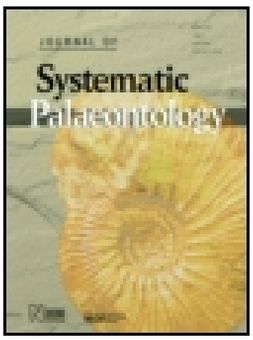

Journal of Systematic Palaeontology

ISSN: 1477-2019 (Print) 1478-0941 (Online) Journal homepage: https://www.tandfonline.com/loi/tjsp20

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To cite this article: Ronald S. Tykoski, Anthony R. Fiorillo & Kentaro Chiba (2019): New data and diagnosis for the Arctic ceratopsid dinosaur *Pachyrhinosaurus perotorum*, Journal of Systematic Palaeontology

To link to this article: https://doi.org/10.1080/14772019.2018.1532464

Journal of Systematic Palaeontology, 2019
Vol. 0, No. 0, 1–20, http://dx.doi.org/10.1080/14772019.2018.1532464

New data and diagnosis for the Arctic ceratopsid dinosaur *Pachyrhinosaurus perotorum*

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(Received 22 March 2018; accepted 13 August 2018)

The pachyrostran centrosaurine dinosaur *Pachyrhinosaurus perotorum* is the geologically youngest (Maastrichtian, 70–68.5 Ma) centrosaurine, and latitudinally highest distributed ceratopsid yet known. Continued preparation of material collected from the type locality, the Kikak-Tegoseak Quarry, has produced more examples of cranial material from multiple individuals, including partial skulls and incomplete parietals. The original reconstruction of the type parietal was incorrect, and the element is similar to that of other *Pachyrhinosaurus* species in bearing medially directed epiparietal 2 processes along its posterior margin. *Pachyrhinosaurus perotorum* is diagnosed by an upturned tip of the rostrum; a dorsally shifted rostral bone lacking a sharply downturned, parrot-like beak; an enlarged median ridge at the posterior end of the nasal boss; and, tentatively, a posterior sulcus on epiparietal 2 and a canal passing dorsoventrally through the base of epiparietal 2. A cladistic phylogenetic analysis incorporating new data from this and other recent studies of centrosaurine relationships recovers a monophyletic *Pachyrhinosaurus* clade. *Pachyrhinosaurus perotorum* and *P. canadensis* are found to be sister taxa, united by the presence of an extra ossification on the lateral surface of the rostrum between the narial fossa and nasal boss, and by enlarged supraorbital bosses that contact or nearly contact the posterior end of the nasal boss. Parietal and squamosal frill ornamentations alone do not adequately address the variables in craniofacial morphology needed to distinguish between species of *Pachyrhinosaurus*.

Keywords: Cretaceous; Alaska; Prince Creek Formation; Centrosaurinae; Pachyrostra; cladistics

Introduction

The Late Cretaceous (Maastrichtian) fossil vertebrate fauna of Alaskan Beringia has been studied for little more than a quarter-century (Brouwers *et al*. 1987; Davies 1987; Clemens 1994; Gangloff 1998; Gangloff *et al*. 2005; Fiorillo *et al*. 2009, 2010, 2016; Fiorillo & Tykoski 2012, 2013, 2014; Tykoski & Fiorillo 2013; Watanabe *et al*. 2013; Flaig *et al*. 2014, 2017; Mori *et al*. 2016; Xing *et al*. 2017), and increasing attention is building a greater understanding of latest Cretaceous fossil vertebrate palaeobiology in the extreme environment north of the Arctic Circle. An early dinosaur discovery in the region was a partial skull of a ceratopsid dinosaur identified as *Pachyrhinosaurus* sp. that came from the Prince Creek Formation along the Colville River just south of Ocean Point, Alaska (Clemens 1994). This find prompted further exploration along the Colville River in the mid-1990s, which resulted in discovery of a monodominant bone bed of *Pachyrhinosaurus* remains many kilometres to the south of Ocean Point (Fiorillo *et al*. 2010). The site, dubbed the Kikak-Tegoseak Quarry (KTQ), was extensively worked, with several tons of rock containing fossils airlifted from the site from 2005 to 2007. Preparation of the KTQ material continues at the Perot Museum of Nature and Science in Dallas, Texas, where hundreds of individual bones have been prepared, including parts of multiple ceratopsid skulls with varying levels of completeness.

The *Pachyrhinosaurus* specimens from the KTQ exhibited morphological features different from the two named species of *Pachyrhinosaurus* known at this time, *P. canadensis* Sternberg, 1950 and *P. lakustai* Currie, Langston & Tanke, 2008. As additional specimens were prepared, including a partial skull lacking the lower

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Published online 24 Jan 2019

jaws and parietosquamosal frill, these morphological differences were more firmly established. In addition, the Prince Creek Formation along this section of the Colville River was younger (68.5–70 Ma with best estimate of 69.1 ± 0.3 Ma (Conrad *et al*. 1990), with additional corroborative work showing 69.2 ± 0.5 Ma (Flaig *et al.* 2014)) than the strata that produced *P. canadensis* (71.25–72.25 Ma: Eberth *et al*. 2013) and *P. lakustai* (73.25 Ma: Currie *et al*. 2008). Taken together, this evidence prompted Fiorillo & Tykoski (2012) to erect a new species, *Pachyrhinosaurus perotorum*, for the Alaskan taxon. Subsequent work established hypotheses of craniofacial ontogenetic development in *P. perotorum* (Fiorillo & Tykoski 2013), as well as details of its braincase and endocranial anatomy (Tykoski & Fiorillo 2013).

New fossils from the KTQ reveal insightful new data that bear on the phylogenetic position of *Pachyrhinosaurus perotorum*. In addition, re-examination of the holotype parietal revealed that its ornamentation, which was considered unique for the taxon (see Fiorillo & Tykoski 2012), was the result of an error made during reconstruction of the fragmented specimen. Given the importance of parietal anatomy in the original diagnosis of the taxon, as well as the increased number of specimens made available since the original description, we offer a new diagnosis of *Pachyrhinosaurus perotorum* and evaluate the impact of the new information on its relationships among pachyrostran ceratopsids.

Material and methods

Institutional abbreviations

DMNH: Perot Museum of Nature and Science, Dallas, USA; **CMN**: Canadian Museum of Nature, Ottawa, Canada; **TMP**: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

Taxonomic definitions

We adhere to ancestry-based definitions for names applied to monophyletic clades and lineages. A list of the supraspecific taxon names and their definitions as used in this work is given in Table 1.

Material

The KTQ is a monodominant bonebed deposit from which several tons of rock and fossil bone were collected between 2005 and 2007 (Fiorillo *et al*. 2010). At least 10 *Pachyrhinosaurus perotorum* individuals are present in the KTQ based on the number of occipital condyles and partial braincases. However, multiple factors prevent us from confidently assigning most of the elements in the quarry to particular individuals. To date, no two skeletal elements have been found in natural articulation with one another, with the exception of coossified cranial bones. Many bones show signs of post-depositional breakage and the highly varied and often high-angle orientation of elements in the deposit

Table 1. Definitions of clade and lineage names used in this work.

Taxon name	Ancestry-based definition of taxon name
Centrosaurinae Lambe, 1915	All ceratopsids more closely related to *Centrosaurus apertus* than to *Triceratops horridus* (Dodson *et al.* 2004)
Centrosaurini Ryan *et al.*, 2017	All ceratopsids more closely related to *Centrosaurus apertus* than to *Pachyrhinosaurus canadensis*
Ceratopsia Marsh, 1890	All marginocephalians more closely related to *Triceratops horridus* than to *Pachycephalosaurus wyomingensis* (Sereno 1998)
Ceratopsidae Marsh, 1888	The last common ancestor of *Triceratops horridus* and *Centrosaurus apertus*, and all of its descendants (Dodson *et al.* 2004)
Chasmosaurinae Lambe, 1915	All ceratopsids more closely related to *Triceratops horridus* than to *Centrosaurus apertus* (Dodson *et al.* 2004)
Dinosauria Owen, 1842	The last common ancestor of *Triceratops horridus* and *Passer domesticus*, and all of its descendants (Padian & May 1993)
Eucentrosaura Chiba *et al.*, 2017	The last common ancestor of *Centrosaurus apertus* and *Pachyrhinosaurus canadensis*, and all of its descendants
Nasutoceratopsini Ryan *et al.*, 2017	All centrosaurines more closely related to *Nasutoceratops titusi* than to *Centrosaurus apertus*
Pachyrhinosaurini Fiorillo & Tykoski, 2012	All ceratopsids more closely related to *Pachyrhinosaurus canadensis* than to *Centrosaurus apertus*
Pachyrostra Fiorillo & Tykoski, 2012	The last common ancestor of *Achelousaurus horneri* and *Pachyrhinosaurus canadensis*, and all of its descendants

suggests they may have experienced 'dinoturbation' subsequent to shallow burial. Further complicating preparation and study of the material, many of the specimens collected near the surface were extensively fractured by the freeze-thaw weathering (Taber 1929, 1930) experienced in the severe Arctic conditions of the area. Even when elements are found within centimetres of each other, or even in physical contact with one another, it is uncertain whether they originated from the same individual.

The holotype specimen of *Pachyrhinosaurus perotorum* (DMNH 21200) is an incomplete parietal preserving part of the midline parietal bar, transverse parietal bar, and epiparietal 2 processes (Fiorillo & Tykoski 2012). Other previously published specimens include: DMNH 21201, a partial parietal and with an epiparietal 2 process; DMNH 21460, a partial nasal and pre-orbital skull roof of an immature individual; DMNH 22194, a partial braincase; and DMNH 22558, a partial skull lacking the parietal-squamosal frill (Fiorillo & Tykoski 2012, 2013; Tykoski & Fiorillo 2013). The catalogued specimens from the KTQ now number in the hundreds, and it is impractical to list them all here. Additional specimens referenced in the present study include: DMNH 24803, a partial skull lacking much of the left side of the skull and the parietal-squamosal frill; DMNH 24252, a partial skull consisting mainly of the dorsal surface of the skull from near the rostrum tip to the supraorbital buttresses; DMNH 24335, a partial skull consisting of a transversely broken section through the rostrum between the orbits and the naris; DMNH 22196, a large, horn-shaped parietal process; DMNH 21689, a section of transverse parietal bar with yet-to-be-identified processes; DMNH 24182, a partial transverse parietal bar including a large epiparietal 3 horn and an associated epiparietal 2 horn; DMNH 21206, a partial parietal including an epiparietal 3 horn, short section of transverse parietal bar, and lateral ramus; and DMNH 24648, an isolated rostral bone.

