Description of Dinosaur Teeth from the Upper Cretaceous Judith River Formation in Montana, U.S.A.

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Abstract

The Upper Cretaceous Judith River Formation is well known for yielding abundant dinosaur fossils. In this study, isolated dinosaur teeth from the formation are described. The specimens come from Site 1, a bonebed in mudstone layer near Winifred, Fergus County, north-central Montana, U.S.A. The studied teeth pertain to Tyrannosauroidea, Dromaeosauridae, Hadrosauridae, basal ornithopod *Orodromeus* and basal Ornithopoda of uncertain genus. This study demonstrates that there were small-bodied dinosaurs at Site 1 for the first time in addition to previously reported large-bodied dinosaurs, namely hadrosaurids and tyrannosauroids.

Key Words: Dinosauria, dentition, Late Cretaceous, Judith River Formation

Introduction

Tooth fossils have often been studied in vertebrate paleontology for the following reasons. First, the outer layer of tooth is enamel, the hardest material in vertebrates, which is most likely to be preserved in a vertebrate body. Second, dental morphology is so useful in the classification of vertebrate that some taxa can be identified only with teeth (Currie et al., 1990; Richter et al., 2012).

The Lower Cretaceous terrestrial fossil beds of western North America contain an extensive record of terrestrial and freshwater vertebrates particularly from the Campanian (Gates et al., 2010). The Upper Cretaceous Montana Group, composed of both marine and terrestrial sediments, is distributed in Montana, U.S.A. (Sahni, 1972). In Montana Group, the Campanian Judith River Formation deposited along the Western Interior Seaway (Rogers, 1998). The Judith River Formation has been well known for the occurrence of numerous vertebrate fossils including dinosaurs (Eberth, 1997; Weishampel et al., 2004).

In 1991, 220 vertebrate fossils were collected from a bonebed in Judith River Formation near Winifred, Fergus Country, north-central Montana, U.S.A., which was named Site 1 (Fig. 1A-C; Suzuki, 1993). The taphonomy of the bonebed at Site 1 has been analyzed by Suzuki (1993) and Kawaguchi (2013). Five teeth of tyrannosauroid theropods from Site 1 have been described in detail by Oniki and Tanoue (2014). In this study, vertebrate fossils were prepared from a block of sandstone collected at Site 1. Among these fossils, tooth specimens were described to clarify their taxonomic affinities.

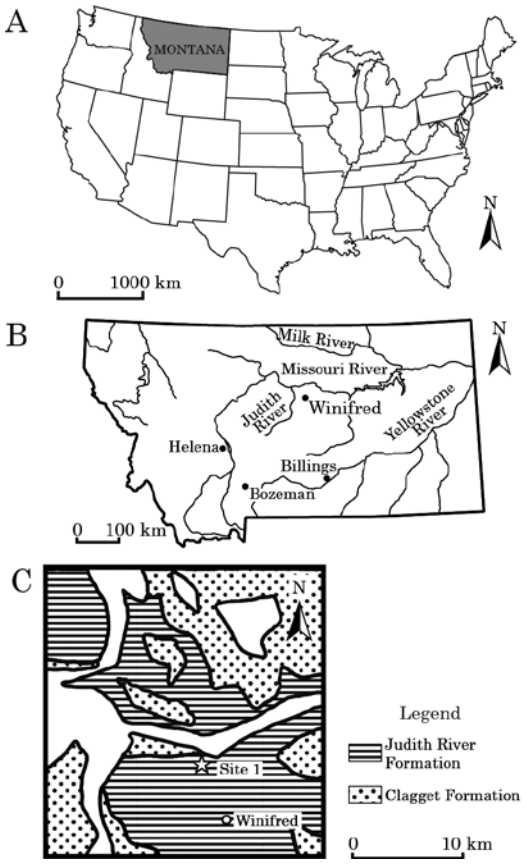

Fig.1. Locality of the studied specimens. A, Map of U.S.A. B, Map of Montana. Modified after Oniki and Tanoue (2014). C, Regional geological map of the Upper Cretaceous near Winifred, Fergus County, north-central Montana, U.S.A. Modified after Rogers (1998).

