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Tooth replacement pattern in maxillary dentition of basal Neoceratopsia

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ABSTRACT — Maxillary dentition of basal neoceratopsians was examined to understand the tooth replacement pattern in the early stage of neoceratopsian evolution. The replacement tooth developed on the lingual side of the functional tooth. For the replacement tooth to grow apically, resorption of the root and eventually the base of crown of the functional tooth was necessary. Having only one replacement tooth for each tooth position and involving resorption of the functional tooth for it to erupt, tooth replacement of basal neoceratopsians was inefficient compared to ceratopsids, the derived neoceratopsians.

KEY WORDS: Maxillary dentition, Tooth replacement, Basal Neoceratopsia

INTRODUCTION

The Ceratopsia is one of the dominant herbivorous dinosaur taxa in Cretaceous terrestrial ecosystems of Asia and western North America (Dodson *et al*., 2004; You and Dodson, 2004). Within the Ceratopsia, Neoceratopsia thrived throughout the Cretaceous. Along with the well-developed horns on the skull ceratopsids, the derived neoceratopsians, have been known for their unique form of mastication. Ceratopsid jaws contain large numbers of teeth, which are mesiodistally compressed for close packing in dental batteries in which files of teeth interlock both vertically and horizontally (Ostrom, 1964; Dodson, 1996). The dental batteries exhibit vertical cutting planes, in which the lingual sides of maxillary teeth occlude against the labial sides of dentary teeth. Ceratopsids have multiple replacement teeth in each tooth position. In contrast, basal ceratopsians lack dental batteries. The closely-spaced teeth merely erupt in a single horizontal line with only one replacement tooth for each functional tooth.

The replacement pattern of ceratopsian dentition has attracted very little attention (Edmund, 1960). Analysis of tooth replacement pattern in basal neoceratopsians is necessary to understand the evolution of the neoceratopsian dentition. The difference in the numbers of replacement teeth in basal and derived neoceratopsians implies that the tooth replacement patterns were also different. However, previous studies of the erupting teeth have concentrated on descriptions of the tooth crown morphology when the functional teeth are already worn.

Discoveries of both complete and fragmentary skulls of basal neoceratopsians from China make possible the examination of their tooth replacement pattern. This study illuminates the tooth replacement pattern in the early stage of neoceratopsian evolution.

Institutional Abbreviations — **CAGS-IG**, Chinese Academy of Geological Sciences, Institute of Geology, Beijing, China; **GSGM**, Gansu Geological Museum, Lanzhou, Gansu Province, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

MATERIALS AND METHODS

Maxillary dentitions of basal neoceratopsians from the Lower Cretaceous of Gansu and Liaoning Provinces, China, with replacement teeth were examined. GSGM-FV-00601 (its cast to be housed at the Kitakyushu Museum of Natural History and Human History, KMNH VP 600,001) is a partial left maxilla. It was collected from "the ceratopsian graveyard" site in the Lower Cretaceous Xinminpu Group in Mazongshan area,

