



# Tooth Structure and Replacement of the Triassic *Keichousaurus* (Sauropterygia, Reptilia) From South China

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The small-sized sauropterygian *Keichousaurus hui* was one of the most abundant marine reptiles from the Triassic Yangtze Sea in South China. Although *Keichousaurus* has been studied in many aspects, including the osteology, ontogeny, sexual dimorphism, and reproduction, the dentition of this marine reptile was only briefly described in external morphology. In this study, we provide new information on *Keichousaurus* tooth implantation, histology, and replacement based on a detailed examination of well-preserved specimens collected in the past decades. The tooth histology has been investigated for the first time by analyzing cross-sections of premaxillary teeth and the tooth attachment and implantation have been further revealed by X-ray computed microtomography. We refer the tooth replacement of *Keichousaurus* to the iguanid replacement type on the basis of the observed invasion of small replacement tooth into the pulp cavity of the functional tooth. Given the resemblance to other extinct and modern piscivorous predators in the morphology and structure of teeth, *Keichousaurus* might mainly feed on small or juvenile fishes and some relatively soft-bodied invertebrates (e.g., mysidacean shrimps) from the same ecosystem.

**Keywords:** pulp cavity, plicidentine, tooth replacement, *Keichousaurus*, Triassic, South China

## INTRODUCTION

Teeth are complex mineralized tissues that originated in jawed vertebrates more than 400 million years ago (Rücklin et al., 2012). The shape, implantation, and replacement of teeth differ widely across vertebrates and promote the radiation of this clade (Owen, 1841, 1842; Edmund, 1960, 1962; Peyer, 1968; Mehler and Bennett, 2003; Maxwell et al., 2012; Buchtová et al., 2013; LeBlanc et al., 2017; McCurry et al., 2019). Reptiles show a diverse array of tooth shapes from homodont to heterodont (Peyer, 1968; Rieppel, 2002) and from simple unicuspid to complex multicuspid teeth (Ungar, 2010; Handrigan and Richman, 2011), reflecting functional adaptation to various diets. Additionally, reptiles exhibit numerous combinations of tooth implantation and attachment (Peyer, 1968; Mehler and Bennett, 2003; Buchtová et al., 2013; LeBlanc et al., 2017), ranging from teeth possessing roots and lying within a socket (thecodonty), to teeth lying against the lingual wall

of the jawbone (pleurodonty), and to teeth without roots or sockets that are attached to the apex of the marginal jawbones (acrodonty). Continuous tooth replacement (polyphyodonty) is common for the vast majority of reptiles, although some groups (e.g., acrodont lepidosaurs) have lost the ability to replace their dentition (monophyodonty) (Edmund, 1960, 1962; Peyer, 1968; Motani, 1997; Rieppel, 2001; Fastnacht, 2008; Maxwell et al., 2012; Buchtová et al., 2013; Neenan et al., 2014; LeBlanc and Reisz, 2015).

The small-sized sauropterygian *Keichousaurus hui* (rarely exceeding 50 cm in total length) is one of the most abundant reptiles from the Triassic Yangtze Sea in South China (Young, 1958; Rieppel and Lin, 1995; Jiang, 2002; Holmes et al., 2008; Cheng et al., 2009; Fu et al., 2013; Xue et al., 2013). The genus was originally classified by Young (1958) in Pachypleurosauridae or in its own family (Keichosauridae) (Young, 1965) before formal phylogenetic analyses. Recent analyses of the sauropterygian phylogeny place *Keichousaurus* either at a relative basal position of the Eosauropterygia (Shang et al., 2020) or within Pachypleurosauridae (Li and Liu, 2020; Lin et al., 2021). Represented by large quantities of well-preserved specimens, *Keichousaurus* has been studied in many aspects including the ontogeny, taphonomy, reproduction, sexual dimorphism, allometry, and living style (Lin and Rieppel, 1998; Cheng et al., 2004, 2009; Holmes et al., 2008; Fu et al., 2013; Xue et al., 2013; Motani et al., 2015). However, the teeth of *Keichousaurus*—significant organs for taxonomy and ethology (Radinsky, 1961; Handrigan and Richman, 2011; Hwang, 2011)—were only briefly described in their external morphology (Young, 1958, 1965; Lin and Rieppel, 1998; Jiang, 2002; Holmes et al., 2008; Fu et al., 2013). Compared with those in other marine reptiles (Maisch and Matzke, 1997; Motani, 1997; Rieppel, 2001; Ciampaglio et al., 2005; Caldwell, 2007; Maxwell et al., 2012; Neenan et al., 2014; Sassoon et al., 2015), the teeth of *Keichousaurus* remain poorly known in their internal structure, function, and replacement.

In this study, through a detailed examination of well-preserved specimens, we aim to describe the tooth morphology, internal structure, and tooth histology of *Keichousaurus* and to discuss the tooth replacement, dental function, and food preference of this taxon.

## MATERIALS AND METHODS

All the studied specimens of *Keichousaurus* are housed in the Resource and Environmental Engineering College of Guizhou University (GZU), China. They were collected from the lower part of the Zhuganpo (lower) member of the Falang Formation in southwestern Guizhou (Dingxiao) and eastern Yunnan (Fuyuan), South China (Figure 1B). This member of fossil beds, composed of dark gray thin-to medium-bedded limestones or muddy limestones with dolomitic limestones, indicates a carbonate platform deposit environment (Liu and Xu, 1994; Wang, 1996, 2002; Rieppel, 1999; Rieppel et al., 2000; Jiang, 2002) (Figure 1A). Also, from the fossil beds, rich invertebrates, bony fishes, and several other types of marine reptiles are also found; the whole fossil assemblage represents the renowned Xingyi Biota (Su,

