A new metriacanthosaurid theropod dinosaur from the Middle Jurassic of Yunnan Province, China (#106452)

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A new metriacanthosaurid theropod dinosaur from the Middle Jurassic of Yunnan Province, China

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Metriacanthosaurid theropods represent a basal-branching lineage of tetanurans. Members of this clade are mainly medium to large-sized and lived in Laurasia during the Middle Jurassic to the Early Cretaceous. In this clade, Sinraptor dongi, Sinraptor hepingensis, and Yangchuanosarus shangyouensis from the Late Jurassic are well represented by the nearly complete specimens, but the incompleteness of Middle Jurassic taxa hinders our knowledge of the origin and early evolution of Metriacanthosauridae. This paper describes a new genus and species of metriacanthosaurids, Yuanmouraptor jinshajiangensis gen. et sp. nov, from the Middle Jurassic Zhanghe Formation of Yunnan Province, China. The new taxon is represented by a cranium and the anterior section of the vertebral column including the complete cervical series and the first dorsal vertebra. Yuanmouraptor jinshajiangensis can be diagnosed based on the following autapomorphies: the anterior process of postorbital is sheet-shaped and keeps consistent depth; gently sigmoidal ventral ramus of postorbital with a laterally twisted trough running along it; processes on the anterodorsal margin of the third and fourth cervical neural spines; strongly posteriorly elongated epipophyses of anterior cervical vertebrae; deeply excavated pleuroceols on the third cervical vertebra; sheet-shaped and subrectangular neural spines of posterior cervical vertebrae. Phylogenetic analysis recovers Yuanmouraptor as the most basalbranching member within Metriacanthosauridae and provides a new alternative phylogenetic topology of non-coelurosaurian tetanurans.

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INTRODUCTION

- 26 Metriacanthosauridae is a family of medium-to-large sized carnivorous dinosaurs and represents a
- 27 basal-branching clade within the Allosauroidea (Holtz et al., 2004; Smith et al., 2007; Benson,
- 28 2010; Carrano et al., 2012; Hendrickx et al., 2015; Coria & Currie, 2016; Rauhut et al., 2016,
- 29 2019, 2024; Lamanna et al., 2020). Members of this clade mainly came from the Middle to Late
- 30 Jurassic strata of western China (Fig. 1), such as Sichuan, Chongqing, Xinjiang, and Yunnan
- 31 (Dong et al., 1978, 1983; Gao, 1992, 1993, 1999; Currie & Zhao, 1993; Wu et al., 2009). Apart
- 32 from these taxa found in China, metriacanthosaurid theropods were also reported in the Late
- Jurassic of England (Huene, 1923; Walker, 1964), the Late Jurassic of Kyrgyzstan (Rauhut et al.,
- 34 2024), and the Early Cretaceous of Thailand (Buffetaut et al., 1996). Recently, Yu et al. (2023)
- 35 reported the probable distribution of this clade in the Tibetan Plateau.
- 36 Here we report a new genus and species of Metriacanthosauridae collected from the Middle
- 37 Jurassic Zhanghe Formation of Jiangyi, Yuanmou county of Yunnan Province, China (Fig. 1 B).
- 38 Material of this new taxon include a relatively complete skull and the first 11 vertebrae including
- 39 10 cervical vertebrae and the anterior-most dorsal vertebra. The Zhanghe Formation also yielded
- 40 sauropods including Yuanmousaurus (Lü et al., 2006), Eomamenchisaurus (Lü et al., 2008), and
- 41 Nebulasaurus (Xing et al., 2015). Our phylogenetic analysis suggests that the new taxon is
- 42 probably one of the two most basal-branching metriacanthosaurids. Furthermore, some characters
- present in the new taxon are also shared with several megalosauroids (*Li et al.*, 2009; *Dai et al.*,
- 44 2020) and non-tetanuran theropods (Colbert, 1989; Marsh & Rowe, 2020), which suggests that
- 45 these shared characters were gained independently by the aforementioned taxa.

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MATERIAL & MATHODS

Material

- The specimens studied here were excavated by a field team of Chuxiong Prefectural Museum from
- 50 a layer of red sandstones within the Zhanghe Formation at Jiangyi Town, Yuanmou County,
- 51 Chuxiong Yi Autonomous Prefecture, Yunnan, China in 2006, and is now on display in the
- 52 museum of Lufeng World Dinosaur Valley in Lufeng City, Yunnan Province. Most cranial bones
- are still in articulation or closely associated. Some of the cranial elements are heavily distorted or
- 54 covered by matrix or other bones, rendering difficult or impossible to determine bone sutures or
- 55 internal structures. The specimen was prepared using mechanical tools (pneumatic chisels) and
- 56 photographed from various perspectives with a Sony DLSR-A700 digital camera. Line drawings
- were made based on the reference photographs and checked against the original specimens.

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Phylogenetic analysis

The new matrix for the phylogenetic analysis in this study was modified based on that of Carrano 60 et al. (2012), which mainly focused on the phylogenetic relationship within tetanurans. We added 61 five new and 26 characters modified from the datasets of Lamanna et al. (2020), Eddy & Clark 62 (2011), Brusatte & Serreno (2008), and Schade et al. (2023) (see the online Supplemental File S1 63 for details). We added the coelophysoid *Panguraptor* (You et al., 2014), Zuolong (Choiniere et al., 64 2010), Guanlong (Xu et al., 2006), and Eoabelisaurus (Pol & Rauhut, 2012) to the matrix to enrich 65 the samples of non-tetanurans, Coelurosauria, and Ceratosauria, respectively. Several basal-66 67 branching tetanurans such as Asfaltovenator (Rauhut & Pol, 2019), Wiehenvenator (Rauhut et al., 2016), and Yunyangosaurus (Dai et al., 2020) were added because these taxa were recently 68 reported tetanurans. Alpkarakush kyrgyzicus (Rauhut et al., 2024) (the most recently named 69 Central Asian metriacanthosaurid) was also added to the dataset. The new matrix, consisting of 70 372 characters and 70 operational taxonomic units (OTUs), was analyzed using TNT v. 1.6 71 (Goloboff & Catalano, 2023). The most parsimonious trees (MPTs) were recovered by a traditional 72 search of 1000 replicates of Wagner trees followed by tree bisection and reconnection, with 10 73 trees saved per replication. Characters were equally weighted, and none of the characters were 74 treated as ordered. 75

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Nomenclatural acts

The electronic version of this article in Portable Document Format (PDF) will represent a 78 published work according to the International Commission on Zoological Nomenclature (ICZN), 79 and hence the new names contained in the electronic version are effectively published under that 80 Code from the electronic edition alone. This published work and the nomenclatural acts it contains 81 have been registered in ZooBank, the online registration system for the ICZN. The ZooBank 82 LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through 83 any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for 84 this publication is: urn:lsid:zoobank.org:pub:2A9F32AD-B671-4F48-8A6E-0A69976A75FB. 85 86 The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS. 87

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RESULTS

90 Systematic paleontology

- 91 Dinosauria Owen, 1842
- 92 Theropoda Marsh, 1881
- 93 Tetanurae Gauthier, 1986



- Allosauroidea Currie & Zhao, 1993 94
- Metriacanthosauridae Paul, 1988 95
- Yuanmouraptor gen. nov. 96
- Diagnosis—As for the only species. 97
- 98 Yuanmouraptor jinshajiangensis gen. et sp. nov.
- **Etymology**—The genus name, 'Yuanmou', refers to Yuanmou County where the holotype was 99
- collected, and 'raptor' is Latin for the robber. The specific name, 'jinshajiang' (the middle region 100
- of Yangtze River) which passes through Yuanmou County and the type locality is located on the 101
- 102 north bank of the river.
- Holotype—LFGT-ZLJ0115: a partial skeleton consists of a nearly complete skull with mandible 103
- and 11 articulated anterior vertebrae including 10 cervical vertebrae and the first dorsal vertebra. 104
- Type Locality and horizon—Jiangyi Town, Yuanmou County, Chuxiong Yi Autonomous 105
- 106 Prefecture, Yunnan Province, China; Zhanghe Formation, early Middle
- Aalenian/Bajocian ((Bureau of Geology and Mineral Resources of Yunnan Province 1990). 107
- medium-sized metriacanthosaurid dinosaur differing other 108
- metriacanthosaurids by the following unique combination of characters (autapomorphies are 109
- indicated with an asterisk): ventral extension of antorbital fossa on maxilla is dorsoventrally deep, 110
- which is shared with non-tetanurans, *Marshosaurus* and *Eocarcharia*, and some basal-branching 111
- coelurosaurs such as *Ornitholestes* and *Proceratosaurus*; an accessory foramen located within 112
- 113 antorbital fossa on lacrimal and ventral to pneumatic foramen, similar to Allosaurus; dorsal part
- of postorbital forming a very low rugosity, similar to megalosaurids; lack of pneumatic fenestra 114
- on lateral surface of jugal, shared with non-tetanurans; the anterior process of postorbital sheet-
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shaped and its depth keeping consistent*; gently sigmoidal ventral ramus of postorbital with a

- laterally twisted trough running along it*; process on anterodorsal margin of the third and fourth 117
- cervical vertebrae*; flattened peripheral band on anterior articular surface of anterior cervical 118
- centra, shared with Yunyangosaurus and megalosaurids; strongly posteriorly elongated 119
- epipophyses on anterior cervical vertebrae*; deeply excavated pleuroceols on the third cervical 120
- 121 vertebra*; sheet-shaped and subrectangular neural spines of posterior cervical vertebrae*.

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General description of the cranium

- The conditions of preservation of LFGT-ZLJ0115 are different between each side, and bones show 124
- 125 many fractures which might be caused during fluvial transportation. On the left side (Fig. 2 A B),
- most parts of the nasal and elements around the orbit and lateral temporal fenestra are missing. On 126
- the right side (Fig. 2 C D), although the nasal is also poorly preserved, other bones are relatively 127
- more complete than those of the left side. The mandibular ramus is well-preserved on both sides. 128
- The remnant elements of the skull and mandible are generally articulated, and thus most of the 129



internal structures are obscured from observation except the right ramus of the mandible. The main 130 fenestrae of the skull, such as the naris, antorbital fenestra, orbit, lateral temporal fenestra, and 131 supratemporal fenestra, are all damaged or largely distorted. The preserved skull is measured 53.9 132 cm in anteroposterior length, and the reconstruction (Fig. 3) of the skull measures 60.-1 cm in 133 anteroposterior length. In comparison, the type specimen of Yangchuanosaurus shangyouensis 134 (Dong et al., 1978) bears a skull length of 78 cm, and the referred specimen (Y. magnus, reported 135 by Dong et al. [1983], was considered to present different ontogenetic stage of Y. shangyouensis 136 by Carrano et al. [2012]) has an estimated skull length of 111 cm. The skull of Sinraptor dongi 137 138 (Currie & Zhao, 1993) is 90 cm long and the skull of S. hepingensis (Gao, 1992, 1999) is 104 cm 139

Based on the closed neurocentral suture, *Yuanmouraptor* is probably a mature individual.

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142 **Premaxilla**—Only the left premaxilla (Fig. 4 A, B) is preserved, with most supranarial process missing except for its risen base. In lateral view, the outline of the premaxillary body (below the 143 external naris) is roughly quadrangular and slightly higher than long (5.65×5.42 cm), with the 144 ventral border of the external naris is nearly paralleled with the premaxillary alveolar margin, 145 which is similar to the condition of Ceratosaurus (Madsen & Welles, 2000), Torvosaurus (Britt, 146 1991), Majungasaurus (Sampson & Witmer, 2007), and many allosauroids, such as Sinraptor 147 (Currie & Zhao, 1993; Gao, 1999), and Acrocanthosaurus (Eddy & Clarke, 2011), but in contrast 148 to Sinraptor (Currie & Zhao, 1993), Allosaurus (Britt, 1991), Neovenator (Brusatte et al., 2008), 149 Dubreuillosaurus (Allain, 2002), Marshosaurus (Madsen, 1976b), and Monolophosaurus 150 (Brusatte et al., 2010a), in which the premaxilla is slightly longer than high. The premaxilla is 151 much longer than high (length/height > 2) in spinosaurids like Suchomimus (Sereno et al., 1998) 152 and Ceratosuchops (Barker et al., 2021). The premaxilla of Yuanmouraptor bears four alveoli, 153 which is a primitive condition for theropods (Allain, 2002; Sampson & Witmer, 2007, Currie & 154 Zhao, 1993), as in Sinraptor, Yangchuanosaurus, but five alveoli are present in Allosaurus and 155 Neovenator (Brusatte et al., 2008). In spinosaurids, the number of alveoli could reach seven. The 156 fourth tooth is broken with only a little part of its base preserved. The other three are complete and 157 compress mediolaterally with slightly backward curvature. The distal carina is well-developed and 158 extended throughout the whole length, whereas the mesial carina is only visible at the epical one 159 third of the second tooth in lateral view (Fig. 4 C). 160 161 The anterodorsal border of the premaxillary body is missing, along with the main part of the supranarial process (nasal process), but the preserved base of the process forms the anteroventral 162 margin of the external naris and indicates the posterodorsal orientation of the process. The narial 163

fossa is located ventrally to the remnant part of the external naris as in Acrocanthosaurus,

Sinraptor, Allosaurus, and Dubreuillosaurus. The complete portion of the anterodorsal rim



suggests that the anterior margin of the premaxillary body is nearly vertical as in Sinraptor, 166 Ceratosaurus, and Allosaurus, whereas that of Torvosaurus, Dubreuillosaurus, and Duriavenator 167 (Benson, 2008) is more rounded and more posterodorsally inclined. The subnarial process 168 (maxillary process) is relatively complete and of triangular-shape tapering posterodorsally in 169 lateral view, resembling that of Ceratosaurus, Neovenator, and Sinraptor in relative size and 170 orientation. The subnarial process in Acrocanthosaurus and Allosaurus is elongated 171 dorsoposteriorly, whereas in *Duriavenator* this process is horizontally elongated without the dorsal 172 inclination. The posteroventral rim of the subnarial process is confluent with the posterior border 173 174 of the premaxillary body, and both form the slightly posterodorsally inclined suture with the maxilla in lateral view. The posterior border of the premaxillary body ventral to the subnarial 175 process presents a rugose surface and indicates the overlying of the maxilla (Fig. 4 B). There is no 176 evident subnarial foramen near the posterior border of the premaxillary body and subnarial 177 178 process, whereas the subnarial foramen is well developed in *Allosaurus*, *Acrocanthosaurus*, Sinraptor, and other theropods. Based on the suture of the premaxilla with the maxilla, there is no 179 subnarial gap between these two bones, and the tooth row of each bone is continuous and at the 180 same level, as in most allosauroids. 181 Numerous foramina are mainly scattered on the lateral surface ventral to the mid height of the 182 premaxillary body and open ventrolaterally, similar to the distribution pattern in Sinraptor and 183 Yangchuanosaurus, whereas in many megalosaurids (Dubreuillosaurus, Torvosaurus and 184 *Marshosaurus*) the foramina are mainly distributed on the anterior half of the premaxillary body. 185 In *Neoventor*, the foramina spread evenly over the lateral surface of the premaxillary body. 186 Recent research (Carr et al., 2017; Barker et al, 2017; Cullen et al, 2023) proposed that these 187 foramina in terrestrial theropods probably house branches of trigeminal nerve linking to 188 integumentary sensory organs, which are related to foraging, intraspecific communication and nest 189 building behavior. 190

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Maxilla—Both the left and right maxillae are adhered to the matrix, and thus the medial surface is obscured. The main body of the left maxilla (Fig. 4 E, F) is well-preserved but lacks most of its ascending ramus. The posterodorsally oriented base of the ascending ramus of the right maxilla (Fig. 4 G, H) is preserved, but the anterodorsal margin of the lateral surface is missing. The anteroposterior length of the preserved part of the left maxilla is measuring 28.87 cm, and the right element is 29 cm.

