New digital anatomical data of *Keichousaurus hui* (Reptilia: Sauropterygia) and its phylogenetic implication (#105294)

First submission

Guidance from your Editor

Please submit by **5 Nov 2024** for the benefit of the authors (and your token reward) .

Structure and Criteria
Please read the 'Structure and Criteria' page for guidance.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

If this article is published your review will be made public. You can choose whether to sign your review. If uploading a PDF please remove any identifiable information (if you want to remain anonymous).

Files

Download and review all files from the materials page.

11 Figure file(s)
2 Table file(s)
2 Other file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- Original primary research within Scope of the journal.
- Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- **Impact and novelty is not assessed.** Meaningful replication encouraged where rationale & benefit to literature is clearly stated.
- All underlying data have been provided; they are robust, statistically sound, & controlled.
- Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

New digital anatomical data of *Keichousaurus hui* (Reptilia: Sauropterygia) and its phylogenetic implication

Jiayu Xu Equal first author, 1, **Yu Guo** Equal first author, 2, **Yucong Ma** [1], **Wei Wang** [3], **Long Cheng** [4], **Fenglu Han** Corresp. 1

[1] School of Earth Science, China University of Geosciences, Hubei, Wuhan, China
[2] The Geological Museum of China, Beijing, China
[3] Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
[4] Hubei Key Laboratory of Paleontology and Geological Environment Evolution, Wuhan Centre of China Geological Survey, Hubei, Wuhan, China

Corresponding Author: Fenglu Han
Email address: hanfl@cug.edu.cn

Three complete skulls of *Keichousaurus hui* from the Middle Triassic Xingyi Fauna of southwestern China are examined using high-resolution CT scanning. The CT images allow a few refinements and supplements in cranial anatomy. Some previously ambiguous anatomical characters are able to be identified, including the presence of an L-shaped ectopterygoid that extends from the lateral side of the pterygoid and bends ventrally, wedge-shaped posterolateral process of the frontal, the pterygoid wedge-shaped for articulating with the palatine, a rodlike basioccipital tuber that extends ventrally. These new features provide a new detailed anatomy for taxonomy. The new phylogenetic analysis of eosauropterygians shows *Keichousaurus* is in the basal location of the clade which includes Nothosauridae and Pistosauroidea, and suggests that *Keichousaurus* is more closely related to Chinese pachypleurosaurs-like eosauropterygians than European pachypleurosaurs and more derived than other Chinese pachypleurosaurs-like forms.

New digital anatomical data of *Keichousaurus hui* (Reptilia: Sauropterygia) and its phylogenetic implication

Jiayu Xu[1,*], Yu Guo[2,*], Yucong Ma[1], Wei Wang[3], Long Cheng[4], Fenglu Han[1]

[1] School of Earth Sciences, China University of Geoscience (Wuhan), Wuhan, Hubei, China
[2] The Geological Museum of China, Beijing, China
[3] Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
[4] Hubei Key Laboratory of Paleontology and Geological Environment Evolution, Wuhan Centre of China Geological Survey, Wuhan, China
* These authors contributed equally to this work.

Corresponding Author:
Fenglu Han[1]
No. 388 Lumo Road, Wuhan, Hubei, 430074, China
Email address: hanfl@cug.edu.cn

Abstract

Three complete skulls of *Keichousaurus hui* from the Middle Triassic Xingyi Fauna of southwestern China are examined using high-resolution CT scanning. The CT images allow a few refinements and supplements in cranial anatomy. Some previously ambiguous anatomical characters are able to be identified, including the presence of an L-shaped ectopterygoid that extends from the lateral side of the pterygoid and bends ventrally, wedge-shaped posterolateral process of the frontal, the pterygoid wedge-shaped for articulating with the palatine, a rodlike basioccipital tuber that extends ventrally. These new features provide a new detailed anatomy for taxonomy. The new phylogenetic analysis of eosauropterygians shows *Keichousaurus* is in the basal location of the clade which includes Nothosauridae and Pistosauroidea, and suggests that *Keichousaurus* is more closely related to Chinese pachypleurosaurs-like eosauropterygians than European pachypleurosaurs and more derived than other Chinese pachypleurosaurs-like forms.

Introduction

Keichousaurus hui is a small marine reptile, normally less than 0.5 m, inhabiting in the eastern Tethys during the Middle Triassic (Lin & Rieppel, 1998). This taxon was first discovered from the Zhuganpo Member of Falang Formation in Dingxiao Village, Xingyi City, Guizhou Province of China (Young, 1958), and after that, abundant materials were collected from neighboring localities between Guizhou and Yunnan provinces (Li & Jin, 2003; Ma et al., 2013). Many aspects of this taxon have been adequately investigated: analysis of the fossil-bearing strata and corresponding paleoenvironment (Young, 1965; Chen, 1985; Wang, 1996; Yang, 1997; Wang, Kang & Wang, 1998; Li & Jin, 2003; Sun, Hao & Jiang, 2005; Ma et al., 2013; Hu, Xie & Yin, 2018), osteological anatomy (Cheng & Pan, 1999; Holmes, Cheng & Wu, 2008; Liao et al., 2021), ontogenetic stages (Fu et al., 2013; Qin, Yu & Luo, 2014), and sexual dimorphism (Cheng et al., 2009; Xue et al., 2013). However, the internal anatomy of the skull is still rarely known due to fossil preservation.

In recent years, computed tomography (CT) has been widely used in studying the osteological morphology of vertebrate fossils, including the Triassic marine reptiles (e.g., Neenan et al., 2015; Čerňanský et al., 2018; Wang et al., 2019; Yin, Zhou & Lu, 2021). Here, we study the cranial morphology in three *Keichousaurus* based on CT scanning. By comparing with the interpretations of the skulls of *Keichousaurus* in Lin and Rieppel (1998) and Holmes, Cheng and Wu (2008) as well as other previous work, we have identified new features on the internal anatomy of the skull elements in more comprehensive views. We supplemented and revised some of the characters in *Keichousaurus*, mainly including the morphological features of the dentition, the hyobranchium, the ectopterygoid and some other bones. We will give a detailed description of these new features and compare them with those of other pachypleurosaurs. Our discovery is significant for clarifying the phylogenetic position of *Keichousaurus* in eosauropterygians.

Materials & Methods

Three well preserved specimens of *Keichousaurus hui* (Fig. S1) are employed for this study. These fossils are collected from the thin limestone of the Middle Triassic Zhuganpo Member of Falang Formation at Mayigou locality, Fuyuan County, Yunnan Province, southwestern China (Fig. S2), and are permanently deposited in the paleontological collection of China University of Geosciences (Wuhan) (CUGW) with specimen numbers of CUGW VH007, CUGW VH009, and CUGW VH017, respectively. These three specimens are not physically prepared to remain the natural preservation and limit artificial damage.

The skulls of *Keichousaurus* were scanned by the micro-CT scanners at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP) and Yinghua Inspection and Testing (Shanghai) Co., Ltd.. Among these specimens, CUGW VH009 was scanned in 225kv micro-CT of IVPP, with a voltage of 180 kV, a current of 100 µA, and a resolution of 21.96 µm per pixel. CUGW VH007 and CUGW VH017 were scanned in the industrial micro-nanometer CT v|tome|x m of Yinghua Inspection and Testing (Shanghai) Co., Ltd. with a voltage of 140 kV, the current of 100 µA, and the resolution of 10.71 µm per pixel. Mimics 19.0 was used to reconstruct the CT data of the three specimens, which were rendered and shown (Figs. 1 and 2). The bony elements can be best reconstructed in CUGW VH009, which were separated, rendered, and illustrated in different colors (Fig. 1). The description and comparison were mainly based on this specimen. Three reconstructions of the CT data are uploaded to MorphoSource (see Supplemental Data).

Ontogenetic variation and sexual dimorphism have been well-studied in previous research (Lin & Rieppel, 1998; Cheng et al., 2009; Qin, Yu & Luo, 2014). according to body length, CUGW VH007 and CUGW VH009 are possibly to be within the adult stage, while CUGW VH017 is among the sub-adult stage (Table 1). CUGW VH007 could be a male individual based on a ratio of humerus to femur about 1.3 and expansion of humeral condyles, whereas CUGW VH009 and CUGW VH017 were assigned to be a female with the ratio of humerus to femur about 1 and smooth distal end of the humerus (Table 1).

Results

Systematic Paleontology

Diapsida Osborn, 1903
Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994
Keichousaurus Young, 1958
Keichousaurus hui Young, 1958

Description and comparison

All skulls are well preserved and are compressed dorsoventrally. The skull of *Keichousaurus* is generally wedge-shaped in dorsal view and the widest part of the skull is located in the posterior orbital region (Figs. 1 and 2A, B, E, F). The skull length of adult individuals (CUGW VH007 and CUGW VH009) can reach more than 20 mm. The external nare is long and narrow with a subtriangular outline. The orbit is very large, about 25 percent of the skull length. The preorbital region is slightly longer than the postorbital region. The supratemporal fenestra is elongated and about 70% of the orbital length, and the posteromedial margin of skull roof is concave. On the basis of previous studies (e.g., Lin & Rieppel, 1998; Holmes, Cheng & Wu, 2008; Liao et al., 2021), novel and revised anatomical interpretations are documented here.

