Comparative anatomy of selected basal ceratopsian dentitions

Kyo Tanoue, Hai-Lu You, and Peter Dodson

Abstract: The dental structure of basal ceratopsians is described. Evolutionary trends in maxillary and dentary teeth of basal ceratopsians include decrease and possible loss of enamel on the occluding side of tooth crowns, increase in the angle of wear facet, development of a prominent primary ridge and deep indentations on mesial and distal sides of the primary ridge, and increase in tooth size in neoceratopsians. Premaxillary teeth in the basalmost ceratopsian Yinlong and basal neoceratopsian Archaeoceratops oshimai exhibit wear facets and denticles along the carina, which imply use for feeding. Maxillary and dentary teeth of basal ceratopsians were probably not as effective in feeding as those in ceratopsids because of the relatively less prominent primary ridges. Some dental characters can be used to identify taxon and tooth position of isolated basal ceratopsian teeth.

Résumé : La structure dentaire des ceratopsiens basaux est décrite. Parmi les tendances évolutives des dents maxillaires et dentaires des ceratopsiens basaux figurent une diminution et une éventuelle disparition de l’émail sur la face occlusive des couronnes des dents, une augmentation de l’angle des facettes d’usure, l’apparition d’une crête primaire éminente et de profondes indentations sur les côtés méssial et distal de la crête primaire, ainsi que l’augmentation de la taille des dents chez les néocératopsiens. Les dents prémaxillaires de Yinlong, le plus basal des ceratopsiens, et du néocératopsien basal Archaeoceratops oshimai présentent des facettes d’usure et des denticules le long de la carène, ce qui indique une fonction alimentaire. Les dents maxillaires et dentaires des ceratopsiens basaux n’étaient probablement pas aussi efficaces pour l’alimentation que celles des ceratopsidés en raison de leurs crêtes primaires relativement moins éminentes. Certains caractères dentaires peuvent être utilisés pour déterminer le taxon et la position de dents isolées de ceratopsiens basaux.

[Traduit par la Rédaction]

Introduction

A unique feature of ceratopsids, the most derived ceratopsians, is the form of mastication. Derived ceratopsian 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). In ceratopsids the enamel is confined to the labial side of the maxillary tooth crown and lingual side of the dentary tooth crown. The dental batteries exhibit vertical cutting planes, in which the lingual sides of maxillary teeth occlude against the labial sides of dentary teeth. (Vertical shear of dental batteries is not found in any other herbivorous vertebrate taxa.) In contrast, basal ceratopsians lack dental batteries; instead, the closely spaced teeth merely erupt in a single horizontal line. Examination of the tooth structure of basal ceratopsians should help to elucidate the evolutionary transformation of dentition within the Ceratopsia. However, compared with theropod dinosaurs, comparative studies on ornithischian dentitions, including those of ceratopsians, have rarely been done (Ostrom 1966; Weishampel 1984; Coombs 1990). Dental structure in the basal Ceratopsia has attracted little attention other than a few thorough descriptions (Zhao et al. 1999; Makovicky and Norell 2006; Godefroit and Lambert 2007). Diagnostic characters of neoceratopsian teeth from North America were identified by Chinnery et al. (1998). Moreover, premaxillary teeth are found only in basal ceratopsians, except for the Psittacosauridae, but the function of these teeth has not been discussed previously.

Recent discoveries of skulls of basal Ceratopsia include Archaeoceratops (Dong and Azuma 1997), Zuniceratops (Wolfe and Kirkland 1998), Chaoyangsaurus (Zhao et al. 1999), Liaoceratops (Xu et al. 2002), Hongshanosaurus (You et al. 2003), Magnirostris (You and Dong 2003), Lamaceratops, Platyceratops (Alifanov 2003), Prenoceratops (Chinnery 2004), Auroraceratops (You et al. 2005), Yinlong (Xu et al. 2006), Xuanhuaceratops (Zhao et al. 2006), Yamaceratops (Makovicky and Norell 2006), and Cerasinops (Chinnery and Horner 2007), whose occurrences range from the Upper Jurassic (Oxfordian; Xu et al. 2006) to the Upper Cretaceous (Campanian; Chinnery and Horner 2007). Subsequent preparation of many of these specimens has revealed new information of the teeth and jaws, allowing us to conduct a comparative study of the early evolution of the ceratopsian dentition.
Institutional abbreviations

AMNH, American Museum of Natural History, New York, N.Y., USA; CAGS, IG, IGCAGS, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; PKUP: Peking University Paleontological Collections, Beijing, China.

Materials and methods

Dentitions of nine basal ceratopsian genera were examined and measured. Phylogenetic relationships among these genera are shown in Fig. 1. In this study, *Yinlong* and *Chaoyangosaurus* are considered the basalmost Ceratopsia, which are here defined as outgroup to Psittacosauridae + Neoceratopsia (Xu et al. 2006). *Psittacosaurus* and *Hongshanosaurus* compose Psittacosauridae. *Hongshanosaurus* is a newly discovered psittacosaurid that differs from *Psittacosaurus* in having greater preorbital length relative to basal skull length (approximately one half) than *Psittacosaurus* (less than 40%; Sereno 2000) and elliptical external naris, orbit, and infratemporal fenestra, whose long axes are oriented posterodorsally (You et al. 2003; You and Xu 2005). The mandible of *Hongshanosaurus* is deeper than the mandible in any species of *Psittacosaurus* (Tanoue et al. in press). The adult specimen (IVPP V12617) examined in this study is attributed to *Hongshanosaurus* since the preorbital length is approximately half of the basal skull length and the orbit and infratemporal fenestra are elliptical, with the long axes sloping anteroventrally as in the holotype (IVPP V12704). IVPP V12617 is unlikely to have undergone distortion, for the skull and mandible are symmetrical and the delicate palatal structure is preserved intact (Dodson et al. in press). In this study *Liaoceratops*, *Archaeoceratops*, *Auroraceratops*, *Leptoceratops*, and *Protoceratops* represent the basal Neoceratopsia. Dental terminology used is shown in Fig. 2.

