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A new Maastrichtian species of the centrosaurine ceratopsid *Pachyrhinosaurus* from the North Slope of Alaska

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The Cretaceous rocks of the Prince Creek Formation contain the richest record of polar dinosaurs found anywhere in the world. Here we describe a new species of horned dinosaur, *Pachyrhinosaurus perotorum* that exhibits an apomorphic character in the frill, as well as a unique combination of other characters. Phylogenetic analysis of 16 taxa of ceratopsians failed to resolve relationships between *P. perotorum* and other *Pachyrhinosaurus* species (*P. canadensis* and *P. lakustai*). *P. perotorum* shares characters with each of the previously known species that are not present in the other, including very large nasal and supraorbital bosses that are nearly in contact and separated only by a narrow groove as in *P. canadensis*, and a rostral comb formed by the nasals and premaxillae as in *P. lakustai*. *P. perotorum* is the youngest centrosaurine known (70–69 Ma), and the locality that produced the taxon, the Kikak-Tegoseak Quarry, is close to the highest latitude for recovery of ceratopsid remains.

Key words: Dinosauria, Centrosaurinae, Cretaceous, Prince Creek Formation, Kikak-Tegoseak Quarry, Arctic.

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Introduction

As with nearly all fossil vertebrates, the fossil record of dinosaurs is biased geographically towards localities in the middle and lower latitudes. Understanding of dinosaurs and their ecosystems at high latitudes is much poorer. This is somewhat ironic because of the intense interest in polar ecosystems and climates at high latitudes today.

Here we present a new pachyrhinosaurian ceratopsian dinosaur from the Prince Creek Formation of the North Slope in Alaska. The Prince Creek Formation ranges in age from latest Campanian to Paleocene (summarized in Flaig et al. 2011) and consists largely of fluvial sediments shed from the uplift of the Brooks Range (Fiorillo et al. 2010; Flaig et al. 2011). This unit was deposited at latitudes similar to, or even higher than the current geographic position (Witte et al. 1987; Lawver and Scotese 1990; Lawver et al. 2002), and it represents a gateway that connected the faunas and floras of the latest Cretaceous of Asia to those of North America (Fiorillo 2008a).

The Cretaceous rocks in the Prince Creek Formation contain the densest known concentrations of dinosaur bones of any high latitude rock unit in the northern or southern hemisphere (Rich et al. 1997, 2002). Though rich in terms of fossil yield, the dinosaur fauna from the Prince Creek Formation shows modest taxonomic diversity compared to similarly

aged faunas at lower latitudes (Fiorillo and Gangloff 2000; Fiorillo 2004). It includes small and large theropods, hypsilophodontids, hadrosaurs, pachycephalosaurs, and ceratopsians (Davies 1987; Parrish et al. 1987; Clemens and Nelms 1993; Fiorillo and Gangloff 2000 2001; Gangloff et al. 2005; Fiorillo 2008a, b; Fiorillo et al. 2009, 2010; Gangloff and Fiorillo 2010; Erickson and Druckenmiller 2011). Additional taxa from the Prince Creek Formation include fishes and mammals (Clemens 1994; Clemens and Nelms 1993), as well as a variety of invertebrates and trace fossils (Flaig et al. 2011).

The diversity of pachyrhinosaurus has increased in recent years. *Pachyrhinosaurus canadensis* Sternberg, 1950 was viewed as a bizarre ceratopsian when first described, being the only ceratopsian then known with enlarged nasal and supraorbital bosses instead of facial horns or similar processes (Sternberg 1950; Langston 1967, 1968, 1975). The discovery of *Achelousaurus horneri* Sampson, 1995 another boss-bearing centrosaurine from the Campanian Two Medicine Formation of Montana showed that pachyrhinosaurus had a greater distribution in time and space (Sampson 1995). *Pachyrhinosaurus lakustai* Currie et al. 2008 was erected upon multiple individuals from the Pipestone Creek bonebed in the Wapiti Formation (Late Campanian) of west-central Alberta, and other *P. lakustai*-like specimens from higher in the Wapiti Formation have yet to be described (Currie et al.

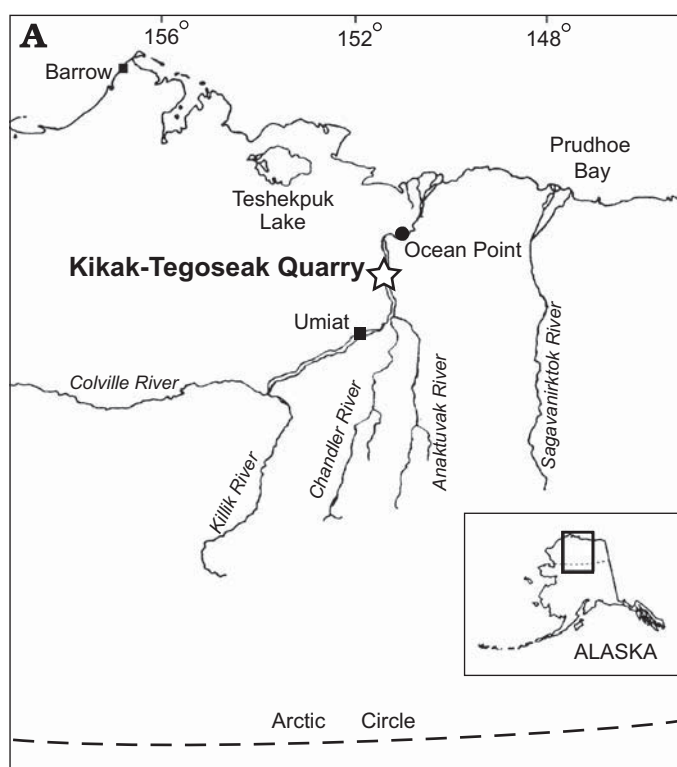


Fig. 1. **A.** Location of the Kikak-Tegoseak Quarry on Alaska's North Slope. Site indicated by open star. **B.** Photograph of Kikak-Tegoseak Quarry during excavation. A large field jacket still in the quarry is seen in the lower left corner of the image.

2008). A recently described specimen (TMP 2002.76.1) from the Dinosaur Park Formation (dated to approximately 75 Ma) of Dinosaur Provincial Park of southern Alberta bears similarities to *A. horneri* and *Pachyrhinosaurus*, and may represent a new taxon (Ryan et al. 2010; Sampson and Loewen 2010).

Here we erect a new pachyrhinosaur species based upon material from the Kikak-Tegoseak site. We present a full description, a justification for erecting a new taxon, and a phylogenetic analysis that compares the new taxon with close relatives.

Institutional abbreviations.—DMNH, Perot Museum of Nature and Science (formerly the Museum of Nature and Science), Dallas, USA; NMC, Canadian Museum of Nature, Ottawa, Canada; TMP, Royal Tyrell Museum of Palaeontology, Drumheller, Canada.

Geological setting

The Kikak-Tegoseak Quarry (Fiorillo et al. 2010) hosts a monodominant, multi-taxic bonebed within the Prince Creek Formation (Fig. 1). The quarry, which extends at least 90 m along the bluff overlooking the Colville River in northern Alaska, was discovered in the mid-1990s. The depositional setting was a low-energy alluvial/coastal plain that was wet but subject to periodic drying (Fiorillo et al. 2010). The Kikak-Tegoseak Quarry has yielded dozens of fossils from a variety of taxa such as osteichthyan fish, the theropod dinosaurs *Dromaeosaurus albertensis*, *Troodon formosus*, cf. *Gorgosaurus libratus*, an ornithomimid, and a hadrosaur, but it has also produced an abundance of skeletal remains of *Pachyrhinosaurus* Sternberg, 1950 (Fiorillo et al. 2010).