197 element is 29 cm.

- On the lateral surface, the ventral wall of the external antorbital fossa is very developed, occupying more than half of the maxillary body ventrally, as in *Masiakasaurus* (*Carrano et al., 2011*),
- 200 Marshosaurus (Madsen, 1976b), and many allosauroids (Currie & Zhao, 1993; Dong et al., 1983;
- 201 Gao, 1999; Madsen, 1976a, Sereno & Brusatte, 2008). This is different from the moderate range



of the antorbital fossa wall reaching nearly half depth of the maxilla body in Afrovenator (Serreno 202 et al., 1994), Acrocanthosaurus (Eddy & Clark., 2011), Neovenator (Brusatte et al., 2008), and 203 Ceratosaurus (Madsen & Welles, 2000). In contrast, the antorbital fossa has very limited exposure 204 on the maxillary body in Torvosaurus (Britt, 1991; Hendrickx & Mateus, 2014), Wiehenvenator 205 (Rauhut et al., 2016), Monolophosaurus (Zhao & Currie, 1993; Brusatte et al., 2010a), and some 206 Carcharodontosarurids (Sereno et al., 1996; Coria & Salgado, 1995; Coria & Currie, 2006; 207 Brusatte & Sereno, 2007). Some abelia surids even totally lack the antorbital fossa on the maxillary 208 body like Majungasaurus (Sampson & Witmer, 2007) and Kryptops (Sereno & Brusatte, 2008). 209 210 The border of the antorbital fossa is better preserved and well-defined by a rim on the left maxilla, while this rim is less developed on the right maxilla due to compression. The antorbital fossa is 211 anteriorly extensive, whose anterior-most border reaches the 3rd alveolus, as in *Sinraptor (Currie* 212 & Zhao, 1993) and Ceratosaurus (Madsen & Welles, 2000), indicating a reduced anterior ramus. 213 214 Above the 3rd tooth the rim gently curves upward, forming a round anteroventral margin of the antorbital fossa as in Sinraptor (Currie & Zhao, 1993), Yangchuanosaurus (Dong et al., 1983), 215 Ceratosaurus (Madsen & Welles, 2000), Marshosaurus (Madsen, 1976b), and Monolophosaurus 216 (Brusatte et al., 2010a). This contrasts with the squared anteroventral border of the antorbital fossa 217 in Eocarcharia (Sereno & Brusatte, 2008), Acrocanthosaurus (Eddy & Clarke, 2011), and 218 219 Dubreuillosaurus (Allain, 2002). Posteriorly this rim flattens gradually throughout the length of the posterior ramus. 220 The preserved ascending ramus of the right maxilla preserves the anteroventral margin of the 221 external antorbital fenestra. From the ventral margin of the antorbital fenestra, the preserved 222 223 ascending ramus is measuring 6.95 cm. The angle between the main axis of the ascending ramus and the jugal ramus of the maxilla is not very sharp, and about 60°. The lateral surface of the 224 225 ascending ramus of the right maxilla is too fragmentary to determine whether it is excavated by pneumatic openings (Fig. 4 G, H). 226 Although the ascending rami are heavily damaged on both maxillae, traces of two openings at the 227 base of the ascending ramus are preserved. On the left maxilla, the anterior concavity on the 228 anterodorsal margin of the maxillary body is smooth, demarcates the ventral rim of the 229 promaxillary fenestra, and its anterior end is adjacent to the anteroventral margin of antorbital 230 fossa. The posterior one only preserves its rounded ventral half. On the right maxilla, the anterior 231 opening only preserves its posterior rim while the posterior one is nearly intact. These two 232 233 openings are separately interpreted as promaxillary fenestra and maxillary fenestra here based on their relative placement (Witmer, 1997). The preserved portion of the promaxillary fenestra 234 indicates that it is larger than the maxillary fenestra, which resembles the condition in Sinraptor 235 (Currie & Zhao, 1993) and Eocacharia (Sereno & Brusatte, 2008). Relatively large promaxillary 236 fenestra is regard as a synapomorphy of Metriacanthosauridae (Carrano et al., 2012), in many other 237



theropod (Allosaurus, Neovenator, Ceratosaurus, Dubreuillosaurus; Currie & Zhao, 1993; 238 Brusatte et al., 2008; Madsen & Welles, 2000; Allain, 2002) the promaxillary feenstra is slit-239 shaped and blocked by lateral wall of maxilla from lateral view. A discrete rounded promaxillary 240 fenestra is present in Acrocanthosaurus (Eddy & Clarke, 2011), Marshosaurus (Madsen, 1976b), 241 and some coelurosaurs (Xu et al., 2006; Brusatte et al., 2009). The promaxillary and maxillary 242 fenestrae seem to merge into one opening in Carcharodontosaurinae (Hendrickx et al., 2015). 243 The ventral margin of the maxilla is slightly convex, with one row of neurovascular foramina 244 aligning right above and in parallel with it, similar to those present in Sinraptor (Currie & Zhao, 245 246 1993), Allosaurus (Madsen, 1976a), and Monolophosaurus (Brusatte et al., 2010a), in contrast to two rows of neurovascular foramina present in Marshosaurus (Madsen, 1976b), Shaochilong 247 (Brusatte et al., 2010b), and Eocarcharia (Sereno & Brusatte, 2008). The foramina dorsal to the 248 anterior four alveoli opens anteroventrally, then the orientation of subsequent foramina gradually 249 250 turns more posteroventrally. Each foramina opens ventrally into a depression but is less extensively than the band-like depress in Ceratosaurus (Madsen & Welles, 2000). After the 10th 251 alveolus, the foramina merge into a discontinuous longitudinal groove. 252 12 and 10 functional teeth are preserved on the left and right maxilla, respectively. Based on the 253 vacant space, each maxilla is estimated to bear at least 14 alveoli, similar to the condition in many 254 Allosauroids (Currie & Zhao, 1993; Madsen, 1976a; Dong et al., 1983). Each tooth is 255 mediolaterally compressed and strongly curved backward. Both mesial and distal carinae are 256 serrated, and the well-preserved nineth maxillary tooth bears 15 and 20 denticles per 5 mm on the 257 distal and mesial carinae, respectively (Fig. 4 D). The distal carina continues to the base of the 258 crown, but the mesial carina reaches less than half length of the crown from the tip, which is a 259 260 common condition in theropod. Among these preserved functional teeth, the fourth tooth is the biggest in both left and right maxillae and reach the axial length of 4.60 cm in left and 3.99 cm in 261 right. The 3rd tooth of the premaxilla, which is the biggest premaxillary tooth, is similar in size to 262 the first maxillary tooth, and manifests that the size of the teeth is continuous from the premaxilla 263 to the maxilla. This case differs from the noticeable reduction in size of the posterior premaxillary 264 265 teeth in Spinosauridae.

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Lacrimal—The right lacrimal is preserved relatively complete (Fig. 5 A, B), whereas the left one lacks most of its dorsal part (Fig. 2 A, B). The dorsoventrally height of the lacrimal is 12.08 cm. The ventral ramus of lacrimal contacts the anterodorsal process of jugal, and forms most of the anterior rim of the orbit. The transverse width of the ventral process constricts at its mid-height, and expends anteroposteriorly through the rest ventral part until it sutures with jugal. The posteroventral margin of antorbital fenestra is broken, so it impossible to determine whether the lacrimal contacts the maxilla. The angle between disconnected ventral ramus of lacrimal and the



jugal ramus of maxilla is approximately 120° (Fig. 2 C, D), such a blunt angle might be caused by 274 the preservation. The anterior ramus lacks most of its anterior end, but the posterodorsal margin 275 of antorbital fenestra is preserved. The remnant base of the anterior ramus and ventral ramus meet 276 at an angle slightly more than 90°. 277 278 The ventral ramus is formed by two laminae as in most other tetanurans: the lateral and the medial. The ridge defined by the boundary of these two laminae forms the posteroventral margin of the 279 antorbital fossa and continues to the jugal. The lateral lamina protrudes anteriorly into the 280 antorbital fenestra at the 2/3 height of the ventral ramus, and separates the antorbital fossa on 281 282 lacrimal into dorsal and ventral part as in Allosaurus (Madsen, 1976a), Monolophosaurus (Brusatte et al., 2010a), and Acrocanthosaurus (Currie & Carpenter, 2000). In contrast, in 283 Torvosaurus (Britt, 1991) the antorbital fossa is continuous on anterior and ventral ramus of 284 lacrimal. 285 286 The posterodorsal part of the lacrimal bears a small, blunt, triangular boss, which lengthened 2.23 cm with rugosity distributed on its dorsal and ventral lateral surface, proportionally larger than the 287

The posterodorsal part of the lacrimal bears a small, blunt, triangular boss, which lengthened 2.23 cm with rugosity distributed on its dorsal and ventral lateral surface, proportionally larger than the small boss seen in *Torvosaurus* (*Britt, 1991*), but much less prominent than the distinct lacrimal horn of *Allosaurus* (*Madsen, 1976a*) and *Ceratosaurus* (*Madsen & Welles, 2000*). A weak flange is right below the posterodorsal boss of lacrimal, resembling that of *Ceratosaurus* (*Madsen & Welles, 2000*) and *Sinraptor* (*Currie & Zhao, 1993*). In many carcharodontosaurids (*Acrocanthosaurus, Giganotosaurus, Mapusaurus:Eddy & Clarke, 2011; Coria & Salgado, 1995; Coria & Currie, 2006*) this flange is more pronounced and forms a process, which marks the lower limit of the eye socket.

Two pneumatic openings excavate the main posterodorsal body of the lacrimal, located at the posterodorsal rim of antorbital fossa. And a third foramen is about 0.8 cm below the larger posterior opening, and falls within the region of antorbital fossa. This combination of foramina is also seen in *Allosaurus* (*Madsen, 1976a*).

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Jugal—The anterodorsal border of jugal are broken on both left and right sides, so it is unclear whether the jugal separates the maxilla and lacrimal and slightly contributes to the antorbital fenestra. The remnant jugal is 17.42 cm long on left (Fig. 5 G, H) and 16.40 cm on right side (Fig. 5 C-F). The anterior ramus of jugal rises dorsally into the lacrimal ramus to contact the lacrimal, and contributes to the anteroventral rim of orbit. Immediately posterior to the base of the anterior ramus the postorbital ramus of jugal is 7.02 cm high from the bottom of orbit on the right side, and contributes to the posteroventral margin of the orbit. The postorbital ramus rises abruptly, forms a steep angle with the jugal body. These two rami result in an acute ventral margin of the orbit, similar to the condition in *Sinraptor (Currie & Zhao, 1993)*, *Yangchuanosaurus (Dong et al., 1983)*, and *Allosaurus (Madsen, 1976a)*. Beneath the ventral rim of the orbit, the dorsoventral



- depth of jugal is 3.3 cm on the left and 2.91 cm on the right.
- Posteriorly, the quadratojugal ramus of jugal bifurcates into an upper branch overlapping the
- anterior ramus of the quadratojugal and a lower branch lying below the quadratojugal as in most
- 313 theropod, but differs from the triradiate posterior ramus of Sinraptor (Currie & Zhao, 1993). In
- better preserved right jugal (Fig. 5 D), the upper branch is slightly shorter than the lower branch,
- which differs from the much shortened upper branch seen in *Allosaurus* (Madsen, 1976a) and
- 316 Monolophosaurus (Brusatte et al., 2010a). The quadratojugal ramus strongly turns upwards on the
- right side, and results in the convex ventral rim of lateral temporal fenestra. This exaggerating
- 318 curvature is more likely the distortion caused by compression. In contrast, on the left side the
- quadratojugal ramus curves slightly downwards near the tip of the upper and lower branches (Fig.
- 320 5 G, H).
- 321 The posteroventral rim of the antorbital fossa is well-developed on jugal, and the rim is demarcated
- by a ridge which is continues onto the ventral ramus of lacrimal. At the base of this ridge, the
- 323 lateral surface of jugal is smooth, and differs from the pneumatic openings seen in Sinraptor
- 324 (Currie & Zhao, 1993) and Monolophosaurus (Brusatte et al., 2010a). Beneath the postorbital
- ramus, near the bottom of the left jugal, the lateral surface is penetrated by a small and flat foramen
- 326 (Fig. 5 H), but this foramen is absent on the right side. This might be considered as break, but a
- similar foramen is present in *Sinraptor*.

- **Quadratojugal**—Both left and right quadratojugals are preserved, the left one (Fig. 5 C-F) is of
- heavy damage on its lateral surface, while the right one (Fig. 5 I) lacks most of its dorsal ramus.
- 331 The quadratojugal is L-shaped in lateral view, and compressed mediolaterally as in most
- theropods. The left quadratojugal is 11.88 cm long and 6.48 cm high, while the right one is 12.96
- cm long and 0.73 cm thick.
- In lateral view, the ventral margin of the quadratojugal is convex, similar to the condition in
- 335 Ceratosaurus (Madsen & Welles, 2000) and Sinraptor hepingensis (Gao, 1992, 1999). The
- posterior end of the bone forms a triangular process oriented posteriorly. The lateral surface of the
- quadratojugal is smooth, with a slight depression (Fig. 5 C, D) extending throughout the base of
- the dorsal ramus and occupy roughly 2/3 ventral depth of the main body. The anterior process
- tapers anteriorly and is wedged into the upper and lower branches of the posterior ramus of the
- 340 jugal. The anterior process extends to be level with the anterior border of the lateral temporal
- 341 fenestra, more anteriorly than those of Allosaurus (Madsen, 1976a) and Sinraptor dongi (Currie
- 342 & Zhao, 1993), but falls shorter than the condition in Monolophosaurus (Brusatte et al., 2010a).
- 343 The dorsal process is preserved on the left quadratojugal, but most of its external surface is broken.
- The remnant dorsal process takes the form of triangular, and tapers dorsally. The articulation with
- the squamosal is not definitive due to the latter's missing.

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In the medial view, the posterior end of the quadratojugal bears slight rugosity, which might be the contact with the quadrate as in *Allosaurus*. Anterior to this rugosity, a deep fossa excavates into the posterior end with a rounded rim (Fig. 5 E, F), and the bony wall is thin as a lamina corresponding to the concave lateral surface.

