

# First report of protoceratopsians (Neoceratopsia) from the Late Cretaceous Judith River Group, Alberta, Canada

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**Abstract:** Protoceratopsians are best known in North America from associated skeletal material of *Montanoceratops* from the early Maastrichtian of Montana and Campanian of Alberta and *Leptoceratops* from the late Maastrichtian of Alberta and Wyoming. We report here the first occurrence of protoceratopsian elements from the middle Campanian (Dinosaur Park Formation) of Alberta. The specimens consist of a fragmentary right dentary and an almost complete left dentary which can be referred to *Leptoceratops* sp. Recent examination of Albertan microvertebrate material has identified cf. protoceratopsians teeth from the latest Santonian (Milk River Formation), extending the record of Albertan protoceratopsians back almost 20 million years. The rarity of these small ornithischians in the fossil record of Alberta may have been due to ecological exclusion from the wet, coastal environments that were preferred by the larger, more abundant ceratopsids.

**Résumé :** Les Protoceratopsiens sont particulièrement bien connus en Amérique du Nord du fait de leur association au matériel squelettique des *Montanoceratops* du Maastrichtien précoce dans le Montana et du Campanien en Alberta, et des *Leptoceratops* du Maastrichtien tardif en Alberta et dans le Wyoming. Nous décrivons ici la première découverte d'éléments protoceratopsiens datant du Campanien moyen (Formation de Dinosaur Park) en Alberta. Les spécimens sont constitués des fragments d'une dent du côté droit et d'une dent presque complète du côté gauche qu'on peut assigner à *Leptoceratops* sp. L'examen récent de matériel de microvertébrés cf. a permis d'identifier des dents protoceratopsiennes datant du Santonien terminal (Formation de Milk River), faisant reculer dans le passé le registre des protoceratopsiens albertains d'environ 20 millions d'années. La rareté de ces petits ornithischiens dans le registre fossile albertain est peut-être due à une exclusion pour des raisons écologiques, car les milieux humides et littoraux étaient préférés par les ceratopsidés plus gros et plus nombreux.

[Traduit par la Rédaction]

## Introduction

The Ceratopsia is a monophyletic group of herbivorous ornithischians comprising the Psittacosauridae and the Neoceratopsia (Serenio 1986). The Neoceratopsia is a monophyletic assemblage consisting of Protoceratopsidae and Ceratopsidae (Serenio 1986; Dodson and Currie 1990). Monophyly of the Protoceratopsidae (Table 1) has been questioned by Serenio (1986), and the recent cladistic analysis of the group by Chinnery and Weishampel (1998) supports the proposition that this group is paraphyletic, with *Montanoceratops* being the sister group of Ceratopsidae and the remaining protoceratopsians being more basal neoceratopsians. With the exception of *Udanoceratops tschizhovi* (Kurzanov 1992), with a skull length greater than 1 m in length, protoceratopsians are small bodied (usually 1.0–2.5 m in length). They typically possess small to moderately developed frills, and lack well-developed orbital or nasal horns. Ceratopsids were large (4–8 m) quadrupeds with variably developed orbital and nasal horns, and large

parietosquamosal frills. The Ceratopsia was one of the last groups of dinosaurs to evolve, with no published accounts of its members being older than late Early Cretaceous. Undisputed neoceratopsians have a restricted distribution to Asia and western North America, although fragmentary remains from the Lower Cretaceous of Australia suggest a protoceratopsian may also have been present in the Southern Hemisphere (Rich and Vickers-Rich 1994).

To date, three protoceratopsian taxa have been reported from western North America: *Leptoceratops gracilis* (Gilmore 1939), *Montanoceratops cerorhynchus* (Brown and Schlaikjer 1942; Sternberg 1951; Chinnery and Weishampel 1998), and *Leptoceratops* sp., the latter being a species of *Leptoceratops* that appears to be different from *L. gracilis* (Gilmore 1939). Horner (1984) reports a new ceratopsian identified only from teeth (PU No. 22459) from the lower Two Medicine Formation of Montana which might be protoceratopsian.

## Locality

Dinosaur Provincial Park (DPP) (Fig. 1), located 48 km north of Brooks in Alberta, Canada, is noted for having one of the most abundant and taxonomically diverse collections of Upper Cretaceous vertebrates remains, including at least 35 dinosaur species (Koster et al. 1987). Ceratopsid remains dominate some bone beds, and are second in abundance only to hadrosaurs in terms of articulated skeletons, individual el-

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**Table 1.** North American protoceratopsians.

