A New Eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan Province

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ABSTRACT: A new eosauropterygian, *Largocephalosaurus polycarpon* gen. et sp. nov., was described based on a skeleton from the Middle Triassic of Luoping (罗平), Yunnan (云南) Province, southwestern China. The new taxon is characterized by a big skull, paired frontal, laterally expanded upper temporal fossa, anterior process of squamosal entering orbit, robust teeth with basally expanded crown and blunt tip, short cervical region, distinctly elongated transverse process of the dorsal vertebrae, short and broad dorsal ribs, stout gastralia, scapula with distinctly posterodorsally extending blade, distinctly robust humerus, eleven carpal ossifications, and a manual fomula of 2-3-4-5-5. A phylogenetic analysis suggests that *Largocephalosaurus* is the basal-most member of a clade including *Wumengosaurus*, European pachypleurosaurs, and Nothosauroidea.

KEY WORDS: Yunnan, Triassic, Guanling Formation, Sauropterygia.

INTRODUCTION

Eosauropterygia, includes most subgroups of Sauropterygia, widely distributed in the Alps and South China during the Middle Triassic (Rieppel, 2000). *Hanosaurus hupehensis* Young, 1965 and *Keichousaurus yuananensis* Young, 1965, which were found from the Lower Triassic Jialingjiang Formation in Hubei Province, represent the oldest records of Eosauropterygia in the world (Rieppel, 1998; Young, 1965). Recently, several faunas of marine reptiles have been found from the Triassic marine strata in Guizhou Province and Yunnan Province: the Panxian/Luoping Fauna (Anisian, Middle Triassic), the Xingyi Fauna (Ladinian, Middle Triassic) and the Guanling Biota (Canian, Late Triassic) (Zhang et al., 2008; Hao et al., 2006; Li, 2006; Wang et al., 2003). Hitherto, only Sauropterygian placodonts has been known from the Guanling Biota with numbers of ichthyosaurs and thalattosaurs (Li and Rieppel, 2002; Li, 2000). For the other two faunas, sauropterygians, especially eosauropterygian fossils are very common (Jiang et al., 2008, 2006a, b; Cheng et al., 2006; Li et al., 2002).

We report here a new eosauropterygian, *Largo-*

cephalosaurus polycarpon gen. et sp. nov., from the Luoping area, Yunnan Province. It is represented by an articulated skeleton collected from the limestone of the Guanling Formation (Anisian, Middle Triassic) (Zhang et al., 2009). The specimen reveals a previously unknown mophotype, very different from pachypleurosaurians and Nothosauroidea. We provide a preliminary report while the postcranial skeleton waits for further preparation and a subsequent full description. The phylogenetic analysis shows its close relationship with *Wumengosaurus* (Jiang et al., 2008).

Systematic Palaeontology

Superorder Sauropterygia Owen, 1860

Order Eosauropterygia Rieppel, 1994

Family incertae sedis

Genus *Largocephalosaurus* gen. nov.

Largocephalosaurus polycarpon gen. et sp. nov. (Figs. 1–3)

Holotype—Wuhan Institute of Geology and Mineral Recourses (WIGM) SPC V 1009, a nearly complete and articulated skeleton (more than 113 cm in length), with most part of the tail missing.

Etymology—The generic name is derived from the Latin, largus, for "large"; cephalus, for "head". The specific name is derived from the Latin, poly, for "many"; carpon, for "ossified carpals".

Type locality and horizon—Luoping County, Yunnan Province, China; upper Member of the Guanling Formation, middle Anisian, Middle Triassic.

Diagnosis—A large eosauropterygian with a big skull; frontals paired; upper temporal fossa expanded laterally; anterior process of squamosal entering orbit; teeth robust with basally expanded crown and blunt tip; cervical region short; transverse process of dorsal vertebrae distinctly elongated; dorsal ribs short and wide; gastralia stout; scapula with pronounced posterodorsally extending blade; humerus distinctly robust; eleven carpal ossifications including small pisiform; and formula of manus 2-3-4-5-5.