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Postorbital—Only the right postorbital has been preserved, and lacks most distal part of its posterior ramus (Fig. 6 A, B). In lateral view, the postorbital is T-shaped in outline consisting of the orbital, posterior and ventral rami. The postorbital measures 9.83 cm in dorsoventrally height and 6.17 cm in anteroposteriorly length from the orbital ramus to the broken base of the posterior ramus.

The postorbital projects anteriorly to form a sheet-shaped process (Fig. 6 A, B), differing from the 356 prominent orbital boss as seen in other derived metriacanthosaurids (Dong et al., 1978, 1983; Gao, 357 358 1992; Currie & Zhao, 1993; Rauhut et al., 2024). From the beginning of the juncture of orbital ramus and ventral ramus of the postorbital, the orbital ramus is 2.69 cm long. Through this planar 359 orbital ramus, the postorbital contacts the frontal medially, and forms the orbital roof along with 360 prefrontal, lacrimal and a slight part of frontal as in Sinraptor (Currie & Zhao, 1993) and 361 Allosaurus (Madsen, 1976a). In contrast, the frontal or prefrontal is excluded from the orbital rim 362 due to the postorbital-lacrimal articulation as in Carcharodontosaurus (Sereno et al., 1996) and 363 Eocarcharia (Sereno & Brusatte, 2008). The orbital ramus maintains a relatively constant 364 thickness with the deepest portion measured 0.99 cm. This constant thickness of the orbital process 365 of postorbital in Yuanmouraptor also differs from conditions in Torvosaurus (Britt, 1991) and 366 Eustreptospondylus (Sadleir et al., 2008), in which the orbital processes increase the dorsoventral 367

depth gradually backwards. 368 The ventral ramus of the postorbital is transversely widened and anteroposteriorly tapered to the 369 distal end, with a prominent lamina (Fig. 6 A-D) running along its posterior border, differing from 370 U-shaped posterior rim of postorbital in many megalosauroids (*Torvosaurus*; 371 Eustreptospondylus; Wiehenvenator: Britt, 1991; Sadleir et al., 2008; Rauhut et al., 2016). 372 373 Through the ventral part of this lamina the postorbital contacts the postorbital ramus of jugal. The upper half of the ventral ramus extends posteroventrally, then the lower half turns downwards with 374 its tip curves backwards, resulting in gently sigmoidal profile in lateral view. The anterior rim of 375 the ventral ramus is smooth and concave, and there is no evidence of any anteriorly projecting 376 377 intraorbital process which defines the ventral border of eyeball as in Acrocanthosaurus (Eddy & Clarke, 2011), Carcharodontosaurus (Sereno et al., 1996), Majungosaurus (Sampson & Witmer, 378 2007). A shallow trough begins at the anterodorsal rim of the orbit, then twists to face laterally on 379 the ventral ramus and shallows ventrally, which is considered as an autapomorphy of 380

Yuanmouraptor.

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The roof of the postorbital body expands laterally into a longitudinal ridge, ventral to which the lateral surface of main body forms a shallow depression (Fig. 6 B). This longitudinal ridge continues onto the posterior ramus of postorbital, and marks the lateral rim of the supratemporal fossa. The remnant of posterior ramus is mediolaterally thin, and its cross section tapers dorsolaterally to form the ridge. The posterior ramus is deflected at an angle of nearly 70° from the posteroventrally pointed ventral ramus.

In dorsal view (Fig. 6 E, F), a medial process contacts frontal anteriorly and laterosphenoid posteromeidally, forms the anterolateral border of the supratemporal fenestra. Between the frontal and laterosphenoid, this process also has a very limited contact with the lateral projection of parietal, similar to the condition of *Sinraptor* (*Currie & Zhao, 1993*). The supratemporal fossa is shown as a shallow, poorly-defined depression, and its anterior rim is formed by postorbital together with frontal, parietal and laterosphenoid.

Prefrontal—The prefrontal is a small element located between lacrimal and frontal, partly lacks its anterior end (Fig. 6 E, F). The remnant prefrontal measures 5.15 cm in length, 2.70 cm in width and 1.88 cm in depth. Due to the damage, the prefrontal is displaced posteriorly relative to frontal, and overlapps the mediodorsal surface of the lacrimal. The nasal is poorly preserved, thus the articulation between the prefrontal and the nasal is not definitive.

In dorsal view, the frontal is sub-rhomboid in outline, and contacts lacrimal laterally and frontal medially, but sutures of these articulations are all broken. The dorsal surface of prefrontal is planar and smooth. The prefrontal's posterolateral rim, which contributes to the orbital roof, is slightly rugose as in *Sinraptor* (*Currie & Zhao, 1993*), this rugosity might continue onto the lacrimal boss. Unlike the fusion with other bones or lateral covering of the lacrimal in carcharodontosaurids and ceratosaurs (*Sereno et al., 1996*; *Sereno & Brusatte, 2008*; *Sampson & Witmer, 2007*), the prefrontal of *Yuanmouraptor* is exposed laterally on the dorsal rim of orbit and forms a supraorbital notch together with frontal, postorbital and lacrimal, a condition close to that in *Allosaurus* (*Madsen, 1976a*), *Sinraptor* (*Currie & Zhao, 1993*), and *Monolophosaurus* (*Brusatte et al., 2010a*).

Frontal—The paired frontals (Fig. 6 E, F) are wedge-shaped in outline in dorsal view, and articulate each other through the suture on the midline, though the structure of this suture is deformed due to the compressional distortion. Both left and right frontals are preserved, but lack their anterior end, thus the articular surface with nasal is not definitive. The right frontal is relatively complete, about twice as long as it is wide, and measures 10.82 cm in length and 5.77 cm in width. Whereas the left frontal lacks its posterolateral part.

In dorsal view, the frontal contacts the prefrontal anteromedially, the postorbital posterolaterally



and the parietal posteromedially. The frontal reaches its great mediolateral width at a point level with its contact with the postorbital, resembling that in *Sinraptor* (*Currie & Zhao, 1993*) and *Allosaurus* (*Madsen, 1976a*). In contrast, the frontal of *Eustreptospondylus* (*Sadleir et al., 2008*) is widest at the supraorbital notch. Prior to the contact with the postorbital, the transverse width of the frontal shrinks abruptly to contribute to the supraorbital notch, this also occurs in *Sinraptor* and *Allosaurus*. At the anterior rim of the supraorbital notch, the frontal expands laterally to form the contact with the prefrontal, then the frontal tapers anteriorly. The dorsal surface of the frontal is smooth, and its posterolateral part was occupied by a poorly-defined shallow recess, which is continues with the recess on the postorbital and contributes to the anterior rim of supratemporal fossa. Although the suture between paired frontals is broken, there is no sign of a midline ridge as displayed in *Shaochilong* (*Brusatte et al., 2010b*). Posteriorly, the suture with the parietal is interdigitating medially and roughly straight laterally, resembles that of *Sinraptor*, *Allosaurus* and *Shidaisaurus* (*Wu et al., 2009*).

Parietal—The paired parietals are fused, and lack most of their posterodorsal part (Fig. 6 E, F). The remnant parietal is similar to that of *Sinraptor* (*Currie & Zhao, 1993*) and *Shidaisaurus* (*Wu et al., 2009*) in outline, and measures 6.69 cm in length and 8.24 cm in width. In dorsal view, the parietal contacts the frontal through an interdigitating suture anteriorly. Posterior to the contact with the frontal, the parietal expands laterally to form two slender projections, contacting the posterolateral part of frontal in transversely straight suture. The tips of these projections reach the postorbital and overlap the laterosphenoid. The dorsal surface between the projections is dorsally convex, and differ from the additional bone deposition which protrudes laterally into the supratemporal fenestra as in *Sinraptor*. Behind these projections the parietal constricts transversally and measures as 2.84 cm in width. Due to the serious damage present on the posterodorsal part of the parietal, the existence of nuchal crest and the border between the parietal and the supraoccipital is not definitive.

Squamosal—Only the right squamosal has been preserved (Fig. 7 A-E), but deviates strongly from the original position, with its anterior and ventral end obscured by sediment. As in many theropods, the squamosal of *Yuanmouraptor* comprises four processes: the anterior process contacting the posterior ramus of the postorbital; the ventral process that extends ventrally to cover the quadrate laterally and contact the ascending process of quadratojugal; the medial process underlapping the parietal; and a posterior process that envelopes the paroccipital process anterolaterally.

In dorsal view (Fig. 7 A, B), the preserved part of squamosal measures 6.24 cm in maximum length and 6.62 cm in width. The dorsal surface of the squamosal is smooth and slightly concave, and



subtriangular in outline. The obscuration of the postorbital and sediment preclude the observation 454 of the medial border of the dorsal surface of the squamosal, which contributes to the posterolateral 455 rim of the supratemporal fenestra. The lateral rim of dorsal surface is demarcated by a ridge (Fig. 456 7 B) which extends posteriorly from the remnant of the anterior process then recurves medially at 457 the base of the posterior process. The articular surfaces for the parietal and the paroccipital together 458 form the posterior border of the squamosal (Fig. 7 D). The medial process protrudes 459 anteromedially and is slightly convex posteromedially. The coarse surface of the medial process, 460 which is not continuous with the dorsal surface of the bone, indicates its contact with the parietal. 461 462 Anteromedial to the posterior process, the articular surface for the tip of the paroccipital process is posteriorly concave and dorsoventrally deep, then becomes posteriorly flat and constricts in 463 depth to continue onto the base of the medial process. 464 In lateral view (Fig. 7 E), the remnant anterior process measures 3.36 cm in length, bears evident 465 466 dorsal and ventral rim, and the former contributes to the border of the concavity on the dorsal surface. The remnant ventral process measures 3.25 cm in depth and inclines anteroventrally. 467 Together the anterior and ventral processes of the squamosal form the posterodorsal rim of the 468 lateral temporal fenestra, these two processes are at an angle of broadly 70°. In contrast, this angle 469 is blunter in basal-branching tetanurans such as Sinraptor (Currie & Zhao, 1993), Allosaurus 470 (Madsen, 1976a), Afrovenator (Sereno et al., 1994), and Eustreptospondylus (Sadleir et al., 2008). 471 The tip of the posterior process projects 1.89 cm posteriorly from the main body of the squamosal, 472 and differs from the posteroventrally oriented posterior process of Sinraptor (Currie & Zhao, 473 1993), Allosaurus and Monolophosaurus (Brusatte et al., 2010a). The lateral surface of the 474 posterior process of the squamosal is rugose and pitted, might for the attachment of ligament. 475 In posterior view (Fig. 6 C, D), the squamosal is dorsoventrally deep along the contact with the 476 exoccipital, and reaches its maximum depth near the posterior process, but becomes shallow 477 toward its medial process. The bottom of the articulate surface for the paroccipital process is 478 concave ventrally, might houses the quadrate head. 479

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Quadrate—Both the left and right quadrate are seriously damage, the former (Fig. 7. F-H) lacks most of its dorsal part and the latter (Fig 2. D) only preserves partial pterygoid flange. The bottom of the left quadrate is well-preserved, with measuring 4.69 cm in mediolateral width, and is separated by an anteromedially oriented intercondylar sulcus into the entocondyle and the ectocondyle (Fig. 7 H). The ectocondyle is larger, which is similar to the condition in *Allosaurus*, but contrasts with that of *Eustreptospondylus* (*Sadleir et al., 2008*) and *Ceratosaurus* (*Madsen & Welles, 2000*) in which the entocondyle is rather larger. The ectocondyle is 2.79 cm wide mediolaterally while the entocondyle is 2.5 cm wide. The long axes of the ento- and ectocondyles are anteromedially oblique in broadly same direction, but slightly more medially directed than the



degree of the intercondylar sulcus. The anterior end of each condyle is at approximately the approximate level, which contrasts with the strongly anterior protruding entocondyle in *Torvosaurus* (*Britt*, 1991) and *Eustreptospondylus*. In lateral view, both mandibular condyles extend anteriorly to form a concavity dorsal to them, while the posterior rim of the remnant quadrate is straight along the shaft.

Palatine—The incomplete left palatine is preserved (Fig. 7 I, J) and lacks most of its posterior processes, with its medial surface obscured by matrix. Whereas the right palatine is present by a bar-like bone, and its structure is impossible to identify. The palatine takes the form of a saddle, with the central part of the bone is lowest in dorsoventral depth. As preserved the palatine is 11.23 cm long anteroposteriorly, 4.5 cm deep dorsoventrally at the vomeropterygoid process, and 2.64 cm deep at the waisted region of the main body.

The anterior vomeropterygoid and maxillary processes are preserved, together define the posterior limit of the internal naris choana. The vomeropterygoid process lacks its distal end, and inclines mediodorsally at its base, then becomes more anteriorly oriented, thus the medial rim of the coana is concave laterally. The maxillary process is more robust than the vomeropterygoid process, and extends anteriorly with a laterally convex surface. The articular surface with the maxilla of the palatine is not definitive due to the damage. In lateral view, a shallow fossa is present at the base of the maxillary process, immediately posterior to the internal naris choana. This fossa might mark the pneumatic recess of palatine, but does not penetrate the surface of bone and lead to the inner space as in *Sinraptor (Currie & Zhao, 1993)* and *Acrocanthosaurus (Eddy & Clarke, 2011)*. A similar fossa is present in *Neovenator (Brusatte et al., 2008)*, but it is located more posteriorly at the juncture of the jugal and medial process.

