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PALEONTOLOGY

Tooth replacement of the filter-feeding pterosaur *Forfexopterus* and its implications for ecological adaptation

CHANG-FU ZHOU & FENGMIN FAN

Abstract: A "comb-dentition", characterized by long, needle-like, and closely-spaced teeth, is found in the ctenochasmatid pterosaurs as an adaptation for filter-feeding. However, little is known about their tooth replacement pattern, hindering our understanding of the development of the filter-feeding apparatus of the clade. Here, we describe the tooth replacement of the pterosaur *Forfexopterus* from the Jehol Biota based on high-resolution X-ray Computed Tomography (CT) reconstruction. As in the ornithocheirid *Coloborhynchus*, the tooth germs are relatively medially positioned along the middle line; the replacement teeth erupt at the posteromedial side of the functional tooth; no more than one replacement tooth present in each alveolus. The replacement teeth are less than half of the length of the full-grown tooth, and alternatively positioned along the tooth row. The alternatively-positioned young and mature functional teeth are dominant and abrased, maintaining the active tooth-tooth occlusion of the filter-feeding apparatus. Reconstruction of Zahnreihen shows an average Z-spacing of 2.02, comparable to that of the simple alternate replacement (Z-spacing = 2) between odd- and even-numbered tooth positions in reptiles. Based on comparisons with *Balaenognathus*, *Ctenochasma*, and *Pterodaustro*, the tooth replacement pattern appears to be varied in ctenochasmatids, and needs to be further studied in the future.

Key words: Ctenochasmatidae, filter-feeding, CT scan, tooth replacement, Jehol Biota.

INTRODUCTION

Tooth replacement pattern is rarely known in pterosaurs (Edmund 1960, Fastnacht 2008). Fastnacht (2008) firstly examined the tooth replacement pattern in the ornithocheirid *Coloborhynchus robustus* by X-ray Computed Tomography (CT), revealing some tooth replacement patterns in pterosaurs, such as the replacement tooth positioned posteromedially against the functional tooth, the replacement process starting while the replacement tooth reaches about two-thirds the size of the functional tooth, the replacement process taking more than two thirds of the tooth life, enlarged anterior teeth have a higher replacement rate than posterior teeth, which are possibly adapted to the fish-grabbing feeding behavior (Fastnacht 2008).

The filter-feeding ctenochasmatids are characterized by long, needle-like, and closely-spaced teeth which form "comb-dentitions" (e.g. Wellnhofer 1991, Zhou et al. 2017, Bestwick et al. 2018). The "comb-dentitions" are highly diverse to filter varied food items from water with exceptionally weak bites (e.g. Henderson 2018), although a more active tooth-tooth occlusion is involved in *Forfexopterus* (Zhou et al. 2022). However, their tooth replacement pattern is still poorly known. Recently, Cerda & Codorniú (2023) examined the dental histology and the iconic ctenochasmatid *Pterodaustro*, revealing an absence of replacement teeth, which demonstrates a monophyodont or diphyodont pattern. Martill et al. (2023) hypothesized that an alternating replacement pattern in the ctenochasmatid *Balaenognathus*, based on the tooth size gradients identified in the tooth row, while the process of tooth replacement is unexplored.

In 2022, a mandibular fragment of the Jehol Biota ctenochasmatid *Forfexopterus* was reported by Zhou et al. (2022) using CT scan and three-dimensional visualization. This specimen preserves the rostral portion of the mandible and associated teeth. Nine pairs of alveoli are occupied by the functional and/or replacement teeth, providing an opportunity to investigate the tooth replacement pattern. Here, the functional and replacement teeth are reconstructed along with the functional teeth based on the CT scan data. Details of the tooth development, tooth replacement, Zahnreihen and Z-spacing are revealed to enrich our knowledge of the tooth replacement pattern in ctenochasmatids.