Taxa	Formation and locality	Age	Specimen No.	Material
<i>Leptoceratops gracilis</i> Brown 1914	Scollard Formation, Alberta (Brown 1914; Sternberg (1951))	Late Maastrichtian	AMNH 5205	Holotype consisting of two associated partial skeletons
			NMC 8887, NMC 8888, NMC 8889	Plesiotypes, three partial skeletons, two with skulls
			TMP 93.95.1, TMP 95.86.1	Two partial skeletons
	Lance Formation, Wyoming (Ostrom 1978)	Late Maastrichtian	YPM 18133	Partial skeleton lacking skull
	Pinyon Conglomerate, Wyoming (McKenna and Love 1970)	Late Maastrichtian	AMNH 2571	Single tooth
<i>Leptoceratops</i> sp. (this paper)	Dinosaur Park Formation, Alberta	Middle Campanian	TMP 95.12.6	Dentary
<i>Montanoceratops cerorhynchus</i> Sternberg 1951 (= <i>L. cerorhynchus</i> Brown and Schlaikjer 1942)	St. Mary's River Formation, Montana (Brown and Schlaikjer 1942; Chinnery and Weishampel 1998)	Early Maastrichtian	AMNH 5464	Partial skull with associated skeleton
			MOR 542	Articulated specimen with skull
	?Belly River Group (this paper)	?Campanian	TMP 82.11.1	Articulated specimen lacking skull
<i>Leptoceratops</i> sp.	Two Medicine Formation, Montana (Gilmore 1939)	?late Campanian	USNM 113863, USNM 13864	Partial skeletons
Protoceratopsian indet.	Milk River Formation, Alberta (Baszio 1995)	Upper Santonian		Teeth
	Cedar Mountain Formation (J. Kirkland, personal communication, 1997)	Lower Cenomanian		Teeth
	Arundel Formation, Maryland (J. Kirkland, personal communication, 1997)	Lower Albian	USNM 337977	Tooth
	Wayan Formation, Idaho (Weishampel et al. 1990)	Albian		Partial skeleton

ements, and specimens recovered from systematic screen washing of fossil microvertebrate localities. However, until this report, protoceratopsians were unknown from the Judith River Group of Alberta (Fig. 1).

During the summer of 1995, an isolated but nearly complete protoceratopsian left dentary was collected by the second author from the trough crossed-stratified sandstones of bone bed 55 (Fig. 2) in a section of badlands at the west end of DPP. Bone bed 55 is a productive microvertebrate locality in the middle of the Dinosaur Park Formation (middle Campanian, Late Cretaceous), approximately 40 m above the contact with the Oldman Formation.

Subsequent examination of the Royal Tyrrell Museum fossil collections uncovered another previously unrecognized protoceratopsian dentary fragment, TMP 74.10.31. This specimen also came from Dinosaur Provincial Park, but the exact locality is uncertain.

## Systematic palaeontology

Superorder Dinosauria Owen, 1842  
 Order Ornithischia Seeley, 1887  
 Suborder Ceratopsia Marsh, 1890  
 Infraorder Neoceratopsia Sereno, 1986

Family Protoceratopsidae Granger and Gregory, 1923  
 Genus *Leptoceratops* Brown, 1914