Supraoccipital—The supraoccipital is seriously broken, with most of its dorsal part missing. The preserved part of the supraoccipital (Fig. 8 A, B) is 2.73 cm deep dorsoventrally and 5.19 cm wide transversely at its base. Despite the heavy damage, the preserved base of the supraoccipital indicates a prominent ridge running on the midline, and flanked by a pair of vertical grooves. Lateral to the paired grooves the bone extends posterolaterally and might continue onto the probable nuchal crest of parietal. The base of the middle ridge is triangular in shape, tapers dorsally, and expands transversely based on the dorsal fracture. The ventral rim of supraoccipital makes a slight contribution to the dorsal border of the foremen magnum as in *Sinraptor* (*Currie & Zhao, 1993*), *Acrocathosaurus* (*Eddy & Clarke, 2011*), *Monolophosaurus* (*Zhao & Currie, 1993*), and *Piatnitzkysaurus* (*Rauhut, 2004*), and this contribution measures 0.83 cm in breadth. On the left side of the base of the bone, there are two foramina penetrates the external surface, but on the opposite side the surface is smooth. The symmetrical paired foramina positioned lateral to the

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midline near the base of supraoccipital are generally referred as exits for external occipital vein 526 (Currie & Zhao, 1993), vena capitis dorsalis (Coria & Currie, 2002; Rauhut, 2004; Brusatte & 527 Serreno, 2007; Eddy & Clarke, 2011) or vena cerebralis media (Sampson & Witmer, 2007). The 528 asymmetrical foramina present in supraoccipital in *Yuanmouraptor* might be caused by pathology 529 or taphonomic process. The supraoccipital expands laterally at its ventral margin to contact 530 otoccipitals. 531

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Otoccipital (Exoccipital-Opisthotic) — The main body of the exoccipital-opisthotic complex is well-preserved, but the tips of left and right paroccipital processes are missing (Fig. 8 D, E). A possible suture between the exoccipital and opisthotic is present. In all preserved vertebrae the neural arch is attached to the centrum and the absence of neurocentral suture in most of them, indicating that this individual is nearly mature or subadult, thus this suture-like boundary is more likely caused by damage. In posterior view (Fig. 8 D, E), the paired exoccipitals are separated by the supraoccipital above the foramen magnum. Then the exoccipitals form the lateral and ventral margin of the foramen magnum, and meet each other at a midline suture throughout the dorsal surface of the occpital condyle. The foramen magnum is 2.47 cm transversely wide and 1.32 cm dorsoventrally high, proprotionally broader than that of Sinrapor (Currie & Zhao, 1993) and Allosaurus (Madsen, 1976a). The paroccipital process is posterolaterally directed, and slightly turns downwards, contrasts more sharply downturned condition with Sinrapor (Currie & Zhao, 1993) and Allosaurus (Madsen, 1976a). The ventral limit of the base of process levels with the bottom of the occipital condyle, as in Allosaurus, Sinraptor, and Piatnitzkysaurus (Rauhut, 2004), but contrasts more dorsally placed ventral base of the paroccipital process with *Dubreuillosaurus* (Allain, 2002), Eustreptospondylus (Sadleir et al., 2008), and Leshansaurus (Li et al., 2009). A depressed area (Fig. 8 C) lies between the paroccipital process and the base of occipital condyle, and houses three foramina for cranial nerves. Among these foramina, the dorsal one is for the vagus (X) and

accessory (XI) cranial nerves, the medioventral one and the lateroventral one is for the two 552 553 branches of the hypoglossal nerve (XII). The ventral part of the exoccipital-opisthotic tapers 554

ventrally, and overlaps the basioccipital laterally at the boundary between the basioccipital and the

basisphenoid. The suture with the basioccipital extends from the base of the occipital condyle to 555

the basal tubera. 556

557 In lateral view (Fig. 9 A, B), the anterodorsal corner of the exoccipital-opisthotic is coverd by the prootic, and the exoccipital-opisthotic forms the posterior boundary of the fenestra ovalis 558 approximately ventral to the crista prootica. The posteroventral rim of the paroccipital process, 559 formed by the metotic strut, is strongly concave posteriorly, and separates lateral and posterior 560 surfaces of the braincase. The suture with the basisphenoid is posteroventrally inclined and slightly 561



562 posteriorly concave.

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573 574 **Prootic**—The prootic is mainly exposed on the lateral surface (Fig. 9), and the right prootic is better preserved than the left one, with a complete prootic pendant. The prootic contacts the laterosphenoid anteriorly, and posterior to the contact a shallow recess is present. Ventral to the suture with the laterosphenoid, a longitudinal groove runs through the ventral part of the prootic. Approximately posterior to the groove, a single foramen penetrating the bone houses the cranial nerve VII, differs from two openings for the cranial nerve VII in Eustreptospondylus (Sadleir et al., 2008). The opening for trigeminal (V) nerve originates in the anterior-most part of the prootic and is even bounded by the laterosphenoid anteriorly in many tetanurans such as Sinraptor (Currie & Zhao, 1993), Eustreptospondylus, Dubreuillosaurus (Allain, 2002), Monolophosaurus (Brusatte et al., 2010a), and Piatnitzkysaurus (Rauhut, 2004), but in Yuanmouraptor this part is obscured by the sediment, preventing the further observation.

The prootic contact the exoccipital-opisthotic posteroventrally with a jagged suture. A prominent 575 crista prootica (Fig. 9 B) marks the posteroventral margin of the prootic. Above the crista prootica 576 the prootic is contiguous with the base of paroccipital process and overlaps the exoccipital-577 opisthotic laterally. The prootic forms the anterior boundary of the fenestra ovalis with the 578 exoccipital-opisthotic forming the posteroventral boundary, approximately ventral to the crista 579 prootica. Anteroventral to the fenestra ovalis, a slight process sits at the boundary between the 580 exoccipital-opisthotic and basisphenoid, and protrudes posteroventrally, similar to that in 581

582 Sinraptor.

> The ventral part of the prootic mainly overlaps the basisphenoid laterally with the prootic pendant, and the space between the pendant and exoccipital-opisthotic is infilled by sediment.

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Basioccipital—The basioccipital is mainly exposed in the posterior view (Fig. 8 D, E), and its central ventral part is incomplete. The basioccipital occupies more than 60 percent of the occipital condyle. The occipital condyle is evidently wider (3.28 cm) than tall (2.3 cm), with rounded and smooth articular surface. Unlike in Sinraptor (Currie & Zhao, 1993), Allosaurus (Madsen, 1976a), and Eustreptospondylus (Sadleir et al., 2008), the basioccipital of Yuanmouraptor does not contribute to the foramen magnum, and the paired exoccipitals meet each other in the midline. Ventral to the neck of the occipital condyle, a shallow fossa is present, and the surface below the neck is posteriorly concave and smooth, but is not as well-defined as the subcondylar recess seen in *Piatnitzkysaurus* (Rauhut, 2004). The ventral rim of the basioccipital on the right side probably represent the basal tuber, though it is not very apparent due to the damage. The remnant basal tuber is level with the ventral limit of exoccipital-opisthotic, in contrast to the unusual condition of Sinraptor, in which the exoccipital-opisthotic extends significantly more ventrally than the basal



tubera. Differs from the relatively narrow width between the basal tubera in *Sinraptor*, *Allosaurus*, and *Monolophosaurus* (*Zhao & Currie*, 1993), the transverse width across the basal tubera is broader than the transverse diameter of the occipital condyle in *Yuanmouraptor*. The suture with the basisphenoid is visible near the basal tubera and could only be observed on the right side.

Basisphenoid—The basisphenoid could be mainly observed on the right side (Fig. 9). Its ventral structures such as the basisphenoid recess and the basipterygoid process are obscured by other bones and sediment. In lateral view, the basisphenoid contacts the exoccipital-opisthotic through a posteriorly curved suture. The suture with the basioccipital is visible on the tip of the basal tubera. The dorsal part of the basisphenoid is overlapped by the prootic. Only the base of the cultriform process is exposed, and the remnant of it is obscured by matrix.

Laterosphenoid—Both left and right laterosphenoids are preserved, but most of their ventral parts are either damaged or obscured by matrix. The laterosphenoid forms the anterior wall of the brancase, and is surrounded dorsally by the parietal, posteriorly by the prootic and laterally by the postorbital. The contact with the forntal is not definitive due to the bloking of the surrounding articulated bones. The laterosphenoid is visible in dorsal and laterodorsal views(Figs 6, 9), and forms the anteromedial rim of the supratemporal fenestra.

Dentary—Dentaries are preserved on both left and right side, but their posterior boundaries are broken, so the suture with the surangular and angular is not clear. The relatively complete right dentary (Fig. 2 C, D) is 34.1 cm long and reaches minimum depth (4.17 cm) at the level of the fourth alveolus. In lateral view, the main part of the upper margin is straight, but a step appears at nearly the fourth dentary teeth leading to a slight dorsoventral expansion as in Eustreptospondylus (Sadleir et al., 2008). In contrast to the square anteroventral rim of dentary in Giganatosaurus (Coria & Salgado, 1995), the tip of the ventral rim of dentary in Yuanmouraptor is rounded. The lower margin of the dentary is concave and inclines more ventrally at the 11th alveolus, posterior to which the dentary body expands vertically throughout its posterior half length. An array of slightly undulate neurovascular foramina (Fig. 10 A, B) excavates the external surface of the bone below anterior seven tooth. Posterior to and level with these foramina, a longitudinal groove extends from the 11th alveolus along the rest dentary and runs upward gradually. Several smaller foramina scatter over the anteroventral margin of the lateral surface. The function of these neurovascular foramina on the dentary might be the same as those on the premaxilla and maxilla. Most of the left and the right dentaries adhere to the matrix or other bones, only a bit of medial surface of the left dentary is observable but poorly-preserved (Fig. 2 D). Through this limit expose of medial surface, two unfused interdental plates are preserved on the exposed medial surface, and



takes form of sub-triangular, as in Sinraptor (Currie & Zhao, 1993), Dubreuillosaurus (Allain, 2002), Marshosaurus (Madsen, 1976b), and Eustreptospondylus (Sadleir et al., 2008). Ventral to the interdental plates a trough represents the paradental groove, which demarcates the ventral border of the interdental plates. A replacement tooth occurs between these two interdental plates, and an unerupted tooth is exposed on the broken surface near the damaged interdentary symphysis, exhibiting serrated distal carina. The Meckelian groove appears as a narrow trough on the remnant dentary, and the foramina anterior to it as in Sinraptor (Currie & Zhao, 1993) and Allosaurus (Madsen, 1976a) might be damaged. The relatively well-preserved left dentary (Fig. 10. A, B) bears nine functional teeth, from gaps among which, at least 14 alveoli are estimated. 14-17 teeth are present in other derived Late Jurassic allosauroids such as Sinraptor (Currie & Zhao, 1993), Yangchuanosaurus (Dong et al., 1983), and Allosaurus (Madsen, 1976a). Similar to the condition in maxillary teeth, the distal carina of dentary teeth continues form the base to the tip while the mesial carina develops along less than half of the teeth from the apex. The dentary teeth are generally smaller in size than maxillary tooth with the largest dentary teeth measures 2.73 cm high. Dentary teeth also have greater curvature than those of maxillary and premaxillary teeth.

Splenial—Only the right splenial is observable, and is poorly-preserved, with most of its anterior part obscured by other elements and the posterior boundary damaged (Fig. 10 E, F). Caused by the compression during burial, the bone covers the anterior end of the prearticular medially. The bone forms a posteroventrally tapering process and its anteroventral rim is slightly concave and smooth.

Surangular—The left surangular (Fig. 10 C, D) are better preserved than the right one, while the latter is heavily compressed dorsoventrally, and the anterior end of each one are obscured or damaged (Fig. 2). The right surangular measures 27.26 cm anteroposteriorly, and its suture with the dentary is not clear due to the compression.

Anterolateral to the contact with the articular a longitudinal surangular ridge (Fig. 10 D) is present

Anterolateral to the contact with the articular, a longitudinal surangular ridge (Fig. 10 D) is present approximately below the dorsal margin of the surangular. The ridge ends posteriorly with a dorsal concavity, which laterally demarcates the lateral glenoid contacting the ectocondyle of the quadrate. Posterior to the lateral glenoid the surangular forms a U-shaped notch deeper than the lateral glenoid, which contributes to the retroarticular process together with the articular, and is similar to but dorsoventrally deeper than that of *Sinraptor* (*Currie & Zhao, 1993*) and *Acrocanthosaurus* (*Eddy & Clarke, 2011*). The posterolaterally opened posterior surangular foramen is exhibited posteroventrally to the surangular ridge and ventrolaterally to the mandibular joint, and a second foramen is found further anteriorly. This resembles that of *Sinraptor* but contrasts with the condition in *Monolophosaurus* (*Brusatte et al., 2010a*), in which the surangular



ridge is absent and the posterior surangular foramen is roofed by an unexpanded and smooth surface.

The surangular forms most of the dorsal and posterior rim of the external mandibular fenestra. At the posteroventral corner of the external mandibular fenestra, the surangular is overlapped laterally by the bony wall formed by the angular. Medially the surangular have a hook like process (Fig. 10 E, F), which forms an angle of nearly 60° with the long axis of the surangular and contacts the prearticular ventrally (Fig. 11 C, D). The posterior rim of the hooked process extends laterally and contributes to dividing the glenoid into two parts. In medial view (Fig. 10 E, F), the surangular thickens transversely to form a bar like dorsal rim, which demarcates the dorsal limit of the adductor fossa. The M. adductor mandibulae externus is estimated to attach the concave surface between this bar and the surangular ridge.

Angular—The left angular lacks most of its anterior part (Fig. 10 C, D), and the right angular is strongly dorsoventrally compressed. The angular forms the posteroventral part of the mandible, it thins dorsally to cover the surangular, and thickens ventrally to overlap the ventral margin of the prearticular, which forms the ventral border of the adductor fossa. The angular is dorsally concave, and forms the ventral rim of the external mandibular foramen. The remnant angular reaches the maximum depth at its central part of the contact with the surangular.

Prearticular—The right prearticular could be observed in medial view (Fig. 10 E, F). The bone is a ventrally bowed element, it dorsoventrally flares at its anterior and posterior ends, but constricts in depth at its central part. The medial surface of the remnant prearticular is obscured by angular anteriorly and surangular posteriorly. The anterior part of the ventral rim of the prearticular is surrounded ventrally by the thickened angular. Whereas posterior to the contact with the angular, the ventral rim of the angular is exposed in lateral view as in *Sinraptor* (*Currie & Zhao, 1993*) and *Acrocanthosaurus* (*Eddy & Clarke, 2011*). The posterodorsal part of the prearticular forms a dorsomedially directed triangular process, which contacts the hooked process of surangular dorsolaterally (Fig. 11 C, D). Posterior to this process the prearticular forms a dorsally concave embayment, which houses the articular.

Articular—The right articular is well-preserved and still in articulation with the prearticular and surangular (Fig. 11). The retroarticular process is well-developed and has a concave dorsal surface, which is dorsally oriented and bordered by sharp ridge, in contrast, this surface faces more posteriorly in *Allosaurus* (*Madsen, 1976a*) and *Acrocanthosaurus* (*Eddy & Clarke, 2011*). In lateral view (Fig. 11 A, B), the lateral rim of the retroarticular process surpasses the lateral wall of the surangular and exposes laterally. In dorsal view, the posterior end of the retroarticular process



is U-shaped in outline, then the process constricts its lateral rim abruptly and then expands medially at its anterior part, forming a lateral notch and a medial blunt process. This medial blunt process is contiguous with the medial rim of the medial glenoid, and the opening for the chordra tympani penetrates it from its posterodorsal surface to its ventral surface. Anteriorly a prominent ridge separates the medial glenoid and retroarticular process as in *Sinraptor* (*Currie & Zhao, 1993*), this ridge is more eminent in *Acrocanthosaurus* (*Eddy & Clarke, 2011*).

General description of the axial skeleton

All vertebrae are well-preserved but none of them bears a rib. Of them the first 10 vertebrae were considered as belonging to the cervical series and the 11th was speculated to be the first dorsal vertebra based on the common condition of 10 cervical vertebra in basal-branching tetanurans (*Holtz et al., 2004*) and the diapophysis of the eleventh vertebra that is more laterally expanded than the preceding one as is the case in *Sinraptor* (*Currie & Zhao, 1993*) and *Yangchuanosaurus* (*Dong et al., 1983*). The neurocentral suture is only partly visible on the eighth and ninth cervicals, indicating that this individual is an adult or subadult.

