Histology and Ontogeny of *Pachyrhinosaurus* Nasal Bosses

by

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Abstract

Pachyrhinosaurus is a peculiar ceratopsian known only from Upper Cretaceous strata of Alberta and the North Slope of Alaska. The genus consists of three described species *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus lakustai*, and *Pachyrhinosaurus perotorum* that are distinguishable by cranial characteristics, including parietal horn shape and orientation, absence/presence of a rostral comb, median parietal bar horns, and profile of the nasal boss. A fourth species of *Pachyrhinosaurus* is described herein and placed into its phylogenetic context within Centrosaurinae. This new species forms a polytomy at the crown with *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus perotorum*, with *Pachyrhinosaurus lakustai* falling basal to that polytomy. The diagnostic features of this new species are an apomorphic, laterally curved Process 3 horns and a thick longitudinal ridge separating the supraorbital bosses.

Another focus is investigating the ontogeny of *Pachyrhinosaurus* nasal bosses in a histological context. Previously, little work has been done on cranial histology in ceratopsians, focusing instead on potential integumentary structures, the parietals of *Triceratops*, and how surface texture relates to underlying histological structures. An ontogenetic series is established for the nasal bosses of *Pachyrhinosaurus* at both relative (subadult versus adult) and fine scale (Stages 1-5). It was demonstrated that histology alone can indicate relative ontogenetic level, but not stages of a finer scale. Through *Pachyrhinosaurus* ontogeny the nasal boss undergoes increased vascularity and secondary remodeling with a reduction in osteocyte lacunar density.

A histological study of ceratopsian cranial elaborations was also performed to better understand the functional and developmental implications of these structures, as well to place the nasal boss of *Pachyrhinosaurus* into the context of ceratopsian elaborations. In centrosaurines, parietal spikes and hooks, postorbital horncores, bosses, and nasal horns are formed as outgrowths of the dermatocranium. Although the bone tissue type remains fibrolamellar across any given specimen, organization of the bone varies (cortex versus core, compact versus spongy) across cranial elaborations. However, epoccipitals (epiparietals and episquamosals) form via metaplasia. This may also be the case for epinasals in chasmosaurines, which do not form from the nasal bone, but instead fuse onto the nasal-rostral complex later in life, indicating that they are not outgrowths of the dermatocranium.

Historically, cranial histology is a poorly studied component of paleohistology and is expanded upon in this thesis. The ontogeny of *Pachyrhinosaurus* nasal bosses is explored in a histological perspective, which gives deeper understanding to how these atypical nasal ornamentations form. New fossil reports have expanded our understanding of *Pachyrhinosaurus* diversity, although their relationship to each other is not entirely clear. This increased understanding has revealed interesting evolutionary patterns, such as the replacement of nasal horns with nasal bosses by the last of the centrosaurines, the Pachyrostra (*Achelousaurus* + *Pachyrhinosaurus*). Here I provide new phylogenetic, historical, and histological research that informs these topics.

Preface

This thesis is an original work by Elizabeth Kruk. No part of this thesis has been previously published.

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Table of Contents

List of Tables

Chapter 1

Chapter 2

Chapter 3

List of Figures

Chapter 1

Chapter 2

Chapter 3

Abbreviations

GPRC, Grande Prairie Regional College, Grande Prairie, Alberta, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada

INTRODUCTION

Pachyrhinosaurus is a genus of centrosaurine ceratopsians found only in Upper Cretaceous strata of Alberta and Alaska of North America. The Pachyrostra (*Achelousaurus* + *Pachyrhinosaurus* sensu Fiorillo and Tykoski, 2012) is the youngest centrosaurine clade to appear in the fossil record (Ryan, et al., 2010). *Pachyrhinosaurus* contains three described species: *Pachyrhinosaurus lakustai* from the Wapiti Formation of northern Alberta (upper Campanian); (Currie et al., 2008); *Pachyrhinosaurus canadensis* from the Horseshoe Canyon Formation of southern Alberta (upper Campanian) (Sternberg, 1950; Langston, 1967, Langston 1975); and *Pachyrhinosaurus perotorum* from the Prince Creek Formation from the North Slope of Alaska (upper Campanian to lower Maastrichtian; Fiorillo and Tykoski, 2013). Additionally, Ryan et al. (2010) tentatively refers to material recovered from the upper Dinosaur Park Formation of Alberta as *Pachyrhinosaurus*. *Pachyrhinosaurus lakustai* is stratigraphically older than *Pachyrhinosaurus canadensis* and is different based on the presence of a rostral comb, an upturned “spout” (in some specimens) on the anterior end of the nasal boss, and an epiparietal Process 3 that twists anterolaterally, as well as horns on the median parietal bar. *Pachyrhinosaurus perotorum* differs from the other named species by the presence of a median hump on the nasal boss, a rostral comb, and an anterior facing parietal horn not seen in any other *Pachyrhinosaurus* specimens (Fiorillo and Tykoski, 2012). *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus perotorum* both have nasal and supraorbital bosses that are nearly in contact, only separated by a narrow groove, whereas *Pachyrhinosaurus lakustai* and the pachyrhinosaur from Dinosaur Park have widely separated nasal and supraorbital bosses. The growth and variation of nasal bosses has never been investigated in a histological context.

Gross morphology is not the only valuable source of information from fossils; histology, the study of tissues, can provide evidence to further our understanding of dinosaurs. The microstructure of bone records the effects of various factors including rate of bone formation, environmental conditions, biomechanics, and lifestyle adaptations (Chinsamy-Turan, 2005). Studies on the histology of dinosaur bone histology show that limb bones often preserve a growth record for the individual (Erickson and Tumanova, 2000; Horner et al., 2000; Padian et al., 2001; Horner and Padian, 2004; Erickson 2005; Chinsamy-Turan, 2005; Klein and Sander, 2007; Erickson et al., 2009; Erickson and Druckenmiller, 2011). Lines of arrested growth are often used with confidence in extant animals to estimate age and the corresponding structures in fossil bones convey similar information (Levitt, 2013). Chinsamy (1994) estimates the age of specimens that span various developmental stages by combining the growth-line counts with measurements of size to produce quantified age-versus-size growth curves for dinosaurs. There has been work done on the long bone histology of ceratopsian dinosaurs (Erickson and Tumanova, 2000; Lee, 2007; Reizner, 2010; Erickson and Druckenmiller, 2011; Levitt, 2011; Levitt, 2013; Zhao et al., 2013). However, long bone histology is still better understood than the skull elements of ceratopsians and their characteristic cranial elaborations (Hieronymus, Witmer, Tanke, Currie, 2009; Scannella and Horner, 2010; Tumarkin-Deratzian, 2010; Horner and Lamm, 2011; Kruk et al., 2013; Kruk et al., 2014).

The first known paleohistological study transpired when Richard Owen took a thin section of a bone from *Scelidosaurus* when he described it in 1861. The study of the microscopic structure of fossil bone was never a large field, but it has steadily been on the rise since the 1960s. Armand de Ricqlès published a series of works based on his dissertation, which were the first systematic studies into the histology of fossil bone. His studies were based on fragmentary bones that often were not identified, but nevertheless Armand de Ricqlès was able to introduce a series of generalizations about patterns of bone growth that still hold up to this day (Francillon-Vieillot et al., 1990). In the 1980s and 1990s Anusuya Chinsamy, Armand de Ricqlès, John R. Horner and their students and colleagues were able to standardize their bone samples and determine what paleohistology could determine about the ages and growth rates of dinosaurs. This increased acceptance and interest in the field of paleohistology also led to a renewed interest in the subject.

Bone is composed of three types of cells: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are the bone-forming cells that cover most surfaces of bones and line the blood channels as well. They also deposit osteoid, which is a collagenous matrix that mineralizes later. Osteocytes are osteoblasts that have become embedded in the bone within small spaces known as lacunae. These osteocytes communicate with other osteocytes/osteoblasts through little channels called canaliculi. Osteocytes are responsible for bone maintenance, mechano-sensory reception, and calcium homeostasis. On the other hand, osteoclasts are large, multi-nucleated bone resorbing cells. They occur on the bone surface in resorption pits and move through the bone secreting enzymes that breakup and resorb organic as well as inorganic structures.

There are three different types of ossification: endochondral, intramembranous, and metaplasia. Endochondral ossification begins from a cartilage model where the primary ossification center develops in the mid-diaphysis. Here blood vessels invade, the cartilaginous model calcifies, and osteoblasts secrete osteoid along the calcified matrix. In intramembranous ossification there is no cartilage precursor, this is typical of flat bones such as skull bones. Within the fibrous connective tissue, mesenchymal stem cells differentiate into osteoblasts forming an ossification center where osteoid is deposited and the periosteum forms; the bone continues to form along the periosteum. Metaplasia differs from the other two forms because it is the direct transformation of one fully formed tissue, such as cartilage or tendon, into another, such as bone. It occurs in areas where no periosteum forms, such as attachment sites of tendons, as well as dense dermis and cartilage can ossify via metaplasia. Metaplastic bone forms without osteoblasts. It can also be defined as a poorly vascularized, amorphous dermal bone tissue in which fibers are numerous and oriented in various directions (Main et al., 2005).

