The oldest record of Saurosphargiformes (Diapsida) from South China could fill an ecological gap in the Early Triassic biotic recovery

Eliminado: s

Cheng Long[1], Benjamin C. Moon[2], Yan Chunbo[1], Ryosuke Motani[3], Jiang Da-yong[4], An Zhihui[1], Fang Zicheng[5]

1 Hubei Key Laboratory of Paleontology and Geological Environment Evolution, Wuhan Centre of China Geological Survey, Wuhan, Hubei, P. R. China
2 Palaeobiology Research Group, School of Earth Sciences, University of Bristol, United Kingdom
3 Department of Earth and Planetary Sciences, University of California Davis, Davis, California, United States of America
4 Department of Geology and Geological Museum, Peking University, Beijing, P. R. China
5 China University of Geoscience, Wuhan, Hubei, P. R. China

Corresponding Authors:
Cheng Long
Wuhan Centre of China Geological Survey, Wuhan, Hubei, P. R. China
Email address: chengl@mail.cgs.gov.cn

Benjamin C. Moon
Life Sciences Building, University of Bristol, Bristol BS8 1TQ, United Kingdom

Email address: benjamin.moon@bristol.ac.uk

ABSTRACT

Diversification following the end-Permian mass extinction marks the initiation of Mesozoic reptile dominance and of modern marine ecosystems, yet major clades are best known from the Middle Triassic suggesting delayed recovery, while Early Triassic localities produce poorly preserved specimens or have restricted diversity. Here we describe *Pomolispondylus biani* gen. et sp. nov. from the Early Triassic Nanzhang-Yuan'an Fauna of China assigned to Saurosphargiformes tax. nov., a clade known only from the Middle Triassic or later, which includes Saurosphargidae, and likely it is the sister taxon to Sauropterygia. *Pomolispondylus biani* is allied to Saurosphargidae by the extended transverse processes of dorsal vertebrae? and a low, table-like dorsal surface on the neural spine, however, it does not have the typical extensive osteoderms. Rather an unusual tuberous texture on the dorsal neural spine and rudimentary ossifications lateral to the gastralia are observed. Discovery of *Pomolispondylus biani* extends the known the geographic range of Saurosphargiformes and increases the taxic and ecological diversity of the Nanzhang-Yuan'an Fauna. Its small size fills a different ecological niche with respect to previously found species, but the overall food web remains notably different in structure to Middle Triassic and later ecosystems, suggesting this fauna represents a transitional stage during recovery rather than its endpoint.

Eliminado: ing

Eliminado: known only from the Middle Triassic or later,

Eliminado: but r

Comentario [GP1]: Correct?

Eliminado: to

Keywords: Early Triassic, Nanzhang-Yuan'an Fauna, Saurosphargiformes, Saurosphargidae, marine reptile, end-Permian mass extinction, ecosystem recovery.

INTRODUCTION

The origin and evolution of marine reptiles in the Early Triassic is the subject of intense study to elucidate the tempo and mode of biotic recovery following the the end-Permian mass extinction, the largest of the Phanerozoic: (EPME; Benton et al., 2013; Ezcurra & Butler, 2018; Alvarez et al., 2019). While several sites preserve Early Triassic strata globally, only those in China have produced substantially complete and articulated remains of marine reptiles to date (Cheng et al., 2015; Ezcurra & Butler, 2018; Li & Liu, 2020). This contrasts with terrestrial vertebrate ecosystems of this time, from which numerous specimens, albeit of a few common "disaster taxa", have been found, e.g. *Lystrosaurus* (Sahney & Benton, 2008; Romano et al., 2020). Key innovations in the Early Triassic oceans include the incursion of several disparate marine reptile groups (Chen et al., 2014c; Scheyer et al., 2017), establishing reptiles in the top tiers of marine ecosystems (Scheyer et al., 2014; Li & Liu, 2020). Despite rapid diversification taxonomically, morphologically, and ecologically (Moon & Stubbs, 2020; Reeves et al., 2021), it is not until the Middle Triassic that clades that will dominate the rest of the Triassic (Ichthyopterygia, Sauropterygia, Thalattosauria) become established and build more complex ecosystems (Fröbisch et al., 2013; Benton et al., 2013). The question about how quickly and smoothly recovery occurred remains, and what roles do biotic and abiotic interactions play. Establishing the taxic and ecological diversity of Early Triassic ecosystems remains integral to understanding recovery patterns following the EPME.

Eliminado: mass extinction

Eliminado: the end-Permian mass extinction

Eliminado: and

Eliminado: remains

Eliminado: : e

Saurosphargidae are an enigmatic family of marine reptiles primarily known from the Middle Triassic of Europe and China. The first specimens were identified from the Alps (Frech, 1903; Huene, 1936; Nosotti & Rieppel, 2003), but recent specimens predominantly from China have increased the diversity of marine reptiles and provided new hypotheses on its origin and relationships to other major groups. Saurosphargidae was erected by Li *et al.* (2011) to include *Saurosphargis volzi* and *Sinosaurosphargis yunguiensis* (Huene, 1936; Nosotti & Rieppel, 2003); *Largocephalosaurus polycarpon* and *L. qianensis* were added later (Cheng et al., 2012; Li et al., 2014). Saurosphargidae are characterized by elongate transverse processes on the neural spine of dorsal vertebrae, a transverse expansion and pachyostosis of the dorsal ribs, and by the presence of osteoderms (Li et al., 2011). *Eusaurosphargis dalsassoi* and *Helveticosaurus zollingeri*, both from the Middle Triassic of Switzerland and Italy, are possibly terrestrial animals that share some features with Saurosphargidae (Peyer, 1955; Rieppel, 1989; Scheyer et al., 2017), however, these two taxa have been excluded by recent phylogenetic analyses (Li et al., 2011, 2014; Chen et al., 2014c). Similarly, the presence of osteoderms and the rib morphology has led to comparisons with the early turtles *Odontochelys* and *Eorhynchochelys* (Li et al., 2008, 2018), but the formation of the plastron in these taxa differs enough to separate them (Li et al., 2014).

In recent years, Wuhan Centre of China Geological Survey (WGSC) has led several field excavations of the Lower Triassic Jialingjiang Formation between Nanzhang and Yuan'an counties, Hubei, China, collecting abundant marine reptiles from the Nanzhang-Yuan'an Fauna (NYF; Cheng et al., 2015). This fauna includes hupehsuchians (*Hupehsuchus* [Carroll & Zhi-Ming, 1991], *Parahupehsuchus* [Chen et al., 2014b], *Nanchangosaurus* [Wu et al., 2003; Chen et al., 2014c], *Eohupehsuchus* [Chen et al., 2014a], *Eretmorhipis* [Chen et al., 2015; Cheng et al., 2019]), sauropterygians (*Hanosaurus* [Young & Dong, 1972; Rieppel, 1998], *Keichousaurus* [Young, 1965], *Lariosaurus* (Chen et al., 2016; Li & Liu, 2020)), and one ichthyosauriform (*Chaohusaurus zhangjiawanensis* [Chen et al., 2013]) (Cheng et al., 2015). Here, we describe a new marine reptile genus and species from the NYF. Although it is only

Código de campo cambiado

Con formato: Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Código de campo cambiado

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Código de campo cambiado

Código de campo cambiado

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Código de campo cambiado

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Código de campo cambiado

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Código de campo cambiado

represented by postcranial elements, it shares critical characters with Saurosphargidae suggesting these evolved earlier than previously thought.

GEOLOGICAL SETTING

The South China Block is composed of the Yangtze Craton and the South China Fold Belt that together formed a stable continent from the Late Proterozoic or early Paleozoic (Shen et al., 2006) into the early Mesozoic. During this time deposition was characterized by shallow-water carbonates. In the Early Triassic, the Yangtze Carbonate Platform extended approximately 1200 km east to west and 500 km north to south, between the deeper-water Guizhou-Guangxi-Hunan (also Nanpanjiang) Basin to the south and the Yangtze Basin to the east (Benton et al., 2013; Feng et al., 2015). This expanse of shallow water was interrupted only occasionally by small banks and potential exposure that formed localized lagoonal areas (Fig. 1B). Sources of clastic material into the basin were dominated by the Cathaysia Land to the south-east and Kangdian Land to the west.

The NYF is present through the upper part of Member II of the Jialingjiang Formation in western Hubei Province, China (Fig. 1C, D). Earlier references indicated that these fossils were from the upper part of Member III, however, the local stratigraphy of the Jialingjiang Formation has recently been revised (Yan et al., 2021). These strata were deposited during the Spathian (Olenekian, Early Triassic) towards the northern margin of the preserved Yangtze Carbonate Platform (Fig. 1B). Despite the extent of this shallow-water platform, occurrences of the NYF are limited to a small region north of Yichang, from six localities (Fig. 1A): Gujing, Songshugou, Baihechuan, Xunjianzhen, Zhangjiawan, and Yingzishan (Cheng et al., 2015; Qiao, Iijima & Liu, 2020). These localities were all deposited in lagoonal

Eliminado: s

Comentario [GP2]: What means “NYF”? you do not explain this previously.