MORPHOLOGICAL DESCRIPTION
Skull

The skull is exposed in the laterodorsal view but the mandible is preserved in the lateral view. The left margin was broken when the specimen was dug out (Figs. 1, 2). The total length of the skull along with the dorsal midline is 201.5 mm, and the total length of the mandible is 245.2 mm (Table 1).

The external naris is elliptical, with a maximal diameter of 26.1 mm. It extends horizontally and was formed by the premaxilla, the maxilla and the nasal.

The premaxilla, relatively long compared with the maxilla, forms the rostum. Its tip is blunt and exceeds anteriorly for 24.7 mm beyond the dentary symphysis. The superficial surface of the premaxilla develops vermiculate ornaments as in other sauropterygians. The posterior end of the premaxilla extends to a point parallel to the middle level of the external naris and contacts the anterior margin of the nasal with an undulated suture. The posterior end of the premaxilla forms the anterodorsal margin of the external naris.

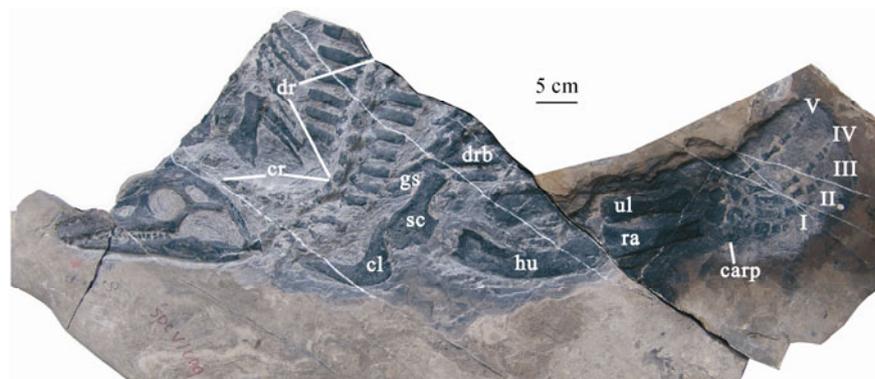The maxilla is an irregular element and slightly shorter than the premaxilla. The anterior part of the

Figure 1. The holotype of *Largocephalosaurus polycarpon* gen. et. sp. nov. (SPC V 1009). carp. ossified carpals; cl. clavicle; cr. cervical region; dr. dorsal region; drb. dorsal rib; gs. gastralia; hu. humerus; ul. ulna; ra. radius; sc. scapula; I–V. metacarpal I–V.
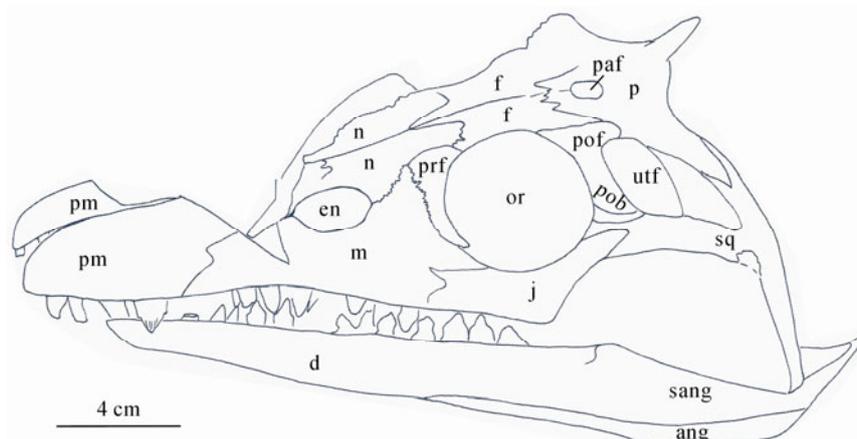
Figure 2. Line drawing of the skull of *Largocephalosaurus polycarpon* gen. et sp. nov. (SPC V 1009). ang. angular; d. dentary; en. external naris; f. frontal; j. jugal; m. maxilla; n. nasal; or. orbit; p. parietal; paf. parietal foramen; pm. premaxilla; po. postorbital; pof. postfrontal; prf. prefrontal; sang. surangular; sq. squamosal; utf. upper temporal fossa.

