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DESCRIPTION OF *PRENOCERATOPS PIEGANENSIS* GEN. ET SP. NOV. (DINOSAURIA: NEOCERATOPSIA) FROM THE TWO MEDICINE FORMATION OF MONTANA

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ABSTRACT—A new basal neoceratopsian genus and species, *Prenoceratops pieganensis*, is described from the Two Medicine Formation of Montana. This material represents the only bone-bed deposition of a basal neoceratopsian currently known, and in addition is almost entirely disarticulated allowing for a more thorough understanding of basal neoceratopsian cranial morphology. The new taxon is characterized by a lower, more sloping head than in *Leptoceratops*, with a nasal that is pinched caudally, a wide, triangular jugal, extremely gracile surangular, and reduced articular among other autapomorphies. A preliminary cladistic analysis unites *Prenoceratops* firmly with the other North American basal neoceratopsians (and one Asian taxon) in the clade Leptoceratopsidae.

INTRODUCTION

Barnum Brown discovered the basal neoceratopsian *Leptoceratops gracilis* in 1910 (Brown, 1914). The type material is from the Edmonton Group, Scollard Formation of Alberta, Canada, and consists of two fragmentary skeletons. At the time, *Leptoceratops* was unlike all other known ceratopsians as it possessed a deep, rounded dentary and lacked even an incipient nasal horn core. In size and some skeletal features it resembled *Protoceratops*, found in Mongolia a decade later, and thus the foundation was laid for understanding the ancestry of the larger ceratopsids.

The most complete specimens of *Leptoceratops gracilis* are the paratypes described by Sternberg (1951), consisting of three well-preserved skeletons and two intact skulls. The skull of one specimen (NMC 8889) is crushed dorsoventrally, while the other skull (NMC 8887) is flattened mediolaterally. Together these specimens permit a nearly complete description of the skull of this genus and species, lacking only internal views of the elements and sutural contacts.

The only other basal neoceratopsian described from North America to date is *Montanoceratops*, discovered in 1916 by Barnum Brown and initially described as *Leptoceratops cerorhynchus* (Brown and Schlaikjer, 1942; Sternberg, 1951; Chinnery and Weishampel, 1998). Other material, including partial skeletons, individual specimens, and isolated teeth, have been variously designated as *Leptoceratops* sp. (Gilmore, 1939; Ryan and Currie, 1998) or basal neoceratopsian indet. (Weishampel et al., 1993; Chinnery et al., 1998), indicating the problems with identification of often similar basal neoceratopsian material.

A recent find of new basal neoceratopsian material in the Two Medicine Formation of Montana provides the first evidence of bone bed deposition of a basal neoceratopsian and indicates the presence of a new taxon—*Prenoceratops pieganensis*. The material was discovered in a monospecific bonebed on privately deeded land on the Blackfeet Indian Reservation, an area from which a surprising variety of neoceratopsian material has been described (Dodson, 1996). The area is predominantly composed of the Two Medicine Formation, which extended in time for approximately 8.6 million years (Rodgers et al., 1993) before being overlain by the marine Bearpaw Shale Formation.

The *Prenoceratops pieganensis* bone-bed includes representatives of nearly every element in the skull and postcranial skeleton, found together but not associated into distinct skeletons. Many elements can be fit together (i.e., vertebrae, metatarsals), but aside from partial skull and limb associations, the elements cannot be combined to form even one complete skeleton. A minimum of four individuals is represented, in varying stages of development. All are immature, based on the lack of fusion of the elements and on bone texture (Sampson et al., 1997). Due to length constraints, the present description only includes skull material. A full description of the postcrania will be completed subsequently.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **MOR**, Museum of the Rockies, Montana; **NMC**, Canadian Museum of Nature, Ottawa, Ontario; **MNHCM**, Mokpo Natural History and Culture Museum, Korea; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; **TCM**, Childrens Museum of Indianapolis, Indiana; **USNM**, United States National Museum; **YPM**, Yale Peabody Museum, Connecticut.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
CERATOPSIA Marsh, 1888
NEOCERATOPSIA Sereno, 1986
PRENOCERATOPS PIEGANENSIS, gen. et sp. nov.

Generic Etymology—Preno (= sloping, Greek) + ceratops (= horn-face, Greek). The generic name refers to the collection of facial features that distinguish this genus and provide it with a long, low head shape.

Specific Etymology—The species name *pieganensis* honors the Piegan tribe of the Blackfeet Indian Nation that resides in Montana, where the specimens were discovered (also known as Piikani).

Diagnosis—Basal neoceratopsian with: caudally oriented external naris; maxillary projection instead of maxillary shelf; rostral position of pterygoid-maxilla contact; constricted caudal portion of the nasal; deep and sharp frontal depression demarcated by straight, transverse border; postorbital bar narrow in dorsal view (at the contact between the frontal and postorbital) and tall in lateral view; wide, triangular jugal; rostral curvature of the ventral tip of the jugal; quadratojugal tall and compressed both mediolaterally and rostrocaudally; very gracile surangular; reduced articular and corresponding inequality of quadrate condyles; entirely convex dorsal border of the articular; and reduced caudal expansion of the coronoid.

Holotype Specimen—Surangular fused with articular, TCM 2003.1.1. The disarticulated nature of the bone-bed material limits the holotype specimen to one skeletal element or complex.

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The surangular and articular elements chosen as the holotype are uncharacteristically fused together, thus allowing the holotype to consist of two diagnostic elements instead of one. These two elements display several of the autapomorphies of this new taxon.

Referred Specimens—Disassociated partial skeletons of at least four individuals found together in a bone-bed deposition, catalogued as MNHCM (unnumbered) and TCM 2001.96.4.

Horizon and Locality—The bone-bed is located approximately 50 meters below the Bearpaw/Two Medicine contact in the Two Medicine Formation. The site is in Pondera County, on privately owned and deeded land of the Blackfeet Reservation. The specimens were privately collected and sold to Canada Fossils, Inc., a commercial company in Calgary, Canada. Canada Fossils kindly allowed for the study of the specimens before building two composite skeletons of the material and selling them to the Mokpo Natural History and Culture Museum, Mokpo, Korea, and the Childrens Museum of Indianapolis, Indiana.

DESCRIPTION OF *PRENOCERATOPS PIEGANENSIS*

Braincase and Basicranium

The only preserved portions of the *Prenoceratops pieganensis* braincase are the basioccipital and the basisphenoid, and the only identifiable palate element preserved is the pterygoid.

Basioccipital—As in other ceratopsians, the occipital condyle is composed of the basioccipital and exoccipitals, the former contributing approximately two thirds of the condyle as in *Protoceratops* and *Montanoceratops* (Chinnery and Weishampel, 1998). The preserved portion of the occipital condyle is subrounded, and exhibits distinct sutural contacts for the exoccipital. The basioccipital tubera form a shelf extending caudoventrally from the neck of the condyle. The position of these tubera are similar in all three North American basal neoceratopsian taxa, but differ from the more vertical position found in other ceratopsians (Makovicky, 2001). As discussed by Makovicky (2001), well-defined grooves wrap around the occiput on the caudal surface of the basioccipital tubera.

The basioccipital of *Prenoceratops* differs from that of *Leptoceratops gracilis* in having one central ridge located directly under the occiput and dividing the tuberal grooves located on the caudal surface (Makovicky, 2001). Sutures are apparent on the rostral side of the shelf for contact with the basisphenoid. In *Prenoceratops* this shelf, composed of contributions from the basioccipital and the basisphenoid, is robust in comparison with that of *Montanoceratops* (Chinnery and Weishampel, 1998) and *Protoceratops* (Brown and Schlaikjer, 1940).

Basisphenoid—The basisphenoid of *Prenoceratops* is similar in shape to those of the other basal neoceratopsians (Brown and Schlaikjer, 1940; Maryańska and Osmólska, 1975; Chinnery and Weishampel, 1998). The internal carotid groove is similar in length to those of *Leptoceratops* and *Montanoceratops* (Makovicky, 2001). In all North American basal neoceratopsians, this groove is located on the lateral surface of the basisphenoid, and is encompassed entirely within this element, contrary to Chinnery and Weishampel (1998). The caudal portion of the basisphenoid forms the ventral half of the basioccipital tubera, indicated by clearly visible sutural contacts on the caudal surface of the basisphenoid and the rostral surface of the basioccipital. Caudally curved basipterygoid processes are separated from the caudal portion of the basisphenoid by deep notches, a condition only found in the North American basal neoceratopsians.

Pterygoid—Two incomplete pterygoids are included with the *Prenoceratops* material. The preserved portions appear similar to those of *Leptoceratops*, but differences in sutural contacts on corresponding elements may indicate differences in palative and quadrate wing lengths. For example, the pterygoid sutural contact on the maxilla is more rostral in position than in *Leptoceratops*.

Facial Elements

Rostral—No rostral elements were recovered with the *Prenoceratops pieganensis* material.

Premaxilla—The four left premaxillae indicate the minimum number of individuals contained in the *Prenoceratops* bone-bed. Two fragmentary right premaxillae are also known. In combination these elements allow for a nearly complete description of the premaxilla, apart from the extremely thin caudodorsal border, which is not completely preserved on any of the six specimens. Measurements of these and other facial elements are listed in Table 1.

The premaxilla extends back from a blunt, rounded rostral end that would be enclosed by the rostral bone in life (Fig. 1A, B). One projection extends upward, forming part of the rostral border of the external naris, and contacts the nasal dorsally. The majority of the element fans out caudally and dorsally behind the naris to the contact with the maxilla, forming the caudal border of the external naris and contacting the nasal dorsally. The element is fairly narrow mediolaterally, although this width varies among the four well preserved premaxillae. This variation is due to a combination of deformation and either individual or ontogenetic variation. The articular surface for the nasal is clearly seen in lateral view, and that element overlaps the premaxilla laterally for at least 20 mm. Although the premaxillae are not complete, the nasal is estimated to form the lateral aspect of the upper two thirds of the rostral border of the external naris.

In ventral view, the ventral border of the element is sigmoidal in shape, curving laterally from the rostral end and then medially towards the caudal end of the contact with the rostral bone. It then flares laterally again briefly and ends medially, directly in line with the rostral end. The ventral border thickens near the middle, at which point a longitudinal groove extends for 8–10 mm and is surrounded by a rugose area. The caudal portion of the rostral contacts the premaxilla in this area. The tongue-in-groove sutural pattern is common to *Prenoceratops* cranial elements, as will be discussed throughout this description.

From a medial view, a ridge curves down and then back horizontally from the rostral border of the external naris, outlining the internal naris and forming the contact for the opposing premaxilla rostrally and the maxilla caudally (Fig. 1B). Again, the characteristic tongue-in-groove pattern is apparent. Contact with the opposing premaxilla is limited to a small, angular articulation at the rostral end of the element. A space is formed caudal to this contact in which sit the rostral projections of the two maxillae. Together these elements form the roof of the rostral portion of the mouth. This is in contrast to the condition depicted in *Leptoceratops gracilis*, in which the premaxillae appear to have more extensive contact with each other (Sternberg, 1951:plate L). The maxillary projections are clearly seen on specimen NMC 8889, however.

The caudal border of the premaxilla of *Prenoceratops* extends further back than in *Leptoceratops gracilis*, even in a specimen very close in size to that of NMC 8887. The caudal portion of the element is shaped differently in the new taxon, as the contact with the maxilla is a straight, vertical line rather than the curved condition seen in *Leptoceratops gracilis* (Sternberg, 1951:plate XLIX). The contribution to the rostral border of the external naris is more highly curved in a caudal direction on all preserved premaxillae of *Prenoceratops*, suggesting a possible lower rostral end of the face of the new genus (Fig. 1A, B). The external naris of *Protoceratops* differs in shape depending on age (size—Brown and Schlaikjer, 1940:fig. 4), so the difference noted above may be due partly to immaturity. A strong, convex spur extends down in

TABLE 1. Measurements of *Prenoceratops pieganensis* skull elements (in mm). Those measurements followed by + are of nearly complete elements or portions of elements, and those followed by ++ are of incomplete elements.

Occipital condyle	Mediolateral width	16.2
Nasal	Length	117.4+
	Thickness at midline suture	5.4
	Width at frontal contact	13.6
	Length of suture betw. premax. and frontal contacts	69.9
Premaxilla	Length	79.1
	Height	70.5+
Maxilla	Maximum length	144.9
	Length—premax. contact caudally	113.9
	Length—tooth row	80.1
	Height—rostral end of tooth row to nasal contact	74.8+
	Height—tooth row to lat. projection	48
	Height— tooth row to antorbital fossa	45.3
	Width—mediolateral, including lateral projection	36.6
Lacrimal	Length	50.3++
	Height	57.9++
Prefrontal	Length	50.6+
	Height	33.9++
Frontal	Length	84.1+
	Skull width at posterior orbit	70.9
	Maximum thickness	16.4
Postorbital	Length—dorsal surface	69.3
	Height— at orbit rim	64.2
	Maximum width	13.3
	Width—at ½ length postorbital bar	9.4
Squamosal	Length	68.9+
	Height	71.2+
Jugal	Length—dorsal	83.3++
	Maximum height	127.9
	Height—orbit rim caudally	107.1
	Maximum mediolateral width	14.3
Quadrate	Height	136.3
	Length condyles	30.5
	Width condyles	13.1
Quadratojugal	Length	31.7
	Height	74.8+
Dentary	Length—rostral end to coronoid process	137.1
	Height—ventral predentary contact to lateral shelf	60.8
	Maximum height with tooth row horizontal	115.9
	Length of predentary contact	88.2
	Width of predentary notch	3.2
	Shelf width at first tooth position	9.3
	Shelf width at rostral coronoid process	23.3
	Maximum width across coronoid process	42.4
Surangular	Length	77.9
	Height—rostral end	45.3+
	Height—caudal end	20.8
	Mediolateral width—rostral end	6.2
	Maximum mediolateral width of articular area	16.4
Articular	Length	35
	Width	11.6
Coronoid	Length	32.6
	Height	34.8++
Predentary	Length	117.7++
	Maximum height	45.2
	Length of cutting edge	69.9+
	Maximum thickness	16.9

front of the tooth row in *Leptoceratops*, while the corresponding one in *Prenoceratops* is very weak. In lateral view the ventral border of the premaxilla is concave in *Prenoceratops* (as in *Protoceratops*), rather than straight as in *Bagaceratops* and convex as in *Leptoceratops* (Maryańska and Osmólska, 1975).

Maxilla—Four partial right, and one left, maxillae are included with the bone-bed material. One is about 90% complete; the others are less so. All have partial tooth rows, but few teeth are preserved, and none of the maxillae are complete dorsally at the contacts with the nasal and lacrimal.

In lateral view, the *Prenoceratops* maxilla is proportionately shorter on average than those in the paratypes of *Leptoceratops gracilis* (Fig. 1C; Sternberg, 1951:plates XLVII, XLIX). This is due to the lower position of the jugal process in *Prenoceratops*. The projection to the jugal corresponds to the wider, more triangular shape of the latter element.

