A new Yuanansuchus Temnospondyli; Capitosauroidea) from the Middle Triassic

Badong Formation of Yuanan, Hubei, China

Jun Liu

Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044, China

Abstract

A second species of Yuanansuchus, Y. maopingchangensis, is erected for new temnospondyl material from the Maopingchang site, Yuanan County, Hubei Province, China. These specimens are from a horizon approximately 20 m below the one that produced Y. laticeps, the type species, Y. maopingchangensis shares the following features with Y. laticeps: tabular horn directed laterally; lateral line sulci continuous, well impressed; supraorbital sensory canal enters lacrimal; preorbital projection of jugal less than half length of the snout; and vomerine plate short. However, Y. maopingchangensis differs from Y. laticeps in having an elongated skull, a frontal that may enter the medial border of the orbit and extend posteriorly to the level of the posterior orbital margin, a closed otic fenestra, and a slender cultriform process. Analysis of a new capitosaur phylogenetic data matrix, containing 56 characters and 29 species, confirms that the two species from Yuanan are sister taxa and that Capitosauroidea can be divided into two major clades: one including Parotosuchus, Eryosuchus, Calmasuchus and Cherninia, and another including Mastodonsaurus, Yuanansuchus, Stanocephalosaurus, Procyclotosaurus, Paracyclotosaurus,

Jean-Sébastien STEYER 15/12/15 09:44

Commentaire [1]: It does not look like
Yuanansuchus, see my remarks below

Jean-Sébastien STEYER 14/12/15 18:21

Mis en forme: Police :Non Italique

Jean-Sébastien STEYER 14/12/15 18:2: Supprimé: maopingchangensis, the second

Jean-Sébastien STEYER 14/12/15 18:21

Mis en forme: Police :Non Italique

Jean-Sébastien STEYER 14/12/15 18:21

Mis en forme: Police :Non Italique

Supprimé: capitosauroid

Jean-Sébastien STEYER 14/12/15 18:21

Jean-Sébastien STEYER 14/12/15 18:21

Supprimé: t

Jean-Sébastien STEYER 14/12/15 18:22

Supprimé: first *Yuanansuchus* species to be described

Jean-Sébastien STEYER 14/12/15 18:32

Supprimé: short

Antarctosuchus, Eocyclotosaurus, Quasicyclotosaurus, Tatrasuchus and Cyclotosaurus.

INTRODUCTION

Temnospondyls are the largest and most speciose group of amphibians. Within this group, the stereospondyl clade Capitosauria produced some of the largest species and dominated many Mesozoic aquatic ecosystems (e.g., Schoch 2008). Capitosaur research has a long history, and more than 120 nominal species have been erected within this group (Damiani 2001; Fortuny et al. 2011; Liu & Wang 2005; Sidor et al. 2014; Sulej & Niedźwiedzki 2013). The taxonomy of Capitosauria was poorly understood for a long time, but recent systematic revisions of the group by Schoch & Milner (2000) and Damiani (2001) have led to a consensus regarding the taxonomic status of most previously named genera and species. Meanwhile, large-scale cladistic analyses of Capitosauria have been undertaken by Schoch (2000) and Damiani (2001). To resolve the position of Yuanansuchus laticeps, Liu and Wang (2005) added Y. laticeps and Quasicyclotosaurus campi to the matrix of Damiani (2001). In later works, researchers modified the character list and data matrix of Damiani (2001) for their own studies (Fortuny et al. 2011; Schoch 2008; Sidor et al. 2014), and they produced the phylogenetic hypotheses that have varied widely in such particulars as the position of Edingerella, the proximity of Eryosuchus to Mastodonsaurus, and the content of the subgroup Capitosauroidea (sensu Schoch, 2013) [figure 8 of Schoch (2008) vs. figure 7 of Fortuny et al. (2011)].

Capitosaurs are widely distributed on the land masses derived from the Pangean supercontinent, and are known from many well preserved specimens (e.g., Damiani 2001; Schoch & Milner 2000). However, this group is poorly represented in east Asia (Ingavat & Janvier 1981; Li et al. 2008), a region from which only two highly informative capitosaur specimens have been described: the posterior part of a skull almost identical to the corresponding cranial region of *Cyclotosaurus posthumus* was reported from Thailand (Ingavat & Janvier 1981), and the nearly complete skull of a taxonomically novel capitosaur was reported from the age? Badong Formation of China (Liu & Wang 2005). The notably broad Chinese skull was collected in Maopingchang Township, Yuanan County, Hubei Province in 2001, and was named *Yuanansuchus laticeps* Liu & Wang, 2005, In 2011, a mandibular fragment was reported from the Lower Triassic of Japan, implying that the dispersal of stereospondyls into China occurred before the latest Early Triassic (Nakajima & Schoch 2011).

In 2011, we (the author and who? please precise) made a second field trip to the Maopingchang locality and collected a considerable number of fossils. In this paper, several new temnospondyl specimens are described and assigned to a new species, *Yuanansuchus maopingchangensis. Y. maopingchangensis* represents the second temnospondyl species from Maopingchang. To evaluate the phylogenetic relationships of these Chinese capitosauroids, a new character list is established based on a revision of previously established characters, and a new matrice, including both *Y. laticeps* and *Y. maopingchangensis* is constructed.