Description

*Yinlong*

*Yinlong* (IVPP V14530) has three premaxillary teeth on each side (Fig. 3A; Xu et al. 2006). The well-preserved left first and right first and second premaxillary teeth are larger than the maxillary teeth in labial view. The lengths of the crown and root are greater than the width. The tooth crown base widens for the first 2 to 3 mm apically in labial and mesial views, then tapers toward the tip (Fig. 3B). Most of the occlusal surface is flat, except at the base where it is lingually concave in the first teeth on both sides (Fig. 3C). The labial side is mesiodistally convex as in *Chaoyangosaurus*, Xu et al. (2006) reported serrations only on the distal carina of the right second tooth, but the mesial carina is also serrated (Fig. 3B). The serrated region is longer and more prominent on the distal carina than on the mesial carina.

The left maxillary tooth row of the type specimen of *Yinlong downsi* is not fully exposed. Thirteen teeth make up the labially convex right maxillary tooth row (Xu et al. 2006). The diastema between the right third premaxillary and the first maxillary teeth measures approximately 4 mm. The right tooth row is 59 mm long. The maxillary teeth are tightly packed with slight overlap of the crowns. The distal end of each tooth is lateral to the mesial end of the subsequent tooth. The unworn crown of a left maxillary tooth is ovate (Figs. 3D, 3E). The low primary ridge is wide at the base and tapers apically toward the crown apex. The base of the primary ridge is confluent with the low cingulum. On
both mesial and distal sides of the primary ridge are shallow depressions, bounded basally by the cingulum. Secondary ridges develop within both depressions. The secondary ridges on the mesial indentation are much longer and more prominent than those on distal depression. The secondary ridges extend toward the primary ridge near the occlusal margin of the crown, but curve to be subparallel to the primary ridge dorsally, near the tooth base.

Dentary teeth are not exposed, except for the rostral part of the right tooth row and the partial crown of an erupting tooth in the left dentary (Figs. 3F, 3G). This partial crown can be observed ventral to the middle of the dentary tooth row on the medial side of the left dentary. It is 5.7 mm wide and 6.0 mm high. The exposed portion is triangular, and its dorsal margin bears denticles. The primary ridge is poorly developed and only slightly wider than the secondary ridges. Secondary ridges are short. Four and five secondary ridges develop mesial and distal to the low primary ridge, respectively, supporting denticles on the occlusal edges of the tooth.

Chaoyangsaurus

The dentition of Chaoyangsaurus is relatively well preserved in the holotype (Fig. 4A; IGCAGS V371). Two teeth compose the premaxillary tooth row (Figs. 4A, 4B). Although the ventral margin of the premaxilla just posterior to the second premaxillary tooth is not preserved on either side, it is unlikely that this specimen bore a third premaxillary tooth, since it lacks any evidence of an alveolus. The two peg-shaped premaxillary teeth are close to each other, with little or no space between them (Zhao et al. 1999). The root is cylindrical. The base of the premaxillary tooth crown is slightly wider than the root. The crown tapers apically. It is enameled on both the labial and lingual surfaces. Along the occlusal margin, the carina extends in a mesiodistal direction. The left second premaxillary tooth preserves a small wear facet on the lingual side of the tip, which is sloped ventrolabially.

The left maxillary tooth row preserves seven distal teeth (Figs. 4C, 4D). Mesial teeth are missing due to poor preservation of the rostral portion of left maxilla. The preserved tooth row measures 36 mm in length. Nine teeth compose the 37 mm long right maxillary tooth row, from which the second tooth is missing. The maxillary tooth rows are slightly concave labially (Fig. 4C). There is a slight overlap in the maxillary teeth, with the distal end of a tooth labially overlapping the mesial end of the subsequent tooth in occlusal view. The maxillary tooth crown is ovoid in labial (Fig. 4D) and lingual views. The length of the maxillary tooth crown is greater than the width. The height of the crown is greater than the length in the mesial teeth, and smaller in the distal teeth (Zhao et al. 1999). In occlusal view, the labial surface is more convex than the lingual surface. The occlusal edge of an unworn, erupting maxillary tooth preserves about 10 denticles. A low vertical ridge extends at the midline on the labial surface (Fig. 4D). This ridge probably represents a remnant of the primary ridge (Zhao et al. 1999). However, this is uncertain due to the preservation of the specimen. On both sides of this low ridge are shallow depressions (Fig. 4D; Zhao et al. 1999: Fig. 4B). A low cingulum separates the crown from the
cylindrical root, which is only slightly narrower than the crown (Zhao et al. 1999). Enamel covers both sides of the maxillary teeth. The enamel thickness appears to be about the same on both the labial and the lingual sides (Zhao et al. 1999). The wear facet is sloped.

