Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: http://www.tandfonline.com/loi/ujvp20

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To cite this article: Jun Liu & Yuan Wang (2005) The first complete mastodonsauroid skull from the Triassic of China: Yuanansuchus laticeps gen. et sp. nov., Journal of Vertebrate Paleontology, 25:3, 725-728, DOI: 10.1671/0272-4634(2005)025[0725:TFCMSF]2.0.CO;2

To link to this article: http://dx.doi.org/10.1671/0272-4634(2005)025[0725:TFCMSF]2.0.CO;2

Journal of Vertebrate Paleontology 25(3):725–728, September 2005

NOTE

THE FIRST COMPLETE MASTODONSAUROID SKULL FROM THE TRIASSIC OF CHINA: *YUANANSUCHUS LATICEPS* GEN. ET SP. NOV.

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The stereospondyl amphibians were distributed worldwide during the late Paleozoic and early Mesozoic, but have been poorly documented in China. Only fragmentary fossils have been reported from the northern part of China (Sun et al., 1992), and the two named taxa of Chinese Triassic stereospondyls, '*Parotosaurus*' *turfanensis* (see Young, 1966) and *Bogdania fragmenta* (see Young, 1978), were referred to the capitosauroids as nomina dubia by Lucas and Hunt (1993).

Based on a nearly complete skull specimen, we here report a new mastodonsauroid, *Yuanansuchus laticeps*, gen. et sp. nov., from the Xinlingzhen Formation of Hubei Province, China. This specimen is referred to the Mastodonsauroidea (as defined by Damiani, 2001; equals Capitosauroidea plus Benthosuchidae of Schoch and Milner, 2000) based on the following features: preorbital region very flat, without lateral slope; presence of deeply incised otic notches on rear border of skull; supratemporal bone excluded from border of otic notch; presence of lacrimal bone and Z-shaped lacrimal flexure; no area asperate on palate bones; transverse row of teeth posterior to apertura praemaxillaris; stout palatine ramus of pterygoid contacting palatine. The taxon differs from all other mastodonsauroids in its truncated skull shape, with a width greater than length. Our phylogenetic analysis regards *Yuanansuchus* as the sister taxon of the *Eocyclotosaurus-Quasicyclotosaurus* clade, a result consistent with traditional biostratigraphic study. The living environment of this animal was likely a river delta.

Abbreviation—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

SYSTEMATIC PALEONTOLOGY

MASTODONSAUROIDEA Lydekker, 1885
HEYLEROSAURIDAE Shishkin, 1980
YUANANSUCHUS, gen. nov.

Etymology—"Yuanan" refers to the county from where the fossil was collected; "suchus," is the Latin word for crocodile.

Type and Only Known Species—*Yuanansuchus laticeps*, sp. nov.

Known Distribution—Middle Triassic, central China.

Diagnosis—As for the species.

YUANANSUCHUS LATICEPS, sp. nov.
(Fig. 1)

Etymology—The specific name derives from the Latin words *latus*, broad, and *ceps*, head, referring to the broad-headed characteristic of the animal.

Holotype—IVPP V 13463, a nearly complete skull (Fig. 1).

Type Locality and Horizon—Maopingchang, Yuanan County, Hubei Province, China; Xinlingzhen Formation of the Badong Group, Anisian, Middle Triassic.

Diagnosis—Autapomorphies: skull wider than its length, with nearly straight posterior edge in dorsal view; entire orbit seen in palatal view. Primitive characters: prefrontal in contact with postfrontal, excluding frontal from inner margin of orbit; cultriform process of parasphenoid flat and relatively broad, extending to level of choanae. Derived characters: occipital sensory canal present; tabular horn laterally directed and posteriorly bordering semi-closed otic notch.

Description—The holotype is a nearly complete skull, but the snout tip and posterolateral corners are broken. The skull is relatively short and wide, contrary to that of most mastodonsauroids (Damiani, 2001). The skull roof is about 260 mm long at the midline (not including the rostral tip), and the estimated skull width is about 310 mm across the posterolateral corners of the quadratojugals. The skull is strongly flattened as preserved, especially the preorbital division.