Geological Settings

Most Upper Cretaceous (Santonian–Maastrichtian) rock units that crop out within Montana are included within the Montana Group (Eldridge, 1889). The Montana Group comprises both marine and nonmarine sedimentary rocks (Sahni, 1972). The Judith River Formation is Campanian in age as determined by its position between the fossilifeous marine Claggett and Bearpaw shales (Sahni, 1972). In north-central Montana, nonmarine sequence of Campanian Judith River Formation correlates to the Oldman Formation in southern Alberta, Canada, which deposited along the western margin of the Western Interior Seaway (Eberth, 1997; Gates et al., 2010).

Various invertebrate and vertebrate fossils were reported from the Judith River Formation (Horner, 1989; Eberth, 1997; Weishampel et al., 2004). Freshwater mollusks including *Unio, Sphaerium, Andonta, Campeloma* and *Goniobasis* were collected (Horner, 1989). Vertebrate fossils from the formation include fishes, amphibians, turtles, crocodilians, dinosaurs, birds and mammals (Eberth, 1997; Horner, 1989). Judith River Formation has yielded dinosaurs including theropods, ankylosaurs, ornithopods, pachycephalosaurs and ceratopsians (Eberth, 1997; Weishampel et al., 2004).

A block of sandstone including vertebrate fossils was collected from the Judith River Formation near Winifred, Fergus County, north-central Montana, U.S.A. (Fig. 1A-C). In this study, tooth specimens in this block were prepared and described.

Materials and Methods

The materials described below are housed at the Kitakyushu Museum of Natural History and Human History (KMNH) in Kitakyushu, Fukuoka Prefecture, Japan. They were collected from Site 1 in the Campanian Judith River Formation (Fig. 1C). Numerous vertebrate specimens were embedded in a block of matrix. The matrix is yellowish-grey very fine sandstone which is very friable. The length along the major axis of the block which includes the studied specimens is approximately 29 cm, the width along the minor axis approximately 27 cm and the height perpendicular to the two axes approximately 13 cm.

First, the matrix up to 1 cm away from the fossil vertebrate specimen was scraped off with a knife. The matrix in contact with the specimen was then removed by a make-up brush to collect the specimen. The removed matrix was sieved to further collect remaining specimens. Collected specimens were measured, photographed either with a digital camera (Canon EOS Kiss X5) or Hitachi TM-1000 Miniscope and described.

Dental terminology of theropods used is shown in Figure 2. In this study, crown base length (CBL), crown base width (CBW) and height of the crown (CH) were measured (Fig. 2). Dental terminology of basal ornithopods used is shown in Figure 3. In this study, root length (RL), crown length (CL), and height of the crown (CH) were measured (Fig. 3). The density of denticles (i.e. number of denticles/mm) along carina was also examined.

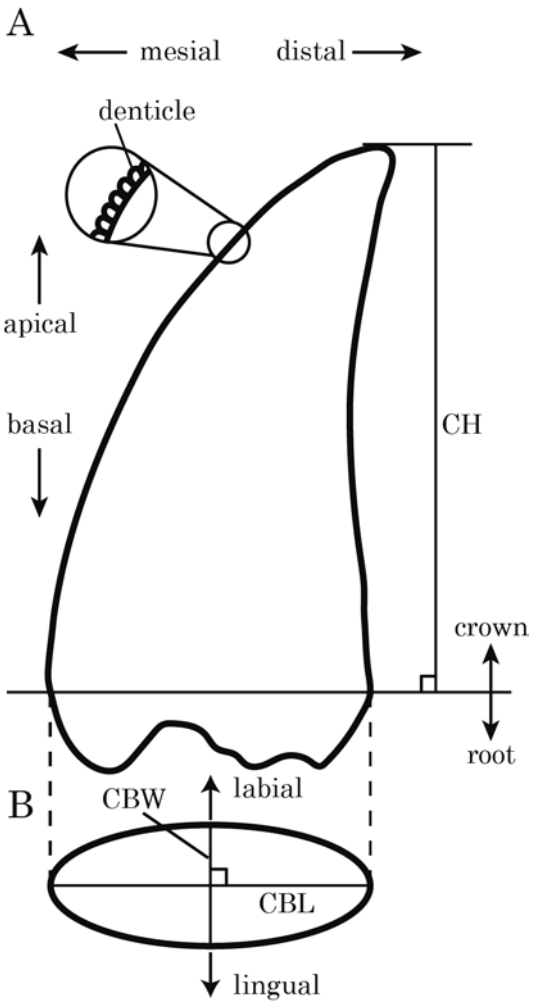

Fig.2. Dental terminology and measurements taken in theropod tooth. Schematic diagram of a theropod tooth is shown. A, Dentary tooth in labial/lingual view. B, Dentary tooth in basal view. Abbreviations: CBL, crown base length; CBW, crown base width; CH, crown height.