A 5 m × 4 m excavation in 2006 yielded several large field jackets, many of which remain to be fully prepared. Collectively these jackets represent approximately 2 tonnes of fossil material. Within the jackets prepared thus far, bones are generally in contact within a fine-grained matrix though no bones have been found articulated. The dense concentrations of bones indicate a high degree of skeletal association. All Voorhies taphonomic groups (Behrensmeier 1975) are represented but a thorough bone census awaits final preparation. The bone surfaces indicate little evidence of prolonged subaerial exposure (i.e., weathering cracks) or rounding from fluvial abrasion. Carbonized root traces are commonly found in the matrix and on the bone surfaces. Less common but present are the shallow borings of dermestid beetles (Fiorillo et al. 2010). Tooth-marked bone is rare in this assemblage and thus far amongst the prepared material only present on the ceratopsian remains. Based on the number of prepared occipital condyles from this quarry, the minimum number of individuals of *Pachyrhinosaurus* is now increased to ten. The range in size of the occipital condyle diameters remains consistent with assigning all remains to *Pachyrhinosaurus* (sensu Fiorillo et al. 2010; Table 1).

Systematic paleontology

Dinosauria Owen, 1842 (sensu Padian and May 1993)

Ornithischia Seeley, 1888 (sensu Padian and May 1993)

Ceratopsidae Marsh, 1888 (sensu Dodson et al. 2004)

Centrosaurinae Lambe, 1915 (sensu Dodson et al. 2004)

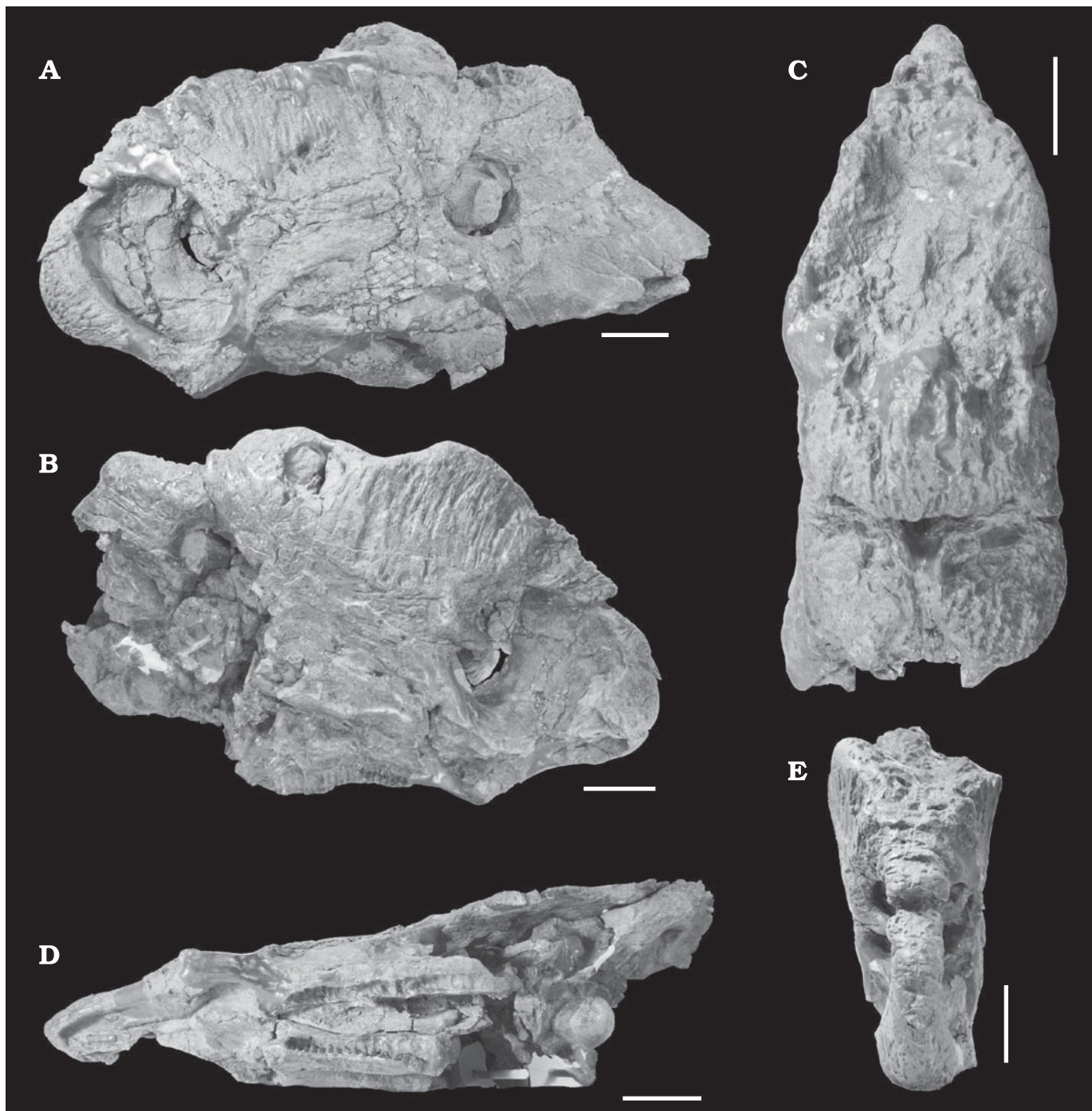


Fig. 2. Centrosaurine ceratopsid *Pachyrhinosaurus perotorum* sp. nov., paratype (DMNH 22558); skull in left lateral (A), right lateral (B), dorsal (C), ventral (D), and anterior (E) views. Scale bars 10 cm.

***Pachyrhinosaurus* Sternberg, 1950**

Type species: *Pachyrhinosaurus canadensis* Sternberg, 1950, north side of Little Bow River, east of Carmongay, Alberta, Canada, Late Cretaceous, Campanian.

***Pachyrhinosaurus perotorum* sp. nov.**

Figs. 2–5.

Etymology: In recognition of members of the Perot family (Margot and H. Ross Perot and their children), who have demonstrated a long history of supporting science and science education for the public.

Type material: Holotype: DMNH 21200, posterior part of parietal including partial median bar, posterior median emargination, and autapomorphic anterior-facing horns. Paratypes: DMNH 22558, partial skull missing parietals, squamosals, right cheek region; DMNH 21201, a short segment of right parietal transverse bar bearing an anterior rim horn.

Type locality: All specimens collected from the Kikak-Tegoseak Quarry along the Colville River, North Slope, Alaska, USA. Exact coordinates on file at the Museum of Nature and Science, Dallas. The palaeolatitude of this quarry places it in the ancient polar world and makes it one of the highest latitude centrosaurine localities known.

Table 1. Maximum diameters of ceratopsian occipital condyles recovered and prepared from the Kikak-Tegoseak Quarry. The incomplete condyle AK 539-V-11 is included here as a voucher for the existence of at least a tenth individual at this site. The means of the population of these occipital condyles and those published by Dodson (1990) are 75.9 mm and 68.9 mm, respectively. The standard deviations are 4.65 mm and 7.08 mm, respectively. The range in size of the Kikak-Tegoseak sample is consistent with the variation observed across centrosaurine taxa.

Specimen no.	Diameter (mm)
DMNH 22558	78.6
DMNH 22194	77.7
DMNH 22195	80.8
DMNH 22198	76.8
DMNH 22257	79.5
AK 539-V-01	65.1
AK539-V-12A	74.7
AK 539-V-28	73.5
AK 539-V-29	76.7
AK 539-V-11	—

Type horizon: The specimens were recovered from lower Maastrichtian rocks (69–70 Ma) within the Prince Creek Formation (Fiorillo et al. 2010; Flaig et al. 2011). This qualifies *P. perotorum* as the youngest known centrosaurine.