The antorbital fossa of *Prenoceratops* is positioned further dorsally and caudally than in *Leptoceratops*, and is more horizontal in orientation (Fig. 1C, D). Consequently, the fossa has a more ovoid shape, is shallow, and has two distinct corners as in *Montanoceratops*, unlike the vertical oval shape of the fossa in *Leptoceratops gracilis* (Sternberg, 1951:plate XLIX).

As mentioned above, the rostral border of the *Prenoceratops* maxilla does not extend as far rostrally as in *Leptoceratops gracilis*, except at the ventral end. The sutural contact between the two elements is relatively vertical from the ventral contact with the premaxilla as in *Protoceratops* and *Bagaceratops* (Brown and Schlaikjer, 1940; Maryańska and Osmólska, 1975), and the large rostral wing of bone seen in the *Leptoceratops gracilis* maxilla is not present (Sternberg, 1951:plate XLIX). The extent of the ascending wing located rostral to the antorbital fossa as well as the sutural contact between the maxilla and the nasal are unknown.

The "maxillary ridge" of Sternberg (1951) is the buccal shelf located lateral to the tooth row and extends caudally to contact the jugal in *Leptoceratops gracilis*. In *Prenoceratops* this ridge is more accurately described as a projection that begins flaring laterally from half way along the tooth row and narrowing quickly to the contact with the jugal, as seen in ventral view (Fig. 1D). In consequence, the tooth row is not as inset, in ventral view, as in other basal neoceratopsians. As the projection narrows rostrocaudally it flares dorsoventrally and caudally to buttress the interior ventral portion of the jugal. The flared part of the projection forms a brace that sits securely in a triangular notch on the inner surface of the jugal, made deep by the formation of a thick ridge on that element. Rostrally, the lateral projection is continuous with a more rostral wing of the maxilla that extends caudodorsally almost to the brace and forms the caudal border of the antorbital fossa. This wing is not complete above the contact with the jugal on the new material.

As in other basal neoceratopsians, a projection of the maxilla of *Prenoceratops* extends rostrally internal to the premaxilla, ending just rostral to the caudal border of the rostral bone. In *Leptoceratops gracilis* (Sternberg, 1951:plate L) this area appears to be composed entirely of the premaxillae, but the projections can clearly be seen on the specimen. In *Protoceratops* this rostral projection ends at the level of the first premaxillary tooth (Brown and Schlaikjer, 1940). In *Prenoceratops* (and *Leptoceratops*) which lacks premaxillary teeth, this area of the ventral premaxilla articulates with the rostral bone, as confirmed by the sutural contacts seen on the ventral border of the *Prenoceratops* premaxillae. Thus the rostral extends further caudally in the later genera than in *Protoceratops*, and the rostral projections of the maxilla are longer.

The foramina on the medial surface of the maxillae are oriented in a horizontal row as in all ceratopsians, but are not situated at the base of the tooth series as is usual—instead they are much closer to the active tooth row. This can be seen clearly on three of the *Prenoceratops* maxillae and one *Montanoceratops*

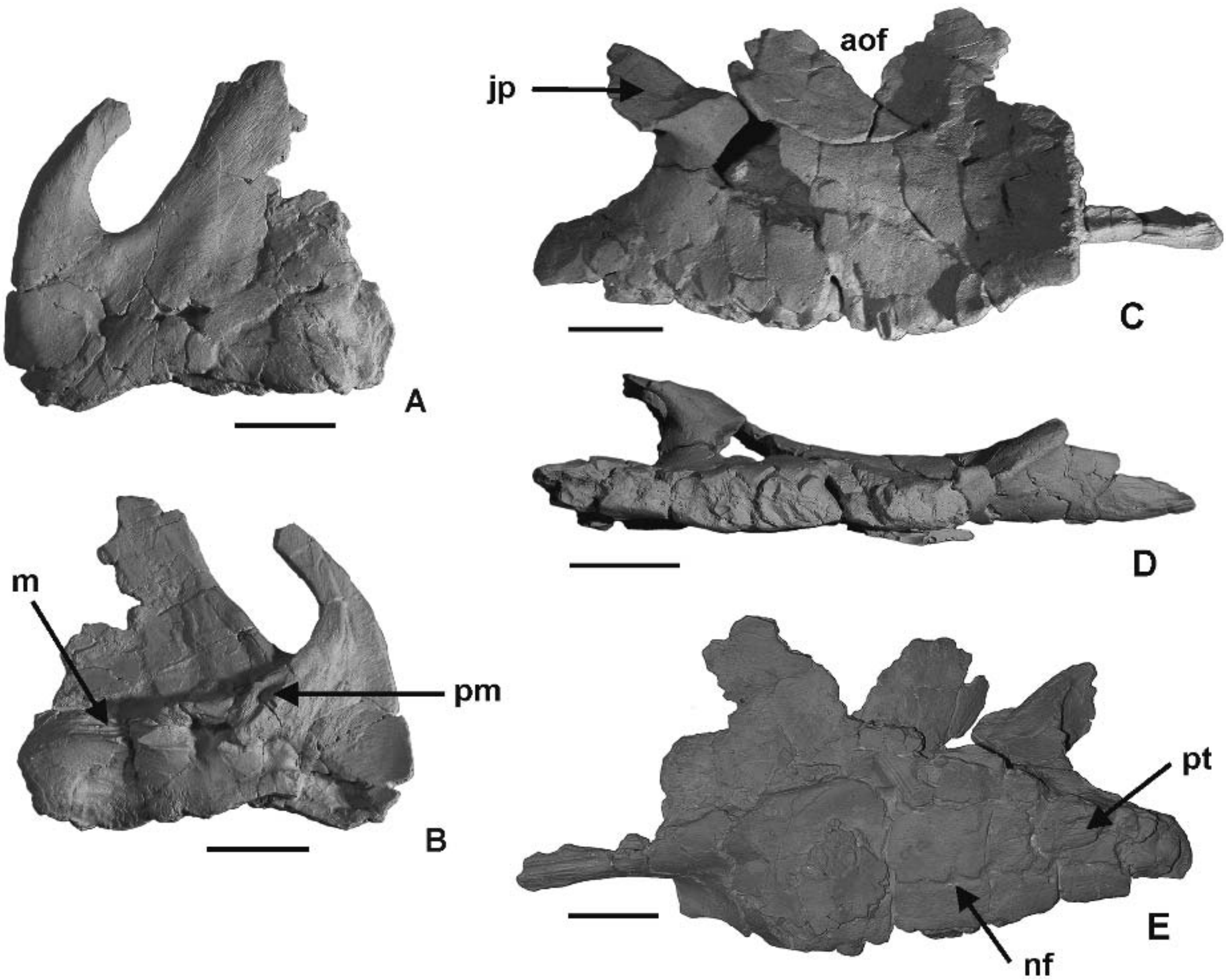

FIGURE 1. *Prenoceratops pieganensis* premaxilla and maxilla, MNHCM (no number). Lateral (**A**) and medial (**B**) views of left premaxilla, and lateral (**C**), ventral (**D**), and medial (**E**) views of right maxilla. Scale bar equals 2 cm. **Abbreviations**: **m**, maxilla articulation; **pm**, premaxilla articulation; **jp**, jugal process; **af**, antorbital fenestra; **nf**, nutrient foramina; **pt**, pterygoid articulation.

maxilla (MOR 542), as the inner surface of the maxilla is broken and well-formed teeth are located partly or mostly above the foramina. Brown and Schlaikjer (1940) describe similar foramina in *Protoceratops* maxillae as a product of bone resorption and possibly nerve and blood vessel transmission. Edmund (1957) refutes this hypothesis and defends an earlier idea that the foramina were for transmission of germinal dental material into the base of the tooth battery (Loomis, 1900; Hatcher et al., 1907). This latter theory is not upheld by the current observation of the position of the foramina, and recent anatomical studies of extant archosaurs clearly indicate that the foramina relay vascular bundles to the alveoli (J. Sedlmayr, pers. comm.). In addition, in a growth series of *Protoceratops* skulls the foramina change position through growth (P. Makovicky, pers. comm.).

Striated areas marking the contact with the pterygoids are located on the inner surface of the *Prenoceratops* maxillae, opposite to the buccal brace for the jugal. The pterygoid articulation extends further rostrally than in *Leptoceratops* and *Protoceratops*, in which the contact occurs only at the very caudal end of the tooth row.

The tooth rows are all incomplete, but the number of alveoli is approximately 12 on the most complete specimen (MNHCM unnumbered). Convex ventral curvature of the tooth row in lateral view has been proposed by some authors as a synapomorphy shared by *Leptoceratops* and *Udanoceratops* (Chinnery and Weishampel, 1998; Makovicky, 2001), and is definitely lacking in *Prenoceratops*, which exhibits a straight maxillary tooth row (Fig. 1C, D).

Nasal—One nearly complete right and two fragmentary left nasals are preserved. No North American basal neoceratopsian nasal is currently known to include even an incipient horn core (Brown, 1914; Gilmore, 1939; Sternberg, 1951), but all have a rugose area where the nasal horn of other neoceratopsians is located.

The nasal of *Prenoceratops* is unique, with a highly constricted caudal end and a nearly straight lateral aspect (Fig. 2A, B). It more closely resembles the nasal of *Leptoceratops* sp. described by Gilmore (1939) than that of the *Leptoceratops gracilis* holotype, as the former exhibits a continuous ventral curve throughout its length and is more constricted caudally than the condition in *Leptoceratops gracilis*. The *Prenoceratops* nasal is long and narrow, the element flattening slightly in the middle portion of the sutural contact with the opposing nasal. Most of the sutural contact with the premaxilla is preserved rostral to the external naris, and the articular surfaces for the frontal and prefrontal are complete. The rostral end of the *Prenoceratops* nasal tapers to a blunt point which contacts the premaxilla, overlapping it to contribute about 60% of the rostral border of the naris. The nasal overlaps the frontal over a distance of one centimeter, with the two elements forming a very straight dorsal aspect of the skull as

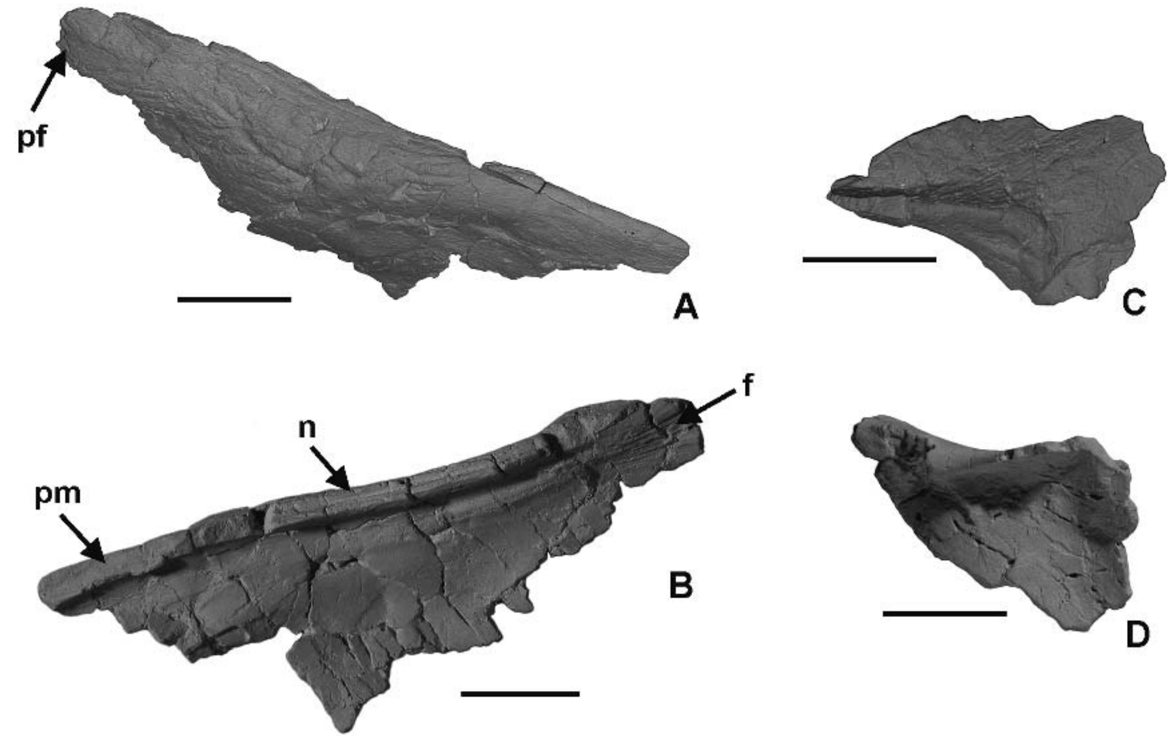

FIGURE 2. Nasal and prefrontal of *Prenoceratops pieganensis* MNHCM (no number); right nasal in dorsolateral (**A**) and medial (**B**) views, and right prefrontal in dorsal (**C**) and ventral (**D**) views. Scale bar equals 2 cm. **Abbreviations**: **n**, articulation for opposing nasal; **pm**, premaxilla articulation; **f**, frontal articulation; **pf**, prefrontal articulation.

in *Leptoceratops gracilis*. Interestingly, the prefrontal lies external to both elements. A very small crest or ridge (one centimeter long) is present about one centimeter from the caudal end of the nasal. The internal aspect of the *Prenoceratops* nasal is smooth, with the nasal vestibule indicated by a groove five millimeters in width running the length of the element and veering slightly from the midline where the element flattens slightly (Fig. 2B).

The *Prenoceratops* nasal is markedly different from that of *Leptoceratops* in having a constricted caudal end that is in line with the rostral end, with hardly any flattening of the element in dorsal view. The type material of *Leptoceratops gracilis* has a slight upturned ridge on the midline similar to the one described for *Prenoceratops*, but it is located further rostrally, about one fifth of the total length from the caudal end. At this point the bone flattens out laterally and rostrocaudally to the point of being slightly concave in all directions and creating a widened area of the skull roof rostral to the orbits (Brown, 1914:fig. 1; Sternberg, 1951:plate XLVIII). The compressed caudal end of the *Prenoceratops* nasal indicates that the genus had a narrower preorbital skull roof. This may be partially due to the immaturity of the specimens, as a widening of the preorbital and orbital skull roof is apparent during growth in *Bagaceratops* (but not in *Protoceratops*—see Discussion). The overall shape of the *Prenoceratops* nasal more closely resembles that of Gilmore's *Leptoceratops* sp. (1939; USNM 13864) except that the latter does not exhibit the midline ridge (although a similar ridge does exist on the *Leptoceratops* sp. frontal; Gilmore, 1939).