Skull Roof—The suture pattern of the skull roof (Fig. 1A) matches that of *Benthosuchus sushkini*. The prefrontal connects to the postfrontal, so that the frontal is excluded from the medial border of the orbit. The postorbital does not extend far anterolaterally and does not reach the prefrontal, so that the jugal comprises about one quarter of the orbit perimeter. The squamosal sutures with the tabular, excluding the supratemporal from the margin of the otic notch.

The outline of this skull is nearly triangular; the posterior margin is nearly straight in dorsal aspect, resembling that of *Quasicyclotosaurus campi* to some extent (Schoch, 2000a). The orbits are small (35 mm along the long axis), rounded and widely separated; the interorbital breadth is 72 mm. The postorbital skull table is elongated compared with that of other mastodonsauroids; thus, the orbits and the pineal foramen are relatively anteriorly positioned.

The tip of the snout anterior to the nares is not preserved, and the premaxilla could not be observed. The anterior border of the nares is broken, but it is clear that they are elongated and oval, located at the lateral margin, and their long axis is anteromedially directed. The nasal is rather broad, with a width-to-length ratio of 0.5. The prefrontal is a little broader than the frontal. The prefrontal has a tapered anterior end. The lacrimal is relatively small. The jugal is a large, elongate element, but the extension of its anterior end is unclear due to preservation.

The posterolateral parts of the skull roof are incomplete, especially on the right side. Only a small part of the quadratojugal is preserved. The posterior margin of the squamosal is broken, so the squamosal should be closer to the tabular horn than preserved. The left tabular horn is complete, and it is laterally directed with a flattened terminal expansion. A round, semi-closed otic notch is probable.

Dermal sculpturing is pronounced on the skull roof, but the surface of some bones, e.g., the left squamosal, is eroded. The lateral-line sensory canals are continuous and obvious. The infraorbital sensory canal (ISC) has a Z-shaped lacrimal flexure, and extends backwards along the lateral margin of the skull roof. The supraorbital sensory canal (SSC) runs across the lacrimal, where it nearly connects with the ISC. A canal-like impression can be seen along the right half of the posterior margin of the skull roof and may represent the occipital sensory canal (OSC). If this interpretation is correct, it is the first report of the OSC in Capitosauroidea (defined by Schoch and Milner, 2000). These canals suggest an aquatic to amphibious lifestyle, more aquatic than that of other capitosauroids.

Palate—The palate is illustrated in Figure 1B. The tip of the snout is not preserved, so it is unclear whether the anterior palatal vacuity is paired or not. The choanae are oval. The prefenestral division of the palate is abbreviated. The two vomers are nearly divided by the cultriform process of the parasphenoid. The fodina vomeralis (Schoch, 1999) is a distinct foramen along with a marked groove in the anterior part of the parasphenoid. This foramen is level with the anterior margin of the choanae. The cultriform process of the parasphenoid is broad and flat; its base forms a broad deltoid as in *Quasicyclotosaurus campi*. The crista