Frontal

The frontal is elongated and flat, forming the medial edge of the orbit. It articulates with the nasal anteriorly and the prefrontal anterolaterally. The posterior end is bifurcated and covered on the parietal (Figs. 1A and 2A, B, E, F). The posterolateral process tapers are inserted into the depression in the anterior region of the parietal as in *Dianmeisaurus*, and contrasts with the previous description that they are arc-shaped (Lin & Rieppel, 1998; Holmes, Cheng & Wu, 2008). And this is similar to those of *Dianmeisaurus* (Shang & Li, 2015) and *Dawazisaurus* (Cheng et al., 2016). The frontal is excluded from the supratemporal fenestra by the postfrontal and parietal. The gradually pointed posterolateral processes of the frontal (Fig.3A, B).

The posterolateral processes of the frontal in *Keichousaurus* are nearly parallel, which are similar to those of *Diandongsaurus* (Shang, Wu & Li, 2011; Sato et al., 2014) and *Dianopachysaurus* (Liu et al., 2011), but are different from European pachypleurosaurs, such as *Anarosaurus* (Klein, 2009), *Serpianosaurus* (Rieppel, 1989) and *Neusticosaurus*, whose posterior end of the frontal is bifurcated into two slender processes with a large angle.

Basioccipital tuber

A pair of short columnar bony processes extending posterolaterally on the ventral side of the basioccipital is identified as basioccipital tuber (Fig. 4). The tuber extends from the anterior end of the ventral side of the basioccipital and lies on the posterodorsal side of the pterygoid. The left tubercle is short and cylindrical, with intact morphology and posterolateral extension. The right tubercle may not be as intact as the left because of the breakage of the occipital region.

Basiocciptial tuber has been described in nothosaurs and plesiosaurs (Rieppel, 1994; Storrs & Taylor, 1996), but it was not found in pachypleurosaurs. Therefore, the new finding confirms the presence of basioccipital tuber in *Keichousaurus* for the first time, suggesting that it may be also present in other early eosauropterygians.

Pterygoid and palatine

The pterygoid of *Keichousaurus* is a long strip, occupying the central position of the ventral side of the skull. In CUGW VH009, the lateral edge of the right pterygoid tapers and contacts with the depressed palatine (Fig. 1B). In CUGW VH007, the pterygoid is inserted into the groove of the palatine in a wedge-shaped process. In CUGW VH017, the pterygoids on both sides did not completely contact with the palatine due to preservation, but they tended to become tapered (Fig. 2G, H). Therefore, the pterygoids should extend outwards to wedge shape and contact the palatine at the position corresponding to the posterior edge of the orbit (Fig. 1A, B and 3C).

In the previous description by Lin and Rieppel (1998) and Holmes, Cheng and Wu (2008), the connection between the two sides of the pterygoids and the palatines is not clear (Fig. 3D). The lateral margin of the pterygoid in European taxa such as *Neusticosaurus* (Carroll & Gaskill, 1985) and *Serpianosaurus* (Rieppel, 1989) did not extend wedge-shaped, while the bilateral sides of the pterygoid of *Neusticosaurus peyeri* did not connect with the palatine (Sander, 1989). In *Diandongsaurus* (Sato et al., 2014; Liu et al., 2021) and *Dianmeisaurus* (Shang & Li, 2015), there are similar laterally extending protrusions on the lateral side of the pterygoid, but they are not wedge-shaped. This suggests that the connection mode between pterygoid and palatal may be an autapomorphy of *Keichousaurus* (Fig. 5).

Ectopterygoid

The ectopterygoid is "L" shape in ventral view, extending from the ventral side of the postorbital, then curved anteroventrally to the dorsal edge of the dentary. The medial surface contacts with the lateral margin of the pterygoid, although their suture is blurred (Fig. 3C). Holmes, Cheng and Wu (2008) described several specimens with the same similar shape of bone behind the palatine but were finally identified to be the medial process of the maxilla (Holmes, Cheng & Wu, 2008). The “L” shaped ectopterygoid is similar to that of *Diandongosaurus acutidentatus* (Sato et al., 2014) and *Dianmeisaurus gracilis* (Shang & Li, 2015). The ectopterygoid was also found in nothosaurs, such as *Nothosaurus rostellatus* (Shang, 2006) from Guizhou and *Simosaurus gaillardoti* (Miguel Chaves, Ortega & Pérez-García, 2018) from Europe, whose ectopterygoids are wide and flaky that are significantly different from the curved "L" shaped slender bones described in *Keichousaurus*.

Hyobranchium

The hyobranchium is well preserved and rod-like in CUGW VH009 (Fig. 1B). The pair of hyobranchium is slightly curved along the shaft. They are slender and expanded on both the proximal and distal ends, although the proximal end is larger. The hyobranchial length is about half the length of the orbit (Fig. 1 and 3C). Noticeably, the expansion of the distal end of hyobranchium described by Holmes, Cheng and Wu (2008) should be the part of the posterior quadrate branch of the pterygoid rather than the hyobranchium (Fig. 1, 2C, D, G, H and 3D). The hyobranchium was previously found in *Serpianosaurus* (Rieppel, 1989), *Neusticosaurus* (Carroll & Gaskill, 1985; Sander, 1989), *Dactylosaurus* (Sues & Carroll, 1985), *Dianmeisaurus* (Shang

& Li, 2015) and *Diandongsaurus* (Liu et al., 2021), but unknown in *Dianopachysaurus* (Liu et al., 2011). The hyobranchium of *Keichousaurus* is more slender, and its ratio to orbital length is similar to that of *Dianmeisaurus* (Shang & Li, 2015) and *Diandongsaurus* (Liu et al., 2021), but is larger than those of *Serpianosaurus* (Rieppel, 1989), *Neusticosaurus* (Sander, 1989) and *Dactylosaurus* (Sues & Carroll, 1985).

Dentition

The premaxilla, maxilla and dentary teeth are all well preserved (Fig. 6). There are five premaxillary teeth as in the description by Lin and Rieppel (1998) and Liao et al. (2021). The premaxillary teeth extend anteriorly with the tip down and recurve. They are generally larger than the maxillary teeth. Teeth size increased posteriorly and be the largest in the fourth tooth, and the fifth tooth is slightly smaller than the anterior four teeth (Fig. 6). CUGW VH007 and CUGW VH009, as adults of different genders, have 1-4 teeth on the right premaxilla gradually increasing. The crown height of the fourth tooth of CUGW VH007 and CUGW VH009 can reach 1.2 mm and 1.4 mm, respectively. Subsequently, the fifth crown of CUGW VH007 decreases to about 0.7 mm, while the fifth crown of CUGW VH009 decreases to about 0.9 mm. The left premaxillary teeth of CUGW VH007 and CUGW VH009 also follow this rule, but the third and fourth teeth are rarely exposed respectively (Fig. 2A, B and 6), which may be caused by tooth replacement. However, CUGW VH017 has no obvious changes, but the fourth tooth is the largest one in the premaxillary teeth.

The anterior maxillary teeth (1-5) of *Keichousaurus* are clearly shown, and the posterior ones (6-15) are either missing or concealed by the maxilla. It can be inferred that there are 15 teeth on each side based on CT reconstruction, which is the same as the description by Holmes, Cheng and Wu (2008), and similar to Liao et al. (2021). In these three specimens, the anterior maxillary teeth are also slightly supine with the tip down, and the first to third teeth are relatively small "conical teeth". In the adult CUGW VH007, the fourth and fifth teeth are widened. The worn crowns of the fourth and fifth teeth are only 0.8 mm and 1.0 mm in height, but the anteroposterior length is more than 0.4 mm, and the transverse width is 0.3 mm and 0.4 mm, respectively, which is significantly thicker than the anterior three teeth. In another adult CUGW VH009, the fourth tooth does not like a canine. The fifth tooth with a crown height of about 1.4 mm, an anteroposterior length and a transverse width of more than 0.4 mm was regarded as a canine (Fig. 6). In CUGW VH017, the fourth teeth are not well preserved, and the crowns of the fifth teeth are also worn. The height of the left and right fifth crowns are only 0.6 mm and 0.7 mm, but the anteroposterior length and transverse width are 0.3 mm, which are significantly larger than the anterior teeth. It could be judged as canine and might continue to grow. In different individuals, the size of teeth may be affected due to tooth replacement and preservation. However, the fourth and fifth teeth of the maxilla of *Keichousaurus* are canines, as described by Holmes, Cheng and Wu (2008) and Liao et al. (2021). From the sixth maxillary tooth, the teeth mutate into small conical shapes, which are smaller than the anterior conical teeth. The crown is cone-shaped forming an angle of 60° with the horizontal level. The canines of the maxilla were found in *Dianopachysaurus* (Liu et al., 2011), *Dawazisaurus*(Cheng et al., 2016), *Diandongosaurus* (Sato et al., 2014; Liu et al., 2021), *Dianmeisaurus* (Shang & Li, 2015). In *Dianopachysaurus*, Liu et al. (2011) simply described that the fourth of the six teeth in the right maxilla was significantly enlarged; In *Dawazisaurus*, the eighth of the twenty teeth was described as the largest of maxillary teeth and fang-like by Cheng et al. (2016); Five teeth were found in the anterior part of the maxilla of *Diandongosaurus*, and the third and fourth teeth were canines. However, according to Sato et al. (2014) and Liu et al. (2021), the space between the anterior edge of canines and the premaxilla can accommodate one or two additional teeth. Therefore, the canines on the maxilla may be located in the position of the fourth and fifth teeth, which is similar to the canines in *Keichousaurus* (Sato et al., 2014). In *Dianmeisaurus*, there are at least four canines on the premaxilla, and the third on the maxilla is canine, which is slightly different from *Keichousaurus*, but the shapes of canine and conical teeth are similar to *Keichousaurus* (Shang & Li, 2015).