Although lateral flaring of the *Prenoceratops* nasal is not evident, a slight rostrocaudal concavity on this material appears similar to that of the *Leptoceratops gracilis* type material, which in effect produces a slight bump in the rostral portion of the nasal as seen in lateral view. The bone surface here is more highly rugose and vascularized. The slight rostrocaudal concavity of the nasal in *Prenoceratops* and *Leptoceratops* is distinguished from the condition seen in *Leptoceratops* sp., which has a nasal that is straight at the midline in lateral view and rugose throughout its length (Gilmore, 1939).

Lacrimal—The one preserved lacrimal is triangular, with the dorsal and orbital borders converging at the apex. Ventrally, the border of the antorbital fossa is distinct, but the thin interior wall of the fossa is not preserved. Articular surfaces for the maxilla and jugal are also incomplete. The orbit rim is straight, differing from the curved rostral orbit rim of *Leptoceratops*.

The orbits of *Prenoceratops* are estimated to be between 60 and 65 mm in length, compared to 80 mm in *Leptoceratops gracilis* (NMC 8889). The rostral border of the *Prenoceratops* orbit is composed of the lacrimal and prefrontal, and is straight up to the sharp top corner on the prefrontal. Two-thirds of the dorsal border are composed of prefrontal and the rest frontal. The postorbital makes up the entire caudal border of the orbit, and is fairly straight as it extends down to the jugal. Finally, the ventral border is formed by the jugal, again a straight border angled rostroventrally.

Only a small amount (25 mm) of the lacrimal contributes to the orbit rim—the dorsal part overlaps the prefrontal, and the jugal articulates with a small groove on the lower part of the element. A thin, medially projecting flange begins about one quarter of the distance down from the dorsal border and gradually extends inward to enclose the top of the maxillary sinus (Witmer, 1997). The rostral surface of this flange forms the wide caudal wall of the antorbital fossa. The rostrodorsal border of the ovoid antorbital fossa is weak on both the lacrimal and the maxilla, while the caudoventral border is wide.

The lacrimal extends further rostrally in *Prenoceratops* than it does in *Leptoceratops gracilis*, and is also angled more rostrally and narrower than in the latter.

Prefrontal—One right prefrontal is preserved with the bonebed material. It is complete except for the tips of the articulations for the frontal and lacrimal, and part of the ventral projection between the nasal and the lacrimal. The prefrontal of *Prenoceratops* is triangular with a pinched caudal contact with the frontal (Fig. 2C). It forms over one half of the dorsal orbit border, the external edge of which extends rostrally in a straight line before curving down at a ninety-degree angle to form a portion of the rostral orbit border. From this sharp outer orbit border the element curves more gently inward, so that from a ventral view the prefrontal and the frontal form a slightly convex and curved orbit roof. From a dorsal view the element flares medially and rostrally from the outer orbit rim to overlap a rostral tongue of the frontal and the caudal aspect of the nasal. The top of the lacrimal contact is preserved, indicating that the lacrimal overlaps the prefrontal.

Ventrally, the tongue of the frontal is buttressed against a sagittal flange on the internal surface of the prefrontal (Fig. 2D). Rostral to the articular area for the frontal the prefrontal is smooth and slightly concave behind the orbit rim.

Frontal—Included with the *Prenoceratops* bone-bed material are two nearly complete frontals, one left and one right, and two partial left frontals. The frontal narrows rostrally, but the element extends internally quite a bit further than is evident from the exposed dorsal portion. It is widest at the lateral contact with the postorbital, caudal to which the frontal extends ventrally to form the rostral border of the supratemporal fossa before contacting the parietal (Fig. 3A). When opposing frontals are in contact, the skull roof between the orbits is slightly concave as in *Leptoceratops*. The contact with the postorbital is a truncated oval facing laterally, the postorbital overlapping the frontal only slightly on the ventral half of the articular surface. In ventral view, the sutural contacts for the ethmoid and laterosphenoid outline the roof of the olfactory tract (Fig. 3C; Gilmore, 1939; Forster, 1990). The median suture on the *Prenoceratops* frontal is again of the tongue-in-groove variety, and is asymmetrical in nature (Fig. 3B). The three left frontals all exhibit a projection that fits into the opposing right element, and the one right frontal contains the requisite notch for this projection. Other midline tongue-in-groove sutural contacts exhibit similar asymmetry, possibly directional in nature, including those of the nasal and the premaxilla.

The frontals of the new specimens differ from those of *Leptoceratops* in several respects. The most notable difference, found in all *Prenoceratops* frontals, is the presence of a marked caudal transverse depression, as deep as that seen in some large *Protoceratops* skulls, with a distinct ridge separating it from the rest of the element (Fig. 3A). This depression is found in older specimens of *Protoceratops*, but only in the oldest does it extend up to one third of the dorsal length of the frontal (Brown and Schlaikjer, 1940). In *Prenoceratops* it extends beyond 37% of the length as measured on an incomplete specimen. The weak ridge that demarkates the depression in *Leptoceratops gracilis* angles back toward the supratemporal fenestra as in *Protoceratops*, unlike the transversely-oriented ridge in *Prenoceratops*.

The frontal of *Prenoceratops* is comparatively narrower than that of *Leptoceratops*, and grades in a relatively straight line from the orbit rim contribution to the rostral end of the bone. Another difference between the frontal of the new taxon and that of *Leptoceratops* is the lack of a midline ridge on the former. The contact with the postorbital is narrower on the *Prenoceratops* frontal than in *Leptoceratops*, and this together with the shape of the postorbital indicates a narrower postorbital bar (from a dorsal view) in *Prenoceratops*.

Postorbital—The *Prenoceratops* postorbital is another relatively flat, triangular element. One partial and two almost complete left postorbitals are included in the bone-bed material, along with two almost complete right elements. The rostral border of the *Prenoceratops* postorbital curves convexly, forming the caudal orbit rim, with the dorsal and ventral corners located more medially than the middle of the orbit rim (Fig. 4A). The ventral corner is narrow where it contacts the jugal, with a tongue on the internal surface that fits into a corresponding groove in the outer surface of the jugal (Fig. 4B). Fully one half of the vertical extent of the postorbital is underlain by a dorsal projection of the jugal, shown by the indentation of the inner surface of the postorbital. The element is more massive dorsally, where a thickening of the bone accentuates the caudodorsal corner of the orbit. Only the lateral border of the supratemporal fenestra is formed by the postorbital, as in *Leptoceratops*. The internal surface of the postorbital is smooth, with deep articular sockets opposite the thickened area (Fig. 4B). The more ventral socket, for articulation with the laterosphenoid, is crescent-shaped and sits parallel to the orbit rim. Several grooves span the

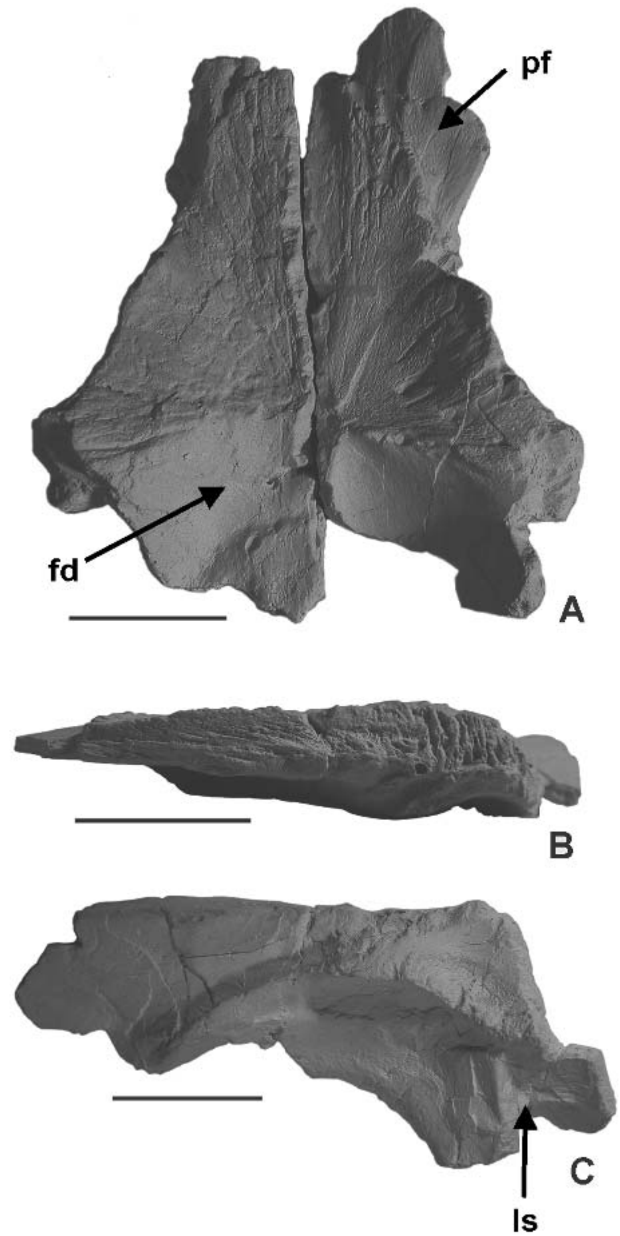

FIGURE 3. *Prenoceratops pieganensis* frontals (MNHCM [no number]) in dorsal view (**A**, both sides), medial view of the sutural contact (**B**, right side), and ventral view (**C**, right side). Scale bar equals 2 cm. **Abbreviations**: **fd**, frontal depression; **pf**, prefrontal articulation; **ls**, laterosphenoid articulation.

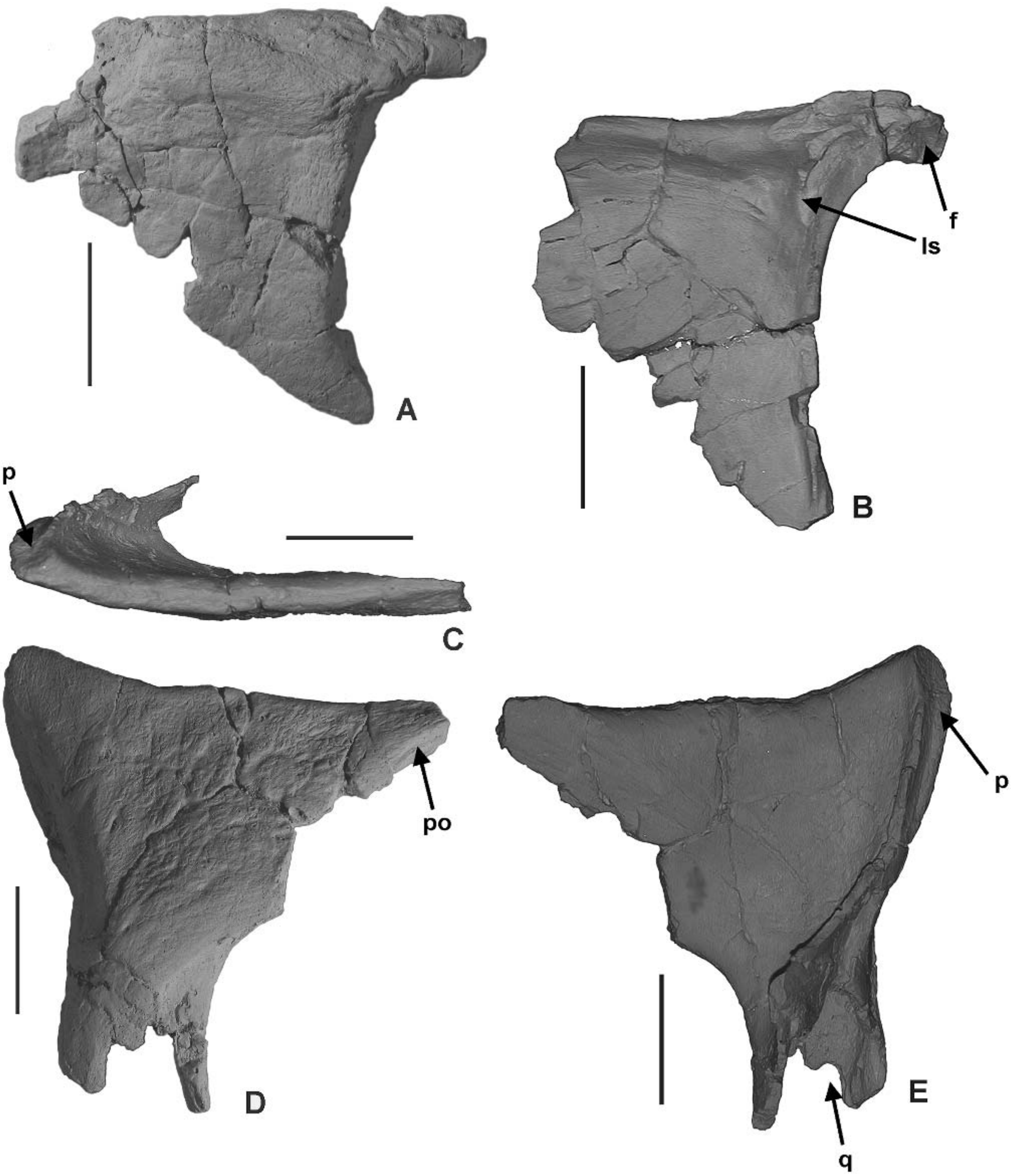

FIGURE 4. *Prenoceratops pieganensis* right postorbital, MNHCM (no number) in lateral (**A**) and medial (**B**) views, and right surangular, MNHCM (no number) in dorsal (**C**), lateral (**D**) and medial (**E**) views. Scale bar equals 2 cm. **Abbreviations**: **p**, parietal suture; **po**, postorbital articulation; **ls**, laterosphenoid articulation; **f**, frontal suture; **q**, quadrate articulation.

inner surface for articulation with the parietal. Only a portion of the articulation with the squamosal is preserved, but a smooth surface indented from the outer, exposed bone surface indicates that the squamosal overlaps the postorbital fairly extensively (also shown by the inner surface of the squamosal). This is in contrast to the condition in *Protoceratops*, in which the postorbital fits into a deep notch on the rostral border of the squamosal (Brown and Schlaikjer, 1940).

The postorbital of *Prenoceratops* differs from that of *Leptoceratops gracilis* in its dimensions: the *Leptoceratops gracilis* postorbital is 2.5 times more massive (mediolateral width of the element in dorsal view adjacent to the orbit corner is 13.3 mm in *Prenoceratops* and 35.5 mm in *Leptoceratops gracilis*). The *Leptoceratops gracilis* postorbital is larger in all other dimensions, but only by approximately 20%. In addition, the *Prenoceratops* frontal-postorbital contact is relatively narrower than in *Leptoceratops*, *Bagaceratops*, or *Protoceratops*. The rostral portion of the postorbital bar of the new taxon is therefore much narrower than in these other basal neoceratopsians. The articular groove for the laterosphenoid is much larger in *Leptoceratops*, and is of a more horizontal oval shape. The frontal suture in *Prenoceratops* is lateral, directly in line with the lateral border of the fenestra and sagittally positioned as in *Bagaceratops*, in contrast to the more angled contact seen in *Leptoceratops gracilis*.

