

524   vertebrae of the basal sauropod *Shunosaurus* (Dong, Zhou & Zhang 1983) and some

525   rebbachisaurids and dicraeosaurids (Ibiricu et al. 2013; Tschopp, Mateus & Benson 2015). The

526   ischium ZMW148 has a relatively slender posteroventral shaft and an acetabular surface that is

527   narrowest in its central portion, as in some diplodocoids (Mannion et al. 2012; Wilson & Allain

528   2015). These features suggest that ZGT002 and ZMW148 may be referable to Diplodocoidea or

529   even Rebbachisauridae. Although the fragmentary nature of the material makes it difficult to

530   draw clear phylogenetic conclusions, the limited evidence available suggests two alternative

531   hypotheses: the Zhuzhou sample may either contain a mixture of titanosauriform and

532   diplodocoid elements or comprise only titanosauriform elements, some bearing features mainly

533   present in basal sauropods and diplodocoids. Because the specimens come from multiple layers

534   within the Daijiaping Formation, some of which have also yielded other dinosaur material, there

535   is no guarantee that all of them pertain to a single species.

536

537   The possibility that some of the Zhuzhou specimens might be of rebbachisaurid or at least

538   diplodocoid origin has intriguing implications. Diplodocoids are among the best-known

539   sauropods, and are found in North America, South America, Africa and Europe (Tschopp,

540   Mateus & Benson 2015). They flourished in the Late Jurassic and survived until the mid-

541   Cretaceous, but then disappeared entirely. Diplodocoids were traditionally thought to be absent

542   from the Asian fossil record. However, the recently discovered dicraeosaurid *Lingwulong* from

543   the Toarcian-Bajocian of Ningxia Autonomous Region in northern China shows that

544   diplodocoids were present in the Jurassic of eastern Asia and that neosauropods had therefore

545   achieved a worldwide distribution by the Middle Jurassic (Xu et al. 2018). Additionally,

546   Mannion et al. (2019) suggested a close relationship between the Jurassic sauropod faunas of

547   East Asia and southern Gondwana. This supposition is supported by the presence of

548   mamenchisaurids in the Jurassic of both China and Tanzania, as well as the similarity between

549   the Tanzanian *Janenschia* and the Chinese *Bellusaurus*. However, only a single diplodocoid,

550   namely *Lingwulong*, is currently known from Asia (Xu et al. 2018). Various specimens from the

551   Cretaceous of Asia were previously suggested to represent diplodocoids, but have been placed in

552   or near Titanosauriformes in recent phylogenetic analyses; this applies, for example, to the

553   holotype of *Nemegtosaurus* (Wilson 2005), and to an isolated anterior caudal vertebra from the

554   Lower Cretaceous of Shandong Province, China (Upchurch & Mannion 2009; Whitlock, D'Emic

555   & Wilson 2011). Nevertheless, the presence of diplodocoids in the Middle Jurassic of Asia lends

556   support to the possibility that Asian members of this clade survived into the Cretaceous

557   alongside the more prevalent titanosauriforms.

558

559   Rebbachisaurids, a group found in South America, Africa, Europe and probably North America

560   (Fanti et al. 2015; Mannion et al. 2019), are among the latest-surviving diplodocoids, the

561   youngest known rebbachisaurids being from the Cenomanian-Turonian of Argentina (Ibiricu et

562   al., 2013; Wilson & Allain 2015). Rebbachisaurids may have originated in South America, and

563   dispersed into Africa and Europe between 135 and 130 Ma (Fanti et al. 2015). However, the

564   oldest known rebbachisaurids, including *Histriasaurus* (Dalla 1998), *Demandasaurus*

565   (Fernández-Baldor et al. 2011; Xu et al. 2018), and an unnamed caudal vertebra (Mannion,

566   Upchurch & Hutt 2011), come from the Upper Hauterivian-lower Barremian of Europe.

567   Additionally, *Xenoposeidon* from the earliest Cretaceous (Berriasian-Valanginian) of England

568   may also be a rebbachisaurid (Taylor 2018), although this putative genus is known only from an

569   incomplete dorsal vertebra. Therefore, it is possible that rebbachisaurids originated in Europe.

570   Although no rebbachisaurids have previously been found in Asia, it is possible that members of

571   this group dispersed into Asia during the Early Cretaceous. The discovery of probable

572   rebbachisaurid material from the Daijiaping Formation indicates that rebbachisaurids may have

573   been present in Asia during the Cretaceous.

574

575   Nevertheless, some if not all of the Zhuzhou sauropod bones are clearly of somphospondylan

576   origin. Somphospondylans were among the most abundant and widespread sauropods, and were

577   particularly diverse in Asia during the Barremian (Poropat et al., 2016). Recent evidence

578   indicates, however, that the basal somphospondylan *Euhelopus* could be as early as Berriasian

579   and to be the oldest known somphospondylan, suggesting that somphospondylans could have

580   originated in eastern Asia (Xu & Li, 2015).