Jean-Sébastien STEYER 14/12/15 18:35 Supprimé: good

Jean-Sébastien STEYER 14/12/15 18:36

Supprimé: (

Jean-Sébastien STEYER 14/12/15 18:36

Supprimé:)

ean-Sébastien STEYER 14/12/15 18:39

Supprimé: s

Jean-Sébastien STEYER 14/12/15 18:39

Supprimé: are

GEOLOGICAL SETTING

Outcrops of the Triassic Badong Formation are widely distributed in Hubei,
Chongqing, and Hunan (Fig. 1). The Badong Formation conformably overlies Lower
Triassic shallow marine carbonates of the Jialinjiang Formation, and in most places
underlies an Upper Triassic terrestrial coal series. The Badong Formation is generally
divided into five members (numbered I to IV), and vertebrate fossils have been
collected from the purplish-red calcareous siltstone and mudstone of Member II in
both Hunan and Hubei (Liu & Wang 2005; Zhang 1975). Member I contains a rich
bivalve fauna, which is generally regarded as Anisian in age. Member III yields the
bivalves *Plagiostoma striatum* and *Placunopsis plana*, the ammonoid *Progonoceratites*, and the conodont *Neospathodus kockeli*, and is considered either as

Progonoceratites, and the conodont Neospathodus kockeli, and is considered either as Anisian (((please give your aguments here, otherwise cite only the publication of Thang et al. 2003))) or Ladinian (Thang et al. 2003) in age. Member II has also been suggested to be Anisian in age, based on its fossil flora (Meng et al. 1995), so the fossil tetrapods from Member II are accepted here as Anisian. Member II has been interpreted as comprising tidal flat sediments (Meng et al. 1995), but the sediments at the Maopingchang locality are more likely to represent a floodplain facies. No tidal-related structures were observed in the field.

The specimens described in this paper were excavated from a <u>spot 400 m away</u> from the <u>type locality</u> of *Yuanansuchus laticeps*, and from a stratigraphic level approximately 20 m lower in the section (Fig. 1). Among the bones collected at this <u>new spot</u>, four skulls, one left lower jaw, three interclavicles, and nine clavicles are of

Jean-Sébastien STEYER 14/12/15 18:42

Supprimé: accepted

Jean-Sébastien STEYER 14/12/15 18:43

Supprimé: in age

Jean-Sébastien STEYER 14/12/15 18:43

 $\textbf{Supprim\'e:} \ although \ Zhang \ et \ al. \ (2003) \ argued$

that it could instead be

Jean-Sébastien STEYER 14/12/15 18:43

Supprimé:

Jean-Sébastien STEYER 14/12/15 18:47

Supprimé: hill

Jean-Sébastien STEYER 14/12/15 18:45

Supprimé: site of the holo

temnospondyl origin. They represent at least six individuals, based on the number of clavicles. In addition to the temnospondyl fossils from the type locality of *Y*.

maopingchangensis, vertebrae with high neural spines were also discovered: they certainly belong to an archosaur similar to *Lotosaurus** from the *age here** Badong

Formation of Sangzhi County in Hunan (Zhang 1975).

Methods—The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. A ZooBank LSID (Life Science Identifier) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub: D68F2D09-0AC0-4AE1-ACE1-EFD0C5680916. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

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

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1887–1890 to be added in the reference list

STEREOSPONDYLI Zittel, 1887–1890

Jean-Sébastien STEYER 14/12/15 18:49

Supprimé: are present on the hill where *Y. maopingchangensis* was discovered, and almost

Jean-Sébastien STEYER 14/12/15 18:50

Supprimé: Member II of

CAPITOSAURIA Yates and Warren, 2000 to be added in the reference list, sensu

Schoch, 2008

CAPITOSAUROIDEA Säve-Söderbergh, 1935 to be added in the reference list sensu

Schoch, 2013

FAMILY?

Yuanansuchus Liu and Wang, 2005

Revised diagnosis (modified from Liu and Wang, 2005)—please precise here that it is a combination of characters Tabular horn directed laterally (character seen in cyclotosaurids); lateral line sulci continuous, well impressed (character seen in many stereospondyls); supraorbital sensory canal enters lacrimal (also seen in Mastodonsaurus); preorbital projection of jugal shorter than half length of snout; vomerine plate short (seen in many temnospondyls); interclavicle wider than long (see in many eryopoids); ventral part of blade of clavicle with convex medial margin.

Yuanansuchus maopingchangensis sp. nov. Figs 2-5

Etymology—From "Maopingchang", name of the village the closest to the type locality.

Holotype—IVPP V 22628, a nearly complete skull. Fig. 2

Type Locality and Horizon—Maopingchang, Yuanan County, Hubei Province,
China; Member II of the Badong Formation, Anisian (according to ???), Middle
Triassic (Fig. 1).

Diagnosis—Differs from *Y. laticeps* <u>a comparative diagnosis is not sufficient to erect</u>

<u>a taxon</u> in having an elongated skull, a large orbit, a closed otic notch <u>according to</u>

Jean-Sébastien STEYER 14/12/15 20:45

Mis en forme: Police :Non Gras

Jean-Sébastien STEYER 14/12/15 20:56

Mis en forme: Police :Non Italique

Jean-Sébastien STEYER 14/12/15 20:56

Mis en forme: Police :Non Italique

Jean-Sébastien STEYER 14/12/15 20:59 **Mis en forme:** Police :Italique

Jean-Sébastien STEYER 14/12/15 21:06

Supprimé: the

Jean-Sébastien STEYER 14/12/15 21:05

 $\textbf{Supprim\'e:}\ a$

Jean-Sébastien STEYER 14/12/15 21:05

Supprimé:

Jean-Sébastien STEYER 14/12/15 21:05

Supprimé: near

Jean-Sébastien STEYER 14/12/15 21:05

Supprimé: quarry

Yuanansuchus, a frontal that may do not integrate "possible" characters in a diagnosis (cf. "that may") contribute to the border of the orbit and extend to the level of the posterior orbital margin, and a short cultriform process of the parasphenoid that extends only to the anterior border of the interpterygoid vacuity already seen in others temnospondyls-> not diagnostic. Also base your diagnosis on the autapomorphies of

"Yuanansuchus" maopingchangensis obtained from your phylogeny.