As discussed previously, the overlapping contact between the postorbital and the jugal along the caudal orbit border is relatively very extensive in *Prenoceratops.* Description of the postorbital is lacking for *Leptoceratops gracilis* (Sternberg, 1951). The contact differs in *Montanoceratops* from that of *Leptoceratops* in the position of the contact for the laterosphenoid (Makovicky, pers. comm.) This articulation is described only as "blunt" in *Protoceratops* (Brown and Schlaikjer, 1940) and the postorbital is described as "covering the jugal . . ." in *Bagaceratops* (Maryańska and Osmólska, 1975) but the extent is not discussed. However, the *Leptoceratops gracilis* paratypes do not exhibit the long ventral corner of the postorbital, but instead show a more horizontal contact between the jugal and the postorbital, suggesting less of an overlap in this genus (Sternberg, 1951:plates XLVII, XLIX).

It is not possible to determine if the *Prenoceratops* postorbital reached the dorsal border of the infratemporal fenestra as in *Leptoceratops* (contrary to Sternberg, 1951; Makovicky, 2001), as the caudoventral edge is not preserved.

Squamosal—Two *Prenoceratops* squamosals are preserved, one right and one left. The element is triangular, extremely narrow except for the ventral contact with the quadrate (Fig. 4C, D, E). This ventral contact is a deep sulcus in which the head of the quadrate sits. The external surface of the squamosal is rugose. Rostrally, the squamosal splits into upper and lower portions, although the lower portion is not preserved in the bone-bed material. The upper portion overlaps the postorbital and sits in a shallow groove on that element. Consequently, on the inner surface of the squamosal the facet for the postorbital is evident as a flattened area with faint horizontal ridges. In dorsal view, the dorsal border extends directly caudally and then curves medially just before the contact for the parietal (Fig. 4C). The sutural contact for the parietal is nearly vertical, indicating that the parietal extended steeply in a rostral direction. This contact faces caudomedially at an angle of 30 degrees, suggesting that the parietal extended only slightly further caudally than the caudal extent of the squamosal, similar to the condition in *Leptoceratops*.

The squamosal of *Prenoceratops* is overall a much more gracile and flatter element than that of *Leptoceratops*, with a straight dorsal margin and a caudal corner that does not extend medially as in *Leptoceratops* (as seen from dorsal view), but is truncated as in *Bagaceratops* and *Protoceratops* (Maryańska and Osmólska, 1975). The largest difference between the *Prenoceratops* squamosal and that of *Leptoceratops gracilis* is the shape of the caudodorsal corner in lateral view (Fig. 4D). This corner is upturned in *Prenoceratops*, as in *Montanoceratops* and *Protoceratops*, which have frills that extend beyond the caudal margin in the skull. In *Leptoceratops gracilis*, which has a shorter frill, this corner is directed straight backwards (Sternberg, 1951:plate XL–VII).

Jugal—Only one partial left jugal is preserved with the *Prenoceratops* material, along with the ventral tip of one right jugal. The element is wide and triangular, and is complete ventrally and caudally (Fig. 5A, C, D). Most of the orbital rim is preserved, but the caudodorsal extension that forms the rostral border of the infratemporal fossa is missing, as is the rostrodorsal corner of the element. The *Prenoceratops* jugal is gracile relative to those of other basal neoceratopsians, less than one centimeter thick apart from the epijugal ridge, but most of the surface is rugose. Lack of robustness could be due to immaturity of the specimens, and rugosity of the *Prenoceratops* elements is not as prominent as in adult specimens of other basal neoceratopsians. The main body of the element extends ventrally from the orbital rim, with a prominent ridge extending from below the orbital rim caudally

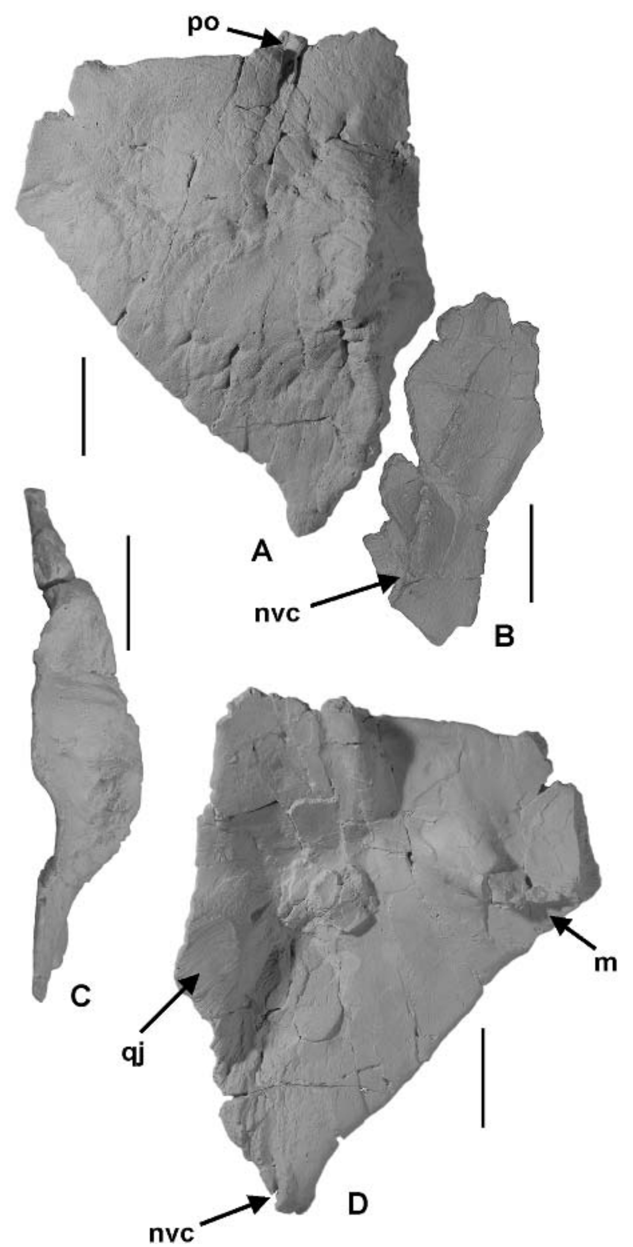

FIGURE 5. Jugal and quadratojugal of *Prenoceratops pieganensis* MNHCM (no number). Left jugal is in lateral (**A**), caudal (**C**) and internal (**D**) views, and quadratojugal (**B**) is in lateral view, in place for articulation with the jugal but shifted caudoventrally. Scale bar equals 2 cm. **Abbreviations**: **po**, postorbital articulation; **m**, maxilla contact; **nvc**, neurovascular canal; **qj**, quadratojugal articulation.

to the ventral tip (Fig. 5A). Caudal to the ridge the jugal extends for only another 20 mm, and the caudal border is irregular where it articulates with the quadratojugal. In dorsal view, looking down on the orbital border, the jugal is shifted medially approximately 10mm just caudal to the orbit border, where the ventral tongue of the postorbital overlaps the element. In lateral view, the bottom of the contact with the postorbital is preserved as a narrow, vertical groove on the external surface. The contact is not a horizontal line at the level of the ventral orbital rim as in *Leptoceratops gracilis* (Sternberg,1951), but instead the postorbital overlaps this area of the jugal with only a narrow tongue ending in a triangular tip. Thus the jugal is seen extending further dorsally caudal to the postorbital to form part of the caudal orbital border and probably most of the rostral border of the infratemporal fenestra.

The internal surface of the *Prenoceratops* jugal is smooth and gently concave, with distinct articular surfaces for contact with the quadratojugal caudally and the lateral projection of the maxilla rostrally (Fig. 5D). The ventral tip of the element partially encloses a neurovascular canal that extends from the medial aspect of the jugal to the outer surface of the face. This canal is entirely enclosed when the quadratojugal is articulated with the jugal.

The jugal of *Prenoceratops* is wider and more vertically positioned than in all other known basal neoceratopsians, with a nearly vertical epijugal ridge. Also, the tip of the ventral corner curves rostrally in front of the quadratojugal articulation in *Prenoceratops* rather than the caudal position seen in other basal forms.

Ostrom (1978) described a specimen of *Leptoceratops gracilis* that included teeth and the articulated caudal half of the skeleton. A jugal was included in the catalogued specimen (PU 18133) but was not mentioned in the article. This jugal is morphologically very similar to that of *Prenoceratops* (P. Makovicky, pers. comm.), which raises a question as to the validity of the referral of the Ostrom skeleton. Described portions of the skeleton include the pelvis, tail vertebrae, and hind limbs, very little of which is diagnostic at the generic level in North American basal neoceratopsians (Chinnery, 2002). In addition, the specimen was originally described as found in the "Lance" Formation (Ostrom, 1978), but may in fact have been from the Mateetse Formation, and thus close to the *Prenoceratops* horizon (C. Forster, pers. comm.).

Quadratojugal—One complete and two fragmentary quadratojugals are preserved. The element is oblong and flat, with a slightly thickened ridge positioned to buttress the jugal and continuing the ventral extent of the epijugal ridge (Fig. 5A, B). As in other basal neoceratopsians, the quadratojugal spans the distance between the jugal and the quadrate, but the *Prenoceratops* quadratojugal is not as thick or caudally broad as in other taxa (Sternberg, 1951; Maryańska and Osmólska, 1975). The mediolateral width and rostrocaudal length are fairly equal throughout the *Prenoceratops* quadratojugal giving it a rectangular shape, and it exhibits no sign of the rostral flange seen in the *Leptoceratops gracilis* jugal (Sternberg, 1951).

The quadratojugal does not contact the squamosal, as it is only approximately half the height of the quadrate. It does, however, extend down past the ventral tip of the jugal to a point level with the articular surface of the quadrate as in *Leptoceratops* and *Bagaceratops*. The quadratojugals of *Prenoceratops* and *Leptoceratops* differ from those of other taxa in that they do not wrap around the quadrate caudally, but fit into a groove on the caudal border. The quadratojugal of *Prenoceratops* is extremely gracile in comparison to that of *Leptoceratops* and is angled in a rostrocaudal direction versus the condition seen in *Leptoceratops*, in which the quadratojugal is angled inward and is much more extensive dorsally. The ". . . heavy, well supported buttress . . ." reported for *Leptoceratops gracilis* (Sternberg, 1951) appears rather fragile in the new genus.

Quadrate—Two partial right quadrates are known. The better-preserved specimen includes the entire caudal portion of the element including the condyles ventrally and the head dorsally. Neither specimen preserves the rostral portion of the element. The condyles are very unequal in size, with the lateral condyle over twice the size of the medial one (Fig. 6). The articulation of the condyles in the mandibular complex is at a caudoventral angle to the dentary (see below), causing the position of the head of the quadrate to be located further caudally than that of the condyles. The quadrate head fits into a socket on the ventral border of the squamosal, and just caudal to this articulation a short process of the quadrate extends caudally for about 8mm. The caudal border of the element is narrow at the dorsal and ventral ends, but thickens two thirds of the distance up from the condyles. The articular surface for the quadratojugal extends from the thickest part of the caudal border down to the condyles.

The quadrate of *Prenoceratops* is similar to those of the *Leptoceratops gracilis* paratypes in being very gracile compared with the quadrate of *Protoceratops*. However, the quadrate of *Prenoceratops* is different in that there is a gentle, even backward arch throughout the length of the shaft as in *Montanoceratops* (Fig. 6;

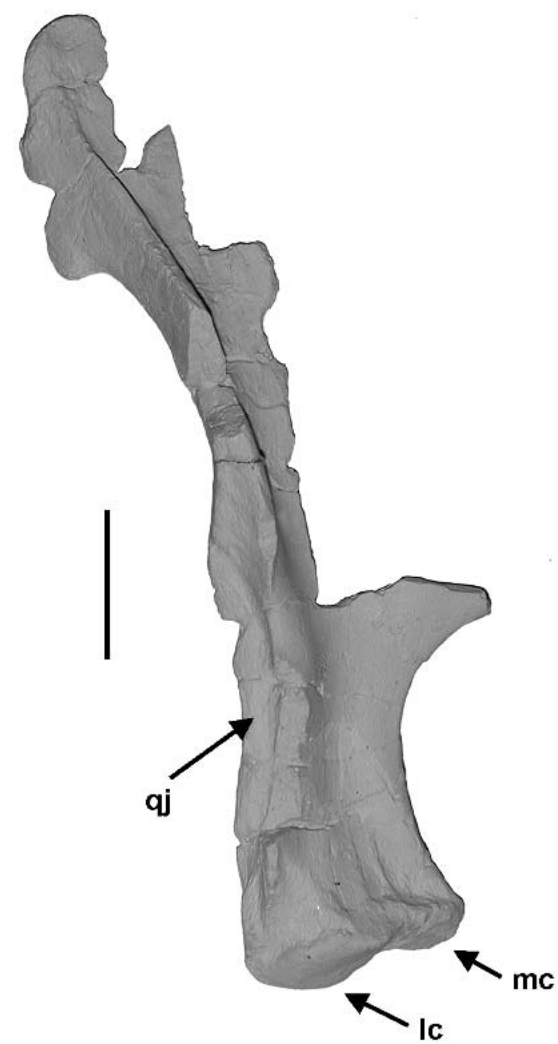

FIGURE 6. Medial view of *Prenoceratops pieganensis* quadrate (TCM 2001.96.4 and MNHCM [no number]). Scale bar equals 2 cm. **Abbreviations**: **qj**, quadratojugal articulation; **lc**, lateral condyle; **mc**, medial condyle.

Chinnery and Weishampel, 1998; Makovicky, 2001). NMC 8887, the smallest of the *Leptoceratops gracilis* specimens, has a quadrate that is nearly vertical. The other paratype exhibits one quadrate with a slight arch, but the specimen in crushed dorsoventrally (Sternberg, 1951). *Protoceratops* and *Bagaceratops* have straight caudal quadrate borders (Makovicky, 2001). The *Prenoceratops* element is further extended caudally by the position of the articular surfaces on the surangular and articular, which effectively tip the quadrate back at a 30-degree angle not seen in *Leptoceratops gracilis*, *Protoceratops*, or *Bagaceratops*. When articulated with the surangular and articular, the *Prenoceratops* quadrate condyles are angled rostromedially with the medial condyle located further rostrally, a condition found only in *Bagaceratops* among other currently known basal neoceratopsians (Maryańska and Osmólska, 1975).

Mandible

The mandible of *Prenoceratops* is unique in many respects, primarily in the caudal elements. The dentary and predentary, however, are very similar to those of *Leptoceratops gracilis* (Brown, 1914; Sternberg, 1951). All mandible elements are disarticulated apart from one surangular-articular complex. The articulation of these two elements is the only such occurrence in the skull elements of *Prenoceratops*, and the complex is designated as the holotype specimen due to the increase of information available with two elements (TCM 2003.1.1).