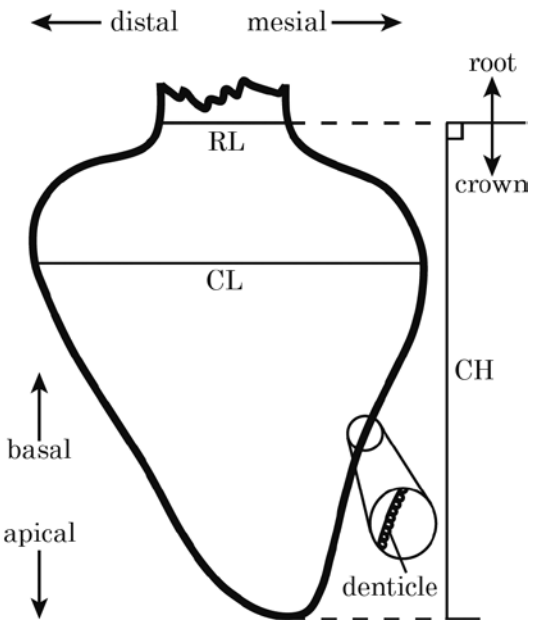

Fig.3. Dental terminology and measurements taken in ornithischian tooth. Schematic diagram of a basal ornithopod premaxillary tooth in labial/lingual view is shown. Abbreviations: RL, root length; CL, crown length; CH, crown height.

Description

Seven dinosaurian teeth were collected from the block of sandstone. These tooth specimens are described below. Measurements of these specimens are shown in Table 1 and 2.

・KMNH VP 600,002 (Fig. 4A-E)

Table 1. Measurements of KMNH VP 600,002, KMNH VP 600,003 and KMNH VP 600,004. See text and Figure 2 for definition of CH, CBL and CBW. Measurements are in millimeters.

specimen	CH	CBL	CBW
KMNH VP 600,002	>56.4	>15.1	>17.3
KMNH VP 600,003	20.4	11.5	10.1
KMNH VP 600,004	6.0	3.3	1.3-1.5

Table 2. Measurements of KMNH VP 600,005, KMNH VP 600,006, KMNH VP 600,007 and KMNH VP 600,008. See text and Figure 3 for definition of CH, RL and CL. Measurements are in millimeters.

specimen	CH	RL	CL
KMNH VP 600,005	4.2	2.5	2.7
KMNH VP 600,006	1.9	1.1	1.5
KMNH VP 600,007	2.4	1.6	2.0
KMNH VP 600,008	>7.8	-	>7.1

KMNH VP 600,002 is broken longitudinally and shows longitudinal section (Fig. 4A, C, D). The mesial portion of the crown is preserved. The complete crown would have been conical. It has mesial carina aligned on a plane parallel to rostro-caudal axis of the skull (Fig. 4A-C). Denticles develop on the mesial carina. The number of denticles per millimeter is approximately 2-2.5 (Fig. 4E). Shallow blood grooves are found between the bases of the denticles.

・KMNH VP 600,003 (Fig. 4F-K)

KMNH VP 600,003 is conical and apicodistally recurved (Fig. 4F, H). It has a worn surface in the apical region (maximum length: 6.5 mm) and therefore is functional tooth (Fig. 4G, H). It has mesial and distal carinae aligned on a plane parallel to rostro-caudal axis of the skull (Fig. 4F-I). Denticles develop both on distal (Fig. 4F, H, I) and mesial carina (Fig. 4F, G, H). The number of denticles per millimeter is approximately 2-3 (Fig. 4J, K). Blood grooves are found between the bases of the denticles. The root of KMNH VP 600,003 is partially preserved.

・KMNH VP 600,004 (Fig. 4L-S)

KMNH VP 600,004 is an incomplete tooth which lacks distal portion of its crown base (Fig. 4L, N). Its root is partially preserved. Crown is labio-lingually compressed and its horizontal cross-section at the base is hourglass-shaped (Fig. 4P). It has mesial and distal carinae aligned on a plane parallel to rostro-caudal axis of the skull. Denticles develop on the distal (Fig. 4L, N, O) and mesial carina (Fig. 4M). The mesial denticles are smaller and denser than distal denticles (Fig. 4Q-S). The numbers of mesial and distal denticles per millimeter are approximately 10 and 7, respectively.