Referred specimens: IVPP V 22629, a nearly complete skull (Fig. 3); IVPP V 22630, an incomplete skull (Fig. 4); IVPP V 22631, an incomplete left lower jaw; IVPP V 22632, a right clavicle articulating with the interclavicle (Fig. 5A-B); IVPP V 22633.1-2, two interclavicles (Fig. 5C partim); IVPP V 22634.1-8, eight clavicles including at least five right ones (Fig. 5D partim).

Description

The following description, except where specified otherwise, is based on the holotype; the other two known skulls are used as a supplementary source of information.

The holotype is a slightly distorted skull missing the posterolateral corner of the right cheek (Fig. 2). As preserved, the skull has an anteroposterior midline length of 275 mm and a width of 215 mm, but the complete skull was probably about 23 cm wide. This skull is slightly longer than IVPP V 13463, the holotype of *Yuanansuchus laticeps*, but is also much narrower. The posterior part of the skull was exposed and damaged by weathering prior to excavation of the rest of the specimen, so that the

Jean-Sébastien STEYER 15/12/15 10:56

Mis en forme: Police :Non Italique

ean-Sébastien STEYER 14/12/15 21:19

Supprimé: 1

occipital and otic regions are poorly preserved. The skull roof is generally well preserved, but white plaster has been inserted between the skull roof and palate to reinforce the skull. None of the marginal or palatal teeth is preserved.

In dorsal and ventral views, the outline of the skull is parabolic and elongate, with straight lateral margins. The outline is very similar to that of the skull of *Quasicyclotosaurus campi* (Schoch 2000). The preorbital region is low in profile and relatively broad. Shape and relative size of the snout? The two sides of the skull are asymmetrical. This anomaly can only partly be explained by distortion, and it seems likely that the preserved shape is similar to the original one. The midline suture between the frontals lies considerably further to the left than that between the nasals, so that the left nasal has a substantial contact with the right frontal. In most capitosaurs, the midline is nearly straight. Other differences in suture pattern exist between the left and right sides of the skull; for example, the right frontal is distinctly longer than the left one.

The dermal sculpturing is well preserved on the skull roof (Fig. 2) and largely consists of a pattern of deep pits, which grade into alternating ridges and grooves near the lateral margins of the skull and the nasal surface. Which individual age is suggested by this ornamentation? (see Steyer 2000, about "ontogeny and phylogeny of temnospondyls" ZJLS) The lateral line sensory sulci are continuous and obvious on the skull roof. The infraorbital sulcus (IS) has a Z-shaped lacrimal flexure, extends backwards along the lateral skull margin on the maxilla, and seems continuous with the jugal sulcus (JS) to the squamosal. The supraorbital sulcus (SS) is better-defined

than the IS, runs across the prefrontal and the lacrimal, nearly contacts the IS, and extends onto the nasal. The SS seems to not meet its counterpart across the midline within the premaxilla. Posteriorly, the SS extends across the frontal and postfrontal, and intersects with the temporal sulcus (TS) on the postorbital. The TS extends downwards on the jugal to meet the IS, and extends posteriorly onto the supratemporal.

Skull Roof

A small interpremaxillary foramen lies on the midline, close to the anterior border of the premaxillae. The nares are elongated and large (the left measuring 314 mm in length, and the right 275 mm), and are situated near the anterior margin of the skull. The external naris is bordered anteriorly and laterally by the premaxilla, dorsally by the nasal, and posteriorly by the maxilla. The posterolaterally directed suture between the premaxilla and the nasal touches the medial margin of the external naris, and the right suture is displaced anteriorly relative to the left one. In dorsal view, the maxilla is restricted to the skull margin and does not extend posterior to the anterior margin of the orbit. No septomaxilla is evident. The nasal contacts the maxilla posterior to the external naris. The lacrimal contacts neither the orbit nor the naris.

The two large orbits are both ovoid, but differ in size, the right orbit being longer (43 mm in length) and more anteriorly positioned than the left (38 mm in length). However, both orbits are situated relatively far anteriorly, lying close to the mid-length of the skull roof. In this characteristic *Y. maopingchangensis* resembles *Y. laticeps* but not based on the snout shape and *Mastodosaurus giganteus* + see also