Lamellar, parallel fibered, and woven bone are the types of bone matrix. Lamellar bone has an one-dimensional structure, flat osteocytes with few canaliculi, and tends to be found in vascular canals. Parallel fibered bone is two-dimensional and has an interbraided structure. Woven bone is three-dimensional, well vascularized, with plump osteocytes, and lots of canaliculi. This is indicative of fast growth and a high metabolic rate. Bone tissue type is a combination of a given bone matrix and vascularity (e.g. radial, laminar, longitudinal, etc.). The two types are lamellar zonal and fibrolamellar bone. Lamellar zonal bone is slow growing, poorly vascularized, and also forms growth marks. It is typically found in ectotherms such as amphibians and reptiles, as well as small mammals. Fibrolamellar bone is fast growing, highly vascularized, with growth marks, and is typical of modern birds, mammals, and also dinosaurs.

In the cortex of the bone, osteoclasts tunnel through bone while osteoblasts centripetally deposit layers of lamellar bone, in which a vascular canal forms. An osteon is the fundamental functional unit of bone; it consists of concentric layers of bone that surround a central vascular canal. The boundary of an osteon is the cement line. With secondary osteons, collagen fibers get deposited in various directions, and at the center of the secondary osteon a vascular canal known as a Haversian canal forms. Another cement line forms as a boundary between the secondary osteon and primary or secondary bone. Haversian bone is defined as bone that is covered entirely by many generations of secondary osteons. Typically, secondary osteons form first within the inner core and over time spread out toward the outer cortex. Bone continues to be remodeled with secondary osteons until death.

Nasal Boss Histology

The crania of *Pachyrhinosaurus* have not been examined histologically in a comprehensive manner. Previous studies have focused on histological changes in the nasal boss during ontogeny (Edwards and Russell, 1994) and possible integumentary structures (Hieronymus et al., 2009. All other cranial histological studies have focused on other ceratopsians such as *Centrosaurus* (Tumarkin-Deratzian, 2010) and *Triceratops* (Horner and Goodwin, 2008; Horner and Lamm, 2011). As such, one focus of this thesis aims to expand the histological understanding of *Pachyrhinosaurus*, describe the morphological and histological differences between juvenile and adult nasal bosses, and use these differences to determine finer ontogenetic stages (e.g. subadult versus adult) than morphology can by itself.

The bosses on *Pachyrhinosaurus lakustai* are polymorphic, ranging from inflated to a flattened mushroom shapes, to elongate, broadly dished out bosses with anterodorsally oriented "spouts" rising from the anterior margins, to thick-walled cups (Currie et al., 2008; Ryan et al., 2010). However, it is unclear whether these extremes are due to taphonomic deformation, possible sexual dimorphism, or ontogenetic variation. Similar to other centrosaurines, juveniles of *Pachyrhinosaurus* have long-based nasal horncores that only differ in the absence of pointed distal ends, instead possessing a broad flattened appearance in lateral view (Sampson et al., 1997; Currie et al., 2008; Fiorillo and Tykoski, 2013). The ontogenetic series of pachyrhinosaurs shows a progression from small, sagittally divided horncores in juveniles to full-fledged pachyostotic bosses in adults (Sampson et al., 1997; Fiorillo and Tykoski, 2013). Furthermore, the highly rugose texture of the boss indicates rapid deposition of bone in combination with the attainment of adult size (Sampson et al., 1997).

Hieronymus et al. (2009) proposes two hypotheses for the integumentary structure on the cranial bosses of *Pachyrhinosaurus*: 1) heavily keratinized skin over the rugose surfaces of the boss; or 2) large, rhinoceros-like keratinous horns on the nasal and supraorbital bosses. Some specimens of adult *Pachyrhinosaurus lakustai* have defined apical notches, pitting, and gradation from dorsal pitting to lateral neurovascular grooves. All of these things indicate that the skin has become a thick pad of keratinized epidermis (Hieronymus et al., 2009). Furthermore, examination of a histological specimen from the dorsal surface of the nasal boss reveals bony spicules deep within the grooves. Hieronymus et al. (2009) attribute this feature to be most similar to that of a frontal boss of muskoxen because the spicules of both are composed of osteonal bone tissue, instead of metaplastically ossified deep dermis as in the case of *Rhinoceros*. Also, on the lateral surface the palisaded texture of ridges and grooves suggests a cornified sheath projecting at a shallow angle from the boss (Hieronymus et al., 2009; Fiorillo and Tykoski, 2013). Therefore, the most likely integumentary structure supported by this evidence suggests that the nasal boss of *Pachyrhinosaurus* likely supported a thick cornified pad with a thinner cornified sheath on the lateral surface.

In extant animals, such as muskoxen, African buffalo, and helmeted hornbills, the presence of a thickened cornified pad may be correlated with head-butting behavior; therefore, a similar function could be inferred for the nasal boss in *Pachyrhinosaurus* based on its proposed associated integumentary structure (Hieronymus et al., 2009). Several authors also suggest that the nasal boss was used as a battering ram, with sexual or social selection as the main function (Sternberg, 1950; Farlow and Dodson, 1975). However, Currie et al. (2008) propose that the nasal and supraorbital bosses could have functioned mainly as a visual display structures to potentially attract mates, deter predators, or for species recognition.

Histological Study of Ceratopsian Cranial Elaborations

The basic elaborations of a ceratopsid skull include posteriorly projecting frills comprised of the parietal and squamosal bones, along with horns above the orbits and the nares (Dodson et al., 2004). Although the function of ceratopsian horns remains unclear, however the most common hypothesis is that the horns were used in intraspecific combat (Lull, 1933; Farlow and Dodson, 1975; Sampson et al., 1997; Farke, 2004; Farke, Wolff, Tanke, 2009). Other possible functions include defense against predators (Hatcher et al., 1907; Lull, 1933), thermoregulation (Barrick et al., 1998), and as aids in knocking down vegetation (Tait and Brown, 1928).

Padian and Horner (2011) test the possibility of facial horns as a mechanism for species recognition using two approaches: (1) the group would need to demonstrate non-directional evolutionary variation of these structures, and (2) include several sympatric species. Most recent phylogenetic analyses of neoceratopsians do not reveal any trends in the morphology of the facial horns that would indicate any directionality in the phylogenetic sense (Xu et al., 2002;

Dodson et al., 2004). Also, the geographical and temporal distribution of ceratopsian clades indicate that bizarre structures existed in groups that lived at around the same time in geographic proximity (Padian and Horner, 2011). Therefore, ceratopsian cranial elaborations pass the two tests for the Species Recognition Hypothesis but not for adaptation or sexual display, due to lacking evidence of sexual dimorphism.

Nasal horns of *Pachyrhinosaurus* increase in size and mass ontogenetically but in different patterns than *Triceratops* (Horner and Goodwin, 2006). Juvenile and sub-adult centrosaurines possess nasal horncores that are largely triangular, laterally compressed, have median sutures, and are either erect or curve somewhat posteriorly (Sampson et al., 1997). Prior to attaining the adult condition, nasal horncore halves fuse entirely, starting from the tip and moving proximally, likely between or within the juvenile and sub-adult growth stages (Sampson et al., 1997; Horner and Goodwin, 2006). Furthermore, the horncores in juvenile centrosaurines overlie most of the narial openings; in adults, they only overlie the posterior margin of this opening (Sampson et al., 1997). In contrast, the base of the *Triceratops* horncore becomes larger than the span of the paired nasal bones beneath it (Horner and Goodwin, 2006). Additionally, the epinasal fusion of the horn to the skull anterodorsally begins during the sub-adult growth stage. Generally, the nasal horn extends anteriorly over the premaxillae but is highly variable in size and profile in adults (Horner and Goodwin, 2006).

Overall, juvenile and sub-adult centrosaurines possess roughly the same form of supraorbital horncore as each other, and only display adult horncore morphology once adult body size is reached (Sampson et al., 1997). Generally, taxonomically/phylogenetically informative characters are thought to be most prominent in somatically mature animals (Sampson et al., 1997). Juvenile supraorbital horncores are long, low rounded processes that are generally even with the external surface of the face whereas the medial surfaces slope sharply toward the midline (Sampson et al., 1997). However, some centrosaurine specimens lack true supraorbital horncores and instead have low masses, simple raised ridges, or concavities that could have resulted from periodic resorption and regrowth, resorption related to age, periodic loss, or pathology (Sampson et al., 1997). In contrast, the postorbital horns of *Triceratops* begin as straight stubs in early ontogeny, which curve posteriorly in juveniles, straighten in subadults, and curve anteriorly in adults (Horner & Goodwin, 2006).