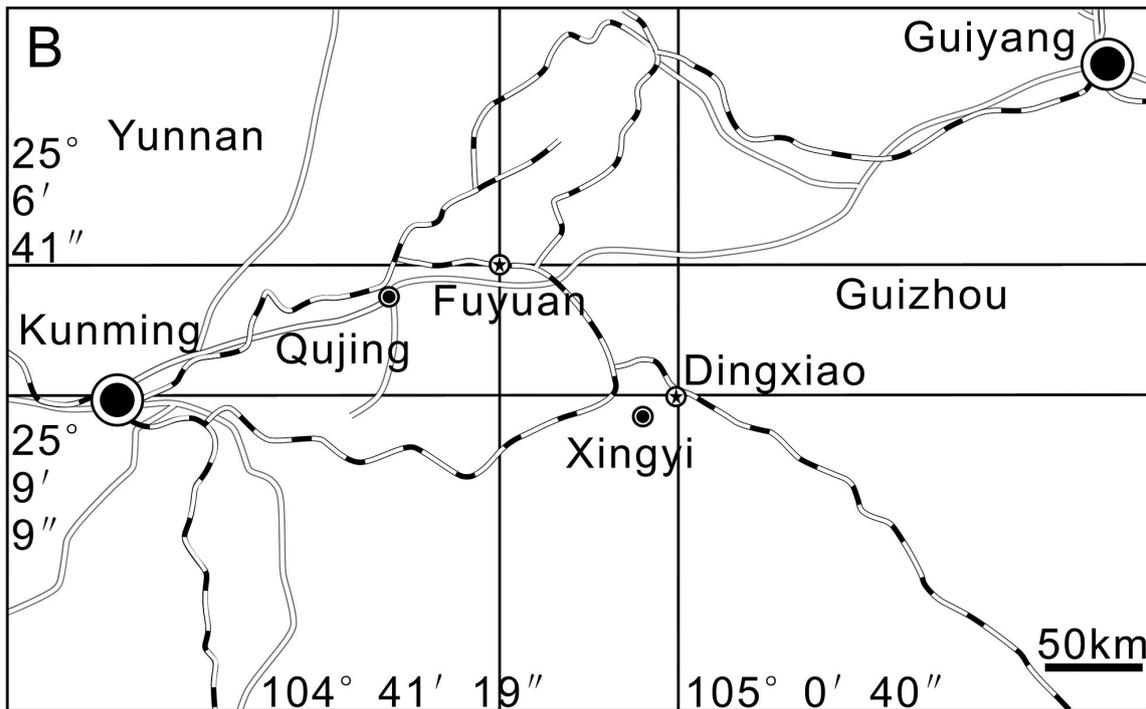
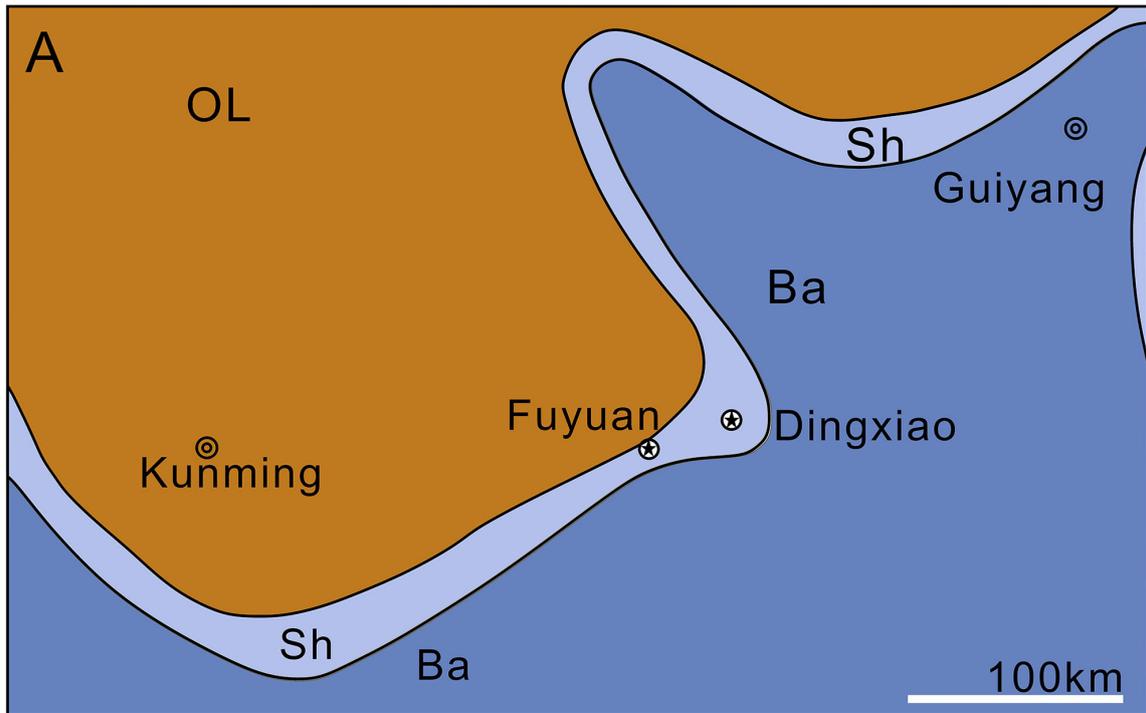
1959; Jin, 2001; Liu et al., 2002, 2003; Li, 2006; Geng and Jin, 2009; Xu et al., 2012, 2015, 2018a,b; Tintori et al., 2015; Sun et al., 2016; Ni et al., 2017; Xu and Ma, 2018; Shang et al., 2020; Xu, 2020). The age of this biota was controversial (Benton et al., 2013). Biostratigraphical studies of marine reptiles and ammonites (Young, 1958; Chen, 1985; Li, 2006; Zou et al., 2015) consistently support a late Middle Triassic (late Ladinian), but conodont biostratigraphy (Yang et al., 1995; Wang, 1996, 2002; Wang et al., 1998) suggests a younger Late Triassic (Carnian) age for this biota. Zou et al. (2015) commented that the previous conodont identification is inaccurate; the conodont "*Paragondolella polygnathiformis*" identified by Wang et al. (1998) is actually a transition *Paragondolella polygnathiformis*-*P. nodosa* recovered from a sample 3 m above the vertebrate-bearing interval. A recent zircon U-Pb age dating ( $240.8 \pm 1.8$  Ma) (Li et al., 2016) supports the determination of late Middle Triassic (Ladinian) for the Xingyi Biota.