Eliminado: s

environments within the broader carbonate platform, although its extent is uncertain, becoming occasionally more restricted (Fig. 1B; Yan et al., 2021). Members II and III of the Jialingjiang Formation correlate approximately to the Nanlinghu Formation found in the eastern Yangtze Platform, which preserves the Chaohu Fauna at Majiashan, Anhui Province (Benton et al., 2013). Despite generic overlap in the marine tetrapod fauna (e.g. *Chaohusaurus*; Huang et al., 2019), no species have been identified at both localities, and Hupehsuchia are unique to the NYF.

MATERIALS & METHODS

Materials

The new taxon is described from a single specimen (WGSC V 1701) in two parts housed at WGSC. The part specimen (WGSC V 1701-1) preserves the articulated trunk portion of the body, prepared in dorsal view, whereas the counterpart (WGSC V 1701-2) mainly shows impressions of some bone fragments posteriorly. This specimen was collected from the Lower Triassic Member II of the Jialingjiang Formation at Songshugou Quarry near Xuanjianzhen (Xuanjian Village), Nanzhang County, Hubei Province (Fig. 1A, D); WGSC V 1701 was found lower in the sequence than other layers that yield fossils marine reptile at Songshugou Quarry (Fig. 1D).

Eliminado: with

Eliminado: fossils

[Insert Figure 1 here]

Methods

We added WGSC V 1701 as a new operational taxonomic unit (OTU) to the cladistic matrix of Li *et al.* (2014) (Analysis 1) that focused on the phylogenetic relationships of Saurosphargidae to

Sauropterygia and other diapsids, and to the matrix of Chen et al. (2014c) as modified most recently by Scheyer et al. (2017) used to assess the relationships of early Mesozoic marine tetrapods. Following Chen et al. (2014c), we run two analyses using this second matrix: (Analysis 2) incorporating all characters, and (Analysis 3) modifying marine-related characters to uncertainty (see Supplemental information). We also added OTUs representing Hupehsuchia and *Hanosaurus* to the matrix of Li *et al.* (2014) and modified two characters (see Supplemental Information). These three analyses provide complementary results for detailed relationships of saurosphargids (Li et al., 2014) and for broader diapsid and marine tetrapod relationships using a recent data set (Chen et al., 2014c; Scheyer et al., 2017). All analyses were implemented using maximum parsimony in TNT version 1.5 (Goloboff & Catalano, 2016), and Bayesian inference in MrBayes version 3.2.7a (Ronquist et al., 2012) using gamma- and log-normal-distributed rates models (see Supplemental Material). Convergence of the analyses in MrBayes was checked using estimated sample size (ESS) > 200 and plotting traces of the MCMC output in R version 4.1.0 (R Core Team, 2021) and package CODA version 0.19.4 (Plummer et al., 2006). Model comparison used a stepping-stone analysis implemented in MrBayes (Xie et al., 2011) and comparisons of Bayes factors (Kass & Raftery, 1995).

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. The ZooBank LSIDs (Life Science Identifiers) 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: zoobank.org:act:42A625CB-EE27-4432-8606-7DD0ADC760D4. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

SYSTEMATIC PALAEONTOLOGY

Diapsida Osborn, 1903 [Gauthier & de Queiroz, 2020]

Saurosphargiformes tax. nov., new clade name

Phylogenetic definition: The maximum clade including *Saurosphargis volzi* Huene, 1936, but excluding *Placodus gigas* Agassiz, 1839, *Plesiosaurus dolichodeirus* Conybeare, 1824, and *Hupehsuchus nanchangensis* Young & Dong, 1972. **Abbreviated definition:** max ∇ (*Saurosphargis volzi* Huene, 1936) | ~ (*Placodus gigas* Agassiz, 1839 & *Plesiosaurus dolichodeirus* Conybeare, 1824 & *Hupehsuchus nanchangensis* Young & Dong, 1972).

Discussion: Diagnostic characters for this new clade are taken from the phylogenetic analyses presented below as well as comparing shared (non-phylogenetic) morphology with the diagnosis of Saurosphargidae presented by Li *et al.* (2014); this is amended below.

Diagnosis: Aquatic diapsids characterized by the following combination of characters: (1) low neural spine of dorsal vertebrae?with table-like top; (2) presence of dorsal osteoderms; (3) transverse processes of dorsal vertebrae distinctly long; (4) anterior ribs developing facets for ossicles dorsally; (5) gastralia elongate and flattened; (6) lateralmost elements of gastral ribs broadened and contacting each other; (7) humerus not expanded at both ends.

Referenced phylogeny: The referenced phylogeny for Saurosphargiformes is shown in Figure 5A in this publication.

Saurosphargidae Li et al., 2011

Phylogenetic definition: The minimum clade including *Saurosphargis volzi* Huene, 1936, *Largocephalosaurus polycarpon* Cheng et al., 2012, and *Sinosaurosphargis yunguiensis* Li et al., 2011, and all its descendants. **Abbreviated definition:** min ∇ (*Saurosphargis volzi* Huene, 1936 & *Largocephalosaurus polycarpon* Cheng et al., 2012 & *Sinosaurosphargis yunguiensis* Li et al., 2011).

Discussion: A phylogenetic definition for Saurosphargidae has not previously been set down; the name is based on inclusion of the type species *Saurosphargis volzi* (Li et al., 2011), and diagnosed based on *Largocephalosaurus* and *Sinosaurosphargis* (Li et al., 2014). We propose a minimum (node-based) clade definition matching the indications of Saurosphargidae in previous phylogenetic hypotheses, differentiating Middle Triassic Saurosphargidae from more plesiomorphic Saurosphargiformes. The diagnosis below is modified from Li *et al.* (2014) based on our phylogenetic analyses and comparing shared characters with the more inclusive Saurosphargiformes.

Diagnosis: Modified from Li *et al.* (2014): (1) dorsal ribs forming a closed basket; (2) presence of large dorsal osteoderms [modified]; (3) external naris retracted; (4) median elements of gastral ribs with a two-pronged lateral process on one side; (5) supratemporal extensively contacting quadrate shaft; (6) posterior margin of skull roof deeply emarginated; (7) jugal-squamosal contact; (8) presence of ectopterygoid; (9) presence of interpterygoid vacuity and open braincase-palatal articulation; (10)

leaf-shaped tooth crown with convex labial surface and concave lingual surface; (11) tip of neural spines covered by osteoderms [modified]; (12) large interclavicle boomerang-like or atypical T-shaped, with a small and sharp posterior process; (13) nine carpals; (14) four tarsals; (15) pachyostosis of dorsal ribs [new]; (16) distal end of transverse process distinctly thickened [new]; (17) deltopectoral crest absent [new]; (18) median gastral rib elements two-pronged with lateral process on one side [new].

Referenced phylogeny: The referenced phylogeny for Saurosphargidae is shown in Fig. 5A of this publication.

Eliminado: in

Pomolispondylus biani gen. et. sp. nov.

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

LSID: zoobank.org:act:42A625CB-EE27-4432-8606-7DD0ADC760D4

Etymology: The generic name *Pomolispondylus* is from the Greek ‘πόμολα σπόνδυλο’ (pómola spóndylo) meaning ‘knobbly vertebra’, referencing the morphology of the neural spines; the specific name *biani* honors Bian He, a famous Chinese historical figure from the locality.

Holotype: Part and counterparts: WGSC V 1701-1 and V 1701-2 (Figs 2, 3). When WGSC V 1701 was removed from the matrix the rock split into two parts along the fossil layer and some elements were broken. Most elements are present on the part specimen (WGSC V 1701-1; Fig. 2A), while four posterior dorsal and two sacral vertebrae are on the counterpart with impressions of the neural spines, ribs, and fore and hind limbs of the right side (WGSC V 1701-2; Fig. 2B). The length of WGSC V 1701-1 is 128.54 mm, and the counterpart WGSC V 1701-2 is 200.8 mm long.

[Insert Figure 2 here]

Locality and Horizon: Member II of the Jialingjiang Formation, Spathian (Olenekian), Early

Triassic; Songshugou Quarry, Xuanjianzhen, Nanzhang County, Hubei Province, China. The definition of the Jialingjiang Formation was revised and three members were recognized based on geological mapping in Nanzhang and Yuan'an counties recently (Yan et al., 2021). The NYF is found at the top layers of Member II in the Jialingjiang Formation (Fig. 1).

Eliminado: to

Eliminado:

Eliminado: in

Diagnosis: Saurosphargiformes with the following unique combination of characters: at least 18 dorsal vertebrae, two sacral vertebrae; neural spine heavily rugose dorsally; vertebral centrum with parallel lateral surfaces; proximal end of dorsal ribs slightly pachyostotic; lateral margin of distal part of dorsal rib developing oval facet; dense, sheet-like gastralia, with four grouped elements corresponding to one centrum; a small ossicle attaching the distal end of the lateral element of gastralia; humerus curved more strongly than straight femur; medial margin of pubis rounded.