MATERIALS AND METHODS

SDUST-V1007 includes the rostral portion of the mandible of *Forfexopterus* from the Jiufotang Formation at the Dayaogou site, Jianchang, western Liaoning Province (Zhou et al. 2022). It is heavily damaged and compressed dorsoventrally, as common in other Jehol pterosaurs. Most of the teeth especially the roots are damaged (Figure 1).

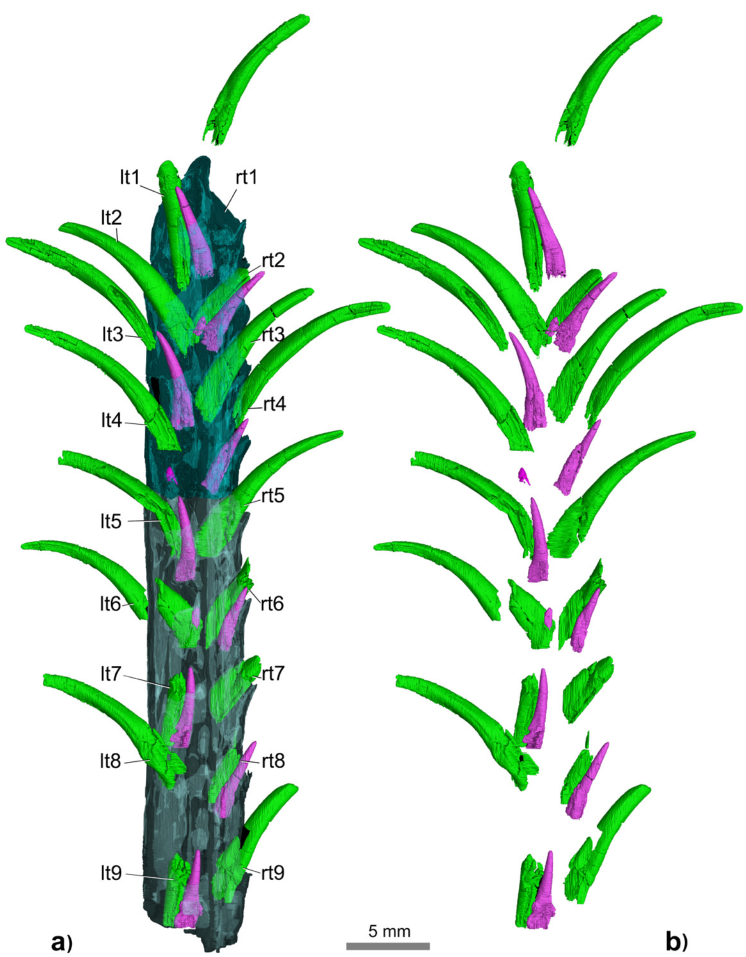

Figure 1. Digital reconstruction of lower teeth in the ctenochasmatid *Forfexopterus* (SDUST-V1007). a) transparent reconstruction of the rostral fragment of the mandible in ventral view; b) lower teeth in ventral view. Colors marked: dark, mandibular body; green, functional teeth; purple, replacement teeth.

The specimen was CT scanned at China University of Geosciences (Beijing) with a High-Resolution X-ray CT scanner (Nikon XT H 225 ST; Nikon, Tokyo, Japan), 150 kV, 46 μA. 4284 slices were acquired with a resolution of 2000×2000 and a voxel size of 16.58 μm. The data was processed with VG Studio 3.0 (Volume Graphics, Heidelberg, Germany).

Zahnreihen and Z-spacing are constructed using the replacement index (Fastnacht 2008), which is the ratio between heights of replacement teeth and functional teeth. As mentioned by Zhou et al. (2022), many of the functional teeth of SDUST-V1007 are worn and some of them are broken off, which undermines their height estimation (Figure 1, Table I). In order to calculate the replacement index, all the functional teeth are assumed to have the same height of the left sixth functional tooth (lt6), which is the longest preserved teeth and is almost completely preserved, as the rostrally-positioned teeth appear subequal in height in most ctenochasmatids (e.g. *Balaenognathus*, *Ctenochasma*, *Feilongus*, *Forfexopterus*, *Gnathosaurus*, *Pterofiltrus*; Wellnhofer 1991, Wang et al. 2005, Jiang & Wang 2011, Jiang et al. 2016, Martill et al. 2023). The replacement index of the dentition of SDUST-V1007 is listed in Table II.

