A JUVENILE HADROSAUR MAXILLA FROM THE DINOSAUR PARK FORMATION (CAMPANIAN) OF DINOSAUR PROVINCIAL PARK (ALBERTA, CANADA)

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ABSTRACT A nicely preserved right maxilla of a juvenile lambeosaurine hadrosaur was found by Junchang Lü from the Dinosaur Park Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada. It came from the *Centrosaurus-Cory-thosaurus* Assemblage Zone (probably equivalent to Megaherbivore Assemblage Zone 1b), suggesting that it is likely referable to either *Corythosaurus* or *Lambeosaurus*. An X-ray Computed Tomography helical scan revealed 23 tooth families of up to four teeth per family. The number of tooth families and number of teeth per family increase during ontogeny in hadrosaurida, and this number is approximately what is expected for either a lambeosaurine, or any other subfamily of the Hadrosauridae for a specimen of this size. A second maxilla with teeth of approximately the same size can be identified as a right maxilla of a hadrosaurine based on the nature of the premaxillary contact. UALVP60543 and UALVP62346 have approximately equivalent tooth row lengths with a similar number of tooth families (22-23). Because it has been established that Lambeosaurines and hadrosaurines can have radically different tooth counts at maturity, these specimens indicate that tooth counts in these two clades were similar at hatching, but rapidly diverged during ontogeny.

KEYWORDS Dinosaur, Hadrosaur, Maxilla, Dinosaur Provincial Park, Late Cretaceous, Campanian

INTRODUCTION

As part of the volume honoring the long career of Louis Jacobs, it seems appropriate to also recognize the all-too short career of one of his star students - Junchang Lü (Conniff 2018; Guangzhou Daily 2021). I originally met Junchang in Beijing in the late 1980s when we were doing the Sino-Canadian Dinosaur Project (CCDP) and he was a student working at the Institute of Vertebrate Paleontology and Paleoanthropology. Over the years I had the pleasure of working with Junchang (both in in the field and on research papers) many times in China and Mongolia. In 2015, three palaeontologists (Junchang Lü, Yoshi Kobayashi and Yuong-Nam Lee) who had been graduate students of Louis Jacobs joined a University of Alberta field party in Dinosaur Provincial Park (referred to henceforth as DPP). On June 17, 2015, Junchang found a nicely preserved, juvenile hadrosaur maxilla with most of the teeth intact.

The bones of small dinosaurs are rare in DPP, where there was a preservational bias that commonly led to the complete

disarticulation and/or loss of small animal remains (Dodson 1975, Brown et al. 2013). This includes baby or juvenile dinosaurs, the articulated or associated remains of which are hard to find in Dinosaur Provincial Park. However, disarticulated, isolated bones of juvenile dinosaurs are not uncommon (Tanke and Brett-Surman 2001). Nevertheless, disarticulated maxillae and dentaries of juveniles are rarely complete and almost never include teeth. For these reasons, the discovery of UALVP60543 was noteworthy in that it is one of the smallest (Table 1) and most complete hadrosaur maxillae with teeth known from DPP. Smaller hadrosaur maxillae with teeth have, of course, been recovered from other sites, including those of embryonic skeletons from Devil's Coulee (Oldman Formation; Horner and Currie 1994), which is approximately 300 km south of DPP.

The specimen (UALVP60543, field number DPP2015.248) was found in a coarse-grained fluvial sandstone. Over the years, several attempts have been made to find associated parts of the skeleton in the vicinity of the discovery site (12U 0465413E, 5621217N), but no other bones have been

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Table 1. Measurements in mm of various small hadrosaur maxillae. Information on CMN 8917 from Sternberg (1956), Warnock-Juteau 2023, and Warnock-Juteau et al. 2023; on MOR 548 from Brink et al. 2011; on MPC-D100/764 by Dewaele et al., 2015; on RAM 14000 from Farke et al., 2013; on TMP 87.79.286 from Tanke and Brett-Surman (2001); on TMP 94.385.1 from Brink et al. 2011; on YPM-PU 22400 from Prieto-Márquez and Guenther (2018); on ROM specimens from Evans 2010. Abbreviations: e, estimate that is approximate only; H, height at jugal suture; L, length; +/-, estimate is close to what the measurement probably was