The specimens were prepared mechanically with sharp steel needles and air scribe under optical microscope and some were washed by dilute oxalic acid to further remove the matrix. Tooth section and photography were performed at the Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Beijing, China. The whole skull of the specimen (GZU V0056) was removed and embedded in resin for preparation of transverse sections. Thin sections of four premaxillary teeth (about 30  $\mu$ m in thickness) were obtained from the bases of tooth crowns (perpendicular or nearly perpendicular to the long axis of the tooth). These sections were analyzed and photographed under cross-polarized light using the Zeiss Imager A2m microscope. X-ray computed microtomography was performed at the Yunnan Key Laboratory for Palaeobiology of the Institute of Palaeontology, Yunnan University, China, using a micro-CT (Xradia 520 Versa) with a pixel size of 14.71  $\mu$ m in three axes.

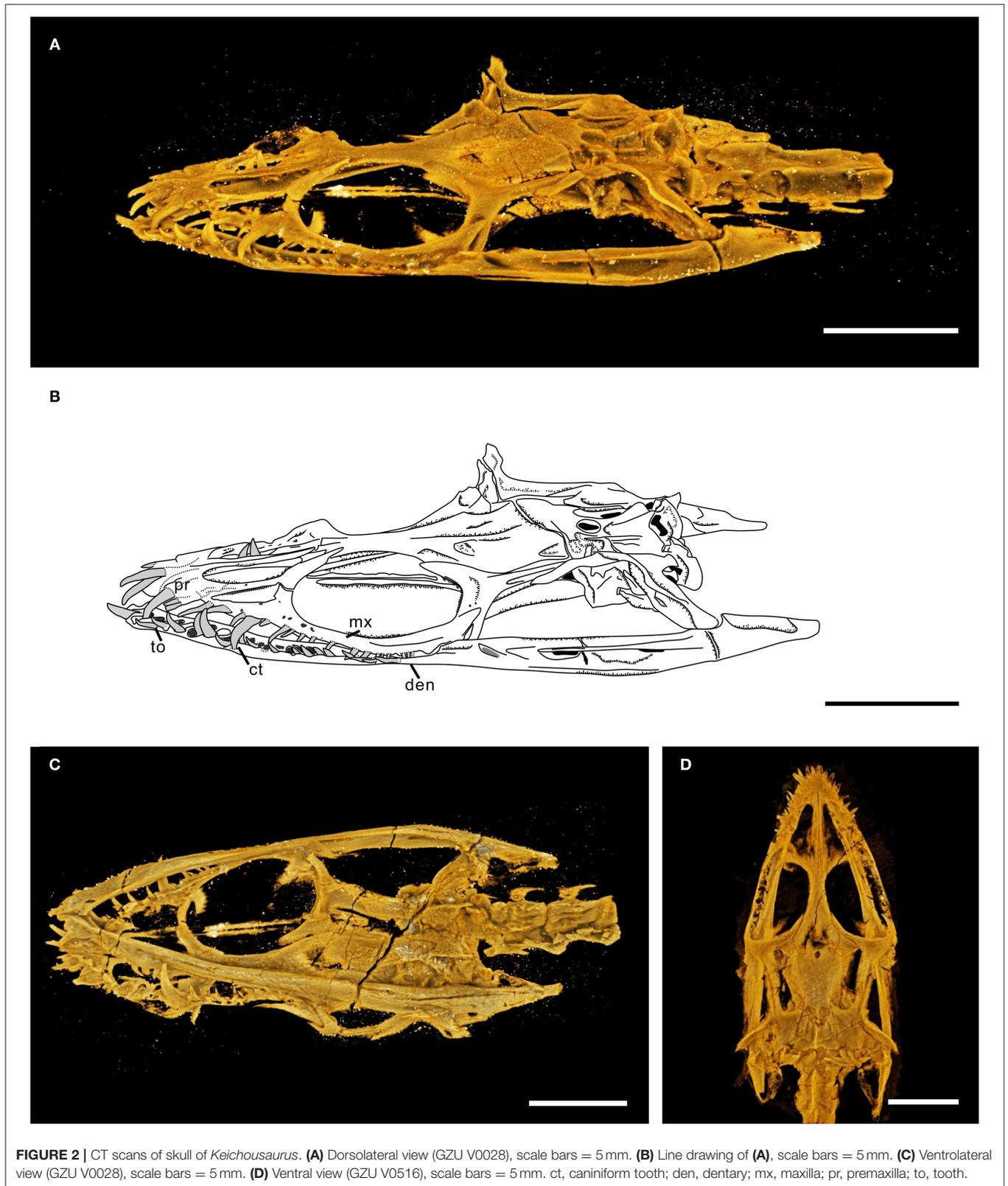
## TOOTH MORPHOLOGY AND INTERNAL STRUCTURE

The general morphology of the dentition of *Keichousaurus* has been described by Holmes et al. (2008) in their revision of the skull of this taxon. The heterodont teeth with variation of sizes are implanted in deep sockets of the premaxilla and maxilla in the upper jaw and the anterior portion of the dentary in the lower jaw (Figures 2A,B). The teeth in the premaxilla are strongly procumbent (visible in dorsal view) and five in number, larger than the anterior three teeth in the maxilla. The fourth and fifth maxillary teeth are fang-like (caniniform), nearly as large as the largest premaxillary teeth in size (Figures 2A–C), and the sixth and remaining (about 10) maxillary teeth are notably smaller, becoming angled more mesial than labial (Figures 2A,C,D). A nearly complete series of 19 dentary teeth is discernable in the specimen GZU V0028 including 6 enlarged teeth near the symphysis followed by 13 smaller teeth posteriorly.