Institutional abbreviations: SDUST, Shandong University of Science and Technology, Qingdao, Shandong Province, China; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

RESULTS

Description of the dentition

Nine pairs of alveoli are preserved in the rostral portion of the mandible of SDUST-V1007. All alveoli except for the first right one are occupied by functional and/or replacement teeth. The first right functional tooth is preserved but is displaced from its alveolus, as a taphonomic artifact. A total of 18 functional teeth and 13 replacement teeth are identified using CT-scan

Table I. **Measurement of the teeth of the ctenochasmatid *Forfexopterus* (SDUST-V1007) (mm). ?: unknown; N/A: not applicable.**

	1	2	3	4	5	6	7	8	9
Right functional tooth	9.14	?	10.86	12.57	11.53	?	?	?	8.5
Right replacement tooth	N/A	5.14	N/A	4.91	N/A	3.8	N/A	5	0.83
Left functional tooth	8.20	11.14	11.26	11.71	?	12.63	?	10.5	?
Left replacement tooth	5.71	0.86	5.71	1.14	5	1.25	5.75	N/A	5

Table II. **Replacement index of the teeth of the ctenochasmatid *Forfexopterus* (SDUST-V1007).**

	1	2	3	4	5	6	7	8	9
Right functional tooth	1.0	1.41	1.0	1.39	1.0	1.30	1.0	1.40	1.07
Right replacement tooth	0	0.41	0	0.39	0	0.30	0	0.40	0.07
Left functional tooth	1.45	1.07	1.45	1.09	1.40	1.10	1.46	1.0	1.40
Left replacement tooth	0.45	0.07	0.45	0.09	0.40	0.10	0.46	0	0.40

(Figure 1). Six functional teeth (rt2, rt6, rt7, rt8, lt7, lt9) are damaged on their crowns, and only the roots remain. The rest of the functional teeth are abrased on their crowns, implying the presence of a tooth-tooth occlusion (Zhou et al. 2022). The functional teeth are comparable in the crown size, but the size of the roots are generally divergent (Figure 1, Table I). The basial surface of the root is closed in the mature functional teeth (rt2, rt4, rt6, rt8, lt1, lt3, lt5, lt7, lt9), but the posteromedial side of the root is secondary open due to resorption. The basial surface of the young functional teeth (rt1, rt3, rt5, rt7, rt9, lt2, lt4, lt6, lt8) is open. The open roots are thin-walled, heavily damaged, making them appear broader than the enclosed roots, as taphonomic artifacts. These two stages of the functional teeth are positioned alternatively along the tooth series and are asymmetrically on both sides (Figure 1).

The replacement teeth are present in thirteen alveoli, and are absent in the rest (rt1, rt3, rt5, rt7, lt8). As in the ornithocheirid *Coloborhynchus*, no more than one replacement tooth is present in each alveolus. The replacement teeth appear to be medially or posteromedially positioned in relative to the functional teeth, but much smaller in size (Figure 1, Table I). Nine replacement teeth are at a relatively developed stage and less than half size of the functional tooth. They erupt against the posteromedial side of the functional teeth. Their crowns are not completely formed, showing a slender and sharp profile in contrast to the relatively robust functional teeth. The nine replacement teeth are positioned in the alveoli along with the mature functional teeth. Other four replacement teeth (rt9, lt2, lt4, lt5) as tooth germs are tiny, cap-like, and deeply imbedded in the bony mandibles. The tooth germs appear more medially positioned in relative to the more developed replacement teeth. A similar condition is highlighted in *Coloborhynchus*, in which the tooth germs are developed even beyond the middle line (Fastnacht 2008).

