

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

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

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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.

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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 pachypleurosaur-like eosauropterygians than European pachypleurosaur and more derived than other Chinese pachypleurosaur-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 pachypleurosaur. 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 μ A, and a resolution of 21.96 μ m 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 μ A, and the resolution of 10.71 μ m 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 *Diandongosaurus* (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.

Basioccipital 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 *Diandongosaurus* (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 *Diandongosaurus* (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 *Diandongosaurus* (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 *Keichousaurus* 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 Pistosauroidae. 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 eosauroptrygians, *Dianopachysaurus*, *Diandongosaurus*, *Dianmeisaurus* and *Dawazisaurus*, than European pachypleurosaurs *Anarosaurus*, *Serpianosaurus*, *Neusticosaurus* 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 forms has been controversial (Li & Liu, 2019). The relationships among not only the pachypleurosaurs, but also the eosauroptrygians, remain open constantly. Here, we discuss the relationship between *Keichousaurus* and three taxa mentioned above with other families of Eosauroptrygia. The European pachypleurosaurs we mentioned, which include *Anarosaurus*, *Serpianosaurus*, *Neusticosaurus*, 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 Eosauroptrygia and the position of the Chinese genera have some differences (Fig. 8A and B). In regard to the internal relationship of the families of Eosauroptrygia, the monophyletic group consists of Nothosauroida and Pistosauroida forming a sister group with the Pachypleurosauria (Liu et al., 2011, 2021; Xu et al., 2022) (Fig. 8A), or the Pistosauroida is the basal clade of the consecutive sister groups of Nothosauroida 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 pachypleurosaur-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 Pistosauroida is positioned at the base of Eosauroptrygia, but the European pachypleurosaurs form a monophyletic group with the branch that is composed of Nothosauroida and Chinese pachypleurosaurs or similar forms and becomes the sister group to Pistosauroida. It shows the four taxa of Chinese pachypleurosaurs-like are more derived than others, and *Keichousaurus* is more related to Nothosauroida 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 Nothosauroidae, 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), Nothosauroidae 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.

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554

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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
Kelesosaurus 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 anteroventrally, 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