Atlas-Axis—In the atlas-axial complex (Fig. 12), the atlantal intercentrum is in articulation with the axial intercentrum and odontoid. The proximal parts of both the left and right neurapophyses are still attached to the atlantal intercentrum and are positioned laterally to the neural canal. There is no evident prezygopophysis on the neurapophysis, indicating the absence of the proatlas as in Sinraptor (Currie & Zhao, 1993). The exposed part of the atlantal intercentrum is similar to that of Shidaisaurus (Wu et al., 2009) and Sinraptor (Currie & Zhao, 1993). In anterior view, the main body of the atlantal intercentrum is slightly wider than deep. The ventrolateral rim is slightly convex, and the ventral rim becomes flat, resulting a sub-rectangular profile of the lower half. The anterior articular surface is concave, for the articulation with the occipital condyle. The dorsal rim of the atlantal intercentrum is ventrally depressed and underlaps the rounded ventral part of odontoid.

The odontoid adheres to the upper half of the anterior articular surface of the axial centrum, and its boundaries with the atlantal intercentrum and axial centrum are visible. The odontoid is divided into a dorsal and an anterior surface by an anteriorly convex rim, and this rim is approximately parallel with the ventral border which contacts the atlantal intercentrum. The dorsal surface of odontoid is dorsally concave and continuous with the floor of the neural canal. The anterior surface arches anteriorly to pass through the dorsal margin of the atlantal intercentrum. A single shallow recess is located laterally on each side of the anterior surface of the odontoid, which differs from the foramina penetrating the same position as these recesses in *Neovenator* (*Brusatte et al., 2008*). In anterior view the odontoid is in shape of semicircle, similar to the condition in *Allosaurus*



(Madsen, 1976a) and Monolophosaurus (Zhao et al., 2009). 742 The axial intercentrum is not observable in anterior view (Fig. 11 C) due to the obscuration of the 743 articulated atlantal intercentrum. In lateral view (Fig. 11 E), the axial intercentrum tapers 744 posterodorsally to form a sub-triangular lateral outline as in Neovenator (Brusatte et al., 2008), 745 Piatnitzkysaurus (Bonapart, 1986), and Yunyangosaurus (Dai et al., 2020). In contrast, the axial 746 intercentrum maintains a constant anteroposterior thickness dorsoventrally, resulting a sub-747 rectangular outline in lateral view in Sinraptor (Currie & Zhao, 1993) and Ceratosaurus (Madsen 748 & Welles, 2000). The suture between the axial intercentrum and centrum is slightly inclined 749 750 anteroventrally, similar to the condition present in Sinraptor (Currie & Zhao, 1993), but in contrast with nearly vertical suture in Allosaurus (Madsen, 1976a), Neovenator (Brusatte et al., 2008), 751 Piatnitzkysaurus (Bonapart, 1986), and Yunyangosaurus (Dai et al., 2020). The ventral surface of 752 the axial intercentrum is flat and ventrally faced, continuous with the ventral surface of the axial 753 754 centrum in lateral view as in Ceratosaurus (Madsen & Welles, 2000), Dilophosaurus (Marsh & Rowe, 2020), Majungasaurus (O'Connor, 2009), Piatnitzkysaurus (Bonaparte, 1986), and 755 Yunyangosaurus (Dai et al., 2020), but differs from Sinraptor (Currie & Zhao, 1993), 756 Monolophosaurus (Zhao et al., 2009), Neovenator (Brusatte et al., 2008), and Acrocanthosaurus 757 (Harris, 1998), in which the ventral surface of the axial intercentrum is nearly horizontal. In ventral 758 759 view (Fig. 11 B), the suture between the intercentrum and centrum is well exposed and arches anteriorly. 760 The axial centrum is longer ventrally than it is dorsally, a similar condition in Sinraptor (Currie & 761 Zhao, 1993). The anterior articular surface is mostly obscured by the odontoid and axial 762 intercentrum. The posterior articular surface is strongly concave, and is as approximately wide as 763 high. In lateral view, the ventral rim of the centrum strongly arches dorsally, and forms an acute 764 angle with the posterior articular surface as in Sinraptor (Currie & Zhao, 1993). The diapophysis 765 is located at the base of the neural arch, just above the centrum, and is present as a lateroventrally 766 oriented pedicle. Anteroventral to the diapophysis the parapophysis protrudes posteroventrally to 767 form a diminutive hump. The lateral surface of centrum is smooth and there is no trace of any 768 pneumatic structure. This contrasts with many allosauroids (Currie & Zhao, 1993; Brusatte et al., 769 2008; Harris, 1998), in which pleurocoels invade the main body of the centrum ventral to the 770 diapophysis. The central part of the centrum tapers its transverse width downwards, resulting an 771 mediolaterally narrow and flat ventral surface as is the case in Yunvangosaurus (Dai et al., 2020). 772 773 This differs from the centrum that bears pronounced ventral keel in *Acrocanthosaurus* (*Harris*, 1998). The transversely narrow and ventrally tapering ventral surface of axial centrum without 774 ventral keel was considered as an autopomorphy of Yunyangosaurus (Dai et al., 2020). 775 The prezygopophyses are obscured by neurapophyses on both left and right sides (Fig. 11 E, F). 776 The postzygopophyseal facets of the axial centrum are well-developed, comparable in size to those 777



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of postaxial cervicals. The V-shaped intrapostzygopophyseal lamina (tpol) medially connects paired postzygopophyses dorsal to the neural canal. The developed epipophysis extends posterodorsally from the distal end of the postzygopophysis and curves laterally. A well-developed axial epipophysis also occurs in Shidaisaurus (Wu et al., 2009), Sinraptor (Currie & Zhao, 1993). The neural spine is transversely thin and posterodorsal inclined. In lateral view, the neural spine deflects at an angle of 50° with the neural canal throughout its ventral half, then the degree of inclination decreases abruptly in rest dorsal part. This transition in the degree of deflection is probably caused by breakage. Prior to the base of neural spine, a rounded eminence rises dorsally, similar to the condition in Neovenator (Brusatte et al., 2008) and Yunyangosaurus (Dai et al., 2020). The anterior end of the neural spine is positioned posterior to the anterior margin of the neural canal, this contrasts the strongly anteriorly flared neural spine in *Dilophosaurus (Marsh &* Rowe, 2020). The spinopostzygopophyseal lamina expands laterally from the neural spine and fills the space between its summit and the epipophysis, resembling that of Sinraptor (Currie & Zhao, 1993; Gao, 1993, 1999), Yangchuanosaurus (Dong et al., 1983), Dilophosaurus (Marsh & Rowe, 2020), and Yunyangosaurus (Dai et al., 2020). In posterior view (Fig. 11 D), an anteriorly excavated and subtriangular fossa is surrounded by the spinopostzygopophyseal lamina and postzygopophyses, such fossa also occurs in Sinraptor (Currie & Zhao, 1993; Gao, 1992, 1999), Yangchuanosaurus (Dong et al., 1983), Ceratosaurus (Madsen & Welles, 2000), and Dilophosaurus (Marsh & Rowe, 2020).

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Postaxial vertebrae—The third to fifth cervical centra are opisthoceolous with dorsally arched ventral surface. In remnant elements of the cervical series the anterior articular surface becomes flat or slightly convex, and their corresponding posterior articular surface becomes less concave, resulting the platycoelous centra. The centra of the postaxial cervicals are anteroposteriorly longer than dorsoventrally high, whereas the length/height ratio gradually decreases posteriorly through the cervical series. A distinct rim (Fig. 13 A-C) is present on the anterior articular surface of the anterior cervicals, and it is especially well defined on the third cervical. This distinct rim also occurs on anterior cervicals of *Yunyangosaurus* (*Dai et al., 2020*), whereas all the postaxial cervical vertebrae bear such rim in *Torvosaurus* (*Britt, 1991*). In all postaxial cervicals, the anterior and posterior articular surfaces are slightly wider than high.

The lateral surface of each of the postaxial cervical centra is excavated by a single pleurocoel, which is positioned posterodorsal to the parapophysis. In the third cervical (Fig. 13 A) the pleuroceol deeply invades the lateral surface of the centrum, leading to a very transversely narrow ventral surface (Fig. 14 C) of central part. But this narrowing ventral surface does not run through the whole length of centrum to form a ventral keel. The ventral surfaces of following cervical vertebrae become broad and flat and by the 10th cervical vertebra the ventral keel appears with a



ventrally vaulted process anterior to it. In the fourth and fifth cervical, the pleuroceol is leading to 814 the neural canal. In the eighth and ninth cervical the pleuroceol is anteroposteriorly elongated and 815 dorsally roofed by a thin lamina. 816 The diapopysis of each postaxial cervical is lateroventrally extended, and bears a smooth articular 817 surface with ellipse profile. The parapophysis is positioned ventral to the mid-height of the centrum 818 and adjacent to the anterior articular surface in each cervical. In the third and the last two cervicals 819 the parapophysis is strongly shortened and ended with oval-shaped surface, whereas it protrudes 820 lateroventrally in other cervicals. The laterally elongated parapophyses in medial cervicals also 821 822 occur in Neovenator (Brusatte et al., 2008). In the last cervical the parapophysis is followed by a prominent ridge, which marks the bottom of the pleurocoel and shallows posteriorly. 823 The prezygopophysis projects anteriorly from the base of diapophysis, and is connected with the 824 diapophysis laterally through the prezygodiapophyseal lamina (prdl). The paired prezygopophyses 825 826 are well separated dorsolateral to the neural arch, and are medially connected by the intraprezygopophyseal lamina (tprl). The prezygopophysis has a sub-ellipse shaped and smooth 827 articular facet, which faces anterodorsally and medially. The spinoprezygopophyseal lamina (sprl) 828 laterally demarcates this facet, and connect the prezygopophysis with the neural spine. Throughout 829 the whole cervical series this facet turns more anteromedially, and the anteroposterior distance 830 831 between pre- and postzygopophysis gradually shortens. The posterodorsally and laterally projected postzygopophysis is more strongly developed than the prezygopophysis, with lateroventrally and 832 posteriorly faced articular surface. In the last three cervicals (Fig. 13 F-H), the postzygopophyseal 833 facets turn to face more posteriorly than that of the preceding elements in the series. The 834 postzygodiapophyseal lamina (podl) runs from the base of the diapophysis posteriorly to the distal 835 836 end of the postzygopophysis or epipophysis. The spinopostzygopophyseal lamina (spol) originates posteriorly form the base of the neural spine and ends at the distal end of the articular surface of 837 the postzygopophysis. Only the first three postaxial cervicals have well developed epipophysis, 838 which emerges posterolaterally and dorsally to the postzygopophysis. In fourth and fifth cervical 839 the epipophysis is extended well beyond the posterior margin of the postzygopophysis and forms 840 841 a dorsoventrally thin plate-like structure. In the third and fourth cervical (Fig. 13 A, B), the anterior rim of the neural spine bears an 842 anterodorsal oriented process, resulting the concave lateral profile above and below this process. 843 Such process positioned at the anterodorsal rim of the anterior cervicals also occurs in 844 845 Acrocanthosaurus (Harris, 1998), but in which this process protrudes more anteriorly and past the base of neural spine. The posterior rim of the neural spine of these two elements is posterodorsally 846 convex, thus the posteriormost point is situated at nearly midheight. In subsequent cervicals the 847 neural spine increases in height gradually, and is dorsoventrally higher than anteroposteriorly long 848 since the sixth cervical. In the eighth, ninth and tenth cervicals (Fig. 13 F-H) the neural spine is 849



prominently dorsally elongated, with the distal end fanning out anteroposteriorly in lateral view. 850 Whereas in derived metriacanthosaurids (Dong et al., 1983; Currie & Zhao, 1993; Gao, 1992, 851 1999), neural spines in posterior cervical vertebrae are slender and rod-like, this condition might 852 provide more spaces for upward mobility of the neck. In ninth (Fig. 14 G-I) and 10th cervicals, a 853 shallow groove runs dorsoventrally along the anterior and posterior rims of the neural spine. 854 Several bony laminae connect the neural arch and the centrum and separate the space between 855 them into several pneumatic chambers as in most Theropods. In the first five postaxial cervicals 856 the anterior centrodiapophyseal lamina (acdl) and centraprezygopophyseal lamina (cprl) are not 857 858 very developed and laterally obscured by the ventrally oriented diapophyses. Due to the short distance between the neural arch and centrum in anterior cervicals, the centrapostzygopophyseal 859 laminae of these elements are poorly-developed. In the rest of the cervical series the distance 860 between the arch and centrum increases with the elevation of the diapophysis from the 861 862 parapophysis, resulting that aforementioned three bony laminae become more prominent. In the first three postaxial cervicals the postzygodiapophyseal laminae (podl) do not continue onto the 863 pedicle of the diapophyses. In the third cervical this lamina is especially weak-developed and even 864 discontinuous to the base of the postzygopophysis. In the last three cervicals, a pneumatic fossa 865 excavates anteriorly into the ventral surface of the postzygodiapophyseal lamina (podl), as in 866 Sinraptor (Currie & Zhao, 1993). All postaxial cervicals bear notable prezygodiapophyseal 867 laminae (prdl) and posterior centradiapophyseal laminae (pcdl). 868 The first dorsal vertebra (Fig. 13 I) is platycoelous, with a flat anterior articular surface and a 869 slightly concave posterior articular surface. The anterior and posterior articular surface are slightly 870 wider than high as in cervical vertebrae. The neural arch and the centrum of the first dorsal vertebra 871 are in further distance compared to those in the cervical vertebrae. This extension is followed by 872 the more elongated bony laminae connecting the neural arch and the centrum. The diapophysis is 873 more laterally and horizontally oriented instead of pointing ventrolaterally. The parapophysis does 874 not protrude laterally and its articular surface is immediately lateral to the anterior articular surface 875 of the centrum and subtriangular in shape. The pre- and postzygopophysis decreases in height, 876 followed by the reduction of inclination of the pre- and postzygodiapophyseal lamina in lateral 877 view. The neural spine is approximately 1.5 times as dorsoventrally high as anteroposteriorly long. 878 with a sub-rectangular lateral profile. The groove running along the anterior rim of the neural spine 879 excavates deeper than those of former cervical vertebrae. As in postaxial cervicals, a single 880 881 pleurocoel penetrates either side of the centrum, but these pelurocoels on both left and right side are straightly connected without any bony walls. The ventral part of the centrum is similar to that 882 of the last cervical vertebra, with a ridge originated from the posterior end of the parapophysis 883 forming the lateral floor of the peurocoel, and a developed ventral keel running through the 884 885 centrum.



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Phylogenetic analysis

The phylogenetic analysis resulted in 1152 MPTs, with each MPTs having a length of 1290 steps (CI = 0.364, RI = 0.660). The strict consensus tree (Fig. 14) places Yuanmouraptor at the most 'basal' position in the Metriacanthosauridae, forming a polytomy with *Xuanhanosaurus* and a monophyletic group defined by Yangchuanosaurus and Sinraptor. The Metriacanthosauridae in our analysis is supported by seven unambiguous synapomorphies: squamosal forms a flange covering quadrate head laterally (character 87-1); acute angle between the occipital condyle and the basal tubera (character 123-1); external mandibular fenestra is 15% longer than the total mandible length (character 133-1); dorsoventral depth of surangular above external mandibular fenestra less than half of the height of mandible (character 134-0); well-developed and broad spinopostzygopophyseal lamina (character 183-0); manus shorter than arm plus forearm (character 268-0); presence of metacarpal IV but lack of IV phalanges and whole digit V (character 269-0). Furthermore, three major lineages of basally branching tetanurans (Megalosauroidea, Coeluerosauria, and Allosauroidea) are supported by this phylogenetic analysis, and recovered a Carnosauria in which Piatnitzkysauridae forms the sister-group to Avetheropoda (Allosauroidea + Coelurosauria).