DESCRIPTION

Size

As preserved the specimen WGSC V 1701 measures 200.8 mm on the counterpart specimen (WGSC V 1701-2), while the dorsal portion is around 150 mm long. This size? is comparable to that of *Keichousaurus yuananensis* from the same formation (dorsal length 145 mm in IVPP V2799; Young, 1965), and to the small Middle Triassic pachypleurosaurs like *Dianopachysaurus dingi* (Liu et al., 2011) and *Dianmeisaurus gracilis* (trunk length 98 mm in IVPP V 18630; Shang & Li, 2015). The humerus impression indicates that it was 31.5 mm in WGSC V 1701. This is notably smaller than the humerus of *Lariosaurus sanxiaensis* (58.02 mm in HFUT YZS-16-01; Li & Liu, 2020) and *Hanosaurus hupehensis* (by way of comparison: the femur is 43.2 mm in IVPP V3231; Young & Dong, 1972; Rieppel, 1998). WGSC V 1701 is also smaller than Hupehsuchia from the same locality: the smallest *Eretmorhipis carrolldongi* has a dorsal length 255 mm (IVPP V4070; Chen et al., 2015) and *Eohupehsuchus brevicollis* is incomplete at 236 mm (WGSC 26003; Chen et al., 2014b), up to *Parahupehsuchus longus* with a dorsal length of 500 mm (WGSC 26005; Chen et al., 2014a). Estimates of presacral length vary given the different morphological proportions of compared taxa, but suggest little more than 200 mm, and likely smaller than 329 mm (Table 1).

Eliminado: s

Ontogenetic assessment

Maturity of the specimen is determined from comparisons with closely related Sauropterygia and modern lepidosaurs and archosaurs. This is made problematic due to the focus on cranial determinants that aren't preserved in the material herein described. However, we identified the following characters that support a mature determination: neural spines fused to the vertebral centrum (Klein, 2012; Griffin et al., 2021); ossified zygantrum-zygosphene articulation, long bone epiphyses (as indicated by the sharp impressions), and ossified? ulnare (Lin & Rieppel, 1998; Griffin et al., 2021), along to humerus as robust as the femur (Lin & Rieppel, 1998).

Eliminado: is

Comentario [GP3]: Sharp end of long bones may be due to immaturity or to the presence of aquatic habits. Thus, if the new species is aquatic, this character is ambiguous for maturity.

Eliminado: ;

Centra & Ribs

In WGSC V1701-1, there are 11 dorsal? centra preserved that are covered by the neural arches dorsally, and six centra in WGSC V1701-2, which are obscured by the gastralia and pelvic elements. Adding two impressions of anterior dorsal? vertebrae gives a total of around 20 presacrals? (Fig. 2). The vertebral centra are oblong in dorsal view with straight lateral faces to the centra, unlike the concave shape seen in later Sauropterygia (e.g. *Dianmeisaurus* [Shang, Li & Wu, 2017] and *Keichousaurus* [Lin & Rieppel, 1998]) and in *Largocephalosaurus* (Li et al., 2014). The anteriormost rib impression does not join to an impression of a vertebra, but more posterior elements are generally well articulated. The first rib impression is much shorter than the posterior neighboring impressions as in *Largocephalosaurus* (Fig. 2B; Li et al., 2014), suggesting that the first rib impression represents the last cervical rib. This is supported by the similarity of a partially preserved rib anteriorly and first completely preserved rib; thus, we interpret the partially preserved rib to be the first dorsal rib. Based on this interpretation, there are 18 dorsal and 2 sacral vertebrae present in both parts of the specimen; this is much fewer than in *Largocephalosaurus* (24 dorsal, 2 sacral centra; Li et al., 2014), *Lariosaurus sanxiaensis* (~26 dorsal; Li & Liu, 2020), and *Anarosaurus* (25 dorsals; Klein, 2012), but similar to the pachypleurosaurs *Keichousaurus yuananensis* (19–20 dorsals; Young, 1965) also from the Early Triassic, and *Dianopachysaurus* (19 dorsals, 3 sacrals; Liu et al., 2011), *Diandongosaurus* (18 dorsals, 3 sacrals; Sato et al., 2014), and *Dianmeisaurus* (18 dorsals, 4 sacrals; Shang & Li, 2015) from the Middle Triassic.

Comentario [GP4]: This is contradictory, please define if the anteriormost rib is the last cervical or the first dorsal.

Con formato: Fuente: Sin Negrita, Francés (Francia)

Con formato: Fuente: Sin Negrita, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Dorsal Vertebrae

The transverse processes of the dorsal vertebrae are elongate: about twice the lateral width of the centrum (e.g., 9.06 vs. 17.22 mm in the anteriormost preserved vertebra), or more than twice the width across the prezygapophyses (e.g., 8.71 vs. 18.52 mm in the eighth preserved vertebra). These are longer than in *Lariosaurus sanxiaensis* (Li & Liu, 2020) and in later small pachypleurosaurs (e.g. *Dianmeisaurus* [Shang, Li & Wu, 2017], *Diandongosaurus* [Liu et al., 2015]), but shorter than in Saurosphargidae. Laterally the transverse processes narrow to a rhombus-like shape in dorsal view (Figs 2B, 3A, B), rather than the more narrow, elongate forms that are found in *Saurosphargis* and *Largocephalosaurus* (Nosotti & Rieppel, 2003; Li et al., 2014). It appears to be rounded in cross section, but the specimen has been dorsoventrally compressed, so the original shape cannot be determined. The zygantrum-zygosphene articulation, as preserved, is present above and between the zygapophyses, as shown between dorsals 4 and 5 (Fig. 3A, B).

[Insert Figure 3 here]

The neural spines of the new taxon are unusual. Each neural spine is very low (just exceeding the height of the neural arch; Figs 2C, 3A, B, 4A), like in *Lariosaurus sanxiaenesis*, *Keichousaurus yuananensis*, and later pachypleurosaurs (Fig. 4D; Young, 1965; Shang, Li & Wu, 2017; Li & Liu, 2020), and does not extend dorsally as in *Sinosaurosphargis* (Fig. 4F; Li et al., 2011). The neural spine then expands horizontally near the neural arch, particularly anteroposteriorly (Figs 3A, C, 4A), so that the neighboring two neural spines contact each other on their anterior and posterior margins (Figs 2A, 3A, B). However, the neural spine differs from *Lariosaurus sanxiaenesis, Keichousaurus yuananensis, Hanosaurus hupehensis*, and pachypleurosaurs by quickly expanding posteriorly and becoming laterally broader towards its posterior (Figs 2A, 3A, B, 4A, D, G; Young, 1965; Rieppel, 1998). Additionally, the size of the neural spines increases posteriorly along the vertebral column (Figs 2A, 3A). The length/width ratios of neural spines 10 to 13 are 8.82/8.23, 8.68/7.27, 9.15/7.78, 9.32/7.62, respectively (Fig. 2A, C).

The dorsal neural spines form an elliptical table (Figs 2C, 3A, 4A), as in *Largocephalosaurus*, *Eusaurosphargis*, Placodontoidea, and *Eorhynchochelys* (Nosotti & Rieppel, 2003; Li et al., 2014, 2018; Cheng et al., 2015; Scheyer et al., 2017). However, the surface of this table in the new taxon is slightly convex dorsally, with abundant tuber-like ornaments in the surface, whereas the dorsal neural spines in

Eliminado: s

Largocephalosaurus, *Eusaurosphargis*, and Placodontoidea are flattened or slightly concave (Figs 3A, B, 4A, C, E). The tubers in the center of the neural spines table are distinctly larger than the surrounding ones and sub-circular, while the surrounding tubers are elongated radially (Fig. 3A, B). In *Largocephalosaurus*, *Eusaurosphargis*, Placodontoidea, and *Eorhynchochelys*, the dorsal neural spines are covered by at least one layer of osteoderms. It is difficult to identify the shape in *Sinosaurosphargis*, because its body trunk is covered by small dense osteoderms (Li et al., 2011). However, there are no osteoderms preserved near the vertebral column in this specimen, indicating that the table of the neural spine was possibly covered by soft tissue.

[Insert Figure 4 here]

Dorsal Ribs

The dorsal ribs are single-headed (shown at their contact with the lateral centra and on anterior broken surfaces of the part specimen), as in *Lariosaurus sanxiaensis, Majiashanosaurus discocoracoideus*, and Middle Triassic pachypleurosaurs (Jiang et al., 2014; Li & Liu, 2020; Liu et al., 2021), and apparently articulate with the vertebral centra ventral to the transverse process (Figs 2A, 3A, B, 4A); however, compaction of the specimen has made the positions of the rib uneven. Proximally, the ribs are somewhat thickened for approximately one-quarter of their length and narrow only slightly to the rather stout, rounded distal end of the rib. In cross section, the ribs are rounded and sub-circular.

The anterodorsal margin of the rib develops a low crest near the distal end in each of dorsal ribs 1 to 15. The crest forms an elliptical facet that extends distally along the shaft of the rib with a flat, smoothed surface (Figs 2A, 4B). This is different from *Saurosphargis*, *Largocephalosaurus*, and

Eliminado: is

Eusaurosphargis in which the dorsal rib develops an uncinate process at the shoulder region (Fig. 4E; Nosotti & Rieppel, 2003; Li et al., 2014), however, no uncinate process is present in *Sinosaurosphargis* (Fig. 4F; Li et al., 2011). The distal rib in *Lariosaurus sanxiaensis* and *Hanosaurus hupehensis* distally narrow (Fig. 4D, G; Rieppel, 1998; Chen et al., 2016), but a small crest is seen in *Eusaurosphargis* and a larger uncinate process the placodont *Paraplacodus* (Rieppel, 2000; Klein & Sichelschmidt, 2014; Scheyer et al., 2017).