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Dinosauria Owen, 1842 (*sensu* Padian & May 1993)
Ceratopsidae Marsh, 1888 (*sensu* Dodson, Forster & Sampson 2004)
Centrosaurinae Lambe, 1915 (*sensu* Dodson, Forster & Sampson 2004)
Eucentrosaura Chiba, Ryan, Fanti, Loewen & Evans, 2017
Pachyrhinosaurini Fiorillo & Tykoski, 2012
Pachyrostra Fiorillo & Tykoski, 2012
Pachyrhinosaurus Sternberg, 1950
Pachyrhinosaurus perotorum Fiorillo & Tykoski, 2012 (Figs 1, 2, 3A–E, 4A–C, 5A–M, 7)

Revised diagnosis. *Pachyrhinosaurus perotorum* is distinguished from other centrosaurine ceratopsids by the following autapomorphies: rostrum anterior tip upturned with anteroventrally directed premaxillary oral margin, resulting in a rostral bone shifted to a level dorsal to the maxillary tooth row; rostral bone lacks the acute, ventrally downturned, parrot-like beak common to other ceratopsians; nasal boss dorsal surface with median ridge near posterior end of boss. Features that we tentatively identify as potential autapomorphies of *P. perotorum* are: epiparietal 2 (P2) posterior margin excavated by enhanced, trough-like, mediolaterally oriented sulcus; epiparietal 2 (P2) horn base penetrated by canal passing dorsoventrally through body of horn. In addition, *Pachyrhinosaurus perotorum* can be differentiated from *P. canadensis* by the presence of a small rostral comb dorsal to the rostral (shared with *P. lakustai*, but absent in *P. canadensis*). *Pachyrhinosaurus perotorum* can be differentiated from *P. lakustai* by the presence of a nasal boss and supraorbital bosses that contact each other on the skull roof (shared with *P. canadensis*, but absent in *P. lakustai*), and by the presence of a supranarial ossification on the lateral surface of the rostrum (shared with *P. canadensis*, but absent in *P. lakustai*).

Description. A partial skull of *Pachyrhinosaurus perotorum* (DMNH 22558) was described and figured by Fiorillo & Tykoski (2012), and it remains the most complete skull from the KTQ (Figs 1A, B, 2A–C). At least four other partial skulls in various levels of completeness have been prepared and catalogued into the collections of the Perot Museum of Nature and Science, in Dallas, Texas, USA. DMNH 24803 (Figs 1C, D, 2D–F) is similar in size and the craniofacial development of the nasal and supraorbital bosses to DMNH 22558 (Supplementary material Table 1). DMNH 24252 (Figs 1E, F, 2G–I) was originally collected in three separate, surface-collected blocks that were later reconnected. It preserves much of the pre-orbital dorsal skull roof. DMNH 24335 (Figs 1G, H, 2J–L) is part of the skull preserving the section of the snout between the orbits and the external naris. DMNH 21460 (Fig. 1I–K) is a section of the dorsal skull roof of an immature individual approximately one-half to two-thirds the size of DMNH 22558. It provides information about the craniofacial ontogeny of *P. perotorum*, as well as insights into the nature and position of facial integument and structures at a 'sub-adult' stage of development (Fiorillo & Tykoski 2013). Numerous pieces of additional skulls,

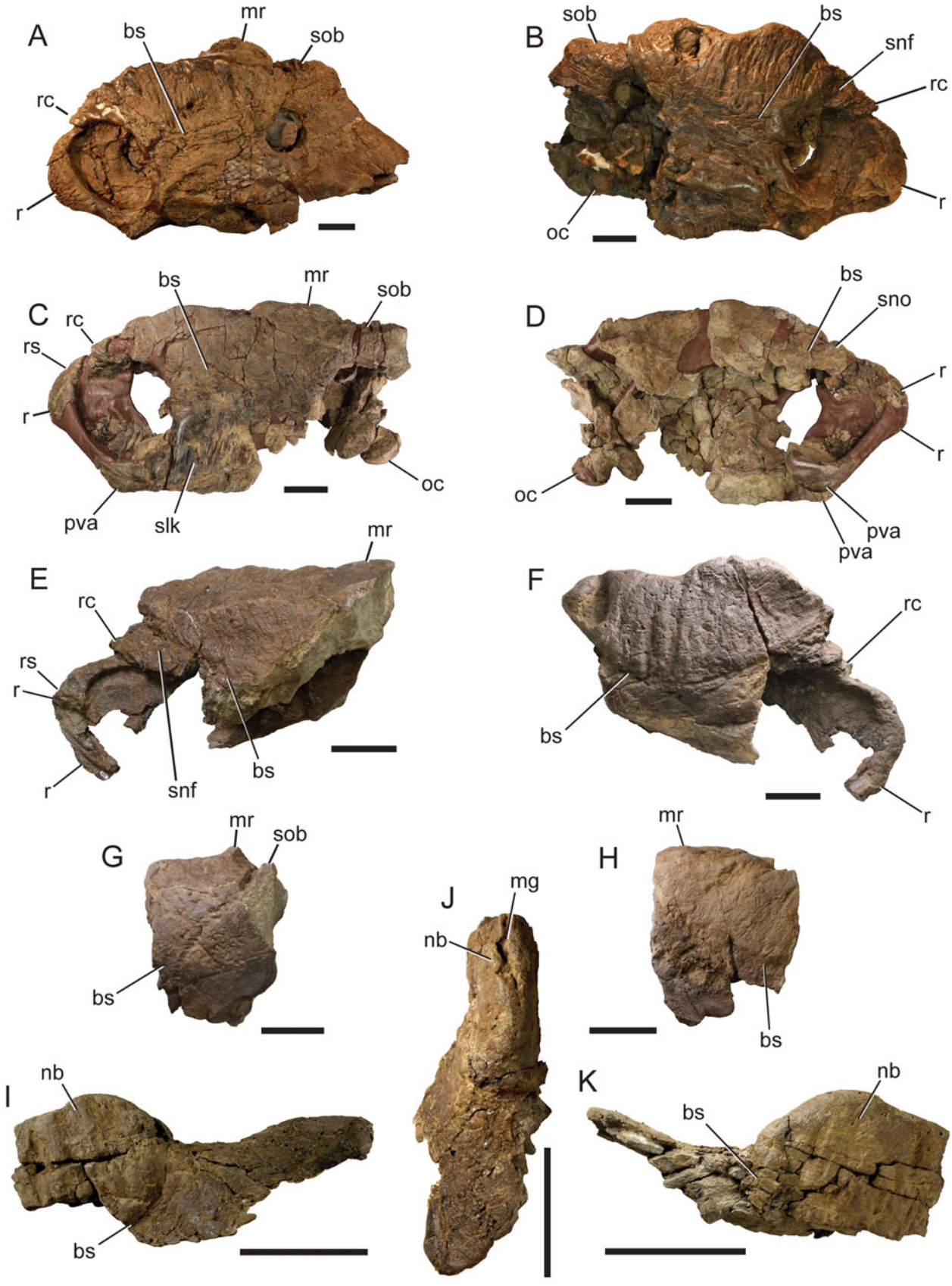

Figure 1. *Pachyrhinosaurus perotorum* partial skulls from the Kikak-Tegoseak Quarry. DMNH 22558 in **A,** left lateral and **B,** right lateral views; DMNH 24803 in **C,** left lateral and **D,** right lateral views; DMNH 24252 in **E,** left lateral and **F,** right lateral views; DMNH 24335 in **G,** left lateral and **H,** right lateral views; DMNH 21460 in **I,** left lateral, **J,** dorsal and **K,** right lateral views. Abbreviations: bs, basal sulcus; mg, median groove; mr, median ridge; nb, nasal boss; oc, occipital condyle; pva, posteroventral angle of premaxilla; r, rostral; rc, rostral comb; rs, rostral suture with premaxilla; snf, supranarial fossa; sno, supranarial ossification; sob, supraorbital boss; slk, slickenside surface. Scale bars = 10 cm.

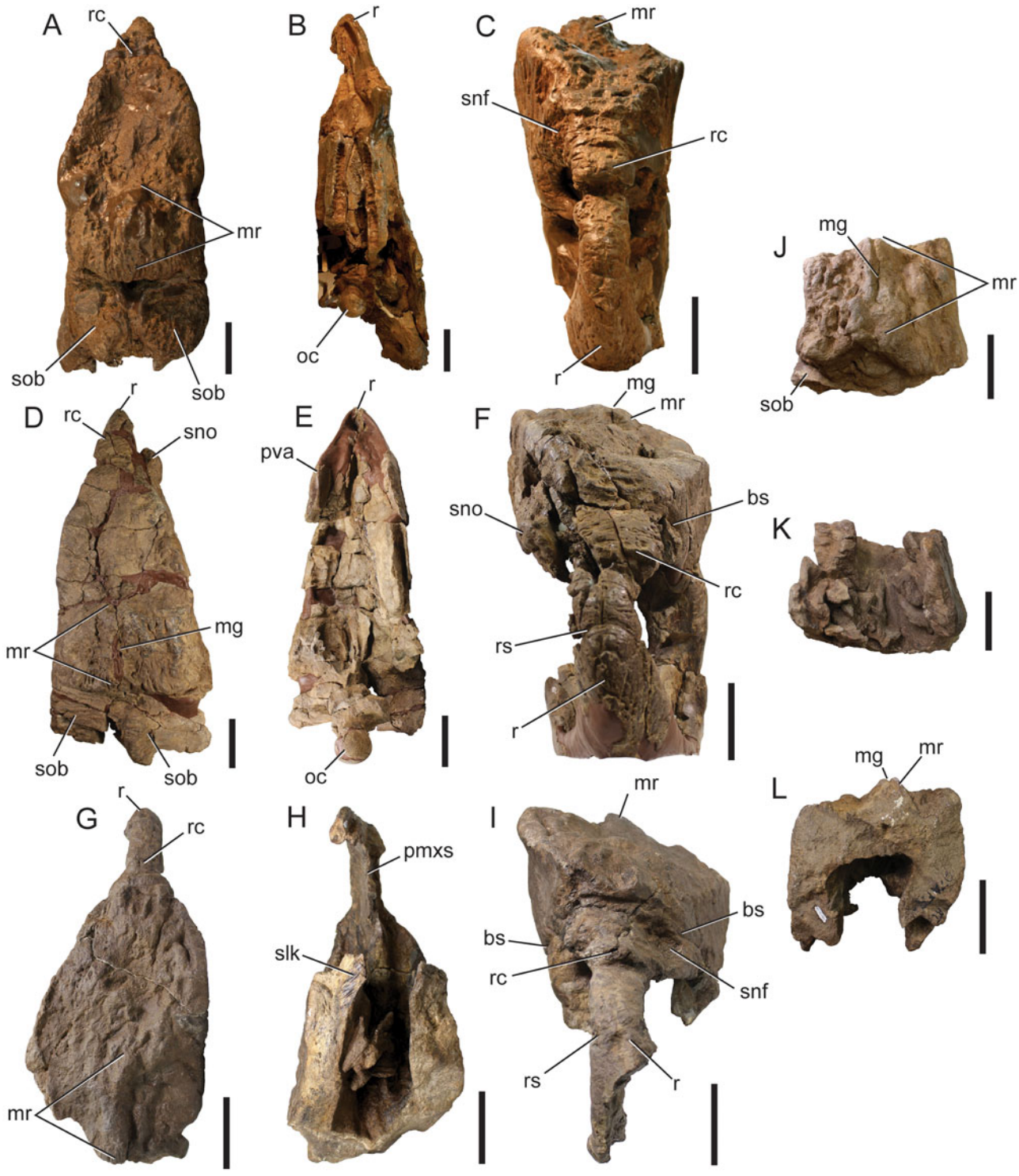

Figure 2. *Pachyrhinosaurus perotorum* partial skulls from the Kikak-Tegoseak Quarry. DMNH 22558 in **A,** dorsal, **B,** ventral and **C,** anterior views; DMNH 24803 in **D,** dorsal, **E,** ventral and **F,** anterior views; DMNH 24252 in **G,** dorsal, **H,** ventral and **I,** anterior views; DMNH 24335 in **J,** dorsal, **K,** ventral and **L,** anterior views. Dorsal and ventral views with anterior to top of image. Abbreviations: bs, basal sulcus; mg, median groove; mr, median ridge; oc, occipital condyle; pmxs, premaxillary septum; pva, posteroventral angle of premaxilla; r, rostral; rc, rostral comb; rs, rostral suture with premaxilla; slk, slickenside surface; snf, supranarial fossa; sno, supranarial ossification; sob, supraorbital boss. Scale bars = 10 cm.