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DISCUSSION

Comparison with Jurassic Metriacanthosauridae in China and morphology transition within Metriacanthosauridae lineage

As shown in the result of our phylogenetic analysis, the metriacanthosaurids excluding 907 Xuanhanosaurus (Dong, 1984) and Yuanmouraptor formed two lineages together to form a 908 clade Metriacanthosauridea. In other 909 monophyletic within words, Yuanmouraptor,

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Xuanhanosaurus, and the clade formed a basal trichotomy within Metriacanthosauridae. The Middle Jurassic Xuanhanosaurus (Dong, 1984) was considered to fall within 911 Megalosauroidea or in close relationship with Piatnitzkysauridae in previous studies (Benson, 912 2010; Rauhut et al., 2016; Rauhut & Pol, 2019; Dai et al., 2020). In our phylogenetic analysis, 913 Xuanhanosaurus was recovered as a member of Metriacanthosauridae, as in Carrano et al. (2012), 914 915 but this placement is poorly supported with only two characters: relatively short manus and developed metacarpal IV with lack of IV phalanges and digit V, shared with CNM V214 (Dong et 916 al., 1983) and 'Szechuanosaurus' zigongensis (Gao, 1993) respectively. Therefore, the 917 phylogenetic position of *Xuanhanosaurus* still needs to be testified by a detailed study of the taxon 918 919 in the future. The overlapping materials of *Xuanhanosaurus* with *Yuanmouraptor* are limited to two posterior cervical vertebrae. The eighth cervical centrum of *Xuanhanosaurus* is evidently 920



opisthocoelous, in contrast with the platyceolous condition in that of Yuanmouraptor. Due to the 921 uncertain phylogenetic position of *Xuanhanosaurus*, *Yuamouraptor* is considered as the most basal 922 representative of Metriacanthosauridae. 923 Sinraptor dongi (Currie & Zhao, 1993), S. hepingensis (Gao, 1992, 1999), and Yangchuanosaurus 924 shangyouensis (Dong et al., 1978, 1983) represent derived members in Metriacanthosauridea and 925 all lived in Late Jurassic. Materials of these taxa reach a high degree of completeness, and provide 926 significant taxonomic information. These three taxa are large-sized theropods, and the skull length 927 could reach approximately two times the condition in Yuanmouraptor. In S. dongi, S. hepingensis, 928 929 and Y. shangyouensis, the skull and vertebrae are highly pneumatized, such as the pneumatic foramen on the lateral surface of the jugal and perforated pleurocoels on the axial centrum. 930 Whereas in *Yuanmouraptor* the jugal and axial centrum are not pneumatized. The ventral process 931 of the postorbital of three derived metriacanthosaurids has a small suborbital flange, which might 932 933 mark the ventral limit of the eyeball, whereas in Yuanmouraptor the ventral process of the postorbital is smooth and slightly concave below the eyeball. All three derived metriacanthosaurids 934 bear rugose ornaments on the upper part of the skull, such as heavy rugosity on the nasal, well-935 developed lacrimal horn, and large rugose boss forming the anterior process of the postorbital. 936 Though the nasal of *Yuanmouraptor* was not preserved, the lacrimal and postorbital only possess 937 938 slight rugosity. The cervical vertebrae of derived metriacanthosaurids are strongly opisthocoelous with ball and socket articular surface, and the axial intercentrum is anterodorsally flexed. This 939 940 condition shows greater mobility than that of *Yuanmourpator*, in which the cervical vertebrae are platycoelous and the ventral surface of the axial intercentrum is continuous with that of the 941 centrum. The anteroposteriorly narrow neural spines in posterior cervical vertebrae also indicate a 942 943 more upward flexible neck in derived metriacanthosaurids. By contrast, the sheet-like neural 944 spines of posterior cervical vertebrae in Yuanmouraptor might limit the upward flexibility of the neck. 945 Within the monophyletic clade excluding Yuanmouraptor and Xuanhanosaurus in the 946 Metriacanthosauridae, one lineage leads to Yangchuanosaurus (Dong et al., 1978, 1983), and 947 another lineage is represented by Sinraptor (Gao, 1992; Currie & Zhao, 1993). The clade 948 comprising the members of the latter lineage was named as Metriacanthosaurinae by Carrano et 949 al. (2012). These two lineages are distinct in many aspects. In the axial skeleton, the anterior dorsal 950 vertebrae of Metriacanthosaurinae have prominent ventral keel, whereas in another lineage the 951 952 keel is weakly developed. In the pelvic girdle, the angle between the long axis of pubis and pubic boot is less than 60° in Metriacanthosaurinae, distinguished from the nearly perpendicular boot 953 and shaft of the pubis in Yangchuanosaurus lineage. In Metriacanthosaurinae the ischial shaft is 954 ventrally curved and the distal end is slightly expended, which differs from that the ischial shaft is 955 straight and the distal end of ischium is notably expended to form an ischial boot in 956



Yangchuanosaurus lineage. Whereas the distal end of the ischium of Yangchuanosaurs 957 shangyouensis is slightly expended and similar to the condition in Metriacanthosaurinae, might 958 suggesting that this trait is gained independently in these taxa. In the hindlimbs, members of 959 Metriacanthosaurinae possess bulbous fibular crest on the tibia, in contrast to the narrow and 960 lamina-like fibular crest of the tibia in *Yangchuanosaurus* lineage. 961 Shidaisaurus (Wu et al., 2009) was found in Chuanjie Formation (Middle Jurassic) in Lufeng City, 962 Yunnan, which is 85 km from the type locality of Yuanmouraptor. Shidaisaurus was the first 963 tetanuran reported in Yunnan Province. The skull roof, dorsal part of the occiput, and axis of 964 965 Shidaisaurus are preserved, and these elements could be compared with Yuanmouraptor. Both Yuanmouraptor and Shidaisaurus possess paired frontals broader than long, which generally occur 966 in Allosauroidea; however, in Megalosauroidea and more basal therapods, the paired frontals are 967 anteroposteriorly longer than transversely wide. Similar to Shidaisaurus, a slight margin of the 968 969 frontal contributes to the dorsal margin of the orbit in *Yuanmouraptor*, this also occurs in *Sinraptor* dongi (Currie & Zhao, 1993). The supratemporal fossa of Shidaisaurus is bounded by abruptly 970 elevated surfaces of the frontals and parietal, which form a very clear border of the supratemporal 971 fossa, this is similar to the condition in Sinraptor dongi (Currie & Zhao, 1993). Whereas in 972 Yuanmouraptor, the border of the supratemporal fenestra does not have well-defined boundary, 973 974 and the surfaces of the surrounding frontals and parietal are plain and gently sloped. The occiput of *Shidaisaurus* and *Yuanmouraptor* share a similar posteroventrally directed paroccipital process, 975 with the ventral base of which located beneath the occipital condyle, a condition generally 976 developed in Allosauroidea. However, the supraoccipital of Yuanmouraptor forms a moderate part 977 of the dorsal rim of the foramen magnum, differing from *Shidaisaurus* in which the supraoccipital 978 979 does not contribute to form the dorsal margin of the foramen magnum. An atlas-axis complex is the only preserved cervical element of *Shidaisaurus*. The axial centrum of *Shidaisaurus* bears 980 some similarities to that of Yuanmouraptor, including broad spinopostzygapophyseal lamina and 981 absence of pleurocoels. The axial intercentrum of *Shidaisaurus* has an anterodorsal inclined ventral 982 surface, followed by an anterodorsally faced anterior articular surface, which resembles the 983 984 condition in derived metriacanthosaurid Yangchuanosaurus (Dong et al., 1983) and Sinraptor (Currie & Zhao, 1993). However, the alignment of the atlas-axis complex is different in 985 Yuanmouraptor, in which the ventral surface of the axial intercentrum is parallel with the axial 986 centrum, but the anterior articular surface of the axial intercentrum also faces anterodorsally, 987 988 resulting in a triangular lateral profile of the axial intercentrum. This indicates that *Yuanmouraptor* could also bring the neck underneath the occipital condyle more or less to support the skull as more 989 derived Late Jurassic metricanthosaurids, and might represent an early stage of the arrangement of 990 the atlas-axis complex during the evolution of Metriacanthosauridae. Although Yuanmouraptor 991 and Shidaisaurus share similar geological distribution and approximately contemporaneous 992



stratigraphic unit which were known as Middle Jurassic (Huang et al., 2005; Fang et al., 2008), 993 the difference in morphology along with the support of our phylogenetic analysis shows the 994 validity of *Yuanmouraptor jinshajiangensis* gen. et sp. nov. 995 The Late Jurassic CNM V214 (Dong et al., 1983) and the Middle Jurassic 'Szechuanosaurus' 996 zigongensis (Gao, 1992) are also positioned as derived metriacanthosaurids by the phylogenetic 997 analysis and form a monophyletic group with Sinraptor dongi (Currie & Zhao, 1993), Sinrptor 998 hepingensis (Gao, 1992), and Yangchuanosaurus (Dong et al., 1978, 1983). The first reports of 999 CNM V214 and 'S.' zigongensis regarded them as the neotype of 'Szechuanosaurus' campi 1000 1001 (Young, 1942) and a new species of the genus 'Szechuanosaurus' respectively. The type species of genus 'Szechuanosaurus', 'S. campi', was based on four isolated teeth, and was considered as 1002 invalid (Wu et al., 2009; Carrano et al., 2012). Due to the lack of detailed restudies and 1003 phylogenetic analyses of these two specimens for decades, CNM V214 and 'S.' zigongensis have 1004 1005 not been given the formal taxonomic names so far. The information about CNM V214 is very limited, with part of the cervical series overlapping with Yuanmouraptor. The axial complex of 1006 CNM V214 is similar to that of S.dongi, S. hepingensis, and Yangchuanosaurus, with the 1007 anterodorsally tilted ventral surface of the intercentrum and well-developed pleurocoels on the 1008 centrum. The maxilla of 'S.' zigongensis is similar to that of Yuanmouraptor, with well-developed 1009 1010 antorbital fossa. However, the morphology of the posterior cervical vertebrae of 'S.' zigongensis resembles the condition in those Late Jurassic forms, in which the neural spines are 1011 1012 anteroposteriorly narrow and rod-like. Many character transitions occurred during the evolution of Metriacanthosauridae from the Middle 1013 Jurassic to the Late Jurassic. First, as shown in Yuanmouraptor, the basal-branching Middle 1014 1015 Jurassic members of this clade do not possess a well-developed pneumatic system as in those Late 1016 Jurassic descendants, such as the lack of pneumatic foramen on jugal and pleurocoels on axial centrum. The latter condition also occurs in basal-branching metriacanthosaurid Shidaisaurus (Wu 1017 et al., 2009). Second, the ornamentations of the skull have been changed from a slight rugose brow 1018 in Yuanmouraptor to a prominent lacrimal horn and heavy rugosity on postorbital in Sinraptor 1019 (Gao, 1992; Currie & Zhao, 1993) and Yangchuanosaurus (Dong et al., 1983). Third, the 1020 alignment of the atlas-axis complex and morphology of cervical vertebrae have been changed to 1021 improve the mobility of the neck. In the primitive stage, as shown in *Yuanmouraptor*, the ventral 1022 surface of the axial intercentrum and centrum are continuous, and subsequent cervical vertebrae 1023 1024 are platycoelous. This condition has been changed to that the ventral surface of axial intercentrum is notably inclined anterodorsally to bring the neck underneath the skull and cervical vertebrae are 1025 strongly opisthocoelous with ball-and-socket articular surface in Yangchuanosaurus and 1026 Sinraptor. Furthermore, to increase the upward flexibility of the posterior part of the neck, the 1027 neural spines of posterior cervical vertebrae altered from sheet-like in Yuamouraptor to rod-like 1028



in those Late Jurassic descendants. Two Middle Jurassic taxa, *Shidaisaurus* and 'Szechuanosaurus' zigongensis (Gao, 1993) could be regarded as transitional forms. In 'Szechuanosaurus' zigongensis (Gao, 1993), the neural spines of posterior cervical vertebrae are also anteroposteriorly constricted and nearly rod-like, but the articular surfaces of cervical centra are platycoelous. *Shidaisaurus* possesses anterodorsally inclined axial intercentrum, but lacks pleurocoels on the axial centrum.

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Implications on phylogeny of basal-branching tetanurans

Since three major lineages (Megalosauroidea, Allosauroidea, and Coelurosauria) within Tetanurae were proposed by Carrano et al. (2012), alternative opinions (Rauhut & Pol. 2019; Lamanna et al., 2020; Schade et al., 2023; Rauhut et al., 2024) upon the interrelationship of tetanurans were put forward in past decade. Although the result recovered by our phylogenetic analysis approaches to the three-major-clade pattern within Tetanurae, this topology of diverging is unstable with relatively low scores of Bremer support in many nodes (see the online Supplemental File S2 for details). Among the nodes within Tetanurae, Spinosauridae and Coelurosauria (with the exception of Lourinhanosaurus) are well-supported, with Bremer support scored 3. Besides, Allosauria (Allosauridea + Carcharodontosauria), and Metriacanthosaurinae (Carrano et al., 2012) are less well supported with Bremer support scored 2. However, the placement of Piatnitzkysauridae within the Allosauroidea is rather stable, with three additional steps needed to recover its affinity to Megalosauroidea. The low Bremer support of many nodes within Tetanurae might suggest that independent acquirements of characters occurred multiple times during Early and Middle Jurassic. At least eight taxa from western China are located near the node Allosauroidea by our phylogenetic analysis, but taxa of other clades of basal tetanurans in this region are scarce, this is probably due to the artificial effects rather than the reflection of real proportion of different clades within basalbranching tetanurans. The finding of Yuanmouraptor provides an example of early stage in tetanuran evolution. Many characters present in Yuanmouraptor are shared with megalosaurid theropods or non-tetanuran theropods, indicating that high level of similarities among these Early and Middle Jurassic theropods. Thus, findings of key taxa to bridge the gap between non-tetanuran ancestors and a variety of derived tetanuran clades are important to testify whether similar character states in different clades are the result of homology or homoplasy. Meanwhile, the construction and sampling of characters, accuracy of state scores, and issues of sampling are also strongly related to alleviate phylogenetic uncertainty (Lovegrove et al., 2024). The review and redescription of the named taxa are of great significance. There are still many taxa (Dong et al., 1978; He, 1984; Dong et al., 1983; Dong & Tang, 1985; Gao, 1992, 1993, 1999; Li et al., 2009) reported in China lacking detailed osteological descriptions. New anatomic information helping to resolve the phylogenetic problems will be extracted after the detailed re-examination and



description of those taxa in future works.