maxilla extends anteriorly along the posteroventral margin of the premaxilla. The suture between them is strongly undulated. The maxilla forms the entire ventral margin of the external naris, as in most nothosauroids. The triangular dorsal process extends dorsally to insert between the nasal and the prefrontal. The sutures with the two bones are finely serrated but become smooth between the posterior margin of the maxilla and the anteroventral margin of the prefrontal. Posteriorly, the maxilla contacts the jugal at the anteroventral corner of the orbit. There is no lacrimal as in other eosauropterigians except for *Wumengosaurus* (Wu et al., 2011).

The nasal is a large and unconstricted element as in most pachypleurosaurs, anteriorly forming the posterodorsal margin of the external naris. The posterior end of the nasal extends posteriorly beyond the anterior margin of the orbit. It inserts the anterior end of the frontal posteriorly and contacts the dorsal margin of the prefrontal laterally.

The orbit is rounded in outline, with a diameter of 52.3 mm. It is mostly formed by the prefrontal, the frontal, the jugal, the postfrontal and the postorbital.

The prefrontal is a slender element. It forms the anterior margin of the orbit. The dorsal part expands in the horizontal plane. The ventral part tapers increasingly.

The unconstricted frontal occupies the roof area between the two orbits in most pachyleurosaurs. The suture between the paired frontals is straight, which is similar to *Wumengosaurus*. The frontal forms the dorsal margin of the orbit. The anteromedial process tapers between the paired nasals and extends anteriorly beyond the orbit. The anterolateral process is shorter and stouter than the anteromedial process. The suture between the frontal and the parietal is strongly serrate. The posterolateral process is close to the upper temporal fossa. It is difficult to distinguish the postfrontal from the postorbital. They form the septum of the orbit and the upper temporal fossa as well as the bar between the orbit and the lower temporal fenestra.

The jugal is a slender and roughly L-shaped element. It extends along the ventral margin of the orbit as in most pachyleurosaurs. The posterodorsal end overlaps the squamosal.

The upper temporal fossa is small and transversely oblong, with a maximal diameter of 34.5 mm. It differs from most eosauropterygians in which the fenestra extends anteroposteriorly. The upper temporal fossa of the new taxon is surrounded by the parietal, the squamosal, the postfrontal and the postorbital.

The parietal is relatively large. The parietal foramen is located at a place slightly anterior to the midpoint of the bone. The suture appears present between the parietal anterior to the parietal foramen although it is not clear. It is difficult to distinguish the parietal suture posterior to the parietal foramen. The lateral margin of the parietal does not constrict and forms the dorsal margin of the upper temporal fossa as in other pachypleurosaurs. Posterolaterally, the parie-

tal expands laterally and contacts the squamosal.

The squamosal is a slender and triangular element with three processes. The dorsal process is the shortest and stoutest among the three. The anterior process is relatedly elongated and extends anteriorly into the posteroventral corner of the orbit. This is peculiar among diapsid reptiles. The posteroventral process is the slenderest one and extends ventrally to the lateral side of the articular condyle of the quadrate.

The mandible is slender. The coronoid is distinctly reduced and located well posteroventral to the postorbital bar. The dentary is the longest element of the mandible. The posterior end of the dentary extends to the coronoid. The slender angular is exposed in the lateral view; it sharply tapers off and reaches a level parallel to the fourth teeth from the back. The angular is slender in the lateral view. The posterior end of the surangular forms a slender retroarticular.