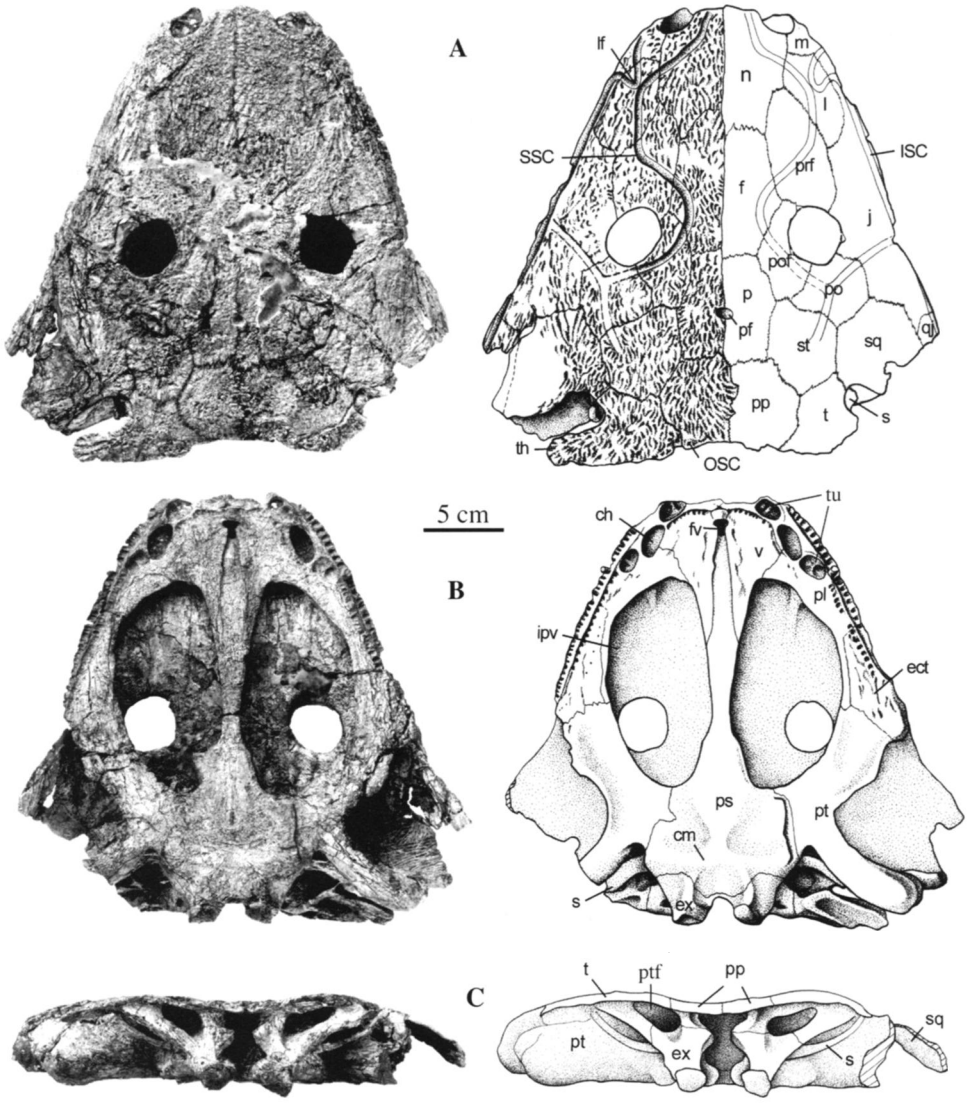

FIGURE 1. Skull of *Yuanansuchus laticeps*, gen. et sp. nov. (IVPP V13463), in dorsal (**A**), ventral (**B**) and occipital (**C**) views. **Abbreviations**: **ch**, choana; **cm**, muscular crest; **ect**, ectopterygoid; **ex**, exoccipital; **f**, frontal; **fv**, fodina vomeralis; **ipv**, interpterygoid vacuity; **ISC**, infraorbital sensory canal; **j**, jugal; **l**, lacrimal; **lf**, lacrimal flexure; **m**, maxilla; **n**, nasal; **OSC**, occipital sensory canal; **p**, parietal; **pf**, pineal foramen; **pl**, palatine; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **ptf**, posttemporal fenestra; **qj**, quadratojugal; **s**, stapes; **sq**, squamosal; **SSC**, supraorbital sensory canal; **st**, supratemporal; **t**, tabular; **th**, tabular horn; **tu**, tusk; **v**, vomer.

muscularis is continuous but not pronounced, and is level with the posterior border of the pterygoid-parasphenoid suture. The ventrally positioned "pockets" (as defined in Damiani, 2001:454) are not so distinct and widely separated. The basicranial region is short and broad.

The pterygoid is separated from the exoccipital in palatal aspect by the posterolateral corner of the parasphenoid body. It contacts a narrow posteromedial process of the palatine, thus excluding the ectopterygoid from the margin of the interpterygoid vacuity. The posterior part of the interpterygoid vacuity is relatively broad, as in *Tatrasuchus wildi* (Schoch, 1997; Damiani, 2001). The entire orbit can be observed through the vacuity.

Although the quadrates are not preserved, judging from the impression of the quadrate on the matrix and the position of the quadrate ramus of the pterygoid, it appears that the quadrate condyles are positioned slightly anterior to the occipital condyles.

A few teeth are preserved on this skull, but more information about the teeth could only be obtained from the sockets. The size of the transversely broadened tooth sockets on the maxilla increases slightly snoutwards. There are four pairs of tusks: one pair on each vomer and a pair on each palatine. The interchoanal (=transvomerine) tooth row is transverse anteriorly and extends posteriorly on both sides to form a curve; the anterior border of the tooth row is level with the vomerine tusks. No tusk is present on the ectopterygoid.