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CONCLUSIONS

A new metriacanthosaurid, Yuanmouraptor jinshajiangensis gen. et sp. nov, is established based 1068 on a relatively complete skull, a complete cervical series, and an anterior-most dorsal vertebra. 1069 Yuanmouraptor is diagnosed by a unique combination of characters, especially six 1070 1071 autapomorphies. Phylogenetic analysis placed Yuanmouraptor at a basal-branching position within Metriancanthosauridae. Although the type locality and living age of *Yuanmouraptor* 1072 resemble those of Shidaisaurus, many characters manifest that these two are different taxa. 1073 Yuanmouraptor presents the most complete craniums among basal-branching tetanurans reported 1074 1075 in Middle Jurassic China, and provides valuable information concerning the morphology transition of cranium and cervical vertebrae during the cause of metriacanthosaurid evolution. In addition, 1076 our phylogenetic analysis recovered that the phylogenetic position of Piatnitzkysauridae is more 1077 closed to Allosauroidea than to Megalosauroidea, and three major lineages within Tetanurae are 1078 supported. However, due to the lack of consensus upon the phylogenetic relationship within basal-1079 branching tetanurans over past decades, more accuracy in character coding and new findings of 1080 early members of this clade are needed to testify this new alternative phylogenetic topology. 1081

INSTITUTIONAL ABBREVIATIONS

- 1083 **CNM** Chongqing Natural History Museum;
- 1084 **LFGT** The Bureau of Natural Resources of Lufeng City, Yunnan, China.

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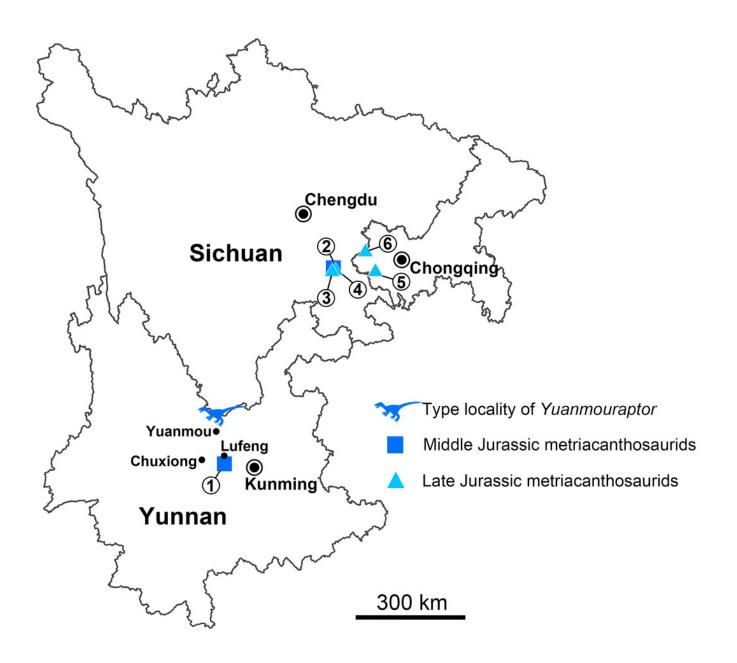
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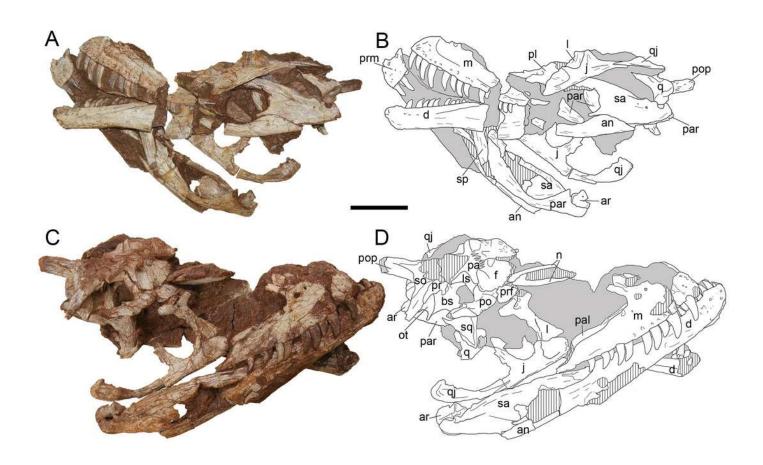
Geographical distribution of metriacanthosaurid theropods in Yunnan, Sichuan, and Chongqing, China.

Each number indicates an individual: 1, *Shidaisaurus jinae*; 2, '*Szechuanosaurus*' zigongensis; 3, CNM V214; 4, *Sinraptor hepingensis*; 5 & 6, *Yangchuanosaurus shangyouensis*.



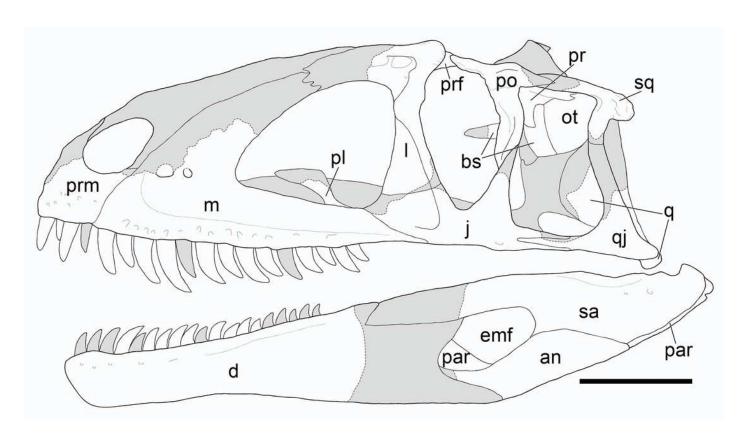
Cranium of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0015).

Cranium in (A) left lateral view with (B) labeled drawing and (C) right lateral view with (D) labeled drawing. Abbreviations: an, angular; ar, articular; bs, basisphenoid; d, dentary; f, frontal, j, jugal; l, lacrimal; lsp; laterosphenoid; m, maxilla; n, nasal; ot, otoccipital; prm, premaxilla; pa, parietal; par, prearticular; pl, palatine; po, postorbital; pop, paroccipital process; pr, prootic; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; so, supraoccipital; sq, squamosal. Striated area indicates damage and grey area indicates matrix. Scale bar represents 100 mm. Photos by Xiao-Chun Wu.



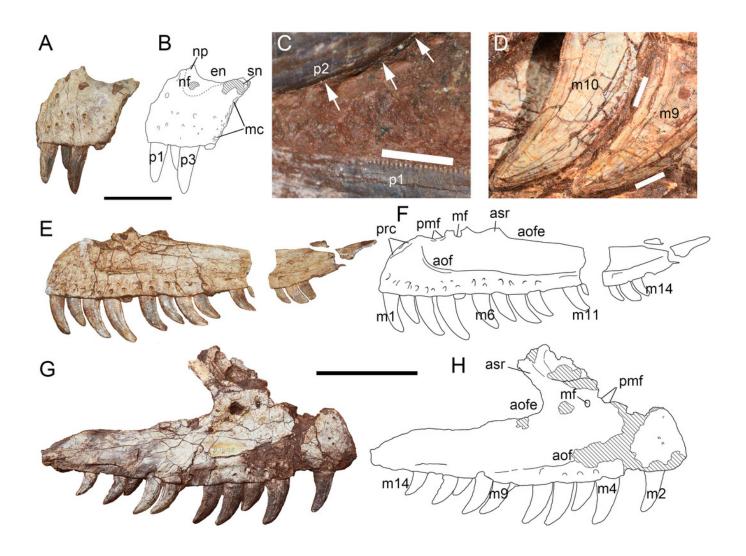
Reconstruction of the cranium of *Yuanmouraptor jinshajiangensis* gen. et sp. nov. (LFGT-ZLJ0015).

Abbreviations: an, angular; bs, basisphenoid; d, dentary; emf, external mandibular fenestra; j, jugal; l, lacrimal; m, maxilla; ot, otoccipital; prm, premaxilla; par, prearticular; pl, palatine; po, postorbital; pop, paroccipital process; pr, prootic; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal. Shaded area indicates the missing part, and dashed line marks the margin of breakage of bone. Scale bar represents 100 mm.



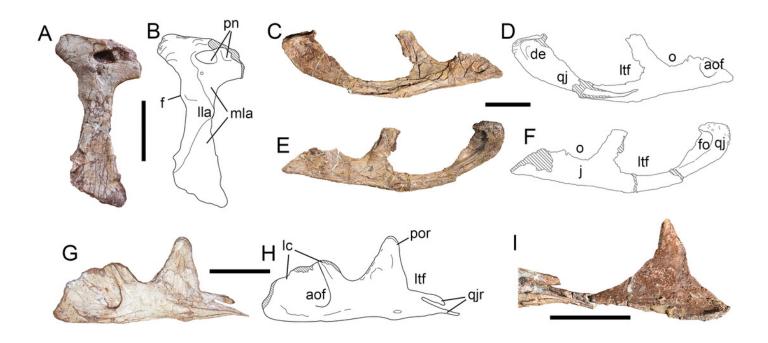
Premaxilla and maxilla of *Yuanmouraptor jinshajiangensis* gen. et sp. nov. (LFGT-ZLJ0015).

Left premaxilla in (A) lateral view with (B) labeled drawing. (C) Serration on the premaxillary teeth, with mesial carina pointed by white arrows. (D) Serration on the mesial and distal carina of the maxillary teeth. Left maxilla in (E) lateral view with (F) labeled drawing. Right maxilla in (G) lateral view with (H) labeled drawing. Abbreviations: aof, antorbital fossa; aofe, antorbital fenestra; asr, remnant ascending ramus of maxilla; en, external naris; mc, maxillary contact; mf, maxillary fenestra; m1-14, maxillary teeth 1-14; nf, narial fossa; np, nasal process; pmf, promaxillary fenestra; prc, premaxillary contact. p1-3, premaxillary teeth 1-3; sn, subnarial process. Striated area indicates damage. Scale bars for A-B present 50 mm, for C-D, 5 mm, and for E-H, 100 mm. Photos by Xiao-Chun Wu and Yi Zou.



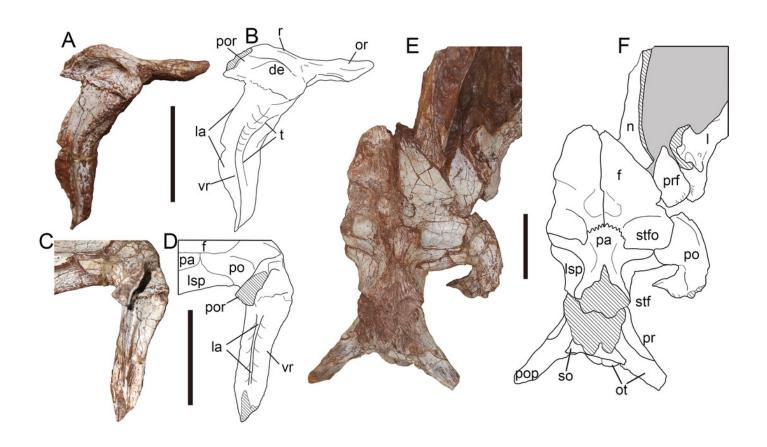
Skull elements of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0015).

Right lacrimal in (A) lateral view with (B) labeled drawing. Articulated right jugal and quadratojugal in (C) lateral view with (D) labeled drawing. Articulated right jugal and quadratojugal in (E) medial view with (F) labeled drawing. Left jugal in (G) lateral view with (H) labeled drawing. (I) Left quadratojugal and partial quadratojugal ramus of left jugal. Abbreviations: aof, antorbital fossa; de, depression; f, flange; fo, fossa; j, jugal; lc, lacrimal contact; lla, lateral lamina; ltf, lateral temporal fenestra; mla, medial lamina; o, orbit; pn, pneumatic foramen; por, postorbital ramus of jugal; qj, quadratojugal; qjr, quadratojugal ramus of jugal. Striated areas indicate damage. Scale bars present 50 mm. Photos by Xiao-Chun Wu and Yi Zou.



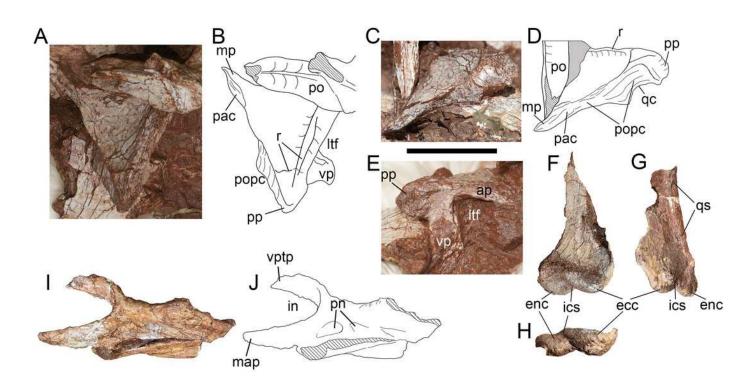
Postorbital and skull roof of *Yuanmouraptor jinshajiangensis* gen. et sp. nov. (LFGT-ZLJ0015)

Right postorbital in (A) lateral view with (B) labeled drawing, and in (C) posterior view with (D) labeled drawing. Skull roof in (E) dorsal view with (F) labeled drawing. Abbreviations: de, depression; f, frontal; l, lacrimal; la, lamina; lsp, laterosphenoid; n, nasal; or, orbital ramus; ot, otoccipital; pa, parietal; po, postorbital; pop, paroccipital process; por, posterior ramus; pr, prootic; prf, prefrontal; r, ridge; so, supraoccipital; stf, supratemporal fenestra; stfo, supratemporal fossa; t, trough; vr, ventral ramus of postorbital. Striated area indicates damage and grey area indicates matrix. Scale bars present 50 mm. Photos by Xiao-Chun Wu.



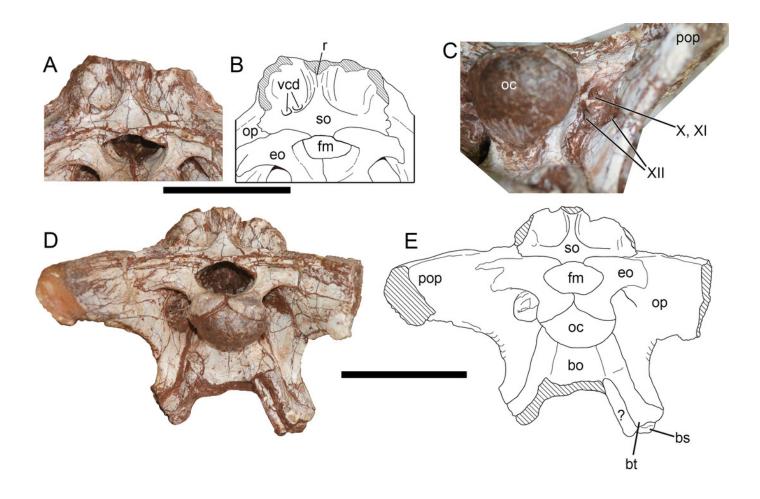
Skull elements of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0015).