including partial nasal bosses, supraorbital bosses, and other cranial elements are also present in the KTQ collection. The additional skulls confirm the presence of autapomorphic features in *P. perotorum* that were only considered tentative by Fiorillo & Tykoski (2012). We detail those features below.

Rostrum. The most visually distinctive and unusual features of *Pachyrhinosaurus perotorum* compared to other centrosaurines involve the anterior end of the rostrum. In a 'normal' centrosaurine rostrum, the premaxilla has a ventrally directed corner or angle that marks the posteroventral tip of the premaxillary cutting surface. The margin of the premaxilla generally rises anterodorsally from the ventral angle to the sutural contact with the rostral bone. The ventral margin of the rostral bone then arcs anteroventrally to a relatively sharp point, resulting in a ventrally directed cutting edge formed by the edentulous margins of the premaxilla and rostral bones. As a result, in normal centrosaurines the ventral margins of the premaxilla and rostral are normally at or near the same horizontal plane as the maxillary tooth row, and the downturned rostral beak may extend below that level (B. Brown 1914, 1917; Dodson *et al*. 2004).

The two most complete *Pachyrhinosaurus perotorum* skulls from the KTQ, DMNH 22558 (Figs 1A, B, 2A–C) and DMNH 24803 (Figs 1C, D, 2D–F) clearly demonstrate two unusual conditions of the rostrum. First, the rostral bone in *P. perotorum* does not have a downturned, ventrally protruding beak. Instead, the anterior and anteroventral profile of the rostral makes an almost continuous, smoothly curved transition to the premaxilla contact along the shared ventral cutting edge (Figs 3A, B, 4A, B). The rostral bones in DMNH 22558 and DMNH 24803 are incomplete, but enough of the smooth, rounded margins of each are present to confirm the absence of a downturned, parrot-like beak in these individuals. There is no sign of pathological bone texture in either specimen. Indeed, the oral margins of the rostrals are transversely rounded and smooth in cross-section, not sharp-edged or roughened. The smooth texture and regular, rounded transverse cross section is evidence against the rostral morphology in these specimens being the result of pre-mortem pathology. The latter was suggested for abnormal rostral bones in TMP 2002.76.1, a *Pachyrhinosaurus*-like specimen from the Campanian (75.1 Ma) sediments of Dinosaur Provincial Park, Alberta, Canada (Ryan *et al*. 2010), and two specimens of *Pachyrhinosaurus lakustai* (Tanke & Rothschild 2010).

The second unusual feature of the rostrum is that the rostral bone is positioned more dorsally than in other ceratopsids, which is visible on DMNH 22558 (Figs 1A, B, 3A), DMNH 24648 (Fig. 3C), and DMNH 24803 (Figs 1C, D, 3B, D). When the skull is oriented with the maxillary tooth row horizontal, the entire body of the rostral bone is positioned dorsal to the plane of the maxilla's alveolar border (Fig. 3A, B). This is especially evident in DMNH 24803 (Figs 1C, D, 3B, D). An incomplete rostral and part of the premaxilla to which it attached, DMNH 24648, preserves the tip of the rostral and a small amount of its oral margin (Fig. 3C). The oral margin slopes posteroventrally from the tip of the bone, much as in DMNH 22558, and there is no evidence of a hooked or pointed beak in DMNH 24648. The relative position and orientation of the element are also confirmed by comparing premaxilla-rostral sutures preserved in DMNH 24648 (Fig. 3C) to those visible in DMNH 24803 (Fig. 3B, D, E). Based on the similar morphology of the elements and their contacts with the premaxilla, the rostral in DMNH 24648 would have also been dorsally positioned on the snout, with the oral margin of the element curved gently posteroventrally towards the ventral angle of the premaxilla as in DMNH 22558 and DMNH 24803.

The combination of a dorsallypositioned rostral and its lack of a pronounced downturned beak results in a bluntly rounded profile with an anteroventrally facing, instead of a ventrally facing, premaxilla-rostral oral margin in *Pachyrhinosaurus perotorum* (Figs 1A–D, 3A, B, D, 4A, B). This differs from the condition in *P. canadensis* (Fig. 3F, G) and *P. lakustai* (Fig. 3H, I), both of which have rostrals in the normal centrosaurine location at the same level as, or ventral to, the maxillary tooth row, and both of which have the typical ceratopsian, parrot-beaked morphology (Langston 1967, 1975; Currie *et al*. 2008), although Currie *et al*. (2008) noted that *P. lakustai* has a relatively smaller rostral than *P. canadensis*. The normal centrosaurine condition is also present in TMP 2002.76.1 (Ryan *et al*. 2010). Given the unusual morphology present in multiple individuals of *P. perotorum* from the KTQ, we consider the dorsal displacement of the rostral and its rounded, 'beakless' profile to be autapomorphies of *P. perotorum*.

Nasal and supraorbital bosses. Mature pachyrostrans are immediately distinguishable from other centrosaurines by the presence of a nasal boss on the dorsal surface of the snout instead of a nasal horn, a feature that expresses through the ontogeny of individuals (Sampson *et al*. 1997; Currie *et al*. 2008; Fiorillo & Tykoski 2013). The presence or absence of these enlarged nasal and supraorbital masses has been included as a character in cladistic analyses testing centrosaurine relationships (Sampson 1995; Dodson *et al*. 2004; Ryan 2007; Currie *et al*. 2008; Ryan *et al*. 2010; Farke *et al*. 2011; Evans & Ryan 2015; Ryan *et al*. 2017). However, there are

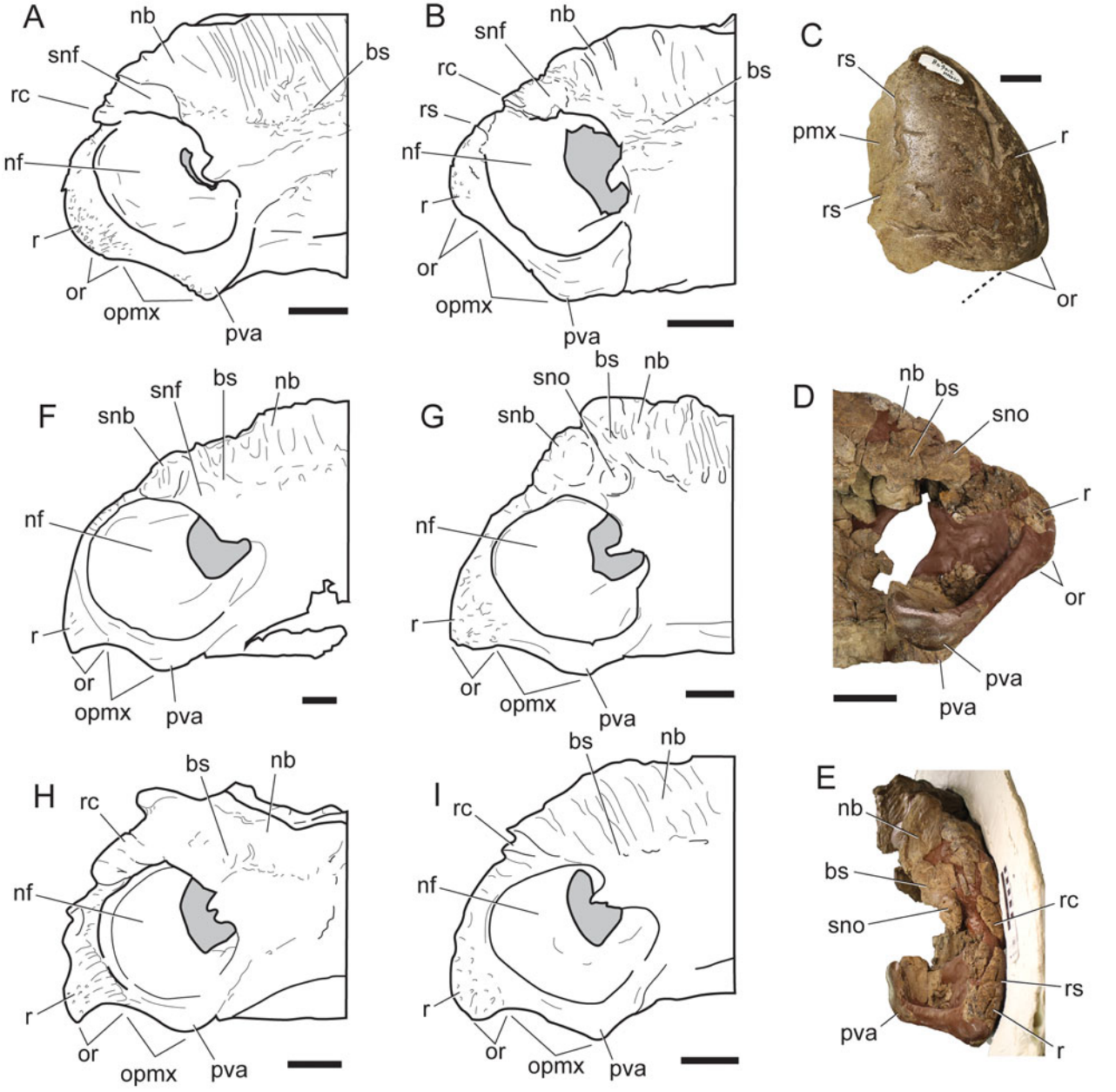

Figure 3. Details of the rostral region in *Pachyrhinosaurus*. **A,** *P. perotorum*, line drawing of DMNH 22558; **B,** *P. perotorum*, line drawing of DMNH 24803; **C,** *P. perotorum*, DMNH 24648, broken rostral in right lateral view. Dashed line is projection of oral margin; **D,** *P. perotorum*, DMNH 24803 right side of rostrum in lateral view; **E,** *P. perotorum*, DMNH 24803, rostral region of skull in anterolateral and slightly dorsal view; **F,** *P. canadensis*, line drawing of Drumheller skull (reversed: redrawn from Langston 1967); **G,** *P. canadensis*, line drawing of CMN 9485 (redrawn from Langston 1975); **H,** *P. lakustai*, line drawing of TMP 1986.55.258 (redrawn from Currie *et al*. 2008); **I,** *P. lakustai*, line drawing of TMP 1989.55.188 (redrawn from Currie *et al*. 2008). Abbreviations: bs, basal sulcus; nb, nasal boss; nf, narial fossa; opmx, oral margin of premaxilla; or, oral margin of rostral; pmx, premaxilla; pva, posteroventral angle of premaxilla; r, rostral bone; rc, rostral comb; rs, rostral suture with premaxilla; snb, supranarial boss; snf, supranarial fossa; sno, supranarial ossification. Scale bars: A, B, D–I = 10 cm; C = 2 cm.

details of the nasal and supraorbital bosses within Pachyrostra that can be used to further differentiate between closely related taxa. We highlight some of the details of these structures in *Pachyrhinosaurus perotorum* and offer comparisons and contrasts with other pachyrostrans.