Dentary—Two nearly complete dentaries are preserved, one right and one left, as well as the coronoid process and two tooth row fragments of a third right dentary. The two complete dentaries exhibit the typical deep, short shape of *Leptoceratops* dentaries, but differ slightly in shape from each other, exhibiting either individual variation or growth changes. The only unrepresented areas of the *Prenoceratops* dentary are the rostrodorsal corner and the caudal border. The contact with the predentary is long and wide, the coronoid process is tall, and the number of alveoli is estimated at 12 or 13 (Fig. 7C, D). The tooth battery extends caudally almost to the caudal border of the coronoid process. The dentaries will be described first in relation to those of other taxa, after which they will be compared with each other.

Several important differences are evident between the dentaries of *Prenoceratops* and *Leptoceratops*. The majority of these are probably due to the immaturity of the new specimens, but some may be taxonomically significant. The left dentary of *Prenoceratops* is much smaller and more gracile than in *Leptoceratops*. It is shorter and deeper, and the coronoid process does not extend as far rostrally as in *Leptoceratops*, although it does extend further rostrally than in *Protoceratops*. The process also does not extend as far medially as in *Leptoceratops*; in the latter it extends almost to the lateral edge of the tooth battery in dorsal view, while in *Prenoceratops* the process is positioned about 10 mm from the tooth row. The most significant difference between the new taxon and *Leptoceratops gracilis* is the possession of a large, C-shaped notch on the upper caudal border of the coronoid process in *Prenoceratops*. This border on the dentary of *Leptoceratops gracilis* is nearly straight. Although it is possible that this is an ontogenetic difference, *Protoceratops* does not exhibit such a prominent notch in younger specimens (Brown and Schlaikjer, 1940). Interestingly, *Montanoceratops* (MOR 542) possesses this notch to a lesser degree. Presumably, the rostral portion of the surangular extends across the notch space in *Prenoceratops* as it does in *Montanoceratops*.

The small *Prenoceratops* dentary has a nearly flat lateral surface. The *Leptoceratops gracilis* dentary bulges out at the coronoid process and at the rostral end, and the lower edge faces laterally. The whole *Leptoceratops* element is sigmoidal in shape

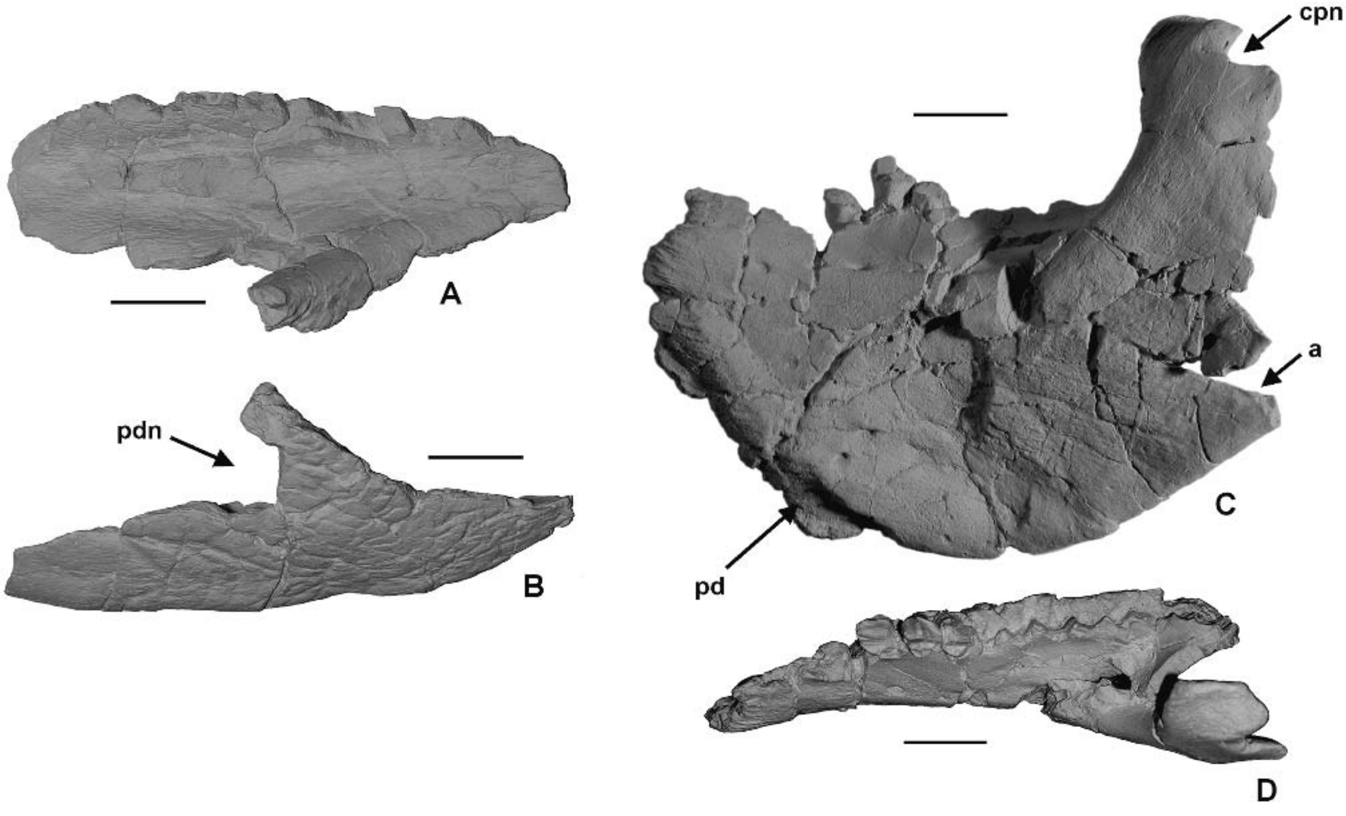

FIGURE 7. *Prenoceratops pieganensis* (MNHCM [no number]) predentary in dorsal (**A**) and right lateral (**B**) views, and left dentary in lateral (**C**) and dorsal (**D**) views. Scale bar equals 2 cm. **Abbreviations**: **pd**, predentary articulation; **cpn**, coronoid process notch; **a**, angular articulation; **pdn**, predentary notch.

in ventral view. The rostrodorsal pit for the predentary extends up higher than the level of the tooth battery in *Leptoceratops* and *Udanoceratops*, nearly as high as the coronoid process, while in *Prenoceratops* the rostrodorsal corner of the element is located no further dorsally than at the level of the tooth row.

A bifurcation of the caudoventral portion of the *Prenoceratops* dentary forms a triangular notch for articulation with the angular. This notch creates a caudally pointing projection of the dentary that is seen in the type of *Leptoceratops gracilis* (Brown, 1914). The internal surface of the dentary in this area contains several strong grooves oriented rostrocaudally, suggesting an extensive overlap of the dentary on to the angular. Dorsal to this grooved area is the mandibular fossa and the Meckelian groove, which is formed between the tooth row and the coronoid process. Although the surangular fits into the dorsal part of this area, it is thin and does not fill much of this space. The mandibular fossa is enclosed medially by the splenial, caudally by the articular and surangular, and ventrally by the angular and predentary.

The inner ventral surface of the tooth battery area of the dentary is strongly grooved for contact with the splenial ventrally and the intercoronoid dorsally (Brown and Schlaikjer, 1940; Sternberg, 1951), although there is no indication of the boundaries of these two elements. This grooved surface extends ventrally to the rostral end of the mandibular fossa, where the inner surface of the tooth battery merges with the main body of the dentary. A ridge continues forward from this point in a curve that follows the shape of the ventral border of the dentary, ending at the rostral border approximately two thirds of the way up from the articulation with the predentary. This ridge would seem to demarcate the upper border of the rostral portion of the splenial as it converges with its opposite at the midline. Rostral to this point the ridge borders the symphyseal area of the dentary, which extends further dorsally than that of *Leptoceratops gracilis*.

At the rostrodorsal corner of the dentary is the sulcus for reception of the buccal process of the predentary. This, together with the extensive symphysis, creates a strong union among the three elements. This sulcus is, however, extremely small in *Prenoceratops* in comparison to that of *Leptoceratops gracilis*. In the dentary of juvenile *Asiaceratops*, this pit is extremely large, which may contradict the argument of ontogenetic change accounting for this discrepancy.

A flange is present on the ventral predentary contact of the *Prenoceratops* dentary which is relatively larger than that of *Leptoceratops gracilis*. A notch separates this flange from the rest of the ventral border of the dentary, which on the inner surface marks the start of the symphyseal area. The dentary-predentary articular surface extends back ventrally and caudally approximately one third of the length of the tooth row. The predentary extends back further in the type of *Leptoceratops gracilis*, to one half the length of the tooth row (Brown, 1914). This difference may be ontogenetic in nature, as in *Protoceratops* the predentary lengthens with age (Brown and Schlaikjer, 1940). The length and angle of this articular surface is shorter on one of the two *Prenoceratops* dentaries, which exhibits several other characters indicative of immaturity, that will be discussed shortly.

In dorsal view the dentary of *Prenoceratops* is much less massive than that of *Leptoceratops gracilis* (Fig. 7D). The shelf between the coronoid process and the tooth row does not extend to the front of the dentary as it does in *Leptoceratops gracilis*, but becomes only a gentle slope by the rostral third of the tooth row. The lateral edge of the *Prenoceratops* dentary is slightly concave in dorsal view, while in *Leptoceratops gracilis* it is convex, and the tooth row of *Prenoceratops* is laterally convex rather than concave as in *Leptoceratops gracilis* (Sternberg, 1951:plate LI).

The *Leptoceratops* sp. material described by Gilmore (1939) includes only two small dentary fragments, both representing the rostroventral corners of the element. Preserved on these fragments is the bottom of the predentary contact on the outer surface, and the front end of the splenial contact and start of the symphysis on the inner surface. On the outer surface of the rostroventral border of this dentary is a bulbous area, instead of the smooth ventral dentary of *Prenoceratops*. Also, the *Leptoceratops* sp. specimens have a less pronounced rostroventral corner, and the splenial seems to converge to more of a point, as the articular surface is more triangular.

Comparison with the *Leptoceratops* sp. dentary described by Ryan and Currie (1998) indicates that the Dinosaur Park Formation dentary is not referable to *Prenoceratops*. Differences between the *Leptoceratops* sp. dentary and that of *Prenoceratops* include a relatively much larger rostral portion in the *Leptoceratops* sp. element, while in *Prenoceratops* the rostral and caudal ends are similar in their dimensions (apart from the coronoid process). The *Leptoceratops* sp. dentary has a larger rostroventral corner, and the extension that articulates with the angular at the caudoventral corner is located further caudally.

Differences between the two *Prenoceratops* dentaries seem to be related to ontogeny. The right, and probably more immature, dentary is not as deep, has a straighter ventral border, and the rostroventral corner is sharper than in the other specimen. In addition, the predentary articulation is shorter and more vertical, and only extends back to the third tooth position, and the coronoid process is lower and less vertical, with no forward curve at all. All of these differences can be seen among *Protoceratops* dentaries from different levels of maturity (Brown and Schlaikjer, 1940). Interestingly, if these are changes are due to growth, they are happening with no overall size increase—the two dentaries are virtually identical in size. Both have an equal number of alveoli, and the preserved teeth are the same size.

Predentary—The predentary of all ceratopsians is similar in shape—beak-like to oppose the rostral and premaxillary bones, with a strong union to the dentary. Basal neoceratopsians typically have longer predentaries relative to dentary length (Brown, 1914; Brown and Schlaikjer, 1940; Sternberg, 1951; Maryańska and Osmólska, 1975). One partial predentary is included with the *Prenoceratops* bone-bed material. The fragment extends from close to the rostral tip back to where the ventral surface splits into two processes. The right side of the dorsal cutting edge is preserved, including part of the articulation with the rostrodorsal corner of the dentary (Fig. 7A, B).

Leptoceratops and *Prenoceratops* predentaries can be distinguished from those of other basal neoceratopsians by a notch in the dorsal part of the articulation with the dentary in the former taxa (Fig. 7B; Brown, 1914). In other basal forms the rostral cutting edge of the bone is more continuous with the extension of the predentary laterally down onto the dentary (Maryańska and Osmólska, 1975). The presence of the notch is possibly a more derived character state, as a very well developed notch is present in ceratopsids, in effect dividing the element into dorsal and ventral extensions (Hatcher et al., 1907). One interpretation of the evolution of this element is the elongation of the superior extension relative to the remainder of the element, as noted by Brown and Schlaikjer (1940).

Prenoceratops pieganensis has a predentary slightly different from those of the paratypes of *Leptoceratops gracilis* in several respects. In dorsal view, the predentary of the new genus is narrower rostrally (Fig. 7A). The dorsal cutting edge is sharp throughout its length; as the caudal projection widens to meet the dentary the edge shifts to the lateral side of the projection. This contrasts with *Leptoceratops gracilis*, which has a rounded caudodorsal surface (Sternberg, 1951; Makovicky, 2001). This dorsal surface is also more concave in lateral view in the new taxon. The other difference is in the shape of the ventral extension of the element on to the dentary. In *Prenoceratops* the angle of the ventral process of the predentary in lateral view is less gradual, with the caudal end of the predentary expanded further dorsally than in *Leptoceratops*.

Although a fragmentary predentary is included with Gilmore's (1939) *Leptoceratops* sp. material (USNM 13864), the only part preserved is the central area—no part of the dorsal cutting edge or articular surfaces are present. The ventral surface forms less of a keel than in *Prenoceratops*, but the element is overall much more robust, as are all parts of USNM 13864 compared to the bone-bed material.

The *Leptoceratops* sp. dentary described by Ryan and Currie (1998) has the distinctive rostral shape associated with a predentary with a long dorsal projection, as the articular surface of the dentary extends forward to a point from the ventral border and from the tooth row. The larger rostroventral corner on this specimen suggests a possible similarity in shape of the caudoventral predentary to that of *Prenoceratops*.

Angular—Only one very fragmentary angular is preserved. Caudally, this element is similar to that of *Leptoceratops*, *Protoceratops* and *Montanoceratops*, and the rostral extent is unknown.

Surangular—Five partial surangulars are preserved: three mostly complete (two right and one left) and two fragmentary. One right surangular is fused with its corresponding articular (TCM 2003.1.1), possibly (but not definitely) signifying greater maturity in one individual of the bone-bed assemblage.

The *Prenoceratops* surangular is roughly triangular, as in *Leptoceratops* and *Protoceratops*, although the full extent of the element is not known, as none is entirely complete. This is undoubtedly due to the unusually gracile, thin nature of the element.

Rostrally the element is deep, with a straight edge at a 90-degree angle to the quadrate articular surface (Fig. 8A). This rostral edge extends up to the top of the coronoid process as in *Leptoceratops*, and fits in a caudal notch formed by the coronoid process of the dentary. The external surface of this notch is formed entirely by the dentary, while the internal surface is composed of the dentary and the coronoid bone. The remainder of the straight rostral edge of the surangular sits on the internal surface of the caudal dentary, the latter element overlapping the surface of the surangular and effectively cutting off the whole rostroventral corner of the element from lateral view when articulated. A small rugose area is present on the external surface where the spur of the dentary that forms the bottom of the lateral notch (discussed in the "Dentary" section) sits. The rostromedial end of the surangular exhibits the articular surface for the coronoid; a raised, semicircular area with a lip formed on the lower edge (Fig. 8B). Below this is another ridge, extending in a rostroventral angle. The surangular foramen is clearly visible.