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

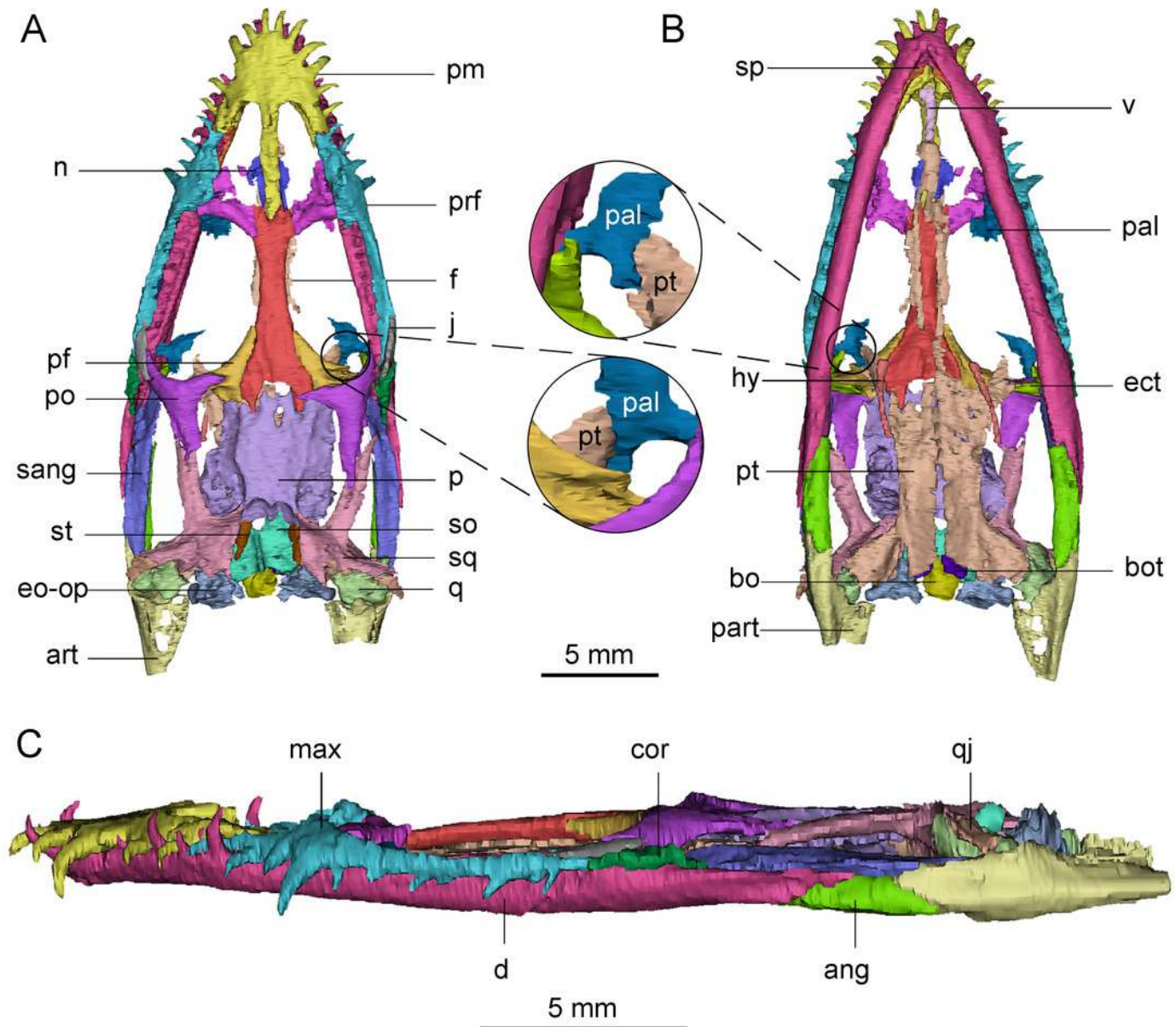


Figure 2