Tooth development process

Based on the variation in morphology and size (e.g. Edmund 1960, Fastnacht 2008, Hanai & Tsuihiji 2019), the tooth development process can be represented by four stages: germ, replaced, young functional, and mature functional (Figure 2). At the first stage, the tooth germ rises medially to the functional tooth along the midline. Its crown apex is formed first, and then enlarged basally. At the replaced stage (stage II), the tooth migrates laterally against its predecessor. The tooth crown is further enlarged until the half of its full-grown length, and partially erupted at the posteromedial side of its predecessor. Subsequently, the tooth continues to develop, and replaces its predecessor completely. At the young functional stage (stage III), the tooth is well functional and evidenced by the occurrence of tooth abrasion, but its root is still unclosed, representing an immature condition. At this stage, the enclosed root is not observable even in the more mature condition when its successor arise. The full-sized root is present in the mature functional stage (Figure 2: stage IV), about one third the length of the entire tooth. Meanwhile, the tooth is resorbed on the posteromedial side, and its successor continuously grows and reaches the replaced stage of the second development cycle. At the end of the fourth stage, the root would be further eroded, resulting the functional tooth shed from the alveolus, but unobservable in SDUST-V1007. Only two mature functional teeth (lt3, rt4) are slightly displaced from their alveoli, as the taphonomic artifacts.

Tooth replacement process

The replacement process matches well with the four tooth developmental stages. At the first two stages (stage I and II), the replacement

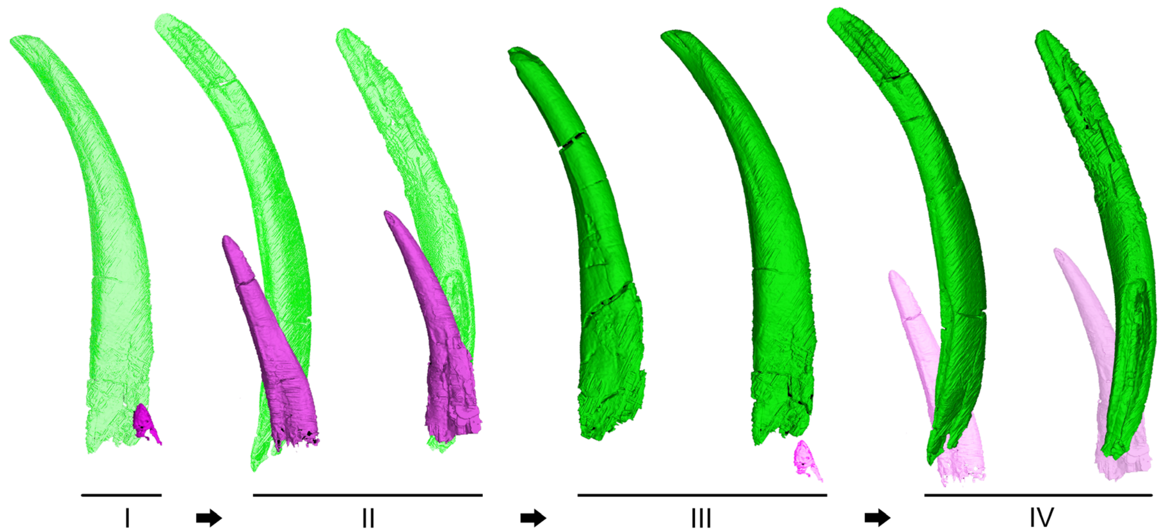

Figure 2. Tooth development process with four stages I-IV in the ctenochasmatid *Forfexopterus* (SDUST-V1007). Colors marked: green, functional teeth, and purple, replacement teeth, in the same developmental circle; light green, functional teeth of the previous developmental circle; light purple, replacement teeth of the next developmental circle.