581

582   Titanosauria, defined as the least inclusive clade containing both *Andesaurus delgadoi* and

583   *Saltasaurus loricatus*, originated in the Early Cretaceous (Mannion et al. 2013). The oldest

584   known valid titanosaurs include *Tapuiasaurus* from the Aptian of Brazil (Zaher et al. 2011),

585   *Malawisaurus* and *Karogasaurus* from Aptian of Africa (Gomani 2005), *Daxiatitan* and

586   *Yongjinglong* from the Early Cretaceous of China (You et al. 2008; Li et al. 2014), and

587   *Tengrisaurus* from the Barremian-Aptian Murtoi Formation of Russia (Averianov & Skutschas

588   2017). A South American origin has been inferred for Titanosauria using a model-based

589   phylogenetic approach (Gorscak & O'Connor 2016). However, the analysis in question did not

590   include the earliest titanosaurian from Asia (*Tapuiasaurus*). Considering that the oldest and

591   many early titanosaurians mentioned above are from Asia, an Asian origin for this clade seems

592   possible.Titanosaurians may subsequently have formed endemic groupings in various parts of the

593   world as the continents moved apart during the Cretaceous.

594

595 Many authors have suggested some degree of endemicity among eastern Asian sauropods in
596 general, and have proposed the existence of putative endemic eastern Asian titanosauriform
597 clades including Euhelopodidae (Wilson & Upchurch 2009; D'Emic, 2012), Nemegtosauridae
598 (Wilson 2005) and Opisthocoelicaudiinae (You et al. 2004). Recent phylogenies support the
599 validity of Euhelopodidae, but the validity of Nemegtosauridae and Opisthocoelicaudiinae
600 remains controversial (Upchurch, Mannion & Taylor 2015; Poropat et al. 2016; González Riga et
601 al. 2018; Mannion et al., 2019).
602
603 Despite this taxonomic uncertainty, the number of different titanosauriforms reported from China
604 attests to the diversity of this group in the Late Cretaceous. However, most of these species are
605 highly incomplete and/or have been described only briefly, which limits their utility for
606 comparisons to other taxa and analyses of sauropod phylogeny. A detailed study of the relevant
607 specimens will be a necessary step in clarifying the phylogenetic affinities of titanosauriforms
608 from eastern Asia.
609

610 **Conclusions**

611 This contribution represents the first detailed study of sauropod material from the Upper
612 Cretaceous Daijiaping Formation of Tianyuan District, Zhuzhou City, Hunan Province, southern
613 China. Some of the individual bones are clearly referable to Titanosauriformes, increasing the
614 known diversity of this clade in eastern Asia. Interestingly, some of the specimens also possess
615 features that occur in basal sauropods and diplodocoids, suggesting that patterns of character
616 evolution in neosauropods during the Late Jurassic and Early Cretaceous must have been
617 complex. Diplodocoids flourished and spread around the world in the Late Jurassic, but declined
618 sharply in the Cretaceous. The last surviving diplodocoids, namely the rebbachisaurids, have
619 been documented in South America, Africa, and Europe, but are not definitively known from
620 Asia. If some of the Zhuzhou sauropod sample is indeed of diplodocoid origin, the existence of
621 diplodocoids in the Daijiaping Formation of south China would drastically extend the known
622 geographic range of this clade during the Late Cretaceous. However, the fragmentary nature of
623 the available material makes the presence of diplodocoids difficult to confirm, and implies a
624 need for further excavation and collecting,
625

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632

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Figure 1

Locality maps showing the site produced sauropod dinosaurs

(A) Map of China showing titanosauriform dinosaur localities, with Hunan Province shaded.

(B) Map of Hunan Province showing the location of Zhuzhou City. (C) Position of dinosaur