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

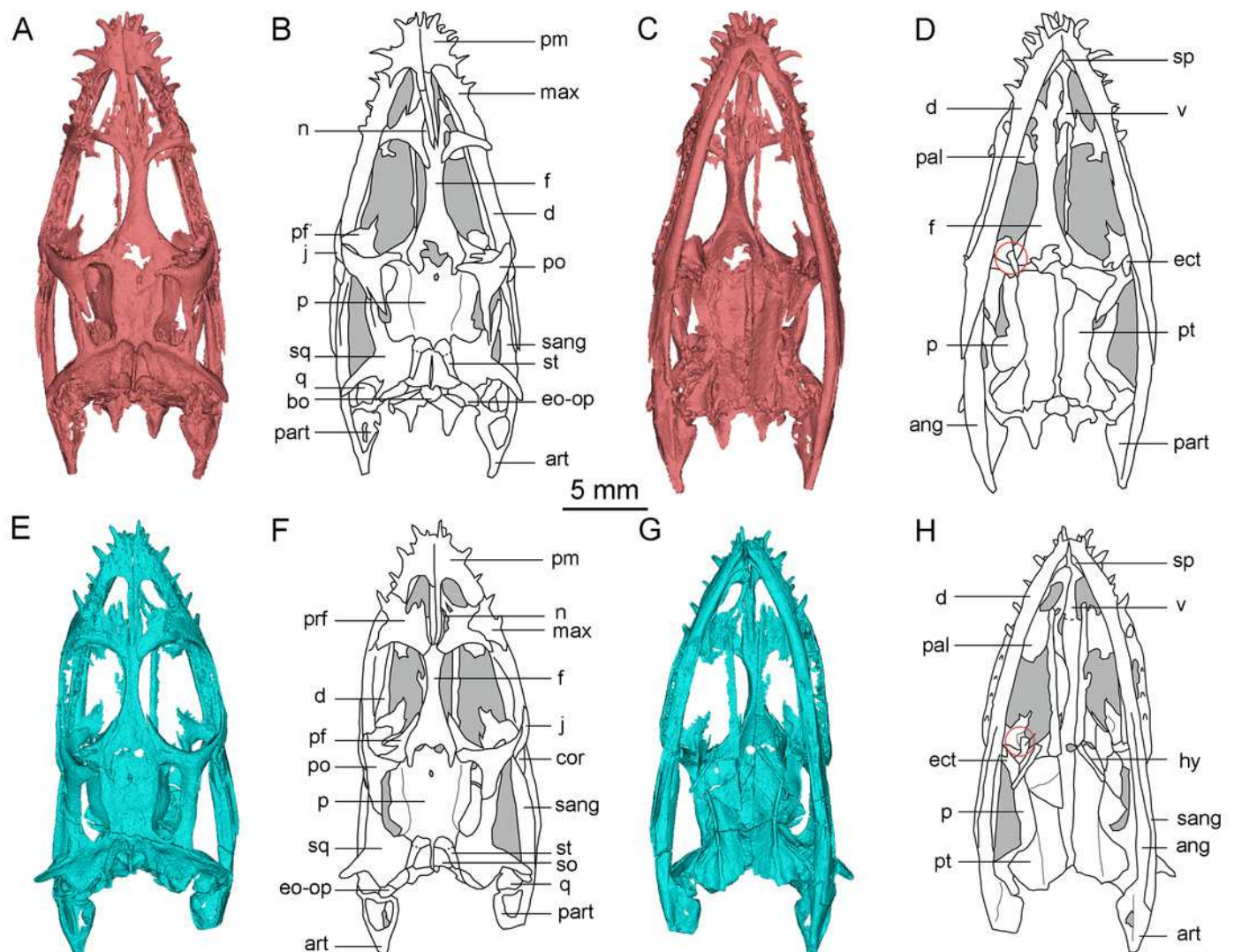
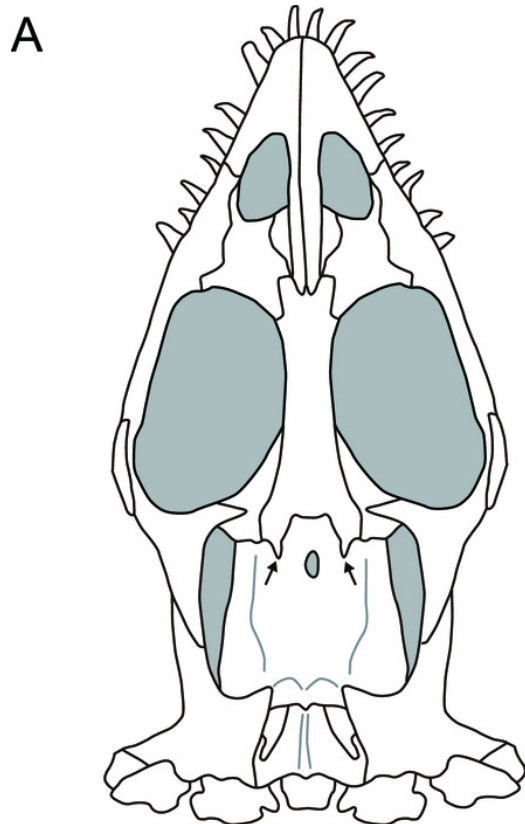