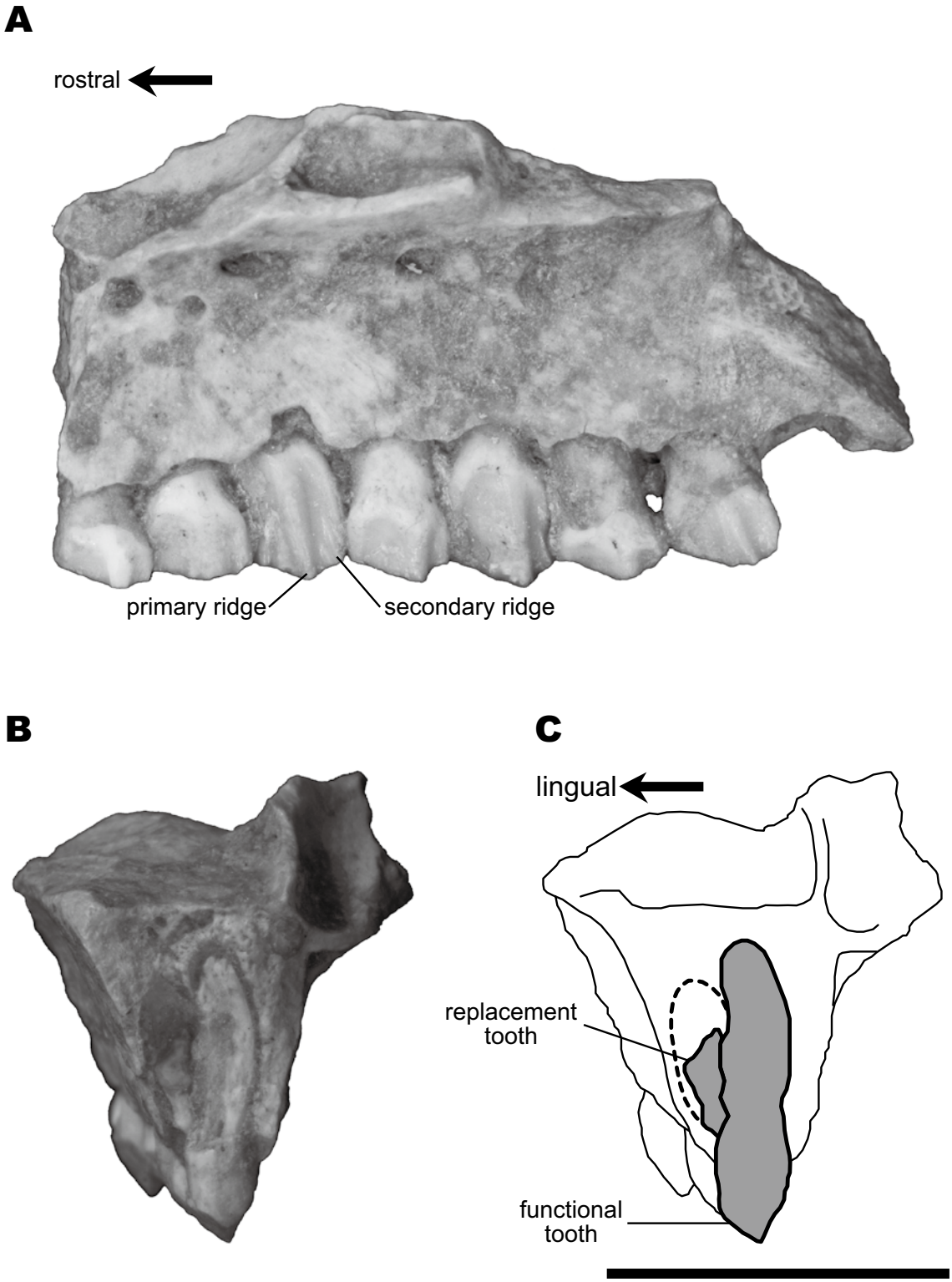

Fig. 1. Left maxilla of *Auroraceratops* (GSGM-FV-00601). A: lateral view. B, C: rostral view. A, B: photographs; C: interpretative outline. Scale bar: 1 cm.

Gansu Province, China (see Tang *et al*., 2001, Fig. 2). Maxillae of *Archaeoceratops yujingziensis* (CAGS-IG-VD-003; You *et al*., 2010) also from the Xinminpu Group in Mazongshan area, Gansu Province and *Liaoceratops yanzigouensis* (IVPP V12738; Xu *et al*., 2002) from the Yixian Formation in Liaoning Province, whose dentitions had previously been described in You *et al*. (2010) and Tanoue *et al*. (2009), respectively, were reexamined to understand the replacement pattern of maxillary teeth in basal neoceratopsians.

DESCRIPTION

GSGM-FV-00601, a partial left maxilla, measures 25.6 mm in length, 13.8 mm in width and 18.6 mm in height as preserved (Fig. 1A, B). The horizontal dorsal surface and the vertical medial surface that contribute to the nasal and oral cavities respectively are preserved. The maxilla lacks the dorsolateral and rostral parts, including the most mesial portion of the tooth row. A shelf extends laterally dorsal to the tooth row, hence the tooth row is inset medially. The relationships with adjacent skull elements are uncertain.