Occiput and Braincase—The occiput (Fig. 1C) is very shallow. The crista muscularis of the parasphenoid is not visible in occipital view. The quadrate ramus of the pterygoid occupies a large part of the occiput lateral to the condyle, but the oblique ridge of the pterygoid is weak as preserved.

The stapes is robust and preserved in situ; its footplate fits into the fenestra ovalis; the shaft curves gently ventrolaterally, with its distal end adjacent to the tabular-squamosal suture in the otic notch as seen in dorsal aspect. The posttemporal fenestrae are large and triangular.

DISCUSSION

The frontal is excluded from the medial border of the orbit in most temnospondyls, but it enters the orbit in most mastodonsauroids except for *Benthosuchus*, *Wetlugasaurus*, *Eocyclotosaurus*, *Odenwaldia*, and *Quasicyclotosaurus* (Bystrow and Efremov, 1940; Ortlam, 1970; Kamphausen and Morales, 1981; Morales and Kamphausen, 1984; Kamphausen, 1989; Schoch, 2000a, b). Compared with the above five taxa, the new specimen differs from *Benthosuchus*, *Wetlugasaurus* and *Oden-*

waldia in having laterally directed tabular horns and from *Eocyclotosaurus* and *Quasicyclotosaurus* in having an open otic notch, while the latter two taxa have closed otic foramina (Schoch, 2000b). Therefore, a new genus of Mastodonsauroidea is erected for this specimen.

Yuanansuchus laticeps retained some juvenile characteristics, such as a skull that was relatively broad and triangular, and anteriorly positioned orbits. Based on the ossification in various endoskeletal elements and the sculpturing on the skull bones (Boy and Sues, 2000), the skull appears to be that of a subadult. In Mastodonsauroidea, *Benthosuchus* and *Parotosuchus* reached adulthood at skull lengths of 20 to 30 cm (Bystrow and Efremov, 1940; Warren and Schroeder, 1995). Allometry continues in the subadult and adult phase of temnospondyls but to a much-reduced extent (Warren and Hutchinson, 1988). The holotype of *Yuanansuchus laticeps* is greater than 26 cm in skull length, so it is most likely to be a post-juvenile specimen; thus, its shape can be interpreted as characteristic of the taxon. Features such as a relatively broad skull could be the result of paedomorphosis. Besides the skull proportion, other possible autapomorphic characters include the presence of a distinct fodina vomeralis, a long palatal exposure of the cultriform process of the parasphenoid, and the presence of a nearly straight posterior border of the skull roof.

A comprehensive review and a phylogenetic analysis of mastodonsauroids were conducted by Damiani (2001); from his study we borrow the character descriptions and the data matrix, but change the coding of character 9 in *Benthosuchus* as '1' (Damiani, 2001:386), character 11 in *Cyclotosaurus* as '0&1', and add our new genus and another newly described taxon, *Quasicyclotosaurus* (Schoch, 2000a). The inclusion of the two new taxa has caused a great change in the mastodonsauroid phylogeny as proposed by Damiani (2001). The result (Fig. 2) shows that the monophyly of the superfamily Mastodonsauroidea is still well supported, but the composition and the in-group relationship of the Mastodonsauridae are different from those defined by Damiani (2001). *Eocyclotosaurus*, formerly paired with *Odenwaldia* and together forming the family Heylerosauridae, is now moved farther crownward and constitutes a monophyletic group with *Quasicyclotosaurus*, with *Yuanansuchus* and *Mastodonsaurus* as successive sister groups to the aforementioned clade. This result is consistent with the temporal distribution of the mastodonsauroid taxa as shown in Figure 2, and it justifies the inclusion of *Yuanansuchus* and *Quasicyclotosaurus* in the family Heylerosauridae (Heylerosaurinae of Milner, 1994). However, *Odenwaldia* should be removed from the group based on our new hypothesis, in agreement with the classification of Schoch and Milner (2000).