locality adjacent to Lianhua Road, Tianyuan District, Zhuzhou City.
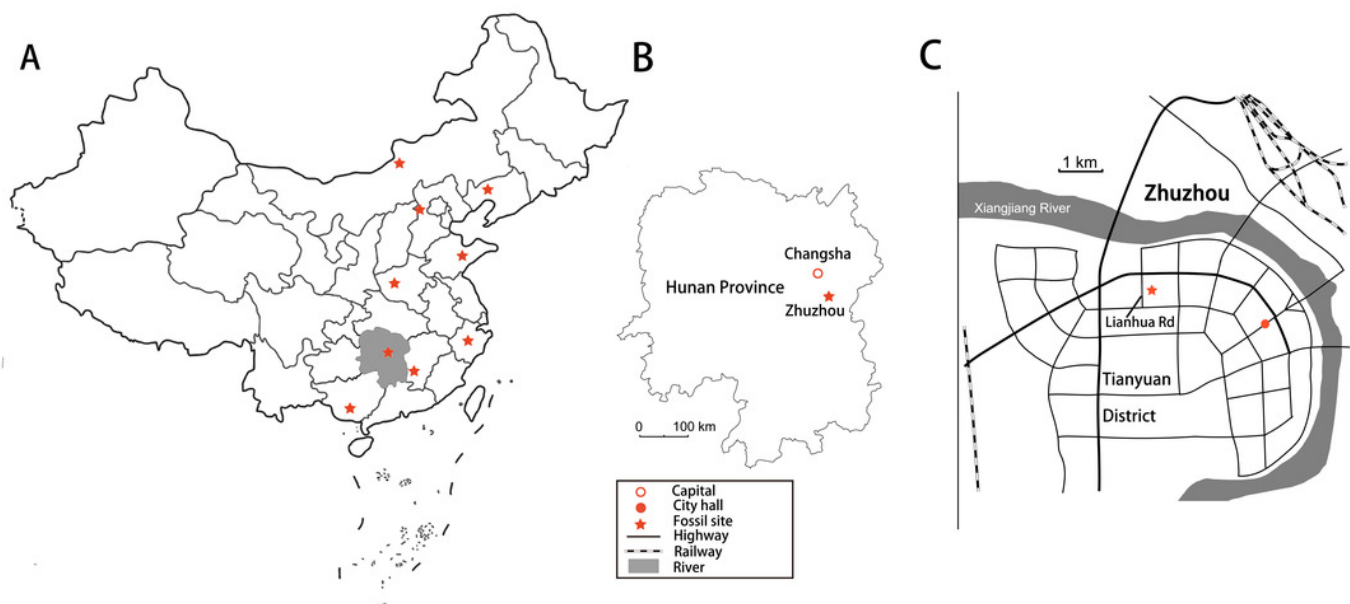
Figure 2

Stratigraphic section through the dinosaur-bearing Daijiaping Formation of Tianyuan District, Zhuzhou City.

Modified from Han et al. (2017). **Abbreviations**: **K$_2$**, Late Cretaceous; **Q**, Quaternary.

age	layer number	thickness	rock type	sedimentary structures
Q_2		>8		
K_2 upper	13	>5		
	12	1.4		
	11	2.2		
K_2 mid	10	1.2 ~ 2.4		
	9	2.1		
	8	1.8 ~ 2.8		ZMW148 ischium / ZMW51-57 fibula
	7	1.5 ~ 2.2		
	6	0 ~ 2.5		
	5	1.8		ZGT56-60 humerus
	4	0 ~ 1.5		ZMW013 ungual
	3	2.0 ~ 2.5		ZGT002, ZGT005 ZGT012, ZGT013 ZGT003, ZGT044
	2	1.5 ~ 2.7		
	1	>1.0		
lower K_2		>7.0		

Legend:
- calcareous siltstone
- conglomerate
- pebbled sandstone
- glutenite
- red clay
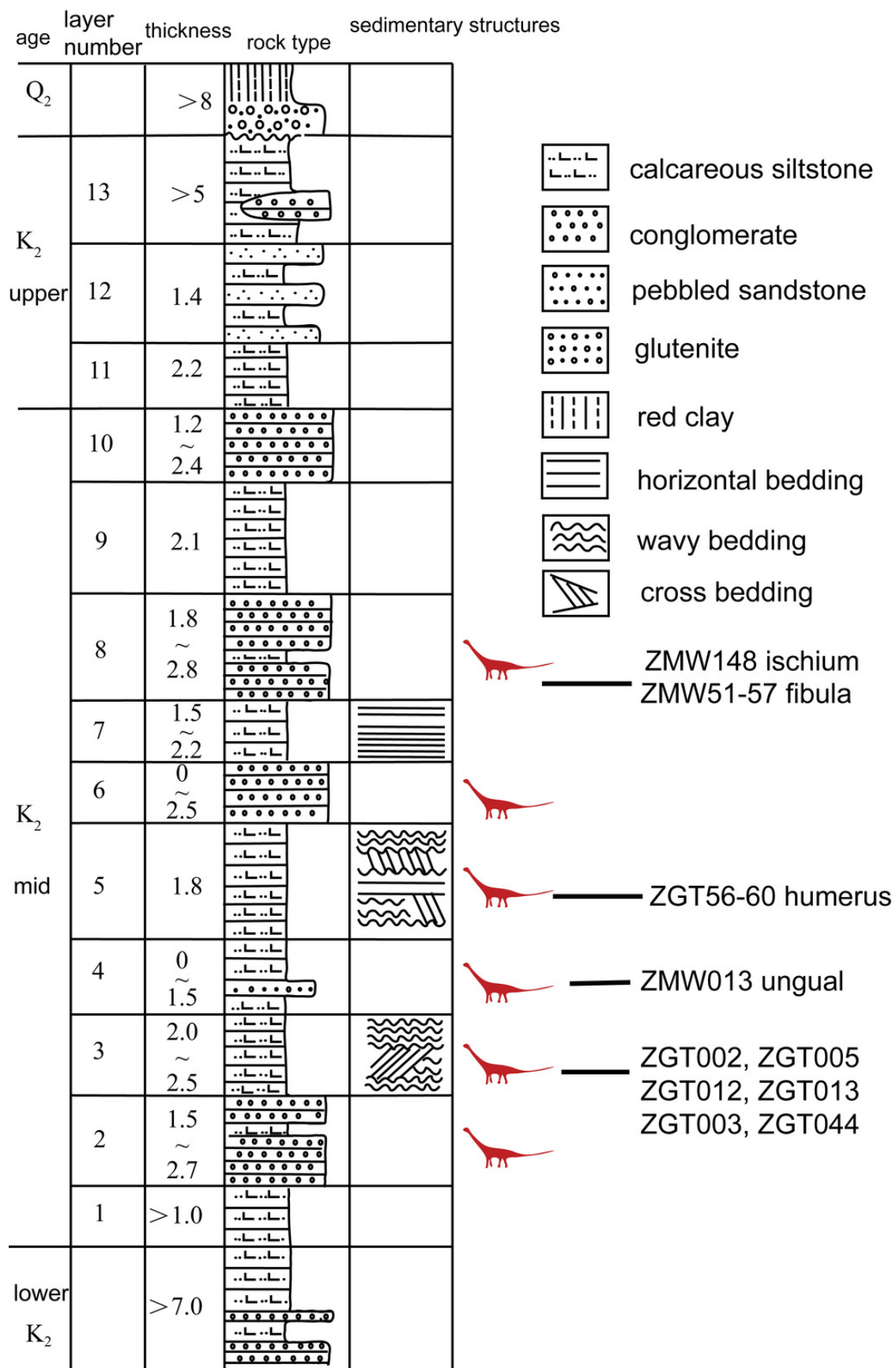- horizontal bedding
- wavy bedding
- cross bedding