Diagnosis.—*Pachyrhinosaurus perotorum* is distinguished from other centrosaurine ceratopsids by the presence of a pair of short, dorsoventrally flattened horns projecting antero-medially and slightly dorsally from the anterior (fenestral) margin of the parietal transverse bar. Potential diagnostic features of *P. perotorum* also include paired fossae dorsal to narial fossa; a narrow median hump on the posterior part of the nasal boss; basal sulcus of nasal boss extends ventrally to a level lower than the dorsal rim of narial fossa; and lack of a P2 horn or process on posterior margin of parietal transverse bar, but this feature may vary as seen in specimens of *P. lakustai* (Currie et al. 2008). The new taxon may also be distinguished by a blunt-tipped profile to the rostrum with an upturned premaxillary and rostral ventral border. However, this condition is so unusual for a ceratopsian that it may prove to be an individual oddity rather than a diagnostic feature. *P. perotorum* may also be differentiated from *P. lakustai* by lack of anterior pommel on nasal boss (pommel present in some specimens of *P. lakustai*), and nasal boss and supraorbital bosses that nearly contact, separated only by narrow groove (shared with *P. canadensis*, but bosses widely separated in *P. lakustai*). The new species is also differentiated from *P. canadensis* by the presence of a rostral comb (shared with *P. lakustai*, but not present in *P. canadensis*).

Description

Much of the fossil material collected from the Kikak-Tegoseak site awaits preparation. This description is based mainly on DMNH 22558, a partial skull missing the parietosquamosal frill and lower right cheek area (Figs. 2, 3), and the holotype partial parietal frill section DMNH 21200 (Fig. 4).

The skull (DMNH 22558) is distorted in an oblique manner, such that the right side is shifted dorsally relative to the left. The sutures between most of the cranial bones are obscured by extensive fusion, a sign of relative maturity in other ceratopsids. In most respects, the skull of *P. perotorum* closely resembles both *P. canadensis* and *P. lakustai*. Therefore, we focus here only on cranial features pertinent to establishing phylogenetic relationships between *P. perotorum* and other pachyrhinosaurids. Measurements of DMNH 22558 are given in Table 2. They are based on the same landmarks used by Langston (1967, 1975) and Currie et al. (2008). Based on these measurements (Table 2) and those of occipital condyles from the quarry (Table 1), the cranial material of *P. perotorum* falls within the size range of specimens of *P. lakustai* (Currie et al. 2008).

Rostral.—The rostral bone is fused to the premaxillae, and the right side is missing its posteroventral portion. The rostral lacks an anterior point or beak-like hook (Figs. 2A, B, 3A, B). Instead, it has an almost continuously convex lateral profile from dorsal to ventral contacts with the premaxillae. In contrast, the rostral of some *P. lakustai* specimens is sharply

Table 2. Measurements (in mm) of DMNH 22558, *Pachyrhinosaurus perotorum* paratype skull. Landmarks are those used by Langston (1975) and Currie et al. (2008). Lowercase “e” after number indicates an estimate, or measured to a reconstructed surface.

A	top of nasal boss to ventral limit of maxilla	536
B	vertical height of narial opening in lateral view	92
C	maximum vertical height of skull	536
D	vertical height of nasal fossa	216e
E	top of orbit to tip of supraorbital boss	72 (left), 25.5 (right)
F	rostrum to posterior edge of naris	310
G	posterior edge of naris to anterior margin of orbit	257 (left), 280e (right)
H	anteroposterior length of orbit	116
I	posterior edge of orbit to supratemporal fenestra	?
J	antorbital length	570
K	height of orbit	111e
L	posterior edge of naris to posterior edge of nasal boss	301
M	bottom of orbit to bottom of jugal	?
N	greatest width of expansions behind nares	199
O	width across lowest flanges of premaxillae	108e
P	least transverse width of narial bridge	53
Q	greatest width of narial aperture	134
R	greatest width of nasal boss	274e
S	least transverse width of face between nares and orbits	190e
T	length of nasal boss	504

Additional measurements relevant to Currie et al. (2008: tables 3 and 4):

Length of skull roof (tip of nasal boss to posterior edge supraorbital bosses)	612
Skull length (rostrum to occipital condyle)	756

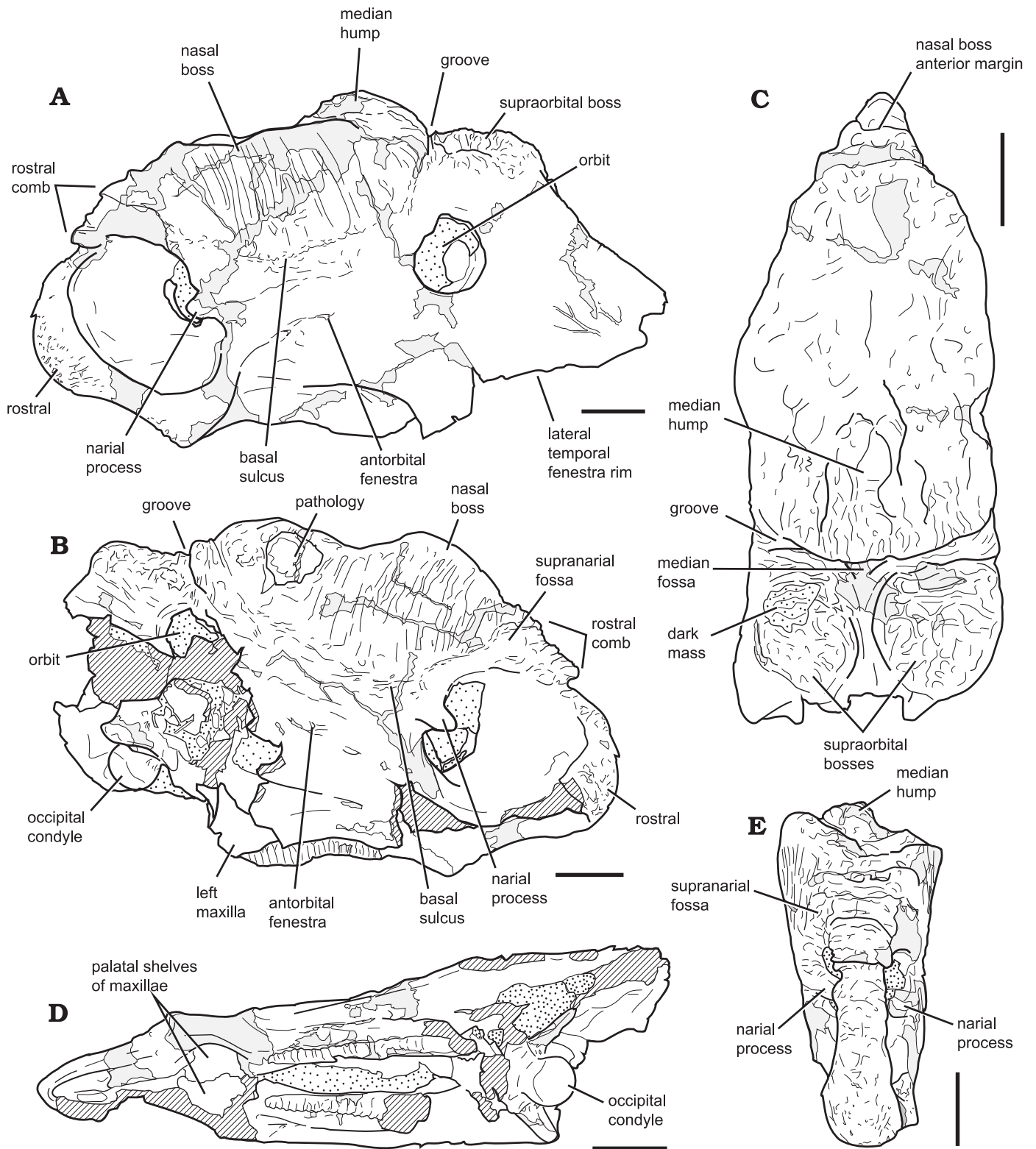


Fig. 3. Labeled line drawings of *Pachyrhinosaurus perotorum* paratype (DMNH 22558) skull in left lateral (A), right lateral (B), dorsal (C), ventral (D), and anterior (E) views. Scale bars 10 cm.

hooked (TMP 1987.55.285, TMP 1986.55.258), and there is a lesser beak on specimens of *P. canadensis* (NMC 9485 and an un-numbered specimen at the Drumheller Valley Interpretive Centre informally referred to in the literature [Currie

et al. 2008] as “the Drumheller skull”). There is no evidence for pre-mortem breaking or pathology of the element. The ventral margins of the rostral have a relatively rounded, broad cross-section (Figs. 2D, 3D).