Dentition

The dentition of *Largocephalosaurus polycarpon* is unique amongst eosauropterygians. All the teeth of the premaxilla, maxilla and dentary are robust. The teeth can be divided into the basal peduncle and the crown. The basal peduncle is robust and more expanded than the crown. Apically, the crowns of the anterior teeth are conical, while the crowns of the posterior fourth teeth are blunt. Most of teeth are located at the surface of the related bones. There is no groove or socket for the teeth. The enamel covering the crown shows distinct striations.

Axial skeleton

Eight cervical vertebrae can be recognized. It is difficult to identify the atlas-axis complex, and several cervical centra may be covered by the displacement of the skull. However, the cervical region appears short, although the exact count of the cervical region is uncertain. The transverse process of the dorsal vertebrae is distinctly elongated. The distal end of the transverse process does not expand. The neural spine is low. The dorsal ribs are very short and wide. The gastralia are exposed because of displacement, and they are short and stout.

Appendicular skeleton (Figs. 1, 3)

The clavicle is L-shaped. The anteroventral part is longer and slenderer than the posterodorsal part. The medial corner is distinctly expanded as in *Wumengosaurus*. The posteroventral margin develops a small notch. The scapula has an extended ventral portion, delimited by a ventrally concave margin that participates in the formation of the dorsal part of the glenoid fossa. The ventral portion of the scapula is set off from the dorsal scapular blade by a distinct constriction, which is very similar to that of *Wumengosaurus* (Jiang et al., 2008, Figs. 2, 4). The humerus bends posteriorly, which is characteristic of sauropterygians (Storrs, 1991; Sander, 1989). However, the humerus is more robust related to the body. The proximal end of the humerus is slightly more expanded than the distal end. The middle portion of the humerus constricts slightly. The preaxial margin is slightly convex while the postaxial margin is strongly concave. The ectepicondylar groove is distinct, which results in a shallow ectepicondylar notch at the distal end of the humerus near its preaxial margin. The shape of the radius is similar to that of *Wumengosaurus*. The ulna is slightly shorter than the radius. The proximal end is somewhat more expanded than the distal end. The preaxial margin is slightly more convex than the postaxial margin. It forms a narrow spatium interosseum between radius and ulna. Measurements of selected elements are shown in Table 1.

Eleven carpal ossifications are present in the hand. All ossified carpals are nearly rounded. The intermedium is the biggest amongst the carpals. The proximal margin of the intermedium is relatively stout to articulate the radius. The radiale is small and lies distal to the radius. The ulnare is much bigger than the radiale. The pisiform is slightly smaller than the radiale, which lies closer to the ulna than the ulnare. Because the radiale articulates the fifth distal carpal, the two centrale should be the second centrale and the third centrale, respectively. The second centrale is distinctly bigger than the third one. The first distal carpal is the smallest one among the five distal carpals. The distal carpals become bigger increasingly from the first to the third. The fourth distal carpal expands laterally and forms an oblong shape. The fifth distal carpal is broken into two parts when fossilized, The first
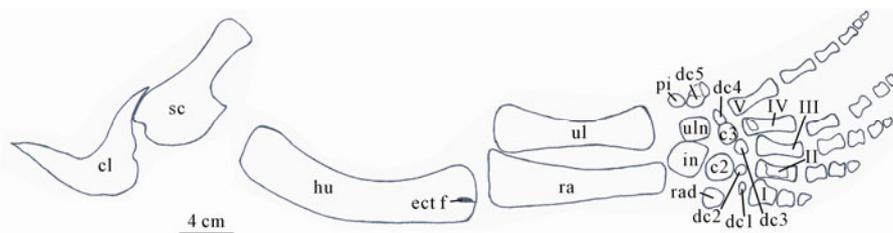
Figure 3. Line drawing of the pectoral girdle and forelimb of *Largocephalosaurus polycarpon* gen. et sp. nov. (SPC V 1009). c. centrale; dc 1–5. distal carpal 1–5; ect f. ectepicondylar foramen; in. intermedium; pi. pisiform; rad. radiule; uln. ulnare; others as Fig. 1.