In the dentary teeth of CUGW VH009, the anterior eight dentary teeth were clearly shown, and they were basically supine with the tip recurved. The dentary teeth are staggered with the premaxillary teeth and the maxillary teeth. The first, second, fifth and seventh teeth are larger than other dentary teeth, and the crown heights are between 0.8 mm and 1.1 mm. The posterior dentary teeth (the ninth and later) were covered by the maxilla. However, some very small teeth can be seen through the orbit. According to CT images, there are 21 dentary teeth.

Compared with the traditional European pachypleurosaurs, the number of premaxillary teeth of *Keichousaurus* is similar to that of *Neusticosaurus pusillus* (5) and *Neusticosaurus peyeri* (5-6), and slightly less than that of *Neusticosaurus edwardsi* (6) and *Serpianosaurus mirigiolensis* (6-8). Compared with the Chinese pachypleurosaurs-like, the number of 5 premaxillary teeth of *Keichousaurus* is same as *Dawazisaurus brevis* (5), and similar to *Dianopachysaurus dingi* (at least 5 premaxillary teeth), *Diandongosaurus acutidentatus* (at least 5 premaxillary teeth) and *Dianmeisaurus gracilis* (at least 4 premaxillary teeth).

Compared with the traditional European pachypleurosaurs, the number of maxillary teeth of *Keichousaurus* is similar to that of *Serpianosaurus mirigiolensis* (15-16), but slightly more than *Neusticosaurus peyeri* (10-12) and *Neusticosaurus pusillus* (12), and maybe less than *Neusticosaurus edwardsi* (19 or more). The number of the maxillary teeth of Chinese pachypleurosaurs-like *Dianopachysaurus dingi* and *Diandongosaurus acutidentatus* were unknown, *Keichousaurus* is slightly less than *Dawazisaurus brevis* (20), and maybe slightly more than *Dianmeisaurus gracilis* (at least 13 teeth).

The number of dentary teeth in *Keichousaurus is* less than the traditional European pachypleurosaurs, such as *Neusticosaurus peyeri* (24), *Neusticosaurus pusillus* (25) and

Serpianosaurus mirigiolensis (31~32). The teeth morphology of *Keichousaurus* is compared with that of other pachypleurosaurs in Table 2.

Phylogenetic analysis

This paper uses the data matrix of Wang et al. (2022) which is mainly based on the data of Neenan, Klein and Scheyer (2013) with the combination of information from other researchers including Liu et al. (2011). Six characters of *Kueichousaurus* have been modified (Table S1, data from Wang et al., 2022).

The new matrix containing 181 characters and 63 genera was analyzed by phylogenetic software TNT (Goloboff, Farris & Nixon, 2008). All the characters are of equal weight, unordered. 181 characteristics of 63 genera were searched by traditional search that ran 100 replications of Wagner trees with one random seed and 10 trees saved per run, and 351 most parsimonious trees (TL = 811, CI = 0.293, RI = 0.685) were obtained (Fig. S3).

In the strict consensus tree, the clades within Sauropterygia are poorly resolved. Five taxa were excluded from the reduced strict consensus tree (Fig. 7), including *Majiashanosaurus*, *Eremtmorhipis*, *Palatodonta*, *Hanosaurus*, and *Chaohusaurus*. The European pachypleurosaurs *Neusticosaurus*, *Serpianosaurus*, *Dactylosaurus*, *Odoiporosaurus*, and *Anarosurua*, form a monophyletic group, but the Pachypleurosauria from China do not form a monophyletic group. *Qianxisaurus* and *Wumengosaurus* are assigned to be Eosauropterygia. They form a polytomy with the European pachypleurosaurs and a branch that consists of the remaining genera of Eosauropterygia. On the contrary, *Dawazisaurus*, *Dianopachysaurus*, *Dianmeisaurus*, *Diandongosaurus*, and *Keichousaurus* all are included in a monophyletic group with the remaining genera of European Eosauropterygia except *Panzhousaurus*, and *Dawazisaurus*, *Dianopachysaurus*, *Dianmeisaurus*, and *Diandongosaurus* forms a polytomy with a monophyletic group that is composed of five genera includes *Keichousaurus*, *Plaudidraco*, *Simosaurus*, *Wangosaurus*, *Germansaurus* and two branches which is Nothosauridae and Pistosauroidea. This branch, which includes the Chinese pachypleurosaurs-like taxa except *Qianxisaurus* and *Wumengosaurus* and the remaining genera of European eosauropterygians, shared derived characters: parietals are fully fused in adults; number of dorsal vertebrae is 16 to 20; ungual phalange in pes is blunt and expanded, and wider than the articulated proximal phalange. The branch of *Keichousaurus* and the remaining genera of eosauropterygians, which is included in the branch above, shared non-ambiguous synapomorphies: nasals are reduced; there are three tarsal ossifications and ungual phalange in pes is short and blunt but not expanded.

Discussion

The CT scanning and skull reconstruction of the three *Keichousaurus* have permitted us to make a few refinements and supplements in cranial anatomy and revealed several new features that were unknown before. We compared *Keichousaurus* with the Triassic eosauropterygians

Anarosaurus, *Dactylosaurus*, *Serpianosaurus*, *Neusticosaurus* from Europe (Carroll & Gaskill, 1985; Sues & Carroll, 1985; Sander, 1989; Rieppel, 1989; Rieppel & Lin, 1995; Klein, 2009; Renesto, Binelli & Hagdorn, 2014) and *Dianopachysaurus*, *Diandongosaurus*, *Dianmeisaurus*, *Dawazisaurus*, *Majiashanosaurus* from South China (Jiang et al., 2008, 2014; Shang, Wu & Li, 2011; Wu et al., 2011; Liu et al., 2011, 2015; Cheng et al., 2012, 2016; Sato et al., 2014; Shang & Li, 2015).

Generally, *Keichousaurus* is more similar to these small-sized Chinese eosauropterygians, *Dianopachysaurus*, *Diandongosaurus*, *Dianmeisaurus* and *Dawazisaurus*, than European pachypleurosaurs *Anarosaurus*, *Serpianosaurus*, *Neuticosaurus* and *Dactylosaurus* by possessing nearly parallel and gradually pointed posterolateral processes of the frontal, laterally extending protrusions on the lateral side of the pterygoid, "L" shaped ectopterygoid, the ratio of hyobranchium to orbital length, the number of premaxillary teeth and the existence of canines. Among them, *Keichousaurus* is more similar to *Diandongosaurus* and *Dianmeisaurus*.

In previous phylogenetic studies, the relationship between *Keichousaurus* and European pachypleurosaurs and other similar Chinese froms has been controversial (Li & Liu, 2019). The relationships among not only the pachypleurosaurs, but also the eosauropterygians, remain open constantly. Here, we discuss the relationship between *Keichousaurus* and three taxa mentioned above with other families of Eosauropterygia. The European pachypleurosaurs we mentioned, which include *Anarosaurus*, *Serpianosaurus*, *Neuticosaurus,* and *Dactylosaurus* that have a stable interrelationship, can form a monophyly well in the majority of studies.

In some studies, the results support the monophyly of Pachypleurosauria, but the internal relationship of Eosauropterygia and the position of the Chinese genera have some differences (Fig. 8A and B). In regard to the internal relationship of the families of Eosauropterygia, the monophyletic group consists of Nothosauroidea and Pistosauroidea forming a sister group with the Pachypleurosauria (Liu et al., 2011, 2021; Xu et al., 2022) (Fig. 8A), or the Pistosauroidea is the basal calde of the consecutive sister groups of Nothosauroidea and Pachypleurosauria (Neenan, Klein & Scheyer, 2013; Li & Liu, 2020; Liu et al., 2021; Hu, Li & Liu, 2024) (Fig. 8B), and the internodes of Chinese pachypleurosaurs or pachypleuosaur-like forms are unstable, except that the position of *Keichousaurus* is closer to the European pachypleurosaurs (Fig. 8A and B).

The monophyly of Pachypleurosauria is invalid in some studies (Fig. 8C and D). In Figure 8C, the Pistosauroidea is positioned at the base of Eosauropterygia, but the European pachypleurosaurs form a monophyletic group with the branch that is composed of Nothosauroidea and Chinese pachypleurosaurs or similar forms and becomes the sister group to Pistosauroidea. It shows the four taxa of Chinese pachypleurosaurs-like are more derived than others, and *Keichousaurus* is more related to Nothosauroidea than European pachypleurosaurs

(Fig. 8C). Holmes, Cheng and Wu (2008) and Shang, Wu and Li (2011) suggested that *Keichousaurus* should be closer to the base of Nothosauroidea, rather than as a sister group close to European pachypleurosaurs. The result of Wu et al. (2011) also supports this result. According to the phylogenetic analysis of Ma et al. (2015) and Jiang et al. (2018), Nothosauroidea and Pistosauroidea are sister groups to each other, and they together constitute a monophyletic clade which is sister to the Chinese pachypleurosaurs-like taxa. Then this clade and Chinese pachypleurosaurs-like taxa form a monophyletic group, and this big group is a sister group to European pachypleurosaurs. *Keichousaurus* is more derived than *Dianophachysaurus* (Ma et al., 2015; Jiang et al., 2018) (Fig. 8D).