Across ceratopsians, nearly two-thirds of the frill is comprised of the parietals with the remaining portion made up of the squamosals (Sampson et al., 1997). There are generally five to seven parietal processes per side, although there is known variation between species, within species, and within individuals across developmental time. In a centrosaurine, the squamosal is roughly rectangular in outline and short in comparison to that of a chasmosaurine squamosal, which is triangular and longer (Sampson et al., 1997). Fusion of the parietals probably occurs at an early ontogenetic stage because there is no indication of any sutural contacts in juvenile specimens (Sampson et al., 1997). Furthermore, only with adult size did the hooks and spikes of the ceratopsian frill develop. Epoccipitals are accessory elements that fuse onto the frill margin during ontogeny and possession of these has been assumed for all chasmosaurines and centrosaurines (Sampson et al., 1997; Horner and Goodwin, 2006). Furthermore, histological studies of *Centrosaurus* (Tumarkin-Deratzian, 2010) and *Triceratops* (Horner and Lamm, 2011) demonstrate similar growth within the parietals of these two genera. In juvenile *Triceratops* parietals consist of cancellous bone with primary osteons and an abundance of radially oriented canals that progresses to heavily remodeled bone (Horner and Lamm, 2011). The epoccipitals undergo considerable change during ontogeny; they begin as triangular bones that fuse sequentially from posterior to anterior to the frill margin creating radiating scallops. With maturity these scallops flatten and take on a sine-wave-like patterns (Sampson et al., 1997; Horner and Goodwin, 2006; Horner and Lamm 2011). It has been suggested that epoccipitals form via metaplasia (Horner and Lamm, 2011).

Hieronymus et al. (2009) completed a comprehensive study on the possible integumentary structures of centrosaurine skulls and explored their possible extant analogs. Overall, the centrosaurines examined with horncores present in adults (*Centrosaurus* and *Einiosaurus*) demonstrated the necessary criteria for cornified sheaths (i.e. prominent neurovascular grooves and obliquely-oriented neurovascular foramina). However, *Achelousaurus*, the sister taxon of *Pachyrhinosaurus*, instead has osteological correlates for a thick epidermal pad (dorsal pitting and lateral neurovascular grooves).

Description of the new taxon from the Wapiti River Bonebed

In the past sixty-five years, the understanding of pachyrhinosaurian diversity has greatly increased. The discovery of *Achelousaurus horneri* in the Two Medicine Formation of Montana increased the temporal and taxonomic range of pachyrhinosaurs (Sampson, 1995). The oldest pachyrhinosaur was found in the Dinosaur Park Formation (75 Ma) of Dinosaur Provincial Park; it bears similarities to *Achelousaurus* and *Pachyrhinosaurus*, and may represent a new taxon (Ryan et al., 2010). *Pachyrhinosaurus canadensis* was described by C.M. Sternberg (1950), and was collected from the St. Mary River Formation (Upper Cretaceous) of southern Alberta. It was the first ceratopsian known to have enlarged nasal and supraorbital bosses instead of facial horns. Additional material was collected from Scabby Butte by Wann Langston, Jr. (1975) and in the Horseshoe Canyon Formation, along the Red Deer River. Material from a monodominant bonebed in the Wapiti River Formation near Grande Prairie, Alberta led to the establishment of *Pachyrhinosaurus lakustai* as a new species of pachyrhinosaur (Currie et al., 2008). The most recently described pachyrhinosaur is *Pachyrhinosaurus perotorum* from the Prince Creek Formation of the North Slope of Alaska (71-68 million years) (Fiorillo and Tykoski, 2012).

The Pipestone Creek *Pachyrhinosaurus* Bonebed has been known since 1975, it is located around 800 m from its confluence with the Wapiti River, and is about 25 km to the southwest of the city of Grande Prairie (Fanti, et al., in press). A second ceratopsian-dominated bonebed occurs along the Wapiti River and is 40 km to the southwest of Grande Prairie. The Wapiti River Bonebed contains at least eight individuals of the genus *Pachyrhinosaurus*. The Pipestone Creek Bonebed has an estimated age of 73.25±0.25 million years, while the Wapiti River Bonebed has an age of 71.89±0.14, meaning there is 1.36 million years and 150 meters of section separating the two bonebeds (Currie et al., 2008; Fanti et al., in press). The age of the Wapiti River Bonebed is equivalent to the Drumheller Member of the lower Horseshow Canyon Formation, and coeval with *Pachyrhinosaurus canadensis* (Fanti et al., in press; Eberth et al., 2013).

In this thesis, a new pachyrhinosaurian ceratopsian dinosaur is described from the Wapiti River Bonebed. The diagnostic features of this pachyrhinosaur include a thick longitudinal ridge between the supraorbital bosses and laterally projecting parietal horns (P3) that sharply curve ventrally, whereas *Pachyrhinosaurus lakustai* parietal twists anterolaterally, and *Pachyrhinosaurus canadensis* points dorsolaterally. The new pachyrhinosaurian lacks the rostral comb and anteriorly projecting pommel that is seen in *Pachyrhinosaurus lakustai*; the lack of a “supranasal boss” and or a “fist sized knob” distinguishes it from *Pachyrhinosaurus canadensis*.

It also lacks the median hump on the nasal boss seen in *Pachyrhinosaurus perotorum* as well as anteromedially projecting horns on the parietal transverse bar.

Summary

Overall, there are several main hypotheses to be tested. With regards to *Pachyrhinosaurus* nasal boss ontogeny will be tested to see if ontogenetic stage (subadult vs. adult) can be determined by histology as well as morphology. The ontogenetic stages of nasal boss development of *Pachyrhinosaurus* were outlined in Table 1 of Fiorillo and Tykoski (2013), and form the basis for comparison. Hopefully relative ontogenetic stage can be determined by histology alone, but can also be conscripted into specific stages of nasal boss development.

Expanding upon this, ceratopsian cranial elaborations will be tested to determine if they grow as extensions of the dermatocranium or are formed metaplastically through mineralization of other tissues. A comparison will be made across various taxonomic groups and will demonstrate that all cranial elaborations, with the exception of epoccipitals and possibly *Triceratops* nasal horns, form in the same way. To do this, samples were selected from chasmosaurine and centrosaurine ceratopsian ornamentations, namely bosses, supraorbital horncores, parietals, squamosals, parietal horns, and an epoccipital. Then a histological analysis was performed where each of the specimens were embedded in epoxy, glued to a plexiglass slides, cut, and ground until they reached the optimal thickness (around 50 μm) to be viewed under a microscope. This was the same technique used in the nasal boss ontogeny study.

Lastly, a description of the new *Pachyrhinosaurus* species from the Wapiti River Bonebed is presented within the framework of ontogenetic, stratigraphic, and taphonomic variability established in the earlier chapters of the thesis. Two partial skulls, a partial parietal bar, and a parietal horn will be used to diagnose this new species. Following the description is a phylogenetic analysis placing the new species into context within the Centrosaurinae.

Overall, ceratopsian long bone histology has not been as well studied as other groups such as the Theropoda. Ceratopsian studies have focused on *Psittacosaurus* (Erickson and Tumanova, 2000; Zhao et al., 2013) and another on *Pachyrhinosaurus* (Erickson and Druckenmiller, 2011). There appears to be a disparity between low and high latitude ceratopsians in terms of number of lines of arrested growth (Levitt, 2011).

As previously mentioned, there has been little work previously on the histology of ceratopsian cranial elaborations; studies on cranial elaborations have focused determining their function and morphological ontogeny. *Pachyrhinosaurus* is a strange and curious ceratopsian that represents the last of the centrosaurines. It is intriguing to note that the species within the crown group of the Centrosaurinae share nasal bosses as a common feature. It raises the question of why there was a deviation from nasal horns to nasal bosses. These structures are poorly understood from a morphological point of view, and are even less understood from a histological perspective. *Pachyrhinosaurus* has some of the most peculiar cranial elaborations seen within ceratopsians and the variety within the genus is increasing as more localities are discovered.

Chapter 1

“Histological and morphological ontogeny of *Pachyrhinosaurus* nasal bosses”

This chapter will be submitted to the Canadian Journal of Earth Sciences for publication.

Introduction

Pachyrhinosaurus is a centrosaurine ceratopsian found only in Alberta and Alaska of North America. Unlike other ceratopsians, which have bony horncores, *Pachyrhinosaurus* has cranial bosses. The specimens examined in this study are juvenile, subadult, and adult nasal bosses of *Pachyrhinosaurus lakustai* from the Pipestone Creek Bonebed. Additional subadult and adult bosses of *Pachyrhinosaurus* sp. nov. from the stratigraphically higher (by 150m) Wapiti Bonebed. Both bonebeds are located near Grande Prairie, Alberta. Superficially, the juvenile nasal boss bears almost no resemblance to those of the adult specimens and more closely resembles a horncore rather than a boss. The juvenile nasal boss is ridge-like in dorsal view and the surface texture includes neurovascular grooves extending predominantly dorsoventrally and foramina for nerves and/or blood vessels. In contrast, the adult bosses are large, coalesced masses that are spongy with resorption pits and are roughly triangular in dorsal view. Histologically, the juvenile nasal boss is composed of mostly fibrolamellar bone. The adult nasal bosses from Pipestone have a combination of spongy bone with thick trabeculae and compact bone consisting of several generations of secondary osteons.