Premaxilla.—The premaxillae are fused to one another, and most of the ventral margin of the right premaxilla has eroded away. A small part of the ventral margin of the left has been reconstructed. The premaxillae give rise to a broad narial septum as in other centrosaurines. A pronounced ventral angle protrudes below the alveolar margin of the maxilla. Dorsally, the premaxillae form part of the narial bridge and contribute to a rostral comb like those seen in some specimens of *P. lakustai* (Currie et al. 2008), but not in *P. canadensis* (Sternberg 1950; Langston 1967, 1975). The rostral comb includes a large, overhanging protrusion even with the anterior margin of the narial fossa. A second but smaller, transversely oriented protrusion is posterodorsal to the first. The lightly eroded dorsal surface of the rostral comb shows a faint median line that marks the sutural contact between premaxillae. The line continues posterodorsally and stops at another transverse ridge that marks the anterior margin of the nasal boss.

Nasal.—The nasal boss in DMNH 22558 is very large, extending from above the anterior part of the narial fossa to above the middle of the orbit (Figs. 2A–C, 3A–C). The boss has no anterior pommel, unlike some specimens of *P. lakustai* (Currie et al. 2008). The basal sulcus (Hieronymus et al. 2009), a system of small grooves and foramina that defines the ventrolateral margin of the boss, curves low on the lateral surface of the face to a level below the dorsal rim of the narial fossa. The lateral surfaces of the boss are marked by extensive dorsoventral grooves and ridges, which produce the palisaded texture typical of *Pachyrhinosaurus* bosses. The sides of the boss are otherwise relatively flat and expand dorsolaterally, making the boss the widest part of the skull anterior to the parietosquamosal frill. There is a large, sub-spherical cavity that deeply invades the bone near the posterior end of the right side of the boss (Figs. 2B, 3B). The edges of this apparent pathology are well rounded, finished bone. Within the cavity are several osseous structures, including multi-layered, onion-skin-like bone, the broken edges of which show they are comprised of coarse fibers generally oriented perpendicular to the outside surfaces.

The dorsal surface of the nasal boss is irregular and pitted as in other *Pachyrhinosaurus* (Figs. 2C, 3C). In dorsal view it is widest at a point over the centre of the maxillae. The anterior part of the boss is relatively flat, and slopes anteroventrally to meet the premaxillae where it contributes to the rostral comb. The asymmetrical dorsolateral edges are raised above the middle of the dorsal surface, producing a concavity in the center of the boss. A low median ridge in the concavity probably marks the union of the two nasals.

Posteriorly, the boss bears a conspicuous median hump, or dome. The hump is sub-triangular in dorsal view, narrows anteriorly, and is the highest point on the skull anterior to the frill (Figs. 2A, C, 3A, C). It is mediolaterally narrow, with lower surfaces of the boss lateral to it. The anterior half of the hump is pitted like the rest of the boss surface, but the posterior half bears anteroposteriorly oriented ridges, or "fins" (Hieronymus et al. 2009) (Figs. 2C, 3C). This matches the texture seen on the posterior surfaces of nasal bosses in both

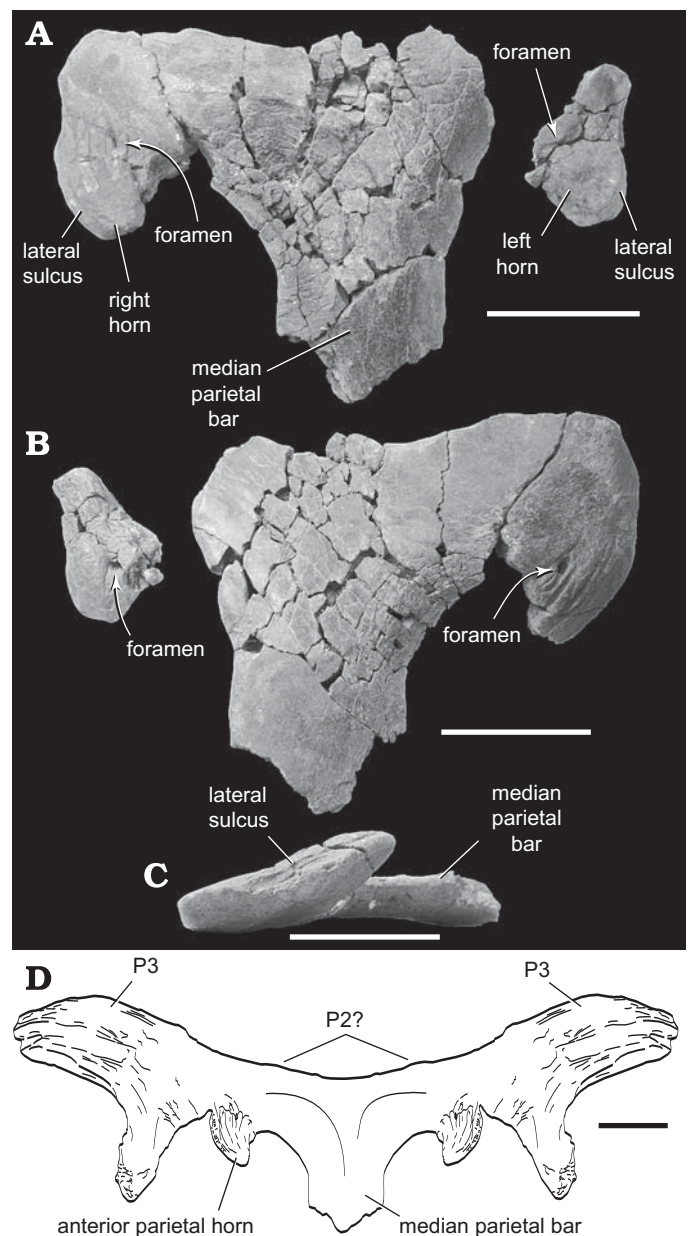


Fig. 4. Centrosaurine ceratopsid *Pachyrhinosaurus perotorum* sp. nov., holotype (DMNH 21200); parietal in dorsal (A), ventral (B), and right lateral (C) views. D. Reconstruction of the posterior parietal frill based upon DMNH 21200 and a yet to be catalogued partial parietal with a P3 horn. Scale bars 10 cm.

P. canadensis and *P. lakustai* (Langston 1967, 1975; Currie et al. 2008; Hieronymus et al. 2009).

The nasal boss extends posteriorly to at least over the midpoint of the orbit. It stops abruptly at a sharp ridge backed on each side by narrow transverse grooves reminiscent of the transverse tunnel described in the same place in *P. canadensis* (Langston 1967, 1975). The grooves are shallow laterally between the nasal and supraorbital bosses, but then enter a deep triangular fossa on the midline (Figs. 2C, 3C). The groove on the left side is interrupted at one point where the nasal and supraorbital bosses actually contact. The trace of

the right-side groove can be followed anteroventrally where it is continuous with the basal sulcus. The groove on the left side may also be continuous with the basal sulcus, but poor surface preservation makes it difficult to discern.

Within the nasal vestibule, the size and orientation of the narial process (= intranarial process) is notable. The narial process is well preserved on the right side, but partially reconstructed on the left. The process is large and robust, with a thick proximal base and triangular, flat-bottomed cross-section. A lateral groove on the lower part is a continuation of faint grooves and foramina that may mark the nasal-premaxillary suture. If so, the premaxilla forms the ventral part of the process, as reported in TMP 2002.76.1 and *Diabloceratops* (Kirkland and DeBlieux 2010; Ryan et al. 2010). The narial process angles anteromedially toward the midline, similar to the condition in *P. canadensis* (Figs. 2E, 3E) (Langston 1975).