As typically in other marine reptiles, the tooth of *Keichousaurus* can be divided into three parts: a crown, a root, and the neck or cervical margin where these two parts



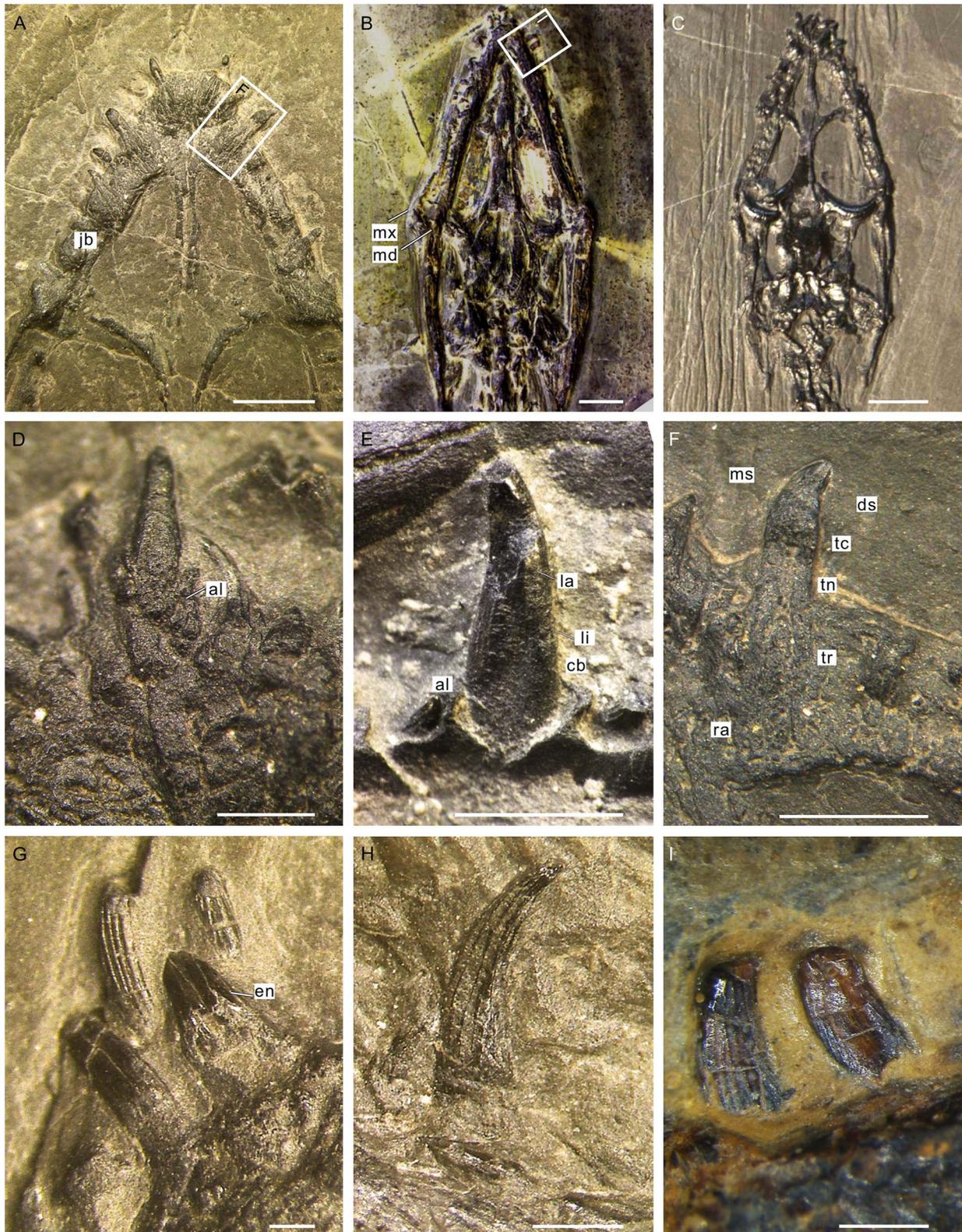
**FIGURE 1** | Maps. **(A)** Paleogeography of Southwest China near the Middle/Late Triassic boundary (modified from Liu and Xu, 1994). **(B)** Traffic map of fossil localities.



**FIGURE 2** | CT scans of skull of *Keichousaurus*. **(A)** Dorsolateral view (GZU V0028), scale bars = 5 mm. **(B)** Line drawing of **(A)**, scale bars = 5 mm. **(C)** Ventrolateral view (GZU V0028), scale bars = 5 mm. **(D)** Ventral view (GZU V0516), scale bars = 5 mm. ct, caniniform tooth; den, dentary; mx, maxilla; pr, premaxilla; to, tooth.

meet. The root is invisible *in situ*, but can be observed when it is detached from the jawbone (**Figures 3A,F**). It has a contracted basal pedicel deeply intercalated within the concave alveolus

(**Figures 3D,E**). The nearly cylindrical root gradually shrinks from near the neck toward the opened root apex (**Figure 3F**). The average length of the root is 0.73 mm, accounting for about half



**FIGURE 3 |** Teeth of *Keichousaurus*. **(A)** Premaxillary teeth (GZU V0036), scale bar = 2 mm. **(B)** Ventral view of the skull (GZU V0095), scale bar = 3 mm. **(C)** Dorsal view of the skull (GZU V0057), scale bar = 4 mm. **(D)** Premaxillary tooth, showing the root inserted into a concaved alveolus (GZU V0043), scale bar = 500  $\mu$ m. **(E)** A  
(Continued)

**FIGURE 3** | caniniform tooth (GZU V0028), scale bar = 1 mm. **(F)** Magnified view of **(A)**, showing an elongated root, scale bar = 1 mm. **(G)** Left mandibular anterior teeth (GZU V0023), showing the tooth neck, scale bar = 250  $\mu\text{m}$ . **(H)** Right mandibular tooth (GZU V0035), showing the apicobasal ridges, scale bar = 500  $\mu\text{m}$ . **(I)** Right mandibular teeth (GZU V0095), showing the transverse furrows, scale bar = 500  $\mu\text{m}$ . al, alveolus; cb, crown base; ds, distal side; en, enamel; jb, jaw bone; la, labial surface; li, lingual surface; md, mandible; ms, mesial side; mx, maxilla; ra, root apex; tc, tooth crown; tn, tooth neck; tr, tooth root.

to two-thirds of the whole length of the tooth. The waist-shaped neck is presented as an annular depression (**Figures 3E,G**), having a depth of 0.21–0.34 mm. The crown is conical with a sharp, slightly recurved dental cusp (**Figures 3E,F,H**). Lingually, it is concave with an arc-shaped mesial surface (**Figures 3G,H**). The crown has a maximal length of 1.51 mm in the premaxillary teeth and the ratio of height to width ranges from 2.5 to 3.5. The external surface of the crown is ornamented with fine, longitudinal ridges separated by multiple regularly spaced grooves (**Figures 3G–I**). These longitudinal ridges, termed as apicobasal ridges (Young et al., 2012, 2014a,b; Zverkov et al., 2018; McCurry et al., 2019), are straight or slightly curved and unbranched; they extend from the crown base to the apex of cusp, tapering in width along the basal–apical direction. The apicobasal ridges are continuous or interrupted by some shallow, transverse furrows (**Figure 3I**).