All dorsal ribs in the present specimen are more slender than other saurosphargiforms, so the inter-rib spacing is distinct to *Pomolispondylus biani*. The posterior two ribs present in the part specimen (WGSC V1701-1) orientated slightly anteriorly in their proximal region with a strong posterior curve strongly distally. Impressions of posterior three slender and short dorsal ribs are preserved to the right of the vertebral column with pointed distal ends (Fig. 2B). The 16th dorsal rib curves posteromedially like the anterior ones. The distinctly short and slender last two dorsal ribs extend anterolaterally (Fig. 2B).

Sacral & Caudal Ribs

There are two impressions of sacral ribs in the counterpart that are almost equal in size and shape (Figs 2B, 3C, D). The sacral rib is distinctly short, stout, and slightly expanded distally. There are three impressions of caudal ribs. The first caudal rib impression extends anterolaterally, with the tip close to the second sacral rib. The latter two caudal ribs are oriented laterally, with conical tips.

Gastralia & Osteoderms

Gastralia are present associated with the vertebrae and ribs between the posterior coracoid and the anterior pubis, packed densely and forming a ventral sheet covering the abdomen (Figs 2A, B, 3, 4A, B).

Most of the gastralia are covered by the vertebral column and dorsal ribs as preserved, however, several of the most posterior gastralia are visible on the counterpart specimen (WGSC V 1701-2; Fig. 2B) and parts of other gastralia can be seen between the ribs (Figs 2A, 3, 4A, B). Each gastral row consists of five elements: one medial and two lateral on each side (named first lateral and lateralmost here).

The median gastral element is relatively broad and slightly bowed with the distal tips curving posteriorly; there is no anterior process as in *Sinosaurosphargis* and *Largocephalosaurus* (Li et al., 2011, 2014), which differs from *Lariosaurus sanxiaensis* and *Hanosaurus hupehensis* (Rieppel, 1998; Chen et al., 2016; Li & Liu, 2020) . The distal tips of the medial element taper to a fine point that inserts between the immediately anterior row and the associated first lateral and lateralmost elements in the same row (Fig. 2A). Laterally the ramus extends to contact the first lateral and lateralmost elements, spreading across about one-half of the width of the trunk; the contact is close but appears to be a simple butt join. The first lateral element is the shortest and fits posterior to the medial and lateralmost elements, extending medially nearly to the trunk midline and laterally approximately ventral to the dorsal ribs. The lateralmost element is slender and straight, with an extensively tapered medial end but a blunt, rounded distal end. This configuration is similar to Saurosphargidae and Early Triassic Sauropterygia (Rieppel, 1998; Li et al., 2014).

The gastral series is very dense: medial elements contact neighboring medial elements anteroposteriorly along the trunk midline (Fig. 2B), while more distally they are inserted between the first lateral and lateralmost elements from the same gastral row and the row immediately anterior to it (Fig. 2A). The lateralmost elements are positioned closely between rows, but do not contact each other distally as they are separated by the first lateral element. Four rows of gastralia correspond to one dorsal vertebra.

A series of small, irregularly shaped bone plates are found lateral to each gastral row that we interpret as rudimentary osteoderms (Figs. 2A, 4B). These plates form two rows along the lateral part of the gastral basket. Some of the more prominent plates are spindle shaped, and the dorsal surface develops ridge-like protrusions along the long axis (Fig. 4B). In *Sinosaurosphargis*, a bony plate covers the entire torso, possibly including the lateral ribs (Fig. 4F; Li et al., 2011). In *Largocephalosaurus*, the distal ribs are not connected to the osteoderms (Fig. 4E; Li et al., 2014), but in *Eusaurosphargis* the lateral rib contact a larger teardrop-shaped osteoderm (Nosotti & Rieppel, 2003; Scheyer et al., 2017). Osteoderms have not been reported for *Lariosaurus sanxiaensis*, *Hanosaurus hupehensis*, and *Keichousaurus yuananensis* (Fig. 4D, G; Young, 1965; Rieppel, 1998; Chen et al., 2016). *Eusaurosphargis* has larger lateral osteoderms than in WGSC V 1701 with distinct processes forming a triangle- or T-shape (Scheyer et al., 2017), while the osteoderms in placodonts like *Cyamodus* are also more strongly developed (Pinna, 1992), although notably absent in the plesiomorphic *Paraplacodus* (Rieppel, 2000; Neenan, Klein & Scheyer, 2013).

Appendicular Skeleton

The posterior portions of the two coracoids can be seen between dorsal vertebra 4 and 5 on the part specimen (WGSC V1701-1) with a convex lateral margin (Figs 2B, 3A, B), but no detail can be determined. Other appendicular elements including much of the right pubis, and fragments of the possible left scapula and ischium together with their impressions preserved in the counterpart (WGSC V 1701-2: Fig. 2B). Only the proximal part of the left scapula is preserved in the counterpart specimen presenting the lateral process, if this is identified correctly based on its association with the humerus (Fig. 2B). The

Comentario [GP5]: Are you sure that fragments of the scapula (anterior girdle) are preserved together incomplete pubis and ischium (pelvic girdle)? Please, verify and modify text.

Eliminado: are

process, together with the responding impression, roughly shows the shape of the whole left scapula. The scapular impression is bow-like, with a slight angle at its mid-length where it is widest and narrows to a sharp distal terminus. This is similar in form to the scapula in dorsal view in *Largocephalosaurus qianensis* (Li et al., 2014), and broadly corresponds to Sauropterygia (e.g. *Placodus*, *Paraplacodus*, *Cyamodus*, *Dianmeisaurus*) and *Eusaurosphargis* (Pinna, 1980; Rieppel, 1995, 2000; Shang, Li & Wu, 2017; Scheyer et al., 2017).

The distal portion of the right pubis is lost, but proximally it is preserved in ventral view (Figs 2A, 3C, D). The medial margin is strongly convex and covers around three vertebral centra. More distally the pubis narrows slightly (seen on the anterior margin). There is only a small fragment and subtle impression of the ischium, but it appears to be a short, bar-shaped element. Impressions of the humerus and femur are also present in the counterpart specimen. The humerus impression is somewhat more robust than the femur impression and has a posteriorly-directed curve (Fig. 2B), like other saurosphargiforms (Li et al., 2011, 2014) and Early Triassic Sauropterygia (Rieppel, 1998; Chen et al., 2016; Li & Liu, 2020), but little sign of a median constriction can be seen. However, the femur is straight and expands somewhat towards the proximal end, like in most Eosauropterygia and all Saurosphargiformes (Li et al., 2011, 2014; Jiang et al., 2014).

PHYLOGENETIC ANALYSES

Pomolispondylus biani could be coded for 41/159 characters (25.8% completeness) in the matrix of Li et al. (2014) and for 32/280 characters (11.4% completeness) in the matrix of Li et al. (2018). Our phylogenetic analyses recovered Saurosphargidae, as defined above, in all analyses except Analysis 2 under parsimony (Supplemental Material Fig. S2), with *P. biani* as its immediate sister taxon (Figs 5, 6; Supplemental Material Figs S1–S15). Support for Saurosphargidae is relatively high where recovered (bootstrap support ≥85%, Bremer support ≥2 under parsimony; credibility value ≥99% under Bayesian inference), but there is lower support for the clade *P. biani* + Saurosphargidae (bootstrap support 45%, Bremer support 2 under parsimony; credibility value ≥54%). All Bayesian inference analyses in MrBayes converged with estimated sample sizes > 1000 for all parameters (Supplemental Material Table S3, Figs. S5, S7, S9, S11, S13, S15). Strong preference for the log-normal model was found in Analysis 2 (Bayes Factor difference = 6.62) and positive support for the log-normal model in Analysis 1 (Bayes Factor difference = 2.64), but neither the gamma nor log-normal model was preferred in Analysis 3 (Bayes Factor difference = 0.42; Supplemental Material Table S4) (Kass & Raftery, 1995). For each analysis, gamma and log-normal models produced near-identical topologies and support values.

In Analysis 1, the topology recovered under parsimony largely matches Li *et al.* (2014) (Fig. 5A), however, *Helveticosaurus* and *Eusaurosphargis* are included within Sauropterygia in a more nested position alongside placodonts, Ichthyopterygia are recovered within Sauropterygia, and Saurosphargidae + *P. biani* are nested with Hupehsuchia and Thalattosauria. The topology is broadly similar under Bayesian inference (Fig. 5B; Supplemental Material Figs S4, S6), however, Saurosphargiformes + Hupehsuchia are positioned within Sauropterygia in a more deeply-nested position than placodonts. In analysis 1 (Fig. 5A), Saurosphargidae have the following synapomorphies: (1) distal transverse process distinctly thickened [char. 68, state 1]; (2) pachyostosis of dorsal ribs [char. 72, state 1]; (3) deltopectoral crest absent [char. 93, state 2]; (4) median gastral rib elements two-pronged with lateral process on one side [char. 119, state 1]; while elongated and narrow transverse processes [char. 66, state 1] is also recovered for only some trees. Saurosphargiformes have the synapomorphies: (1) sacral ribs without distinct expansion of the distal head [char. 74, state 1]; (2) scapula with constriction separating the glenoid [char. 84, state 1]; and humerus curved [char 92, state 1]. Seven characters are shared between Hupehsuchia + Saurosphargiformes (see Supplemental Material) but homoplastic in these phylogenetic hypotheses, some of which are likely ecologically convergent with *Pomolispondylus biani* and other Saurosphargiformes (e.g. straight femoral shaft [char. 104, state 0]; osteoderms [char. 136, state 1]; closely-associated gastral sets [char. 158, state 1; see Supplemental Material). Constraining a monophyletic Ichthyopterygia + Hupehsuchia resulted in trees of length 611 (three steps longer) but causes Sauropterygia to collapse almost completely.