Although *Pachyrhinosaurus* nasal bosses differ superficially in juvenile versus adult specimens, histologically similar tissues may be found in both. It is possible, based on the differences observed in these specimens, that nasal boss microstructure may be useful in determining ontogenetic stages (e.g. subadult versus adult) than morphology alone.

Abbreviations

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

Materials and Methods

Several partial nasal bosses described by Currie et al. (2008) were identified as juvenile based on size, surface bone textures, and cranial ornamentation. The remaining specimens were identified as adults based on their relative size. Histological samples from several juvenile and adult specimens (Table 1) of *Pachyrhinosaurus lakustai* from the Pipestone Creek Bonebed and *Pachyrhinosaurus sp.* from the Wapiti River Bonebed (both representing the Campanian/Maastrichtian Wapiti Formation) near Grande Prairie, Alberta, Canada were examined. All specimens were embedded in epoxy resin (EpoThin™, Low Viscocity Resin and Hardener Buehler, Lake Bluff, IL), vacuum impregnated (Welch Duo-Seal), then left to cure for 24 hours. The embedded samples were rough-cut on a tile saw then stabilized with PaleoBond Penetrant Stabilizer. The billets were ground on a lapidary wheel and glass plate using 240, 400, and 600 grit SiC powder (E.T. Enterprises, Calgary, AB) until the majority of scratches had been removed. The billets were glued to glass or plexiglass slides using EpoThin™. The section was cut and rough-ground on a Hillquist, stabilized further (PaleoBond, Penetrant Stabilizer), ground by hand on a glass plate using 600 and 800 grit SiC, and polished against denim with CeO_2 Grit GPP Tumble Polish for 2-3 minutes.

Sections were examined and photographed on a Nikon Eclipse E600POL trinocular polarizing microscope with an attached Nikon DXM 1200F digital camera. Whole slide scans were taken with a Nikon Super Coolscan 5000 ED.

Table 1.1. List of specimens.

Specimen No.	**Histological No.**	**Ontogenetic Stage**	**Locality**	**Taxon**
TMP 1989.55.894	TMP 1993.55.2	Juvenile (1)	Pipestone Creek Bonebed	*P. lakustai*
TMP 1989.55.174	TMP 1993.55.11	Juvenile (1)	Pipestone Creek Bonebed	*P. lakustai*
TMP 1986.55.048	TMP 1993.55.12	Juvenile (1)	Pipestone Creek Bonebed	*P. lakustai*
TMP 1987.55.161	TMP 1993.55.13	Juvenile (1)	Pipestone Creek Bonebed	*P. lakustai*
TMP 1989.55.1240		Juvenile (2)	Pipestone Creek Bonebed	*P. lakustai*
TMP 1989.55.1038	TMP 1993.55.8	Subadult (3)	Pipestone Creek Bonebed	*P. lakustai*
UALVP 55138		Subadult (4)	Wapiti River Bonebed	*P.* sp. nov.
TMP 1989.55.1342	TMP 1993.55.16/17/18/20	Subadult (4)	Pipestone Creek Bonebed	*P. lakustai*
UALVP 53300		Adult (5)	Wapiti River Bonebed	*P.* sp. nov.
TMP 1985.112.119		Adult (5)	Pipestone Creek Bonebed	*P. lakustai*

Table 1.2. Ontogenetic stages of nasal boss development in *Pachyrhinosaurus*

Growth Stage	Characteristics
Stage 1	Low, paired demihorns with minimal lateral texturing in form of neurovascular grooves Demihorn essentially covers nasal from anterior process to posterior edge Posterior surface of demihorn not strongly deflected medially and only slightly sculptured
Stage 2	Isometric growth of paired (not fused) demihorns, that extend most of the length of nasal Lateral surface texturing with larger neurovascular grooves with variable orientation Posterior sculptured surface larger, more distinctly sculpture, and deflected medially
Stage 3	At least" two-thirds" adult size Fusion of nasals begins anteriorly and progress posteriorly? Thickening of lateral surfaces, "broad tumid expansion" of demihorns into an incipient boss Boss precursor enlarges posteriorly but not yet to posterior edge of nasal Posterior sculpted area apparently coalesced into expanding incipient boss Dorsal margins with lateral ridges bounding medial depression
Stage 4	Lateral surfaces of boss migrate rapidly away from midline, accompanied by rapid deposition of spongy bone between them to form obvious boss structure Boss gross rapidly posteriorly to or nearly to posterior edge of nasals Boss defined ventrolaterally by distinct basal sulcus Lateral surfaces show signs of palisade texture comprised of parallel dorsoventrally-oriented ridges and grooves
Stage 5	Boss mediolaterally as wide or wider dorsally than ventrally along basal sulcus Full nasal boss extends from premaxillary process to posterior edge of nasals, may contact supraorbital bosses in *P. canadensis* and *P. perotorum* Lateral surfaces extensively marked by palisade texture of dorsoventrally oriented grooves and ridges Remodeling of boss dorsal surface

Results

Nasal bosses were sorted into more specific stages of growth using the descriptions in Table 1.2 (modified from Fiorillo & Tykoski, 2013; originally derived from Currie et al. 2008).

Stage 1

Stage 1 is characterized by the smallest and most immature demihorns, which closely resemble the small nasal horncores of juvenile centrosaurines. However, the demihorns take on an anteroposteriorly elongated fin or ridge appearance. Overall, these are composed of fibrolamellar bone, with dense osteocyte lacunae, and the bone is somewhat trabecular (Figure 1.1). Also, the osteons are primary and there is no evidence of secondary remodeling. Each of the Stage 1 demihorns is relatively flat and low in lateral profile. Within the scans of the thin sections there does not appear to be much differentiation within a single slide, except for Figure 1.1 B. The more vascular region is located in the middle of the demihorn, so it is not surprising to find a slight differentiation before core and cortex.

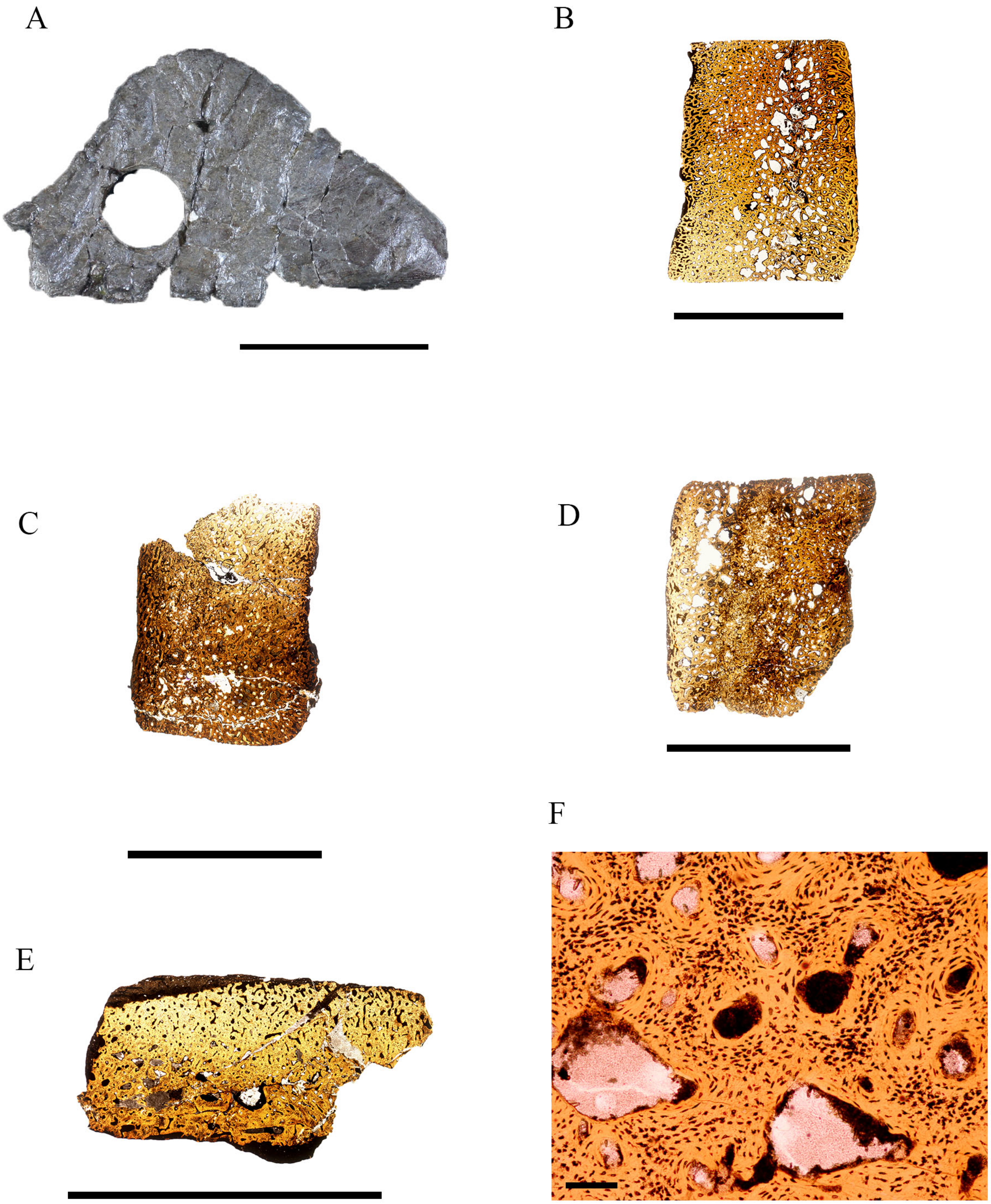

Figure 1.1. Stage 1. Image of TMP 1989.55.174 (A). Coronal sections of TMP 1989.55.894 (PP9-1) (B), TMP 1989.55.174 (PP11-3) (C), TMP 1987.55.161 (PP13-2) (D), TMP 19855.894 (PP2-3) (E), and microscope image of TMP 1989.55.894 (PP2-3). Scale bars equal 5 cm (A), 1 cm (B, C, D, E), and 0.1 mm (F)