Table 1   Selected measurements (mm) of *Largocephaloosaurus polycarpon* gen. et. sp. nov. (SPC V 1009)

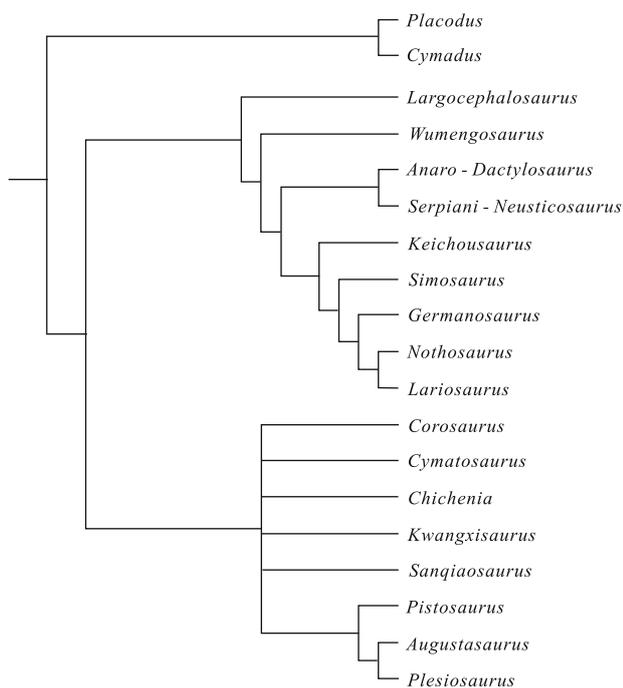|			h	ra	ul
Length of the skull along with the dorsal midline	201.5	Length	174.4	128.6	119.9
Length of the mandible	245.2	Proximal width	42.9	43.6	35.5
Maximal diameter of the external naris	26.1	Minimal width	31.1	–	17.9
Maximal diameter of the orbit	52.3	Distal width	37.2	21.5	32.8
Maximal diameter of the upper temporal fossa	34.5	I	II	III	IV	V
		20.6	30.2	35.6	39.8	36.3

Abbreviations as Fig. 3.

Figure 4. Sauropterygian part of the strict consensus tree, depicting the relationships of *Largocephalosaurus polycarpon* gen. et. sp. nov. (60 MPTs).

metacarpal is the shortest of the five metacarpals. The metacarpals in general are straight elements with concave anterior and posterior margins and correspondingly expanded proximal and distal ends. The proxi-

mal end of the first metacarpal is distinctly more expanded than the distal end. The fourth metacarpal is the longest (Table 1). The distal phalangeal elements are very short. The distal tips of the claw are conical. The phalangeal fomula of the manus is 2-3-4-5-5.

DISCUSSION

Cheng et al. (2010) attributed an incomplete forelimb (YIGM SPC V 0832-2) to a thalattosaur, cf. *Anshunsaurus*, which came from the same horizon and locality where *Largocephalosaurus polycarpon* was collected. The forelimb is comparable in morphology to that of *L. polycarpon*, with similar carpal ossification. However, it is distal carpal 1 that is the largest, differing from the condition seen in *L. polycarpon* in which distal carpal 4 is the largest. So the YIGM SPC V 0832-2 should belong to the new taxon. The condition of the carpal ossifications is similar to primitive reptiles (Romer, 1956, Fig. 179 therein).

Holmes et al. (2008) restudied the *Keichousaurus hui*, and hypothesized that *Keichousaurus* was closer to Nothosauroidea than to Pachypleurosauria. Wu et al. (2011) confirmed the hypothesis in their restudy of *Wumengosaurus delicatomandibularis* based on well-prepared new specimens. Jiang et al. (2008) con-

sidered *Wumengosaurus* as a pachypleurosaur, which was not supported by Wu et al. (2011), although its relationships with other eosauropterygians remained uncertain in the study of the latter.