Seven functional maxillary teeth, identified here as the eighth from the last to the penultimate teeth, are preserved along the ventral border (Fig. 1A). Although the last functional maxillary tooth is missing, the replacement tooth is preserved in its alveolus. A partial replacement tooth of the eighth from the last maxillary tooth is also preserved.

The tooth crowns are closely-spaced, with the distal end of each tooth overlapping the mesial end of the subsequent tooth. Between the roots are little spaces, which are mostly filled with matrix. The well-developed primary ridges of all functional teeth are located distal to the midpoint of the tooth. Each ridge is wide at its base, tapers apically, and is confluent with the cingulum at the base. The functional tooth crowns have indentations on both mesial and distal sides of the primary ridge. At least two secondary ridges are present on each side of the primary ridge, each arising at the case of the crown and converging with the primary ridge on sixth from the last tooth. They are short and do not reach half the length of the primary ridge. In rostral view, the teeth show steep but not vertical wear facets. The set of dental characters seen in GSGM-FV-00601, especially the presence of indentations on the mesial and distal lobes bounded by the primary ridge and cingulum indicates that its teeth pertain to a neoceratopsian (You and Dodson, 2004; Godefroit and Lambert, 2007; Tanoue *et al*., 2009). Although most of the observed characters are shared by iguanodontians and neoceratopsians, the maxillary tooth crown of iguanodontians is lanceolate in labial view, whereas that of GSGM-FV-00601 would have been ovate when complete, resembling more closely those of a neoceratopsian (see Norman and Weishampel, 1990; Norman, 2004; Tanoue *et al*., 2009). In addition, maxillary tooth crowns of iguanodontians lack indentations on the mesial and distal lobes, unlike neoceratopsians (Godefroit and Lambert, 2007). Moreover, the base of the primary ridge is not bulbous and thus does not pertain to a psittacosaurid (Sereno, 1990; You and Dodson, 2004). To date, three basal neoceratopsian species, namely *Archaeoceratops oshimai, A. yujingziensis,* and *Auroraceratops rugosus*, have been reported from the Xinminpu Group in Mazongshan area (Dong and Azuma, 1997; You *et al*., 2005, 2010). Among the basal neoceratopsians from the Xinminpu Group, only *Auroraceratops* has maxillary tooth crowns with short secondary ridges, which are only about half the length of the primary ridge (Tanoue *et al*., 2009). Therefore, we identified GSGM-FV-00601 as a maxilla of *Auroraceratops*.