The dentary tooth rows are concave labially (Fig. 4E). The right tooth row, bearing 11 teeth, is 46 mm long. The left tooth row, which is 39 mm long, preserves only nine teeth. Lack of an alveolus distal to the last tooth indicates that the distal teeth of the left tooth row are completely preserved. The length of the dentary teeth increases distally up to the seventh tooth in the left tooth row and eighth tooth in the right tooth row, and decrease to the last tooth. The length is greater than the width, as on the maxillary teeth. The tooth crown is round or oval in lingual view (Fig. 4F). The occlusal margin bears several denticles. The denticles are supported by short secondary ridges extending ventrally toward the tooth base. The wear facet is concave apicobially. Fully exposed dentary teeth including the root show that these teeth are single-rooted.

Psittacosaurus

The dentitions of five of the eight named species of Psittacosaurus, P. lujiatunensis, P. major, P. mongoliensis, P. neimongoliensis, and P. sinensis, were examined in this study. None of the specimens studied possess premaxillary teeth. The maxillary and dentary teeth are single-rooted. There is only one replacement tooth in each tooth position, as in other basal ceratopsians. Although the maxillary and dentary teeth are closely spaced, there is a small gap between the basal portions of the tooth crowns in some specimens. The crown length is greater than the width in all teeth.

The tooth rows of most species are nearly straight in occlusal view, but in P. sinensis and P. lujiatunensis, they are concave labially (Sereno and Chao 1988; Zhou et al. 2006). The maxillary tooth crowns are aligned at a shallow angle to the long axis of the tooth row. The distal end of each crown labially overlaps the mesial end of the subsequent crown (Sereno et al. 1988; Sereno 1990; Zhou et al. 2006; You et al. 2008). Although no fully exposed unworn maxillary tooth crown was observed in this study, the crown is oval in labial view in P. meileyingensis and P. mongoliensis (Sereno et al. 1988). A low primary ridge separates the mesial and distal lobes on the labial side of the crown. It tapers toward the apex, except for P. lujiatunensis (PKUP V1053) and P. sinensis (IVPP V738), in which the widths of the primary ridges remain constant (Figs. 5A, 5B). In P. neimongoliensis (Fig. 5C; IVPP 12-0888-2) and P. major (Fig. 5D; CAGS-IG-VD-004), long deep grooves are present on both sides of the primary ridge (You et al. 2008). The mesial lobe is flat and broader than the distal lobe. The distal lobe is swollen and can be more prominent than the primary ridge. Several secondary ridges, separated from each other by shallow longitudinal grooves, extend toward the tooth base from the occlusal margins of the two lobes. They do not reach the cingulum. The mesial lobe displays more secondary ridges than the distal lobe. Denticles are present at the occlusal ends of the secondary ridges and can be observed in relatively unworn crowns (Fig. 5B; Sereno and Chao 1988; Sereno et al. 1988). In relatively well-preserved maxillary teeth, enamel layers cover both labial and lingual surfaces of the crown, with the thicker layer on the labial side (Sereno and Chao 1988; Sereno 1990; Averianov et al.
The wear facet on the lingual side of the crown is oblique rather than vertical. The number of teeth in the dentary tooth row usually equals the number in the maxillary tooth row. The size of the dentary teeth is comparable to that of the maxillary teeth. Unworn dentary tooth crowns are circular to oval in outline in lingual view (Sereno and Chao 1988; Averianov et al. 2006; You et al. 2008). The crown is symmetrical, with the bulbous primary ridge in the middle of the lingual surface (Fig. 5E). The primary ridge is more prominent on the dentary teeth than on the maxillary teeth (Sereno 1990). It narrows toward the apex, as in the maxillary tooth crown. Mesial and distal lobes are of about the same size. Several secondary ridges supporting the denticles along the occlusal margin are present on both lobes, but they do not reach the basal half of the lobe (Fig. 5E). These short secondary ridges are visible on the labial surfaces of relatively unworn dentary teeth (Fig. 5C). The enamel layer is thicker on the lingual side than on the labial side of the tooth (Sereno and Chao 1988; Sereno 1990; Averianov et al. 2006). The wear facet is sloped to occlude against that of maxillary tooth.

**Hongshanosaurus**

The adult specimen of Hongshanosaurus (IVPP V12617) was examined. As in all other psittacosaurids, Hongshanosaurus lacks premaxillary teeth (Fig. 6A). Juvenile specimen was not included in this study.

The maxillary tooth rows are poorly preserved compared with the dentary tooth rows in IVPP V12617. The maxillary tooth row probably consists of eight or nine teeth. Five functional teeth are preserved in both maxillary tooth rows (Fig. 6A). Several replacement teeth are partially exposed, with one for each tooth position. The length of the maxillary tooth crown is greater than its width. The primary ridge is low and widens toward the tooth base (Fig. 6B). The primary ridge is shifted distally, resulting in a wider mesial lobe than distal lobe. Short vertical secondary ridges extend from the occlusal margin of the crown. At least three secondary ridges are present on the mesial lobe, and one secondary ridge on the distal lobe. In unworn maxillary teeth, the occlusal margin bears denticles supported by the secondary ridges. The enamel covers the labial and lingual surfaces of the crown, but it is thicker on the labial side (You and Xu 2005).