[Insert Figure 5 here]

In analyses 2 and 3 (Fig. 6; Supplemental Material Figs S2, S3, S8, S10, S12, S14), the main marine reptile groups are present in a polytomous clade, with Analysis 2 additionally resolving a sister relationship between Thalattosauria and other marine reptiles (e.g. Sauropterygia, Ichthyosauromorpha, Saurosphargiformes; Supplemental Material Fig. S8, S10). Saurosphargiformes are united by: (1) the zygosphene-zygantrum articulation [char. 44], (2) curved humerus [char. 60], and (3) presence of osteoderms [char. 193], while Saurosphargidae are further united by (1) holocephalous ribs only articulating with the neural arch [char. 104], (2) pachyostosis of the dorsal ribs [char. 189], and (3) contact between the dorsal ribs forming a “rib basket” [char. 197]. Saurosphargiformes are allied with Thalattosauria by (1) a displaced mandibular articulation [char. 22], (2) slender supratemporal [char. 115], and (3) ossified atlantal ribs [char. 144].

[Insert Figure 6 here]

Saurosphargiformes are not recovered as a distinct clade in Analysis 2 under maximum parsimony (Supplemental Material Fig. S2) or Analysis 3 under Bayesian inference (Fig. 5; Supplemental Material Fig S12, S14). These cases correspond to a lack of resolution among the marine reptiles more generally that most likely results from the inclusion and different treatment of homoplastic characters between the two phylogenetic methods. The phylogenetic hypothesis resulting from exclusion of the marine-related characters (Figs 6B; Supplemental Material Figs S3, S12, S14) was favored by Chen et al. (2014c) because these characters are frequently homoplastic, representing convergences from pressures of aquatic habitats.

DISCUSSION

The Nanzhang-Yuan'an Fauna (NYF) is located in a restricted platform lagoonal setting, thus shallow water marine reptiles dominate (Fig. 1B; Young & Dong, 1972; Chen et al., 2013; Cheng et al., 2015). In recent years discovery of additional Hupehsuchia have extended the taxic and ecological diversity with features including edentulism (e.g. *Hupehsuchus*, *Nanchangosaurus*: Chen et al., 2014c, 2015) and pachyostotic ribs for body protection (e.g. *Parahupehsuchus*: Chen et al., 2014a). *Pomolispondylus biani* is among the smaller species in the NYF, with an intergirdle length around 110 mm, comparable to *Keichousaurus* from South China (Cheng et al., 2009). Estimates by comparison to other Saurosphargiformes and Sauropterygia suggests a total presacral length around 200 mm (see Table 1 and Supplemental Material), making *P. biani* one of the smaller Early Triassic marine tetrapods (Scheyer et al., 2014).

Pomolispondylus biani shares the following traits with Sauropterygia: elongation of the neural arches, low neural spine, medially curved humerus, five-part gastralial rows. The present specimen, however, shows several differences to most Sauropterygia: a laterally-widened dorsal neural spine only found in the placodont *Placodus* (Jiang et al., 2008) and that is more typical of *Largocephalosaurus*, *Eusaurosphargis* (Li et al., 2014; Scheyer et al., 2017), and the stem turtle *Eorhynchochelys* (Li et al., 2018). Neither proximal expansion of the dorsal ribs nor the tuberosity of the dorsal neural spines occur in the holotype of *Eorhynchochelys* (Li et al., 2018), whereas these are present in Sauropterygia such as *Keichousaurus* (Cheng et al., 2009).

Despite this, there are differences between WGSC V 1701 and Saurosphargidae, including no strongly developed dorsal ossified dermal plates and shorter transverse processes of the neural spine. As this specimen is Early Triassic in age, it is older than other Saurosphargidae, known from the Middle Triassic (Li et al., 2011, 2014). Although there is uncertainty in the resolution of plesiomorphic Sauropterygia in our phylogenetic analyses, a clade including Saurosphargidae and *P. biani* is recovered either within Sauropterygia (Fig. 5A) or in close relation (Figs 5B, 6), which we name Saurosphargiformes.

Eliminado: dorsally

The relationships between the major marine reptile groups Hupehsuchia, Thalattosauria, Sauropterygia, and Saurosphargiformes are also uncertain (Figs. 5, 6). Hupehsuchia are found as sister to Saurosphargiformes in analysis 1 using the matrix from Li *et al.* (2014) (Fig. 5). Some of the synapomorphies of this Hupehsuchia + Saurosphargiformes clade likely represent homoplasy among ecologically-adapted characters, such as presence of osteoderms (analysis 1, char. 136, state 1; analyses 2 and 3, char. 193, state 1) and gastralia closely associated (analysis 1, char. 158, state 1) both associated with the development of carapace-like structures (Chen et al., 2014c; Scheyer et al., 2017). This likely results from the focus of the phylogenetic matrix in Analysis 1 on Sauropterygia and terrestrial ancestors, so doesn't fully account for specialization of Ichthyosauriformes, particularly in the skull and limb structure, related to modification of their primary locomotory mode (Chen et al., 2014c; Motani et al., 2015; Scheyer et al., 2017). In the NYF, Hupehsuchia and *Hanosaurus* co-occur with *Pomolispondylus* and share morphological characters with it and Saurosphargiformes typical of the Middle Triassic: the abdominal ribs are widened laterally and are closely arranged in contact, and the pubis is rounded. The clade Thalattosauria + Hupehsuchia + Saurosphargiformes is supported in analysis 1 (Fig. 5A) by a posteriorly displaced mandibular articulation [char. 22], slender supratemporal [char. 115], and ossified atlantal ribs [char. 144]. However, homoplasy is indicated by several reversals of characters between Thalattosauria, Hupehsuchia, and Saurosphargiformes.

The relationship between *Pomolispondylus* and Saurosphargidae allows inference of the transformation that the "carapace" underwent in Saurosphargiformes. We propose that initially cartilaginous plates developed dorsally on the neural spines and around the dorsal ribs, as in *Pomolispondylus*, then became ossified into the small bony plates found in *Largocephalosaurus* (Cheng et al., 2012; Li et al., 2014), or ossified extensively and extended across the dorsal trunk region in *Sinosaurosphargis* (Li et al., 2011). This is supported by recovery of osteoderms present in Saurosphargiformes as a character change (and Hupehsuchia when sister taxa: char. 136 in analysis 1; char. 193 in analyses 2 and 3), with subsequent modification to dense osteoderms in *Sinosaurosphargis* (Figs 5, 6; see Supplemental Material). Presence of osteoderms in Triassic marine reptiles is relatively labile, sometimes alongside other pachyostotic morphology interpreted as adaptation to a shallow marine habitat (Scheyer, 2007; Houssaye, 2009). There remains the possibility, however, that osteoderms in placodonts and saurosphargiforms share the same phylogenetic origin. Other Hupehsuchia from the NYF have been noted for their dorsal armor, indicating selection pressures from predation (Chen et al., 2014a) that may have driven the evolution of dermal ossicles in Saurosphargiformes.

This new find highlights the presence of a diverse Early Triassic fauna and the filling of different niches within the NYF, which is otherwise dominated by hupehsuchians (Cheng et al., 2015; Reeves et al., 2021). This increasingly complex ecosystem marks the beginnings of recovery following the EPME and establishing the reptile-dominated ecosystems found through the Mesozoic. The NYF also supports a different complement of taxa than other Early Triassic localities (e.g. Majiashan, Anhui, China [Jiang et al., 2014; Zhou et al., 2017]; Spitsbergen, Svalbard [Maxwell & Kear, 2013; Ekeheien et al., 2018]), particularly in the presence of diverse Hupehsuchia and small reptile taxa (i.e. *Keichousaurus* and *Pomolispondylus*). There is currently no evidence for large macropredators above 2 m in the NYF, which have been identified in other Early Triassic faunas (Scheyer et al., 2014). Hupehsuchia are the largest representatives of the NYF, but have an unusual slender “duck-billed” skull (Qiao, Iijima & Liu, 2020), while *Lariosaurus sanxiaensis* and *Hanosaurus* are the largest piscivores (Cheng et al., 2015; Li & Liu, 2020). As the NYF represents a restricted lagoon, this may skew the feeding modes present. The lack of fish and macroinvertebrates in the NYF precludes establishing the full food web, however, the diversity of sizes and feeding modes supports limited but productive ecosystem.