Compared to previous studies, the result of our phylogenetic analysis is similar to that of Jiang et al (2018; Fig. 8D), but the position of *Keichousaurus* is more derived than *Diandongosaurus* and *Dianmeisaurus*, and is basal to the clade including Nothosauridae and Pistosauroidea. But the support for the branch including *Keichousaurus*, Nothosauridae and Pistosauroidea is generally low, which suggests this clade is not stable (Fig, S3). Therefore, it still needs more research to explore the characters of *Keichousaurus* and relevant eosauropterygians to solve the phylogenetic position of *Keichousaurus* within the Eosauropterygia.

Conclusion

Here we provide additional anatomy of *Keichousaurus* based on CT scanning of three skulls, including the L-shaped ectopterygoid, the wedge-shaped posterolateral process of the frontal, the wedge-shaped pterygoid that is for articulating with the palatine, and the rodlike basioccipital tuber. Adding these new features in a new phylogenetic analysis of Eosauropterygia, *Keichousaurus* seems to be more closely related to Chinese pachypleurosaurs-like, while it may be more derived than other Chinese pachypleurosaurs-like forms that are located basal to the clade including Nothosauridae and Pistosauroidea.

Acknowledgements

We thank Feng Yun from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences and Yinghua NDT (Shanghai) Co., Ltd. for CT scanning of fossils. This project is supported by the National Natural Science Foundation of China (41530104, 41688103, 42002019, and 41972014) and China Geological Survey (DD20230006).

References

Carroll RL, Gaskill P. 1985. The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 309:343–393. DOI: 10.1098/rstb.1985.0091.

Čerňanský A, Klein N, Soták J, Olšavský M, Šurka J, Herich P. 2018. A Middle Triassic pachypleurosaur (Diapsida: Eosauropterygia) from a restricted carbonate ramp in the Western Carpathians (Gutenstein Formation, Fatric Unit): paleogeographic implications. *Geologica Carpathica* 69:3–16. DOI: 10.1515/geoca-2018-0001.

Chen Z. 1985. Stratigraphical position of Kueichousaurus hui Young of Middle Triassic and its significance in Southwestern Guizhou. *Geology of Guizhou* 2:289–290.

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, Holmes R, Wu X, 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 X, Pan G. 1999. Skeleton features and life habit of Keichousarus-hui. *Journal of Guizhou Normal University (Natural Science)* 17:49–53.

Cheng Y, Wu X, Sato T, Shan H. 2016. *Dawazisaurus Brevis*, A New Eosauropterygian From the Middle Triassic of Yunnan, China. *Acta Geologica Sinica - English Edition* 90:401–424. DOI: 10.1111/1755-6724.12680.

Fu W, Zhang X, Ji C, Jiang D, Sun Z, Hao W. 2013. Morphology of Keichousaurus hui from the Middle Triassic of Xingyi, Guizhou Province with Comments on Its Reproduction Mode. *Acta Scientiarum Naturalium Universitatis Pekinensis* 49:839–846. DOI: 10.13209/j.0479-8023.2013.112.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786. DOI: 10.1111/j.1096-0031.2008.00217.x.

Holmes R, Cheng Y, Wu X. 2008. New information on the skull of *Keichousaurus hui* (Reptilia: Sauropterygia) with comments on sauropterygian interrelationships. *Journal of Vertebrate Paleontology* 28:76–84. DOI: 10.1671/0272-4634(2008)28[76:NIOTSO]2.0.CO;2.

Hu YW, Li Q, Liu J. 2024. A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of southwestern China and its phylogenetic and biogeographic implications. *Swiss Journal of Palaeontology* 143:1. DOI: 10.1186/s13358-023-00292-4.

Hu Z, Xie T, Yin F. 2018. Carbon and oxygen isotopic studies of the horizon of Kueichousaurus Fauna. *Geology in China* 45:1039–1048.

Jiang D, Lin W, Rieppel O, Motani R, Sun Z. 2018. A new Anisian (Middle Triassic) eosauropterygian (Reptilia, Sauropterygia) from Panzhou, Guizhou Province, China. *Journal of Vertebrate Paleontology* 38. DOI: 10.1080/02724634.2018.1480113.

Jiang DY, Motani R, Tintori A, Rieppel O, Chen GB, Huang JD, Zhang R, Sun ZY, 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.

Jiang DY, Rieppel O, Motani R, Hao WC, Sun YL, Schmitz L, Sun ZY. 2008. A new Middle Triassic eosauropterygian (Reptilia, Sauropterygia) from southwestern China. *Journal of Vertebrate Paleontology* 28:1055–1062. DOI: 10.1671/0272-4634-28.4.1055.

Klein N. 2009. Skull morphology of *Anarosaurus heterodontus* (Reptilia: Sauropterygia: Pachypleurosauria) from the Lower Muschelkalk of the Germanic Basin (Winterswijk, The Netherlands). *Journal of Vertebrate Paleontology* 29:665–676. DOI: 10.1671/039.029.0327.

Li J, Jin F. 2003. New progress in the study of Keichousaurus Vertebrate Fauna. *Progress in Natural Science* 13:14–18.

Li Q, Liu J. 2019. Study of Sauropterygia (Reptilia: Diapsida) in China: A review. *Journal of Hefei university of technology (Natural Science)* 42:355-360+375.

Li Q, Liu J. 2020b. An Early Triassic sauropterygian and associated fauna from South China provide insights into Triassic ecosystem health. *Communications Biology* 3:63. DOI: 10.1038/s42003-020-0778-7.

Liao J, Lan T, Xu G, Li J, Qin Y, Zhao M, Li Y, Wang Y. 2021. Tooth Structure and Replacement of the Triassic Keichousaurus (Sauropterygia, Reptilia) From South China. *Frontiers in Ecology and Evolution* 9:741851. DOI: 10.3389/fevo.2021.741851.

Lin K, Rieppel O. 1998. *Functional morphology and ontogeny of Keichousaurus hui (Reptilia, Sauropterygia)*. Chicago. Ill: Field Museum of Natural History. DOI: 10.5962/bhl.title.5174.

Liu Q-L, Cheng L, Stubbs TL, Moon BC, Benton MJ, Yan C-B, Tian L. 2023. Rapid neck elongation in Sauropterygia (Reptilia: Diapsida) revealed by a new basal pachypleurosaur from the Lower Triassic of China. *BMC Ecology and Evolution* 23:44. DOI: 10.1186/s12862-023-02150-w.

Liu X, Lin W, Rieppel O, Sun Z, Li Z, Lu H, Jiang D. 2015. A new specimen of Diandongosaurus acutidentatus (Sauropterygia) from the Middle Triassic of Yunnan, China. *Vertebrata PalAsiatica* 53:281–290. DOI: 10.19615/j.cnki.1000-3118.2015.04.002.

Liu J, Rieppel O, Jiang DY, Aitchison JC, Motani R, Zhang QY, Zhou CY, Sun YY. 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.

Ma L, Ji C, Sun Z, Yang P, Zou X. 2013. Biodiversity and stratigraphic distribution of the Triassic Xinyi marine reptile fauna, Guizhou province. *Journal of s* 37:178–185. DOI: 10.19839/j.cnki.dcxzz.2013.02.006.

Ma LT, Jiang DY, Rieppel O, Motani R, Tintori A. 2015. A new pistosauroid (Reptilia, Sauropterygia) from the late Ladinian Xingyi marine reptile level, southwestern China. *Journal of Vertebrate Paleontology* 35:e881832. DOI: 10.1080/02724634.2014.881832.

Miguel Chaves C de, Ortega F, Pérez-García A. 2018. Cranial variability of the European Middle Triassic sauropterygian Simosaurus gaillardoti. *Acta Palaeontologica Polonica* 63:315–326. DOI: 10.4202/app.00471.2018.

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.

Neenan JM, Li C, Rieppel O, Scheyer TM. 2015. The cranial anatomy of Chinese placodonts and the phylogeny of Placodontia (Diapsida: Sauropterygia): Placodont Cranial Anatomy and

Phylogeny. *Zoological Journal of the Linnean Society* 175:415–428. DOI: 10.1111/zoj.12277.

Qin Y, Yu M, Luo Y. 2014. Ontogenesis of Keichousaurus Hui. *Guizhou Geology* 31:210-214+205.

Renesto S, Binelli G, Hagdorn H. 2014. A new pachypleurosaur from the Middle Triassic Besano Formation of Northern Italy. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 271:151–168. DOI: 10.1127/0077-7749/2014/0382.

Rieppel O. 1989. A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 323:1–73. DOI: 10.1098/rstb.1989.0001.

Rieppel O. 1994. The Braincases of Simosaurus and Nothosaurus: Monophyly of the Nothosauridae (Reptilia: Sauropterygia). *Journal of Vertebrate Paleontology* 14:9–23.

Rieppel O, Lin K. 1995. *Pachypleurosaurs (Reptilia: Sauropterygia) from the lower Muschelkalk, and a review of the Pachypleurosauroidea*. Chicago, Ill: Field Museum of Natural History. DOI: 10.5962/bhl.title.3474.

Sander PM. 1989. The Pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the Description of a New Species. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 325:561–666.

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

Shang Q. 2006. A new sprcies of Nothosaurus from the early middle Triassic of Guizhou, China. *Vertebrata PalAsiatica* 44:237–249. DOI: 10.19615/j.cnki.1000-3118.2006.03.002.

Shang Q, Li C. 2015. A new small-sized eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan, southwestern China. *Vertebrata PalAsiatica* 53:265–280. DOI: 10.19615/j.cnki.1000-3118.2015.04.001.