Figure 3

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



5mm



5mm

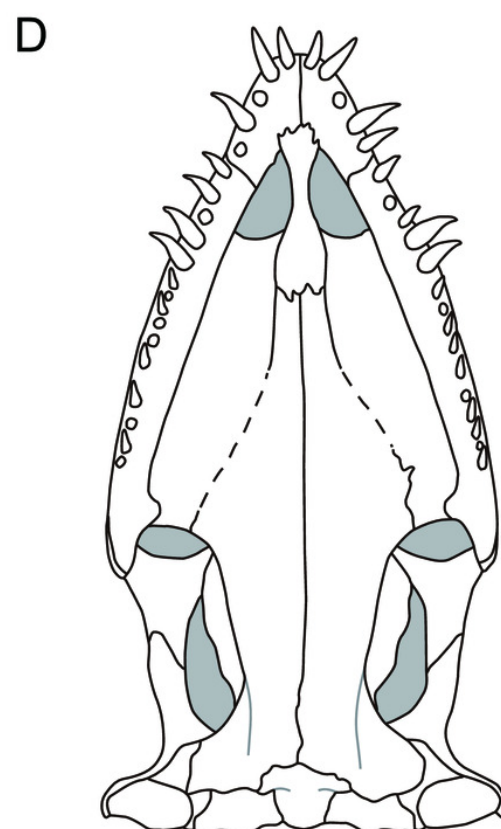
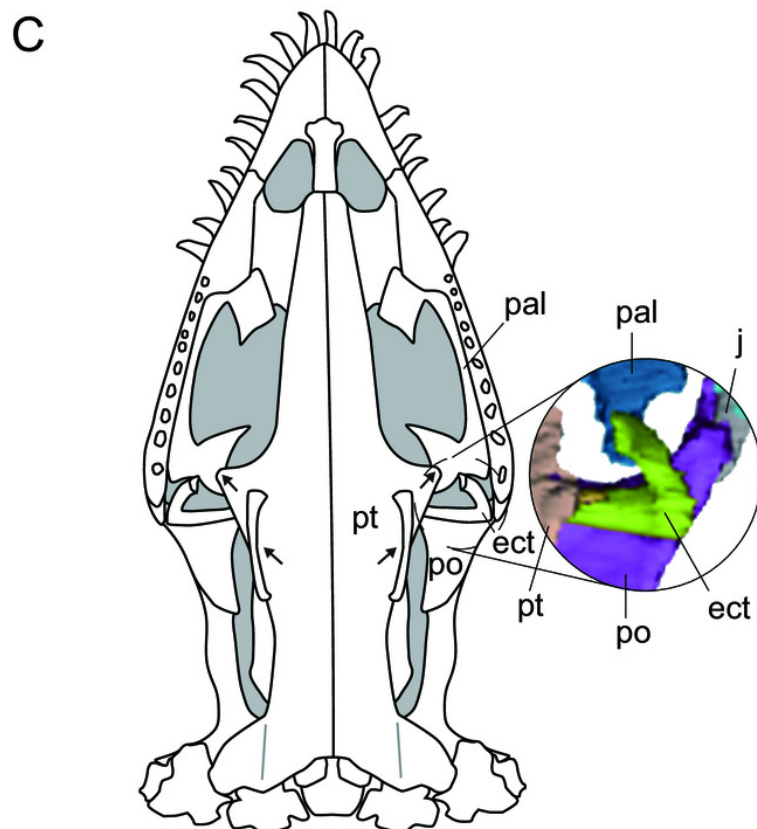