Figure 3

Cervical vertebrae and ribs of sauropod dinosaurs from Zhuzhou City.

(A-G) ZGT002. (A) left lateral view. (B) ventral view. (C) left dorsolateral view. (D) dorsal view. (E) anterior view. (F) posterior view. (G) right lateral view. (H-I) ZGT012. H, centrum and associated rib in left lateral view; I, vertebra without rib in left lateral view and detached rib in medial view. (J-L) ZGT044, large posterior cervical rib. (J) dorsal view. (K) posterior view. (L) ventral view. (M-O) ZGT013, small posterior cervical rib. (M) dorsal view. (N) ventral view. (O) medial view. **Abbreviations**: **dp**, diapophysis; **fo**, fossa; **ipozf**, infrapostzygapophyseal fossa; **LCPOL**, lateral centropostzygapophyseal lamina; **lprf**, lateral fossa of the prezygapophyseal process; **nc**, neural canal; **PCDL**, posterior spinodiapophyseal lamina; **PODL**, postzygodiapophyseal lamina; **pp**, parapophysis; **ppr**, prominent posterodorsally oriented ridge; **PRDL**, prezygodiapophyseal lamina; **rid**, ridge; **SPRL**, spinoprezygapophyseal lamina; **wvr**, weak vertically oriented ridge.
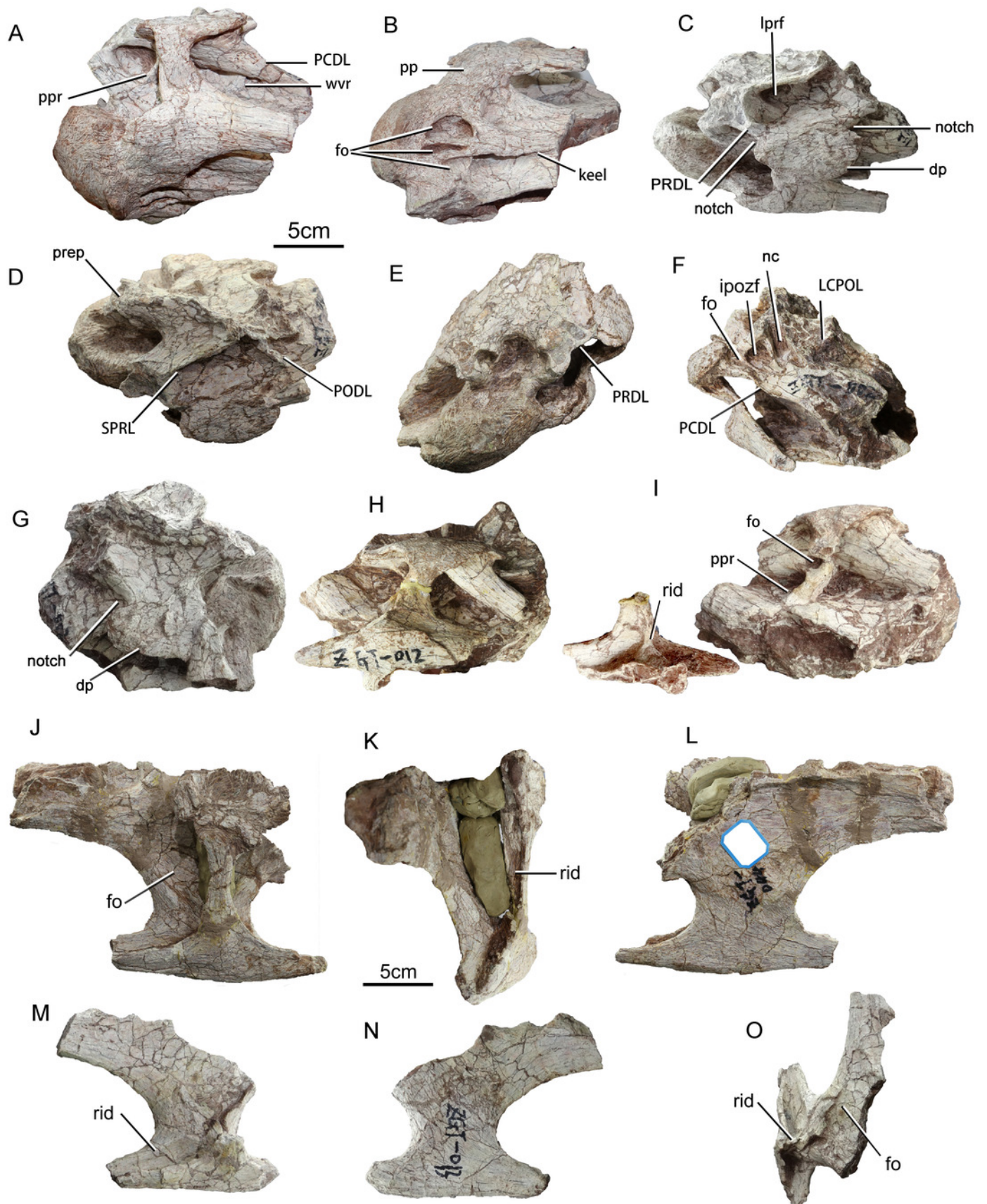
Figure 4