many juvenile capitosauroids (such as Edingerella), but differs from many other taxa (Liu & Wang 2005; Schoch 1999). The orbits are almost dorsally directed and are raised above the rest of the skull roof, indicating an aquatic or semiaquatic lifestyle in which the animal habitually positioned itself near the water surface or at the bottom. The highest point on the skull roof is located on the postfrontal, just posterior to the orbit. The prefrontal is relatively long (measuring about one quarter of the midline length of the skull), tapers to an anterior point, and is elevated just anterior to the orbit. The frontal participates in the orbital margin, as is the case in many other capitosaurs (Damiani 2001; Schoch 2008) but not in Y. laticeps another character which does not go for an assignment to Yuanansuchus (Liu & Wang 2005). The frontal is subequal in length to the nasal, although the left frontal is shorter than the right one. However, in contrast to the condition in all other capitosaurs, the frontal extends posteriorly beyond the posterior margin of the orbit (Schoch 2008; Schoch & Milner 2000). The postfrontal is a nearly quadrangular in shape, and forms the posteromedial margin of the orbit. The postorbital is wide, and its lateral margin extends beyond that of the orbit. However, the postorbital does not extend as far anterolaterally as in many other capitosaurs, but narrows anteriorly and makes only a small posterior contribution to the orbital margin. The jugal forms most of the lateral border of the orbit, and has a long anterior process that extends far anteriorly to the orbit and reaches nearly the same level as the tip of the prefrontal. However, the length of the preorbital part of the jugal is less than half that of the snout. Although the suture between the jugal and quadratojugal is unclear, the former is definitely the longest bone of the skull roof did

Jean-Sébastien STEYER 15/12/15 11:15
Supprimé:

Jean-Sébastien STEYER 15/12/15 11:16

Mis en forme: Police :Italique

Jean-Sébastien STEYER 15/12/15 11:20

Supprimé: bone

ean-Sébastien STEYER 15/12/15 11:21

Supprimé: nevertheless

Jean-Sébastien STEYER 15/12/15 11:22

Supprimé: in

you compare witht the maxilla?

The parietal foramen is round and small relatively to the skull table size?, with a diameter of 6.5 mm, and lies on the midline near the anteroposterior midpoint of the parietals. The parietal is short, and is similar in length to the postparietal, the supratemporal, and the tabular. The postparietal is relatively long, its length exceeding its width. The posterior margin of the left postparietal is incompletely preserved but Jooks transversely aligned (the right postparietal looks relatively complete and suggests a posterior margin not so straight than that you reconstructed) as in Y. laticeps and Mastodonsaurus giganteus and juvenile capitosauroids (ex. Edingerella, see Steyer 2002 about "W." madagascariensis in JVP) (Liu & Wang 2005; Schoch 1999). The tabular is short and wide, and its lateral process is only slightly posteriorly directed. As a result, the posterior margin of the skull roof is nearly straight in dorsal view not according to the right postparital as in Y. laticeps, Mastodonsaurus giganteus and juvenile capitosauroids, rather than distinctly concave as in most adult capitosaurs (e.g., Schoch 2008). The tabular contacts the squamosal, enclosing an otic fenestra and preventing the supratemporal from entering the dorsal margin of this opening. The otic fenestra embays the squamosal more deeply than the tabular. Shape and size of this otic fenestra? Please describe and compare more, especially with the others taxon, which show a closed otic notch. The squamosal is a large bone in the posterolateral part of the skull roof. The posterior margin of the squamosal is poorly preserved, but this bone does extend far enough posteriorly to reach the occiput. The posterior margin of the postparietal, tabular and squamosal appears thick (~7 mm)

Jean-Sébastien STEYER 15/12/15 11:28

Supprimé:

Jean-Sébastien STEYER 15/12/15 11:28

Supprimé: is nearly

Jean-Sébastien STEYER 15/12/15 11:34

Mis en forme: Police :Italique

ean-Sébastien STEYER 15/12/15 11:41

Supprimé: clearly

Jean-Sébastien STEYER 15/12/15 11:41

Supprimé: overhang

relative to the total height of the occiput (47 mm). Please compare more the skull table (especially its size/proportions) with those of the others taxon.

Palate

The palate is moderately vaulted, with the lateral edges slightly below the level of the middle portion. The maxilla bears many how many? marginal tooth sockets, but no teeth are preserved. The anterior palatal vacuities are paired, oval in outline and completely separated by the premaxilla and the vomer, as in *Mastodonsaurus* giganteus (Schoch 1999). Compare more these paired anterior palatal vacuities with those of *Parotosuchus* and/or *Stanocephalosaurus*. A small fossa lies on the midline, crossing the suture between the premaxilla and the vomer. This structure may be the fossa subrostralis media, a feature present in *Eocyclotosaurus woschmidti* (Kamphausen 1989).

The vomerine plate is longer than wide. The plate is in contact with the premaxilla anteriorly, the maxilla laterally, and the palatine posterolaterally, and it sends out a long posteromedial process that runs lateral to the cultriform process. The vomerine tusk pair is large, and situated at the anterolateral corner of the vomer. The transvomerine tooth row is not preserved, but the protruding base shows it is slightly convex posteriorly (please draw it on Fig. 2B otherwise it is not visible) + compare it. The left side of the plate is poorly preserved, but on the right side a depression is situated posterior to the transvomerine tooth row.

The choana is elliptical in outline, and relatively long as in?. It is bordered by the

Jean-Sébastien STEYER 15/12/15 11:46

Supprimé: paired

Jean-Sébastien STEYER 15/12/15 11:50

Mis en forme: Police :Italique

Jean-Sébastien STEYER 15/12/15 11:50

Mis en forme: Police : Italique

Jean-Sébastien STEYER 15/12/15 11:51

Supprimé: a

ean-Sébastien STEYER 15/12/15 11:51

Mis en forme: Police : Italique

maxilla laterally, the vomer medially, and the palatine posteriorly. The interpterygoid vacuities are well-developed, measuring nearly 50% of the midline length of the skull, and are approximately as wide posteriorly as anteriorly. Comparison here Each vacuity is bordered laterally by the palatine and pterygoid, and medially by the vomer and parasphenoid. The orbits are located at the level of the posterior half of the vacuities, as in? Apart from a small portion of the right orbit, they can be seen through the vacuities in their entirety.