The upper temporal fossa is distinctly smaller than the orbit, the posterior part of the parietal skull table is broad and flat, and the jugal extending anteriorly along the ventral margin of the orbit exclude *Largocephalosaurus polycarpon* gen. et. sp. nov. from Nothosauroidea and Pistosauroidea (Holmes et al., 2008; Rieppel, 2000). Instead, the new taxon shares many interesting characteristics with European pachypleurosaurs, especially with *Wumengosaurus delicatomandibularis*.

Eosauropterygia has a long tail in general. *Largocephalosaurus polycarpon* would have exceeded 200 cm if the tail was complete. The adult *Wumengosaurus* and the pachypleurosaur *Neusticosaurus edwardsii* can reach 120–130 cm (Jiang et al., 2008; Carroll and Gaskill, 1985), obviously much smaller than *Largocephalosaurus*. The new taxon has an elongated rostrum, which is most similar to that of *Anarosaurus heterodontus* (Rieppel and Lin, 1995). In pachypleurosaurs, the fusion of the frontals and/or parietal is universal except for *Wumengosaurus*. However, the condition of the frontals and parietals of *L. polycarpon* is similar to *Wumengosaurus*. The upper temporal fossa of *L. polycarpon* is peculiar amongst pachypleurosaurs and nothosauroids. It is relatively small but expands transversely. In all other pachyleurosaurs and nothosauroids, the upper temporal fossa extends anteroposteriorly. *L. polycarpon* retains a relatively narrow upper temporal arch, which is similar to most of pachypleurosaurs.

The pectoral girdle has the same general morphology seen in pachypleurosaurs. The scapula blade has the same characteristics as *Wumengosaurus*. The distal end of the humerus undistinctly expands, which is similar to the female adult of *Serpianosaurus*, *Neusticosaurus* and *Keichousaurus hui* (Cheng et al., 2009, 2004; Sander, 1989). The biggest difference between *Largocephalosaurus polycarpon* and pachyleurosaurs and Keichousaurus is that there are eleven ossified carpals in the former, in contrast, there are three to five ossified carpals in the latter.

In order to establish the phylogenetic relation-ships of *Largocephalosaurus polycarpon* within Sauropterygia, we conducted a phylogenetic analysis based on the data matrix in Rieppel et al. (2002) and Wu et al. (2011). The analysis includes all taxa used by Wu et al. The coding of the 137 characters for *Largocephalosaurus* was as follows (in groups of five): 100?0   00020   11301   1?301   11001 22011 ????? ????? ????? ??100 ??100 10??? ????? 1?0?? ????? ?0??0 1??10 ????? 01??? 0?1?? ????? ????? ????? ????? 0???? 0??0? ?110? ?0. We analyzed the matrix using PAUP* version 4.0b10 for Macintosh (Swofford, 2002), implementing a heuristic parsimony search that yielded sixty equally parsimonious trees (Tree length=428; Consistency index= 0.420 6; Retention index=0.695). The strict consensus tree confirms that *Keichousaurus* is the basal-most nothosauroid (Fig. 4). The pachyleurosaurs are only represented by the European taxa (*Anarosaurus-Dactylosaurus* and *Serpianosaurus-Neusticosaurus*). *Largocephalosaurus* forms the basal-most taxon of the clade including *Wumengosaurus*, the European pachypleurosaurs and the Nothosauroidea. The phylogenetic position of *Largocephalosaurus* is supported by the following autopomorphies: 11(1), dorsal exposure of prefrontal reduced; 26(2), postfrontal with reduced lateral process and hence more of an elongated shape; 66(1), transverse processes of neural arches of the dorsal region distinctly elongated; 137(0), total number of carpal ossifications more than three. *Wumengosaurus* is crowner than *Largocephalosaurus* within the clade. The eosauropterygian interrelationships are weakly supported (bootstrap support<50%) except for Nothosauridae (*Nothosaurus* and *Lariosaurus*; bootstrap support>92%) and Pistosauridae (bootstrap support>99%), which may have been caused by some poorly known taxa, such as *Chinchenia*, *Kwangsisaurus* and *Sanchiaosaurus* from China.

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