Both left and right dentary tooth rows bear 10 teeth and are 38 mm and 41 mm long, respectively (Fig. 6C). They extend along the medial side of the dentaries. The tooth rows are slightly concave labially in occlusal view. In most dentary teeth, the distal end of the tooth crown labially overlaps the mesial end of the subsequent crown. Unworn dentary tooth crowns are round or oval in lingual view (Fig. 6D). The bulbous primary ridge of a dentary tooth crown is widest at the base and tapers dorsally. It is more prominent than that of a maxillary tooth, as in Psittacosaurus (Fig. 6D; Sereno 1990). The primary ridge separates the mesial and distal lobes of the crown. It generally extends near the midline, but it is shifted distally in some teeth. As many as eight mesial and six distal denticles are present. A secondary ridge stretching toward the tooth base from the
occlusal margin of the dentary tooth crown supports each denticle. The secondary ridges develop only in the apical third of the crown. Both labial and lingual surfaces of the crown are enameled, with the enamel layer being thicker on the lingual side (You and Xu 2005). The wear facet is flat and slopes labially.

**Liaoceratops**

The dentition of *Liaoceratops* was examined in three specimens: IVPP V12738, IVPP V12633, and CAGS-IG-VD-002 (Xu et al. 2002; You et al. 2007: Figs. 1C, 2C). The holotype (IVPP V12738) is an adult skull and the other two are juvenile skulls, with CAGS-IG-VD-002 being the smallest of the three specimens.

Two premaxillary teeth are preserved on both sides in the holotype (Fig. 7A). Sockets are present rostrolateral to the right first tooth and caudolateral to the second right tooth, which may represent alveoli for additional premaxillary teeth, but no alveoli are preserved for more than two teeth in the left premaxillary tooth row. In both juvenile specimens the premaxillary tooth rows each contain three teeth (You et al. 2007). The premaxillary teeth are peg-shaped with a cylindrical root (Fig. 7B). Both labial and lingual sides of the premaxillary tooth crown are covered with enamel. The carina extends along the mesiodistal axis of the crown. The first right premaxillary tooth exhibits the serrated distal carina reported by Makovicky and Norell (2006). Both the mesial and distal carinae of the left second tooth display denticles, as in *Yamaceratops* and a new species of *Archaeoceratops* (Fig. 7B; Makovicky and Norell 2006; You et al. in press). The serrated region is longer on the distal carina than on the mesial carina. No wear facets are present on any premaxillary tooth.

The left and right maxillary tooth rows of the holotype (adult) skull consist of 11 and 12 teeth, respectively. All maxillary tooth rows of juvenile specimens contain 10 teeth. No unworn tooth is preserved in the holotype. Enamel covers the labial surface of the crown, but not the lingual surface. The primary ridge is shifted distally (Fig. 7C) and is confluent with the cingulum at the base. The primary ridges are poorly differentiated from secondary ridges on the maxillary teeth of the juvenile skulls. Two or three secondary ridges are located mesial to the primary ridge and at least one lies distally. In occlusal view, the maxillary teeth show steep but not vertical wear facets.

At least 12 teeth are preserved in the left dentary tooth row of the holotype (Fig. 7D). The right dentary tooth row consists of 15 teeth. Only the lingual surface of the oval crown is covered with enamel. The primary ridge is mesial to the midline in lingual view (Fig. 7E). The primary ridges in the dentary teeth of juvenile mandibles are only slightly more prominent than the secondary ridges, as is also the case in the maxillary teeth. As many as six and seven secondary ridges develop mesial and distal to the primary ridge, respectively. The wear facets are concave dorsolabially in...
all three specimens. Some dantary teeth exhibit wear facets with shelf structure.

**Archaeoceratops**

Well-preserved teeth can be observed in the holotype of *Archaeoceratops oshimai* (Fig. 8A; IVPP V11114). The dentition of a new species of *Archaeoceratops* will be described by You et al. (in press). Three teeth compose the premaxillary tooth row (Figs. 8A, 8B). All three right premaxillary teeth are preserved, but only the second premaxillary tooth remains on the left side. In occlusal view, the second tooth is slightly labial to the first tooth and the third tooth is slightly lingual to the first tooth. Both labial and lingual sides of the crown are covered with enamel (You and Dodson 2003). The premaxillary teeth are peg-shaped. In labial view, the premaxillary teeth first narrow ventrally from the base, then widen, and the crowns then taper to a narrow apex. The length is greater than the width. The carina extends mesiodistally along the occlusal edge. No denticles were observed along the carina, unlike in the new species of *Archaeoceratops, Liaoceratops,* and *Yamaceratops* (Makovicky and Norell 2006; You et al. in press). The right second and third teeth exhibit ventrolabially sloping, oval wear facets on the lingual side of the apex of the crown (Fig. 8B). When the skull and mandible are articulated, the premaxillary tooth rows are lateral to the posterior half of the dorsal margin of the predentary (Fig. 8A). Thus, the lingual surfaces of the premaxillary crowns will have contacted the outer face of the lower beak.

The left maxillary tooth row comprises 13 teeth and is 46 mm long. Fourteen teeth compose the 47 mm long right maxillary tooth row. In occlusal view, the tooth rows are lenticular, widest a little distal to the middle of the tooth rows and tapering both mesially and distally. Enamel covers both surfaces of the crown. Unworn crowns are oval in labial view. Unlike the new species of *Archaeoceratops,* in which the maxillary teeth lack a primary ridge, maxillary teeth of *A. oshimai* show a primary ridge (Fig. 8C; You et al. in press). However, it is only slightly broader than the secondary ridges. The primary ridge is slightly distal to the midline of the crown, and merges basally with the cingulum. In some teeth, the primary ridge curves ventrodistally. Three secondary ridges are present on each side of the primary ridge, forming denticles along the occlusal margin (Fig. 8C). The secondary ridges stretch dorsally toward the tooth base, and toward the primary ridge. Roots of some teeth are partially exposed. They narrow slightly toward the root apex. Replacement teeth for the left 10th and 12th, and right eighth and 10th tooth positions are partially exposed on the medial surface of the maxilla. Only one replacement tooth is present for each tooth position. The wear facets of maxillary teeth are steeply inclined.