Right squamosal in (A) dorsal view with (B) labeled drawing, in (C) posterodorsal view with (D) labeled drawing, and in (E) lateral view. Left quadrate in (F) anterolateral, (G) posterolateral, and (H) ventral views. Left palatine in (I) lateral view with (J) labeled drawing. Abbreviations: ap, anterior process; ecc, ectocondyle; enc, entocondyle; ics, intercondylar sulcus; in, internal naris; ltf, lateral temporal fenestra; mp, medial process; map, maxillary process; pac, parietal contact; po, postorbital; popc, paroccipital process contact; pn, pneumatic foramen; pp, posterior process; qc, contact for quadrate; qs, quadrate shaft; r, ridge; vp, ventral process; vptp, vomeropterygoid process. Striated area indicates damage and grey area indicates matrix. Scale bar presents 50 mm. Photos by Xiao-Chun Wu and Yi Zou.



Occiput of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0015).

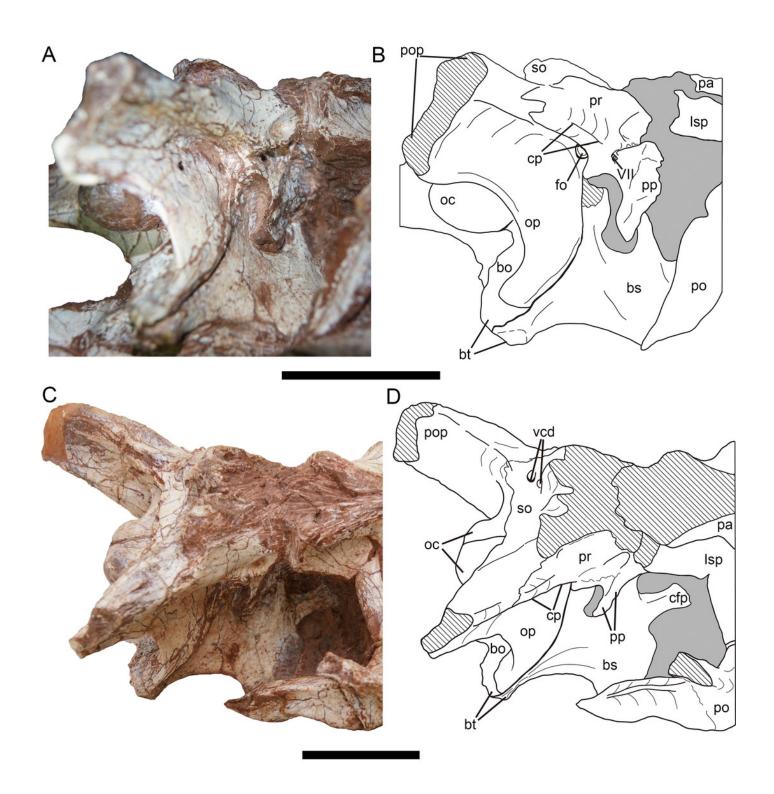
Supraoccipital and adjacent bones in (A) posterodorsal view with (B) labeled drawing. (C) Depression housing cranial nerves. Braincase in (D) posterior view with (D) labeled drawing. Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; fm, foramen magnum; oc, occipital condyle; op, opisthotic; pop; paroccipital process; r, ridge; so, supraoccipital; vcd, foramen vena capitis dorsalis; X, X(I) XI(I) foramina for cranial nerves; ?, unknown bone. Striated area indicates damage. Scale bar presents 50 mm. Photos by Xiao-Chun Wu.





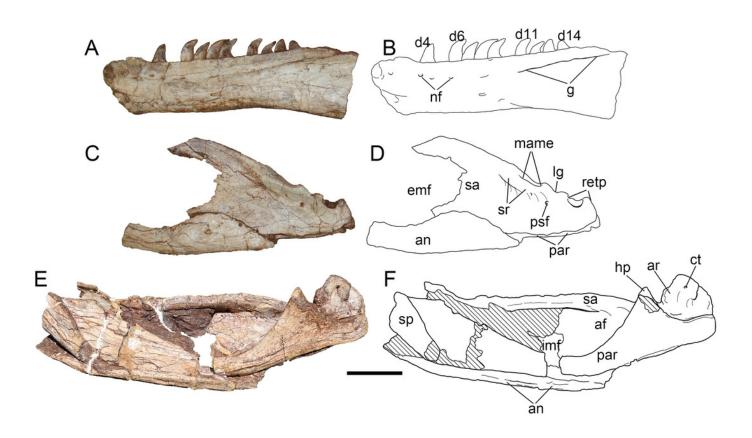
Braincase of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0015).

Braincase in (A) lateroposterior view with (B) labeled drawing and in (C) laterodorsal view with (D) labeled drawing. Abbreviations: bo, basioccipital; bs, basisphenoid; bt, basal tuber; cfp, cultriform process; cp, crista prootica; fo, fenestra ovalis; lsp, laterosphenonid; oc, occipital condyle; op, opisthotic; pa, parietal; po, postorbital; pop, paroccipital process; pp, prootic pendant; pr, prootic; vcd, foramen vena capitis dorsalis; VI(I) cranial nerve VII (facial nerve); so, supraoccipital. Straited area inidcates damage and grey area indicates matrix. Scale bar presents 50 mm. Photos by Xiao-Chun Wu.



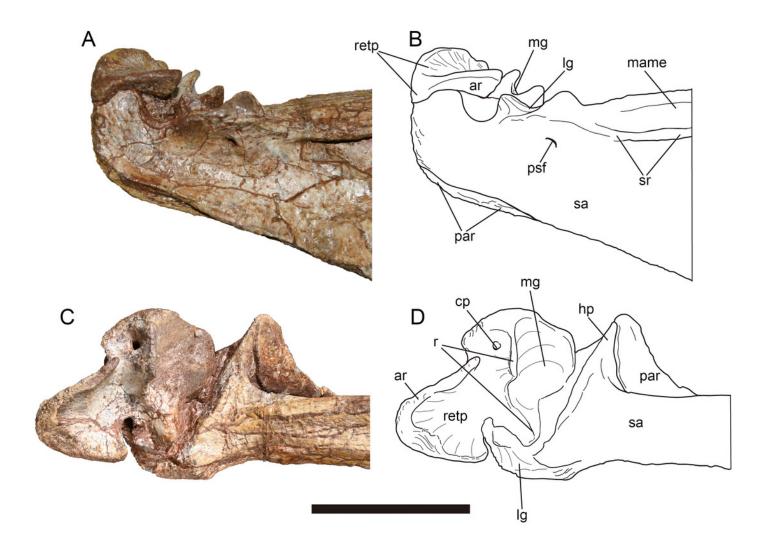
Mandibular elements of *Yuanmouraptor jinshajiangensis* gen. et sp. nov. (LFGT-ZLJ0015).

Left dentary in (A) lateral view with (B) labeled drawing. Left posterior part of mandible in (C) lateral view with (D) labeled drawing. Right posterior part of mandible in (E) medial view with (F) labeled drawing. Abbreviations: af, adductor fossa; an, angular; ar, articular; ct, foramen of condra typamni; d4-14, dentary teeth 4-14; emf, external mandibular fenestra; g, groove; hp, hook like process of surangular; imf, internal mandibular fenestra; lg, lateral glenoid; mame, attachment of M. adductor mandibulae externus; nf, neurovascular foramina. par, prearticular; psf, posterior surangular foramen; retp, retroarticular process; sa, surangular; sp, splenial; sr, surangular ridge. Striated area indicates damage. Scale bar presents 50 mm. Photos by Xiao-Chun Wu and Yi Zou.



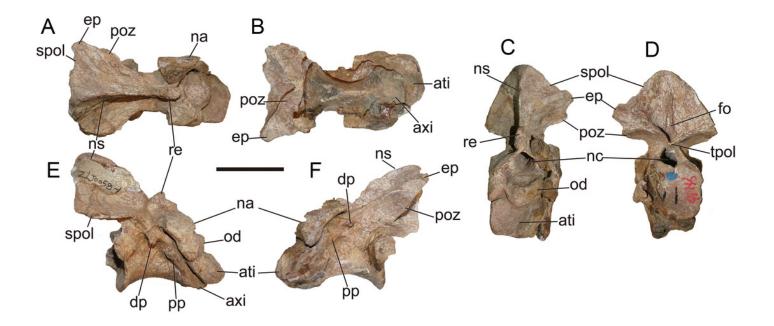
Mandibular joint of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0015).

Right mandibular joint in (A) lateral view with (B) labeled drawing and in (C) dorsal view with (D) labeled drawing. Abbreviations: ar, articular; ct, foramen of condra typamni; hp, hook like process of surangular; lg, lateral glenoid; mame, attachment of M. adductor mandibulae externus; mg, medial glenoid; par, prearticular; psf, posterior surangular foramen; r, ridge; retp, retroarticular process; sa, surangular; sr, surangular ridge. Scale bar presents 50 mm. Photos by Xiao-Chun Wu and Yi Zou.



Atlas-axis complex of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0115).

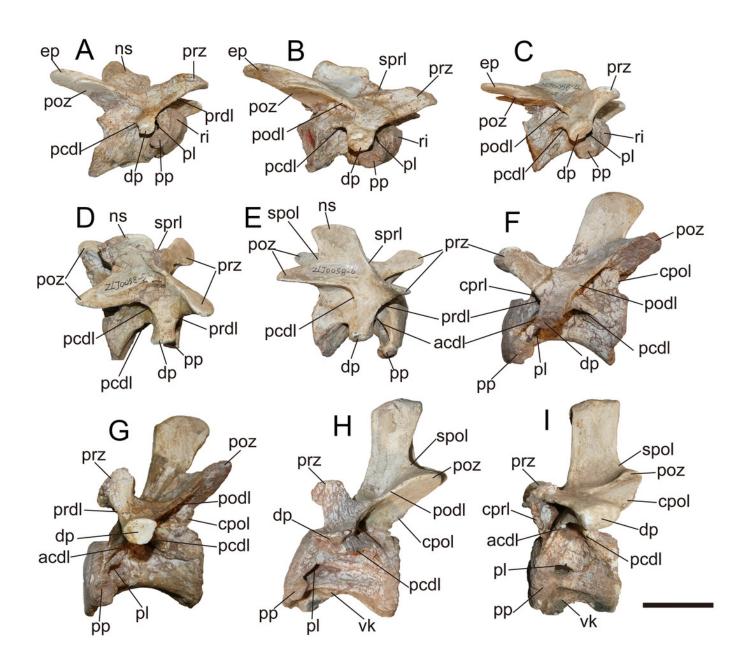
Atlas-axis complex in ((A)), dorsal, (B) ventral, (C) anterior, (D) posterior, (E) right lateral and (F) left lateral views. Abbreviations: ati, atlantal intercentrum; axi, axial intercentrum; dp, diapophysis; ep, epipophysis; na, neurapophysis; nc, neural canal; od, odontoid; poz, postzygopophysis; pp, parapophysis; re, rounded eminence; spol, spinopostzygipophyseal lamina; tpol, intrapostzygopophyseal lamina. All names of the bony laminae follow terminologies in *Wilson* (1999). Scale bar presents 50 mm. Photos by Xiao-Chun Wu.





Postaxial vertebrae of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0115).

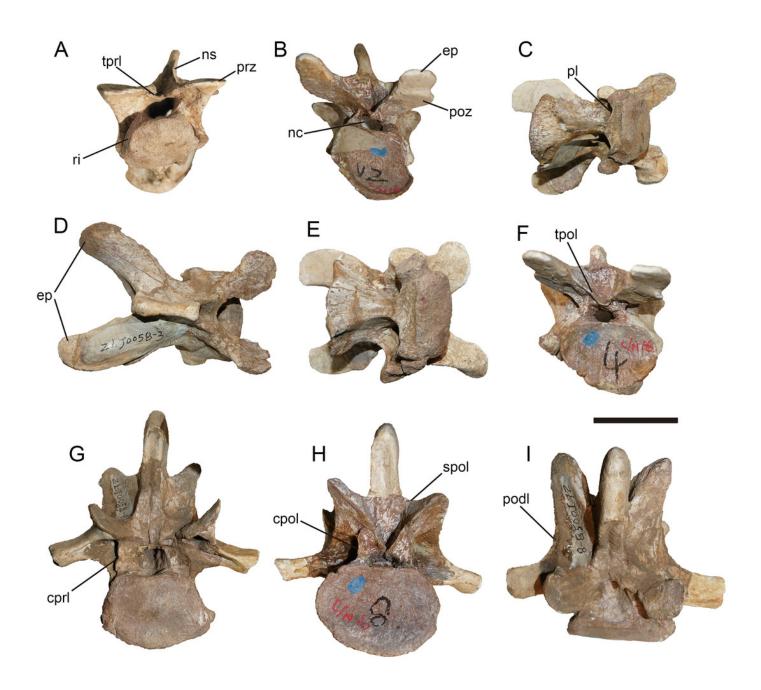
Postaxial vertebrae in lateral view. (A) Cervical 3; (B) Cervical 4; (C) Cervical 5; (D) Cervical 6; (E) Cervical 7; (F) Cervical; (G) Cervical 9; (H) Cervical 10; (I) Dorsal 1. Abbreviations: acdl, anterior centrodiapophyseal lamina; cpol, centropostzygopophyseal lamina; cprl, centroprezygopophyseal lamina; dp, diapophysis; ep, epipophysis; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; podl, postzygodiapophyseal lamina; poz, postzygopophysis; pp, parapophysis; prdl, prezygodiapophyseal lamina; prz, prezygopophysis; spol, spinopostzygopophyseal lamina; ri, distinct rim on the anterior articular surface; sprl, spinoprezygodiapophyseal lamina; vk, ventral keel. All names of the bony laminae follow terminologies in *Wilson (1999)*. Scale bar presents 50 mm. Photos by Xiao-Chun Wu.





Postaxial vertebrae of Yuanmouraptor jinshajiangensis gen. et sp. nov. (LFGT-ZLJ0115).

Cervical 3 in (A) anterior, (B) posterior, (C) ventral, (D) dorsal views. Cervical 5 in (E) ventral, (F) posterior views. Cervical 9 in (G) anterior, (H) posterior, (I) dorsal views. Abbreviations: cpol, centropostzygopophyseal lamina; cprl, centroprezygopophyseal lamina; ep, epipophysis; nc, neural canal; ns, neural spine; pl, pleurocoel; podl, postzygodiapophyseal lamina; poz, postzygopophysis; prz, prezygodiapophyseal lamina; ri, distinct rim on the anterior articular surface; tpol, intrapostzygopophyseal lamina; tprl, itraprezygopophyseal lamina; spol, spinopostzygopophyseal lamina. All names of the bony laminae follow terminologies in *Wilson (1999)*. Scale bar presents 50 mm. Photos by Xiao-Chun Wu.





Result of phylogenetic analysis

Time-Calibrated strict consensus tree showing the phylogenetic position of *Yuanmouraptor* with the latest geological time scale.