Figure 4

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

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

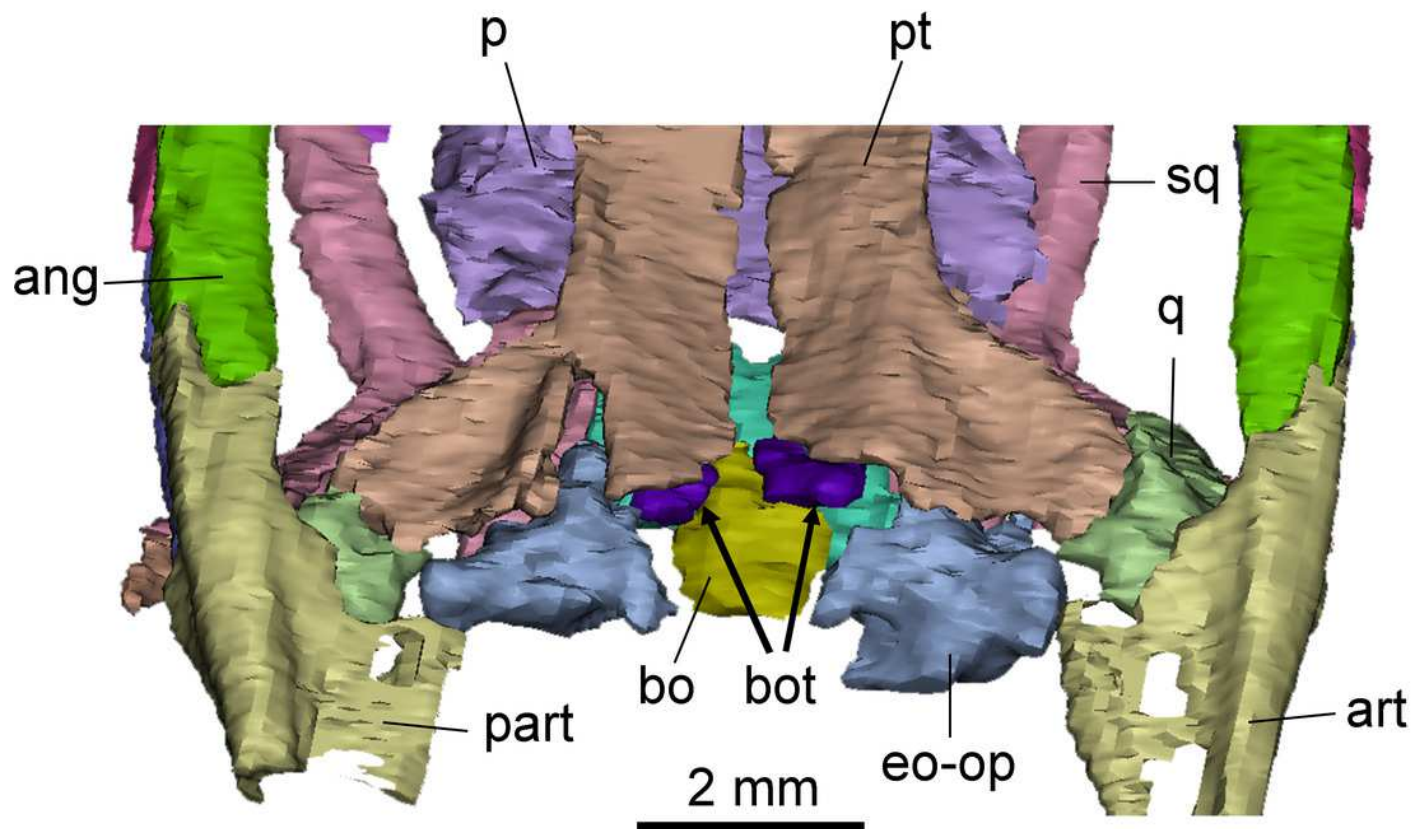


Figure 5

Reconstruction of pterygoid and palatine in marine reptiles