Above the narial fossa and posterolateral to the rostral comb is a shallow depression best seen on the right side (Figs. 2B, 3B). The fossa is defined dorsally and posteriorly by a curved ridge and a series of grooves and foramina that are continuous with the basal sulcus. The ridges from each side meet on the midline to mark the anterior tip of the fused nasals, and together form the third horizontal protrusion that makes up the rostral comb. The fossa on each side is located in the same place as the “tumescent bulge” or “supranasal” boss (Langston 1975: 1582) in *P. canadensis* (Sternberg 1950; Langston 1967, 1975). There is no “fist-sized knob” (Sternberg 1950: 111) posterodorsal to the narial fossa. No supranasal boss or fossa is present in *P. lakustai* (Currie et al. 2008).

Supraorbital bosses.—The supraorbital bosses of DMNH 22558 are large and asymmetrical. Both are highest along the medial and posteromedial edges, and slope anterolaterally. They are separated from one another by a midline groove that rises from the same deep median fossa as the grooves that separate the nasal and supraorbital bosses. The T-shaped pattern of grooves and ridges created by the transverse and median grooves matches that in *P. canadensis*, but which are re-

portedly absent in *P. lakustai* (Sternberg 1950; Langston 1967, 1975; Currie et al. 2008).

The right supraorbital boss is almost circular in dorsal view (Figs. 2C, 3C), with clearly defined edges. The anterior edge is sharp and steep walled with a deeply recessed surface posterior to it. The posterior and posteromedial margins are raised abruptly above the adjacent skull surface. The dorsal surface is nearly planar and marked by pits and ridges, some of which are weakly aligned anterolaterally to posteromedially. The left boss is well defined medially and posteriorly, but has only a low anterior rim and almost indiscernible lateral and posterolateral margins (Figs. 2C, 3C). The dorsal surface bears pits and ridges, but the center is much lower than that of the right boss. An unusual mass of dark-coloured, pitted material was found in the center of the left supraorbital boss during preparation (Figs. 2C, 3C). The dark material averages 10 mm or less in thickness, and appears to follow the contours of the underlying bone ridges.

Parietal.—The holotype parietal (DMNH 21200) consists of the posterior part of the median parietal bar, part of the right-side transverse parietal bar, and a horncore from the left side of the transverse parietal bar found in position but separated from the rest of the parietal by an interval of missing bone (Fig. 4). The dorsal surface of the parietal is marked by faint vascular grooves, while the ventral surface is nearly smooth. The median bar is relatively broad with an asymmetrical cross-section. The right side of the median bar is dorsally excavated by a broad fossa where it curves to become the transverse bar. The fossa overlaps the midline. There is no such fossa on the left side of the median bar.

We follow the convention of Sampson (1995) when referencing parietal horns and processes. The posterior edge of the parietal has only a very shallow median emargination. There is no P1 horn or enlargement, a character shared with other pachyrhinosaurids. There is little development of a process at the P2 locus, in contrast to most other centrosaurines which bear at least rudimentary P2 spines or hooks (Sampson

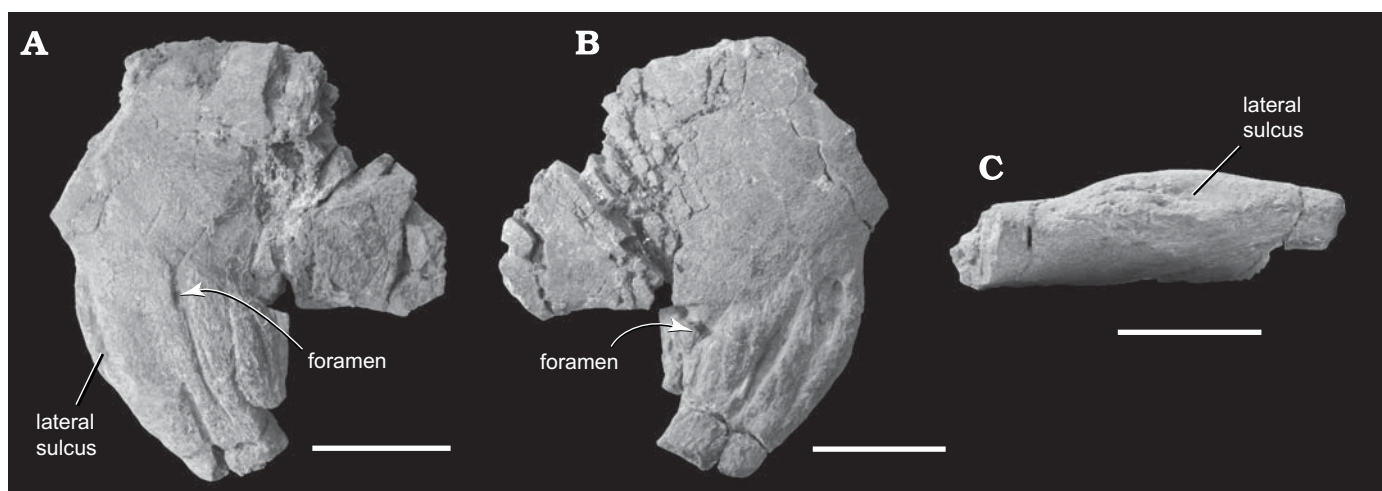


Fig. 5. Centrosaurine ceratopsid *Pachyrhinosaurus perotorum* sp. nov., paratype (DMNH 21201); partial parietal preserving portion of right transverse parietal bar and anterior rim horn in dorsal (A), ventral (B), and right lateral (C) views. Scale bars 5 cm.

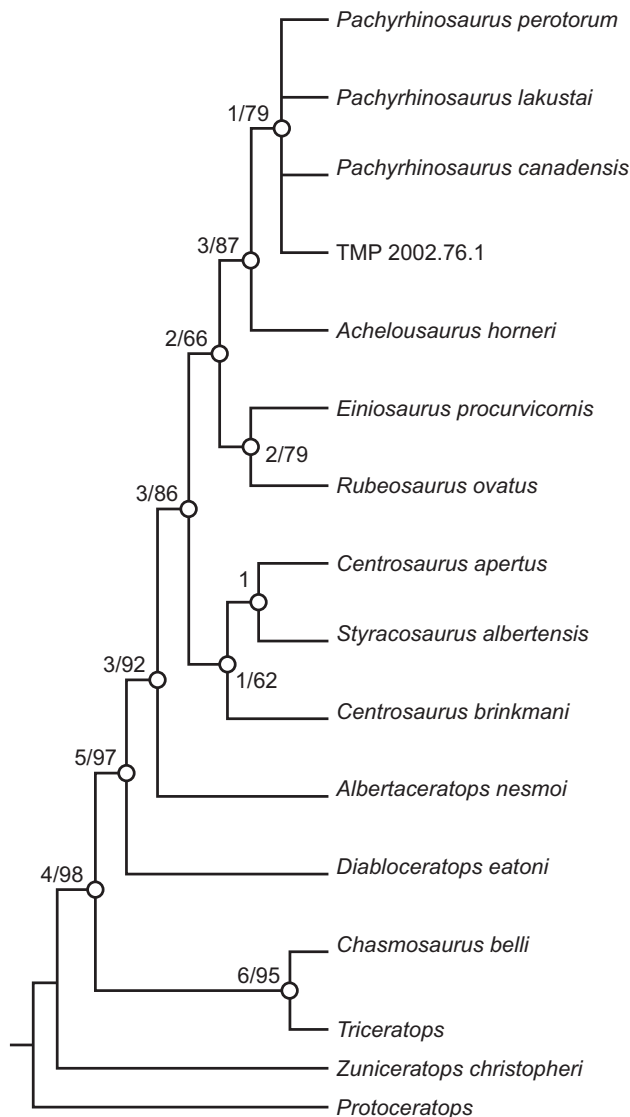


Fig. 6. Results of phylogenetic analysis. Strict consensus of the three equally most parsimonious trees generated by our analysis (length = 107, C.I. (consistency index) = 0.8131, R.I. (retention index) = 0.8291). Numbers at nodes are Bremer support values / Bootstrap percentages recovered from 1000 replicates.