Caudal vertebra of titanosauriform dinosaur from Zhuzhou City (ZGT013).

(A) left lateral view. (B) right lateral view. (C) anterior view. (D) posterior view. (E) dorsal view. (F) ventral view. **Abbreviation**: **rid**, ridge.
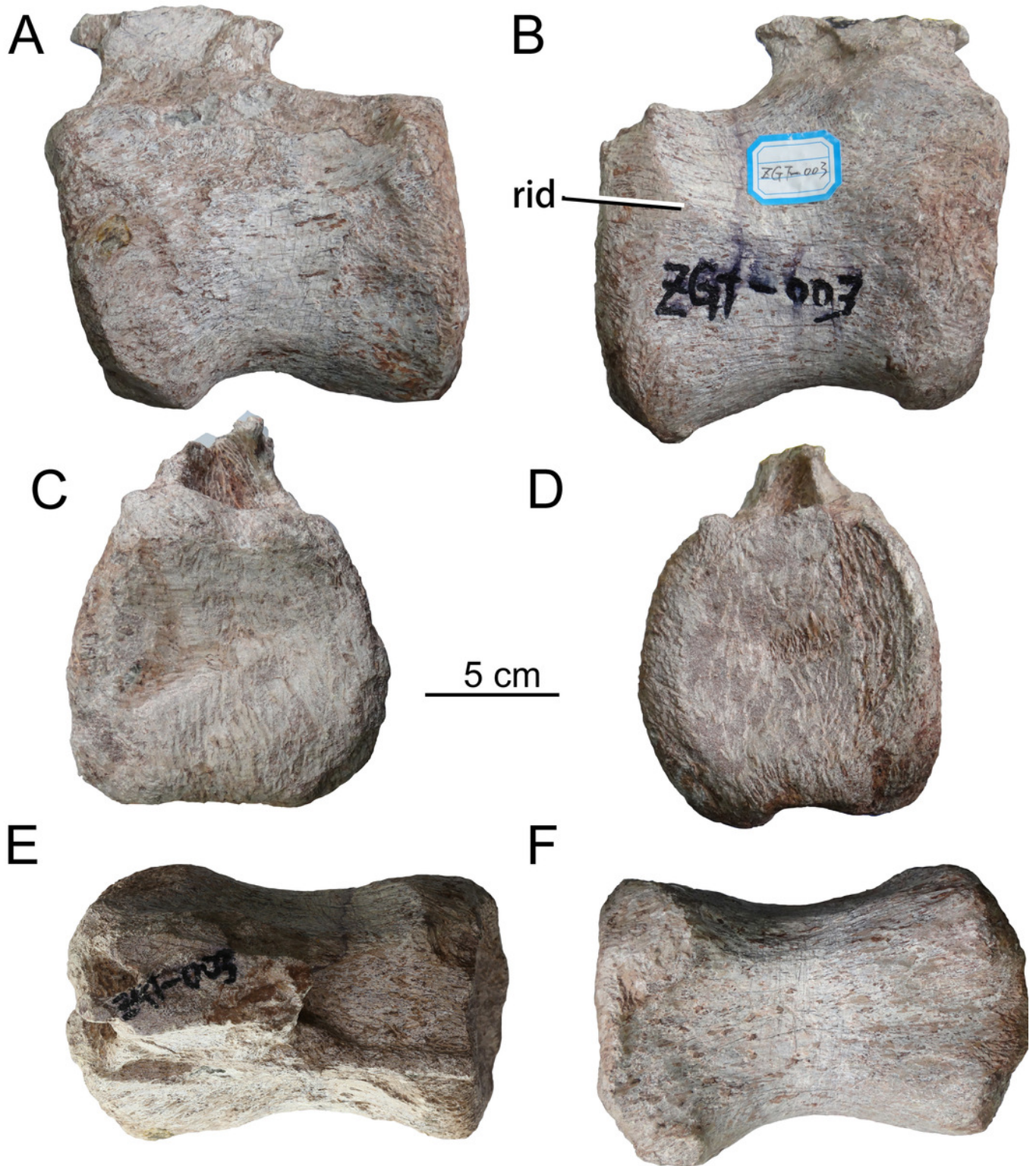
Figure 5