Shang Q, Wu X, Li C. 2011. A New eosauropterygian from middle Triassic of eastern Yunnan province, southwestern China. *Vertebrata PalAsiatica* 49:155–171. DOI: 10.19615/j.cnki.1000-3118.2011.02.002.

Storrs GW, Taylor MA. 1996. Cranial Anatomy of a New Plesiosaur Genus from the Lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England. *Journal of Vertebrate Paleontology* 16:403–420.

Sues H-D, Carroll RL. 1985. The pachypleurosaurid *Dactylosaurus schroederi* (Diapsida: Sauropterygia). *Canadian Journal of Earth Sciences* 22:1602–1608. DOI: 10.1139/e85-169.

Sun Z, Hao W, Jiang D. 2005. Conodont Biostratigraphy Near the Ladinian-Carnian Boundary in Terval in Guanling of Guizhou. *JOURNAL OF STRATIGRAPHY* 29:257-263+313-314.

Wang L. 1996. A Discussion on Horizon and AGE of Kueichousaurus hui Occurrence. *Guizhou Geology* 13:209–212.

Wang C, Kang P, Wang Z. 1998. Conodont-based age of the Kueichousaurus hui Yang, 1958. *Acta Micropalaeontologica Sinica* 15:90–92.

Wang W, Li C, Scheyer TM, Zhao L. 2019. A new species of *Cyamodus* (Placodontia, Sauropterygia) from the early Late Triassic of south-west China. *Journal of Systematic Palaeontology* 17:1457–1476. DOI: 10.1080/14772019.2018.1535455.

Wang W, Shang Q, Cheng L, Wu XC, Li C. 2022. Ancestral body plan and adaptive radiation of sauropterygian marine reptiles. *iScience* 25:105635. DOI: 10.1016/j.isci.2022.105635.

Wu XC, Cheng YN, Li C, Zhao LJ, Sato T. 2011. New information on *Wumengosaurus delicatomandibularis* Jiang et al., 2008 (Diapsida: Sauropterygia), with a revision of the osteology and phylogeny of the taxon. *Journal of Vertebrate Paleontology* 31:70–83. DOI: 10.1080/02724634.2011.546724.

Xu GH, Ren Y, Zhao LJ, Liao JL, Feng DH. 2022. A long-tailed marine reptile from China provides new insights into the Middle Triassic pachypleurosaur radiation. *Scientific Reports* 12:7396. DOI: 10.1038/s41598-022-11309-2.

Xue Y, Jiang D, Motani R, Rieppel O, Sun Y. 2013. New information on sexual dimorphism and allometric growth in Keichousaurus hui, a pachypleurosaur from the Middle Triassic of Guizhou, South China. *Acta Palaeontologica Polonica* 60:681–687. DOI: 10.4202/app.00006.2013.

Yang R. 1997. On paleoecological environment of Kueichousaurus Fauna in Dingxiao of Xingyi area, Guizhou. *Guizhou Geology* 14:35–39.

Yin Y, Zhou M, Lu H. 2021. A dataset of the skull μCT scanning of Keichousaurus hui (Reptilia: Sauropterygia) from the Middle Triassic of Guizhou Province, China. *Science Data Bank* 6:135–141.

Young CC. 1958. On the new Pachypleurosauroidea from Keichou, South-West China. *Vertebrata PalAsiatica* 2:69–81.

Young CC. 1965. On the new nothosaurs from Hupeh and Kweichou, China. *Vertebrata PalAsiatica* 9:315–367. DOI: 10.19615/j.cnki.1000-3118.1965.04.001.

Table 1 (on next page)

Measurement record of *Keichousaurus hui*

Specimens	Humerus (mm)		Femur (mm)		Snout-vent length (mm)	Stage	Gender
	Left	Right	Left	Right			
CUGW VH007	22.8	22.7	17.2	17.0	150.4	Adult	Male
CUGW VH009	15.8	16.1	15.6	16.0	154.2	Adult	Female
CUGW VH017	11.0	12.6	10.5	12.1	114.7	Subadult	Female

Table 2 (on next page)

Comparison of tooth characteristics of *Keichousaurus hui* with other pachypleurosaurs

	premaxillary teeth	maxillary teeth	dentary teeth
Keichousaurus hui (CUGW VH007, VH009, VH017)	five teeth are supine with the tip down, and the tips of the teeth tend to bend backward. One to four of them gradually become larger and the fifth one reduced in size.	15 in total. The fourth and fifth are canines. The anterior teeth are also slightly supine. From the sixth, it suddenly becomes smaller, slightly extending anterioventrally, and is about 60 degrees to the horizontal level.	Among the 21 teeth, the first, third, fifth and seventh teeth were relatively large, and all of them were supine with the tip upward.
Serpianosaurus mirigiolensis (Rieppel, 1989)	six to eight teeth. The front teeth are larger and obviously curved medially, and the back teeth are slightly smaller than the maxillary teeth.	15-16 teeth.	31-32 teeth that are similar to the premaxillary teeth. The anterior teeth are larger and curved medially, and the posterior teeth were smaller, but all larger than the maxillary teeth.
Neusticosaurus pusillus (Sander, 1989)	5 teeth similar in size (about 1.5 mm), with longitudinal ornamentation on the surface.	12 teeth. Anterior teeth are large, similar to canines. The teeth are pointed and curved toward the tip, with longitudinal ornamentation. The length is generally less than 1.5 mm, but it can reach 2mm in adult.	25 teeth. The tooth row of the dentary reaches further back than that of the maxillary and premaxillary.
Neusticosaurus peyeri (Sander, 1989)	5-6 teeth	10-12 teeth	24 teeth. Some teeth are larger.
Neusticosaurus edwardsi (Carroll & Gaskill, 1985)	6 teeth, large and supine.	19 teeth or more, the front teeth are as large and supine as the premaxillary teeth, and the back teeth become smaller and straight.	unknown
Diandongosaurus	At least five teeth, large and	Six or seven maxillary teeth that are	The anterior teeth are similar to

acutidentatus (Sato et al., 2014; Liu et al., 2021)	supine, similar to canines.	large and supine. The fourth and fifth teeth are canines.	the premaxillary teeth, but the posterior teeth are not preserved.
Dianopachysaurus dingi (Liu et al., 2011)	At least five teeth, slightly supine, with the most anterior teeth bent inward.	Six teeth. The fourth increased significantly, and the rest of the teeth are smaller than the premaxillary teeth. The last one is at the end of the orbit.	unknown
Dianmeisaurus gracilis (Shang & Li, 2015)	At least four canines. The crown of canines is slightly curved dagger shaped, with longitudinal ridges on the surface.	At least 13 teeth with one canine, two maxillary teeth in front of canine and more than 10 teeth behind the canine.	The front canines correspond to the premaxillary teeth, and the rear teeth are small conical teeth. The posterior edge of the dentition is located in the anterior part of the posterior edge of the orbit.
Dawazisaurus brevis (Cheng et al., 2016)	5 teeth, sub-conical and curve medially and slightly posteriorly, with fine striations on the crown surface. The fourth and fifth are the largest and the smallest, respectively. The fourth is fang-like.	20 teeth in total, and the description is same as premaxillary. The shape of eighth just like the fourth of premaxillary, but slightly smaller than latter. And others are much smaller and have similar size.	unknown

1

Figure 1

3D reconstruction of the skull of *Keichousaurus hui* (CUGW VH009). The colors denote different bones.

A. dorsal view; B. ventral view; C. left lateral view. The circle shows that pterygoid contacts with palatine. **Abbreviations**: ang. angular; art. articular; bo. basioccipital; bot. basioccipital tuber; cor. coronoid; d. dentary; ect. ectopterygoid; eo-op. exoccipital-opisthotic; f. frontal; hy. hyobranchium; j. jugal; max. maxilla; n. nasal; p. parietal; pal. palatine; part. prearticular; pf. postfrontal; pm. premaxilla; po.postorbital; prf. prefrontal; pt. pterygoid; q. quadrate; qj. quadratojugal; sang. surangular; so. supraoccipital; sp. splenial; sq. squamosal; st. supratemporal; v. vomer