1995; Currie et al. 2008; McDonald and Horner 2010). This resembles some parietals referred to *P. lakustai* (Currie et al. 2008). Another incomplete parietal still under preparation bears a large, triangular P3 horn that would project posterolaterally from a complete frill (Fig. 4D). The location and size of this horn matches the P3 horn in other *Pachyrhinosaurus*, especially *P. canadensis* (Langston 1975; Currie et al. 2008). It does not exhibit the anteroventral twist described in many P3 horns of *P. lakustai* (Currie et al. 2008).

The holotype parietal bears small but well-developed horns on the anterior rim of transverse parietal bar (Fig. 4), which is a diagnostic character for *Pachyrhinosaurus perotorum*. This anterior horn is best preserved on the right hand side of the holotype. It is dorsoventrally flattened with a narrower lateral margin and bears numerous longitudinal grooves on both dor-

sal and ventral surfaces. It arises from the anterior rim of the transverse bar lateral to the P2 position on the posterior rim of the parietal, curves anterodorsally and medially, and projects dorsally only a little above the plane of the frill (Fig. 4C). This differs from the P1 spikes and processes in *Centrosaurus* or *Styracosaurus*, which rise from the dorsal surface of the parietal nearer the midline (Sampson 1995; Sampson et al. 1997). We refrain from applying or modifying the convention of Sampson (1995) for describing these processes because of the unique position of this horn in *P. perotorum*.

A large foramen penetrates the dorsal surface of the anterior parietal rim horn of *Pachyrhinosaurus perotorum* near the base. The foramen leads to a canal that passes through the horn core and exits through a more anteromedially positioned foramen on the ventral surface (Fig. 4A, B). Smooth sulci issue from both foramina, suggesting a large vascular element passed through the horn in life. The dorsolateral edge of the horn is marked by a wider longitudinal sulcus broader than the other grooves on the surface, which results in a weak lateral keel for the horn.

The left horn is much smaller than the right, has fewer longitudinal grooves, but retains a broad lateral sulcus like that on the right horn. Its base is also penetrated by large foramina on the dorsal and ventral surfaces in the same relative positions as those on the right side horn. Asymmetry of parietal ornamentation in the same individual was evidently not uncommon in centrosaurines (Sampson et al. 1997; Ryan et al. 2001; Currie et al. 2008).

Another specimen (DMNH 21201) is identified as a short section of a second right side parietal transverse bar that also bears an anterior rim parietal horn (Fig. 5). It shares the presence of foramina on the dorsal and ventral sides of the horn in the same locations as in the holotype. The horn on DMNH 21201 also has a broad sulcus along the dorsolateral edge, although it is smaller and restricted to the proximal end of the horn. The axis of the horn does not angle as far dorsally as in the holotype, and projects almost directly anteriorly and medially. The presence of at least two individuals from the Kikak-Tegoseak quarry that bear anterior parietal horns is strong evidence against either specimen being from an aberrant individual. Instead, it suggests that these specimens preserve a taxonomically diagnostic frill autapomorphy that differentiates *Pachyrhinosaurus perotorum* from all other centrosaurines.

Geographic and stratigraphic range.—Type locality and horizon only.

Phylogenetic analysis

We performed a phylogenetic analysis to determine the relationships between *Pachyrhinosaurus perotorum* and other centrosaurines. We based our analysis on that of Currie et al. (2008) which was derived in large part from previous works by Sampson (1995), Dodson et al. (2004), and Ryan (2007). We expanded the taxonomic content of the analysis to encom-

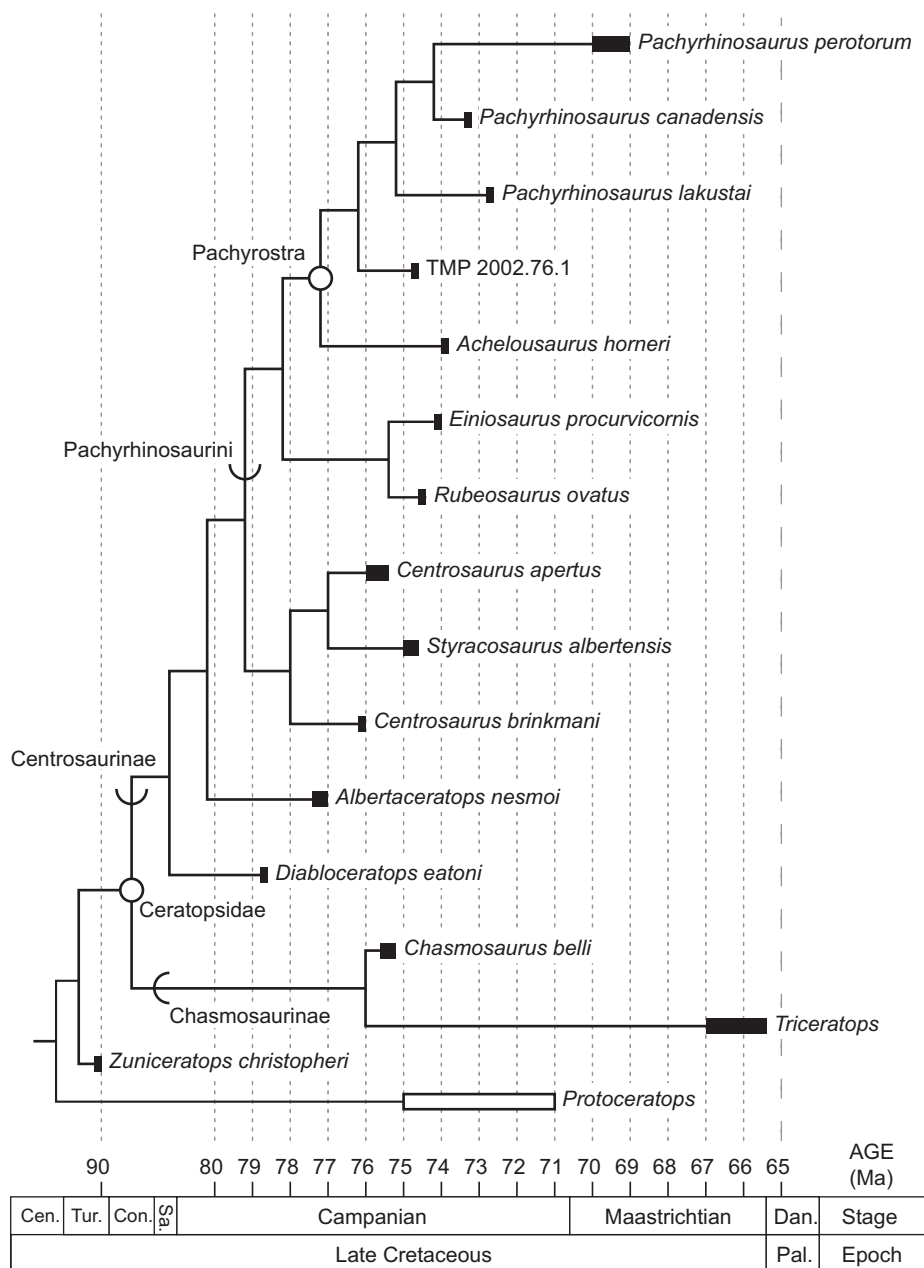


Fig. 7. Results of phylogenetic analysis. One of three equally most parsimonious trees (length = 107, C.I. (consistency index) = 0.8131, R.I. (retention index) = 0.8291) from our analysis set upon the Late Cretaceous timescale. Ranges of ceratopsian taxa other than *Pachyrhinosaurus perotorum* from Sampson and Loewren (2010). Timescale dates derived from Walker and Geissman (2009). Solid thick bars indicate well constrained range of a taxon. Open thick bars indicate poorly constrained or estimated range of a taxon. Open circles at nodes indicate named node-defined clades. Arcs on branches indicate stem-defined lineage names. Divergence points on tree are arbitrarily drawn, and are not based on calculations of lineage divergence dates. Abbreviations: Cen., Cenomanian; Con., Coniacian; Dan., Danian; Pal., Paleocene; Sa., Santonian; Tur., Turonian.

pass recently described centrosaurine taxa and specimens that have added to our understanding of centrosaurine diversity and relationships (*P. perotorum*, TMP 2002.76.1, *Diabloceratops eatoni*, *Centrosaurus brinkmani*, and *Rubeosaurus ovatus*) (Ryan and Russell 2005; Ryan 2007; Currie et al. 2008; Kirkland and Deblieux 2010; Ryan et al. 2010; McDonald and Horner 2010). This brought the number of taxa to 16, with *Protoceratops andrewsi* and *Zuniceratops christopheri* designated as outgroups. The added taxa were coded from the literature.