tooth coexists with its functional predecessor in the alveolus. After the predecessor shed, the replacement tooth is functional at the last two stages, and preserved associated with its successor of the next circle. The replacement circle is identified along the tooth series, as Zahnreihe defined by Edmund (1960). Zahnreihen are revealed based on the replacement index in Figure 3. Five complete Zahnreihen are identified on the right side, while four complete Zahnreihen present on the left side. They include a range of 2-4 tooth positions. The first Zahnreihe involves 2 tooth positions on both sides. The following two Zahnreihen have a longer range of 4 tooth positions on the right side, and a range of 3 tooth positions on the left side. The last two Zahnreihen are shorter to involve 3 tooth positions on the right side. In contrast, the last Zahnreihe involves 4 tooth positions on the left side. Caudally, a partial Zahnreihe involves one or two tooth positions on the both sides respectively. The Z-spacing is calculated between each Zahnreihen, with a mean value of 1.97 on the left side and 2.06 on the right side. The mean value of Z-spacing is 2.02 in the whole dentition, comparable to the Z-spacing (2) of the simple alternative replacement between odd- and even-numbered tooth positions in reptiles (Edmund 1960).

DISCUSSION

The ctenochasmatid pterosaurs are adapted to a filter-feeding behavior, showing a highly-diversified dentition, but little is known about their tooth replacement pattern. Recently, Cerda & Codorniú (2023) revealed that the iconic *Pterodaustro* lacks replacement teeth, showing a monophyodont or diphyodont pattern, which is unusual among reptiles and is possibly related to its numerous filamentous teeth. As a contrast, *Forfexopterus* exhibits a tooth replacement pattern similar to other reptiles.

Tooth replacement pattern

The tooth replacement of *Forfexopterus* (SDUST-V1007) is comparable to that of the ornithocheirid *Coloborhynchus*, in that the