Humeri of sauropod dinosaurs from Zhuzhou City.

(A-E) ZGT056-060, partial right humerus. (A) anterior view. (B) lateral view. (C) posterior view. (D) proximal view. (E) preserved distal view. (F-H) ZGT089, partial left humerus. (F) cross section in distal view. (G) anterior view; (H) posterior view. **Abbreviations**: **dp**, deltopectoral crest; **hh**, humeral head, **lbh**, lateral bulge of humerus; **hplc**, humeral proximolateral corner.

Figure 6

Complete left ischium of sauropod dinosaur from Zhuzhou City (ZMW148).

(A) left lateral view. (B) enlargement of the proximal region in lateral view, (C) proximal region in dorsolateral view. (D) proximal region in posterolateral view.
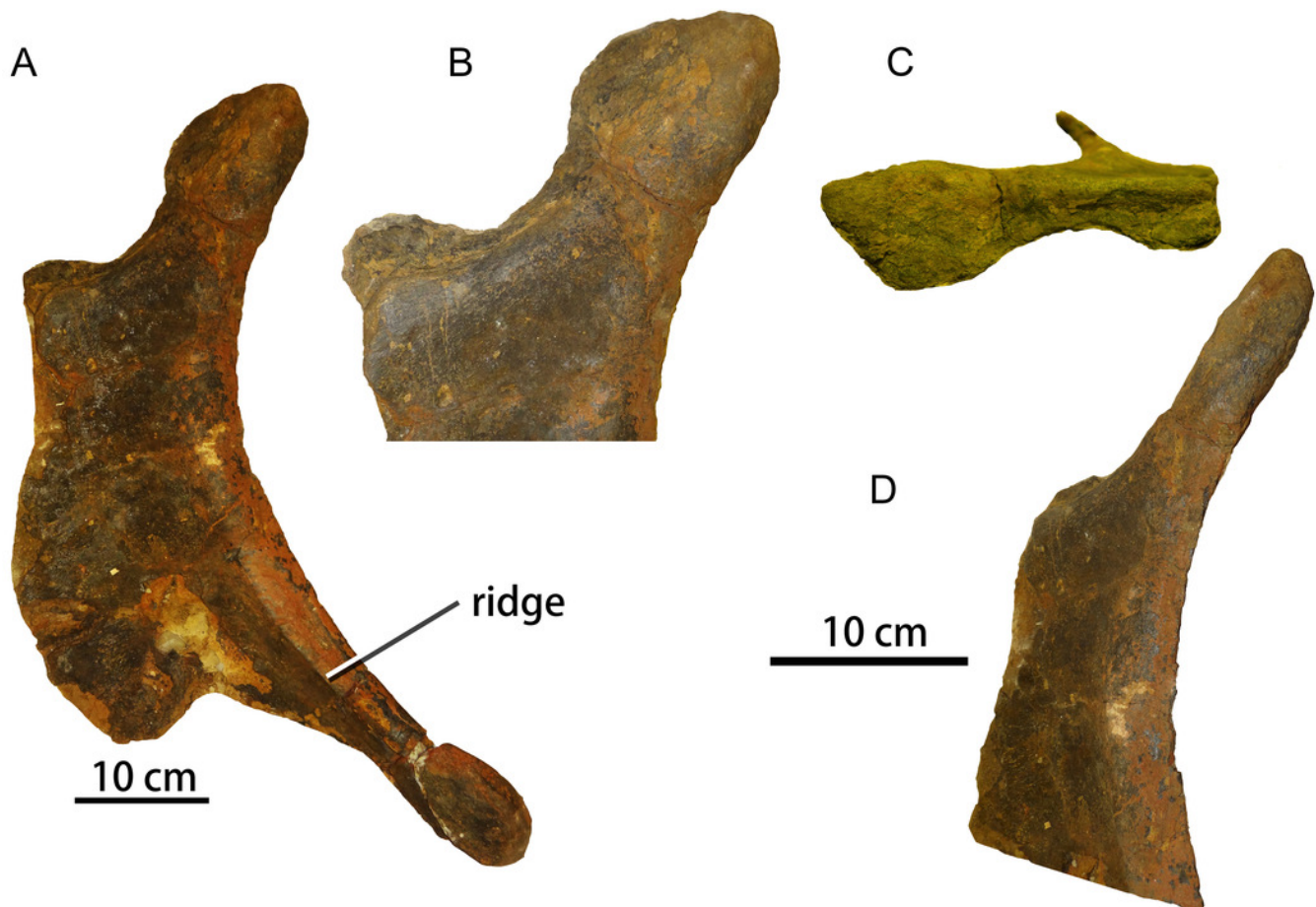
Figure 7