The increased number of taxa required modification of characters 21, 34, and 36 from the dataset of Currie et al. (2008) in order to accommodate wider variation in these characters. We also added eight characters (characters 47 through 54) applicable to putative pachyrhinosaurians in order to more thoroughly test ingroup relationships. The entire character list is given in the Supplementary Online Material (SOM: http://app.pan.pl/SOM/app57-Fiorillo_Tykoski_SOM.pdf), as is the taxon-character matrix. All multistate characters were treated as unordered. Two characters were polymorphic in two

taxa, and these were treated as polymorphisms and not as uncertainties. Non-applicable characters were coded as missing data rather than given the discrete character state “N” as done by Currie et al (2008). The taxon-character matrix was created and manipulated in MacClade 4.08 (Maddison and Maddison 2005), and a branch and bound parsimony analysis run using PAUP 4.0b10 (Swofford 2002). Bootstrap (1000 replicates) and Bremer support values were also calculated for the resulting trees.

Results of analysis.—The analysis produced three equally most parsimonious trees (MPTs) with a length of 107 evolutionary transformations, a consistency index (C.I.) of 0.8131, and a retention index (R.I.) of 0.8291. The three trees differ in the relative position of *Pachyrhinosaurus lakustai* which is determined either as the sister taxon to *P. perotorum*, or to TMP 2002.76.1, or to a clade comprising *P. canadensis* and *P. perotorum*. A strict consensus of the three MPTs is given in Fig. 6. One of the three MPTs is shown in Fig. 7, set on a geological timescale and showing the temporal distribution of centrosaurine taxa as listed by Sampson and Loewren (2010). A list of apomorphies diagnosing the clades in the tree shown in Fig. 7 is provided in the SOM. Relationships and character distributions discussed below are also based on the cladogram in Fig. 7.

Centrosaurine monophyly was recovered, with *Diabloceratops eatoni* the most basal taxon of the lineage, followed by *Albertaceratops nesmoi*. A weakly supported clade consisting of *Centrosaurus apertus*, *Centrosaurus brinkmani*, and *Styracosaurus albertensis* was found to be on the sister lineage to the branch containing *Einosaurus procurvicornis*, *Rubeosaurus ovatus*, and the nasal boss-bearing pachyrhinosaur, a result consistent with some prior analyses (Sampson 1995; Dodson et al. 2004; McDonald and Horner 2010).

Einosaurus procurvicornis and *Rubeosaurus ovatus* formed a clade at the base of the pachyrhinosaur stem, a result consistent with McDonald and Horner (2010). *Achelousaurus horneri* was recovered as the most basal of the nasal boss-bearing taxa, a clade united by the presence of enlarged nasal ornamentation covering the rostrum, and transformation of the nasal and supraorbital ornamentation into bosses in adults. There was weak support for placement of the un-named taxon represented by TMP 2002.76.1 as either the sister to the three *Pachyrhinosaurus* species, or for *P. lakustai* and TMP 2002.76.1 together forming a clade that is the sister group to a *P. canadensis* + *P. perotorum* clade. TMP 2002.76.1 was united with the *Pachyrhinosaurus* taxa by reduction of the antorbital fenestra to a small foramen, or its outright loss.

The three *Pachyrhinosaurus* species were united by the presence of a nasal boss that reaches posteriorly to a point over the orbit. The clade was ambiguously diagnosed by premaxillae bearing a rostral comb, adult nasal ornamentation that is the mediolaterally widest part of the rostrum, the presence of large, medially curled P2 hooks (uncertain in *P. perotorum*), and laterally or anterolaterally directed P3 horns. *P. canadensis* and *P. perotorum* were found to be sister taxa

(54% Bootstrap support) united by having nasal and supraorbital bosses that are nearly in contact, separated by only a very narrow groove. In contrast, the nasal and supraorbital bosses in *P. lakustai* are separated by a relatively wide, smooth trough and by an even wider expanse in TMP 2002.76.1 (Currie et al. 2008; Ryan et al. 2010). The clade was ambiguously diagnosed by loss of an anteriorly or anterodorsally protruding “pommel” on the nasal boss. There is a distinct pommel on the nasal bosses of both TMP 2002.76.1 and some specimens of *P. lakustai* (Currie et al. 2008; Ryan et al. 2010). It should be noted that an equally parsimonious hypothesis from our analysis recovered *P. perotorum* and *P. lakustai* as sister taxa, united by the presence of a rostral comb.

Discussion

Phylogeny and systematics.—Our analysis was unable to fully resolve relationships between *P. perotorum* and previously described species of *Pachyrhinosaurus* (Fig. 6). Some differences between the three taxa include a rostral comb in *P. perotorum* (a feature absent in *P. canadensis* but shared with *P. lakustai*), and nasal and supraorbital bosses that are nearly in contact with each other (a condition shared with *P. canadensis*, but not by *P. lakustai*) (Fig. 8). The nasal boss of *P. perotorum* is also relatively deeper dorsoventrally than in the other taxa, as indicated by the basal sulcus of the boss that extends ventrally on the face to a level lower than the dorsal rim of the nasal fossa (Figs. 2, 3, 8). The large P3 processes of the parietals resemble those of *P. canadensis* in that the horns curve mostly laterally (Langston 1975), and do not exhibit the anteroventral twist present in some *P. lakustai* specimens (Currie et al. 2008).

A diagnostic character of *P. perotorum* is the presence of anteromedially directed horns projecting into and over the parietal fenestrae from the anterior margin of the transverse parietal bar (Figs. 4, 8). The latter is especially important in justifying the establishment of *P. perotorum* as distinct from other pachyrhinosaur, because of the importance of frill ornamentation in distinguishing ceratopsid taxa. The anterior edge parietal horn in *P. perotorum* is not only unique among pachyrhinosaur, but is also unknown among other ceratopsids generally.

The diversity of the centrosaurine lineage leading to *Pachyrhinosaurus* to the exclusion of *Centrosaurus* and its closest kin has expanded in recent times. Sternberg (1950) considered *P. canadensis* so unlike other horned dinosaurs that he erected a separate family for it, Pachyrhinosauridae. The family-rank name was later dropped when it was demonstrated that *P. canadensis* was allied with the “short-frilled” centrosaurines (Langston 1968, 1975). Recent cladistic analyses, including ours, demonstrate there is a basal divergence of the centrosaurine lineage between those taxa more closely related to *Centrosaurus* and those closer to *Pachyrhinosaurus* (Sampson 1995; Dodson et al. 2004; McDonald and Horner 2010). The recognition of this divergence, and the in-