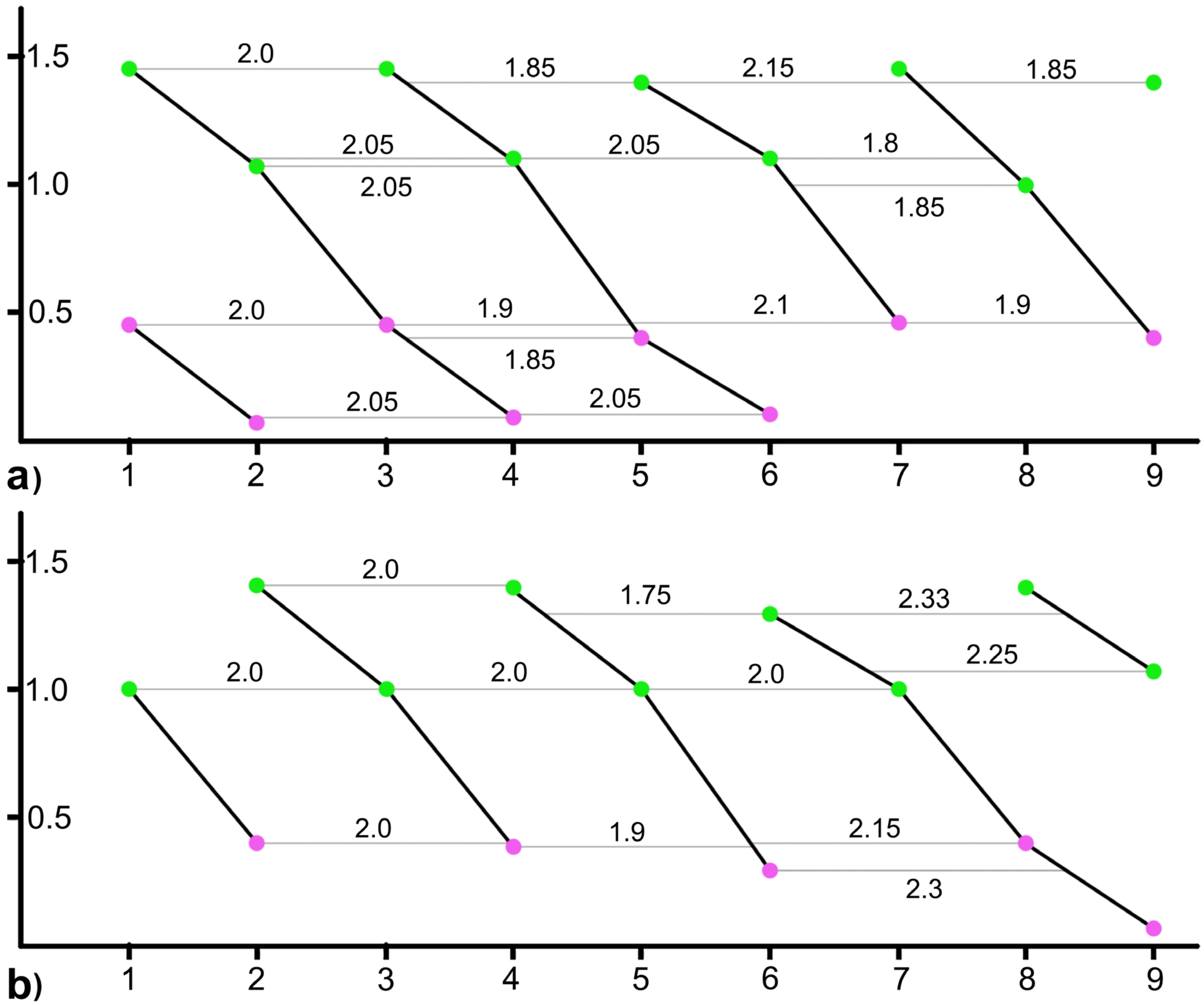

Figure 3. Z-Spacing diagrams of the ctenochasmatid *Forfexopterus* (SDUST-V1007). a) the left and b) the right lower dentition. X-axis is the tooth position, Y-axis is the replacement index.

tooth germ is more medially positioned along the middle line, the replacement tooth erupting at the posteromedial side of the functional tooth, and no more than one replacement tooth present in each alveolus. The pathway of the replacement tooth appears to be in a lateral-anterior direction to replace its predecessor and occupy the alveolus, which is also known as “varanid method” (Edmund 1960, Bertin et al. 2018). It seems to be widely distributed in pterosaurs, evidenced by the replacement tooth erupted posteromedial to the functional tooth frequently known in the Jurassic-Cretaceous pterosaurs (e.g. *Anhanguera*, Fastnacht 2008; *Ctenochasma*, *Pterodactylus*, *Rhamphorhynchus*, *Scaphognathus*, Edmund 1960; *Jianchangnathus*, Zhou 2014). However, a lateral-vertical replacement path, as an alternative pattern, is reported in the basal pterosaur *Eudimorphodon* (Wild 1978; Figure 4), which is common in other archosaurs (e.g. crocodiles, dinosaurs, toothed birds; Edmund 1960, Dumont et al. 2016, Bertin et al. 2018). One or less replacement tooth in each alveolus is not frequently known in archosaurs (e.g. Edmund 1960, 1962, Dumont et al. 2016). In contrast, multiple generations of the replacement