Specimen #	Skull L	Maxilla L	Tooth Row L	Maxilla H	# tooth families
AMNH 5461			162		
CMN 2247	362		149		
CMN 8917		57.5	46e	_	15
MOR 548		69			
MPC-D100/764		20.6			5-7
RAM 14000	246		117.7		20
ROM 759			187		
ROM 758	384		184		
TMP 81.22.6					
TMP 82.16.177					
TMP 87.79.286		45	_	_	12
TMP 88.36.4					
TMP 89.79.52		40e	35e	9.5e	10e
TMP 94.385.1		158			31
YPM-PU 22400		60	_	20	15
UALVP 60543		139	124.5+/-	57	23
UALVP 62346		124	110.8		22

recovered that can be associated with the maxilla. The specimen was found at elevation 688masl in the Dinosaur Park Formation (DPF), and the closest measured contacts with the underlying Oldman Formation (OF) are 0.7 to 1.2 km from the site, mostly on a west to north arch. The elevation of the contacts range from 660 masl to 672 masl, and the average is 668 masl. The specimen was, therefore, recovered approximately 20 m above the OF/DPF contact, which suggests it is part of the Corythosaurus-Centrosaurus assemblage zone (75.77-76.47 Ma) (Ryan and Evans 2005, Eberth et al. 2023), or Megaherbivore Assemblage Zone 1b (MAZ-1b) of Mallon et al. (2012). Hadrosaur species reported from this interval include Corythosaurus intermedius, Gryposaurus notabilis, Lambeosaurus (L. clavinitialis and L. lambei are both in MAZ-1b) and Parasaurolophus walkeri. However, the specimen was also found only 73m to the NE of Q213, where a Prosaurolophus maximus skeleton was collected (TMP 1993.081.0001) only 10 m higher in section in MAZ- 2a. Although the elevation of the excavation site of UALVP60543 probably came from MAZ-1b, there is enough uncertainty that hadrosaur species from MAZ-1a and MAZ-2a need to be considered as possible identifications of UALVP60543.

The second specimen (UALVP) was found when this paper on UALVP60543 was nearing completion. It was also recovered from the *Corythosaurus-Centrosaurus* Assemblage Zone, but was found in Bonebed BB150 at the northwest end of DPP. This specimen had only been prepared from the medial side by the time this paper was written. Its morphology suggests it is probably a hadrosaurine, and its most likely identification is *Gryposaurus*.

Institutional Abbreviations — CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; MOR, Museum of the Rockies, Bozeman, Montana, USA; MPC-D, Mongolian Paleontological Center, Dinosaur Collection (of the Institute of Paleontology, Mongolian Academy of Sciences), Ulaanbaatar, Mongolia; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory of Vertebrate Palaeontology, Edmonton, Alberta, Canada; YPM-PU, Yale Peabody Museum (collection that was formerly in the Museum of Natural History, Princeton University), New Haven, Connecticut, USA.

METHODOLOGY

An X-ray Computed Tomography (XCT) helical scan of the maxilla (UALVP60543) was taken at the Permafrost Archives Science (PACS) lab at the University of Alberta using a Nikon XT H 225 ST Industrial CT Scanner. The scan used a beam energy of 220 kV, current of 191 μ A, and exposure of 4 fps with 8 frames averaging and a total of 5591 projections (3132 per rotation). A 36 μ m effective pixel size was achieved. A 3mm copper filter was also attached to the target head to reduce artefact effects caused by higherdensity minerals.

Primary images were reconstructed through Nikon's CT 3D Pro software, where minor beam hardening effects were applied and volume files were exported to be used for visual analysis in ORS Dragonfly 4.0, and were polished using Zbrush 2018.