The nasal boss that inspired Sternberg (1950) to coin the name *Pachyrhinosaurus* is relatively large in mature

specimens of *P. perotorum*, as most clearly seen in DMNH 22558, DMNH 24803 and DMNH 24252 (Figs 1A–F, 2A, C, D, F, G, I, J, L, 4A–C). The ventral border of the nasal boss is marked on the lateral surface of the skull by a band of foramina and grooves that likely trace the path of neurovascular structures along and through the bone surface. This band was termed the basal sulcus and was identified as the likely starting point for dorsally growing keratinous tissue that sheathed the lateral surfaces of the nasal boss in *Pachyrhinosaurus* (Hieronymus *et al*. 2009). The basal sulcus in mature specimens of *P. perotorum* traces a ventrally bowed path along the lateral surface of the skull, dipping well below a line drawn from the dorsal edges of the narial fossa and the middle of the orbit in DMNH 22558 and DMNH 24252 (Figs 1A, B, E, F, 4A, C). In DMNH 24803 the basal sulcus dips below the dorsal rim of the orbit but not to the mid-orbit level (Figs 1C, D, 4B).

The basal sulcus does not descend as far ventrally onto the lateral surface of the skull in described specimens of *Pachyrhinosaurus canadensis* (Sternberg 1950; Langston 1967, 1975, fig. 4D–F). The basal sulcus instead remains near or dorsal to a plane through the dorsal rims of the orbit and narial fossa. The dorsoventral depth of the nasal boss varies considerably in specimens of *Pachyrhinosaurus lakustai* (Fig. 4G–I), apparently in part because of deformation of some specimens (Currie *et al*. 2008). In most specimens of *P. lakustai* the nasal boss does not descend any farther than to a plane through the dorsal rims of the orbit and narial fossa, much as in *P. canadensis* (Fig. 4H, I). However, there are examples (Fig. 4G) in which the trace of the basal sulcus appears to dip farther ventrally (Currie *et al*. 2008). The relative dorsoventral height of the nasal boss in *P. lakustai* specimens is usually proportionally less than in some specimens of *P. perotorum* (DMNH 22558 and DMNH 24252) but can be comparable to that in DMNH 24803. The basal sulcus of the smaller nasal boss in TMP 2002.76.1 dips slightly below a line drawn between the dorsal rims of narial fossa and orbit (Ryan *et al*. 2010).

The posterior end of the nasal boss in all three *Pachyrhinosaurus* species extends posteriorly on the dorsal skull surface to a point even with or above the orbit (Sternberg 1950; Langston 1967, 1975; Currie *et al*. 2008; Fiorillo & Tykoski 2012). By contrast, the smaller nasal boss in TMP 2002.76.1 does not extend posteriorly to the orbit, a condition more similar to the rugose boss of *Achelousaurus horneri* (Sampson 1995; Ryan *et al*. 2010). The posterior end of the nasal boss in *Pachyrhinosaurus* is also marked by vertical and anteroposteriorly oriented ridges or 'fins' that may indicate the overall direction of keratinous horn growth on that part of the boss (Hieronymus *et al*. 2009).

The posterior end of the dorsoventrally deep nasal boss of *P. perotorum* is further accentuated by a median ridge rising along the dorsal surface of the boss (Figs 1A, C, E, G, 2A, C, D, G, I, J, L). This was previously described as a dorsal 'hump' and cited as a diagnostic feature of *P. perotorum* based on DMNH 22558 (Fiorillo & Tykoski 2012). We confirm that a median dorsal ridge on the posterior end of the nasal boss is present in multiple specimens of *P. perotorum*, including DMNH 24335 (Fig. 2J, L), DMNH 24803 (Fig. 2D, F) and DMNH 24252 (Fig. 2G, I). The degree of development and expression of the median ridge differs between individuals, which is not surprising given the amount of variation expressed in other craniofacial structures of *Pachyrhinosaurus* (Sternberg 1950; Langston 1967, 1975; Currie *et al*. 2008). The dorsal median ridge is about one-third the transverse width of the nasal boss, and is flanked by lower, flatter surfaces of the boss to each side. The ridge is marked by a clear median groove in DMNH 24335 (Fig. 2J), which can be seen particularly well in the broken cross section of the skull (Fig. 2L). A similar but less pronounced median groove in the dorsal ridge is present in DMNH 24803 (Fig. 2D, F), and perhaps in DMNH 22558. The anterior part of the median ridge is partly reconstructed in DMNH 22558, and only a small trace of what may be a median groove is preserved (Fig. 2A, C).

A low median ridge near the posterior end of the nasal boss was noted in a specimen of *P. canadensis* (Langston 1975), and there is a low median ridge on the middle to anterior parts of the nasal bosses of some *P. lakustai* specimens, including the holotype skull (TMP 1986.55.258: Currie *et al*. 2008). However, in these specimens of *P. lakustai*, the median ridge does not rise prominently above the rest of the nasal boss. Instead, it tends to be a raised median structure within an otherwise concave depression on the dorsal surface of the boss (TMP 1986.55.258, TMP 1987.55.285). In others, such as TMP 1989.55.427, the median ridge is expressed in a nasal boss that was heavily weathered or eroded, suggesting it may be an artefact of more resistant bone along the nasal suture.

The supraorbital bosses of *Pachyrhinosaurus perotorum* are large, mediolaterally broad, and subcircular to ovoid in dorsal view, and extend anteriorly above at least the midpoint of the orbit (Figs 1A, C, 2A, D, 4A, B). The supraorbital bosses butt up against the posterior surface of the nasal boss as in specimens of *P. canadensis* (Fig. 4D–F: Sternberg 1950; Langston 1967, 1975). The nasal and supraorbital bosses are separated from each other by a narrow groove that delineates the

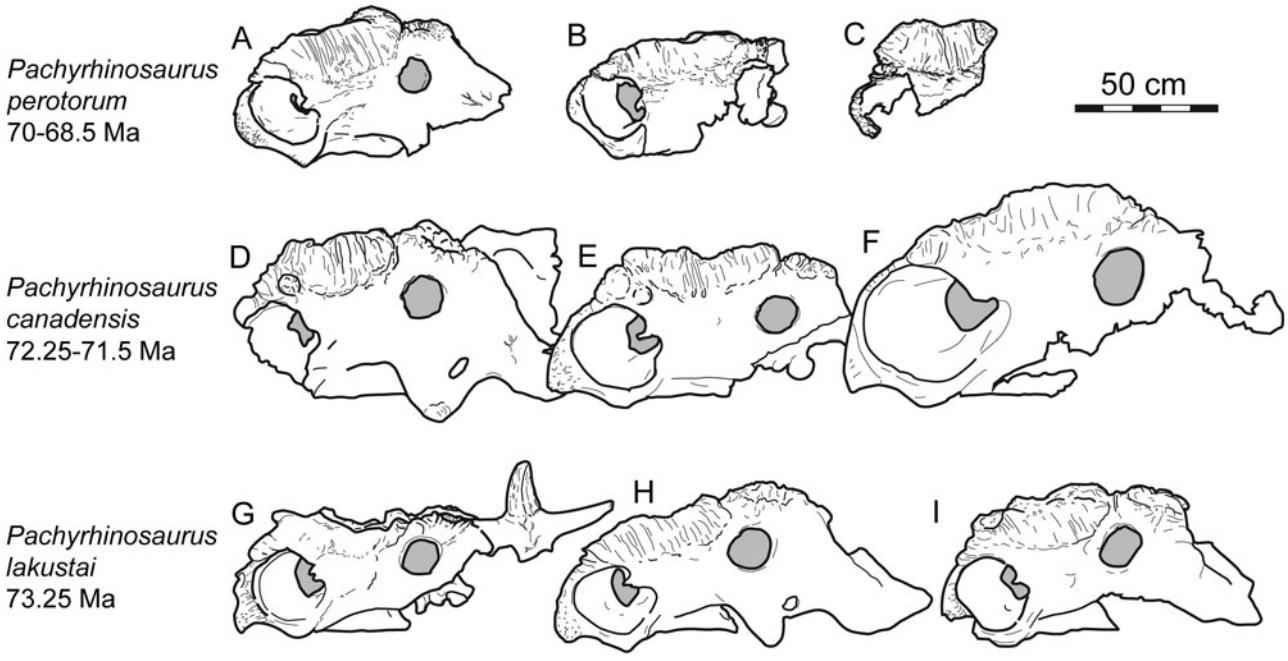

Figure 4. Craniofacial variation between species of *Pachyrhinosaurus*. Line drawings of *Pachyrhinosaurus* skulls in left lateral view. **A,** DMNH 22558; **B,** DMNH 24803; **C,** DMNH 24252 (reversed); **D,** CMN 8867 (redrawn from Sternberg 1950); **E,** CMN 9485 (redrawn from Langston 1975); **F,** Drumheller skull (redrawn from Langston 1967); **G,** TMP 1986.55.258; **H,** TMP 1989.55.188; **I,** TMP 1989.55.1234 (G–I redrawn from Currie *et al*. 2008). Scale bar = 50 cm with 10 cm increments.

boundaries between these dorsal extravagances, but the supraorbital bosses are so enlarged they may actually be overlapped by the nasal boss or extend anteriorly beyond the posterior limit of the nasal boss in some cases (Fig. 4A–C; Supplementary material Fig. 1). A similar groove dividing the bosses was reported in *P. canadensis* (Sternberg 1950; Langston 1967, 1975). The supraorbital bosses and nasal boss are more widely separated from each other on the dorsal surface of the skull in *P. lakustai* (Fig. 4G–I; Supplementary Fig. 1) (Currie *et al*. 2008). An even wider expanse divides the smaller nasal boss and supraorbital bosses in TMP 2002.76.1 (Ryan *et al*. 2010).