Photographs of the right fibula and an ungual of sauropod dinosaurs from Zhuzhou City.

((A-D) ZMW51-57, nearly complete right fibula. (A) right lateral view. (B) medial view. (C) proximal view. (D) distal view. (E-G) ZMW013, a pedal ungual . (E) left lateral view. (F) right lateral view. (G) dorsal view. (H) proximal view. (I) ventral view. **Abbreviation**: **lt**, lateral trochanter..
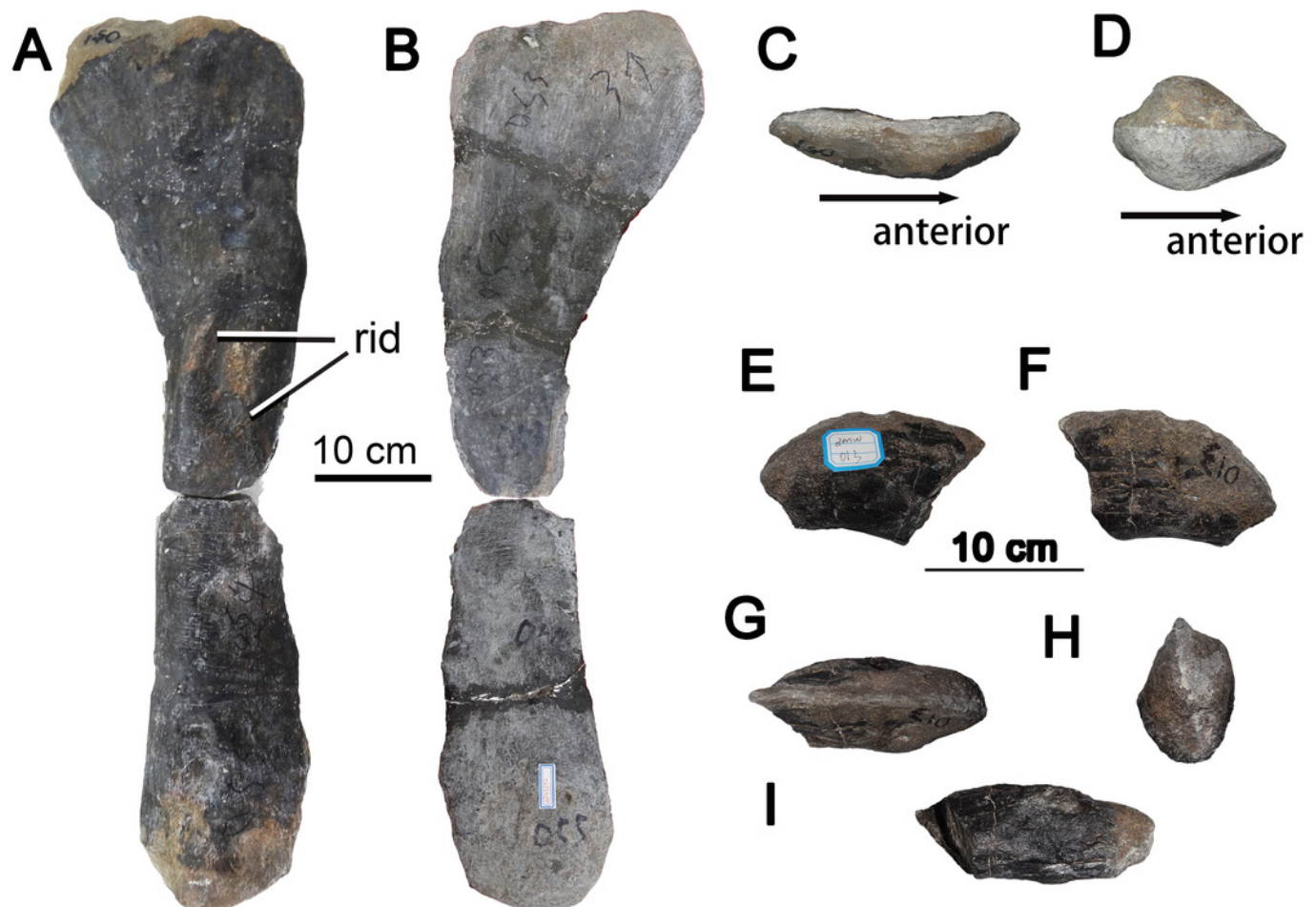
Table 1(on next page)