The oval cross-section of the tooth crown (viewed from its basal part) has two dark-colored layers (enamel and dentine layer) surrounding a light-colored pulp cavity (**Figures 4A,B,F, 5A,B**). A relatively bright and transparent (unevenly mineralized) globular zone is discernable between the enamel and dentine layers (**Figures 5A,B**). The enamel layer is densely mineralized and very thin (about 5  $\mu\text{m}$ ), indicated by a black ring in the tooth section (**Figures 5A,B**); it gradually becomes sparse toward the neck (**Figure 4C**). The dentine layer, as the main component of the tooth, is relatively low in density and bears some ridges and cracks in its internal wall (**Figures 4A,B**). In tooth sections, the annular dentine is simply folded, in which irregular white calcites and centripetally curved, fibril-like dentinal tubules are also present (**Figures 5A,C**). The circumpulpal dentinal tubules are closely packed near the pulp cavity to make this area darker in color than the surrounding areas of the dentine layer. It appears that some tubules nearly extend into the center of the pulp cavity, indicated by some irregular dark patches in the cavity (**Figures 5A,D**).

The pulp cavity (including pulp chamber and root canal) is largely spindle shaped (**Figures 4A,B,E**), completely filled with euhedral crystal grains of white calcites after the internal connective tissue decayed. The average length from the recurved tip of the pulp chamber to the apical portion of the dental cusp (**Figures 4A,B,D,E**) is 0.36 mm. At the horizontal level of the base of the tooth crown, the pulp cavity reaches its maximum width, which ranges from 0.16 to 0.27 mm and accounts for about fourth-fifths of the width of the tooth crown.

## TOOTH REPLACEMENT

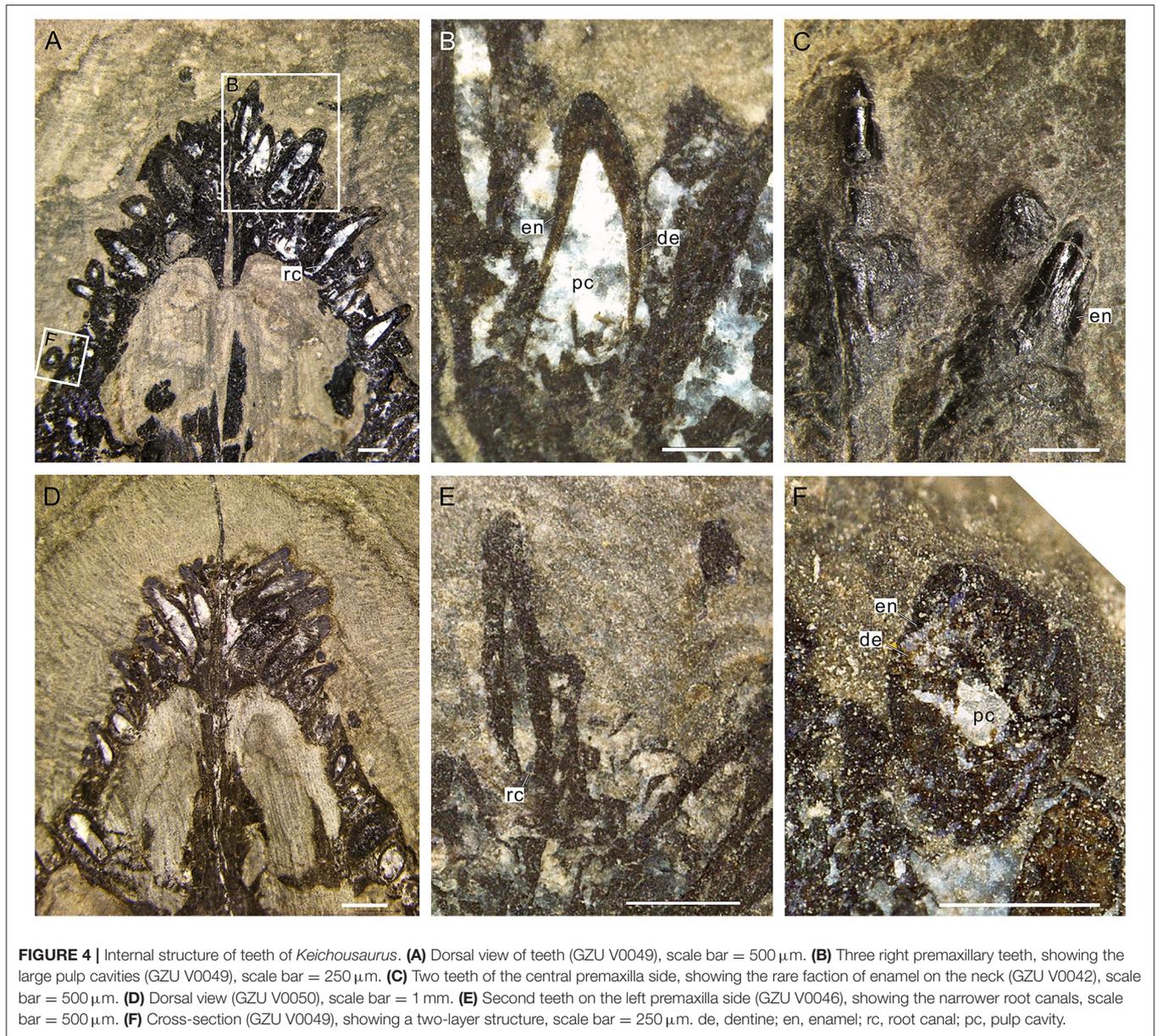
The tooth replacements of *Keichousaurus* are traceable in some specimens (GZU V0021, 0044, 0049, 0053), in which small replacement teeth are associated with the pulp cavities of larger