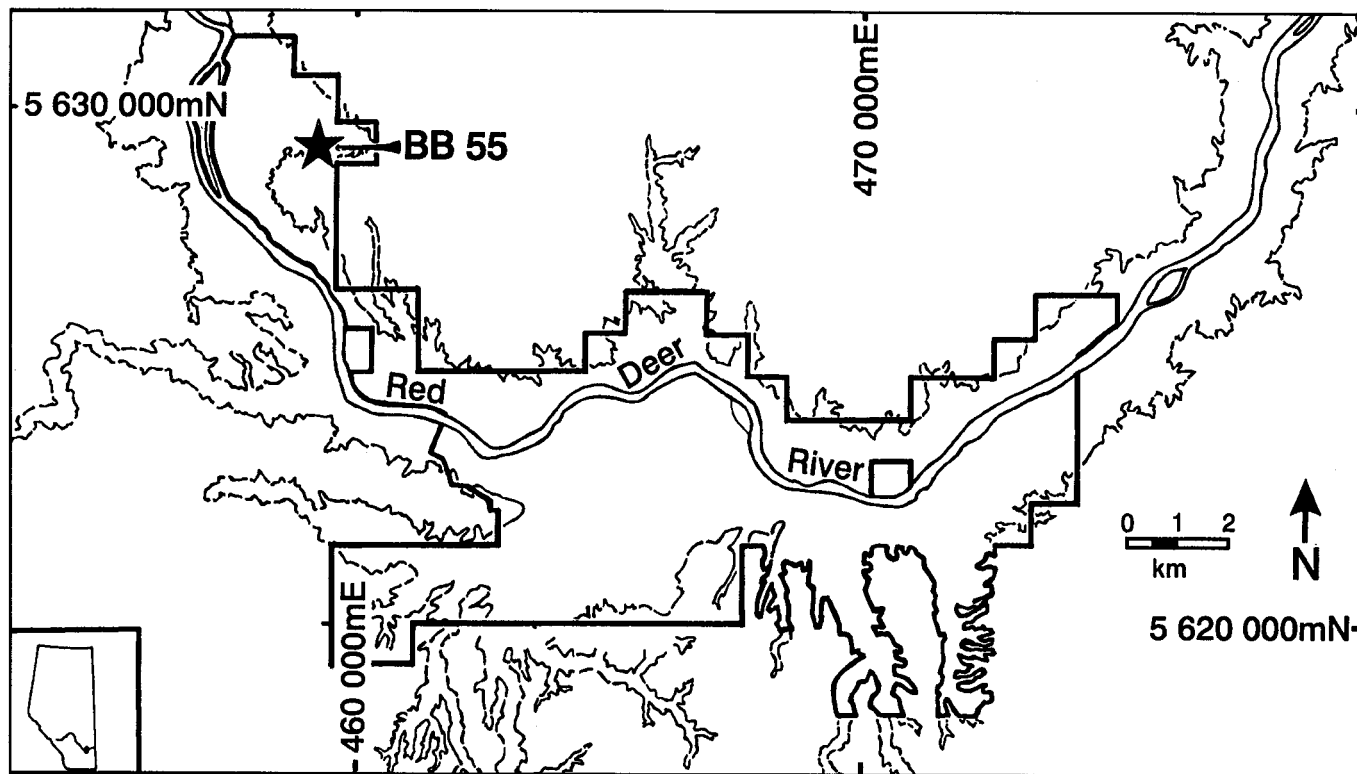
## Institutional abbreviations

American Museum of Natural History (AMNH); Canadian Museum of Nature (NMC); Princeton University (PU); Royal Tyrrell Museum of Palaeontology (TMP); Smithsonian Institution (USNM); Yale Peabody Museum (YPM).

## Description

TMP 95.12.6 (Figs. 3A, 3B) is a nearly complete right dentary lacking most of the coronoid process and the extreme posterior portion of the tooth row due to weathering. Total preserved length is 159 mm, with an estimated complete length of 175 mm. This dimension falls within the range of other *Leptoceratops* dentaries: 235 mm for the holotype AMNH 5205, 200 mm for NMC 8889, and 150 mm for NMC 8887 (Sternberg 1951). Although broken posteriorly, the tooth row appears complete with 15 alveoli preserved, with the tooth row being curved in occlusal view. Teeth are still in situ at positions 2, 6, 7, 8, 9, and 11, probably representing replacement teeth exposed when the erupted teeth were lost after death. Teeth in positions 7, 9, and 11 are only partially exposed. The dentary closely re-

Fig. 1. Locality map of Dinosaur Provincial Park, Alberta, Canada. ★, bone bed 55 (BB 55) where TMP 95.12.6 was found.