Stage 2

Bigger in size than the Stage 1 demihorns, there are more prominent neurovascular grooves visible at Stage 2 and it is more sculpted with a slight medial curvature. However, with regard to histology not much has changed since Stage 1. Primary osteons are numerous whereas the osteocyte lacunar density is quite high (Figure 1.2). For the most part there is not much of a differentiation between core and cortex except for a slight increase in trabecular bone towards the center of the section.

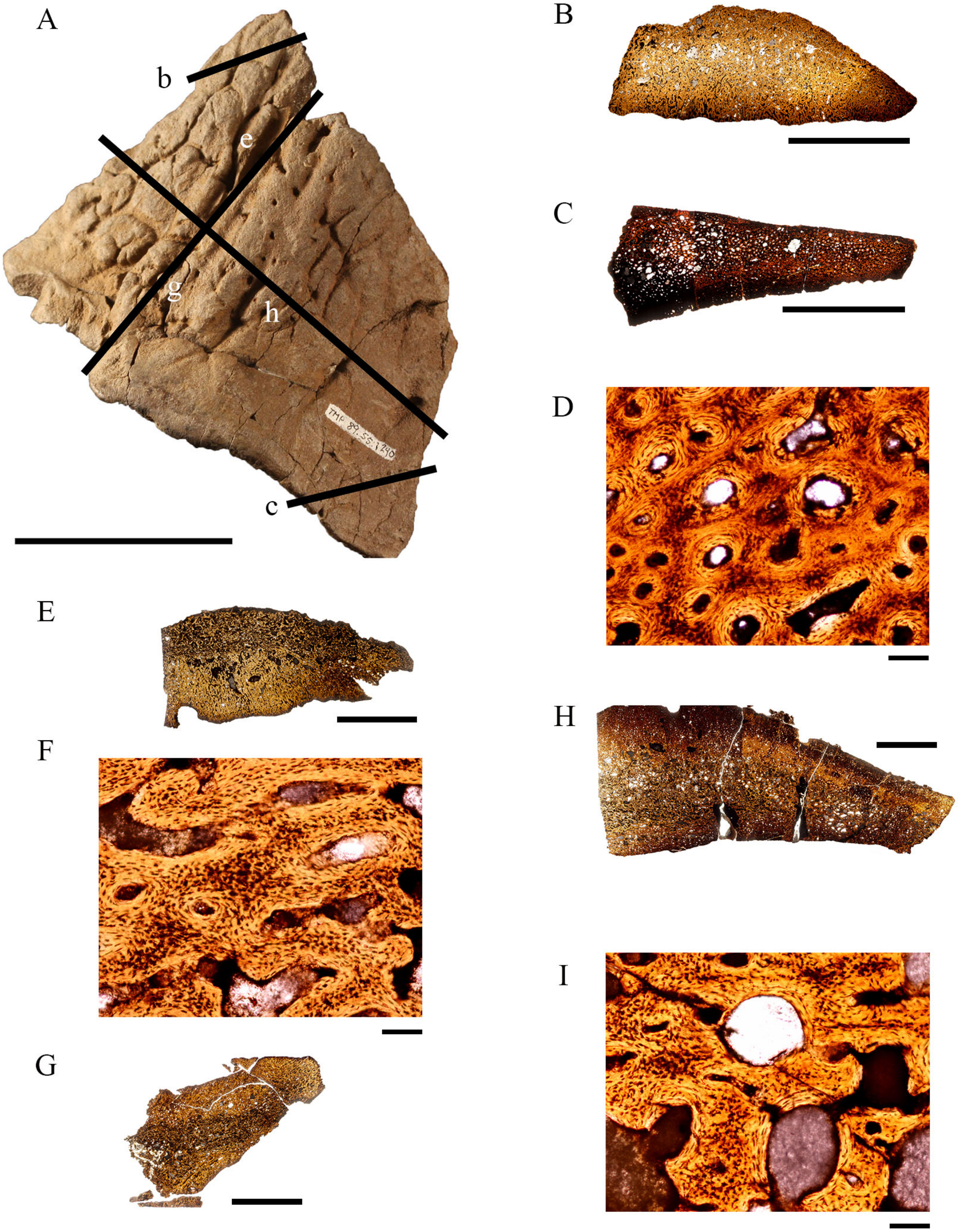

Figure 1.2. Stage 2. TMP 1989.55.1240. TMP 1989.55.1240 showing planes of section (A). Large letters associate with small letters. Microscope image of C (D). Microscope of E (F). Microscope image of H (I). Scale bars equal 5 cm (A), 1 cm (B, C, E, G, H), and 0.1 mm (D, F, I).

Stage 3

TMP 1989.55.8 is categorized into Stage 3 based upon the thickening of the lateral surfaces into an incipient boss (Figure 1.3). An interesting note on the histology of this section, there is some division of tissue textures, the tissues closer to the dorsal surface appear more compact and not as trabecular as tissue positioned ventrally. There is evidence of zones; dorsally the vascular canals are oriented transversely then ventrally large vascular spaces occur and crosscut the primary tissues. Closer in, the texture resembles the rope-like appearance of more mature nasal bosses however there is still a large number of osteocyte lacunae.