predecessor teeth (functional teeth) (**Figures 6A–D**). Among them, the replacement teeth in the specimens GZU V0049 (**Figures 6A,E**) and GZU V0021 (**Figures 6B,F**) are the smallest ones, which are exposed near the mesial-lingual side of the pulp cavities of the predecessor teeth, accounting for slightly less than half of the cavity of predecessor teeth in size. Both have only a loose dentine layer without a distinct enamel layer. In the specimen GZU V0044 (**Figures 6C,G**), the replacement tooth is larger, accounting for slightly more than half of the pulp cavity of the predecessor tooth. Within the predecessor tooth, the replacement tooth extends anterodorsally from the posteroventral edge of the root to the mesial-labial margin of the pulp cavity. The replacement tooth (GZU V0044) (**Figure 6C**) bears a triangular pulp cavity larger than that in the replacement tooth of specimens GZU V0021 (**Figure 6B**). In specimen GZU V0053 (**Figures 6D,H**), the replacement tooth is the largest one, nearly occupying the whole space of this pulp cavity. The replacement tooth has enamel and dentine layers with an even larger pulp cavity.

Two typical tooth replacement types are present in reptiles (Edmund, 1960; Rieppel, 1978; De Ricqlès and Bolt, 1983): iguanid and varanid tooth replacement types. In the former, a replacement tooth germinates at the lingual surface of root of a functional tooth and then invades into the pulp cavity of its related functional tooth during tooth growth; in the latter, the replacement tooth erupts in the interdental location and does not migrate into the pulp cavity during tooth development. Moreover, there is an intermediate replacement type in some reptiles, in which the replacement tooth adopts the replacement path of the iguanid type (existence of an invasion into the pulp cavity of the functional tooth), but the erupting position is similar to that of replacement tooth in the varanid type, with a distal deviation (Rieppel, 1978; Bertin et al., 2018). Based on the presence of replacement teeth inside the pulp cavity of the functional teeth (**Figures 6A–H**), we conclude that the tooth replacement of *Keichousaurus* can largely be referred to the iguanid replacement type. This replacement type was also found in plesiosaurs, Jurassic ichthyosaurs, *Platypterygius*, and extant crocodylians (Edmund, 1960, 1962; Motani, 1997; Fastnacht, 2008; Maxwell et al., 2012).

## TOOTH FUNCTION AND FOOD PREFERENCE

The teeth of *Keichousaurus* are thecodont and their roots deeply insert into individual alveoli (**Figures 3D,E**), such as those of some other eosauroptrygians (e.g., *Nothosaurus* and *Simosaurus*) and crocodiles (Rieppel, 2001; LeBlanc et al., 2017). The waist-shaped tooth neck has a certain depth (0.21–0.34 mm) and the interdental gap is likely filled by gums, which contribute