Rostral comb and supranarial structures. Currie *et al*. (2008) coined the term 'rostral comb' for a structure comprised of a set of protrusions or transverse ridges across the narial bar between the nasal boss and rostral in some specimens of *Pachyrhinosaurus lakustai*. This structure immediately distinguishes *P. lakustai* from *P. canadensis*, because skulls of the latter do not have a rostral comb (Sternberg 1950; Langston 1967, 1975). DMNH 22558 also has a rostral comb (Figs 1A, B 3A, 4A), as does DMNH 24252 (Figs 1E, F, 4C). There is only a weakly developed rostral comb in DMNH 24803 (Figs 1C, D, 3B, D, 4B), hinting that much as in *P. lakustai* there may be considerable variation in the expression of this feature in *P. perotorum* (Currie *et al*. 2008). In *P. perotorum*, the rostral comb is dorsal to the external naris and anterior to the main body of the nasal boss, the anteroventral border of which is defined by the trace of the basal sulcus.

The lateral surface of the rostrum dorsal or posterodorsal to the narial fossa but anteroventral to the nasal boss is marked in DMNH 22558 by a shallow but distinct fossa (Figs 1B, 3A, 4A; Fiorillo & Tykoski 2012). Similar fossae are present in DMNH 24252 (Figs 1E, 4C), and on the left side of DMNH 24803 (Figs 1C, 3B, 4B). On the right side of DMNH 24803 the fossa is filled by a rounded, laterally protruding mass of smooth, finished bone (Figs 1D, 3D, E). Sternberg (1950, p. 111) noted a "knob about the size of a man's fist" in approximately this place in the paratype of *Pachyrhinosaurus canadensis* (CMN 8866), and a similar mass is present in the holotype (CMN 8867). Langston (1967) described the Drumheller skull of *P. canadensis* as having a fossa above the rim of the narial fossa on the right side of the skull, but the corresponding location on the left side of the skull was occupied by a bony mass he identified as an 'osteoscute' (Fig. 3F). Langston (1975) noted the same bony structures in approximately the same place in other specimens of *P. canadensis* (Fig. 3G), identifying them as osteoderms that only sometimes coossified to the skull. There are no comparable fossae or ossifications in specimens of

Pachyrhinosaurus lakustai (Currie *et al*. 2008, fig. 3H, I). The extra ossification above the right narial fossa of DMNH 24803 is not an extension of the nasal boss, as the basal sulcus separates the two structures, and a faint suture is barely discernible inside the border of the fossa along the base of the ossification. We identify this mass as a supranarial ossification that occupies the supranarial fossa, like those present in some specimens of *P. canadensis*. However, since DMNH 22558 lacks the ossifications, the expression or preservation of this character is variable in *P. perotorum* as in *P. canadensis.*

Although *Pachyrhinosaurus perotorum* and *P. canadensis* share the presence of supranarial ossifications on the lateral surface of the rostrum dorsal to the narial fossa, they differ in another feature of the narial bridge. Langston (1975, p. 1582) described a "large, flattened tumescent bulge" to each side of the midline dorsal to the narial fossa in *P. canadensis*, and applied the term "supranasal bosses" to them. These structures protrude dorsolaterally, are separated from one another by a shallow median sulcus, and are distinctly different from the laterally positioned supranarial ossifications and their corresponding fossae (Langston 1975). No *P. perotorum* specimens have bilateral supranasal bosses on the narial bridge (Figs 1A–F, 2A, C, D, F, G, I, 3A, B, 4A–C). Instead, *P. perotorum* has a rostral comb structure in approximately the same part of the narial bar. There are no supranasal bosses in *P. lakustai* either (Currie *et al*. 2008), and the presence of these additional paired structures on the dorsolateral edges of the narial bar is best considered an autapomorphy of *P. canadensis*.

Parietal morphology. Epiparietals (*sensu* Horner & Goodwin 2008; Sampson *et al*. 2013; Evans & Ryan 2015; Lund *et al*. 2016a) along the margins of the parietal are common among ceratopsid dinosaurs, with the expression of these processes ranging from small crescentic ossifications to enlarged horns and spikes (Dodson *et al*. 2004). Sampson *et al*. (1997) established a numbering system for the location of parietal processes in centrosaurine ceratopsids, numbering them consecutively from medial to lateral positions. The first process, P1 (epiparietal 1 in this paper) of Sampson *et al*. (1997) was the most medial process. In *Centrosaurus* and *Styracosaurus* P1 is positioned on the posterior margin of the parietal immediately lateral to the median bar, and projects or curls dorsally or anterodorsally over the parietal. However, Sampson *et al*. (1997) also argued that *Einiosaurus*, *Achelousaurus* and *Pachyrhinosaurus* lack the homologous process to P1 in *Centrosaurus* and *Styracosaurus*, and assigned the medial-most process of the three pachyrhinosaurin taxa as a P2. We follow this scheme of homology in this paper.

The holotype parietal of *Pachyrhinosaurus perotorum* (DMNH 21200) was extensively broken by natural processes prior to collection, and was reassembled from numerous fragments. The specimen included a pair of small, asymmetrical horns, the smaller of which appeared to lack a clear connection to the rest of the specimen. Believing the pieces were originally found in approximately life position, the specimen was subsequently reconstructed with a unique arrangement of small horns that jutted anteriorly and slightly dorsally from the anterior margin of the transverse parietal bar, above and over the parietal fenestra. This unusual parietal ornamentation was cited as an autapomorphy for the newly erected species (Fiorillo & Tykoski 2012).

Subsequent examination of the holotype parietal revealed that the original reconstruction of the specimen was incorrect. A good connection was found between the smaller of the two processes and the portion of the specimen that had been erroneously identified as the median parietal bar. When correctly restored, the small horns of the holotype are the left and right epiparietal 2 processes connected by a span of the median portion of the transverse parietal bar (Fig. 5A–C). The transverse parietal bar between the epiparietal 2 horns is excavated by a semicircular fossa on the dorsal surface, a condition reminiscent of some specimens of *Centrosaurus* (Ryan *et al*. 2001; Chiba *et al*. 2015). The two epiparietal 2 processes of DMNH 21200 point medially (Fig. 5A, B) and slightly dorsally (Fig. 5C) towards each other, and exhibit asymmetry similar to some specimens of *Pachyrhinosaurus lakustai* (Currie *et al*. 2008). Unlike in *P. lakustai*, each epiparietal 2 horn is pierced by a narrow canal that passes dorsoventrally through the base of the horn via a single foramen on both the dorsal and ventral surfaces (Fig. 5A, B). The posterior surface of each epiparietal 2 in DMNH 21200 is marked by a distinct mediolaterally oriented sulcus (Figs 5A, C, D, 6A, B). The sulcus was labelled the "lateral sulcus" by Fiorillo & Tykoski (2012, fig. 4), based on the reconstruction of the holotype at the time. In DMNH 21200, these posterior sulci span the entire length of each epiparietal 2 process (Fig. 6A, B). The surface texture of the bone inside the posterior sulcus of the left epiparietal 2 horn is marked by a dense pattern of fine striae oriented perpendicular to the axis of the sulcus (Fig. 6A). This differs from what is normally seen in vascular grooves and canals, including those in other *P. perotorum* specimens from the KTQ.

Based on the revision of the holotype, the small horn on the paratype specimen DMNH 21201 (Fig. 5D, E) is also re-identified as a left epiparietal 2 process. As seen in DMNH 21200, a foramen is present at the base of epiparietal 2 process on DMNH 21201 (Fig. 5D, E).