Measurements of the cervical and caudal vertebrae of sauropod dinosaurs from the Upper Cretaceous Daijiaping Formation of southern China (All measurements are in millimetres).

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Elements	Dimension	Measurements
Cervical vertebra ZGT002	Preserved centrum length (including ball)	159
	Preserved centrum length (excluding ball)	106
	Anterior centrum height	62.0
	Anterior centrum width	122
	Preserved posterior centrum height	77.7
	Preserved posterior centrum width(dorsal)	64.5
	Preserved posterior centrum width(mid shaft)	32.7
	Neural arch height anteriorly	58.5
	Neural arch width anteriorly	33.6
	Width across prezygapophyses	85.7
	Anterior pneumatopore length	31.6
	Anterior pneumatopore height	22.4
	Posterior pneumatopore length	67.7
	Septum to posterior margin	105
	Posterior pneumatopore height(anterior)	21.3
	Anterior condyle width	55.7
	Anterior condyle height	98.6
	Preserved cervical rib length	105
Caudal vertebra ZGT003	Centrum length	143
	anterior centrum height (without chevron facets)	106
	anterior centrum width (ventral/mid/dorsal regions)	103/106/70
	posterior centrum height (without chevron facets)	106
	posterior centrum width (ventral/mid/dorsal regions)	92/99.6/76.8
	Centrum height at the mid region	96.2
	Centrum width at the mid region	82.6
	Neural arch length (shortest)	67.9
	Neural arch width (mid region)	55.0
	Neural arch height	43.4
	Neural canal width/height (proximal end)	35.0/38.4
	Neural canal width/height (distal end)	19.9/36.4

Table 2(on next page)

Measurements of the humeri of sauropod dinosaurs from the Upper Cretaceous Daijiaping Formation of southern China (All measurements are in millimetres).

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Elements	Dimension	Measurements
Right humerus ZGT56-60	Preserved length (medial/lateral margin)	552/470
	Proximal end maximum mediolateral width	345
	Proximal end maximum anteroposterior thickness	92.9
	Distance from proximal end to distal edge of dtp crest	420
	Preserved mimimum shaft circumference	410
	Mediolateral width at midshaft	175
	Anteroposterior width at midshaft	43.95
	Dtp crest width (largest)/humerus width	94.0/215
Left humerus ZGT089	Preserved length	318
	Largest transversely width as preserved	151
	Distance from proximal end to distal edge of dtp crest	260
	Preserved mimimum shaft circumference	
	Mediolateral width at midshaft	68.3
	Anteroposterior width at midshaft	48.9
	Dtp crest width (largest)/humerus width	56.7/151

3

Table 3(on next page)

Measurements of the ischium, fibula and ungual of sauropod dinosaurs from the Upper Cretaceous Daijiaping Formation of southern China (All measurements are in millimetres)

1

Elements	Dimension	Measurements
Left ischium ZMW148	Length	595
	Anteroposterior length of iliac peduncle	79.2
	Maximum mediolateral width of iliac peduncle	90.7
	Dorsoventral height of iliac peduncle	167
	Anteroposterior length of acetabulum	76.8
	Anteroposterior length of proximal plate	153
	Dorsoventral height of pubic peduncle	340
	Maximum dorsoventral height of distal blade	225
	Maximum mediolateral width of distal blade	31.4
	Maximum anteroposterior length of distal blade	60.2
Fibula ZMW51-57	Length	736
	Length from the proximal end to the proximal / distal end of the lateral trochanter	250/330
	Mediolateral width of proximal end	43.3
	Anteroposterior length of proximal end	225
	Mediolateral width at midshaft	32.2
	Anteroposterior width at midshaft	92.6
	Minimum shaft circumference	228
	Mediolateral width of distal end	75.6
	Anteroposterior width of distal end	129
Pedal ungula ZMW013	Maximum proximodistal length	137
	Proximal end dorsoventral height	83.5
	Proximal end mediolateral width	47.9

2