The palatine forms a slender posterior process that meets the ectopterygoid laterally and the pterygoid posteriorly. The palatine tusk pair is not preserved, and even the shapes of their alveoli are unclear so why are they reconstructed Fig. 2B?. The right ectopterygoid is a slender elongate bone situated medial to the maxilla.

Tooth sockets seem visible by zooming your Fig. 2B. However, the part of the palate forming the lateral margin of the left interpterygoid vacuity is so mediolaterally compressed that even the suture between the maxilla and the ectopterygoid is unclear. This left side should be re-examined because the pterygoid is not suturing usually the maxilla.

Although the middle portion of the vomerine plate is not well-preserved, the length of the midline suture between the two vomers shows that the parasphenoid extends anteriorly to around the level of the anterior margin of the interpterygoid vacuities. The anterior tip of the parasphenoid is far more posteriorly positioned than in most capitosaurians, including *Y. laticeps*. The parasphenoid seems smoothly sutured with the vomer, and the fodina vomeralis (please explain in two words)

Jean-Sébastien STEYER 15/12/15 12:05

Supprimé: triangular

Jean-Sébastien STEYER 18/12/15 11:5

Supprimé: in the vicinity of its midpoint

should be absent here. The cultriform process is a flat bar which narrows laterally at midlength, and whose triangular base is smoothly continuous with the vaulted basal plate of the parasphenoid. The width of the basal plate is subequal to its length. The crista muscularis is a transversely oriented ridge located on the posterior rim of the basal plate. The ventrally positioned 'pockets' mentioned by Watson (1962) are indistinct and widely separated. The parasphenoid contacts the pterygoid laterally at an anteroposteriorly long suture, the length of the suture is slightly greater than the width of the corpus of the parasphenoid.

The palatine ramus of the pterygoid tapers anteriorly, and contacts the posterior margin of the palatine along a short suture located roughly at the level of the anterior margin of the orbit. The corpus of the pterygoid curves ventrally towards its lateral side; its lateral margin is granular and forms a roughened area. The quadrate ramus has an oblique surface, and extends posterolaterally to form a sutural contact with the main body of the quadrate. The palatine and quadrate rami of the pterygoid participate in medially delimiting the subtemporal fenestra, which is bordered posteriorly by the quadrate and laterally by the quadratojugal and maxilla. Both quadrates are preserved. This bone is nearly triangular in palatal view, and the medial side which contacts the pterygoid is much wider than the lateral side which contacts the quadratojugal. The ventral condyle for the articular is saddle-like. The quadrate bears a boss (hyoid tubercle) above the medial part of the condyle. The occipital condyles are separated from one another and are formed by the exoccipitals, which are in sutural contact with the parasphenoid anteriorly. The occipital condyles are positioned posteriorly to the

level of the quadrate condyles. A long, slender, unidentified piece of bone is preserved on the left ventral margin of the skull. The anterior end of this unidentified element covers the posterior portion of the upper alveolar row. Any idea(s)? If this bone is complete, it looks like a rib. If this is a remain of a (bigger) bone, this could belong to the mandible based on its position.

More importantly: the holotypic skull must be figured also in occipital view.

This will allow a better description of the occiput (which bears important characters)

and a more exhaustive comparison with others taxon.

The skull of IVPP V 22629 is nearly complete, with a midline length of 21 cm and a width of approximately 15 cm (Fig. 3). The long axis of the orbit measures 27 mm, and the short axis measures 20 mm. Another skull (IVPP V 22630) is slightly smaller (Fig. 4). Both specimens are similar to the holotype in their general features, but differ from the holotype in that the frontal merely comes close to the orbit rather than entering the orbital margin. The frontal extends only to the level of the posterior margin of the orbits, rather than continuing posteriorly beyond this level as in the holotype. In IVPP V 22629, only one vomerine tusk socket lies anterior to the choana, and there is no socket lying posterior to the choana (Fig. 3B). In IVPP V 22629, the area of the contact between the vomer and the cultriform process is poorly preserved, and the anterior extent of the cultriform process is uncertain.

The occipital region is preserved in two specimens. The posttemporal fenestra is triangular. The occipital condyle is poorly preserved, and is situated at the same

dorsoventral level as the quadrate condyle. The foramen magnum is low (what do you mean?) and wide. The right stapes is preserved in situ in both specimens, and that of JVPP V 22630 is complete. The stapedial footplate is large, and the stapedial shaft is slab-like as in *Tatrasuchus wildi* (Schoch 1997). The foramen for nerves IX-X (the glossopharyngeal and the vagal nerves) is visible on the lateral side of the exoccipital.

Lower jaw

IVPP V 22631 is a robust and long left lower jaw, missing the anterior tip and the postglenoid region (Fig. 4). The intact specimen is estimated to have measured 266 mm in length and 65 mm in height. The lower jaw increases in height posteriorly until the posterior end of the coronoid, then begins to decrease in height on the lateral side of the adductor fossa. As a result, the dorsal margin of the lateral wall of the adductor fossa is strongly convex. The lateral surface of the angular shows well—developed radial ornamentations, which become less evident on the postsplenial. A distinct mandibular sulcus extends posterodorsally across the lateral surface of the angular, beginning at the ventral margin.