The labially concave dantary tooth rows are aligned along the medial borders of the dentaries in occlusal view. Four-

---

Fig. 7. *Liaoceratops yanzigouensis* (IVPP V12738). (A) Skull in left lateral view. (B) Left premaxillary teeth in labial view. (C) Left maxillary teeth in labial view. (D) Mandible in dorsal view. (E) Right dantary teeth in lingual view. dt, dantary teeth. See Fig. 3 for other abbreviations. Scale bars = 5 mm in B, C, and E.
teen teeth compose the 55 mm long left tooth row. The right tooth row comprises 14 teeth and is 53 mm long. Both the labial and lingual sides of the dentary teeth are covered with enamel, as is the case on the maxillary teeth. Each dentary preserves two or three small rostral teeth, which are isolated from each other and from the closely packed tooth rows (Fig. 8D). When the skull and mandible are articulated, the first two dentary teeth are mesial to the first maxillary tooth. The first maxillary tooth occludes with the third dentary tooth. In lingual view, the subtriangular crowns of the first two teeth lack both primary and secondary ridges and only show denticles along the apical margins. The third tooth also displays a subtriangular crown outline, but there are secondary ridges on the lingual surface. The fourth tooth preserves a wear facet, but it lacks the primary ridge. The primary ridges are preserved on teeth distal to the fifth tooth on both dentaries. With the exception of the third tooth, the teeth of the closely packed tooth row exhibit oval crowns. The primary ridges in teeth 5–14 extend vertically in the mesial third of the crown (Fig. 4E). However, the primary ridge is only slightly more prominent than the secondary ridges, which converge basally toward the primary ridge. Three secondary ridges are located mesial and four distal to the primary ridge. In the new species of Archaeoceratops, the dentary teeth lack primary ridges (You et al. in press). The cingulum is poorly developed in A. oshimai. Unworn erupting teeth display more denticles than the number of secondary ridges. Only one replacement tooth is present for each tooth position. The wear facet is sloped as in maxillary tooth.

*Auroraceratops*

The teeth of *Auroraceratops* (Fig. 9A; IG-2004-VD-001) are the largest among the known Chinese basal ceratopsians. The premaxillary teeth are better preserved on the left side (Fig. 9B). Three or four left premaxillary teeth are present. There is a shallow depression mesial to the preserved teeth, which possibly is an alveolus for the first tooth. The second and third teeth are aligned along the lateral margin of the premaxilla in occlusal view, with the first alveolus and fourth tooth lingual to them. The length and width of the second tooth are 7.2 mm and 5.2 mm, respectively. The length of the third tooth is 7.6 mm, and the width is 4.5 mm. The heights of the second and third teeth are approximately 7 mm and 8 mm, respectively, in labial view. The third peg-shaped tooth is the best preserved in this specimen. The blunt mesial and distal carinae extend lingually toward the tip, unlike in Liaoceratops. As a result, the tip of the third premaxillary tooth is situated on the lingual side of the crown in occlusal view. Serrations are not present along the carina. Only three premaxillary teeth are present in the right premaxilla, represented by two alveoli and the root of the third premaxillary tooth. The second alveolus is slightly labial to the first alveolus and to the third tooth.
The axes of the maxillary teeth slope ventrodistally (Fig. 9C). Thirteen maxillary teeth form the 65 mm long left tooth row. The right maxillary tooth row consists of 12 teeth. It is 65 mm long. Both the length and width of the maxillary teeth increase distally, except for the distalmost two or three teeth in both maxillary tooth rows. The ovate crown of the left third tooth displays an unworn labial surface. The primary ridge is situated distal to the midline (Fig. 9C). It widens toward the tooth base and is basally confluent with the cingulum. Mesial and distal to the primary ridge are shallow depressions. The concave surface of the mesial lobe extends closer to the tooth base than does the distal one. Three secondary ridges are located mesial and two distal to the primary ridge. They stretch toward the base from the occlusal margin of the crown but are only about half the length of the primary ridge. Enamel covers only the labial surfaces of the maxillary teeth, but this may be due to preservation. Replacement teeth are not exposed in lingual view. Although small spaces are found between adjacent roots, adjacent crowns are in contact and form a tightly packed tooth row. The tooth height decreases mesially and distally from tooth position 8 in lingual view. The wear facet is nearly vertical.

The dentary teeth are poorly preserved. Twelve teeth form the dentary tooth row on either side (Fig. 9D). The length and the width of the teeth increase up to the seventh or eighth tooth and then decrease distally in both tooth rows. In labial view, the better preserved left tooth row is highest at the middle, with the seventh and eighth teeth being the highest. In dorsal view, the tooth rows are lingually convex (Fig. 9D). No unworn teeth are present. The roots of the first four teeth in the left tooth row are longer than they are wide. The crown is asymmetrical in lingual view, with the primary ridge developing mesial to the midline (Fig. 9E). The primary ridge is confluent with the cingulum. Three secondary ridges lie distal to the primary ridge in relatively well-preserved teeth. The secondary ridges do not reach the cingulum. Enamel is preserved only on the labial sides of the dentary teeth. The presence of an enamel layer on the lingual surface is uncertain because of poor preservation. The wear facet appears to be vertical.