The dorsal border of the element rises at a slight angle from the quadrate articulation, more so than in *Montanoceratops* and *Bagaceratops* (Maryańska and Osmólska, 1975), but less so than in *Protoceratops* (Brown and Schlaikjer, 1940). The rostral end of this border, the coronoid process of the dentary, and the coronoid bone extend to equal heights. As in *Leptoceratops* and *Protoceratops*, the *Prenoceratops* surangular sends a projection medially from just over half of the length from the rostral end. This supports the rostral end of the articular and forms part of the caudal border of the mandibular fossa.

The entire *Prenoceratops* surangular is extremely narrow. The rostral portion of the element is extremely gracile, with a maximum thickness of less than a centimeter, and as thin as two mm. The surangular of *Leptoceratops gracilis* (NMC 8889) is much more robust, with ". . . a very broad, heavy process up behind, and to the top of, the coronoid process" (Sternberg, 1951). It appears that the robust rostral ridge on other basal neoceratopsian surangulars may be replaced by an increase in overlap of the dentary in *Prenoceratops* and/or a change in the jaw musculature. Contrary to the condition in *Leptoceratops gracilis* and other basal neoceratopsians, no lateral shelf is displayed on these elements except on the one fused with the articular, and even this is very weakly developed (Fig. 8A). This variably sized lateral shelf is positioned above the articulation to the angular, forming a hollow that is possibly for attachment of the m. depressor mandibulae (Brown and Schlaikjer, 1940). In *Protoceratops* this shelf is more robust on mandibles from older individuals (Brown and Schlaikjer, 1940), but even very immature *Protoceratops* and *Bagaceratops* (as well as *Asiaceratops*) surangulars exhibit a better developed ridge than seen on *Prenoceratops*. *Leptoceratops gracilis* has a relatively weak surangular shelf (Makovicky, 2001), but it is still more developed than in *Prenoceratops*.

Caudal to the articular area for the quadrate, the medial aspect of the surangular gives rise to a projection of bone caudally. This projection is long in *Prenoceratops*—accounting for about one fifth the total length of the element, and is thus more similar to the condition seen in *Protoceratops* than in *Leptoceratops* (Fig. 8D). However, in *Protoceratops* the surangular wraps around the articular at the caudal end of this projection. *Leptoceratops* dis-

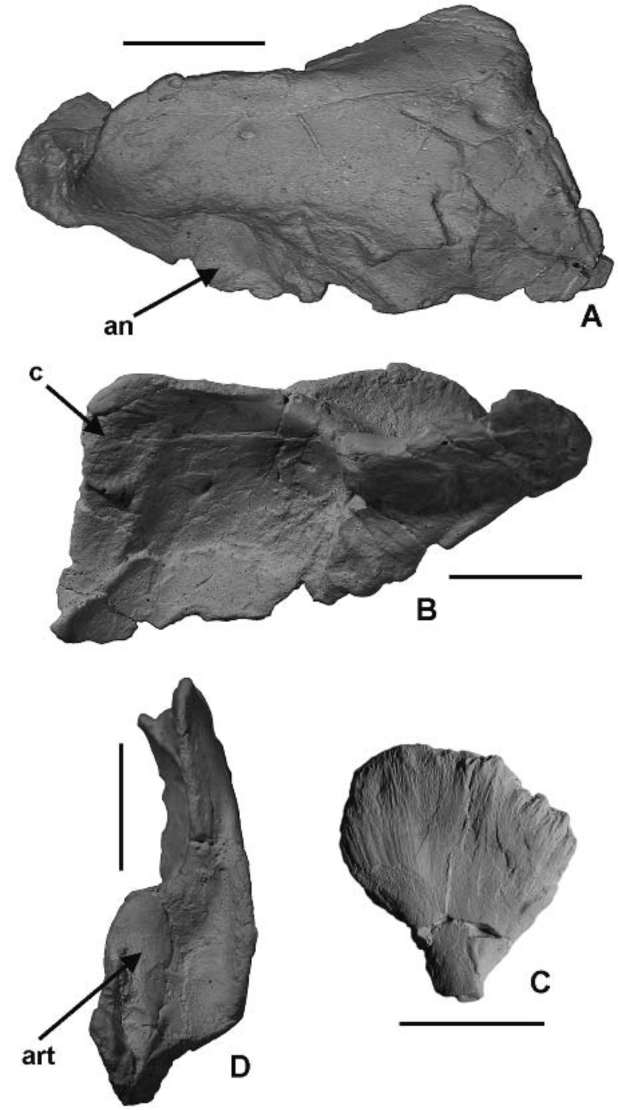

FIGURE 8. Mandible elements of *Prenoceratops pieganensis*. Right surangular and articular complex (holotype specimen, TCM 2003.1.1) in lateral (**A**), medial (**B**), and dorsal (**D**) views, and right coronoid in medial view (**C**). Scale bar equals 2 cm. **Abbreviations**: **art**, articular; **c**, coronoid articulation; **an**, angular articulation.

plays the opposite condition, with the articular extending very slightly beyond the surangular. The elements are exactly the same length in the new genus.

Unlike the condition in *Protoceratops* and *Leptoceratops*, the surangular of *Prenoceratops* forms more than half of the quadrate articulation. The articular is thus reduced, a condition corroborated by the preserved quadrate condyles, of which the lateral one is twice the size of the medial one. The ridge dividing the quadrate articular area in *Leptoceratops* and *Bagaceratops* is not present in *Prenoceratops*.

Included in the *Leptoceratops* sp. material described by Gilmore (1939) is one partial surangular. This surangular is unlike almost all other ceratopsian surangulars in that the bone does not expand rostrally at all, but abruptly folds inwards forming a stout shelf that comprises its rostral border. The element would have been buttressed against the caudal aspect of the coronoid process, rather than surrounded by it as described for *Prenoceratops*. In addition, this surangular has a very robust lateral shelf, more so than in any other basal neoceratopsian. The uniqueness of this element alone precludes referral of the *Leptoceratops* sp. material to *Prenoceratops*. This unique surangular is, however, exactly like the surangular of an undescribed basal neoceratopsian (MOR 300, Chinnery, pers. obs.).

Articular—The articular of *Prenoceratops* is an elongated oval in dorsal view (Fig. 8D). It is reduced in size compared with the articulars of *Leptoceratops*, *Montanoceratops*, and *Protoceratops*.

The articular extends from the medial wing of the surangular back to the most caudal point of that element. It is tightly articulated with the surangular laterally and presumably the prearticular and splenial medially, although these elements are not preserved (only the rostral splenial is known for *Prenoceratops*—see below).

The rostral and ventral projections of the element, and the demarcated pit at the caudodorsal end are similar to those of *Leptoceratops gracilis* (Sternberg, 1951). However, the pit extends across the entire width of the *Prenoceratops* articular, and rostral to it the element does not widen as markedly as in *Leptoceratops gracilis*. The *Prenoceratops* articular is primarily convex, with only the slightest upward curve at the medial edge of the articular area for the quadrate condyle. The surface shows no indication of a ridge positioned between the two quadrate articular areas as in *Leptoceratops* and *Bagaceratops* (Maryańska and Osmólska, 1975). Rather, the convex nature of the bone provides a natural division between the small rostral articular area and larger caudal one.

The articular of *Prenoceratops* forms less than half of the articulation for the quadrate. In *Protoceratops* and *Montanoceratops* the articular provides half of the articular surface for the quadrate, while in *Leptoceratops*, *Microceratops* and ceratopsids it forms the greater part of this articulation.

Coronoid—The only preserved *Prenoceratops* coronoid is a thin, fan-shaped bone that is expanded dorsally and constricted ventrally (Fig. 8C). The inner surface is rugose, with two distinct facets for articulation with the surangular caudally and the coronoid process of the dentary rostrally. A lip of the element extends beyond the dentary, running along the rostral border and front half of the dorsal border. When articulated with the dentary, a groove is provided for insertion of part of the capitimandibularis muscle (Brown and Schlaikjer, 1940). No indication of a spur extending down past the intercoronoid is seen in the *Prenoceratops* coronoid, in contrast to *Bagaceratops* (Maryańska and Osmólska, 1975). The dorsal portion of the *Prenoceratops* coronoid is expanded further rostrally than caudally, unlike those of *Leptoceratops* and *Protoceratops* where it is more expanded caudally relative to the constricted ventral "neck."

Splenial—The ventral border of the preserved splenial fragment is gracile and of equal thickness to the corresponding dentary border, except at the rostral end where it widens slightly in ventral view. At this point a ridge appears on the medial surface, probably for contact with the opposing splenial, although the rostral end is not preserved. In ventral view the bone curves in a slightly sigmoidal fashion in order to form the inner wall of the mandibular fossa and then cover the ventral part of the tooth battery. The preserved portion of the splenial appears to be similar to that of the type of *Leptoceratops gracilis*. However, the articular border on the *Prenoceratops* dentary shows that this element was lower at the rostral end than in *Leptoceratops* (Brown, 1914).

Teeth

The teeth of *Prenoceratops* are similar to those of *Leptoceratops*, with a prominent primary ridge and several secondary ridges on both maxillary and mandibular teeth. Enamel coats the buccal aspect of the maxillary teeth and the lingual side of the mandibular teeth. The *Prenoceratops* teeth exhibit the vertical-shear wear pattern found in *Leptoceratops* and *Montanoceratops*, with a horizontal shelf forming through wear on the dentary teeth as in those taxa.

Postcranial Skeleton

The postcranial skeleton of Prenoceratops will be described elsewhere. However, it should be noted that the *Prenoceratops* postcranium does not differ markedly from that of *Leptoceratops* (Brown, 1914; Sternberg, 1951) for current descriptions. Immaturity is evident in the *Prenoceratops* postcranial elements, as most vertebral neural arches are unfused and the majority of limb elements are more gracile than in *Leptoceratops*. A few unique fusions, including one entirely fused scapulocoracoid, indicate that fusion may be a variable feature, not to be relied upon as an indicator of maturity.

Postcranial elements of *Prenoceratops* and *Leptoceratops* were compared directly using the shape methods Least-Squares Theta-Rho Analysis, Resistant-Fit Theta-Rho Analysis, and Euclidean Distance Matrix Analysis (Chinnery, 2002). Slight differences are apparent in some elements, including a difference in orientation of the deltopectoral crest on the humerus, but the distinctions between taxonomic and developmental differences are unclear at present.

DISCUSSION

A cladistic analysis was conducted using PAUP* version Beta 10 (Swofford, 2002), including 16 taxa and 102 cranial and postcranial characters. A representative of Pachycephalosauria (*Stegoceras*) was included as the outgroup, and *Centrosaurus apertus* and *Triceratops horridus* were included to represent the two subfamilies within Ceratopsidae. All currently recognized basal neoceratopsian taxa were included except for *Breviceratops kozlowskii* (which may be synonymous with *Bagaceratops rozhdestvenskyi*; Sereno, 2000; Makovicky, 2001), and *Turanoceratops tardabilis* (excluded due to lack of material). The Branch and Bound option was chosen for the analyses, and the characters were equally weighted and ordered unless otherwise stated in Appendix 2. One most-parsimonious tree was generated, with a tree length of 180, a consistency index of 0.67 and a retention index of 0.73. Characters were coded from the literature, including Chinnery and Weishampel (1998) and Makovicky (2001), and personal observation. Characters were coded for *Zuniceratops* by Doug Wolfe (pers. comm.).

The most parsimonious tree generated by this analysis (Fig. 9) agrees with other recent analyses in some respects, but differs in others. *Chaoyangosaurus youngi* is a member of Neoceratopsia, unlike in Makovicky (2001) and Xu et al. (2002), and Protoceratopsidae includes only the Asian taxa *Protoceratops* and *Graci-*

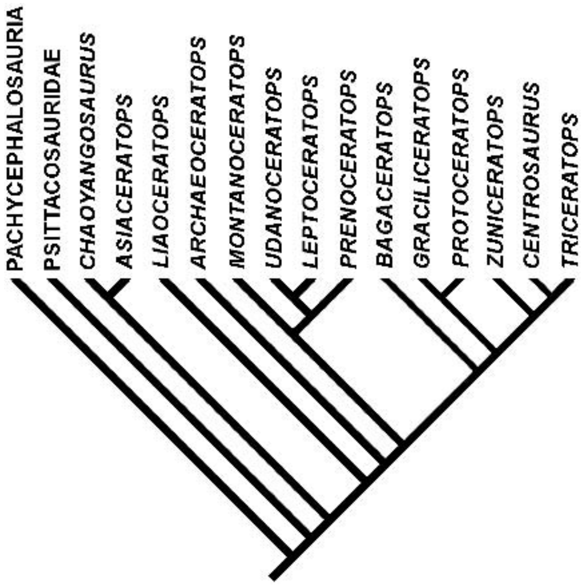

FIGURE 9. Consensus cladogram of relationships within Ceratopsia generated by PAUP* version Beta10 (CI: 0.65, RI: 0.72, tree length = 133). Character descriptions are listed in Appendix 1, taxon states are listed in Appendix 2, and node-supporting characters are listed in Appendix 3.

liceratops. Additionally, Leptoceratopsidae of Makovicky (2001) and Xu et al. (2002) are supported, with the addition of *Prenoceratops*. This clade thus includes all North American basal taxa and *Udanoceratops tschizhovi* from Asia. Again, as in Makovicky (2001) and Xu et al. (2002), Ceratopsidae are monophyletic, with *Zuniceratops christopheri* forming their sister group. The current analysis unites *Asiaceratops* with *Chaoyangosaurus* rather than with the lineage of Leptoceratopsidae.

Leptoceratopsidae and Ceratopsidae are strongly supported (see Appendix 3 for node support). The positions of *Asiaceratops*, *Archaeoceratops*, and *Graciliceratops* are only weakly supported, and when all characters were left unordered these nodes collapsed to polytomies. Neoceratopsia are not well supported in this analysis, most likely due to the position of Chaoyangosaurus (see Xu et al., 2002).

This cladogram supports the hypothesis of multiple dispersal events of early ceratopsians from Asia to North America (Chinnery and Weishampel, 1998; Chinnery et al., 1998; Makovicky, 2001). Specifically, this analysis supports the hypothesis of two dispersal events from Asia to North America, one with the ancestor of Leptoceratopsidae and one of the ancestor to the *Zuniceratops* and the Ceratopsidae lineage. In addition, one dispersal event back to Asia of an ancestor of *Udanoceratops* is also supported.