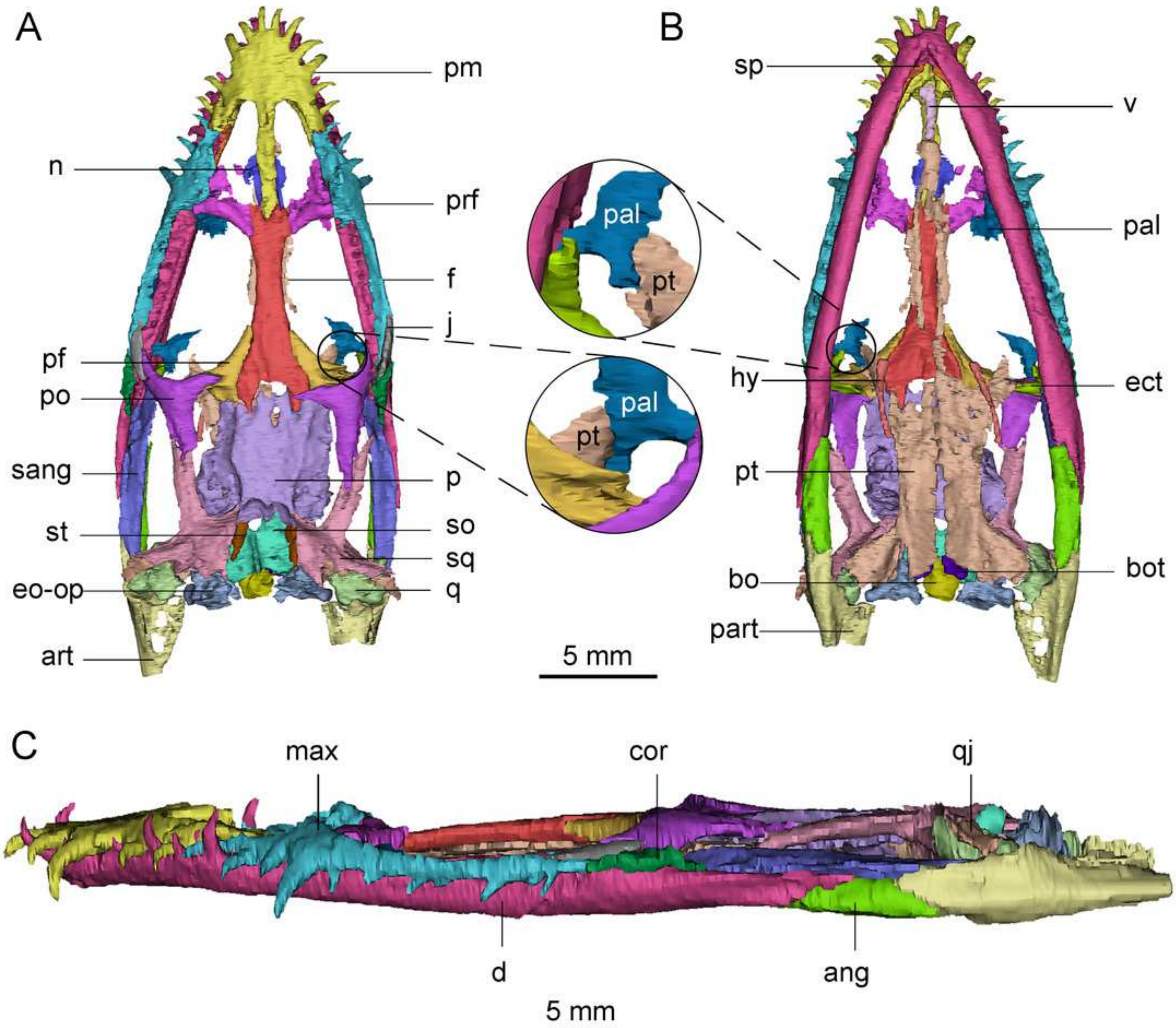
A
pm
n
prf
f
j
pf
po
sang
p
st
so
sq
eo-op
q
art
B
sp
v
pal
pt
pal
pt
pal
hy
ect
pt
bo
bot
part
5 mm
C
max
cor
qj
d
ang
5 mm

Figure 2

3D reconstruction and outline drawing of the skulls of *Keichousaurus hui*.

A-D. CUGW VH007; A, B. dorsal view; C, D. ventral view. E-H. CUGW VH017; E, F. dorsal view; G, H. ventral view. The circle is where the pterygoid connects the palatine. The dashed line represents the uncertain suture. The shadow region denotes cavities and/or unreconstructed bones. For abbreviations, see Fig. 1

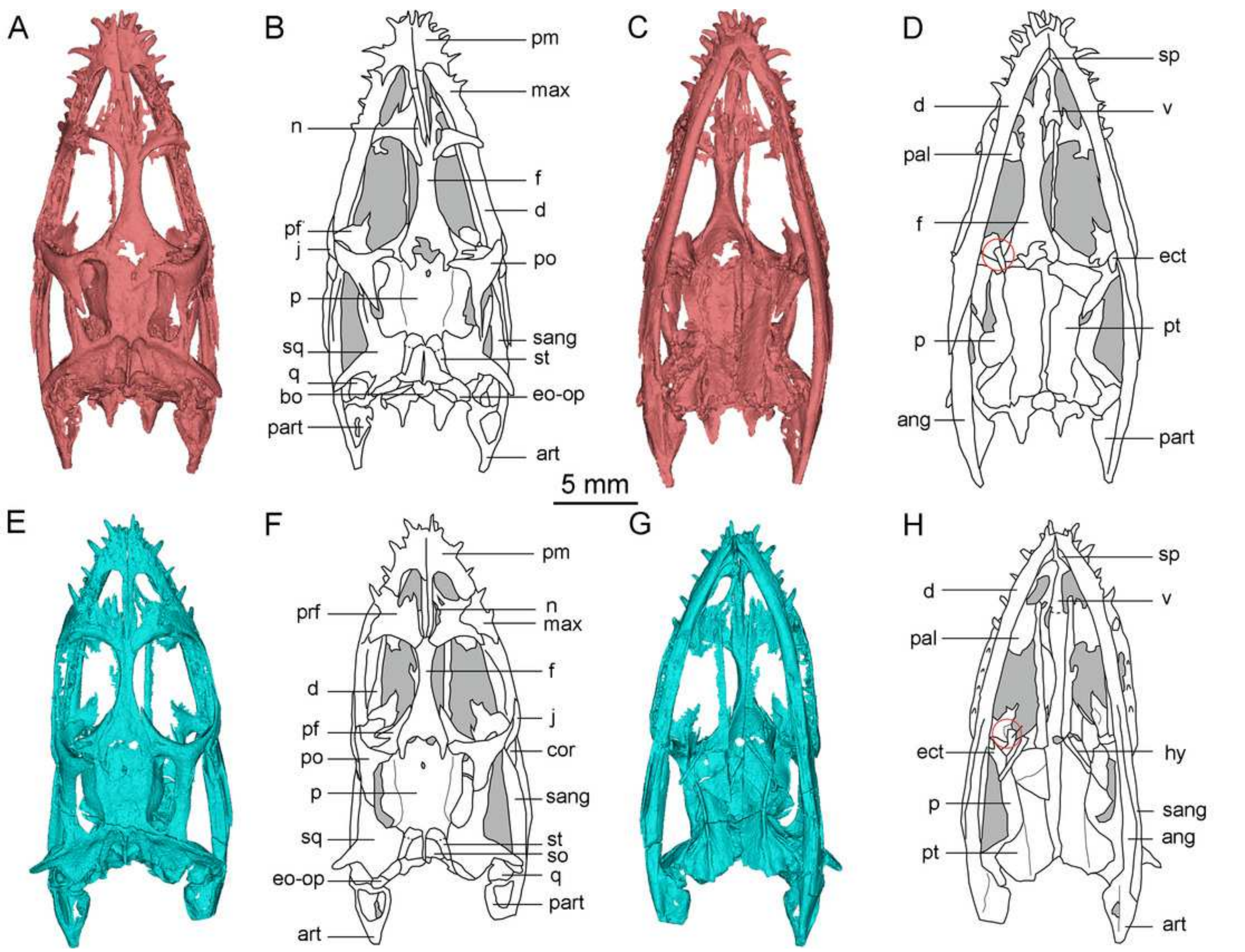

Figure 3

Reconstruction of the skull of *Keichousaurus hui*.

A, B. dorsal view; A. according to our study; B. from Holmes, Cheng and Wu (2008) . C, D. ventral view; C. according to our study; D. from Holmes, Cheng and Wu (2008) .Arrows point differences between our study and Holmes, Cheng and Wu (2008) . The circle shows the ectopterygoid bone**.** The shadow area denotes no bone. For abbreviations, see Fig. 1

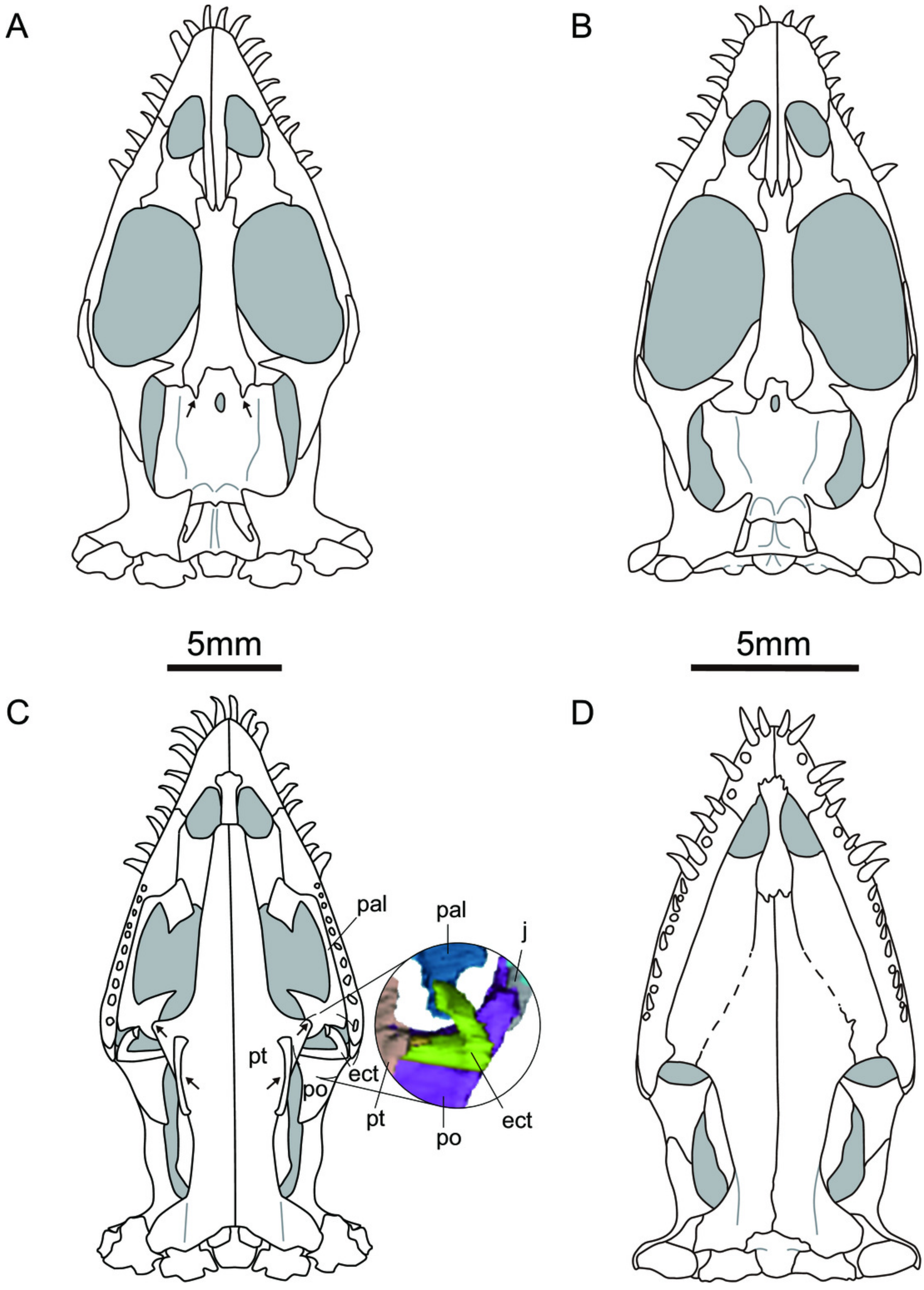
A
B
5mm
5mm
C
D
pal
pal
j
pt
ect
po
pt
po
ect