Two sockets are located mesial to the right dentary tooth row (Fig. 9D). The diameters of these sockets are approximately 2 to 3 mm, with the interval between them of about the same length. These may be alveoli for small mesial teeth that were set off from each other and from the more distal tooth row. They would have fit in the diastema between premaxillary and maxillary teeth.

**Leptoceratops**

The description of the dentition of *Leptoceratops* is based primarily on CMN 8889 (Fig. 10A). Isolated teeth of *Leptoceratops* (CMN 8889, CMN 52781) are single-rooted and among the largest in basal ceratopsians. *Leptoceratops* lacks premaxillary teeth (Sternberg 1951).
Both maxillary tooth rows of CMN 8889 consist of 17 teeth. The left tooth row is 157 mm long and the right tooth row 160 mm. In occlusal view, the tooth rows are slightly concave labially. The width of the tooth crown exceeds the length (Sternberg 1951). The primary ridge is shifted distally and is curved in some teeth (Fig. 10B). Some primary ridges show striations parallel to the ridge axis. At least three secondary ridges are situated mesial to, and one distal to, the primary ridge. The secondary ridges are subparallel to the primary ridge, and some of them turn away from the primary ridge as they approach the tooth base. They are relatively long in Leptoceratops, but do not reach the cingulum. The cingulum is well developed. In some maxillary teeth, the cingulum is notched in the middle (Fig. 10B). The base of the primary ridge does not quite extend to the lingual edge of the cingulum (Godefroit and Lambert 2007). In occlusal view, the wear facet is steeply inclined in most teeth, but vertical in a few teeth in the second quarter of the tooth row. The left 14th and 16th and the right 14th maxillary teeth exhibit narrow horizontal shelves at the base of the subvertical wear facets.

Sixteen teeth compose both dentary tooth rows (Fig. 10C). The tooth row is slightly concave labially in occlusal view, as in the maxillary tooth row, but the tooth rows of Leptoceratops are much less curved than those of other basal neoceratopsians. The width of the dentary tooth is greater than the length. The primary ridge is mesial to the midline of the dentary tooth crown, as in other basal neoceratopsians (Fig. 10D). It is more prominent than that of a maxillary tooth and widens basally, just dorsal to the junction with the cingulum. The primary ridge is confluent with the cingulum, unlike the condition in maxillary teeth. Up to four mesial and three distal secondary ridges are present. The secondary ridges develop in a way that is unique among the basal ceratopsians. Secondary ridges mesial to the primary ridge converge toward the primary ridge, whereas those distal to the primary ridge are parallel to it. These features of the junction between the primary ridge and the cingulum and the secondary ridges are illustrated in Brown (1914, fig. 2) as those of a maxillary tooth; however, it appears to be a dentary tooth. Similarly, the dentary tooth illustrated by Brown (1914, fig. 6) appears to be a maxillary tooth. As on the maxillary teeth, wear facets are steeply inclined or vertical (Sternberg 1951). At the base of the wear facet, there is a horizontal shelf, as is also seen in other North American basal neoceratopsians and some Asian forms, including Udano ceratops and Archaeoceratops (Sternberg 1951; Kurzanov 1992; Chinnery and Weishampel 1998; Chinnery 2004; Chinnery and Horner 2007; You et al. in press). It is difficult to confirm the distribution of enamel in the teeth of CMN 8889 since the entire specimen is stained black. However, isolated teeth of CMN 8888, whose dentine portion is brown, show distinct enamel layers on both labial and lingual surfaces of the crown.

Protoceratops

Two peg-shaped teeth are present in each premaxilla in Protoceratops (Figs. 11A, 11B; Gregory and Mook 1925; Brown and Schlaikjer 1940). The second tooth is slightly labial to the first tooth. There is little or no space in between the two teeth (Fig. 11B). The long cylindrical root is nearly round in horizontal section. Among the observed premaxillary teeth, the right first tooth of AMNH 6433 is the largest with a width of 7.6 mm.

The maxillary tooth row is labially concave mesially, but is straight distally. There are up to 15 maxillary tooth positions (You and Dodson 2004). Each maxillary tooth crown is oval in labial view. The primary ridge is prominent (Fig. 11C). It is shifted distally from the midline. The primary ridge widens at the base and merges with the cingulum. In some teeth, it is sinuous. The cingulum mesial to
the primary ridge is often basal to the distal cingulum. The indentations on both mesial and distal lobes of the crown are deep. The secondary ridges on both lobes extend from the occlusal margin toward the basal part of the primary ridge. Isolated teeth are single-rooted and show longitudinal grooves on mesial and distal surfaces of the root about one-third the width of the root (Brown and Schlaikjer 1940). These grooves would have accommodated the distal and mesial edges of preceding and subsequent teeth, respectively.

Enamel covers the labial surface of the crown and the apical half of the lingual surface of the crown; the lingual enamel band is only preserved on unworn teeth. The wear facet is steeply inclined or vertical.

Maxillary and dentary dentition

Maxillary teeth of Yinlong resemble those of pachycephalosaurs in that the low primary ridge of maxillary tooth is wide at the base (Figs. 3D, 3E). Crowns of unworn dentary tooth of Yinlong and mesial dentary teeth of A. oshimai are subtriangular as in pachycephalosaurs (Figs. 3F, 3G, 8D). All other maxillary and dentary teeth of basal ceratopsians examined, however, exhibit ovate crowns. Additionally, the labial surface of pachycephalosaurian maxillary tooth crowns is concave vertically (Sues and Galton 1987; Maryańska et al. 2004), in contrast to the convex labial surface of ceratopsian tooth crowns (Chinnery et al. 1998).