Acknowledgements - Like so many vertebrate palaeontologists, the first author owes a great debt of gratitude to Dr. Louis Jacobs (Southern Methodist University, Dallas, Texas). In addition to being a great scholar with broad-based experiences in collecting and researching fossil vertebrates, Lou has been a great teacher and friend to many, has a great sense of humour, and is a tireless supporter of the Society of Vertebrate Paleontology. UALVP60543 was found by Junchang Lü on June 17, 2015, and was collected by the first author on June 22, 2015. Further searching in the same area both that day and over subsequent years failed to turn up any additional associated material that can be attributed to this individual. It was prepared by Susan Kagan in the UALVP. UALVP62346 was found by Colton Coppock in 2023 and was prepared initially by the first author. We thank Duane Froese, Joel Pumple, and Jordan Harvey of the PACs CT Lab at the University of Alberta for CT scanning and imaging. Many thanks to Jordan Mallon (Canadian Museum of Nature, Ottawa, Canada) and Trystan Warnock-Juteau (Carleton University) for providing unpublished information on (and a cast of) CMN8917, and to Brandon Strilisky (Royal Tyrrell Museum of Palaeontology) and to Howard Gibbons (University of Alberta Laboratory of Vertebrate Palaeontology) for their assistance in finding specimens and cataloguing data in the collections of their respective institutions. Finally the authors would like to thank the reviewers (Phil Bell and Michael Ryan) for many good suggestions that improved the quality and readability of the paper.

SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen, 1842 Ornithischia Seeley, 1887 Ornithopoda Marsh, 1881 Iguanodontia Dollo, 1888 Hadrosauridae Cope, 1870 Lambeosaurinae Parks, 1923

Comparative Material

- CMN 8917 is a partial skull collected by G.E. Lindblad in 1953 from what is now Dinosaur Provincial Park. It has recently been CT-scanned and redescribed by Warnock-Juteau (2023), who suggests that it probably represents *Gryposaurus notabilis*. The locality suggests it was recovered from the Dinosaur Park Formation.
- MPC-D 100/764 are *Saurolophus angustirostris* perinates from Mongolia that were described by Dewaele et al (2015). Presumably they were collected from the Nemegt Formation.
- TMP 1989.079.0052 is an embryonic skull of *Hypacrosaurus* stebingeri described by Horner and Currie (1994). It is from time-equivalent (Oldman Formation) sediments of Devil's Coulee, which is some 300 km south of Dinosaur Provincial Park. Other Tyrrell Museum specimens from Dinosaur Provincial Park and Devil's Coulee have also been referred to.
- UALVP62346 (Figs. 1E and 3E, F) is a right maxilla with an intact tooth bank of a juvenile hadrosaur found at the base of the Dinosaur Park Formation in BB150 in Dinosaur Provincial Park by Colton Coppock in June, 2023. The specimen was still in preparation at the time of writing.



FIGURE 1. Right maxilla (UALVP60543) in right lateral (A), medial (B), dorsal (C) and ventral (D) views. E, right maxilla (UALVP62346) in medial view. **Abbreviations: dmf**, dorsomedial flange; **dp**, dorsal process; **er**, ectopterygoid ridge; **es**, ectopterygoid shelf; **if**, internal antorbital fenestra; **laf**, maxillary foramen; **plp**, palatine process; **vt**, ventral jugal tubercle.

YPM-PU 22400 is a single number that includes perinatal specimens of *Maiasaura peeblesorum* from Egg Mountain (Two Medicine Formation; Montana) and includes six left maxillae, eight right maxillae and three maxillary fragments (Prieto-Marquez and Gunther 2018). The most complete maxilla is 60mm long.

DESCRIPTION

UALVP60543 (Fig. 1) is an almost complete right maxilla (lacking small fragments around the periphery of the bone that were lost to erosion before the specimen was found). It is 124.9 mm long as preserved, and the height between the alveolar margin and the top of the dorsal process is 55.3mm. The tooth row seems to be complete (judging from the arch of "special foramina", Fig. 1B) and is 124.5 mm long. It

includes alveoli for 23 tooth families, which is in the range of other hadrosaur juveniles of similar size (Table 1). The edentulous anteroventral process was lost to erosion. It can compose about 11% of the maxillary length (Wagner and Lehman 2010). However, the process can also be much longer in some specimens, and in "*Tetragonosaurus*" is 17% the length of the tooth row (Evans et al., 2005). Using the more conservative estimate of 11%, the total estimated length of the maxilla of UALVP60543 is 139 mm.