Figure 4

Posterior part of *Keichousaurus hui* (CUGW VH009) in ventral view.

Arrows denote basioccipital tuber. For abbreviations, see Fig. 1

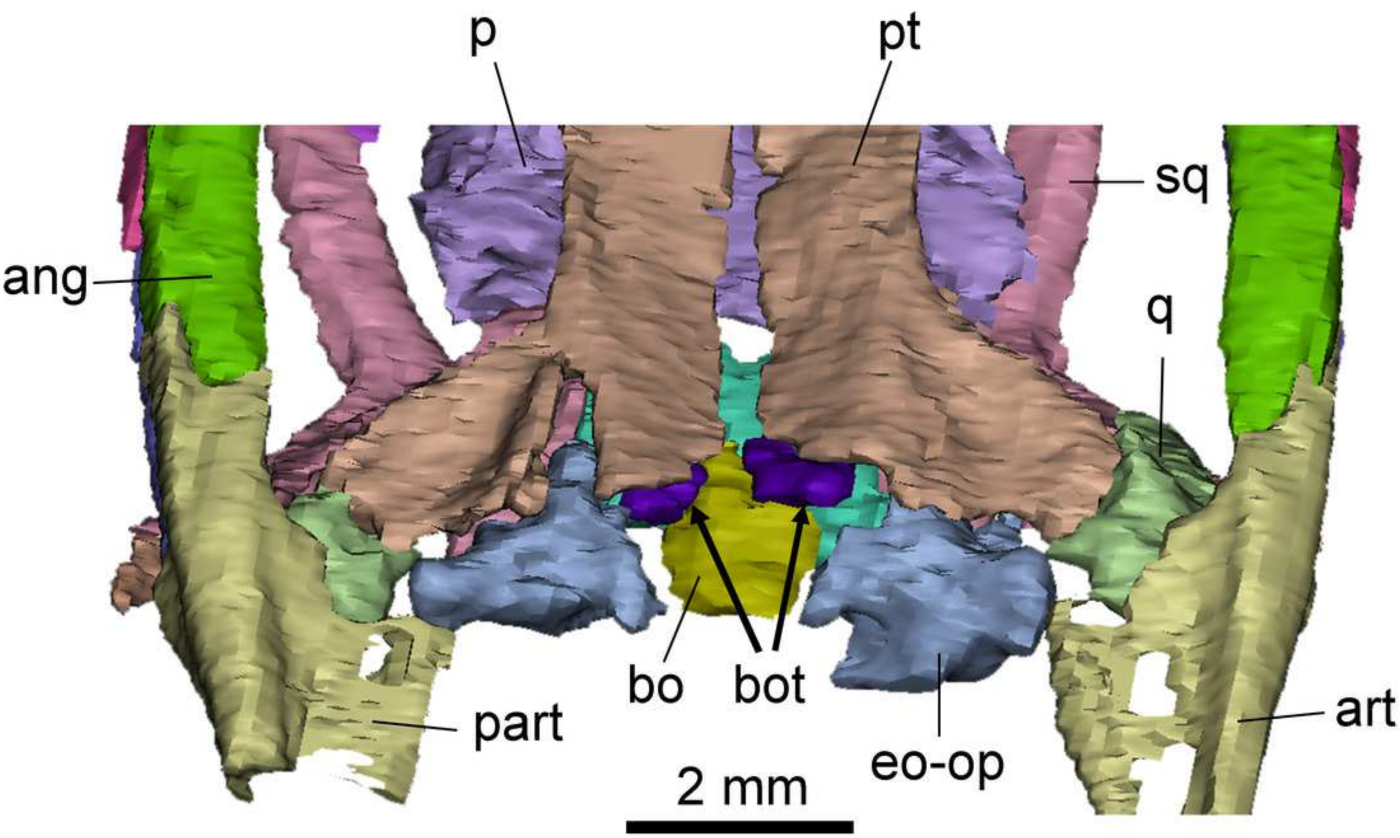

Figure 5

Reconstruction of pterygoid and palatine in marine reptiles

A. *Keichousaurus hui*; B. *Serpianosaurus mirigiolensis*; C. *Neusticosaurus peyeri*; D. *Dianmeisaurus gracilis*; E. *Diandongsaurus acutidentatus*. For abbreviations, see Fig. 1

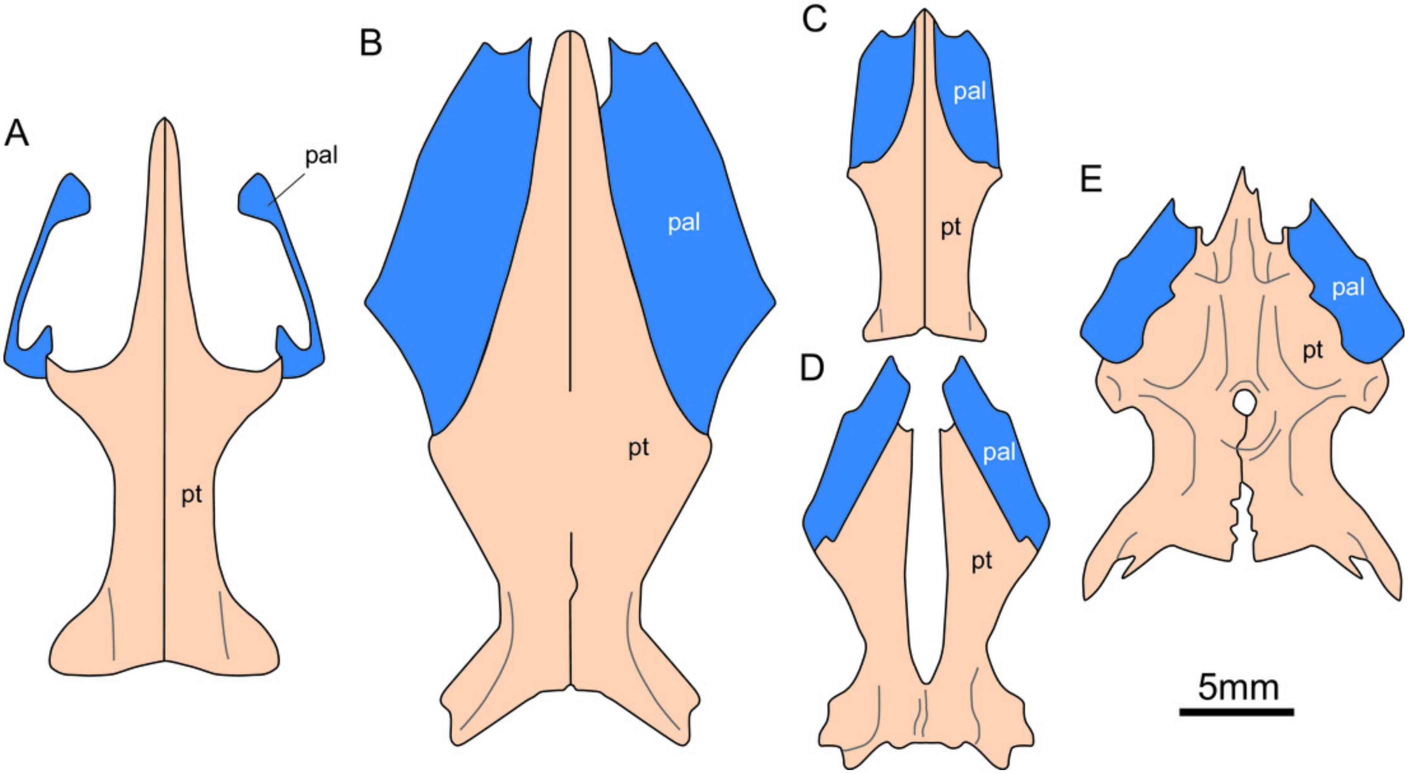

Figure 6

3D reconstruction of anterior teeth of *Keichousaurus hui* (CUGW VH009).