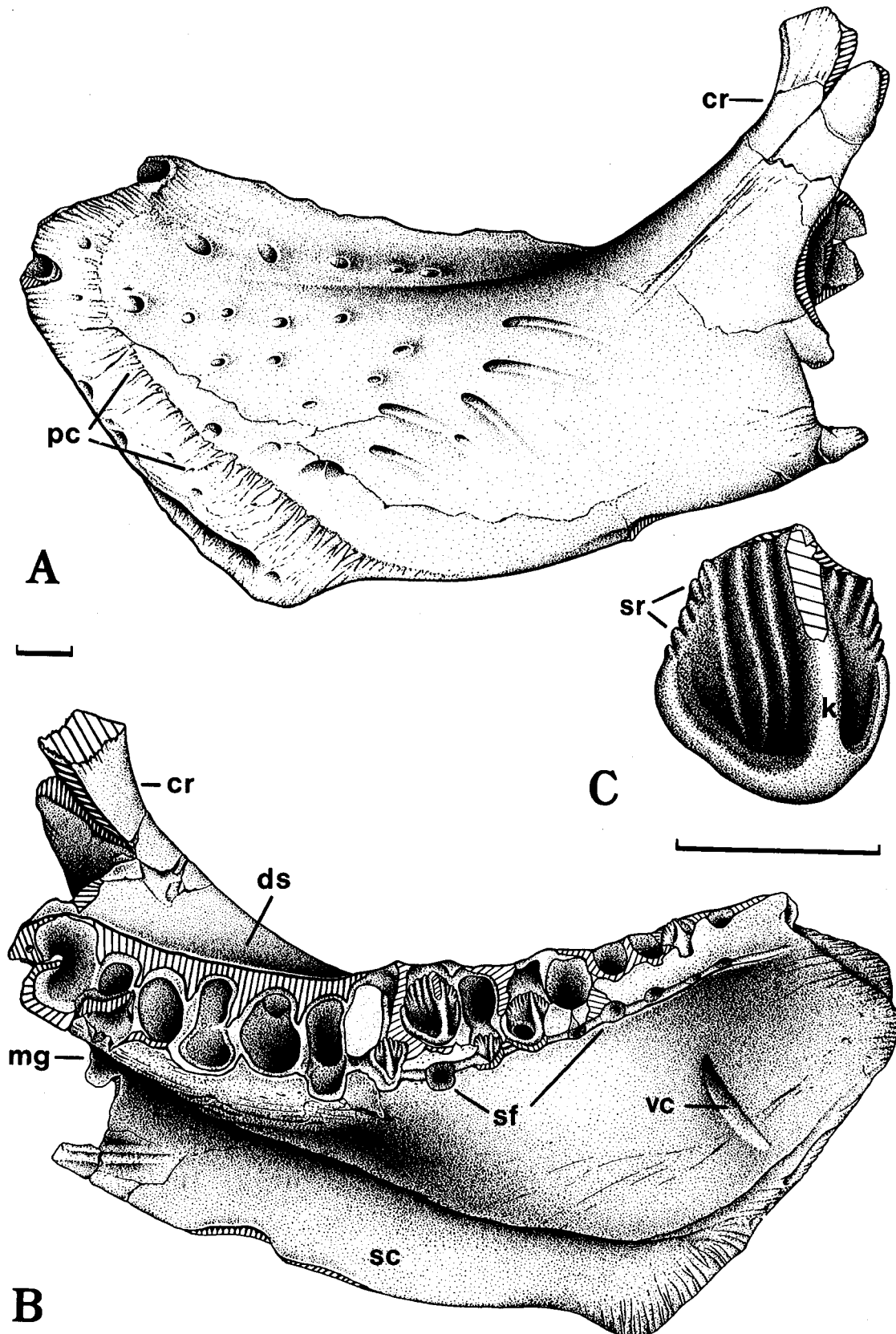


sembles those described by Brown (1914) and Sternberg (1951) in being short, relatively deep, and sharply upturned at the front where it meets the predentary. *Leptoceratops* possesses the distinctive curvature of the ventral border (a character shared with *Protoceratops*) which differentiates *Leptoceratops* from *Montanoceratops*. In lateral view, this dentary has a triangular appearance because the ventral part of the predentary articulation is extended on a point of bone. The articulating surface for the predentary thus divides the anteroventral surface of the dentary into two relatively straight portions. The ventrally descending anterior edge is approximately 30 mm long and the caudally directed ventral margin measures approximately 80 mm in length. The anterodorsal margin borders a short, shallow groove for the overlap of the posteriorly projecting flange of the predentary. The posteromedial portion of this groove (10 mm) is bordered by a short anterior projection of the tooth row (Fig. 3B). The symphyseal surface is narrow. The tooth row is offset from the medial surface by a broad, slightly dorsal concave dental shelf that overhangs the medial surface. The preserved portion of the coronoid ramus slopes up laterally from the superior posterolateral margin, and is broken where the head of the process begins. The Meckelian groove extends from the preserved tip of the medial surface of the coronoid process to about tooth position 9. Its upper margin overhangs the inferior one third of the medial surface, marking the contact with the splenial. Shallow grooves on the posteroventral surface of the coronoid ramus mark the point of attachment for the *M. intramandibularis*. The posterior margin of the dentary is not completely preserved.