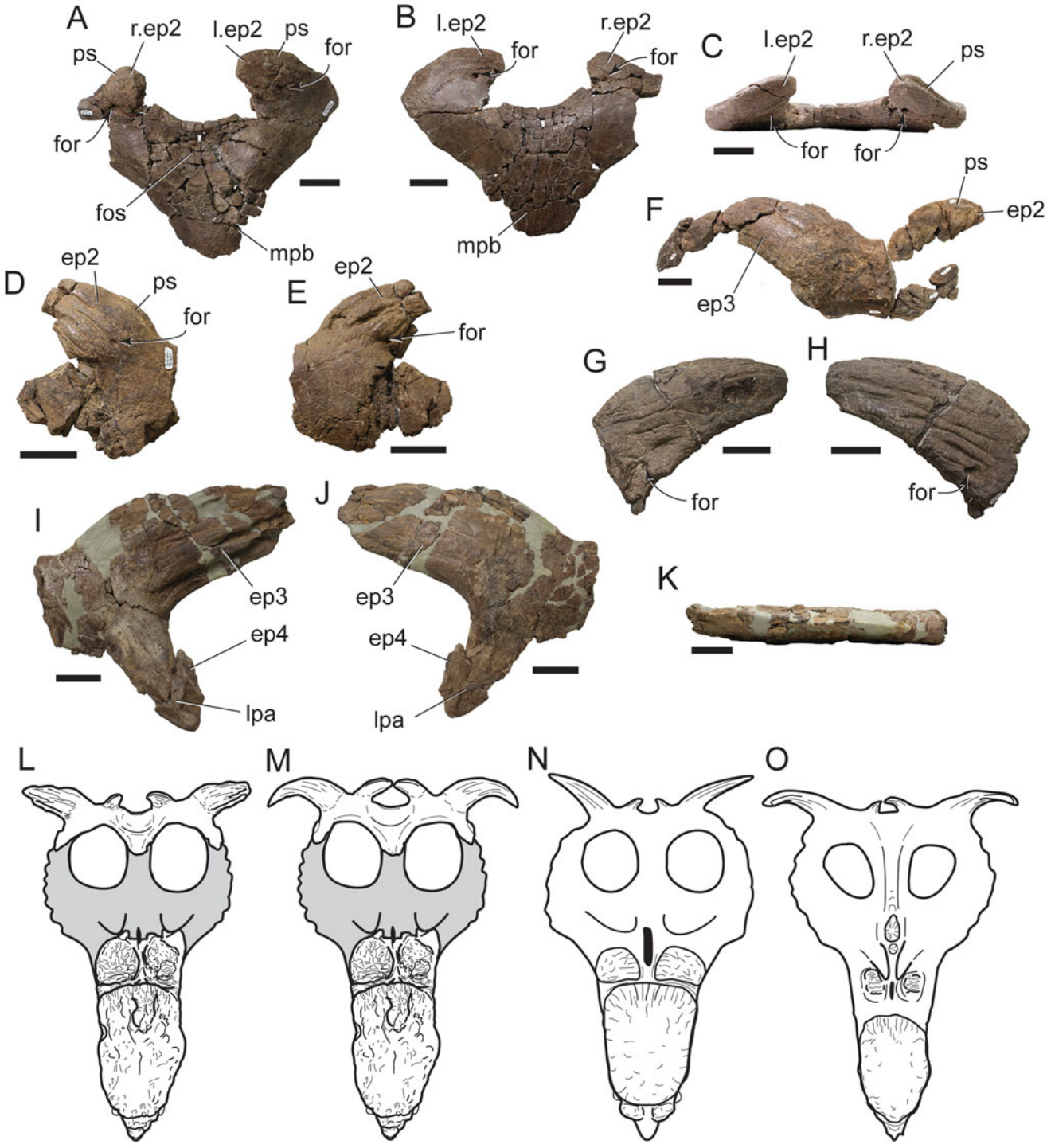

Figure 5. *Pachyrhinosaurus perotorum* parietals. DMNH 21200 *P. perotorum* holotype in **A,** dorsal, **B,** ventral and **C,** posterior views; DMNH 21201, *P. perotorum* paratype parietal piece with left epiparietal 2 horn in **D,** dorsal and **E,** ventral views; **F,** DMNH 24182, incomplete parietal with epiparietal processes 2 and 3 preserved in position found during preparation; DMNH 22196, a large epiparietal 2 process in assumed **G,** dorsal and **H,** ventral views; DMNH 21206, partial parietal with left epiparietal 3 horn, lateral ramus and epiparietal 4 in **I,** dorsal, **J,** ventral and **K,** posterior views; **L,** stylised line drawing of *P. perotorum* skull in dorsal view, based on DMNH 22558, DMNH 21200 and DMNH 21206; **M,** stylised line drawing of *P. perotorum* skull in dorsal view, based on DMNH 22558, DMNH 24182 and DMNH 21200; **N,** stylised line drawing of *P. canadensis* skull in dorsal view (after Currie *et al.* 2008); **O,** stylised line drawing of *P. lakustai* skull in dorsal view (after Currie *et al.* 2008). L–O drawn to same length from rostrum tip to midline of transverse parietal bar. Abbreviations: ep2, epiparietal 2 horn; ep3, epiparietal 3 horn; ep4, locus for epiparietal 4 process; for, foramen; fos, fossa; l.ep2, left epiparietal 2 horn; lpa, lateral ramus of parietal; mpb, median parietal bar; ps, posterior sulcus on epiparietal 2 horn; r.ep2, right epiparietal 2 horn. Scale bars = 5 cm.

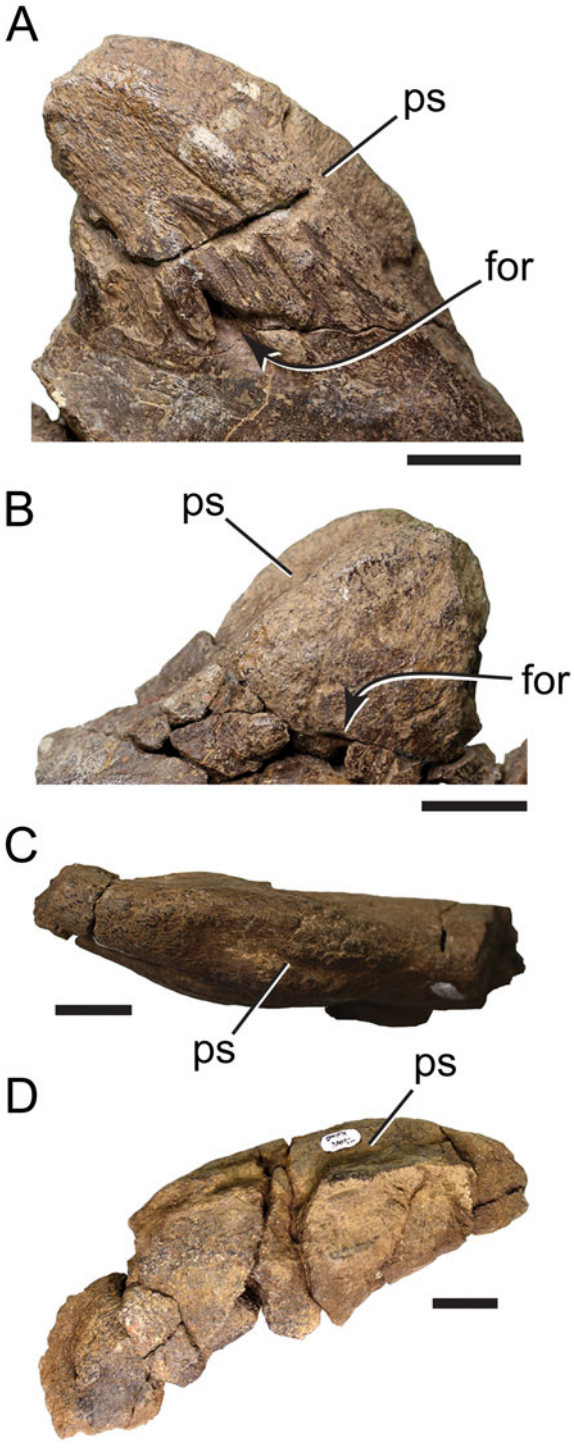

Figure 6. *Pachyrhinosaurus perotorum*, epiparietal 2 horns. **A,** DMNH 21200 holotype left epiparietal 2 horn in dorsal view; **B,** DMNH 21200 holotype right epiparietal 2 horn in dorsal view; **C,** DMNH 21201 paratype left epiparietal 2 horn in posterior view (medial to left, dorsal to bottom); **D,** DMNH 24182 incomplete right epiparietal 2 horn in dorsal view. Abbreviations: for, foramen; ps, posterior sulcus. Scale bars = 2 cm.

As with the epiparietal 2 processes in DMNH 21200, a similar sulcus is present on the posterior surface of the epiparietal horn of DMNH 21201, but is restricted to the proximal half of the process (Fig. 6C).

Another partial parietal, DMNH 24182, bears a large, laterally directed epiparietal 3 horn, a section of transverse parietal bar, and was found with an *in situ* epiparietal 2 (Fig. 5F). Unfortunately, the base of the epiparietal 2 process of DMNH 24182 was destroyed prior to collection, and the presence of a canal through the process cannot be assessed. However, the association between the process and the rest of the parietal was maintained during preparation and curation. The damaged epiparietal 2 horn of DMNH 24182 is excavated by a posterior sulcus as in DMNH 21200 and DMNH 21201 (Figs 5F, 6D). There is no canal through the base of the large epiparietal 3 horn in DMNH 24182 (Fig. 5F).

DMNH 22196 (Fig. 5G, H) is a large, flattened, horn-like process that bears a single large foramen on both sides in approximately the same locations seen in the second epiparietals of DMNH 21200 and DMNH 21201, but it lacks a posterior sulcus. We tentatively identify DMNH 22196 as either an isolated epiparietal 3 or a large epiparietal 2. Although this isolated horn is superficially similar to a midline horn from a median parietal bar of *P. lakustai* (Currie *et al*. 2008), the cross-section of median parietal horns of *P. lakustai* is more square or rectangular (the transverse width of median parietal bar horns is over 60% of the anteroposterior length of the horns), compared to the flattened ovoid cross section of DMNH 22196. In contrast, the horn base width is only 40–50% of horn length in examples of epiparietal 2 in *P. perotorum*.

A partial parietal, DMNH 21206 (Fig. 5I–K), also preserves a large, flat, sharp-edged epiparietal 3 horn and a short section of the lateral ramus of the parietal that bears a low undulation marking the locus for an epiparietal 4 process. The epiparietal 3 horns of *P. lakustai* often have a twist (e.g. TMP 1987.55.141 and TMP 1989.55.1241; figs 32D and 33A, respectively, in Currie *et al*. 2008), but there is no twist in the epiparietal 3 of DMNH 21206 (Fig. 5K) or DMNH 24182 (Fig. 5F). There are no large foramina passing through either surface of the epiparietal 3 processes in DMNH 21206 or DMNH 24182. Based on these specimens, we assume this is the general condition for the epiparietal 3 horns of *P. perotorum*.

Another parietal specimen from the KTQ is puzzling because of its unusual arrangement of parietal processes. DMNH 24653 (Fig. 7) is a section of parietal that includes the base of a robust epiparietal horn with a

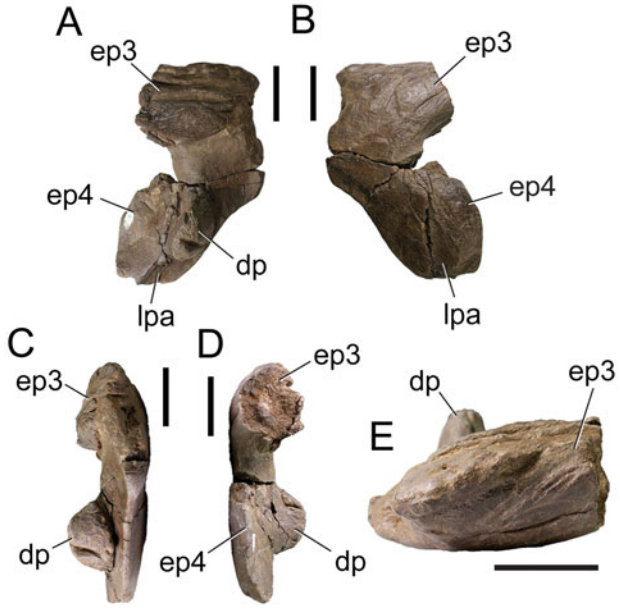

Figure 7. *Pachyrhinosaurus perotorum*, DMNH 24653, a partial parietal with broken right epiparietal 3, epiparietal 4 locus, piece of lateral ramus and unusual horn-like process projecting dorsally from lateral ramus. **A,** dorsal view; **B,** ventral view; **C,** medial view; **D,** lateral view; **E,** posterior view. Abbreviations: dp, dorsal process; ep3, epiparietal 3 horn; ep4, epiparietal 4 locus; lpa, lateral ramus of parietal. Scale bars = 5 cm.

broadly oval to nearly circular cross section. We identify this as the broken base of an epiparietal 3 horn, with a short section of the lateral parietal ramus attached. The lateral edge of the lateral ramus bears a low undulation for an epiparietal 4 locus, while what we interpret as the medial margin of the ramus thins to a narrow edge that is marked by a long-grained bone texture previously associated with still-growing bone surfaces in juvenile and subadult centrosaurines (Sampson *et al*. 1997; C. M. Brown *et al*. 2009; Tumarkin-Deratzian 2010).