The evolutionary transition toward the ceratopsid dental structure can also be observed in basal neoceratopsians. In most basal ceratopsians, enamel covers both sides of maxillary and dentary teeth. In Chaoyangsaurus, enamel layers on both sides of maxillary and dentary teeth exhibit almost the same thickness, but in other basal ceratopsians with tooth crowns enameled on both sides, the enamel layer on the labial side of the maxillary tooth crown and the lingual side of the dentary tooth crown is thicker than that on the opposing
side. Only the labial side of the maxillary and the lingual side of the dentary teeth in Auroraceratops and Liaoceratops are enameled, but it may be due to poor preservation of the known specimens. The thickness of enamel layers in Leptoceratops is uncertain. In contrast, ceratopsid teeth develop the enamel only on the non-occluding side. Having the non-occluding side of the tooth crown covered with thicker enamel layer to resist abrasion and preserve the apex of the crown, while covering the occluding side with less or no enamel would have facilitated effective shearing in ceratopsians.

In general, it is difficult to measure the inclination of wear facets on maxillary and dentary teeth of specimens because of deformation during fossilization. However, among basal ceratopsians, the wear facets for all teeth seem to be steeper in Auroraceratops, Leptoceratops, and Protoceratops. It appears that an increase of the wear facet angle took place in basal neoceratopsians, and it is possible that a bite producing a vertical wear pattern typical of ceratopsids may have evolved in basal Neoceratopsia.

Although the condition is unclear in Chaoyangsaurus, the primary ridges of maxillary and dentary teeth in Yinlong and most psittacosaurids are relatively wider than those of basal neoceratopsians. This feature appears to have helped protect the apex of the tooth crown from abrasion, especially on the dentary teeth of psittacosaurids (Figs. 5E, 6D). However, these primary ridges taper apically and many of the deeply worn teeth with narrow or low primary ridges show nearly horizontal apical margins (Fig. 5D). As for basal neoceratopsians, in large individuals of Leptoceratops and Protoceratops, the teeth show pointed apical edges, even when worn, because of the presence of prominent primary ridges (Figs. 11C, 11D). However, some maxillary teeth of Leptoceratops, in which the primary ridge is the most prominent of any seen among all the taxa studied, still can exhibit horizontal apical margins (Fig. 10B). Overall, the primary ridges of basal ceratopsians are less developed than those of ceratopsids. The high primary ridges of ceratopsids remain as high points along the cutting edge of each tooth as the tooth is worn down. The mesial and distal lobes of each tooth slope away from the high point supported by the primary ridge, to abut the distal or mesial lobe of the adjacent tooth in the dental battery. The net effect is that the cutting edge of the scissor-like occlusal surface is serrated; this serration might have been more effective at slicing through vegetation than a horizontal occlusal edge would have been.

The maxillary teeth of basalmost ceratopsians and the maxillary and dentary teeth of some basal neoceratopsians show shallow indentations on mesial and distal sides of the primary ridges (Figs. 3D, 4D, 7C, 8C). In contrast, the maxillary and dentary teeth of derived basal neoceratopsians, including Leptoceratops and Protoceratops, have deep indentations on both sides of the primary ridges, as in ceratopsids (Figs. 10B, 10D, 11C, 11D). Development of deep indentations in neoceratopsians is associated with that of prominent primary ridges. The function of deep indentations, however, is uncertain.

Shallow longitudinal grooves on the roots of maxillary and dentary teeth in Protoceratops, which have also been reported in Zuniceratops (Wolfe and Kirkland 1998), may be precursor of ceratopsid bifid roots if they became deeper and eventually split a root into two prongs. Replacement tooth fit between the bifid roots of ceratopsids, allowing each tooth position to accommodate more teeth and possibly increasing the rate of tooth replacement compared with that in basal ceratopsians (Ostrom 1966). However, dentition with transitional morphology, such as tooth with deep longitudinal grooves or single-rooted teeth with more than one replacement tooth at each position has not been discovered so far (Ostrom 1966; You and Dodson 2004). Further examination of well-preserved teeth is required to understand the evolution of double-rooted teeth in Ceratopsidae.

Tooth counts in maxillary and dentary tooth rows of adult basal ceratopsians range from eight in Psittacosaurus xinjiangensis (Sereno and Chao 1988) to 17 in Leptoceratops (Sternberg 1951). In ceratopsids, the number of functional teeth forming tooth rows increased, and the maximum tooth count is 40 in Triceratops (Ostrom 1966). Increase in tooth size associated with that in absolute skull size also occurred among Neoceratopsia. Derived basal neoceratopsians, including Auroraceratops, Leptoceratops, and Protoceratops, have larger maxillary and dentary teeth than more basal forms, but the teeth are smaller than in ceratopsids. Increase in the number of teeth and tooth size resulted in the progressive elongation of tooth rows in neoceratopsians. Tooth rows extended distally, even beyond the coronoid process in ceratopsids (Ostrom 1964; Ostrom 1966).