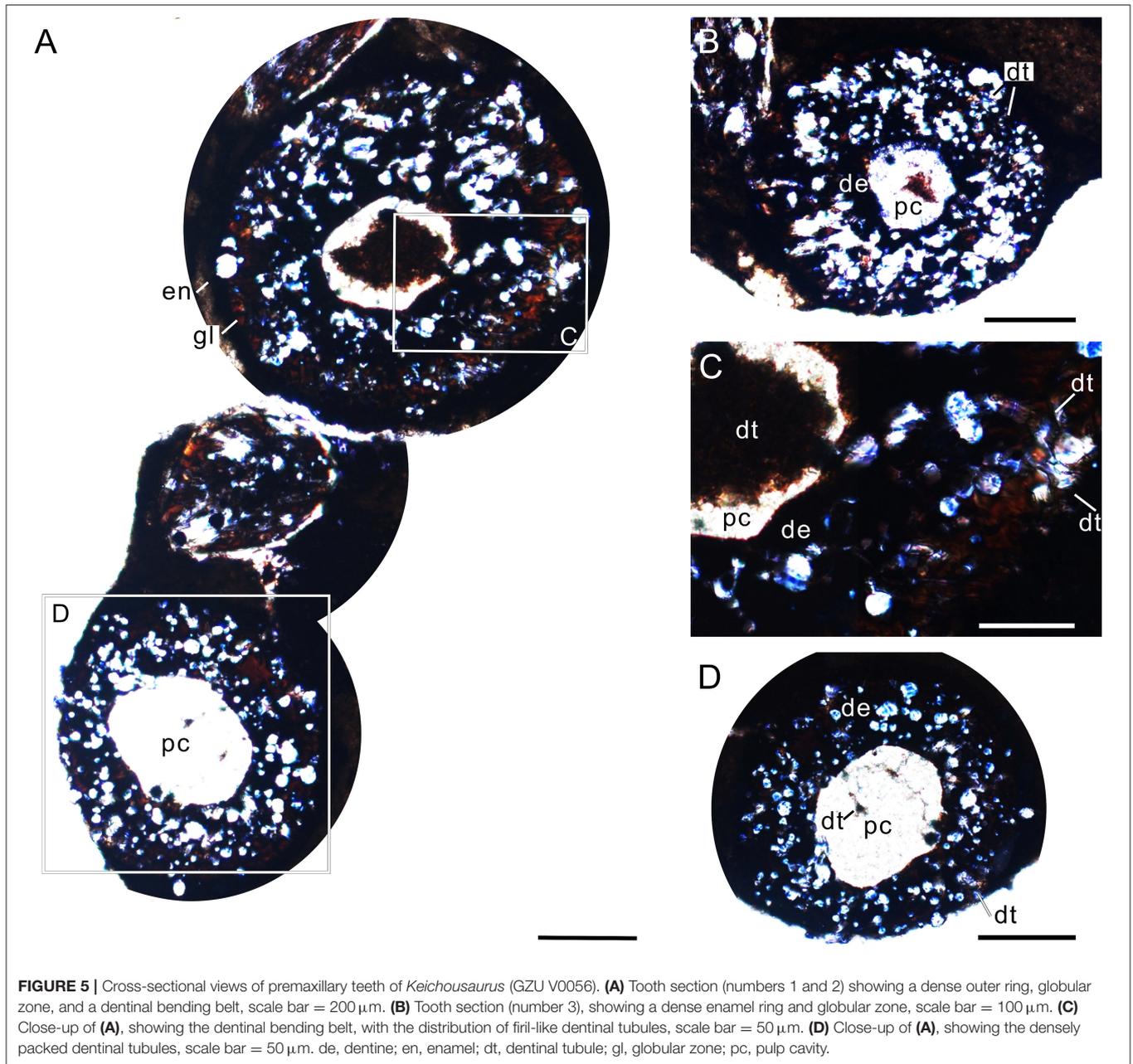


to the tooth stability (Chung et al., 2006; Carnio et al., 2007; Bourie et al., 2008). The teeth of *Keichousaurus* in anterior portions of jaws are elongated, fang like, and loosely arranged (Young, 1958, 1965; Jiang, 2002; Holmes et al., 2008; Fu et al., 2013). These teeth might exert the main force used to control prey by latching onto it and preventing escape (Figures 2A,B,D). The small teeth in posterior portions of jaws (Figures 2A,C) could act as a ratchet, transporting the prey posteriorly to the esophagus (Taylor, 1987; Taylor and Cruickshank, 1993).

The crowns of *Keichousaurus* are ornamented with apicobasal ridges (Figures 3G,H). These ridges, also present in other sauropterygians (e.g., *Pliosaurus* and *Helveticosaurus*) and some crocodylomorphs (Young et al., 2012, 2014a,b), might help pierce slippery or scaly struggling prey, facilitate blood drain, and prevent the prey from escaping (Frazzetta, 1966; Wright et al.,

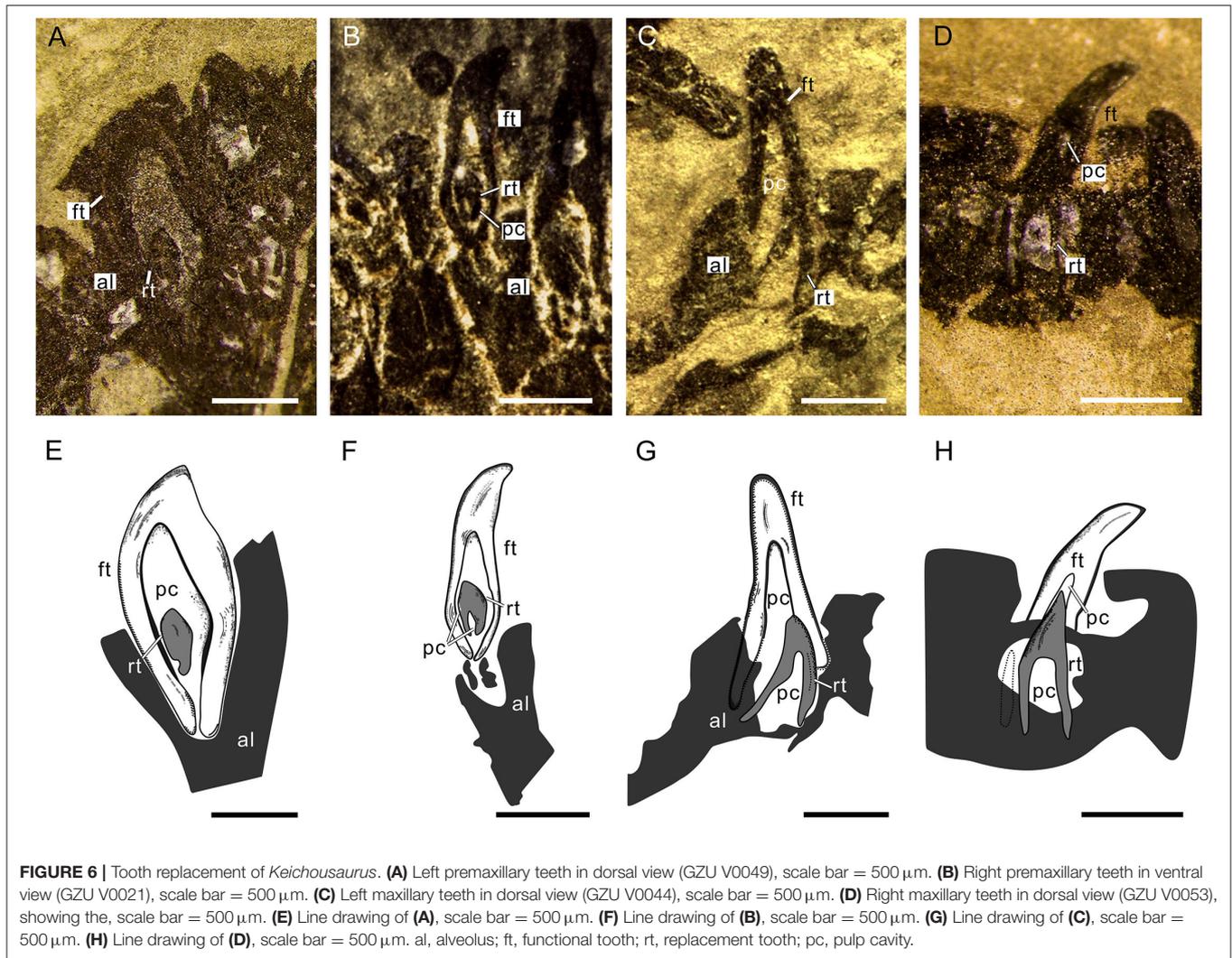
1979; Vaeth et al., 1985; Kardong and Young, 1996; Massare, 1997; Young et al., 2014b; McCurry et al., 2019). Plicidentine manifested as apicobasal ridges externally (Figures 3H, 5A,C; Tomes, 1878; Maxwell et al., 2012; Macdougall et al., 2014; McCurry et al., 2019) is regarded as a functional property of large predators (Scanlon and Lee, 2002; Modesto and Reisz, 2008). It, commonly seen in labyrinthodonts (Owen, 1841, 1842), mosasaurs (Schultze, 1970), ichthyosaurs (Maxwell et al., 2011), plesiosaurs (Owen, 1841), extant varanoids (Zaher and Rieppel, 1999), and snakes (Scanlon and Lee, 2002), could enhance the stress resistance and strength of the tooth-to-jaw anchoring (Peyer, 1968; Scanlon and Lee, 2002; Maxwell et al., 2011; Macdougall et al., 2014).