・KMNH VP 600,005, KMNH VP 600,006 and KMNH VP 600,007 (Fig. 5A-O)

The crowns of KMNH VP 600,005 (Fig. 5A-E), KMNH VP 600,006 (Fig. 5F-J) and KMNH VP 600,007 (Fig. 5K-O) expand apical to the roots, forming bulbous crown base. The crown has slightly concave lingual surface and convex labial surface in mesial and distal views (Fig. 5B, D, H, J, L, N). Weak longitudinal striations are distributed both on labial and lingual surfaces of three specimens, which range from the base of the crown to the apical region, but not at the apex (Fig. 5A, C, G, I, K, M). KMNH VP 600,005 and KMNH VP 600,006 bear very small denticles on mesial carina (Fig. 5B, C, E, F-I). KMNH VP 600,005, KMNH VP

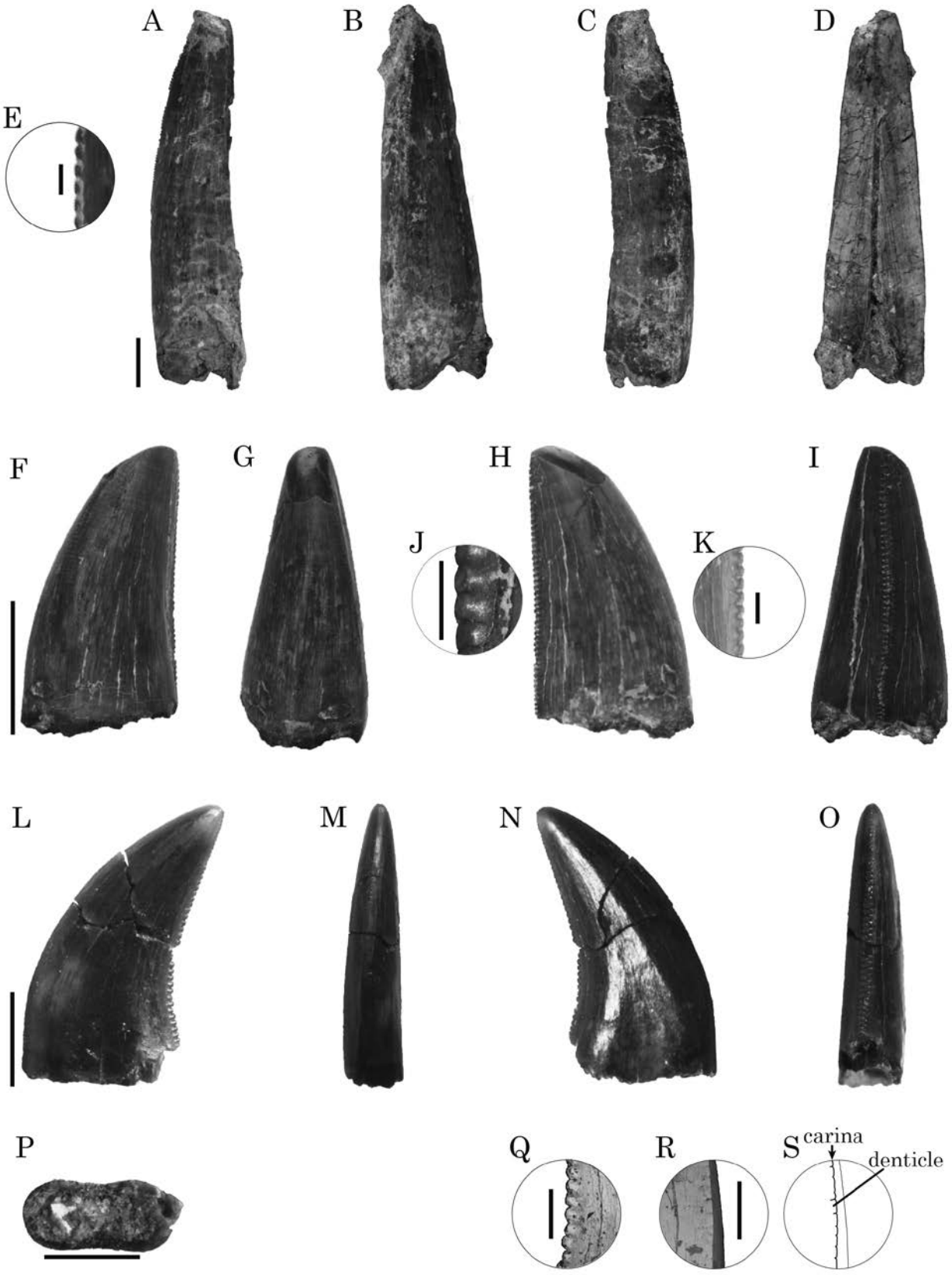

Fig.4. Photographs of theropod teeth. A-E, KMNH VP 600,002. A, lingual/labial view, B, mesial view, C, labial/lingual view, D, distal view, E, mesial denticles. F-K, KMNH VP 600,003. F, lingual/labial view, G, mesial view, H, labial/lingual view, I, distal view, J, distal denticles, K, mesial denticles. L-S, KMNH VP 600,004. L, lingual/labial view, M, mesial view, N, labial/lingual view, O, distal view, P, basal view, Q, distal denticles, R, mesial denticles, S, interpretative outline of denticles in S. Scale bars equal 1 cm for A-D, F-I, 1 mm for E, J, K, 2 mm for L-P and 0.5 mm for Q, R.

Fig.5. Photographs of ornithopod teeth. A-E, KMNH VP 600,005. A, labial view, B, mesial view, C, lingual view, D, distal view, E, apical view. F-J, KMNH VP 600,006. F, apical view, G, labial view, H, mesial view, I, lingual view, J, distal view. K-O, KMNH VP 600,007. K, labial view, L, mesial view, M, lingual view, N, distal view, O, apical view. P-Q, KMNH VP 600,008. P, lingual/labial view, Q, apical view. Scale bars equal 2 mm.

600,006 and KMNH VP 600,007 have wear facet, which indicates they are functional teeth. The wear facet slopes apicolabially in the distal region (Fig. 5C-E, F, I, J, M-O). In all three specimens, the wear facet is mostly flat except at its base, which is convex.

・KMNH VP 600,008 (Fig. 5P, Q)

KMNH VP 600,008 is a partial tooth. Only the basal part of the crown is preserved (Fig. 5P). It has a straight and well-developed primary ridge (Fig. 5P, Q). The cingulum at the base of the crown, in contrast, is poorly-developed. Its mesial or distal margin bears four knob-like projections (Fig. 5P). Mesial and distal lobes of the crown separated by the primary ridge are depressed. In occlusal view, the wear facet is preserved indicating KMNH VP 600,008 is a functional tooth (Fig. 5Q).