The dentary bears more than 20 tooth sockets, which are anteroposteriorly compressed. Only two broken teeth are preserved on the dentary. The middle and posterior coronoids each bear a single row of teeth, but only a few conical teeth are actually preserved. The medial side of the postsplenial bears a small anterior Meckelian foramen, posterior to which is an additional tiny foramen. The posterior Meckelian foramen is bordered by the postsplenial anteriorly and ventrally, the

Jean-Sébastien STEYER 18/12/15 12:04

Supprimé: the

Jean-Sébastien STEYER 18/12/15 12:05

Supprimé: ne

Jean-Sébastien STEYER 18/12/15 12:05

Supprimé: in

Jean-Sébastien STEYER 18/12/15 12:05

Supprimé: area

prearticular dorsally, and the angular posteroventrally. It is ovate??? and much larger than the anterior Meckelian foramen, but still far less than half as long as the adductor fossa. The prearticular extends anteriorly beyond the anterior margin of the posterior Meckelian foramen, and contacts the postsplenial below the posterior coracoid. The hamate process of the prearticular is not complete, but still rises above the level of the glenoid fossa. Most of the glenoid facet lies above the level of the dorsal surface of dentary.

The mandible should be more compared with other capitosauroid mandibles (ex. shape, proportions, bone contacts and especially the postglenoid region, see Damiani 2000) to help for the identification.

Postcranial skeleton

Many complete isolated bones have been discovered at this locality, but only a limited number have been successfully excavated because they are quite fragile and the matrix is very hard. Among the elements that have been recovered, three interclavicles and nine clavicles have been identified as temnospondyl in origin and tentatively referred to *Y. maopingchangensis* (see Discussion).

The interclavicle is well preserved in IVPP V22632 (Fig. 5). It is rhomboidal in shape, lacking a distinct anterior stylus, and is much wider than long. In contrast, the interclavicle is longer than wide in *Mastodonsaurus giganteus* (Schoch 1999). On the dorsal side, this bone bears three converging ridges (Figs. 5B, C). The anterior two ridges lie in the anteroposteriorly middle portion of the bone, and the posterior one is

Jean-Sébastien STEYER 18/12/15 12:09

Commentaire [2]: How many?

Jean-Sébastien STEYER 18/12/15 12:12

Commentaire [3]: For preparators on the field, fragility of the remains and hardness of the sediment should not be problems with time.

longitudinally aligned. The anterior and posterior margins of the interclavicle are broad and nearly straight. The ventral surface displays the characteristic temnospondyl dermal sculpture pattern, with furrows and ridges radiating outwards from the ossification centre.

Among the nine clavicles, only two right clavicles are nearly complete (Fig. 5). The ventral blade of the clavicle is slightly longer than wide, and shows a radial ornamentation on the ventral surface. The medial margin is convex, making the blade fanlike in shape rather than triangular. The dorsal process is posterodorsally directed and similar to that of *Eryosuchus pronus* (Damiani 2001; Howie 1970). The lateral surface of the dorsal process combines with the ventral blade to form a prescapular cavity, and the dorsal process tapers to form a sharp dorsal tip.

DISCUSSION

The only previously reported tetrapod species from the Maopingchang locality is *Yuanansuchus laticeps*. The specimen IVPP V 22628 is quite do you mean relatively or very? different from the only known specimen of *Yuanansuchus laticeps*, and cannot be referred to this species neither to this genus (see remarks above). IVPP V 22628 differs from *Yuanansuchus laticeps* in possessing the following features: elongated skull, large orbit, frontal entering the medial border of the orbit, closed otic fenestra, and short cultriform process. Particularly considering that IVPP V 22628 is similar in skull length to the holotype of *Y. laticeps*, the differences between the two specimens are too great in magnitude to represent intrageneric variation, implying that

IVPP V 22628 represents a new taxon. This specimen has a laterally directed tabular

Jean-Sébastien STEYER 18/12/15 12:13

Supprimé: a

Jean-Sébastien STEYER 18/12/15 12:13

Supprimé: central point

an-Sébastien STEYER 15/12/15 09:46

Supprimé: intraspecific

Jean-Sébastien STEYER 14/12/15 21:22

Supprimé: the holotype of

horn, as in *Y. laticeps*, and the lateral orientation of the horn is a unique feature not known in other capitosaurs No: see Cyclotosaurus, Eocyclotosaurus, Stanocephalosaurus and others! Although such capitosaurs as *Eryosuchus* and *Mastodonsaurus* have been described as having laterally directed tabular horns (Damiani 2001; Schoch 2008), their tabular horns in fact differ from those of the two Chinese taxa in being directed posterolaterally. OK but you need to consider the closure degree of the otic notch as an important character (e.g., Schoch & Milner 2000).

The two small skulls collected from the same small hill (IVPP V 22629, 22630) are very similar to IVPP V 22628 in most features but differ in that the frontal is excluded from the orbital margin in both specimens. As shown by Kamphausen (1994), however, frontal asymmetry can be present even in a single skull, so these two specimens are referred to *Y. maopingchangensis* here. The lower jaw and postcranial bones are tentatively also referred to *Y. maopingchangensis* because they came from the same small hill (=same strata?) where the skulls described in this paper were found it is not a sufficient criteria. You need to give at least arguments dealing with taphonomy. All of the cranial material from this spot is referable to *Y. maopingchangensis*. Because postcranial morphology is relatively stable within most small temnospondyl clades not according to Pawley (2007), Pawley & Warren 2004, the postcranial features observed in the new Maopingchang specimens probably characterize the entire genus *Yuanansuchus* rather than only *Y. maopingchangensis*.