Based on the conical crown shape, sharp cusp (Figures 3E,H), moderate size (crown height to width between 2.5 and 3.5), and



ornamentation of apicobasal ridges (**Figures 3G,H**), the teeth of *Keichousaurus* could be categorized as pierce II (Massare, 1987). This type of piercing teeth (**Figures 3A,D,H**), unlike those in the filter-feeder *Atopodentatus* with needle-like teeth (Cheng et al., 2014) or those in durophagous placodontian predators with bulbous teeth (Neenan et al., 2013), are similar to the “fish-trap” teeth of exclusively piscivorous predators such as many mesozoic marine reptiles (ancient plesiosaurs, pliosauroids, teleosaurs, geosaurs, and nothosaurs) and extant river dolphins and gavia (Massare, 1987, 1997; Taylor and Cruickshank, 1993; Sander, 1999; Rieppel, 2002; Ciampaglio et al., 2005; Shang, 2007).

The teeth of *Keichousaurus* with large pulp cavities (**Figures 4A,B,F**) might have had sound microcirculation systems and keen sensory nerves to perform well in many respects including eliciting endogenous mechanisms of defense, moderating inflammation, providing pain tolerance, and promoting postinjury healing (Gazelius et al., 1987; Silverman and Kruger, 1987; Kimberly and Byers, 1988; Byers et al., 1990; Olgart, 1990; Taylor and Byers, 1990; Byers and Taylor, 1993; Chen et al., 1994; Walton and Nair, 1995; Evans et al., 1999; Hahn and Liewehr, 2007; Caviedes-Bucheli et al., 2008; Couve et al., 2013; Satoko et al., 2013). The large pulp cavities



**FIGURE 6 |** Tooth replacement of *Keichousaurus*. (A) Left premaxillary teeth in dorsal view (GZU V0049), scale bar = 500 μm. (B) Right premaxillary teeth in ventral view (GZU V0021), scale bar = 500 μm. (C) Left maxillary teeth in dorsal view (GZU V0044), scale bar = 500 μm. (D) Right maxillary teeth in dorsal view (GZU V0053), showing the, scale bar = 500 μm. (E) Line drawing of (A), scale bar = 500 μm. (F) Line drawing of (B), scale bar = 500 μm. (G) Line drawing of (C), scale bar = 500 μm. (H) Line drawing of (D), scale bar = 500 μm. al, alveolus; ft, functional tooth; rt, replacement tooth; pc, pulp cavity.

are prevalent among aquatic carnivores such as dolphins and the crocodylian *Alligator* (Westergaard and Ferguson, 1990; Slooten, 1991). Considering the large pulp cavity is surrounded by a thin wall, the bending resistance and strength of the tooth might be achieved by the radial foldings of the dentine (Plicidentine) (Figures 5A–C) (Preuschoft et al., 1991). The teeth of *Keichousaurus*, thus, might respond sensitively to external stimuli and have a relatively strong piercing force.

A rich diversity of small scaly or naked ray-finned fishes has been recovered from the same fossiliferous layer as *Keichousaurus* including thoracopterids, peltopleurids and laganoids (Xu et al., 2012, 2015, 2018b; Xu, 2020), holosteans (Liu et al., 2002, 2003; Xu et al., 2018a), and stem teleosts (Tintori et al., 2015). These fishes, as primary consumers in the food web of the Xingyi Biota, appear the potential prey of *Keichousaurus* and other piscivorous marine reptiles (e.g., nothosaurs). Other primary consumers in the same ecosystem include mysidaceans, gastropods, brachiopods, bivalves, ammonoids, etc. Among them, the small and relatively soft-bodied mysidaceans are probably the alternative prey of

*Keichousaurus*, but other invertebrates with hard shells are unlikely in the diet of *Keichousaurus*.

## CONCLUSION

Our detailed examination of well-preserved specimens of *Keichousaurus* provides new information on its tooth implantation, histology, and replacement. The thecodont teeth of *Keichousaurus* resemble the “fish-trap” teeth of other extinct and modern piscivorous predators: the cylindrical root deeply inserts into the alveolus with its depth accounting for about a half to two-thirds of the tooth; the dental neck is presented as an annular depression (0.21–0.34 mm in depth); and the conical, thin-enameled crown bears apicobasal ridges on its surface with a sharp, slightly recurved tooth cusp apically. These ridges might help pierce slippery or struggling scaly prey, facilitate blood drain, and prevent the prey from escaping. In the cross-section of the basal portion of the crown, the tooth has two dark-colored layers (dense enamel and radially folded dentine) surrounding a light-colored large pulp cavity, with some dentinal tubules

invading the cavity. The tooth replacement of *Keichousaurus* can largely be referred to the iguanid replacement type on the basis of the invasion of small replacement tooth into the pulp cavity of the predecessor tooth. Deduced from the functional morphology of the tooth, the potential prey of *Keichousaurus* is mainly composed of small or juvenile fishes and some relatively soft-bodied invertebrates (e.g., mysidacean shrimps) from the same ecosystem.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

## AUTHOR CONTRIBUTIONS

YW and TL put forward the concept. J-IL wrote this manuscript with comments from G-hX. Y-jQ performed data analysis. JL proposed some suggestions to the article. M-sZ and Y-IL made contributions to data visualization. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

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