Discussion and Conclusion

The roughly conical morphology of KMNH VP 600,002, KMNH VP 600,003 and KMNH VP 600,004 shows that they are the teeth of carnivorous vertebrates. Among the toothed carnivorous vertebrates from the Judith River Formation including amiiforms, lepisosteiforms, champsosaurids, crocodiles, lepidosaurs, pterosaurs, theropods and mammals, only theropod teeth have denticles (Eberth, 1997; Norman et al., 2004; Weishampel et al., 2004; Gates et al., 2010). Therefore, KMNH VP 600,002, KMNH VP 600,003 and KMNH VP 600,004 pertain to Theropoda. In Theropoda, Coelurosauria including Ornithomimosauria, Troodontidae, Tyrannosauroidea and Dromaeosauridae have been collected from the Judith River Formation (Weishampel et al., 2004). Ornithomimosauria is toothless (Fastovsky and Weishampel, 2005). The height of crown of Troodontidae does not exceed 20 millimeters (Holtz et al., 1998). Tyrannosauroids are the large-bodied theropods with largest teeth among the four taxa from the formation. The horizontal section of tyrannosauroid maxillary and dentary teeth is lenticular (Fastovsky and Weishampel, 2005). Both mesial and distal carinae of tyrannosauroid maxillary and dentary teeth have denticles (Currie, 1990; Fastovsky and Weishampel, 2005). The number of denticles per millimeter is approximately 2 (Currie et al., 1990). In KMNH VP 600,002 and KMNH VP 600,003, the number of denticles per millimeter is 2-3 (Fig. 4E, J, K). Therefore, KMNH VP 600,002 and KMNH VP 600,003 are maxillary or dentary teeth of Tyrannosauroidea. Dromaeosaurid tooth crown is labio-lingually compressed and horizontal section is hourglass-shaped (DeMar and Breithaupt, 2006). Additionally, the distal denticles of dromaeosaurid teeth are distinctly larger than mesial denticles (Currie et al., 1990). In basal view, KMNH VP 600,004 is longer mesiodistally than labiolingually and its central region of constricted (Fig. 4P). Moreover, denticles on distal carina are more developed than those of mesial carina (Fig. 4Q-S). KMNH VP 600,004 is thus maxillary or dentary tooth of Dromaeosauridae.