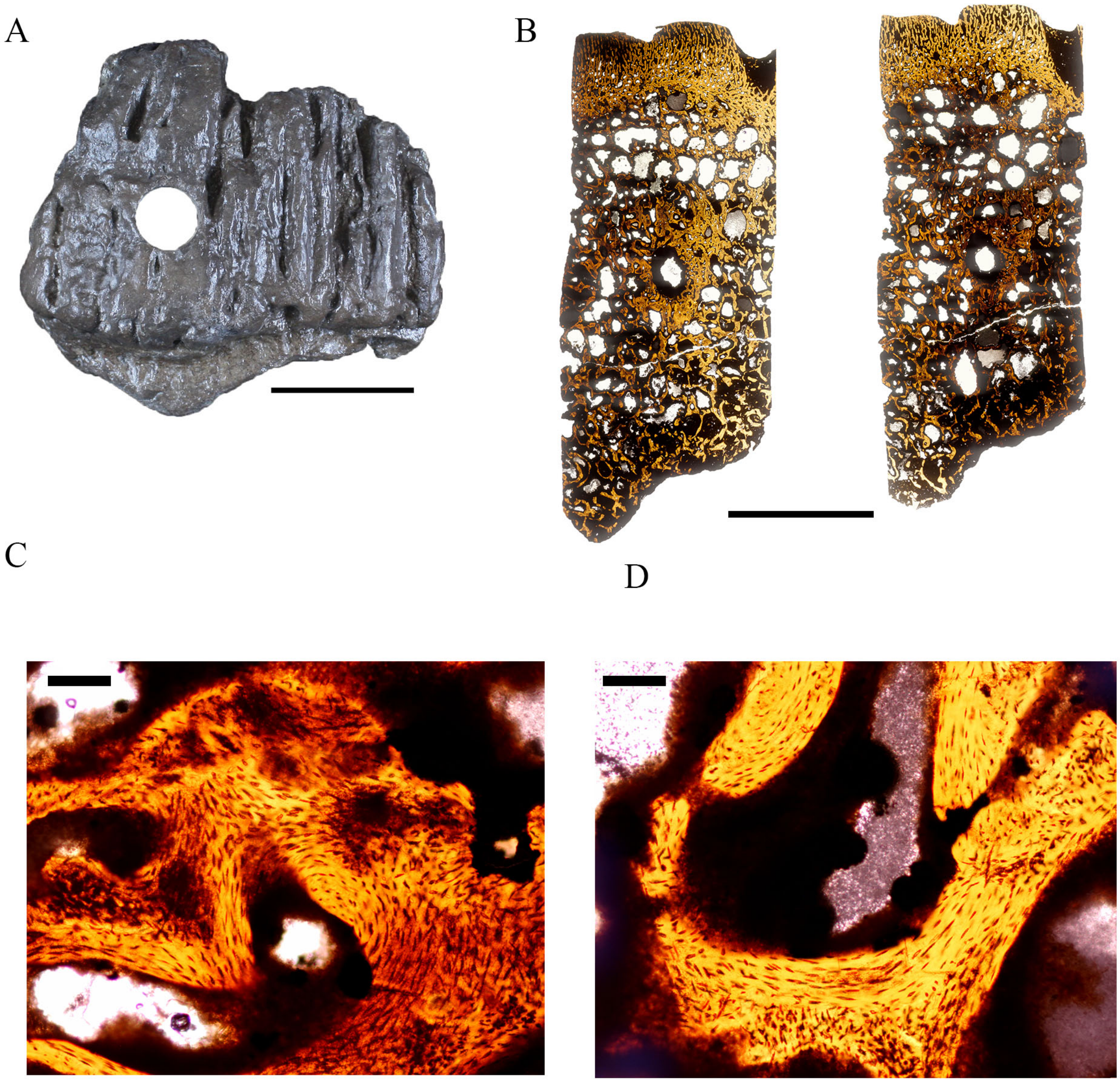

Figure 1.3. Stage 3. TMP 1989.55.1038 (A). Thin sections oriented dorsal edge up (B). Microscope images of B (C, D). Scale bars equal 5 cm (A), 1 cm (B), and 0.1 mm (C, D).

Stage 4

TMP 1989.55.1342 is classified as Stage 4 based on the distinct basal sulcus and overall size (Fig. 1.4 A). However, UALVP 55138 (Fig. 1.4) is a well-worn nasal boss that is placed into Stage 4 based only on histological evidence. Both specimens have a mixture of primary and secondary osteons but are not as trabecular as Stage 5 nasal bosses. Two interesting points to note with UALVP 55138, there is a resorption pit with a clear resorption line (Fig. 1.4 G, I) as well as differing orientations of vascular canals in the coronal section (Figure 1.4 H). Towards the outside of the slide (Fig. 1.4 H) the canals are circular and oriented perpendicular to the field of view, but towards the center the canals are longitudinal. The slides of TMP 1989.55.1342 (B, C, D) exhibit differentiation between the cortex and core. The tissues at the cortex are more compact than the interior and the canals are oriented dorsoventrally at the dorsal most edge. Moving ventrally the tissue becomes more trabecular and looks most similar to an adult boss at its most ventral edge. It should also be noted that the difference in shading across slides B, C, and D is due to the slide being polished too thin, the lighter areas represented thinner portions of the section. In both TMP 1989.55.1240 and UALVP 55138 the density of osteocyte lacunae is less than that of the previous stages but denser than the Stage 5 slides.

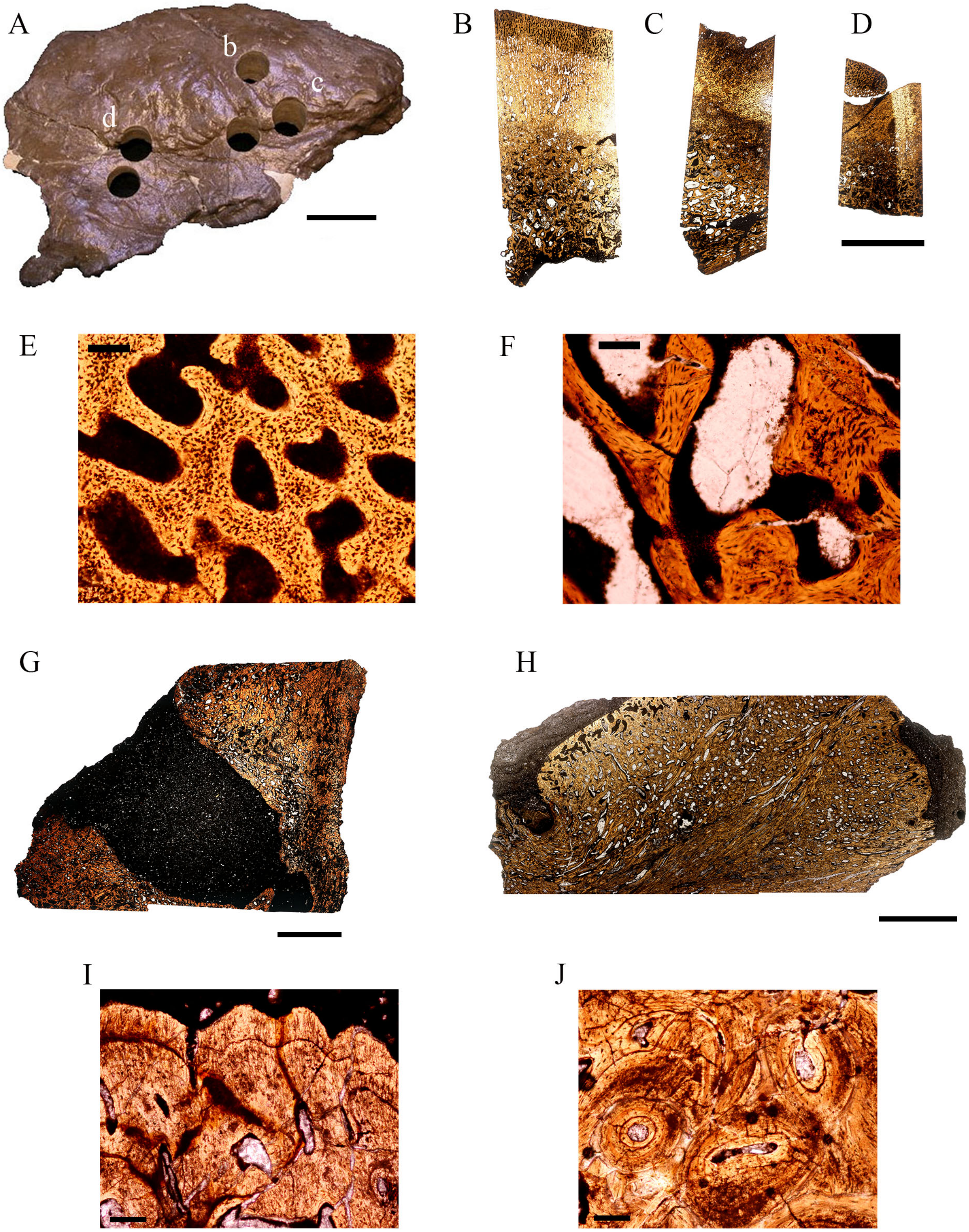

Figure 1.4. Stage 4. TMP 1989.55.1342 (A), Thin sections (B, C, D) from TMP 1989.55.1342, oriented dorsal edgeup. Microscope images for TMP 1989.55.1342 (E, F). UALVP 55138 thin sections (I, J), oriented dorsal edge up. Microscope images of UALVP 55138 (I, J). Scale bars equal 5cm (A), 1cm (B, C, D, G, H), and 0.1mm (E, F, I, J).

Stage 5

Stage 5 sections were taken from a fully developed nasal boss from a partial skull (UALVP 53300) and an isolated nasal boss (TMP 1985.112.119) (Fig. 1.5). Microscopically there are several generations of secondary remodeling and the amount of vascular space is greater than the earlier stages. Also, the density of osteocyte lacunae has decreased as well. The fibrolamellar bone has taken on a rope-like appearance. Several generations of secondary osteons are visible in the thin sections (Fig. 1.4 C, E, F). In Figure 1.4 D, a resorption cavity has resorbed part of several osteons.