A. right side view; B. left side view. The third tooth on the left dentary is absent.

Abbreviations: D. dentary teeth; M. maxillary teeth; P. premaxillary teeth

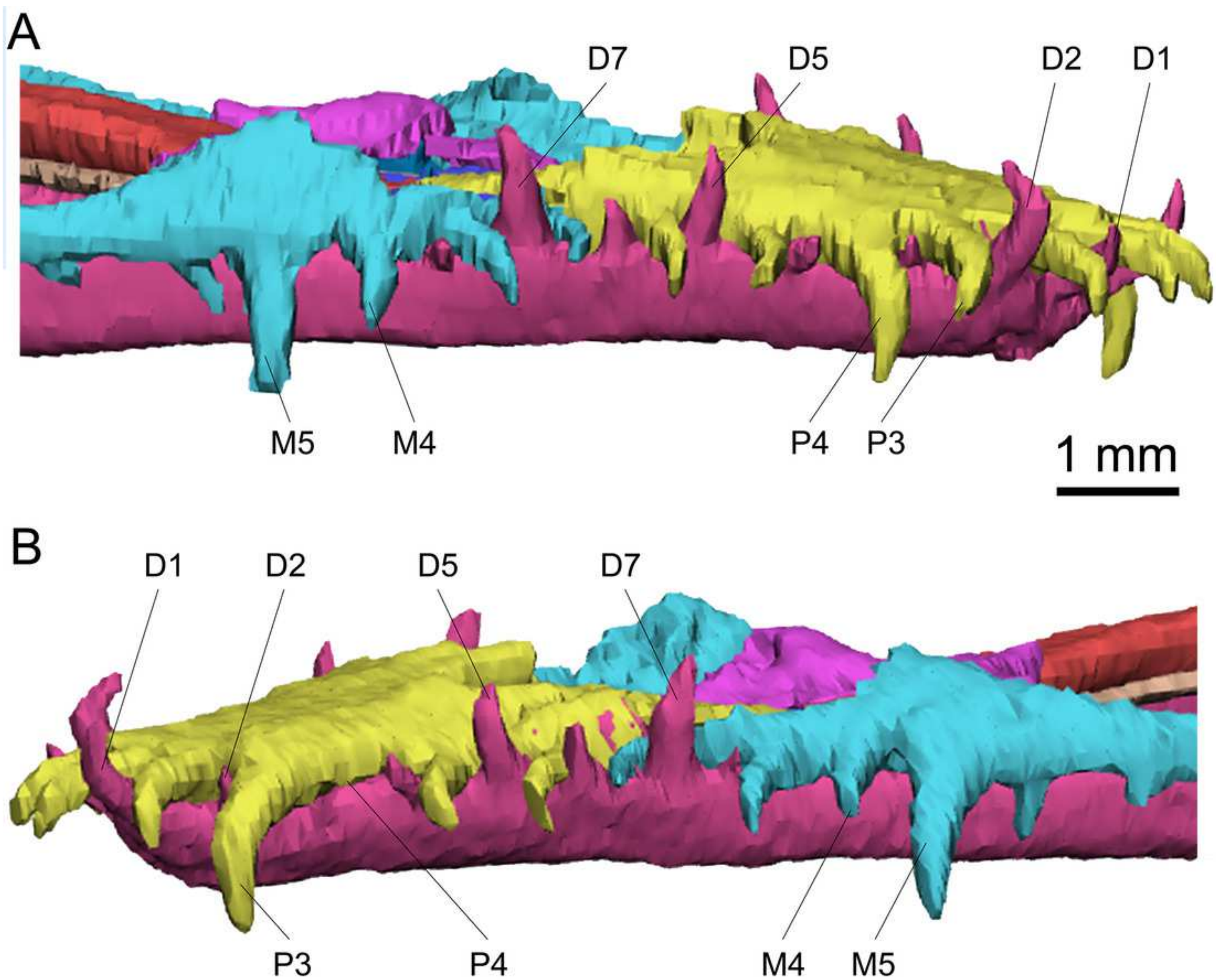

Figure 7

Reduced Strict consensus tree of 351 MPTs showing the phylogenetic relationships of *Keichousaurus* in Sauropterygia.

Five taxa excluded, including *Majiashanosaurus*, *Eremtmorhipis*, *Palatodonta*, *Hanosaurus*, and *Chaohusaurus*

TL = 811, CI = 0.293, RI = 0.685

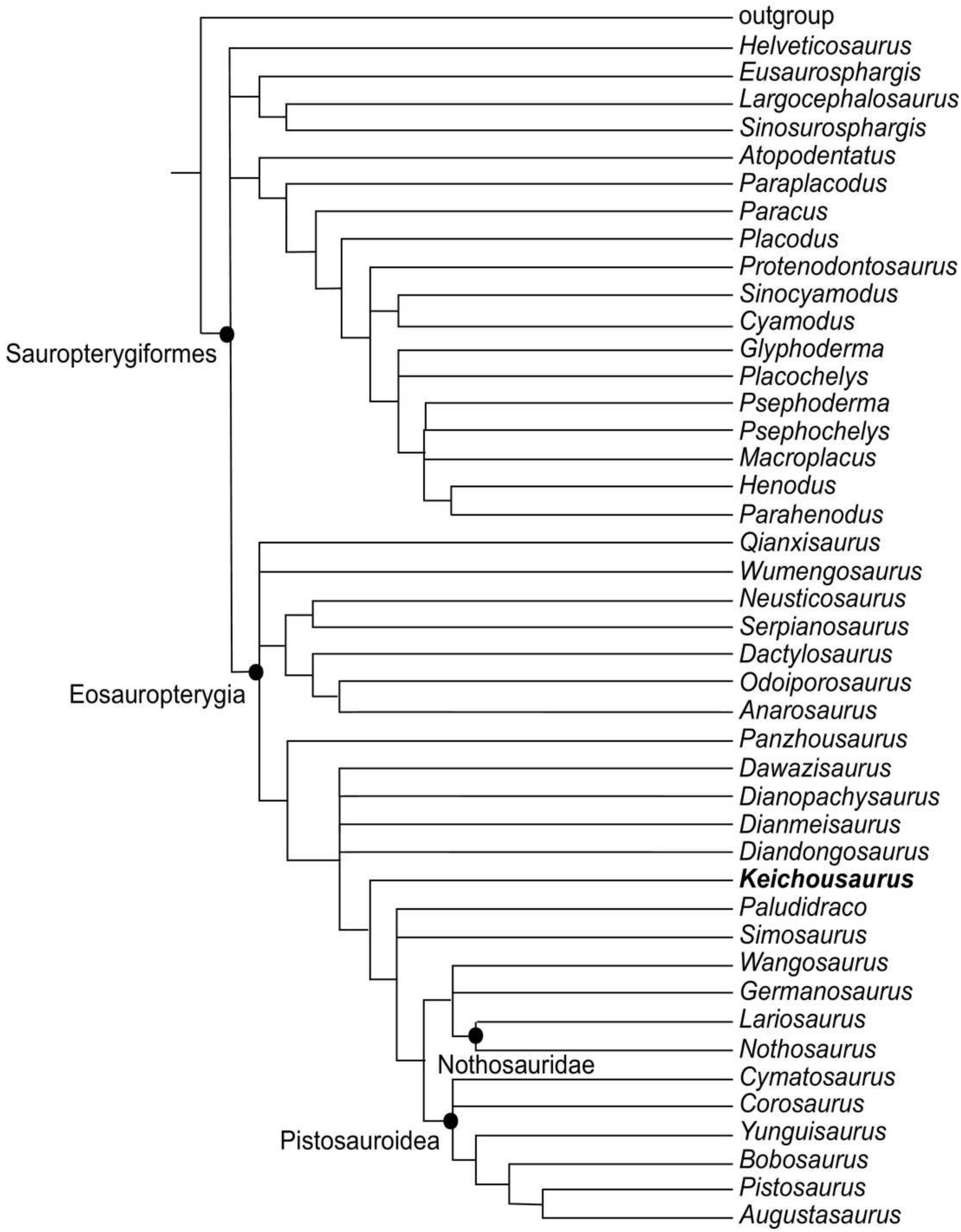
outgroup
Helveticosaurus
Eusaurosphargis
Largocephalosaurus
Sinosurosphargis
Atopodentatus
Paraplacodus
Paracus
Placodus
Protenodontosaurus
Sinocyamodus
Cyamodus
Glyphoderma
Placochelys
Psephoderma
Psephochelys
Macroplacus
Henodus
Parahenodus
Qianxisaurus
Wumengosaurus
Neusticosaurus
Serpianosaurus
Dactylosaurus
Odoiporosaurus
Anarosaurus
Panzhousaurus
Dawazisaurus
Dianopachysaurus
Dianmeisaurus
Diandongosaurus
Keichousaurus
Paludidraco
Simosaurus
Wangosaurus
Germanosaurus
Lariosaurus
Nothosaurus
Cymatosaurus
Corosaurus
Yunguisaurus
Bobosaurus
Pistosaurus
Augustasaurus
Sauropterygiformes
Eosauropterygia
Nothosauridae
Pistosauroidea

Figure 8

Phylogenetic cladograms showing the relationship of Sauropterygia.

The dotted box shows taxa of Chinese pachypleurosaurs or pachypleuosaur-like forms.