Phylogenetic analysis

To assess the phylogenetic position of Yuanansuchus maopingchangensis, I incorporated this taxon into the data matrices of Schoch (2008) and Sidor et al. (2014), both of which represent modifications of that of Damiani (2001). The original dataset of Damiani (2001) included 47 characters. Fortuny et al. (2011) analyzed a modified version of this matrix, which excluded Damiani's (2001) characters 22 and 34 but added eight new characters. Subsequently, Sidor et al. (2014) added Antarctosuchus to the matrix of Fortuny et al. (2011). When I ran the matrix of Sidor et al. (2014) using the same software (PAUP 4.0 beta 1.0 for PC) (Swofford 2001) and settings specified in the paper, the results differed from those reported by Sidor et al. (2014) in that A. polyodon was found to be the sister taxon of Mastodonsaurus giganteus rather than that of Paracyclotosaurus crookshanki, this may be because you don't use the same outgroup (3 real taxon in Sidor et al. vs. one artificial "outgroup" in your work -> please precise and specify) although the parameters two equally most parsimonious trees were the same (145 steps, a consistency index of 0.40, and a retention index of 0.70). Except with respect to the position of Antarctosuchus, however, the two trees are topologically identical with each other and with the cladogram published by Fortuny et al. (2011). The two species of Yuanansuchus were added to the dataset (see Supplemental Data), which was analyzed in PAUP 4.0 beta 1.0 for Mac or PC? please precise using the same settings as before. This analysis recovered two most

ean-Sébastien STEYER 15/12/15 10:14

Supprimé: Paup

parsimonious trees, the strict consensus of which is almost identical to figure 7B of Fortuny et al. (2011) except in that *Antarctosuchus* appears as the sister taxon of *Mastodonsaurus* and the Chinese clade comprising *Y. laticeps* and *Y. maopingchangensis* appears as the sister taxon of *Xenotosuchus africanus*.

Schoch (2008) revised the characters of Damiani (2001) and added 19 further characters and used a slightly different list of taxa. He obtained results quite very or relatively? different from those of Fortuny et al. (2011) and Sidor et al. (2014), one key difference being that *Edingerella* was recovered as a trematosaur rather than a capitosaur by Schoch (2008). However, when Schoch's (2008) small matrix of 25 taxa was analyzed in Paup 4.0b10 (see remarks above), the shortest trees were found to be only 152 steps long, whereas the single most parsimonious tree reported by Schoch (2008) was 162 steps. The strict consensus of the trees obtained is similar to the topology depicted in Schoch's (2008) figure 8, but includes the monophyletic clade (((Cyclotosaurus (Eocyclotosaurus, Quasicyclotosaurus)), Mastodonsaurus), Paracyclotosaurus). The matrix of Schoch (2008) including Yuanansuchus laticeps resulted in an unresolved strict consensus tree which is logic because, by definition, a consensus tree is never solved!

To resolve the interrelationships of Capitosauria, a new data matrix was constructed using a revised list of 56 characters (Appendix 1). The codings of the characters were mostly adopted from previous analyses, though the matrix incorporates a few novel codings based on examination of the Chinese specimens only, photos and the literature (Table 1). The problem (cf. lines 4-5 of the caption of

Jean-Sébastien STEYER 15/12/15 10:17 Supprimé: i

your Table 1) is that you are revising a matrix based on indirect observations only (i.e. literature and photos). This leads to unjustified modifications (ex. character 16 should be coded as "1" for Antarctosuchus, as previous authors proposed, because its vomerine plate as preserved is clearly longer than wide) -> if you want to revise a matrix, please base your revision on all the specimens used in this matrix. Otherwise use it as it. Y. maopingchangensis was coded primarily based on the holotype, and secondarily with reference to the other specimens described in this study. The matrix was analyzed with Paup 4.0b10 see corrections above (Swofford 2001) and TNT 1.1 (Goloboff et al., 2003), and all characters were equally weighted and left unordered. Each program recovered the same two most parsimonious trees, which were 188 steps in length. One tree (Fig. 6A) is similar in its basic pattern to that depicted in figure 7A of Fortuny et al. (2011). Both topologies obtained here posit the two Chinese taxa as a monophyletic clade, supporting referral of the new species to Yuanansuchus this needs to be checked carefully because you do not give any phylogenetical argumentation (ex. a list of the synapomorphies supporting your "Yuanansuchus clade"). The positioned recovered for this clade is more basal than that recovered for Y. laticeps by Liu and Wang (2005) and Schoch (2008), but still falls on the branch of capitosauroid phylogeny that includes Cyclotosaurus. Schoch (2013) defined Capitosauroidea as the least inclusive clade containing Parotosuchus nasutus and Cyclotosaurus robustus. Here, Capitosauroidea can be divided into two clades: a relatively small one containing *Parotosuchus*, and a much larger one containing Cyclotosaurus. Capitosauroidea includes Edingerella, Watsonisuchus,

Jean-Sébastien STEYER 15/12/15 10:44

Mis en forme: Police : Italique

Xenotosuchus in one most parsimonious tree (fig. 6A) but not in the other (fig. 6B). In the phylogenies of Fortuny et al. (2011) and Sidor et al. (2014), Parotosuchus and Cyclotosaurus are positioned close to one another, resulting in a restricted Capitosauroidea that excludes Paracyclotosaurus and many other taxa recovered as capitosauroids in the present analysis. The present analysis did not recover a close relationship between Eryosuchus and Mastodonsaurus.