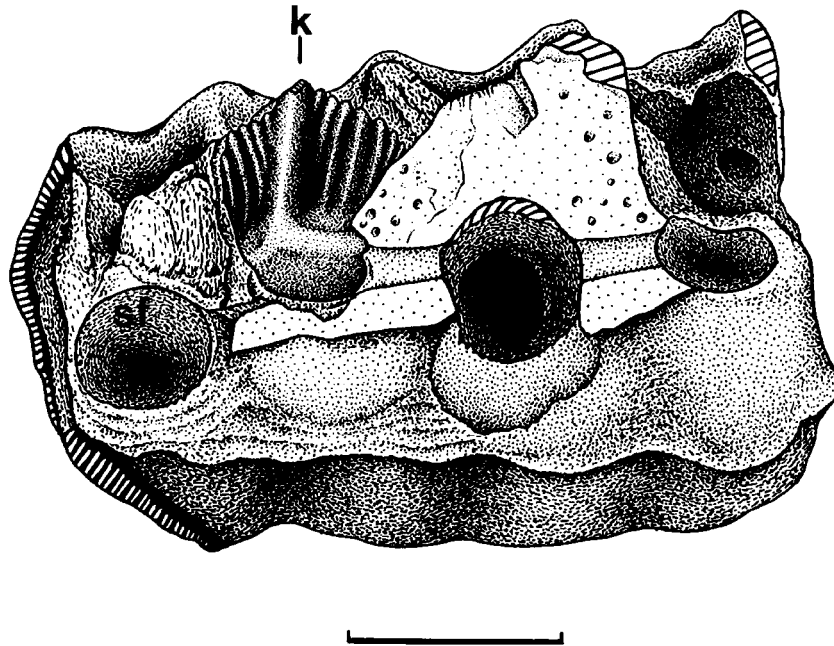
Fig. 2. Geologic columns for southern Alberta (after Braman et al. 1995).

Foothills Alberta		Plains Alberta		
Porcupine Hills		Paskapoo		
Willow Creek	Edmonton Grp.	Scollard		64 Ma
		Battle		
		Whitemud		67 Ma
ST. Mary River		Horseshoe Canyon		
Bearpaw		Bearpaw		
Belly River Group	Judith River Grp.	Dinosaur Pk.		74 Ma
		Oldman		
		Foremost		
	Pakowki			
	Milk River Fm.	Deadhorse Coulee mbr.		83 Ma
		Virgelle mbr.		
		Telegraph Creek mbr.		

**Fig. 3.** Left dentary of cf. *Leptoceratops* sp. (TMP 95.12.6) in (A) lateral and (B) medial views. (C) Close-up of tooth 8. Hatched lines indicate broken bone surface. cr, coronoid ramus; ds, dental shelf; k, median keel; mg, Meckelian groove; pc, contact surface for prementary; sc, contact surface for splenial; sf, special foramina; sr, secondary ridges; vc, vascular canal. Scale bars = 1 cm.



**Fig. 4.** Partial right protoceratopsian dentary, TMP 74.10.31, in medial view. Hatched lines indicate broken bone surface. k, median keel; sf, special foramina. Scale bar = 1 cm.



Sternberg (1951) noted the presence of 17 alveolar positions in each of the mandibles and maxillae of *Leptoceratops* (NMC 8889 and NMC 8887). Although TMP 95.12.6 is approximately the same size as NMC 8887, it appears to have had only 15 teeth, as the posterior margin of the tooth row is almost intact. The broken bone at this point does not show any indication of additional alveoli or teeth. Tooth counts in ceratopsians are not taxonomically meaningful (Maryanska and Osmolska 1975; Dong and Currie 1993), because alveolar positions are added during growth. Using this criteria, TMP 95.12.6 was most likely younger than NMC 8887 at the time of its death, although the possibility of taxonomic difference cannot be completely ruled out. Behind tooth position 5, most of the labial bone surface that covered the teeth and roots down to the special foramina groove has been broken away (Fig. 3A). Special foramina (with the associated groove) numbers 1–5 and 8 are preserved along with portions of numbers 6, 7, 9, 11, and 13. The two most visible teeth are of typical protoceratopsian shape (Figs. 3B, 3C). The teeth are short, leaf-shaped, and recurved lingually. Each bears a strong median keel extending from base to apex on the lingual surface. This keel divides the lingual surface into a small anterior portion, and a wide posterior one that is approximately three times the area of the former. Less prominent secondary ridges are visible on either side on tooth 8 (Fig. 3C) of the median keel. On the posterolingual surface, these ridges are subparallel to the medial keel. The anterior ridges are shorter and are set at oblique angles, so they appear as short extensions of the crown. The base of the lingual surface has an upturned margin that borders small pockets anterior and posterior to the medial keel. X-ray imaging of the dentary showed tooth 2 to have the primitive single root of protoceratopsians.

The ceratopsian holdings of the TMP collections were examined to determine if any protoceratopsian material had

been collected but misidentified. The only unequivocal protoceratopsian element found is a fragmentary right dentary (TMP 74.10.31, Fig. 4) collected from Dinosaur Provincial Park in 1974. Locality data are incomplete, but the specimen is most certainly from the Dinosaur Park Formation. The specimen is 38 mm long and preserves alveolar numbers ?5–?8 and a portion of the dorsolateral bone surface. Tooth position 6 contains an unerupted replacement tooth of typical protoceratopsian form.