Like all hadrosaur maxillae, the outline of UALVP60543 is triangular in lateral view (Figs. 1, 2, 3). The angle between the alveolar margin and the premaxillary shelf is 33 degrees, whereas that between the alveolar margin and the ectopterygoid shelf is 30 degrees. The angles are higher in neonate specimens of *Hypacrosaurus stebingeri* (Horner and Currie 1994, Warnock-Juteau 2023) and other younger hadrosaurids, which is a consequence of their relatively shorter, deeper preorbital regions. The alveolar margin is essentially straight in lateral view, and the dorsal process is centered above the midpoint of the bone. Although the apex was lost to erosion, the dorsal process clearly tapered into a pointed dorsal termination as in all lambeosaurines. Even so, the dorsal process is still taller than it is anteroposteriorly long, which is characteristic of lambeosaurines (Horner et al. 2004). The roughly rhomboidal sutural surface for the jugal has a sharply-defined anteroventral margin. There is a well-defined ventral jugal tubercle on the lateral surface of the dorsal process below the ventral limit of the jugal suture. It is separated by a gap from the straight, well-developed ectopterygoid ridge (Figs. 1, 2). Posterior to the base of the dorsal process is the mediolaterally widest part of the maxilla. Here the medial edge rises into a prominent palatine process that is separated from the dorsal process by a troughlike longitudinal groove that extends from what is sometimes referred to as the internal antorbital fenestra to the back of the palatine process (Fig. 1B). The palatine process is continuous with the dorsomedial flange that slopes posteroventrally until it disappears into the posteromedial surface of the ectopterygoid shelf. There is a weak suggestion of a pterygoid flange projecting posteriorly from the back of the dorsomedial flange. The medial surface has a dorsally arched row of alveolar ("special") foramina as in other hadrosaurids. Although the margins of some of the foramina were destroyed by erosion, the number of foramina correlates with the low number of alveoli and consists of only about 20 preserved openings.

Unfortunately, the anterior edge of the dorsal process is broken at the base, thereby obscuring the details of the foramina that are normally present in this area of hadrosaurid maxillae (Warnock-Juteau 2023). As noted by Evans (2010), the number, sizes and positions of these foramina are highly variable in lambeosaurines. Nevertheless, the posteroventral edge of a large foramen is visible. It is possible that the opening was closed anteriorly and dorsally by the premaxilla, but it is more likely that it was entirely surrounded by the maxilla. The opening is equivalent to what some workers (Xing et al. 2017) have termed the internal antorbital fenestra. Horner et al. (2004) stated that this maxillary foramen is not homologous to the antorbital fenestra because less derived taxa like *Iguanodon* possess both an antorbital fenestra and a maxillary foramen. Galton (1973), Horner et al. (2004) and Warnock-Juteau (2023) suggest that foramina in this region may have transmitted vasculature or the maxillary branches of the trigeminal nerve. However, CT scans suggest that a foramen entered the bone level with the maxillary foramen, and continued forward within the main body of the maxilla as a long channel. The course of this channel does not provide evidence as to whether it was either for vascularizing or innervating musculature, skin, or teeth. These functions were more likely attributable to a second, narrow canal that extends mediodorsally from the maxillary foramen across a ridge and then joins a broad, longitudinal groove that extends between the medial wall of the dorsal process and the lateral surface of the palatine process. As in other lambeosaurines, the maxillary foramen presumably led anterodorsally into a groove on the premaxilla. No other foramina are evident on the lateral surface of the maxilla.

The "special foramina" (Edmund 1957) between the medial dental plate and the main body of the maxilla form an arch of twenty or more foramina (erosional damage to the medial surface of the maxilla left only the lower margins of the foramina, making an exact count uncertain). The most posterior three alveoli were exposed by loss of the front part of the medial dental plate.