This low? diversity has been argued to indicate the earlier recovery of marine vertebrate ecosystems than previously thought (Jiang et al., 2014), however, the relative abbreviation of food chains found in these Early Triassic ecosystems instead supports changing constructions of ecosystems between the Early and Middle Triassic and a more delayed recovery (Benton et al., 2013; Cheng et al., 2015; Song,

Código de campo cambiado

Con formato: Inglés (Estados Unidos)

Comentario [GP6]: Fish and macroinvertebrate absent may have indicate harsh environments, where only opportunistic species can live (see Piñeiro et al. 2012)
Piñeiro, G., Ramos, A., Goso, C., Scarabino, F., & Laurin, M. 2012. Unusual environmental conditions preserve a Permian mesosaur-bearing Konservat-Lagerstätte from Uruguay. *Acta Palaeontologica Polonica*, 57 (2): 299-318. doi.org/10.4202/app.2010.0113

Wignall & Dunhill, 2018; Li & Liu, 2020). The size and morphology of *P. biani* follows from infilling of ecological niches while there is spare carrying capacity prior to the building up of the ecosystem (Song, Wignall & Dunhill, 2018; Reeves et al., 2021), however, the geographical restriction and temporal brevity in which the taxa present in the NYF are found otherwise indicate the brief flourishing of a transitional fauna before later turnover.

Comentario [GP7]: Both scenarios are possible considering the evidence provided. So, I would leave this conclusion with some kind of uncertainty until more discoveries can be made. Besides, it is possible that not all the taxa found in the lagoon lived in the ecosystem.

ACKNOWLEDGEMENTS

We thank Michael Benton (University of Bristol), Xiao-chun Wu (Canadian Museum of Nature), and Li Tian (China University of Geosciences, Wuhan) for discussion on this specimen. We also thank Dongyi Niu for fossil collection and preparation.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Funding was provided by China National Natural Science Foundation grant 41972014, China Geological Survey DD20190811 and DD20221634 to C.L., C.B.Y., Z.H.A., R.M., D.Y.J., Z.C.F.; B.C.M. was funded by NERC BETR grant NE/P013724/1 and ERC grant 788203 (INNOVATION).

Competing Interests

The authors declare no competing interests.

Authors' Contributions

C.L. conceived the project; all authors examined the specimens. C.L. and B.C.M. ran the phylogenetic analyses. C.L. and B.C.M. wrote the first draft of the manuscript and all authors contributed to subsequent versions.

Supplemental Information

Data and implementation code for this paper is available in the Supplemental Material file.

REFERENCES

Agassiz L. 1839. *Recherches sur les Poissons Fossiles*. Neuchâtel: Imprimerie de Petitpierre.

Alvarez SA, Gibbs SJ, Bown PR, Kim H, Sheward RM, Ridgwell A. 2019. Diversity decoupled from ecosystem function and resilience during mass extinction recovery. *Nature* 574:242–245. DOI: 10.1038/s41586-019-1590-8.

Benton MJ, Zhang Q, Hu S, Chen Z-Q, Wen W, Liu J, Huang J, Zhou C, Xie T, Tong J, Choo B. 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth-Science Reviews* 125:199–243. DOI: 10.1016/j.earscirev.2013.05.014.

Carroll RL, Zhi-Ming D. 1991. *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences* 331:131–153. DOI: 10.1098/rstb.1991.0004.

Chen X-H, Cheng L, Wang C, Zhang B. 2016. *Triassic Marine Reptile Faunas from Middle and Upper Yangtze Areas and Their Co-evolution with Environment*. Geological Publishing House.

Chen X, Motani R, Cheng L, Jiang D, Rieppel OC. 2014a. A carapace-like bony body tube in an Early Triassic marine reptile and the onset of marine tetrapod predation. *PLoS ONE* 9:e94396. DOI:

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Código de campo cambiado

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

10.1371/journal.pone.0094396.

Chen X, Motani R, Cheng L, Jiang D, Rieppel OC. 2014b. A small short-necked hupehsuchian from the Lower Triassic of Hubei Province, China. *PLoS ONE* 9:e115244. DOI: 10.1371/journal.pone.0115244.

Chen X, Motani R, Cheng L, Jiang D, Rieppel OC. 2014c. The enigmatic marine reptile *Nanchangosaurus* from the Lower Triassic of Hubei, China and the phylogenetic affinities of Hupehsuchia. *PLoS ONE* 9:e102361. DOI: 10.1371/journal.pone.0102361.

Chen X, Motani R, Cheng L, Jiang D, Rieppel OC. 2015. A new specimen of Carroll's mystery hupehsuchian from the Lower Triassic of China. *PLoS ONE* 10:e0126024. DOI: 10.1371/journal.pone.0126024.

Chen X, Sander PM, Cheng L, Wang X. 2013. A new Triassic primitive ichthyosaur from Yuanan, South China. *Acta Geologica Sinica* 87:672–677. DOI: 10.1111/1755-6724.12078.

Cheng L, Chen X, Zeng X, Cai Y. 2012. A new eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan Province. *Journal of Earth Science* 23:33–40. DOI: 10.1007/s12583-012-0231-z.

Cheng Y-N, Holmes R, Wu X-C, Alfonso N. 2009. Sexual dimorphism and life history of *Keichousaurus hui* (Reptilia: Sauropterygia). *Journal of Vertebrate Paleontology* 29:401–408. DOI: 10.1671/039.029.0230.

Cheng L, Motani R, Jiang D, Yan C, Tintori A, Rieppel O. 2019. Early Triassic marine reptile representing the oldest record of unusually small eyes in reptiles indicating non-visual prey detection. *Scientific Reports* 9:152. DOI: 10.1038/s41598-018-37754-6.

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Cheng L, Yan C, Chen X, Zeng X, Motani R. 2015. Characteristics and significance of Nanzhang/Yuanan Fauna, Hubei Province. *Geology in China* 42:676–684.

Conybeare WD. 1824. On the discovery of an almost perfect skeleton of the *Plesiosaurus*. *Transactions of the Geological Society of London* S2-1:381–389. DOI: 10.1144/transgslb.1.2.381.

Ekeheien CP, Delsett LL, Roberts AJ, Hurum JH. 2018. Preliminary report on ichthyopterygian elements from the Early Triassic (Spathian) of Spitsbergen. *Norwegian Journal of Geology* 98:219–237. DOI: 10.17850/njg98-2-07.

Ezcurra MD, Butler RJ. 2018. The rise of the ruling reptiles and ecosystem recovery from the Permo-Triassic mass extinction. *Proceedings of the Royal Society B* 285:20180361. DOI: 10.1098/rspb.2018.0361.

Feng Z-Z, Bao Z-D, Zheng X-J, Wang Y, Liu M. 2015. There was no “Great Bank of Guizhou” in the Early Triassic in Guizhou Province South China. *Journal of Palaeogeography* 4:99–108. DOI: 10.3724/SP.J.1261.2015.00070.

Frech F. 1903. Trias. In: *Lethaea Geognostica. Handbuch der Erdgeschichte. II Teil. Das Mesozoicum*. Stuttgart: Verlag der E. Schweizerbart’schen Verlagsbuchhandlung, 623.

Fröbisch NB, Fröbisch J, Sander PM, Schmitz L, Rieppel OC. 2013. Macropredatory ichthyosaur from the Middle Triassic and the origin of modern trophic networks. *Proceedings of the National Academy of Sciences* 110:1393–1397. DOI: 10.1073/pnas.1216750110.

Gauthier JA, de Queiroz K. 2020. Diapsida H. F. Osborn 1903 [J. A. Gauthier and K. de Queiroz], converted clade name. In: Queiroz K de, Cantino PD, Gauthier JA eds. *Phylonyms: a Companion to the PhyloCode*. Boca Raton: CRC Press, 1033–1040.

Goloboff PA, Catalano SA. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32:221–238. DOI: 10.1111/cla.12160.

Griffin CT, Stocker MR, Colleary C, Stefanic CM, Lessner EJ, Riegler M, Formoso K, Koeller K, Nesbitt SJ. 2021. Assessing ontogenetic maturity in extinct saurian reptiles. *Biological Reviews* 96:470–525. DOI: 10.1111/brv.12666.

Houssaye A. 2009. “Pachyostosis” in aquatic amniotes: a review. *Integrative Zoology* 4:325–340. DOI: 10.1111/j.1749-4877.2009.00146.x.

Huang J, Motani R, Jiang D, Tintori A, Rieppel O, Zhou M, Ren X-X, Zhang R. 2019. The new ichthyosauriform *Chaohusaurus brevifemoralis* (Reptilia, Ichthyosauromorpha) from Majiashan, Chaohu, Anhui Province, China. *PeerJ* 7:e7561. DOI: 10.7717/peerj.7561.

Huene F von. 1936. *Henodus chelyops*, ein neuer placodontier. *Palaeontographica Abteilung A* A084:99–147.

Jiang D-Y, Motani R, Hao W-C, Rieppel O, Sun Y-L, Schmitz L, Sun Z-Y. 2008. First record of Placodontoidea (Reptilia, Sauropterygia, Placodontia) from the Eastern Tethys. *Journal of Vertebrate Paleontology* 28:904–908. DOI: 10.1671/0272-4634(2008)28[904:FROPRS]2.0.CO;2.

Jiang D, Motani R, Tintori A, Rieppel OC, Chen G, Huang J-D, Zhang R, Sun Z-Y, Ji C. 2014. The Early Triassic eosauropterygian *Majiashanosaurus discocoracoidis* gen. et sp. nov. (Reptilia, Sauropterygia), from Chaohu, Anhui Province, People’s Republic of China. *Journal of Vertebrate Paleontology* 34:1044–1052. DOI: 10.1080/02724634.2014.846264.

Kass RE, Raftery AE. 1995. Bayes factors. *Journal of the American Statistical Association* 90:773–795. DOI: 10.2307/2291091.