Maxillary and dentary teeth of examined basal ceratopsians (except in Leptoceratops) clearly differ from those of ceratopsids in that the crowns are longer than they are wide; these proportions are the opposite in ceratopsids. Maxillary and dentary teeth of basal ceratopsians occlude individually with each other. Having a mesiodistally elongated crown would have increased the surface area for contact, presumably increasing the efficiency of mastication. In ceratopsids, mesiodistally narrow crowns form a tightly packed dental battery that functions as a single unit thus maximizing the area available to process food. There is no space between adjacent teeth in ceratopsids, whereas adjacent crown bases and roots are not in contact with each other in basal ceratopsians.

In some basal neoceratopsians observed, the first dentary tooth is mesial to the first maxillary tooth when the skull and mandible are articulated (Fig. 8A). This also seems to be the case with Chaoyangsaurus. Archaeoceratops and possibly Auroraceratops possess dentary teeth mesial to and apart from the packed tooth rows. These isolated mesial teeth lack primary ridges and are structurally somewhat similar to the premaxillary teeth with no wear facets (Fig. 8D). When the mouth of the animal was closed, they fit in the diastema between premaxillary and maxillary tooth row, which is distal to the upper beak. Hence, they may have been vestigial teeth.

Worn dentary teeth of North American basal neoceratopsians, as well as Udaceratops and a new species of Archaeoceratops from Asia, exhibit horizontal shelves in addition to vertical or subvertical wear facets (Sternberg 1951; Kurzanov 1992; Chinnery and Weishampel 1998; Chinnery 2004; Chinnery and Horner 2007; You et al. in press), which suggests that shearing and crushing functions were combined in these taxa (Sternberg 1951; Ostrom 1966). However, the apex of the maxillary tooth bears no
horizontal wear facet to occlude with the horizontal shelf of the
dentary tooth. The horizontal shelf appears to be formed by
food-to-tooth occlusion (Varriale 2008).

Although isolated teeth are considered of little taxonomic utility, dental characters, including the notch on cingulum of
maxillary teeth in Leptoceratops (Fig. 10B), V-shaped indentation of the maxillary tooth crown in Bagaceratops
rather than U-shaped depressions in other basal ceratopsians (Maryańska and Osmólska 1975), and a primary ridge on the
labial side of dentary tooth crown in Montanoceratops (Chinnery and Weishampel 1998), can be utilized for identification.
In addition, the various species of Psittacosaurus differ in the relative sizes of the primary ridges in maxillary and
dentary tooth crowns (Sereno 1990). Some differences have been observed in the maxillary and dentary teeth of
several other genera. In Hongshanosaurus, the primary ridges of the dentary teeth are more prominent than those of the
maxillary teeth, as in Psittacosaurus (Figs. 6B, 6D). In Leptoceratops, the orientation of the secondary ridge is
different on the maxillary and dentary teeth. The secondary ridges in maxillary teeth are subparallel to the primary ridge
(Fig. 10B). On the dentary teeth, however, secondary ridges mesial to the primary ridge converge toward the primary ridge,
whereas those distal to the primary ridge extend parallel to it (Fig. 10D). In Protoceratops, the indentations on mesial and distal sides of the primary ridge are deeper on the maxillary teeth than on the dentary teeth (Figs. 11C, 11D). These features can be used to distinguish isolated maxillary and dentary teeth.

Conclusions

Some premaxillary teeth show wear facets and serrated carina, which imply that they were utilized for feeding in concert with the predentary beaks. Evolutionary trends in maxillary and dentary teeth of basal ceratopsians include

(1) decrease and possible loss of enamel on the occluding side of tooth crowns,
(2) increase in the angle of wear facets,
(3) development of a prominent primary ridge,
(4) development of deep indentations on the mesial and distal sides of the primary ridge, and
(5) increase in tooth size in neoceratopsians.

Overall, the dentitions of basal ceratopsians appear to be less effective for cutting than those of ceratopsids because of the shorter tooth rows and less developed primary ridges. In ceratopsids, the prominent primary ridges contribute to the serration of the dental battery when it is considered as a single blade, retaining pointed apices on the individual crowns. Basal ceratopsid dentition differs from ceratopsids in that the teeth occluded individually in general unlike the packed tooth row forming a dental battery in ceratopsids. Horizontal shelves in dentary teeth, which imply crushing function, are confined to some basal neoceratopsian genera. Additionally, some dental characters can be utilized to identify isolated teeth of basal ceratopsians.

Acknowledgements

The authors are grateful to C. Mehling (AMNH), K. Shepherd and M. Feuerstack (CMN), X. Xu (IVPP), and K.-Q. Gao (Peking University, Beijing, China) for providing access to their collections. B. Grandstaff (University of Pennsylvania, Philadelphia, Pa.) and R. Holmes (University of Alberta, Edmonton, Alberta) kindly reviewed the early version of the manuscript. Thanks are due to D. D’Amore (Rutgers University, New Brunswick, N.J.) and F. Varriale (Rowan University, Glassboro, N.J.) for valuable discussions. The authors also appreciate Associate Editor H.-D. Sues and reviewers A. Averianov, B. Chinnery-Allgeier, and M. Ryan for helpful suggestions which greatly improved the manuscript. K. Tanoue was funded by Summer Research Stipends in Paleontology (University of Pennsylvania), School of Arts and Sciences Dissertation Research Fellowship (University of Pennsylvania), Jurassic Foundation Research Grant, and Government of Canada Post-Doctoral Research Fellowship. Funding was provided by the Basic Outlay of Scientific Research Work and 973 Project from Ministry of Science and Technology, the National Natural Science Foundation of China (40672007), and Hundred Talents Project of Ministry of Land and Resources of China to H.-L. You. P. Dodson thanks his chairman, N. Avadhani, for support.

References