The most unusual feature of DMNH 24653 is the presence of a small, horn-like process jutting perpendicularly from the assumed dorsal surface of the parietal (Fig. 7A, C, D). The process is asymmetrical in dorsal view, with a flatter lateral surface and a convexly rounded medial surface, and a longer anteroposterior axis. The lateral surface blends smoothly into the surface of the parietal ramus (Fig. 7D), but the medial surface has an abrupt lip overhanging the base of the process (Fig. 7C). The process somewhat resembles small horns on the median parietal bars of some *Pachyrhinosaurus lakustai* specimens (Currie *et al*. 2008). None of the other parietal specimens from the KTQ have processes protruding perpendicular to the dorsal surface of the parietal. The only comparable processes arising perpendicularly from the dorsal surface of the parietal in other centrosaurines are the large dorsally protruding epiparietal 1 processes on the transverse parietal bar of *Centrosaurus apertus* and the much smaller epiparietal 1 processes of *Styracosaurus albertensis* (Dodson *et al*. 2004). We consider this specimen to be an aberrant case for the time being but remain open to the possibility that additional specimens from the KTQ may require further assessment of parietal morphology of *P. perotorum*.

The revised interpretation of the previous described specimens and descriptions of new material in this paper reveals that *P. perotorum* frill ornamentation (Fig. 5L, M) is generally consistent with previous hypotheses of frill morphology in *P. canadensis* (Fig. 5N) and with the larger sample of specimens representing *P. lakustai* (Fig. 5O). There are no processes along the interior margin of the transverse parietal bar. The medial-most epiparietal is the medially projecting small epiparietal 2 process based on DMNH 21200, with a large laterally projecting epiparietal 3 horn lateral to epiparietal 2. Because of the lack of attached or fused examples of an epiparietal 4, and the lack of a complete lateral parietal bar in the sample, the morphology of epiparietals lateral to epiparietal 3 is uncertain in *P. perotorum*. Even the limited sample of specimens from the KTQ shows that parietal ornamentation was variable in *P. perotorum*, although given the smaller sample size we cannot say if it was as variable as in *P. lakustai* (Currie *et al*. 2008).

Phylogenetic analysis

The strict consensus tree generated by the cladistic analysis of Fiorillo & Tykoski (2012) showed *Pachyrhinosaurus perotorum* in an unresolved polytomy with *P. canadensis*, *P. lakustai* and TMP 2002.76.1. Later analyses supported the monophyly of the *Pachyrhinosaurus* clade as new centrosaurine taxa were discovered and described, and subsequent cladistic analyses became larger and more detailed (Ryan *et al.* 2012, 2017; Sampson *et al*. 2013; Evans & Ryan 2015; Lund *et al*. 2016a, b; Chiba *et al*. 2017). However, the sister taxon relationships between the three *Pachyrhinosaurus* species remained uncertain, with analyses sometimes recovering a *P. perotorum* + *P. lakustai* clade to the exclusion of *P. canadensis* (Lund *et al*. 2016a, b; Ryan *et al*. 2017; Chiba *et al*. 2017), or with the three species in a polytomy (Evans & Ryan 2015). The increased number of specimens from the KTQ provides an opportunity to better assess more characters for *P. perotorum*

and to incorporate these data in a more recent analysis to better resolve the relationships of pachyrostran centrosaurines.

Methods

Our phylogenetic analysis was based upon the data set of Chiba *et al*. (2017), which itself was derived from a series of previous analyses of centrosaurine relationships (Farke *et al*. 2011; Sampson *et al*. 2013; Evans & Ryan 2015; Ryan *et al*. 2017). We re-evaluated character state scores for *Pachyrhinosaurus perotorum* to reflect new information revealed by recently prepared specimens from the KTQ. TMP 2002.76.1, which was included in the phylogenetic analysis of Fiorillo & Tykoski (2012), is also scored into the matrix. Character state scoring for *P. perotorum* was changed for 29 of the 101 characters included in the analysis of Chiba *et al.* (2017). A full list of those characters with revised scoring is provided in the Supplementary material. Four new characters (characters 102–105) were added to the taxon-character matrix to encompass morphologies with the potential to further differentiate pachyrostran taxa and are also listed in the Supplementary material. The taxon-character matrix was built and manipulated using the freely available software MacClade 4.08a (D. R. Maddison & Maddison 2005) for OSX and Mesquite (W. P. Maddison & Maddison 2017). Cladistic analyses of the data were performed using PAUP* version 4.0b10 (Swofford 2002) for Macintosh (PPC/Altivec) on a Macintosh iBookG4 computer. The data matrix tested here is available in NEXUS format as Supplementary material (TykoskietalMtx2018-01-02.nex).

The analysis evaluated 27 ingroup and four outgroup taxa (*Leptoceratops*, *Protoceratops*, *Magnirostris*, *Bagaceratops*) for a total of 105 morphological characters. We followed Chiba *et al*. (2017) in keeping a single multistate character (character 20) designated as ordered. All other multistate characters were treated as unordered. Character 7 was found to be constant in its coding, and character 67 was variable but uninformative. There were, therefore, 103 parsimony-informative characters. The analysis used a heuristic branch-swapping algorithm with tree-bisection-reconnection (TBR). Character distribution was determined post analysis based on one of the recovered trees, under both ACCTRAN and DELTRAN character state optimization criteria. Strict, 50% majority-rule and Adams consensus trees were generated to evaluate patterns of clade recovery and quickly identify the presence of 'wildcard' taxa. A bootstrap analysis using fast-stepwise methods and 100,000 replicates was conducted. Bremer support/decay indices were computed using MacClade to generate a PAUP* Decay Command file from the treefile saved out in PAUP*, which was then opened and executed in PAUP* to calculate decay indices.

Results of cladistic analysis

The analysis recovered 717 most parsimonious trees, each with a length of 188 steps, a consistency index of 0.6277, and a retention index of 0.7923. A strict consensus tree of these trees superimposed on the geological time scale is shown in Figure 8. The relationships of taxa in successive sister taxon relationships within Pachyrhinosaurini are fully resolved. *Einiosaurus procurvicornis* is recovered as the sister taxon to a monophyletic Pachyrostra. The clade Pachyrostra (*Achelousaurus horneri* + *Pachyrhinosaurus canadensis* and all descendants of their most recent common ancestor) is diagnosed by nasal ornamentation in adults taking the form of a pachyostotic boss (character 20, state 2), epiparietal 3 curving laterally (character 62), and the presence of a nasal boss that does not extend posteriorly to a point even with or above the orbits (character 103, state 1). The next more derived node among pachyrostrans is that comprised of TMP 2002.76.1 + the clade consisting of all three *Pachyrhinosaurus* species. Characters uniting TMP 2002.76.1 with the *Pachyrhinosaurus* clade include a postorbital horn core/structure centred posterodorsal to the orbit, with the posterior margin of the structure located well posterior to the rim of the orbit (character 26), and the presence of a rostral comb *sensu* Currie *et al*. (2008) (character 102). The three *Pachyrhinosaurus* species are united by a single synapomorphy, the presence of a nasal boss that extends posteriorly at least as far as the anterior rim of the orbit (character 103, state 2). *Pachyrhinosaurus perotorum* was recovered as the sister taxon to *P. canadensis* in all trees. Synapomorphies uniting these two taxa included supraorbital bosses enlarged anteriorly to contact or nearly contact the posterior end of the nasal boss (character 104), and the presence of a rugose ossification on each side of the rostrum dorsal or posterodorsal to the narial fossa of adults (character 105). However, the sister-taxon relationship between *P. canadensis* and *P. perotorum* is tenuously supported in our analysis (decay index =1, bootstrap value =53), taking only one additional step to collapse the three species of *Pachyrhinosaurus* into an unresolved polytomy.

Discussion

Distinguishing species of *Pachyrhinosaurus*

The close relationship and morphological similarity between *Pachyrhinosaurus canadensis* and *P. perotorum* raise the obvious question, is there a chance that

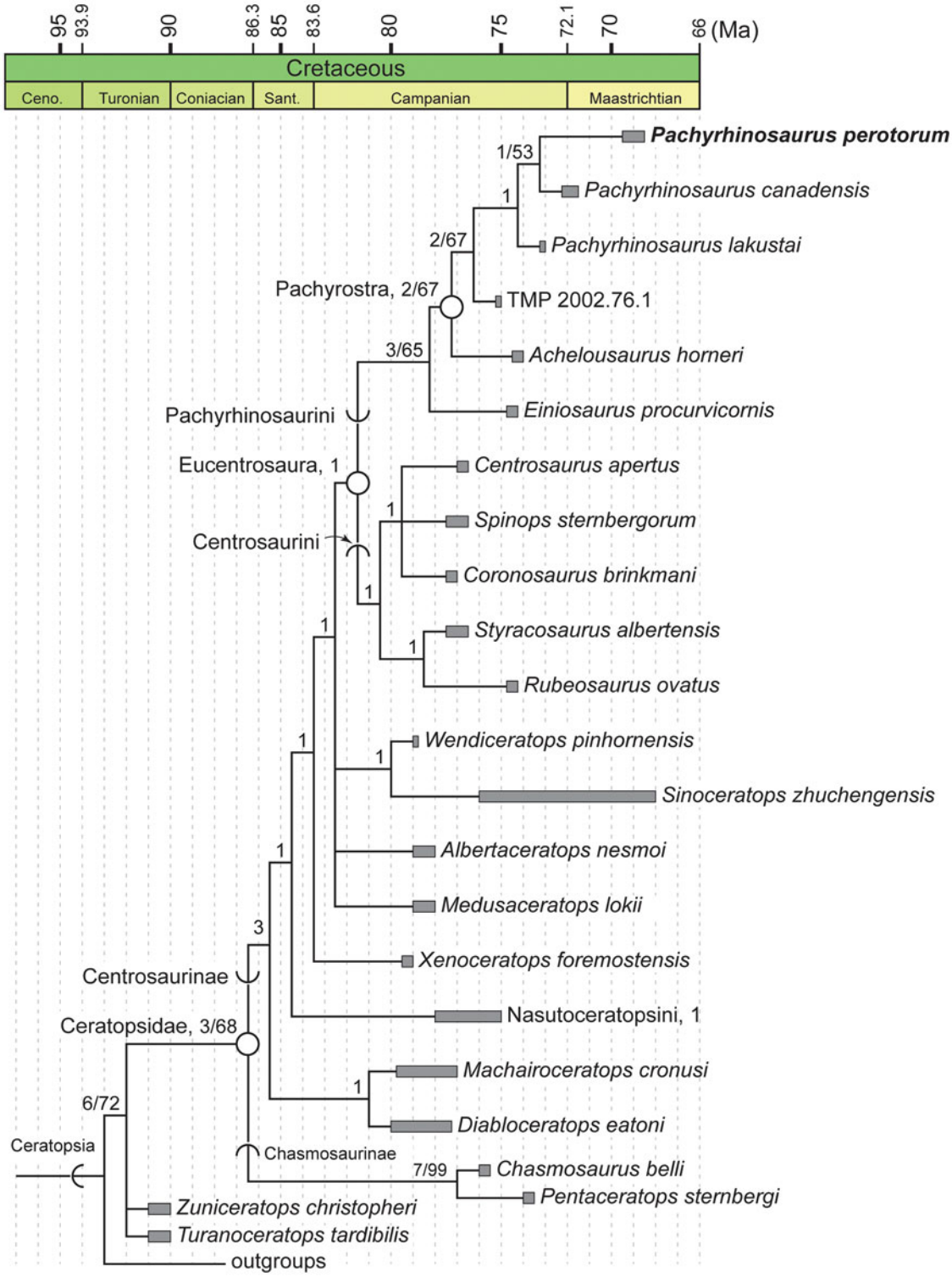

Figure 8. Results of cladistic analysis. Strict consensus of 717 most parsimonious trees, each of 188 steps with a consistency index of 0.6277 and a retention index of 0.7923. Bremer support values given at supported nodes and bootstrap values at nodes with >50% support. Open circle at node indicates a node-defined taxon name. Arc segment on a branch indicates a stem-defined lineage name. Tree is calibrated on the geological time scale of Gradstein *et al*. (2012). Faint, vertical, dashed lines at 1 million year intervals. Grey bars on branches indicate estimated geological range of a taxon based mainly on Evans & Ryan (2015) and Ryan *et al*. (2017). Geological range of *P. perotorum* from Fiorillo *et al*. (2010), *P. canadensis* from Eberth *et al*. (2013) and Fanti *et al*. (2015), *P. lakustai* from Currie *et al*. (2008) and TMP 2002.76.1 from Ryan *et al*. (2010).