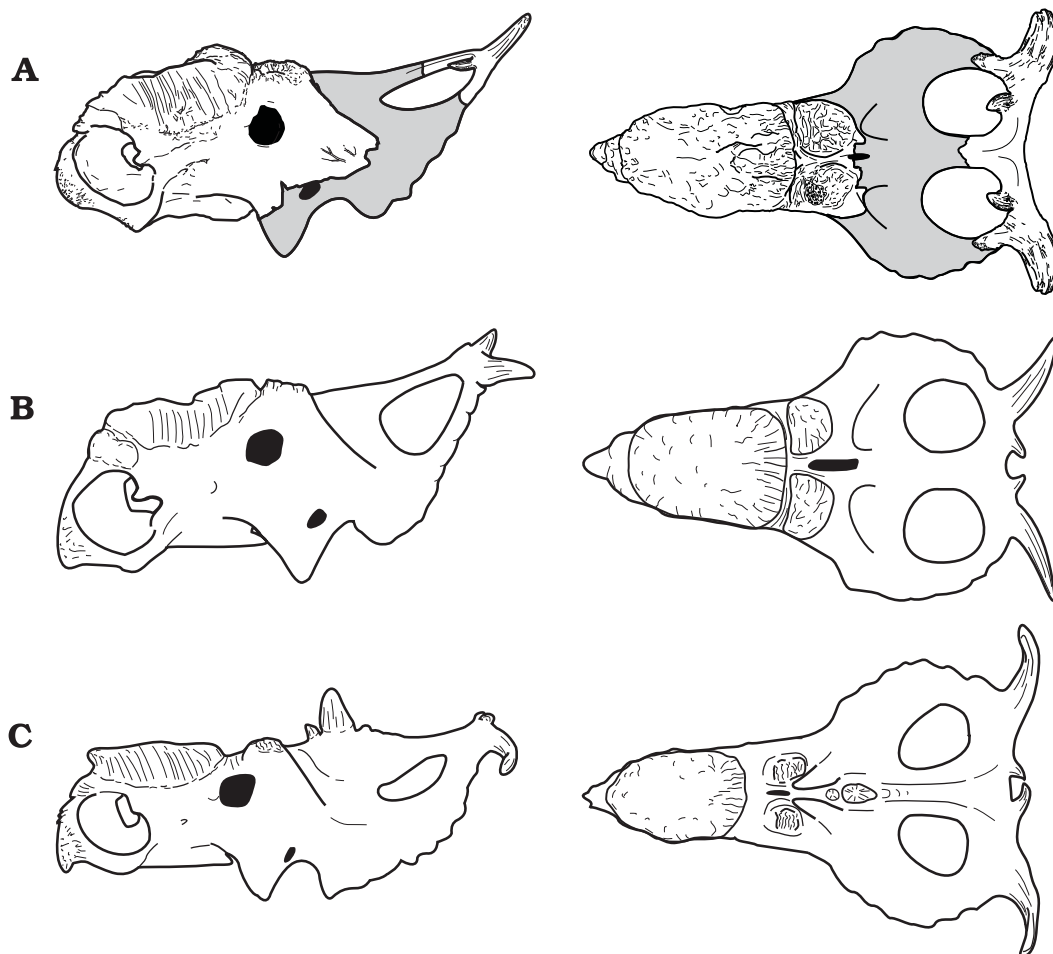


Fig. 8. Comparison of line-drawing reconstructions of skulls of *Pachyrhinosaurus perotorum* (A), *Pachyrhinosaurus canadensis* (B), and *Pachyrhinosaurus lakustai* (C) in left lateral and dorsal views. A. Based on DMNH 21200 and DMNH 22558. B. Based upon NMC 9485, NMC 9602 as shown in Langston (1975), and from Sampson and Loewen (2010). C. Derived from Currie et al. (2008). Gray fill indicates hypothetical morphology not preserved in currently known specimens of *P. perotorum*. Drawings not to scale.

creased number of derived centrosaurines now known, suggest that it may be useful to establish some formally defined clade names within Centrosaurinae.

We choose not to resurrect or re-define the name *Pachyrhinosauridae* Sternberg, 1950, so as to avoid potential confu-

sion with earlier literature. We instead propose the name *Pachyrhinosaurini*, a modification of *Pachyrhinosauridae*, to be defined as the stem-lineage of all centrosaurine ceratopsids more closely related to *Pachyrhinosaurus canadensis* than to *Centrosaurus apertus* (Table 3, Fig. 7). Within *Pachyrhino-*

Table 3. Taxonomic definitions used in this work. We recognize only monophyletic clade and lineage names with explicit ancestry-based definitions. Names are given with reference to the original work in which they were coined, followed by the work that first provided an explicit and widely accepted phylogenetic definition for the name. Taxonomic names are also identified as either node-based or stem-based, and defined.

Dinosauria Owen, 1842 – Padian and May 1993 (node):	the most recent common ancestor of <i>Triceratops</i> and Aves, and all of that ancestor’s descendants.
Ornithischia Seeley, 1888 – Padian and May 1993 (stem):	all taxa more closely related to <i>Triceratops</i> than to Aves.
Ceratopsia Marsh, 1890 – Sereno 1998 (stem):	all marginocephalians more closely related to <i>Triceratops</i> than to <i>Pachycephalosaurus</i> .
Ceratopsidae Marsh, 1888 – Dodson et al. 2004 (node):	the most recent common ancestor of <i>Centrosaurus apertus</i> and <i>Triceratops horridus</i> , and all of that ancestor’s descendants.
Centrosaurinae Lamb, 1915 – Dodson et al. 2004 (stem):	all ceratopsids more closely related to <i>Centrosaurus apertus</i> than to <i>Triceratops horridus</i> .
<i>Pachyrhinosaurini</i> nov. (stem):	all centrosaurine ceratopsids more closely related to <i>Pachyrhinosaurus canadensis</i> than to <i>Centrosaurus apertus</i> .
<i>Pachyrostra</i> nov. (node):	the most recent common ancestor of <i>Achelousaurus horneri</i> and <i>Pachyrhinosaurus canadensis</i> , and all of that ancestor’s descendants.

sauroini is a division between basal forms with enlarged nasal horns and low supraorbital horns (*Einosaurus*, *Rubeosaurus*), and more derived taxa with nasal and supraorbital bosses in adults (*Achelousaurus*, TMP 2002.76.1, *Pachyrhinosaurus*). There is relatively good support for the clade that includes the boss-bearing pachyrhinosaurins (Fig. 6), so we propose the name Pachyrostra and define it as the node-clade consisting of the most recent common ancestor of *Achelousaurus horneri* and *Pachyrhinosaurus canadensis* and all of that ancestor's descendants (Table 3, Fig. 7).

Biogeography.—For over 200 years, observations on the geographic distribution of organisms have been intimately linked to ecology and evolutionary biology (Lomolino et al. 2004). A useful concept is the ecoregion, defined by Bailey (1998) in such a way that the processes responsible for ecosystem differentiation make biogeographic patterns a predictable phenomenon. In terms of the large-scale paleontological applications of biogeography in the Cretaceous of North America, Lehman (2001) presented evidence for latitudinal zonation in the pattern of dinosaur distribution, perhaps linked to habitat loss or fragmentation.

In recent work on the histology of *Pachyrhinosaurus* from northern Alaska, Erickson and Druckenmiller (2011: 7) suggested a new faunal province to encompass the “distinctive, northern-most early Maastrichtian North American fauna”. Their evidence is very limited, including a single partial pachycephalosaurian left squamosal (Gangloff et al. 2005), later named *Alaskacephale gangloffii* (Sullivan 2006), as well as possible size increase in the small theropod *Troodon* as an adaptation to the ancient polar environment (Fiorillo 2008b). Perhaps our new work provides additional evidence for this northern faunal province. It is important to note, however, that there is a substantial temporal, as well as geographic, gap between *P. perotorum* (69–70 Ma) and other *Pachyrhinosaurus* species (72.5–74 Ma) (Fig. 7) (Sampson and Loewen 2010). Centrosaurines at lower latitudes underwent rapid diversification through the late Campanian and early Maastrichtian, with some centrosaurine taxa appearing in intervals of substantially less than 1 million years and perhaps as little as 500,000 years (Sampson and Loewen 2010). The presence of a new *Pachyrhinosaurus* species from deposits two to three millions years younger than the previously known species is not then a surprise, and probably reflects evolution of a lineage independent of geographic distance or faunal provinciality. Until further work demonstrates that taxonomic diversity patterns in the ancient Arctic were indeed unique, we suggest that a conservative approach be taken when discussing biogeographic patterns for dinosaurs in far northwestern North America during the Maastrichtian.

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