Despite intensive screen washing of Late Cretaceous microvertebrate localities in Alberta (Brinkman 1990; Peng 1997; Baszio 1997a, 1997b; Brinkman et al. 1998) and Montana (C. Forster, personal communication, 1998), protoceratopsian teeth are extremely rare. The only documented specimens are six teeth from the Milk River Formation (University of Alberta preliminary Nos. 67–72), one tooth from the Horseshoe Canyon Formation (TMP preliminary No. 1015), and three teeth from the Scollard Formation (University of Alberta preliminary Nos. 81, 83, and 87) identified by Baszio (1997b), with the University of Alberta material having been collected by R. Fox of the University of Alberta. Additional protoceratopsian teeth have been surface collected from microvertebrate localities in the Milk River Formation of southern Alberta (M.J.R., unpublished data).

## Discussion

TMP 95.12.6 can be identified as protoceratopsian and distinguished from Ceratopsidae, based on its close resemblance to the *L. gracilis* dentaries described by Gilmore (1914, Figs. 4A and 5) and Sternberg (1951, Pls. XLIX and LI) and the form of the single-rooted dentary tooth described by Gilmore (1914, Fig. 2). Specifically, TMP 95.12.6 is short and deep relative to the dentaries of adult ceratopsids

(ratio of maximum depth of premaxillary contact to dentary length is  $>0.3$ : estimated as 0.44 for TMP 95.12.6, 0.39 for *L. gracilis* NMC 8887 (Sternberg 1951, Pl. XLIX) and USNM 5205 (Gilmore 1914, Fig. 4A), 0.36 for *Protoceratops andrewsi* AMNH 6438 (Brown and Schlaikjer 1940, Fig. 18E), and 0.36 for *M. cerorhynchus* (Chinnery and Weishampel 1998, Fig. 3;  $<0.3$  for adult ceratopsids, e.g., 0.21 for *Centrosaurus apertus*, TMP 80.18.265 (M.J. Ryan and P.J. Currie, personal observation)). As in other protoceratopsians, the coronoid process slopes up gradually, unlike the strongly offset ramus of ceratopsids (Dodson and Currie 1990). TMP 95.12.6 can be distinguished from the dentary of *Montanoceratops*, the only other recognized North American protoceratopsian genera, by possessing a ventral extension marking the posterior contact point of the prementary, giving it a characteristic "curved" ventral border shared only with the Asian *Protoceratops*. Specific designation beyond *Leptoceratops* sp. is not possible without associated cranial or postcranial material. The small right dentary fragment, TMP 74.10.31, can also be indentified as protoceratopsian but generic designation could not be determined.

*Leptoceratops* is known from the Scollard Formation of Alberta from at least six partial skeletons and a small number of referred isolated teeth and elements. The type of *L. gracilis* (AMNH 5205) was described from two partially "commingled" articulated specimens collected in 1910 (Brown 1914). Brown describes one specimen as including a partial skull, the right forelimb, and a series of caudal vertebrae, but his holotype includes these elements as well as parts of the hind limbs. It is unclear from Brown's description if the holotype of *L. gracilis* is based solely on elements from one individual or is a composite of the two individuals (making each individual a syntype). In keeping with the International Code of Zoological Nomenclature (1985, Article 74), AMNH 5205 should be designated as the individual containing the skull, right forelimb, and partially articulated tail, and should be made the lectotype of *L. gracilis* because it provides more information than the less complete second specimen. The latter specimen (recognized by the difference in size of the duplicated elements) should be designated a pleisiotype of *L. gracilis*.

*Leptoceratops* has previously been recognized in the late Maastrichtian of Alberta based on a number of articulated specimens (Table 1). Baszio (1997b, Pl. IX) has identified six rare occurrences of protoceratopsian teeth from the Deadhorse Coulee Member (latest Santonian) of the Milk River Formation (Fig. 2) of Alberta which appear to represent two morphs of different sizes. Together with TMP 95.12.6, these records extend the Canadian protoceratopsian record through almost 20 million years, from the latest Santonian to the latest Maastrichtian. *Leptoceratops* is also recognized from the late Maastrichtian of Wyoming and possibly from the late Campanian of Montana (Table 1). The other North American protoceratopsian, *M. cerorhynchus*, is known from the early Maastrichtian of Montana (Dodson and Currie 1990). Of note is a previously unreported, partial skeleton of *Montanoceratops* sp. (TMP 82.11.1). This specimen was not collected in situ and probably originated in sediments of the Belly River Group (Fig. 2) near the town of Cowley, in the foothills of southern Alberta. The Campanian

age of these sediments makes this specimen the youngest occurrence of *Montanoceratops* reported to date.