Based on previous stratigraphic work (Meng et al., 1995), the fossil horizon of *Yuanansuchus laticeps* is of Anisian, Middle Triassic age, the time when *Eocyclotosaurus* and *Quasicyclotosaurus* are also known (Schoch, 2000a; Schoch and Milner, 2000; Damiani, 2001); furthermore, *Eocyclotosaurus* has been widely used as a biostratigraphic marker for the Anisian stage (Ochev and Shishkin, 1989). Thus, the result of the phylogenetic analysis on our new taxon is consistent with traditional biostratigraphic study.

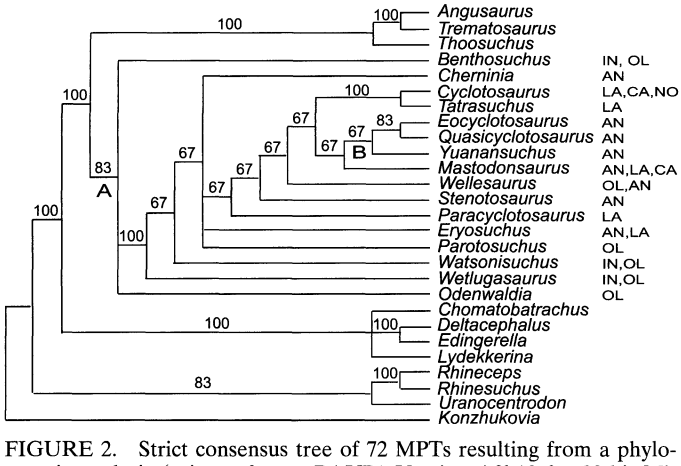

FIGURE 2. Strict consensus tree of 72 MPTs resulting from a phylogenetic analysis (using software PAUP* Version 4.0b10 for 32-bit Microsoft Windows; Swofford, 2003; Branch-and-Bound search; ACCTRAN optimization) based on the data matrix of Damiani (2001) with two new taxa *Yuanansuchus* and *Quasicyclotosaurus* added (codings see Appendix 1), character 9 of *Benthosuchus* changed to "1", and character 11 of *Cyclotosaurus* to "0&1". TL = 116, CI = 0.44, RI = 0.77. Temporal distribution is indicated for related taxa of mastodonsauroids. **Abbreviations**: **A**, Mastodonsauroidea; **B**, Heylerosauridae; **AN**, Anisian; **CA**, Carnian; **IN**, Induan; **LA**, Ladinian; **NO**, Norian; **OL**, Olenekian.

This skull was collected from storm-tide facies (Meng et al., 1995). Many isolated fossil bones were associated with the skull, but no complete skeleton could be found. Among the bones, some vertebrae with high spines may belong to the archosauromorph *Lotosaurus*. *Lotosaurus* has been reported from the same horizon in Furongqiao, Sangzhi, Hunan Province (Zhang, 1975). Complete skeletons of *Lotosaurus* from Hunan Province were also found in storm-tide facies (Meng et al., 1995). Although *Yuanansuchus laticeps* was found in marine deposits, it probably was a nonmarine tetrapod as were other mastodonsauroids. This argument can be further supported by the terrestrial nature of *Lotosaurus* from the same horizon. Based on the well-preserved skull material, it is estimated that *Yuanansuchus laticeps* should had lived in a fluvial environment close to the sea (e.g., river delta).

Acknowledgments—The authors thank Wang Haijun and Wang Zhao for their help in collecting the fossil. Thanks are given to Ding Jinzhao for preparing, Zhang Jie for photographing, and Yang Mingwan for illustrating the specimen. We thank Li Jinling and other colleagues in our division for commenting on the manuscript and Ross Damiani for his valuable information. Anne Warren and Rainer Schoch offered many useful suggestions that improved the manuscript significantly. The grammar was improved by Anne Warren. This study is supported by the Natural Science Foundation of China (J9930095) and the Ministry of Science and Technology of China (G2000077700).

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Submitted 7 October 2004; accepted 23 November 2004.

APPENDIX 1

Codings of *Yuanansuchus* and *Quasicyclotosaurus* based on Damiani's (2001) character descriptions. Information on the latter taxon is drawn from Schoch (2000a).

Yuanansuchus
01011 01211 01010 0100? 01000 11101 11?01 10111 ????? ??

Quasicyclotosaurus
01021 01201 01021 01001 01010 11?11 1100? ?0111 ????? ??