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Klein N. 2012. Postcranial morphology and growth of the pachypleurosaur *Anarosaurus heterodontus* (Sauropterygia) from the Lower Muschelkalk of Winterswijk, The Netherlands. *Paläontologische Zeitschrift* 86:389–408. DOI: 10.1007/s12542-012-0137-1.

Klein N, Sichelschmidt OJ. 2014. Remarkable dorsal ribs with distinct uncinate processes from the early Anisian of the Germanic Basin (Winterswijk, The Netherlands). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 271:307–314. DOI: 10.1127/0077-7749/2014/0391.

Li C, Fraser NC, Rieppel OC, Wu X. 2018. A Triassic stem turtle with an edentulous beak. *Nature* 560:1–13. DOI: 10.1038/s41586-018-0419-1.

Li C, Jiang D-Y, Cheng L, Wu X-C, Rieppel O. 2014. A new species of *Largocephalosaurus* (Diapsida: Saurosphargidae), with implications for the morphological diversity and phylogeny of the group. *Geological Magazine* 151:100–120. DOI: 10.1017/S001675681300023X.

Li Q, Liu J. 2020. An Early Triassic sauropterygian and associated fauna from South China provide insights into Triassic ecosystem health. *Communications Biology* 3:1–11. DOI: 10.1038/s42003-020-0778-7.

Li C, Rieppel O, Wu X-C, Zhao L-J, Wang L-T. 2011. A new Triassic marine reptile from southwestern China. *Journal of Vertebrate Paleontology* 31:303–312. DOI: 10.1080/02724634.2011.550368.

Li C, Wu X-C, Rieppel O, Wang L-T, Zhao L-J. 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature* 456:497–501. DOI: 10.1038/nature07533.

Lin K, Rieppel O. 1998. Functional morphology and ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia). *Fieldiana Geology* 39:1–44.

Liu X-Q, Lin W-B, Rieppel OC, Sun Z-Y, Li Z-G, Lu H, Jiang D-Y. 2015. A new specimen of

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Diandongosaurus acutidentatus (Sauropterygia) from the Middle Triassic of Yunnan, China. *Vertebrata PalAsiatica* 53:281–290.

Liu J, Rieppel O, Jiang D-Y, Aitchison JC, Motani R, Zhang Q-Y, Zhou C-Y, Sun Y-Y. 2011. A new pachypleurosaur (Reptilia: Sauropterygia) from the lower Middle Triassic of southwestern China and the phylogenetic relationships of Chinese pachypleurosaurs. *Journal of Vertebrate Paleontology* 31:292–302. DOI: 10.1080/02724634.2011.550363.

Liu Q, Yang T, Cheng L, Benton MJ, Moon BC, Yan C, An Z, Tian L. 2021. An injured pachypleurosaur (Diapsida: Sauropterygia) from the Middle Triassic Luoping Biota indicating predation pressure in the Mesozoic. *Scientific Reports* 11:21818. DOI: 10.1038/s41598-021-01309-z.

Maxwell EE, Kear BP. 2013. Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. *GFF* 135:85–94. DOI: 10.1080/11035897.2012.759145.

Moon BC, Stubbs TL. 2020. Early high rates and disparity in the evolution of ichthyosaurs. *Communications Biology* 3:68. DOI: 10.1038/s42003-020-0779-6.

Motani R, Jiang D-Y, Chen G, Tintori A, Rieppel O, Ji C, Huang J-D. 2015. A basal ichthyosauriform with a short snout from the Lower Triassic of China. *Nature* 517:485–488. DOI: 10.1038/nature13866.

Neenan JM, Klein N, Scheyer TM. 2013. European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nature Communications* 4:1621. DOI: 10.1038/ncomms2633.

Nosotti S, Rieppel OC. 2003. *Eusaurosphargis dalsassoi* n.gen. n.sp., a new, unusual diapsid reptile from the Middle Triassic of Besano (Lombardy, N Italy). *Memorie della Societa Italiana di Scienze*

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Naturali e del Museo Civico di Storia Naturale di Milano Ile 31:1–33.

Osborn HF. 1903. On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* 17:275–276. DOI: 10.2307/1629860.

Peyer B. 1955. Die Triasfauna der Tessiner Kalkalpen. XVIII. *Helveticosaurus zollingeri* n.g. n.sp.. *Schweizerische Paläontologische Abhandlungen* 72:3–50.

Pinna G. 1980. Lo scheletro postcraniale di *Cyamodus hildegardis* Peyer, 1931 descritto su un esemplare del triassico medio Lombardo. *Atti della Società Italiana di Scienza Naturali e del Museo Civico di Storia Naturale di Milano* 121:275–306.

Pinna G. 1992. *Cyamodus hildegardis* Peyer, 1931 (Reptilia, Placodontia). *Memorie della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 26:1–21.

Plummer M, Best N, Cowles K, Vines K. 2006. CODA: convergence diagnosis and output analysis for MCMC. *R News* 6:7–11.

Qiao Y, Iijima M, Liu J. 2020. The largest hupehsuchian (Reptilia, Ichthyosauromorpha) from the Lower Triassic of South China indicates early establishment of high predation pressure after the Permo-Triassic mass extinction. *Journal of Vertebrate Paleontology* 0:e1719122. DOI: 10.1080/02724634.2019.1719122.

R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reeves JC, Moon BC, Benton MJ, Stubbs TL. 2021. Evolution of ecospace occupancy by Mesozoic marine tetrapods. *Palaeontology* 64:31–49. DOI: 10.1111/pala.12508.

Rieppel OC. 1989. *Helveticosaurus zollingeri* Peyer (Reptilia, Diapsida) skeletal paedomorphosis,

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

Con formato: Español (Uruguay)

Con formato: Fuente: Sin Cursiva, Español (Uruguay)

functional anatomy and systematic affinities. *Palaeontographica Abteilung A* 208:123–152.

Rieppel OC. 1995. The genus *Placodus*: systematics, morphology, paleobiogeography, and paleobiology. *Fieldiana Geology* 31:1–44.

Rieppel O. 1998. The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. *Journal of Vertebrate Paleontology* 18:545–557. DOI: 10.1080/02724634.1998.10011082.

Rieppel OC. 2000. *Paraplacodus* and the phylogeny of the Placodontia (Reptilia: Sauropterygia). *Zoological Journal of the Linnean Society* 130:635–659. DOI: 10.1111/j.1096-3642.2000.tb02204.x.

Romano M, Bernardi M, Petti FM, Rubidge B, Hancox J, Benton MJ. 2020. Early Triassic terrestrial tetrapod fauna: a review. *Earth-Science Reviews*:103331. DOI: 10.1016/j.earscirev.2020.103331.

Ronquist F, Teslenko M, Mark P van der, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542. DOI: 10.1093/sysbio/sys029.

Sahney S, Benton MJ. 2008. Recovery from the most profound mass extinction of all time. *Proceedings of the Royal Society B: Biological Sciences* 275:759–765. DOI: 10.1098/rspb.2007.1370.

Sato T, Cheng Y-N, Wu X-C, Shan H-Y. 2014. *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauropterygians. *Geological Magazine* 151:121–133. DOI: 10.1017/S0016756813000356.

Scheyer TM. 2007. Skeletal histology of the dermal armor of Placodontia: the occurrence of ‘postcranial fibro-cartilaginous bone’ and its developmental implications. *Journal of Anatomy* 211:737–753.

DOI: 10.1111/j.1469-7580.2007.00815.x.

Scheyer TM, Neenan JM, Bodogan T, Furrer H, Obrist C, Plamondon M. 2017. A new, exceptionally preserved juvenile specimen of *Eusaurosphargis dalsassoi* (Diapsida) and implications for Mesozoic marine diapsid phylogeny. *Scientific Reports* 7:1–22. DOI: 10.1038/s41598-017-04514-x.

Scheyer TM, Romano C, Jenks J, Bucher H. 2014. Early Triassic marine biotic recovery: the predators perspective. *PLoS ONE* 9:e88987. DOI: 10.1371/journal.pone.0088987.

Shang Q-H, Li C. 2015. A new small-sized eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan, southwestern China. *Vertebrata PalAsiatica* 53:265–280.

Shang Q-H, Li C, Wu X-C. 2017. New information on *Dianmeisaurus gracilis* Shang & Li, 2015. *Vertebrata PalAsiatica* 55:17.

Shen Z, Ding J, Ye C, Wen J, Wang Z, Chen Z. 2006. New Early Triassic paleomagnetic data from Huangben section, Guangdong and its tectonic implications. *Chinese Science Bulletin* 51:1894–1902. DOI: 10.1007/s11434-006-2033-0.

Song H, Wignall PB, Dunhill AM. 2018. Decoupled taxonomic and ecological recoveries from the Permo-Triassic extinction. *Science Advances* 4:eaat5091. DOI: 10.1126/sciadv.aat5091.

Wu X-C, Li Z, Zhou B-C, Dong Z-M. 2003. A polydactylous amniote from the Triassic period. *Nature* 426:516–516. DOI: 10.1038/426516a.

Xie W, Lewis PO, Fan Y, Kuo L, Chen M-H. 2011. Improving marginal likelihood estimation for Bayesian phylogenetic model selection. *Systematic Biology* 60:150–160. DOI: 10.1093/sysbio/syq085.