The apex of the dorsal process is at mid-length of the maxilla, although the center of the base (between the maxillary foramen and the front of the ectopterygoid shelf) is anterior to the midpoint of the bone (as expected in lambeosaurines). There is a deep depression on the lateral surface of the dorsal process for the contact with the jugal. It is sharply defined ventrally and posteroventrally by a ridge. The surface of the maxilla has the texturing expected of juvenile, rapidly growing hadrosaurs. The dorsal surface of the anterior maxillary process is broad (for contact with the premaxilla), shallowly concave (mediolaterally), relatively smooth (although there are weak longitudinal ridges), and preserves the base of the anteromedial process found in lambeosaurines. At its broadest point the premaxillary contact is 41mm mediodorsally to lateroventrally. It is underlain laterally by a strong longitudinal ridge that is 16mm above the alveolar margin. The lateral surface of the dorsal process is deeply excavated by the suture for the anterior process of the jugal. The concave sutural surface is roughened by ridges and channels for a strong contact.

UALVP62346 (Figs. 1E and 3E, F) is the right maxilla of a juvenile hadrosaur with an intact tooth bank. It was found



FIGURE 2. Rendered CT Images of UALVP60543 in lateral (A) and ventromedial (B) views. C, D, tooth family 8 showing worn, erupted tooth (I, green), an unerupted tooth (II, light blue), the crown and developing root of another tooth (III, dark blue) and the tip of a newly developing crown (IV, red)

at the base of the Dinosaur Park Formation in Bonebed BB150. The specimen was still in preparation at the time of writing. The fact that it has a separate anterior process medial to the posteroventral process of the maxilla that forms part of the medial floor of the external naris shows that this is a hadrosaurine (Horner et al., 2004). Other characters that support the hadrosaurine identification include the maxillary apex being low and gently rounded, and positioned behind the centre of the maxilla; and, the poor development of the ectopterygoid ridge.

Teeth — Twenty-three tooth families are preserved in the maxillary tooth battery (Fig. 1B), held to each other by periodontal ligaments (LeBlanc et al. 2016; Bramble et al. 2017). There are three teeth in the tooth family of the third alveolus (Fig. 2B). However, the CT scans show that there

are as many as four teeth in tooth families of the larger alveoli (Fig. 2C, 2D). Each erupted tooth shows tooth wear on its apex, and the presence in each tooth of enamel, orthodentine, mantle dentine and coronal cementum maintained a suitably rough occlusal surface (Erickson et al. 2012). The presence of these tissues can be seen as elevated ridges for enamel, mantle dentine and coronal cementum in worn occlusal surfaces (Figs. 3A, 3B, 3D) whereas orthodentine can be identified by its basin-like wear (Fig. 3D) and radiating lines from the center of the tooth (Figs. 3A, 3B). There is a strong medial, longitudinal ridge on the lateral surface of each (Figs. 1, 2, 3). There do not appear to be any secondary longitudinal (vertical ridges), but that may be because it is difficult to see the enameled surfaces in most teeth, and the CT scanned cross-sections may not be at the right levels. The anterior and posterior rims of the enameled



FIGURE 3. Anteroposterior CT scans (A, B) and photographs (C, D, E, F) of UALVP60543 (C, D) and UALVP62346 (E, F). A, Slice 782 of 1880. B, Slice 220 of 1880. C, medial photograph of the central part (tooth positions 8 to 13) of the tooth battery of UALVP60543. D, Occlusal surface of tooth battery (tooth positions 8 to 13). E, medial photograph of tooth positions 8 to 14. F, occlusal surface of tooth battery (tooth positions 8 to 13).

parts of the teeth are all smooth, and there is no evidence of denticulation (Fig. 1A). The unenameled medial surfaces of many of the teeth also seem to have each had a weak medial ridge (Figs. 3B, 3D). The tooth crowns are largest at midlength of the maxilla (the anteroposterior lengths of the twelfth and fourteenth maxillary teeth are the largest teeth, but decrease progressively in size towards the front and back of the tooth row (Figs. 2A, 2B).