A paleobiogeographical section is missing here

Jean-Sébastien STEYER 15/12/15 10:59

Mis en forme: Gauche

CONCLUSION

The new temnospondyl specimens collected from the Maopingchang site (Yuanan, Hubei, China) are assigned here to a new capitosaur species, *Yuanansuchus maopingchangensis* The assignment of this species to *Yuanansuchus* is doubtful. This species is the second to be named from the site, and shares the following features with *Y. laticeps*: tabular horn directed laterally; lateral line sulci continuous, well impressed; supraorbital sensory canal enters lacrimal; preorbital projection of jugal less than half length of snout; and vomerine plate short. *Y. maopingchangensis* differs from *Y. laticeps* in having the following characteristics: elongated skull; large orbit; frontal that may enter medial border of orbit; closed otic fenestra; and short cultriform process. A phylogenetic analysis confirms that the two species form a monophyletic clade, and supports the existence of a major dichotomy between separate *Parotosuchus* and *Cyclotosaurus* lineages within Capitosauroidea.

ACKNOWLEDGEMENTS

I thank my field team (LI Lu, JIA Zhenyan, LI Yan, XU Xu) for collecting the specimens, WU Yong and FU Hualin for preparing the specimens, XU Yong for helping to illustrate the paper. Corwin Sullivan kindly read the draft of this paper and significantly improved the language. Boris Morkovin (Borissiak Paleontological Institute, Moscow, Russia) kindly sent some photos and references.

REFERENCES

- Damiani RJ. 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). Zoological Journal of the Linnean Society 133:379-482.
- Fortuny J, Galobart À, and De Santisteban C. 2011. A new capitosaur from the Middle Triassic of Spain and the relationships within the Capitosauria. *Acta Palaeontologica Polonica* 56:553-566.
- Goloboff, P., Farris, J., Nixon, K.. 2003b. T.N.T.: Tree Analysis Using New Technology. Program and documentation, available at http://www.zmuc.dk/public/phylogeny/tnt.
- Howie AA. 1970. A new capitosaurid labyrinthodont from East africa. *Palaeontology* 13:210-253.
- Ingavat R, and Janvier P. 1981. *Cyclotosaurus* cf. *posthumus* Fraas (Capitosauridae, Stereospondyli) from the Huai Hin Lat Formation (Upper Triassic), Northeastern Thailand: With a note on capitosaurid biogeography. *Geobios* 14:711-725.
- Kamphausen D. 1989. Der Schädel von *Eocyclotosaurus woschmidti* ORTLAM (Amphibia, Stegocephalia) aus dem Oberen Buntsandstein (Trias) des Schwarzwaldes (SWDeutschland). *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 149:1-65.
- Kamphausen D. 1994. Eine Schädelasymmetrie bei Cyclotosaurus Fraas (Amphibia, Stegocephalia) aus dem Stubensandstein (Trias) von Württemburg (SW-Deutschland). Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 210:1-12.
- Li J, Wu X, and Zhang F. 2008. The Chinese Fossil Reptiles and Their kin (second edition). Beijing: Science Press. p 473.
- Liu J, and Wang Y. 2005. The first complete mastodonsauroid skull from the Triassic of China: *Yuanansuchus laticeps* gen. et sp. nov. *Journal of Vertebrate Paleontology* 25:725-728.
- Meng F, Zhang Z, and Xu A. 1995. Nonmarine biota and sedimentary facies of the Badong Formation in the Yangzi and its neighbouring areas. Wuhan: China

- University of Geosciences Press.
- Nakajima Y, and Schoch RR. 2011. The first temnospondyl amphibian from Japan. *Journal of Vertebrate Paleontology* 31:1154-1157.
- Schoch RR. 1997. A new capitosaur amphibian from the Upper Lettenkeuper (Triassic: Ladinian) of Kupferzell (Southern Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 203:239-272.
- Schoch RR. 1999. Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian of Germany (Baden-Württemberg, Bayern, Thürbingen). *Stuttgarter Beitrage zur Naturkunde Serie B* 278:1-175.
- Schoch RR. 2000. The status and osteology of two new cyclotosaurid amphibians from the Upper Moenkopi Formation of Arizona (Amphibia: Temnospondyli; Middle Triassic). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 216:387-411.
- Schoch RR. 2008. The Capitosauria (Amphibia): characters, phylogeny, and stratigraphy. *Palaeodiversity* 1:189-226.
- Schoch RR. 2013. The evolution of major temnospondyl clades: an inclusive phylogenetic analysis. *Journal of Systematic Palaeontology* 11:673-705.
- Schoch RR, and Milner AR. 2000. *Stereosondyli*. Munchen: Verlag Dr. Friedrich Pfeil.
- Sidor CA, Steyer JS, and Hammer WR. 2014. A new capitosauroid temnospondyl from the Middle Triassic upper Fremouw Formation of Antarctica. *Journal of Vertebrate Paleontology* 34:539-548.
- Sulej T, and Niedźwiedzki G. 2013. A new large capitosaur temnospondyl amphibian from the Early Triassic of Poland. *Acta Palaeontologica Polonica* 58:65-75.
- Swofford, D.L. 2001. PAUP: Phylogenetic Analysis Using Parsimony, Version 4.0b10. Smithsonian Institution, Washington DC.
- Watson DMS. 1962. The Evolution of the Labyrinthodonts. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 245:219-265.
- Zhang F-K. 1975. A new thecodont Lotosaurus, from Middle Triassic of Hunan. *Vertebrata Palasiatica* 13:144-147.
- Zhang W-T, Chen P-J, and Palmer AR. 2003. Biostratigraphy of China. Beijing: Science Press. p 603.