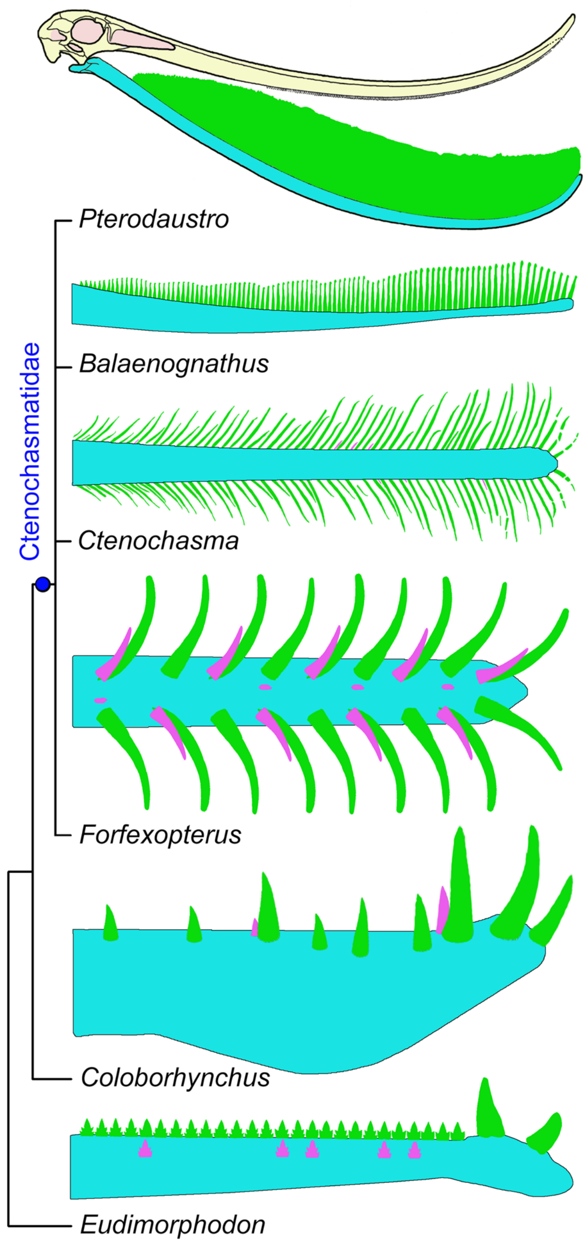

Figure 4. Comparisons of the tooth replacement of *Forfexopterus* with selected pterosaurs in a simple cladogram. Colors marked: blue, mandibular body; green, functional teeth; purple, replacement teeth. Line drawings of the lower dentitions of *Ctenochasma* is based on SMNS 81803; *Balaenognathus*, *Coloborhynchus*, *Eudimorphodon*, and *Pterodaustro* are modified or reconstructed from the literatures (Wild 1978, Fastnacht 2001, 2008, Zhou et al. 2017, Martill et al. 2023).

tooth are well known in some ornithischian dinosaurs (e.g. ceratopsids, hadrosaurians), associated with a high replacement ratio (e.g. Erickson 1996a). The tooth replacement rate can be measured based on the dentinal growth line counts between functional and replacement teeth (e.g. Erickson 1996a, b, D'Emic et al. 2019, Kosch & Zanno 2020, Maho et al. 2022). The tooth replacement rate is not yet known in pterosaurs, due to the lack of histological data of the teeth. A preliminary histological study in *Hamipterus* only reveals a tooth formation time of about 80 days, without any information on the tooth replacement (Chen et al. 2023). Furthermore, Cerda & Codorniú (2023) reported that the dentinal growth lines could not be identified in the teeth of *Pterodaustro*, which could either be a taphonomic artifact or an adaption related to its filamentous teeth. Based on values of Z-spacing, the relative tooth replacement ratio has been estimated in *Coloborhynchus* by Fastnacht (2008) that the enlarged anterior teeth are replaced faster with a lower value of Z-spacing than the posterior teeth along the tooth row, to maintain the fish-grabbing feeding behavior. In *Forfexopterus* (SDUST-V1007), however, the values of Z-spacing are comparable, implying the replacement ratio is relatively stable along the preserved tooth row to adapt to the filter-feeding strategy.