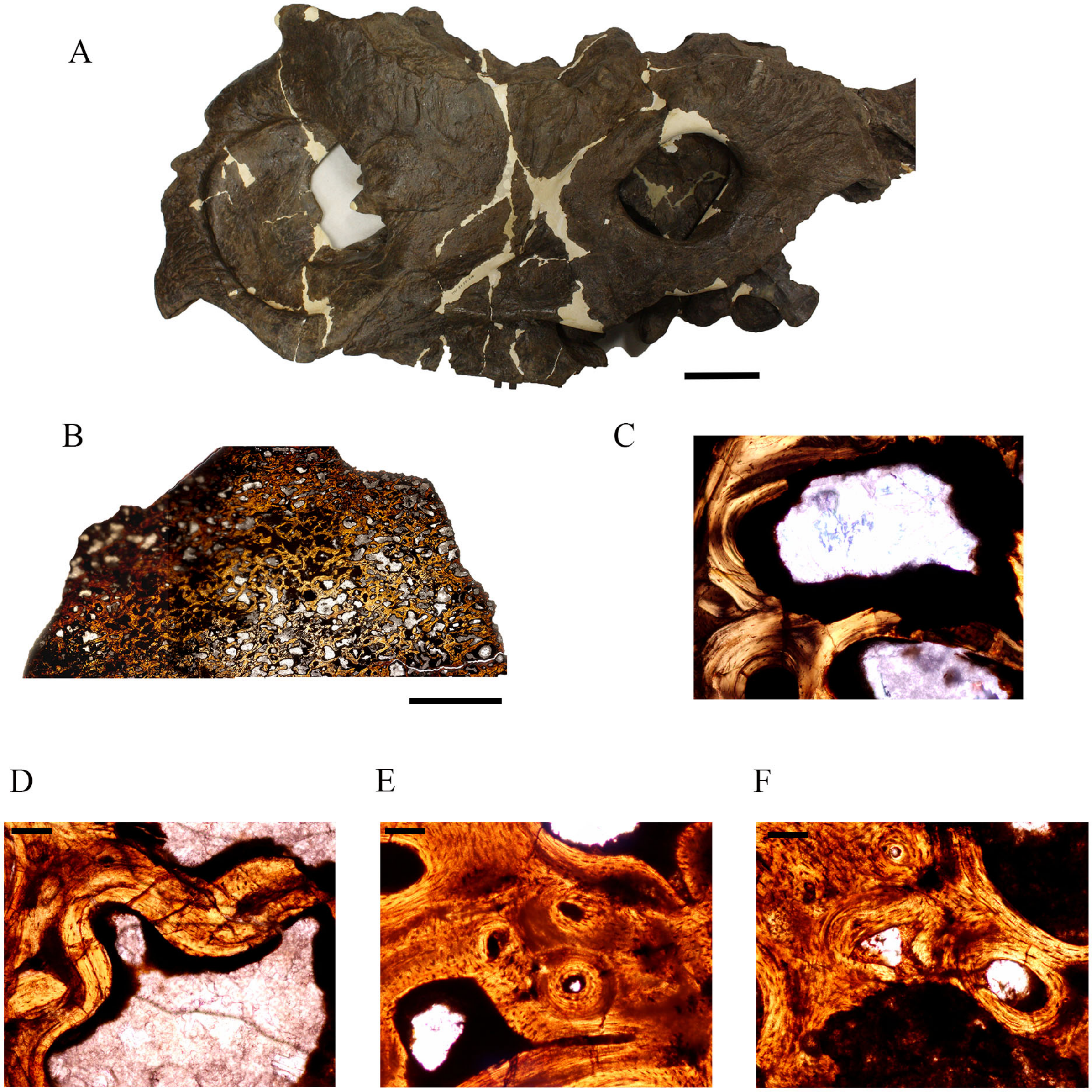

Figure 1.5. Stage 5. TMP 1986.55.258, *Pachyrhinosaurus lakustai* holotype skull (A). UALVP 53300 thin section (B). Microscope images of B (C, D) and TMP 1985.112.119 (E, F). Scale bars equal 10 cm (A), 1 cm (B), 0.1 mm (C, D, E, F).

Discussion

There is an overall increase in vascularity (sponginess), as the *Pachyrhinosaurus* gets older. Secondarily remodeling increases as well but it is not seen until Stage 3 at the earliest. Also osteocyte lacunar density decreases with age as well, tapers off at Stage 5. The presence of osteoblasts in all stages of ontogeny indicates that these structures are ossified intramembranously, are outgrowths of the nasal bone, and are not formed through metaplasia.

Based on these results, I am proposing that the ontogenetic stages based on nasal boss development from Fiorillo and Tykoski (2013) can be divided into three traditional stages of ontogeny. Stage 1 and 2 can be considered juvenile due to dense osteocyte lacunae, extensive primary tissue, and minimal amounts of differentiation between core and cortex. The demihorns are laterally compressed and take on a ridge-like appearance when viewed dorsally. Stage 1 maintains a fairly linear shape dorsally, while Stage 2 curves medially in a concave fashion. Neurovascular grooves are distinctly visible in lateral view on TMP 1989.55.1240, a feature not seen in the Stage 1 demihorns. All specimens in Stage 1 and 2 do not resemble the future nasal boss it would eventually progress to.

Stage 3 and 4 are described as subadults because there is an increase in vascular space as well as secondary remodeling. In Figure 1.3 B, TMP 1989.55.1038's dorsal surface has latitudinal vascular canals that display the "broad tumid expansion" of the incipient nasal boss described by Currie et al. (2008). Furthermore, in Figure 1.4 H the coronal section of UALVP 55138 shows a difference in orientation of vascular canals between the outside and middle of the section. This difference indicates that the nasal boss does not have a point of origination with regards to growth and shows that the vascular canals do not have a particular orientation. Also the resorption pit seen in Figure 1.4 (G, I) is a true resorption pit because it shows a distinct resorption line around the edge, cutting across the surrounding osteons, and it is further evidence of secondary remodeling.

Finally, Stage 5 represents adulthood due to the extensive amount of remodeling, multiple generations of secondary osteons, rope-like texture, and large vascular spaces. Macroscopically an adult *Pachyrhinosaurus* nasal boss's lateral surface has extensive, dorsoventrally oriented grooves and ridges, as well as remodeling on the dorsal surface of the boss including resorption pits or even entirely "scooped out" bosses that have undergone extensive remodeling. Extreme amounts of resorption are an indicator of senescence.

Pachyrhinosaurus has one of the more extreme ontogenetic sequences with regards to the development of its nasal ornamentation. It begins with a horn that resembles those of closely related centrosaurine species but morphs into a structure that is unlike any other found outside the Pachyrostra. It is curious that the last of the centrosaurines evolved their nasal ornamentation to be a boss instead of a horn core.

Conclusions

Nasal boss histology is poorly understood, but our understanding was improved by thin sectioning an ontogenetic series of nasal bosses, as well as placing the specimens into finer ontogenetic stages (Table 1.1, Table 1.2) than just juvenile, subadult, and adult based on gross morphology. As the pachyrhinosaurs progress through ontogeny secondary remodeling and vascularity increase while osteocyte lacunar density decreases. It was determined that relative ontogenetic stage (subadult vs. adult) can be determined by histology alone, but not into finer ontogenetic stages (Fiorillo and Tykoski, 2013). However, further subdivision of ontogenetic stages (Stage 1-5, Table 1.2) leads to three traditional stages of ontogeny --juvenile, subadult, and adult-- based on the histology of individual specimens. All ontogenetic stages are composed of fibrolamellar bone and progress to have many generations of secondary osteons, which causes the heavily remodeled and rope-like appearance.

Prior to this study, the only systematic histological study of ceratopsian nasal ornamentation ontogeny was performed on *Triceratops* (Horner and Goodwin, 2008). Now it has been expanded to include *Pachyrhinosaurus*. However, more histological studies need to be performed on the ontogeny of ceratopsian cranial elaborations. There is an immense amount of information that can be found by using histology that adds to our overall knowledge of dinosaurs.

Chapter 2

“Histological study of cranial elaboration in ceratopsian dinosaurs: Functional and developmental implications”

Introduction

Hypotheses for the developmental processes of cranial elaborations in ceratopsians have relied upon gross morphology and studies of morphological changes in taxa with relatively complete growth series. To date, these hypotheses have not been tested using histology. A study on the cranial epidermal coverings of centrosaurine skulls, however, did investigate the nasal boss histology of *Pachyrhinosaurus* as a correlate for the keratinized covering of that unique structure (Hieronymus et al., 2009). Here the histological data available is expanded for the cranium of *Pachyrhinosaurus*, a centrosaurine ceratopsian dinosaur that has cranial bosses in place of bony horn cores. In addition, other cranial material from Late Cretaceous Albertan ceratopsians of various ontogenetic stages is examined.

The focus of this study is to test whether morphologically diverse cranial elaborations in ceratopsians demonstrate similarly diverse developmental processes via paleohistological analysis. Overall, cranial elaborations in ceratopsians are observed to be intramembranous in origin, not metaplastic, with the exception of epoccipitals. This is in contrast to some other dinosaurs, such as the ankylosaurs, whose cranial elaborations form via combinations of metaplastic mineralization of the dermis and intramembranous outgrowth of the cranial vault bones.

In the specimens examined, these structures generally contain trabecular bone at maturity, but the nasal bosses show thicker trabeculae than the other cranial material sectioned. Secondarily remodeled bone is common among all elements examined, with occasional interstitial primary fibrolamellar bone preserved. Periosteal bone was observed in only two horn core specimens (UALVP 49545 and UALVP 52658). Trabecular bone in the examined specimens is mostly associated with mature structures, commonly found with resorption pits and spicules. An immature horn core examined exhibited radial fibrolamellar bone, which suggests that the bone was growing quickly at the time of the animal's death. Secondary remodeling in this specimen (UALVP 52658) is restricted to the core and retains a high proportion of the primary fibrolamellar bone. This study proposes that all ceratopsian cranial elaborations grow rapidly as primary, fibrolamellar outgrowths of the dermatocranium and remodel, later in ontogeny, into mature, largely trabecular structures.