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

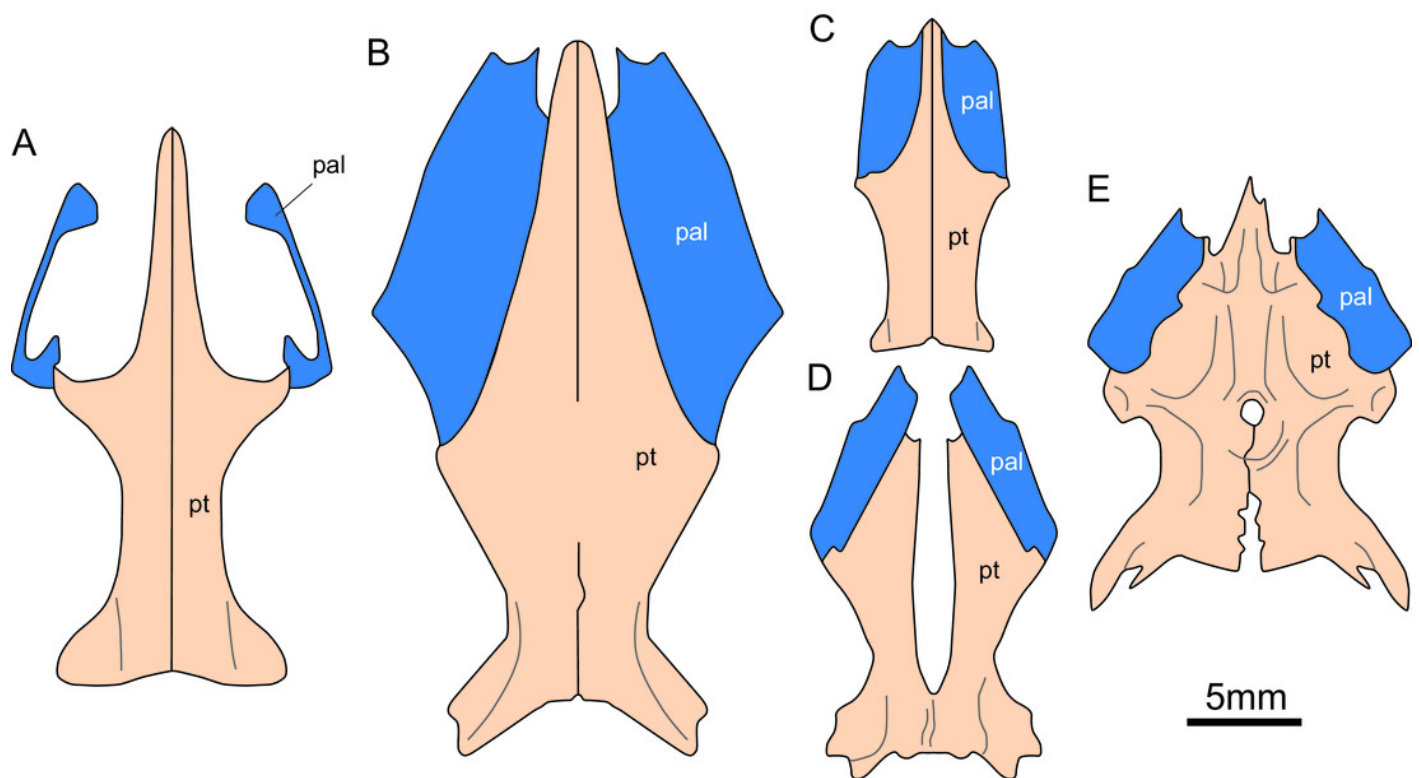


Figure 6

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

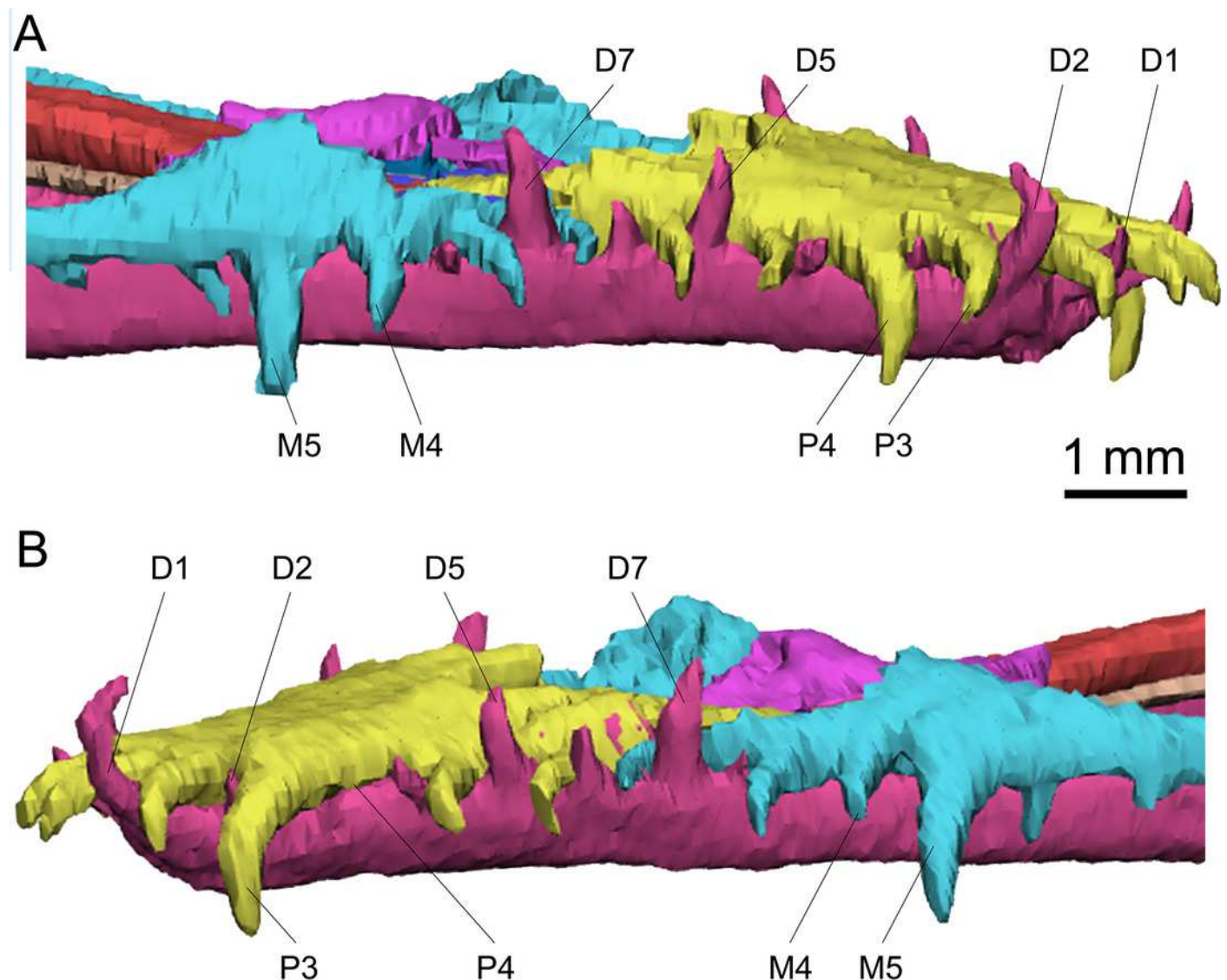


Figure 7