In addition to *Leptoceratops* and *Montanoceratops*, North American protoceratopsian material includes undescribed teeth collected by Kirkland and Parrish (J. Kirkland, personal communication, 1996) from the Cedar Mountain Formation (probably basal Cenomanian, based on pollen correlation) from central Utah (Table 1). J. Kirkland (personal communication 1996) also reported a tooth (USNM 337977) collected by D. Krantz from the Arundel Formation (lower to middle Albian) of Maryland with protoceratopsian affinities. Weishampel et al. (1990) reported a partial skeleton of a possible protoceratopsian from the Wayan Formation (Albian) of Idaho. If valid, these occurrences would place protoceratopsians in North America at least as early as the late Early Cretaceous. This age rivals that of the Asian genus, *Archaeoceratops* (?Aptian-Albian; Dong and Azuma 1997), the oldest known protoceratopsian.

Eberth (1990) has demonstrated that microvertebrate assemblages associated with trough cross-stratified sandstones, such as those comprising bone bed 55, are most likely to have been derived from distances less than 10 km away, well within the palaeogeographic area of the current Dinosaur Provincial Park boundaries. The occurrence of TMP 95.12.6 in bone bed 55 suggests that at least one species of protoceratopsian either lived within the immediate area of ancient DPP or occasionally wandered into it. Supporting the supposition that the dentary was not transported over a great distance is the unabraded nature of the specimen and the presence of several teeth in the jaw. Isolated ceratopsid dentaries rarely preserve any teeth (Ryan 1992), suggesting that they were lost early in the process of disarticulation. It is possible that protoceratopsian teeth were also lost in a similar manner. Additionally, the almost complete lack of protoceratopsian material from within the extremely well sampled Campanian-aged DPP microvertebrate localities (Brinkman 1990) argues for protoceratopsians living outside of this coastal-plain environment and only occasionally entering this region.

Protoceratopsians are also rare in the older sediments of the Milk River Formation of Alberta (Baszio 1997b). These specimens were recovered from a fluvial channel similar in many ways to depositional environments of the Campanian-aged Judith River Group. We postulate that these protoceratopsians were also ecologically excluded from the immediate environment and constituted a minor component of the fauna in this region.

The rarity of protoceratopsian material from the Judith River Group and the Milk River Formation in Alberta, and their rare but possible presence in Aptian through Cenomanian beds of the United States, suggests that while these dinosaurs were members of the Late Cretaceous dinosaur assemblages, their low preservation rate was a result of their reduced numbers and (or) relative isolation from sites of potential preservation. Asian protoceratopsians are common as articulated skeletons in eolian deposits, but are rare or unknown from fluvial deposits. Eolian deposits are rare to unknown in the predominately nearshore dinosaur-bearing Cretaceous strata of Alberta and Montana. During the Late Cretaceous of North America, the drier habitats that seem to have been preferred by protoceratopsians would tend to be

found in regions more distal to the Western Interior Seaway, such as that of the Scollard Formation of Alberta. These factors support the suggestions made by Sternberg (1951) and others that protoceratopsians preferred arid to semiarid environments such as those found in central Asia.