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Portugués (Brasil)

Con formato: Fuente: Sin Cursiva, Portugués (Brasil)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Con formato: Francés (Francia)

Con formato: Fuente: Sin Cursiva, Francés (Francia)

Yan C, Li J, Cheng L, Zhao B, Zou Y, Niu D, Chen G, Fang Z. 2021. Strata characteristics of the Early Triassic Nanzhang-Yuan'an Fauna in western Hubei Province. *Earth Science* 46:122–135. DOI: 10.3799/dqkx.2020.023.

Young C-C. 1965. On the new nothosaurs from Hupeh and Kweichou, China. *Vertebrata PalAsiatica* 9:315–367.

Young C-C, Dong ZM. 1972. On the Triassic marine reptiles of China. *Memoires of the Nanjing Institute of Geology and Palaeontology* 9:1–34.

Zhou M, Jiang D, Motani R, Tintori A, Ji C, Sun Z-Y, Ni P-G, Lu H. 2017. The cranial osteology revealed by three-dimensionally preserved skulls of the Early Triassic ichthyosauriform *Chaohusaurus chaoxianensis* (Reptilia: Ichthyosauromorpha) from Anhui, China. *Journal of Vertebrate Paleontology* 37:e1343831. DOI: 10.1080/02724634.2017.1343831.

FIGURE CAPTIONS

Figure 1. Locality information for *Pomolispondylus biani* get. et sp. nov. holotype specimen (WGSC V1701). (a) location of Songshugou Quarry, Nanzhang County, Hubei. China. (b) palaeogeographical reconstruction of the South China platform during the Early Triassic after Yan et al. (2021). (c, d) stratigraphical sections and correlation between Zhangjiawan Quarry, Yuan'an County (c) and the holotype locality at Songshugou Quarry, Nanzhang County (d). *Pomolispondylus biani* is found lower in the Songshugou section than other marine tetrapods. Abbreviations: **Ob**, oolitic beach; **Op**, open carbonate platform; **Rp**, restricted carbonate platform.

Figure 2. Holotype specimen of *Pomolispondylus biani* gen. et sp. nov. (WGSC V1701). (a) Part specimen (WGSC V1701-1) in dorsal view. (b) Counterpart specimen (WGSC V1701-2) in ventral view. Both images are shown to the same scale with anterior to the top of the image. (c) Transverse thin section through a vertebra. Abbreviations: **co**, coracoid; **cr**, impression of caudal ribs (1 and 3 are numbered); **dr**, dorsal rib; **drc**, dorsal rib crest; **fe**, impression of femur; **gr**, gastralia; **hu**, impression of humerus; **ic**, impression of straight-faced centrum; **idr**, impression of dorsal rib; **is**, impression of ischium; **los**, lateral ossification; **ns**, neural spine; **pu**, pubis; **ra**, impression of radius; **sc**, scapula; **sr1/2**, impressions of sacral ribs; **tp**, transverse process; **ul**, impression of ulna.

Figure 3. Holotype specimen of *Pomolispondylus biani* gen. et sp. nov. (WGSC V1701). (a, b) oblique dorsal-right lateral view of the anterior of the part specimen (WGSC V1701-1) (a) with interpretation (b). (c, d) oblique ventral-left lateral view of the posterior counterpart specimen (WGSC V1701-2) (c) with interpretation (d). All images are shown at the same scale with anterior to the right of the image.

Eliminado: *Strumospina*

Eliminado: a

Eliminado: b

Eliminado: c

Eliminado: d

Eliminado: c

Eliminado: d

Eliminado: *Strumospina*

Eliminado: sequence

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Eliminado: *Strumospina*

Eliminado: a

Eliminado: (d) Left lateral view side of the part specimen. Both images are shown to the same scale with anterior to the top of the image.

Eliminado: **co**, coracoid; **cl**, clavicle;

Eliminado:

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Con formato: Texto en negrita, Fuente: Sin Cursiva, Color de fuente: Rojo

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Con formato: Texto en negrita, Fuente: Sin Cursiva, Color de fuente: Rojo

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Eliminado: *Strumospina*

Abbreviations: **co**, coracoid; **ga**, gastralia; **icr**, impression of first caudal rib; **idr**, impression of dorsal rib; **ins**, impression of dorsal neural spine; **isr**, impression of sacral rib; **itp**, impression of transverse process; **ns**, neural spine; **pu**, pubis; **tp**, transverse process; **zg**, zygapophyses; **zy**, zygosphene-zygantrum articulation.

Figure 4. Dorsal vertebrae and osteoderms of selected marine reptiles. (a, b) *Pomolispondylus biani* gen. et sp. nov. (WGSC V1701), dorsally exposed (a) dorsal neural spine (b) crest in dorsal rib and lateral ossification. (c) *Placodus inexpectatus* (GMPKU-P-1054), dorsally exposed. (d) *Lariosaurus sanxiaensis* (HFUT YZS-16-01), dorsally exposed. (e) *Largocephalosaurus polycarpon* (WIGM SPC V 1009), dorsally exposed. (f) *Sinosaurosphargis yunguiensis* (IVPP V 17040), ventrally exposed. (g) *Hanosaurus hupehensis* (WGSC V 2010), dorsally exposed. Abbreviations: **cn**, centrum; **dos**, dorsal ossification; **drc**, crest in dorsal rib; **ga**, gastralia; hu, humerus; **los**, lateral ossification; **ns**, neural spine; sc, scapula; **tp**, transverse process; **zg**, zygapophyses.

Figure 5. Phylogenetic affinities of *Pomolispondylus biani* gen. et sp. nov. relative to other marine reptiles modified from the matrix of Li et al. (2014). (a) parsimony analysis in TNT, (b) Bayesian inference analysis in MrBayes using log-normal-distributed rates model. *Pomolispondylus biani* is consistently found in a clade as the sister taxon to Saurosphargidae, although relationships to other marine reptiles are variable. Bootstrap (%)/Bremer node support values are given to the right of the relevant nodes (a). Gamma- and log-normal-distributed rates analyses resulted in the same topology and almost identical clade credibility values, so we only show the preferred log-normal-distributed analysis here (see Supplemental Material Figs S4, S6). Clade credibility values (%) are given to the right of the relevant

Eliminado: a

Con formato: Figure caption, Interlineado: sencillo

Eliminado: b

Eliminado: *Strumospina*

Eliminado: a

Eliminado: b

Eliminado: c

Eliminado: d

Eliminado: e

Eliminado: f

Eliminado: g

Con formato: Color de fuente: Rojo

Con formato: Color de fuente: Rojo

Con formato: Color de fuente: Rojo

Eliminado: ***Strumospina***

Con formato: Color de fuente: Rojo

Eliminado: **using maximum parsimony**

Con formato ...

Con formato: Color de fuente: Rojo

Con formato ...

Eliminado: A

Eliminado: using modified matrix of ...

Con formato: Color de fuente: Rojo

Con formato ...

Eliminado: B

Con formato ...

Eliminado: parsimony analysis in ...

Con formato: Color de fuente: Rojo

Con formato ...

Con formato: Color de fuente: Rojo

Con formato: Color de fuente: Rojo

Con formato ...

Con formato ...

Con formato ...

nodes (b).

Figure 6. Phylogenetic affinities of *Pomolispondylus biani* gen. et sp. nov. relative to other marine reptiles modified from the matrix of Scheyer et al. (2017) with marine-related characters coded as uncertainty. (a) parsimony analysis in TNT. (b) Bayesian inference analysis in MrBayes using log-normal-distributed rates model. *Pomolispondylus biani* is not consistently found as the sister taxon to Saurosphargidae. Relationships are more variable between analysis methods and whether marine-related characters are incorporated (see Supplemental Material Figs S8, S10, S12, S14). Bootstrap (%)/Bremer node support values are given to the right of the relevant nodes (a). Gamma- and log-normal-distributed rates analyses resulted in the same topology and almost identical clade credibility values, so we only show the log-normal-distributed analysis here. Clade credibility values (%) are given to the right of the relevant nodes (b).

Con formato: Color de fuente: Rojo

Eliminado: ***Strumospina***

Con formato: Color de fuente: Rojo

Eliminado: **using Bayesian-inference maximum likelihood**

Con formato: Fuente: Sin Negrita, Color de fuente: Rojo

Eliminado: A

Eliminado: modified matrix of Li *et al.* (2014)

Con formato: Color de fuente: Rojo

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Eliminado: .

Eliminado: (B) Bayesian inference analysis in MrBayes using modified matrix of Li *et al.* (2018). Like under maximum parsimony, *Strumospina*

Con formato: Color de fuente: Rojo

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Con formato: Color de fuente: Rojo

Con formato: Color de fuente: Rojo

Con formato: Fuente: Sin Cursiva, Color de fuente: Rojo

Eliminado: Gamma- and log-normal-distributed rates analyses resulted in the same topology and almost identical clade credibility values, so we only show the gamma-distributed analysis here (see Supplemental Material). Clade credibility values (%) are given to the right of the relevant nodes.¶

TABLE CAPTIONS

Table 1. Estimated presacral length of *Pomolispondylus* *biani* (WGSC V 1701). Comparisons of humeral lengths to other Early–Middle Triassic Sauropterygia and Saurosphargidae.

Eliminado: ***Strumospina***