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

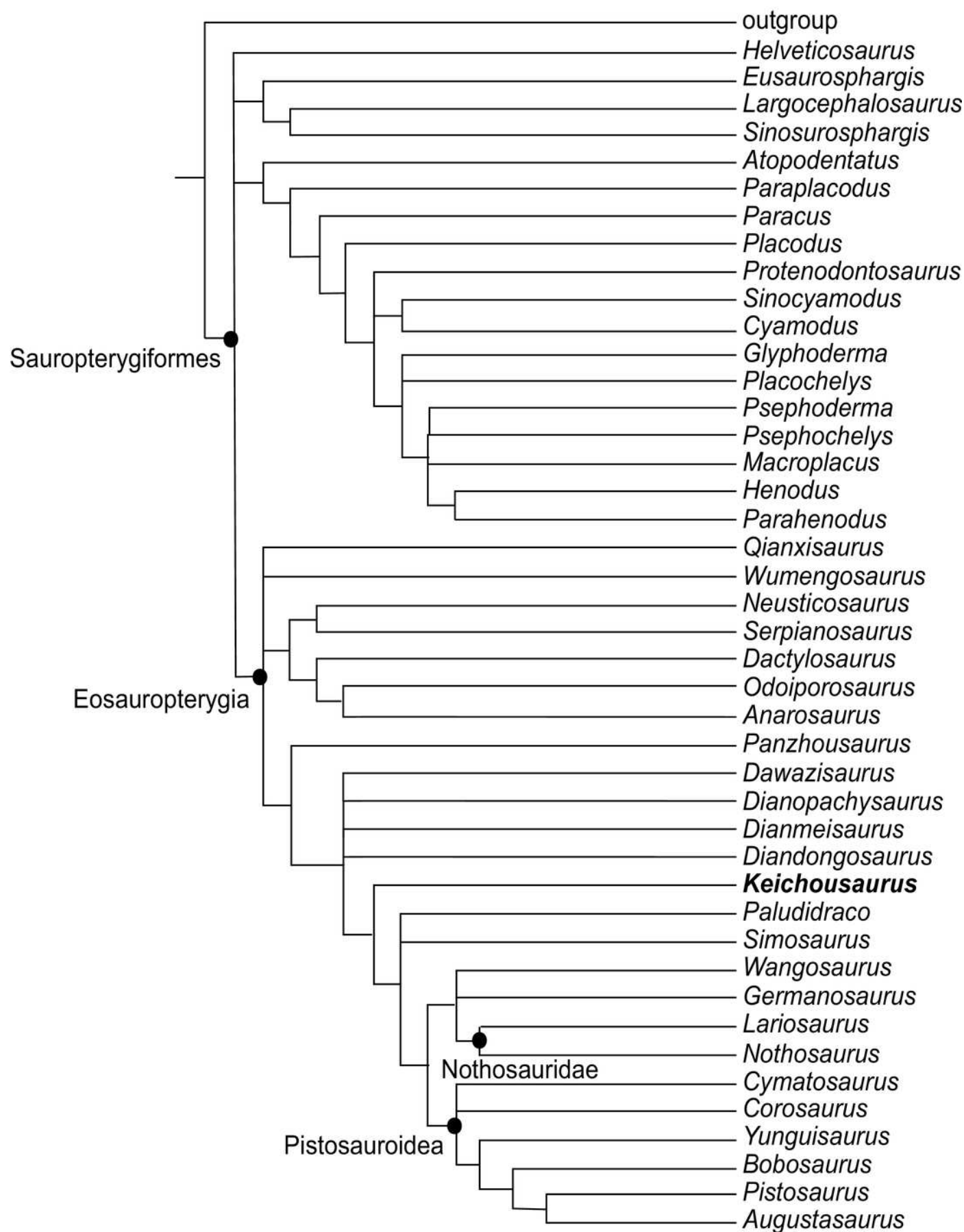


Figure 8

Phylogenetic cladograms showing the relationship of Sauropterygia.

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