The ornithischian crown expands above the root (Benton, 2015). Therefore, KMNH VP 600,005, KMNH VP 600,006 and KMNH VP 600,007 are ornithischian teeth. Ankylosauria, basal Ornithopoda (*Orodromeus* and *Thescelosaurus*), Hadrosauridae, Pachycephalosauridae and Ceratopsidae are the ornithischians reported from the Judith River Formation (Eberth, 1997; Norman et al., 2004; Weishampel et al., 2004). The ornithischian maxillary and dentary teeth have primary ridge or the secondary ridges and thus KMNH VP 600,005, KMNH VP 600,006 and KMNH VP 600,007, which lack these ridges, are premaxillary teeth. Among the ornithischians reported from the Judith River Formation, Pachycephalosauridae and basal Ornithopoda have premaxillary teeth (Maryańska et al., 2004; Norman et al., 2004). Premaxillary tooth of Pachycephalosauridae lacks vertical striations, instead bears three or four distinct facets both laterally and labially, and has relatively large 8-11 denticles both on mesial and distal carinae (Maryańska et al., 2004). Premaxillary tooth crowns of *Orodromeus* and *Thescelosaurus* have weak longitudinal striations and are convex labially and slightly concave lingually (Scheetz, 1999; Brown and Druckenmiller, 2011). However, morphology of denticles differs between *Orodromeus* and *Thescelosaurus*. Premaxillary crown of *Thescelosaurus* lacks distinct denticles (Sternberg, 1940). On the other hand, the mesial and distal carinae of *Orodromeus makerai* tooth bear very small denticles (Scheetz, 1999). Premaxillary crown of *Thescelosaurus* also has low faint ridges extending from the base of the crown to the apex on both labial and lingual surfaces (Galton, 1997; Boyd, 2014). KMNH VP 600,005 and KMNH VP 600,006 have bulbous crown, weak longitudinal striations, and bear very small denticles only on mesial carina, with distal carina worn (Fig. 5A-J). Although distal denticles are not preserved, KMNH VP 600,005 and KMNH VP 600,006 are identified as left premaxillary teeth of *Orodromeus makerai*. Since denticles are not preserved in KMNH VP 600,007, it is identified here as basal ornithopod premaxillary tooth.

KMNH VP 600,008 has a primary ridge and knoblike

projections at its mesial or distal margin. Maxillary and dentary teeth of Hadrosauridae have a primary ridge and marginal papillae (Weishampel and Horner, 1990; Prieto-Márquez and Norell, 2010). Therefore, KMNH VP 600,008 is maxillary or dentary tooth of Hadrosauridae.

Kawaguchi (2013) reported the presence of Hadrosauridae at Site 1. Five teeth of tyrannosauroid theropods from Site 1 have been described in detail by Oniki and Tanoue (2014). This study proves the presence of Tyrannosauroidea, Dromaeosauridae, basal ornithopod *Orodromeus* and Hadrosauridae at Site 1. Dromaeosauridae and *Orodromeus* are small-bodied dinosaurs. This study demonstrates that there were small-bodied dinosaurs at Site 1 for the first time in addition to previously reported large-bodied dinosaurs, namely hadrosaurids and tyrannosauroids (Kawaguchi, 2013; Oniki and Tanoue, 2014).

In contrast to hadrosaurids, which could reach high vegetation, *Orodromeus* fed on low vegetation, possibly up to 1 m in height. Therefore, hadrosaurids and *Orodromeus* must have fed on different vegetation. This study shows the diversity of taxa and niches to be higher than previously thought. *Orodromeus* is the taxon which has not been well understood for its poor fossil record (Scheetz, 1999). More specimens of *Orodromeus* are necessary for further studies in detail.

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