We still know little of basal neoceratopsian diversity in North America. Neoceratopsian remains are known from as early as the Albian, including teeth from the Arundel Formation of Maryland (Chinnery et al., 1998) and skeletal remains from the Wayan Formation of Idaho (Weishampel et al., 1993). Only three basal neoceratopsian genera are currently known from North America: *Leptoceratops*, *Montanoceratops*, and *Prenoceratops*. *Montanoceratops cerorhynchus* is represented by material from the St. Mary River Formation of Montana and Horseshoe Canyon Formation of Alberta, both early Maastrichtian in age. *Leptoceratops* material includes a dentary from the middle Campanian of Alberta (Ryan and Currie, 1998) and partial skeletons from the Two Medicine Formation of Montana (Gilmore, 1939). The holotype and paratypes of *Leptoceratops gracilis* are all from the late Maastrichtian Scollard Formation in Alberta, Canada, and other *Leptoceratops gracilis* material is known from the contemporaneous Lance Formation and Pinyin Conglomerate. The material described here is from the Two Medicine Formation, roughly nine million years older than previously known *Leptoceratops gracilis* horizons.

The validity of a taxon based on juvenile material may be subject to some doubt. Several ceratopsian taxa have been named on the basis of immature specimens, but have usually been found to be invalid or synonymous with other established taxa. *Brachyceratops montanensis* was discovered in 1913 by Charles Gilmore. The material was described as similar to *Monoclonius* and other centrosaurines, but with anatomical differences due either to immaturity of the specimen or to taxonomic variation (Gilmore, 1939). However, Gilmore, as well as others, concluded early on that *Brachyceratops* may be a juvenile member of another centrosaurine genus (Dodson, 1996). *Avaceratops lammersi* is another ceratopsian taxon described on the basis of juvenile material, but is currently regarded as a valid taxon, though this is debated (Sampson et al., 1997; Chinnery, 2002). Even *Monoclonius*, a genus that survived more than a century of study from its description (Cope, 1876) is now believed to be based on juvenile material of another centrosaurine (Sampson et al., 1997). Juvenile specimens of ceratopsids are extremely rare, and little is known about ontogeny within Ceratopsidae, accounting for the controversies listed above.

Basal neoceratopsians, in contrast, are represented by a great deal of juvenile material, exemplified by the fabulous growth series of *Protoceratops andrewsi* skulls (Brown and Schlaikjer, 1940). The determination of taxonomic validity of *Prenoceratops* is based on an exhaustive comparison with juvenile *Protoceratops* and *Bagaceratops* material, among others. Some of the characteristics of the *Prenoceratops* material are explained by the immaturity of the specimens (see above). Others can not be explained as ontogenetic in nature, and are thus considered to be valid taxonomic characters.

The caudal orientation of the naris in *Prenoceratops* may be due to immaturity, as may be the generally gracile nature of the elements. Constriction of the nasal caudally may also be due, in part, to ontogenetic stage. In *Bagaceratops*, the distance between the rostrodorsal corners of the orbits increases from 27.8% to 50.3% of the width of the skull across the postorbitals among the three specimens described (Maryańska and Osmólska, 1975). *Protoceratops* does not, however, exhibit a similar trend during growth (Brown and Schlaikjer, 1940; information on unpublished hatchling material will eventually help to clarify this; Makovicky, pers. comm.). Some differences that may possibly be due to immaturity, such as the lack of a lateral shelf on the *Prenoceratops* surangular, are not found in even the smallest individuals of *Protoceratops* or *Bagaceratops*. No indication of a difference in quadrate articular condyle size is apparent in smaller specimens of either *Bagaceratops* or *Protoceratops*, and the corresponding surangular and articular of these genera do not change greatly in relative robustness through growth.

CONCLUSIONS

The first occurrence of a basal neoceratopsian bone-bed provides sufficient material for the diagnosis of a new genus and species, *Prenoceratops pieganensis*. A minimum number of four individuals are present in the bone-bed material as immature partial skeletons. Elements are mainly unfused, and associations are tentative, but this material provides for a more thorough understanding of basal neoceratopsian cranial morphology.

Autapomorphies of *Prenoceratops pieganensis* include: caudally oriented naris; lateral projection instead of maxillary shelf; rostral position of pterygoid-maxilla contact; constricted caudal portion of nasal; deep and sharp frontal depression with nearly straight border; postorbital bar narrow at frontal-postorbital contact; wide, triangular jugal; rostral curvature of ventral tip of jugal; gracile quadratojugal; caudally angled quadrate; extremely gracile surangular; reduced articular; and convex dorsal border of articular.

The premaxillary contribution to the external naris suggests a more caudally-oriented external naris, and the straight nasal and caudally angled quadrate together suggest a lower, longer head in *Prenoceratops* than in *Leptoceratops*. The short maxilla, more horizontally oriented antorbital fossa, and more upright, triangular jugal also support this hypothesis. Some, but not all, smaller specimens of *Protoceratops* exhibit a lower rostral end of the face; therefore, the caudally oriented external naris and short maxilla may be due, in part, to immaturity of the bone-bed specimens. However, the angle of the quadrate does not seem to differ markedly among *Protoceratops* specimens, nor does the jugal change shape to a large degree (Brown and Schlaikjer, 1940). In addition to the backward angle of the quadrate, the lateral condyle is more than twice the size of the medial one, and the condyles are angled medially, again indicating a difference in jaw articulation in *Prenoceratops*. The surangular and articular are extremely gracile, but the teeth of *Prenoceratops* appear similar to those of *Leptoceratops*, with the same wear patterns in the same planes.

Internal features of the cranial elements and sutural contacts between them are now better known for North American basal neoceratopsians. The *Prenoceratops* material shows that skull elements of this taxon have primarily tongue-in-groove sutures that are asymmetrical, and that the elements overlap to a much greater extent than previously known in other taxa. Neurovascular canals are now suggested to be the reason for the maxillary and dentary "special foramina" of Edmund (1957). Additional neurovascular canals are found in other facial elements, including one encompassed by the jugal and quadratojugal.

In general, the *Prenoceratops* elements are very similar to those of *Leptoceratops*, and when the elements are articulated into a composite skull the result looks remarkably like a low version of the *Leptoceratops gracilis* paratype NMC 8887 (Sternberg, 1951:pl. XLIX).

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APPENDIX 1

Characters and character states included in the preliminary cladistic analysis including *Prenoceratops pieganensis*.

1. Presence of rostral ventral process (Makovicky, 2001): absent (0), present (1).
2. Nasal septum formed by nasals and premaxillaries (Lull, 1933): absent (0), present (1).
3. Nasal horn (Granger and Gregory, 1923): absent (0), small (1), large (2).
4. External naris size (Gregory and Mook, 1925): width less than 10% basal skull length (0), width more than 10% (1).
5. Choanae shape, or extent of internal nares (Brown and Schlaikjer, 1940): positioned at anterior end of tooth row (0), or caudally and more elongated (1). Unordered.
6. Height of premaxilla relative to orbital region of face (Makovicky, 2001): low (0), deep (1).
7. Shape of ventral border of premaxilla: ventrally convex (0), straight (1), concave (2). Unordered.
8. Position of premaxilla-maxilla suture (Makovicky, 2001): caudal to convex buccal process in lateral view (0), extends through process (1).
9. Presence of depression rostroventral to the external naris (Makovicky, 2001): absent (0), present (1).
10. Ventral contact of maxillae at rostral border of internal nares (Makovicky, 2001): not present, separated by vomers (0), present (1).
11. Pterygoid-maxilla contact (Makovicky, 2001): absent (0), at caudal end of tooth row (1), rostral to caudal end of tooth row (2). Unordered.
12. Shape of tooth bearing margin of maxilla (Makovicky, 2001): straight (0), ventrally convex (1).
13. Antorbital fossa size (Granger and Gregory, 1923): less than 10% basal skull length (0), greater than 10% (1).
14. Antorbital fossa shape: round (0), ovate (1).
15. Palatal exposure of the ectopterygoid (Sereno, 1984): exposed (0), not exposed (1).
16. Orbit size (Granger and Gregory, 1923): large, width 20% or more of basal skull length (0), less than 20% (1).
17. Lacrimal contribution to orbit (Sereno, 1984): over ½ of anterior orbit rim (0), less than ½ (1).
18. Palpebral attachment (Granger and Gregory, 1923): free articulation of palpebral to prefrontal (0), fused to prefrontal (1).
19. Shape of rostrodorsal orbit (Hatcher et al., 1907): rounded (0), angular (1). Unordered.
20. Shape of rostral orbit border: curved (0), straight (1). Unordered.
21. Orbital horns (Granger and Gregory, 1923): absent (0), present (1).
22. Infratemporal fenestrae (Sereno, 1984): width greater than 10% basal skull length (0), width less than 10% (1).
23. Midline prefrontal suture (Sereno, 1984): absent (0), present (1).
24. Orientation of frontal depression border: curved or caudolateral (0), directly lateral (1). Unordered.
25. Shape of postorbital (Makovicky, 2001): inverted and L-shaped (0), triangular (1).
26. Angle of frontal-postorbital suture: craniocaudal (0), angled (1). Unordered.
27. Contribution of postorbital to infratemporal fenestra (Makovicky, 2001): postorbital forming part of border (0), postorbital excluded from border (1).
28. Parietal frill (Chinnery and Weishampel, 1998; Makovicky, 2001): absent (0), less than 70% of basal skull length (1), greater than 70% (2).
29. Shape of squamosal in lateral view (Makovicky, 2001): subtriangular (0), T-shaped (1).
30. Orientation of squamosals (Makovicky, 2001): parasaggital (0), caudally divergent (1).
31. Parietal fenestrae (Hatcher et al., 1907): absent (0), present (1). Unordered.
32. Basioccipital (Hatcher et al., 1907; Makovicky, 2001): contributes to foramen magnum (0), forms ⅔ or more of occipital condyle (1), forms less than ⅔ (2).
33. Basal tubera formation (Makovicky, 2001): basisphenoid only (0), basioccipital and basisphenoid (1).
34. Basal tubera shape (Makovicky, 2001): flat (0), everted caudally (1). Unordered.
35. Orientation of basipterygoid (Makovicky, 2001): rostral (0), ventral (1), caudoventral (2). Unordered.
36. Depth of groove caudal to basipterygoid processes (Makovicky, 2001): deep (0), shallow (1).
37. Supraoccipital position (Brown and Schlaikjer, 1940): contributes to the foramen magnum (0), does not contribute (1).
38. Supraoccipital shape (Makovicky, 2001): tall and triangular (0), trapezoid (1), square (2).
39. Presence of secondary skull roof (Lull, 1933): absent (0), present (1).
40. Presence of epoccipital bones (Lull, 1933): absent (0), present (1).
41. Cranial foramina number in exoccipitals (Brown and Schlaikjer, 1940): three (0), two (1).
42. Quadrate-exoccipital contact (Brown and Schlaikjer, 1940): contacting (0), not contacting (1).
43. Squamosal position (Ostrom, 1966): extends to caudal border of parietals (0), shortened (1).
44. Paroccipital process length (Brown and Schlaikjer, 1940): less than 40% basal skull length (0), more than 40% (1). Unordered.
45. Jugal-lacrimal and lacrimal-maxilla contacts (Sereno, 1984): jugal-lacrimal shorter, lacrimal-maxilla longer (0), former longer, latter shorter (1).
46. Squamosal-jugal contact above or beside infratemporal fenestra (Sereno, 1984): absent (0), narrow (1), wide (2).
47. Presence of ectopterygoid-jugal contact (Sereno, 1984): present (0), absent (1).
48. Epijugal ossification (Makovicky, 2001): absent (0), present (1).
49. Shape of epijugal (Makovicky, 2001): crest-shaped (0), conical (1).

50. Shape of quadratojugal (Makovicky, 2001): mediolaterally constricted (0), triangular in coronal section (1), triangular with rostral flange (2). Unordered.
51. Quadrate shape in lateral view (Makovicky, 2001): caudally arching (0), straight (1).
52. Angle of quadrate condyles: transverse (0), angled rostromedially (1). Unordered.
53. Shape of mandible ventral border (Chinnery and Weishampel, 1998): slightly curved (0), greatly curved (1), no curvature (2). Unordered.
54. Predentary length (Lull, 1933): below 67% of dentary length (0), close to or above 67% of length of dentary (1). Unordered.
55. Predentary caudal border shape: straight (0), slightly divided (1), very divided (2). Unordered.
56. Predentary buccal margin (Makovicky, 2001): sharp (0), rounded and beveled (1), grooved and triturating (2).
57. Presence of diastema between predentary and first dentary tooth (Makovicky, 2001): absent (0), present (1).
58. Dentary depth relative to length (Gregory and Mook, 1925): depth less than 40% length (0), greater than 40% (1). Unordered.
59. Large pit at rostral end of dentary (Makovicky, 2001): absent (0), present (1).
60. Coronoid process shape (Lull, 1933): gently curved, convex summit (0), cranial hook present (1).
61. Coronoid process position (Granger and Gregory, 1923; Makovicky, 2001): close to tooth row, and caudal to it (0), lateral, with cranial process level with end of tooth row (1), lateral, with posterior process level with end of tooth row (2).
62. Dentary-prearticular contact (Sereno, 1984): absent (0), present (1).
63. Jaw articulation position relative to tooth row (Chinnery and Weishampel, 1998): below tooth row level (0), at or above tooth row (1). Unordered.
64. Lateral ridge on surangular (Makovicky, 2001): absent or nondistinct (0), well-developed (1).
65. Articular proportions (Chinnery and Weishampel, 1998): one half or less of quadrate articulation (0), more than ½ (1). Unordered.
66. Presence of premaxillary teeth (Gregory and Mook, 1925; Makovicky, 2001): three or more (0), two (1), absent (2).
67. Cheek tooth root number (Gregory and Mook, 1925): one (0), two (1).
68. Cheek tooth spacing (Brown and Schlaikjer, 1940): uneven and wide (0), closely packed and interlocked (1).
69. Tooth occlusion direction (Ostrom, 1966): oblique sheer (0), vertical sheer (1), vertical-notch sheer (2). Unordered.
70. Number of teeth in battery: two or three (0), more than three (1).
71. Tooth enamel placement (Sereno, 1984): both sides of teeth (0), lateral maxillary and medial mandibular (1).
72. Grooves on cheek tooth roots (Sereno, 1984): present (0), absent (1).
73. Maxillary alveoli number in adults (Chinnery and Weishampel, 1998): less than 20 (0), more than 20 (1).
74. Fusion of first three cervical vertebrae in adult (Sereno, 1984; Makovicky, 2001): no (0), centra only (1), complete (2).
75. Atlas intercentrum shape (Brown and Schlaikjer, 1940): semicircular (0), ring-shaped (1).
76. Number of sacral vertebrae (Sereno, 1984): eight or less (0), more than eight (1).
77. Midcaudal vertebral spine length (Brown, 1914): similar in length to dorsal vertebrae spines (0), significantly longer than dorsals (1). Unordered.
78. Presence of clavicles (Chinnery and Weishampel, 1998): present (0), absent (1).
79. Lateral curvature of scapula (Makovicky, 2001): significant lateral curvature (0), straighter (1).
80. Angle of scapular blade relative to glenoid fossa (Makovicky, 2001): acute (0), almost perpendicular (1).
81. Glenoid fossa formation (Brown and Schlaikjer, 1940): equal contributions from scapula and coracoid (0), greater contribution from coracoid (1), greater contribution from scapula (2). Unordered.
82. Olecranon process development compared to total ulna length (Hatcher et al., 1907): not well developed (0), well developed (1).
83. Shape of distal ulna: relatively straight shaft (0), pronounced medial bend of distal shaft (1). Unordered.
84. Pubis shape (Hatcher et al., 1907; Lull, 1933): prepubis rod-like and short, pubic body size relatively large (0), prepubis expanded and pubic body relatively reduced (1).
85. Fourth femoral trochanter size (Dodson and Currie, 1990): large and pendant (0), reduced (1).
86. Ratio of femur versus tibia length (Hatcher et al., 1907): less than 1.0 (0), greater than 1.0 (1).
87. Ungual phalanx shape (Brown, 1914): narrow (claw-shaped) (0), hoof-like (1).
88. Manus versus pes (Dodson and Currie, 1990): pes significantly larger than manus with compressed metatarsals (0), pes close to manus size and uncompressed metatarsals (1).
89. Head size relative to body size (Dodson and Currie, 1990): small (0), large (1).
90. Head shape from a dorsal view (Dodson and Currie, 1990): ovoid (0), more triangular (1).
91. Shape of rostral keel (Xu et al., 2002): rounded (0), sharp (1).
92. Shape of premaxillary palatal region (Xu et al., 2002): flat in ventral view (0), vaulted dorsally (1).
93. Extension of ectopterygoid (Xu et al., 2002): ectopterygoid contacts jugal (0), reduced and contacts maxilla only (1).
94. Presence of "eustachian canal" groove on ventral aspect of pterygoid (Xu et al., 2002): absent (0), present (1).
95. Contact point of angular, surangular, and dentary on lateral surface (Xu et al., 2002): triradiate contact point (0), dentary-surangular suture at acute angle to angular-surangular suture (1).
96. Presence of median primary ridge on teeth (Xu et al., 2002): absent (0), weak and present only on maxillary teeth (1), distinct and on both maxillary and dentary teeth (2).
97. Shape of dentary tooth crowns (Xu et al., 2002): crown with smooth, continuous transition to root (0), bulbous labial expansion of crown at transition (1).
98. Shape of axial neural spine (Xu et al., 2002): low (0), tall and hatchet-shaped (1), elongate and caudally inclined (2).
99. Position of ventral border of external naris relative to that of infratemporal fenestra (Xu et al., 2002): naris border significantly below fenestra (0), same level (1), significantly above (2).
100. Shape of rostral aspect of squamosal (Xu et al., 2002): solid (0), bifurcate around caudal process of postorbital (1).
101. Relative position of rostral (Xu et al., 2002): rostral tip at same level as maxillary tooth row (0), located dorsal to tooth row (1).
102. Shape of tip of predentary (Xu et al., 2002): flat (0), upturned (1).