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## References

- Baszio, S. 1997a. Paleo-ecology of dinosaur assemblages throughout the Late Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, **196**: 1–31.
- Baszio, S. 1997b. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, **196**: 33–77.
- Braman, D.R., Johnston, P.A., and Haglund, W.M. 1995. Upper Cretaceous paleontology, stratigraphy and depositional environments at Dinosaur Park and Drumheller, Alberta. Field Trip Guidebook 4, Drumheller '95, 5th Canadian Paleontology Conference, 29 Sept. – 2 Oct. 1995, Royal Tyrrell Museum of Palaeontology, Drumheller, Alta.
- Brinkman, D.B. 1990. Paleogeology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **78**: 37–54.
- Brinkman, D.B., Ryan, M.J., and Eberth, D.A. 1998. The paleogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the Upper Judith River Group of western Canada. *Palaios*, **13**: 160–169.
- Brown, B. 1914. *Leptoceratops*, a new genus of Ceratopsia from the Edmonton Cretaceous of Alberta. *Bulletin of the American Museum of Natural History*, **33**: 567–580.
- Brown, B., and Schlaikjer, E.M. 1940. The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Sciences*, **40**: 133–266.
- Brown, B., and Schlaikjer, E.M. 1942. The skeleton of *Leptoceratops* with the description of a new species. *American Museum Novitates*, No. 1169, pp. 1–15.
- Chinnery, B.J., and Weishampel, D.B. 1998. *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsidae) and relationships among Asian and North American basal neoceratopsians. *Journal of Vertebrate Paleontology*, **18**: 569–585.
- Dodson, P., and Currie, P.J. 1990. Neoceratopsia. In *The Dinosauria*. Edited by D.B. Weishampel, P. Dodson, and H. Osmolska. University of California Press, Berkeley, pp. 593–618.
- Dong, Z.-M., and Azuma, Y. 1997. On a primitive neoceratopsian from the Early Cretaceous of China. In *The Sino-Japanese Silk road dinosaur expedition*. Edited by Z. Dong. China Ocean Press, Beijing, pp. 68–89.
- Dong, Z.-M., and Currie, P.J. 1993. Protoceratopsian embryos from Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2248–2254.
- Eberth, D.A. 1990. Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **78**: 1–36.
- Gilmore, C.W. 1914. A new ceratopsian dinosaur from the Upper Cretaceous of Montana, with a note on *Hypacrosaurus*. *Smithsonian Miscellaneous Collections*, **63**: 1–10.
- Gilmore, C.W. 1939. Ceratopsian dinosaurs from the Two Medicine Formation, Upper Cretaceous of Montana. *Proceedings of the United States National Museum*, **87**: 1–18.
- Granger, W., and Gregory, W.K. 1923. *Protoceratops andrewsi*, a pre-ceratopsian dinosaur from Mongolia. *American Museum Novitates*, No. 72, pp. 1–9.
- Horner, J.R. 1984. Three ecologically distinct vertebrate faunal communities from the Late Cretaceous Two Medicine Formation of Montana, with discussion of evolutionary pressures induced by interior seaway fluctuations. In *Proceedings of the 1984 Montana Geological Society Field Conference*, Northwestern Montana, Billings, Montana, pp. 299–303.
- International Commission on Zoological Nomenclature. 1985. International code of zoological nomenclature adopted by the 20th General Assembly of the International Union of Biological Sciences. General Trust for Zoological Nomenclature, London.
- Koster, E.H., Currie, P.J., Eberth, D., Brinkman, D., Johnson, P., and Braman, D. 1987. Sedimentology and palaeontology of the Upper Cretaceous Judith River/Bearpaw Formations at Dinosaur Provincial Park, Alberta. Geological Association of Canada – Mineralogical Association of Canada, Joint Annual Meeting, Saskatoon, Saskatchewan, 28–31 May 1987, Field Trip 10.
- Kurzanov, S.M. 1992. Gigantic protoceratopsid from the Upper Cretaceous of Mongolia. *Palaeontological Journal*, **1992**(3): 81–93.
- Maryanska, T., and Osmolska, H. 1975. Protoceratopsidae (Dinosauria) of Asia. *Palaeontologica Polonica*, **35**: 133–181.
- McKenna, M.L., and Love, J.D. 1970. Local stratigraphic and tectonic significance of *Leptoceratops*, a Cretaceous dinosaur in the Pinyon Conglomerate, Northwestern Wyoming. United States Geological Survey, Professional Paper 700D, pp. 55–61.
- Ostrom, J.H. 1978. *Leptoceratops gracilis* from the "Lance" Formation of Wyoming. *Journal of Palaeontology*, **52**: 697–704.
- Peng, J.-H. 1997. Palaeogeology of vertebrate assemblages from the Upper Cretaceous Judith River Group (Campanian) of south-eastern Alberta, Canada. Ph.D. thesis, University of Calgary, Calgary.
- Rich, T.H., and Vickers-Rich, P. 1994. Neoceratopsians and Ornithomimosaurs: Dinosaurs of Gondwana origin? *National Geographic Society Research and Exploration*, **10**: 129–131.
- Ryan, M.J. 1992. The taphonomy of a *Centrosaurus* (Reptilia: Ornithischia) bone bed (Campanian), Dinosaur Provincial Park, Alberta, Canada. M.Sc. thesis, University of Calgary, Calgary.
- Seren, P.C. 1986. The phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Society Research and Exploration*, **2**: 234–256.
- Sternberg, C.M. 1951. Complete skeleton of *Leptoceratops gracilis* Brown from the Upper Edmonton Member on the Red Deer River, Alberta. *National Museum of Canada Bulletin*, **123**: 225–255.
- Weishampel, D.A., McCrady, A., and Akersten, W.A. 1990. New ornithischian dinosaur material from the Wayan Formation (Lower Cretaceous) of Eastern Idaho. *Journal of Vertebrate Palaeontology*, **10**(3): 48.