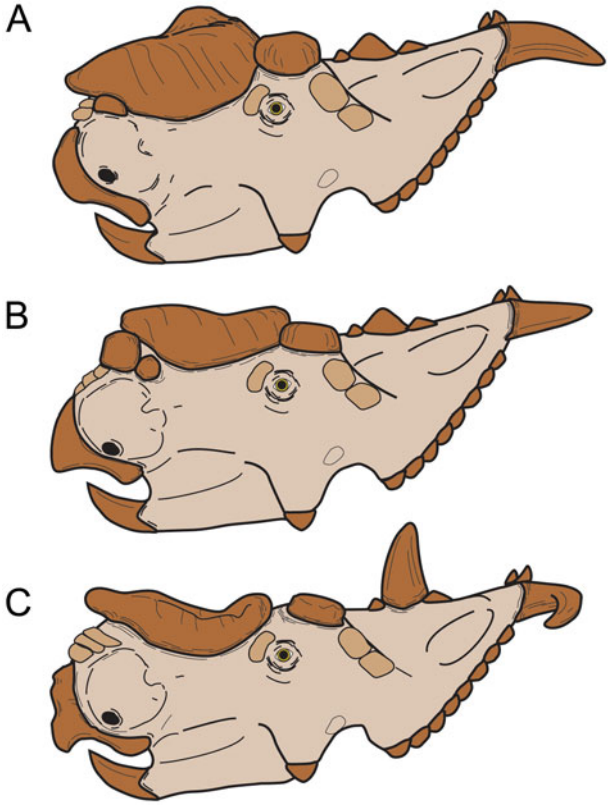

Figure 9. Diagrammatic stylised renderings of craniofacial integument structures in the three named species of *Pachyrhinosaurus*. **A,** *Pachyrhinosaurus perotorum*; **B,** *Pachyrhinosaurus canadensis*; **C,** *Pachyrhinosaurus lakustai*. Light fill indicates 'normal' scaly skin. Medium-dark fill indicates enlarged, keratinized scales. Dark fill indicates keratinous or horn covering. Drawn to same rostrum tip-to-orbit length.

these two taxa might actually be conspecific? As noted above, *P. perotorum* can be diagnosed and distinguished from other *Pachyrhinosaurus* species by a suite of characters including the rostral in a raised position dorsal to the maxillary tooth row; rostral lacking the downturned, pointed ventral tip or beak; the upturned, anteroventrally facing margin of the premaxilla oral margin; epiparietal 2 horn penetrated by a canal passing dorsoventrally through the base of the horn; and epiparietal 2 horn posterior margin excavated by a longitudinal sulcus.

The canal passing through the base of the epiparietal 2 in *Pachyrhinosaurus perotorum* is not described in specimens of *P. lakustai* (Currie *et al*. 2008). There is no mention of any such feature in the epiparietal 2 horn of CMN 9602, a partial parietal frill likely referable to *P. canadensis* (Langston, 1975). There are small neurovascular foramina in many processes and bosses of *Pachyrhinosaurus* specimens (Sternberg 1950; Langston 1967, 1975; Currie *et al*. 2008; Hieronymus *et al.* 2009; Tanke & Rothschild 2010) and the elements in the sample from the KTQ reflect that. However, the relatively consistent presence of a small canal passing dorsoventrally through the second epiparietal horns of *P. perotorum* might be autapomorphic compared to the other *Pachyrhinosaurus* species. The mediolaterally oriented posterior sulcus on the epiparietal 2 horn may also represent an additional potential autapomorphy in the parietal of *P. perotorum*.

Importantly, *P. canadensis* bears at least two autapomorphies that distinguish it from *P. perotorum*. The first of these is the lack of a rostral comb in specimens of *P. canadensis* (Sternberg 1950; Langston 1967, 1975). This structure is present in variable forms in multiple specimens of *P. lakustai* and at least two specimens of *P. perotorum*, and is present to a lesser degree in TMP 2002.76.1 (Currie *et al*. 2008; Ryan *et al*. 2010). Its absence in *P. canadensis* represents a reversal to the more primitive centrosaurine condition. The second autapomorphy diagnosing *P. canadensis* is the presence of a pair of enlarged, bilateral, but distinct supranarial bosses (Sternberg 1950; Langston 1967, 1975). These paired bosses, referred to as a "tumescent bulge" and "supranasal bosses" by Langston (1975, p. 1582), flank each side of the narial bar dorsal to the narial fossa in *P. canadensis*. The bosses should not be confused with the more laterally placed supranarial ossifications in both *P. canadensis* and *P. perotorum*. Both *P. perotorum* and *P. lakustai* lack supranarial bosses. The results here show *Pachyrhinosaurus perotorum* from the Arctic of Alaska and the older *P. canadensis* from southern Alberta are separate, diagnosable sister taxa and are not simply geographical variants of a single, long-lived *Pachyrhinosaurus* species.

The results of the cladistic analysis presented here support the case that *Pachyrhinosaurus perotorum* is diagnosable from other species of *Pachyrhinosaurus* and other pachyrhinosaurins. However, it does not require computational analysis to qualitatively discern the differences in craniofacial anatomy among the three *Pachyrhinosaurus* species. The relative height and extent of the nasal and supraorbital bosses, the presence or absence of supranarial structures and the rostral comb, the shape and position of the rostral, and the orientation of the premaxilla-rostral oral margin can readily distinguish the species visually (Figs 3, 5L–O).

As pointed out by Hieronymus *et al*. (2009), the osseous craniofacial horns, processes and bosses of centrosaurines underlie soft-tissue structures that can be reconstructed based upon comparison with similar bone tissues in extant analogues. Following Hieronymus *et al*.

(2009), we can develop hypotheses about the general pattern of craniofacial integumentary structures in *Pachyrhinosaurus perotorum* (Fig. 9A) and compare them to those of *P. canadensis* (Fig. 9B) and *P. lakustai* (Fig. 9C). Doing so reveals the more subtle visual cues differentiating these taxa, which fall within the level of variation expected between closely related species that span approximately 4 million years of time and were separated by over 2000 km. This relatively conservative pattern of craniofacial change in *Pachyrhinosaurus*, especially with regard to frill ornamentation, contrasts markedly with the rapid morphological changes in frill ornamentation that occurred in the evolution of non-pachyrostran centrosaurines from the middle and late Campanian (e.g. Ryan & Evans 2005; Mallon *et al*. 2012; Eberth *et al*. 2013; Evans & Ryan 2015; C. M. Brown & Henderson 2015).

Conclusions

Pachyrhinosaurus perotorum, from the middle Maastrichtian of the North Slope, Alaska, USA, is represented by a growing sample of multiple individuals from a single locality, the Kikak-Tegoseak Quarry (KTQ). Although the holotype partial parietal was first reconstructed and described incorrectly (Fiorillo & Tykoski 2012), details of the correctly restored specimen still allow it to be distinguished from comparable elements of *P. lakustai* (Currie *et al*. 2008) and those referred to *P. canadensis* (Langston 1975). New cranial specimens reinforce other diagnostic features of *P. perotorum* and allow further refinement of character scoring of the taxon in the recently published analysis of Chiba *et al*. (2017). A parsimony analysis of the revised taxon-character matrix based on Chiba *et al*. (2017) yields a fully resolved Pachyrostra, the clade of nasal boss-bearing centrosaurines that includes the last common ancestor of *Achelousaurus horneri* and *Pachyrhinosaurus canadensis*, and all of that ancestor's descendants. Within the pachyrostran clade there is weak support for *P. perotorum* as the sister taxon to *P. canadensis* to the exclusion of *P. lakustai*. *Pachyrhinosaurus perotorum* and *P. canadensis* are united by the shared presence of a supranarial ossification on the lateral surface of the face between the narial fossa and nasal boss, and by anteriorly enlarged supraorbital bosses that contact or nearly contact the posterior end of the nasal boss. In addition, we find that *P. canadensis* can be diagnosed by the absence of a rostral comb (present in *P. perotorum*, *P. lakustai* and TMP 2002.76.1), and by the presence of paired supranarial bosses on the narial bridge dorsal to the narial fossa and separated from each other by a median sulcus on the narial bridge. Although parietal-squamosal frill ornamentation is important in establishing relationships among centrosaurine taxa, other craniofacial features provide the information necessary to make species-level determinations and diagnoses in *Pachyrhinosaurus*.

Acknowledgements

We thank the numerous members of the various field crews that contributed to the data collection for this project. Particularly, we thank Thomas Adams, Christopher Strganac, Kent Newman and Jason Petula. We also thank fossil preparators Briana Smith, Rory Leahy and Thomas Diamond, as well as Olivia Fiorillo and the multitude of Perot Museum Paleo Lab volunteers who helped extract and prepare many of these specimens for study. Notwithstanding these acknowledgements, the authors take all responsibility for the conclusions drawn here. We also thank Jane and Ron Gard, Cathey and Donald Humphreys, and Virginia and Ansel Condray for their original support of this Perot Alaska dinosaur project. We thank Michael Ryan (Cleveland Museum of Natural History) and David Evans (Royal Ontario Museum) for discussion and Caleb Brown (TMP) for providing specimen photos. The Barrow Arctic Science Consortium (BASC) and CH2M Hill (formerly Veco Polar Resources) provided logistical support for this project. Funding was provided by the National Science Foundation Office of Polar Programs [OPP 0424594], as well as the National Geographic Society [W221-12]. Lastly, the Arctic Management Unit of the Bureau of Land Management provided administrative support. The specimens discussed here were collected under BLM permit number AA–86367.

Supplementary data

Supplemental material for this article can be accessed at: http://dx.doi.org/10.1080/14772019.2018.1532464.

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