The maxillary teeth are typical of lambeosaurines in that each unworn crown has a dorsoventrally elongate, lanceolate (diamond-shaped) enameled labial surface. Each alveolus has a stack (family) of three to four developing and functional teeth (Fig. 3), two of which generally take part in the ventromedially inclined occlusal surface as in other, similarsized lambeosaurine taxa (Farke et al. 2013). In contrast, only a single tooth in each family forms the occlusal surface in embryonic and hatchling tooth batteries (Horner and Currie 1994, Erickson and Zelenitsky 2014), each of which wears into a simple basin-like structure. The complex ridge and basin occlusal surfaces of subadult and adult hadrosaur teeth (Fig. 3A) are produced by different hardness values of the enamel and multiple types of dentine (Erickson et al. 2012; Erickson and Zelenitsky 2014). The enameled labial surface with its prominent, straight vertical carina (central in its anteroposterior position) was covered by the root of the previous tooth in the stack (Fig. 3A). However, the worn stubs of the roots of the most mature teeth of many of the tooth families were not preserved in UALVP60543, and presumably had fallen out before burial and fossilization of the specimen. Therefore, the edge of the dental battery is more jagged than it would have been in the living animal, and the longitudinal ridges are visible in many of the maxillary teeth (Figs. 1A, 3B). The largest teeth are in the centre of the tooth battery, but decrease in size towards the front and the back (Lambe 1920; Lull and Wright 1942, Ostrom 1961; LeBlanc et al. 2016). This is true in all subfamilies of hadrosaurids.

DISCUSSION AND CONCLUSIONS

UALVP60543 is one of the smallest hadrosaur maxillae with teeth presently known from DPP, and can be identified as belonging to one of the many lambeosaurine species known from the Dinosaur Park Formation. At this level (the *Corythosaurus-Centrosaurus* Assemblage Zone), it is likely from either *Corythosaurus* or *Lambeosaurus*. UALVP62346 is from about the same level in the DPF, but is relatively deeper, has a relatively lower but anteroposteriorly more elongate dorsal process, and is more likely identifiable as *Gryposaurus*.

Hadrosaurid teeth went through many changes in ontogeny, including the presence or absence of secondary ridges, denticulation of the margins of the lanceolate enameled surfaces of the crowns, orientations of the occlusal surfaces, height to width ratios of crowns, and even tissue compositions of the teeth themselves. The number of tooth families also increases dramatically with body size (Horner and Currie 2004, Suzuki et al. 2004, Warnock-Juteau 2023), as does the number of teeth that make up each tooth family. These changes have been hypothesized as evidence of ontogenetic and interspecific differences in dietary preferences, which may have allowed for more efficient niche partitioning (Hall 1993, Erickson et al. 2012, Erickson and Zelenitsky 2014, Mallon et al. 2022, Wyenberg-Henzler 2022, Warnock-Juteau 2023).

Estimates of tooth growth, wear and replacement rates (Erickson 1996, Horner et al. 2000) for hadrosaurs this small range between 0.24 mm to 0.40 mm per day. Warnock-Juteau (2023) calculated that a single tooth crown in CMN8917 was worn out between 27 to 45 days, whereas young *Maiasaura peeblesorum* wore out their teeth in 46 days, but adults of the same taxon had to replace their teeth in 58 days (Erickson 1996)

The absence of a pronounced anterodorsal process, and the proportions of the dorsal process that is taller than anteroposteriorly long, identify UALVP60543 as a lambeosaurine. Several species of *Corythosaurus* and *Lambeosaurus* are present in the *Corythosaurus-Centrosaurus* assemblage zone (75.77-76.47 Ma) (Ryan and Evans 2005, Eberth et al. 2023), or Megaherbivore Assemblage Zone 1b (MAZ-1b). However, there are currently no characters known in the maxilla to refine the identification of UALVP60543. As pointed out by Warnock-Juteau (2023), dental characters like secondary ridges and denticulation are no longer considered variable enough to identify the teeth to subfamily level.

UALVP60543 and UALVP62346 have tooth row lengths that are roughly equivalent, and even though the specimens represent two different subfamilies that can have radically different tooth counts at maturity, they have equivalent numbers of tooth families at this size. These specimens indicate that tooth counts in these two clades were similar at hatching, but rapidly diverged during ontogeny. The juveniles of both subfamilies presumably had similar diets, but the morphological divergences during ontogeny suggests there were fundamental differences in the diets of the adults. It is beyond the scope of this paper to determine whether those differences were because of dietary differences, because of differences in how they processed the food, or differences in both.

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