APPENDIX 2

Character codes for the cladistic analysis including *Prenoceratops pieganensis*. Character states are 0, 1, or 2, dashes indicate inapplicability, and question marks indicate lack of information for that taxon.

	10	20	30
Pachycephalosauria	- 0 0 0 1 0 0 - 0 0	0 0 0 - 0 0 0 1 0 0	0 1 0 - - 0 - 0 0 0
Psittacosauridae	0 0 0 0 1 1 1 - 0 1	1 0 0 - 1 0 1 0 0 0/1	0 0 0 - 0 1 0 0 0 0
Chaoyangosaurus	0 0 ? ? ? ? ? 0 0 ?	0 0 ? ? ? 0 ? ? ? ?	0 0 0 ? ? ? ? ? ? ?
Archaeoceratops	0 0 0 0 ? 1 ? 1 0 ?	? 0 1 - ? 0 ? 0 0 0	0 0 0 ? 1 0 ? 1 0 ?
Graciliceratops	? ? ? ? 0 ? ? ? ? ?	? ? ? ? ? 0 ? ? ? ?	? 0 ? ? ? ? ? ? 1 1
Bagaceratops	1 0 1 0 0 1 1 1 0 1	1 0 1 0 0 0 0 0 1 0	0 0 0 0 1 0 0 1 1 1
Protoceratops	1 0 1 0 0 1 2 1 0 1	1 0 1 0 0 0 0 0 1 1	0 0 0 0 1 0 0 2 1 1
Asiaceratops	? ? ? ? ? ? ? 1 0 ?	? 0 1 ? ? ? 0 ? ? ?	? ? 0 ? ? ? ? ? ? ?
Udanoceratops	1 0 0 0 0 1 1 - 0 ?	? 1 ? ? ? ? 0 ? ? 0	? ? 0 ? ? ? ? ? ? ?
Leptoceratops	1 0 0 0 0 1 0 0 0 1	1 1 1 0 0 0 0 0 1 0	0 0 0 0 1 0 1 1 0 0
Montanoceratops	? ? ? ? 0 1 ? ? 0 ?	? 0 1 1 ? ? 0 0 1 ?	? ? ? ? 1 ? 1 ? 0 ?
Prenoceratops	? 0 0 0 ? 1 2 0 0 ?	2 0 1 1 ? 0 0 0 1 1	0 0 0 1 1 1 ? ? 0 1
Centrosaurus	1 1 1 1 1 1 0 0 1 1	1 0 0 - 1 1 1 1 0 0	1 1 1 - 1 - 0 2 1 1
Triceratops	1 1 1 1 1 1 0 0 1 1	1 0 0 - 1 1 1 1 0 0	1 1 1 - 1 - 0 2 1 1
Zuniceratops	? 1 0 1 ? 1 ? ? 1 ?	1 0 1 - ? 1 ? ? 0 0	1 1 ? - ? ? ? 2 ? 1
Liaoceratops	1 0 0 0 0 1 ? 1 0 ?	0 0 1 0 0 0 ? 0 ? 0	0 0 0 - 1 ? 1 1 - 0

	40	50	60
Pachycephalosauria	- 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 - ?	0 0 0 0 ? ? 0 0 0 0
Psittacosauridae	0 0 1 0 0 0 0 1 0 0	0 1 0 0 0 0 0 0 - 0	0 0 0 0 1 0 0 1 0 0
Chaoyangosaurus	? 0 1 0 ? ? ? ? ? ?	? ? ? ? ? ? ? 0 - 0	? ? 2 0 ? 0 0 ? 1 0
Archaeoceratops	? 1 1 0 1 1 0 1 0 ?	? 1 - ? ? ? ? 1 0 1	1 ? 2 0 ? 1 0 ? ? 0
Graciliceratops	1 ? 1 ? ? ? ? ? ? 0	? ? 0 ? ? ? ? ? ? 1	1 ? 2 ? ? ? ? 1 ? 0
Bagaceratops	1 1 1 0 1 1 0 1 0 0	0 1 0 1 0 1 0 1 1 2	1 0 2 1 0 1 1 0 0 0
Protoceratops	1 1 1 0 1 1 0 1 0 0	0 1 0 1 0 0 0 1 1 2	1 0 1 1 1 1 1 1 0 0
Asiaceratops	? 1 1 0 ? 0 ? ? ? ?	? ? 0 ? ? ? ? ? - ?	? ? ? ? ? ? 0 0 1 ?
Udanoceratops	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 0 1	1 ? 1 ? 1 ? ? 1 1 0
Leptoceratops	0 1 1 1 2 0 0 0 0 0	0 1 0 1 0 0 ? 1 0 1	1 0 1 1 1 1 0 1 1 0
Montanoceratops	? 1 1 1 2 0 0 0 ? ?	0 ? ? 1 ? 1 ? 1 0 1	1 0 2 ? ? ? ? ? ? 0
Prenoceratops	? 1 1 1 2 0 ? ? ? ?	? ? 0 ? ? ? ? 1 0 0	0 1 1 1 1 0 0 1 0 0
Centrosaurus	1 2 1 0 1 1 1 2 1 1	1 0 1 0 1 2 1 1 1 1	1 0 2 0 2 2 1 0 0 1
Triceratops	0 2 1 0 1 1 1 2 1 1	1 0 1 0 1 2 1 1 1 1	1 0 2 0 2 2 1 0 0 1
Zuniceratops	1 ? ? ? ? ? ? ? 1 0	? ? ? ? ? ? ? ? - ?	? ? 2 0 2 ? 1 0 0 0/1
Liaoceratops	0 0 1 0 1 1 0 1 0 0	0 ? 0 1 0 1 0 0 - 0	0 ? 2 ? 1 0 0 ? 0 0

	70	80	90
Pachycephalosauria	0 0 0 ? ? 0 0 0 0 0	0 0 0 ? ? 0 0 ? 1 0	? 0 ? 0 0 0 0 ? 0 0
Psittacosauridae	1 0 0 0 ? 2 0 0 0 0	0 0 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 1 1
Chaoyangosaurus	0 ? ? 0 ? 1 0 0 0 0	1 0 0 0 0 ? ? ? ? ?	? ? ? ? ? ? ? ? 1 1
Archaeoceratops	1 ? ? 1 ? 1 0 0 0 ?	? ? 0 0 0 0 1 ? ? ?	? ? ? 0 ? ? 0 1 1 1
Graciliceratops	1 ? 0 1 1 ? 0 0 0 0	0 ? 0 ? ? ? ? ? ? ?	2 ? ? 0 0 0 0 0 1 1
Bagaceratops	1 1 0 1 ? 2 0 0 0 0	1 1 0 ? ? ? ? ? ? ?	? ? ? ? 0 ? ? ? 1 1
Protoceratops	1 1 1 1 0 1 0 0 0 0	1 1 0 1 0 0 1 0 0 1	1 0 0 0 0 0 1 0 1 1
Asiaceratops	? ? 1 0 ? 2 0 0 0 0	0 1 0 ? ? ? 0 ? ? 1	? ? ? ? ? ? 0 ? ? ?
Udanoceratops	1 ? 1 0 0 2 0 ? 2 0	1 1 0 ? ? ? ? ? 0 1	? 0 1 ? ? ? ? ? 1 ?
Leptoceratops	1 1 1 0 1 2 0 0 2 0	1 1 0 1 0 0 1 0 0 1	1 0 0 0 0 0 0 0 1 1
Montanoceratops	1 1 0 1 1 2 0 0 2 0	1 1 0 1 0 0 1 0 0 1	2 0 0 0 0 0 0 0 1 ?
Prenoceratops	1 ? 0 0 0 2 0 0 2 0	1 ? 0 ? ? ? ? 0 0 1	2 0 0 0 0 ? 0 0 1 1
Centrosaurus	2 1 0 1 1 2 1 1 1 1	1 1 - 2 1 1 0 1 1 1	2 1 0 1 1 1 2 1 1 1
Triceratops	2 1 0 1 1 2 1 1 1 1	1 1 - 2 1 1 0 1 1 1	2 1 0 1 1 1 2 1 1 1
Zuniceratops	2 ? 0 ? ? 2 0 1 1 1	1 1 - ? ? ? ? ? 1 1	? ? 0 ? ? ? ? ? 1 1
Liaoceratops	1 0 0 1 ? 0 0 0 1 0	0 0 0 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?

	100	102
Pachycephalosauria	? 0 0 ? 0 0 0 ? 0 0	? ?
Psittacosauridae	0 1 0 0 0 0 0 0 2 0	0 0
Chaoyangosaurus	0 1 ? 0 ? 0 0 0 2 ?	0 1
Archaeoceratops	1 1 ? ? ? 1 ? ? 0 0	0 1
Graciliceratops	? ? ? ? ? 2 0 ? ? 0	? ?
Bagaceratops	1 1 0 1 1 2 0 ? ? 0	? 1
Protoceratops	1 1 1 1 1 2 0 1 2 0	1 1
Asiaceratops	? 1 ? ? ? ? 0 ? ? ?	? ?
Udanoceratops	1 1 ? ? 0 2 1 ? ? ?	1 ?
Leptoceratops	1 1 0 1 0 2 1 1 2 1	1 1
Montanoceratops	? ? 0 ? ? 2 1 1 ? 1	? ?
Prenoceratops	? 1 ? 1 0 2 1 ? ? 1	? 1
Centrosaurus	1 1 1 1 0 2 0 1 1 0	1 1
Triceratops	1 1 1 1 0 2 0 1 1 0	1 1
Zuniceratops	1 ? ? ? ? 2 0 ? ? ?	? ?
Liaoceratops	? ? ? ? ? ? ? ? ? ?	? ?

APPENDIX 3

Character support for cladogram nodes in the cladistic analysis including *Prenoceratops pieganensis*.

Node 1 (Ceratopsia) supported by twelve characters: 6, 10, 18, 22, 33, 42, 61, 79, 80, 89, 90, and 92.
Node 2 (Neoceratopsia) supported by three characters: 13, 53, and 102.
Node 3 (*Chaoyangosaurus* plus *Asiaceratops*) supported by one character: 59.
Node 4 (*Liaoceratops* plus all closer to Ceratopsidae) supported by nine characters: 5, 25, 28, 35, 36, 44, 46, 64, and 96.
Node 5 (*Archaeoceratops* plus all closer to Ceratopsidae) supported by seven characters: 32, 48, 50, 51, 56, 77, and 91.
Node 6 (Leptoceratopsidae plus all closer to Ceratopsidae) supported by ten characters: 19, 54, 62, 71, 72, 74, 81, 96, 98, and 101.
Node 7 (Leptoceratopsidae) supported by nine characters: 8, 27, 34, 35, 36, 38, 69, 97, and 100.
Node 8 (*Prenoceratops*, *Udanoceratops*, and *Leptoceratops*) supported by three characters: 53, 58, and 64.
Node 9 (*Udanoceratops* plus *Leptoceratops*) supported by three characters: 12, 59, and 63.
Node 10 (*Bagaceratops* plus all closer to Ceratopsidae) supported by six characters: 3, 29, 30, 31, 49, and 57.
Node 11 (Protoceratopsidae plus all closer to Ceratopsidae) supported by two characters: 28 and 93.
Node 12 (Protoceratopsidae) supported by one character: 58.
Node 13 (*Zuniceratops* plus Ceratopsidae) supported by 16 characters: 2, 4, 9, 16, 19, 20, 21, 22, 39, 54, 55, 61, 69, 70, 73, and 79.
Node 14 (Ceratopsidae) supported by 34 characters: 5, 8, 14, 15, 17, 18, 23, 32, 37, 38, 40, 41, 42, 43, 44, 45, 46, 47, 56, 60, 67, 68, 74, 75, 76, 77, 78, 82, 84, 85, 86, 87, 88, and 99.