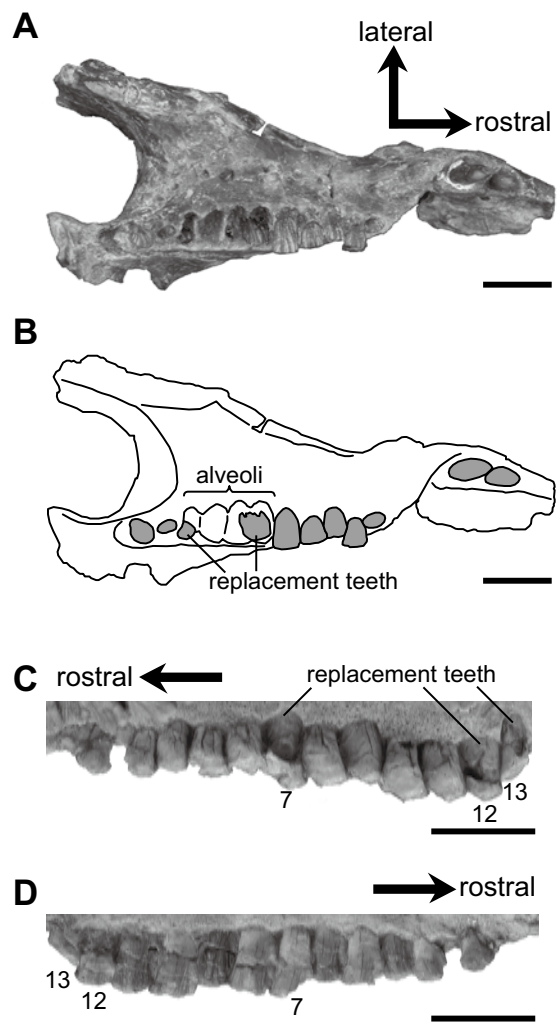

Fig. 2. A, B: Right upper jaw of *Archaeoceratops yujingziensis* (CAGS-IG-VD-003) in ventral view. C, D: Right maxillary dentition of *Liaoceratops yanzigouensis* (IVPP V12738) in lingual (C) and labial (D) views. Numbers indicate the tooth positions with both functional and replacement teeth. A, C, D: photographs; B: interpretative outline. Scale bars: 1 cm.

The transverse section of both functional and replacement tooth of the eighth from the last tooth position can be observed in rostral view (Fig. 1B, C). A portion of the replacement tooth is preserved in its crypt, which is approximately 5 mm deep and 2 mm wide at most. The crypt is widest at its convex base and tapers apically, indicating that the complete replacement tooth would have been wedge-shaped in transverse section. It is lingual to the root of the functional tooth. Moreover, the labial border of the replacement tooth is in contact with the lingual side of the root of the functional tooth.

The right maxillary dentition of *Archaeoceratops yujingziensis* (CAGS-IG-VD-003) is composed of 12 teeth (You *et al*., 2010; Fig. 2A, B). Preserved replacement teeth are exposed in ventral view within the sixth and ninth alveoli. The replacement teeth are in contact with the lingual border of the alveoli, but not with the labial border. Although the sixth replacement tooth is still within the alveolus, its crown is fully developed.

The right maxillary tooth row of *Liaoceratops yanzigouensis* (IVPP V12738; Xu *et al*., 2002) comprises 13 teeth (Fig. 2C, D). Both functional and replacement teeth are present at the seventh, twelfth, and thirteenth positions. Each replacement tooth crown is exposed basal to the partial crown of the functional tooth (Fig. 2C). They erupt on the lingual side of the alveolus and cannot be observed labially (Fig. 2D).

DISCUSSION

In all basal neoceratopsian specimens examined in this study, the replacement teeth are on the lingual side of the alveoli and are lingual to the functional teeth. In GSGM-FV-00601, the replacement tooth tapers apically without enough space for its crown to grow in transverse section (Fig. 1B, C). The size of the replacement tooth at the sixth position in the upper jaw of *Archaeoceratops yujingziensis* is comparable to that of the functional tooth, even though it is completely within the alveolus (Fig. 2A, B). In order for a replacement crown to reach the size of functional crown prior to eruption, resorption of the root of the functional tooth is necessary. In the final stage of tooth replacement the apical portion of the functional crown caps the replacement tooth, indicating that there has been a loss of both the root and the basal portion of the crown from the functional tooth (Fig. 2C). The resorption of the base of the functional tooth is also seen in modern crocodilians, and may be the plesiomorphic state of tooth replacement pattern in archosaurs (Edmund, 1960). During replacement, the newly erupted tooth needs to move or grow labially to fill the space once occupied by the replaced functional tooth.

In ceratopsids, the crown of each replacement tooth fits between the bifid roots of the preceding tooth, allowing each tooth position to accommodate multiple replacement teeth and possibly increasing the rate of tooth replacement compared to basal neoceratopsians (Ostrom, 1966). This relationship between the replacement tooth and the roots of the functional tooth renders resorption unnecessary during tooth replacement in ceratopsids. Basal neoceratopsians have only one replacement tooth for each tooth position. The root and basal crown of the functional tooth required resorption before the replacement tooth could erupt, rendering tooth replacement in basal neoceratopsians inefficient compared to that in ceratopsids.

Dentary teeth of basal neoceratopsians show a similar replacement pattern in that the replacement teeth erupt on the lingual side of the alveolus, and eruption of the replacement tooth involves resorption of the functional teeth (e.g. Tanoue *et al*., 2009, Figs. 7E, 8E, 10D, 11D). Morphological similarities of maxillary and dentary dentitions suggest that they had similar, if not the same, replacement patterns.

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