The tooth replacement of *Forfexopterus* (SDUST-V1007) is alternative between odd- and even-numbered tooth positions on both sides, and showing an asymmetrical pattern on both sides of the lower jaw. In contrast, it is more complex in *Coloborhynchus* (Fastnacht 2008). However, the replacement pattern is varied in ontogeny: a simple alternative pattern is frequently reported in young individuals, and becomes more irregular in adults (e.g. Edmund 1960, 1962, Hanai & Tsuihiji 2019). Unfortunately, this variation is untestable here, lacking the information of the mature specimen of *Forfexopterus* and the young specimen of *Coloborhynchus*. Asymmetry of the tooth replacement between both sides in *Forfexopterus* (SDUST-V1007) is similar with that of *Coloborhynchus*, possibly in order to maintain the functional occlusion on at least one side of the lower jaws. Actually, all young and mature functional teeth are worn somewhat on their crown, fully functioning during the replacement circle in each tooth position in *Forfexopterus* (SDUST-V1007; Figures 2 and 4). In addition, as hypothesized by Lawson et al. (1971), the tooth count in each stage may reflect the relative duration of the stage in the replacement cycle. The relative duration of teeth in function of *Forfexopterus* can be estimated by the percentage of the tooth count in stages III and IV as about 58%, which is longer than the relative duration of the tooth formation.

Ecological adaptation

Generally, there is a functional gap between the shedding of the former tooth and the full growing of the replacement tooth in gnathostomes (e.g. Berkovitz & Shellis 2017). To increase the duration of the functional tooth and the growth time of the replacement tooth, it would be appropriate to reduce the functional gap between tooth generations. As documented by Fastnacht (2008), the replacement tooth is positioned posteromedial to the functional tooth, commonly in pterosaurs, as functional for increasing the duration of the functional tooth and further improving the growth of the replacement tooth. This strategy may be highlighted in *Forfexopterus* by the strong ligamentous anchoring in the alveolus, evidenced by the full functionality of the young functional tooth with incompletely-developed root. In contrast to other ctenochasmatids, *Forfexopterus* feeds more actively, having a tooth-tooth occlusion evidenced by the tooth abrasion, and with a larger interdental space of about 6 mm (Zhou et al. 2022). Larger prey are expected to be more challenging for filter feeding. Therefore, the fully functioning dentition may play a significant role in maintaining the active feeding of *Forfexopterus*.

The tooth replacement is poorly known in other ctenochasmatids. Based on new fossil observation, the tooth replacement may be more complex than we prospected previously. Recently, a study of the dental histology of *Pterodaustro* has been performed by Cerda & Codorniú (2023), revealing that the replacement tooth is absent in *Pterodaustro* evidenced as a monophyodont or diphyodont pattern, possibly representing its extremity in feeding adaption. Another case is present in the bizarre *Balaenognathus* (Martill et al. 2023), in which an alternative replacement pattern is hypothesized based on the tooth size gradients identified along the exposed tooth row on the mandible. The tooth size gradients are unusual, in having a long period of 10-13 teeth (Martill et al. 2023, Figure 4). The small teeth in the size gradients were interpreted as “replacement teeth” in the original literature. However, the tooth replacement process is unknown in *Balaenognathus*. In contrast, more information of the tooth replacement is revealed in *Ctenochasma* (Bennett 2007, Figure 4). As in *Balaenognathus*, the dentitions of *Ctenochasma* is exposed on the jaws. Along the dentition, the tooth size gradients can be identified, implying an alternative pattern of replacement. Each size gradient involves two or three succeeding teeth. The anterior teeth are larger, and the posteriormost tooth is smallest, varied from one third to more than half the size of the anteriormost tooth. Some replacement teeth are tiny and just erupted posterior to the associated functional teeth (SMNS 81803; Figure 4). In contrast to *Forfexopterus*, the young functional teeth that are varied from one third to more than half-size of the mature functional teeth of *Ctenochasma* are not fully functional, evidenced as a functional gap during the tooth replacement process, which hinder more or less the functional occlusion of the filter feeding apparatus. These variations in the tooth replacement of the ctenochasmatids need to be further studied in the future.

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Author contributions

Chang-Fu Zhou designed the research; Chang-Fu Zhou wrote the paper; Chang-Fu Zhou and Fengmin Fan conducted micro-CT Scan and 3D reconstruction of the specimen. All authors gave final approval for publication.