Abbreviations

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

Materials and Methods

Chasmosaurine and centrosaurine specimens from Upper Cretaceous strata of Alberta were chosen to cover a range of cranial elaborations. All specimens were embedded in epoxy resin (EpoThin™, Low Viscocity Resin and Hardener Buehler, Lake Bluff, IL), vacuum impregnated (Welch Duo-Seal), then left to cure for 24 hours. The embedded samples were rough-cut on a tile saw then stabilized with PaleoBond Penetrant Stabilizer. The billets were ground on a lapidary wheel and glass plate using 240, 400, and 600 grit SiC powder (E.T. Enterprises, Calgary, AB) until the majority of scratches had been removed. The billets were glued to glass or plexiglass slides using EpoThin™. The section was cut and rough-ground on a Hillquist, stabilized further (PaleoBond, Penetrant Stabilizer), ground by hand on a glass plate using 600 and 800 grit SiC, and polished against denim with CeO_2 Grit GPP Tumble Polish for 2-3 minutes.

Sections were examined and photographed on a Nikon Eclipse E600POL trinocular polarizing microscope with an attached Nikon DXM 1200F digital camera. Whole slide scans were taken with a Nikon Super Coolscan 5000 ED.

Table 2.1. List of specimens

Specimen Number	Species	Element
TMP 1981.16.499	*Chasmosaurus sp.*	Orbital horncore
TMP 1982.16.215	*Chasmosaurus sp.*	Parietal
TMP 1985.112.119	*Pachyrhinosaurus lakustai*	Nasal boss
TMP 1989.55.1240	*Pachyrhinosaurus lakustai*	Horncore (juvenile)
TMP 1998.93.034	*Styracosaurus albertensis*	Postorbital/Supraorbital
TMP 2000.57.009	*Anchiceratops sp.*	Squamosal/Frill
UALVP 49545	Ceratopsian	Horncore
UALVP 52526	*Pachyrhinosaurus sp.*	Frill
UALVP 52658	*Centrosaurus sp.*	Orbit & Orbital horncore
UALVP 53300	*Pachyrhinosaurus sp.*	Nasal boss
UALVP 54165	*Pachyrhinosaurus sp.*	Parietal horn (P3)
UALVP 54208	*Pachyrhinosaurus sp.*	Postorbital
UALVP 54894	Ceratopsian	Epoccipital
UALVP 55138	*Pachyrhinosaurus sp.*	Nasal boss

Results

TMP 1998.93.034

The *Styracosaurus albertensis* postorbital/supraorbital has fairly dense osteocyte lacunae with a few secondary osteons, showing at least one generation of remodeling (Figure 2.1). It is composed of fibrolamellar bone and is not greatly vascularized.

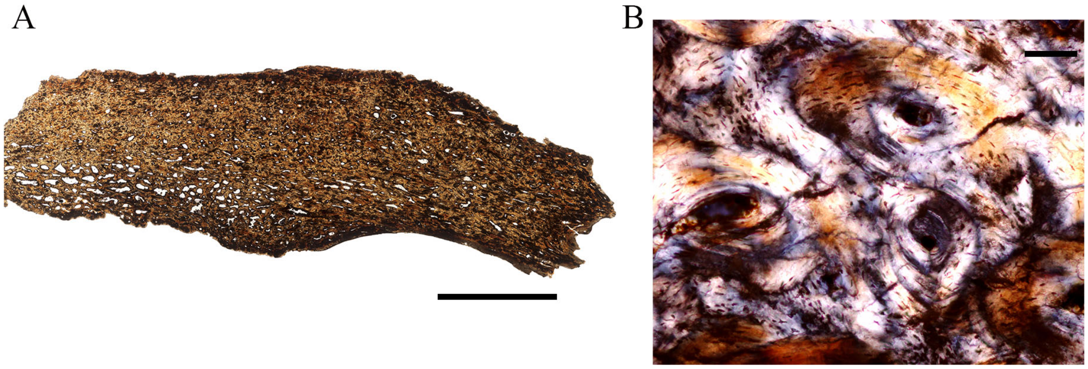

Figure 2.1. TMP 1998.93.34 (*Styracosaurus albertensis*) postorbital/supraorbital, thin section (A) and microscope image (B). Scale bars equal 1 cm (A) and 0.1 mm (B).

UALVP 54208

The *Pachyrhinosaurus* postorbital (Figure 2.2) is riddled with microfractures and cracks (most likely acquired postmortem, due to no evidence of remodeling). The bone is heavily remodeled through fossilization processes, however at least one secondary osteon was visible.

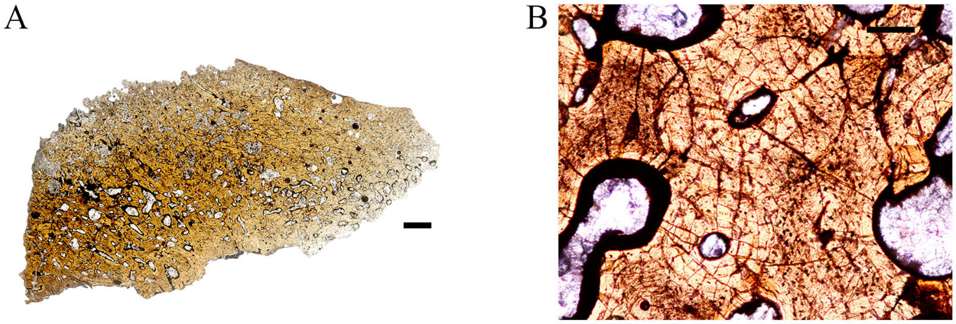

Figure 2.2.UALVP 54208 (*Pachyrhinosaurus sp.*) thin section (A) and microscope image (b). Scale bars equal 1 cm (A) and 0.1 mm (B),

UALVP 52658

This specimen is a juvenile *Centrosaurus* (Figure 2.3). The orbital region is composed of mostly woven bone with some secondary remodeling. However it is still primary bone in the interstitial spaces (Figure 2.3 A,C). Also it has a fine-grained texture, not many vascular openings, and periosteal bone is found on the external edges. The orbital region of bone shows histology expected of a developing skull bone. The orbital horncore primarily consists of woven bone with little fibrolamellar bone and has slightly higher relative vascularity with some radial canals, in comparison to some of the larger specimens (Figure 2.3 B, D). Dense osteocyte lacunae are visible in patches; more would be seen if the slide was not as thin.

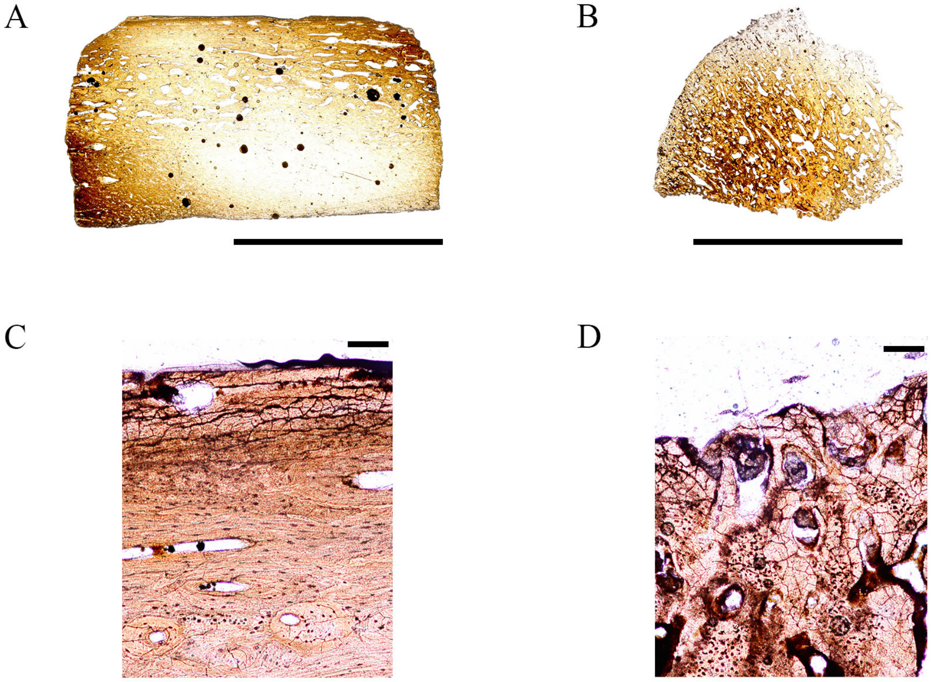

Figure 2.3. UALVP 52658 (*Centrosaurus sp.*). Thin sections of orbital skull bone (A) and associated horncore (B). Microscope images of A (C) and B (D). Scale bars equal 1 cm (A, B) and 0.1 mm (C, D).

UALVP 49545

The cortical area of the ceratopsian horncore (UALVP 49545, Fig. 2.4) consists of compact fibrolamellar bone, which is radial out to the surface along with periosteal bone at its external edge. In the core exist secondary remodeling resorption cavities that form spongy or trabecular bone. Overall, ceratopsian horncores have a compact cortex and a spongy core. There are dense osteocyte lacunae, indicative of rapid growth.

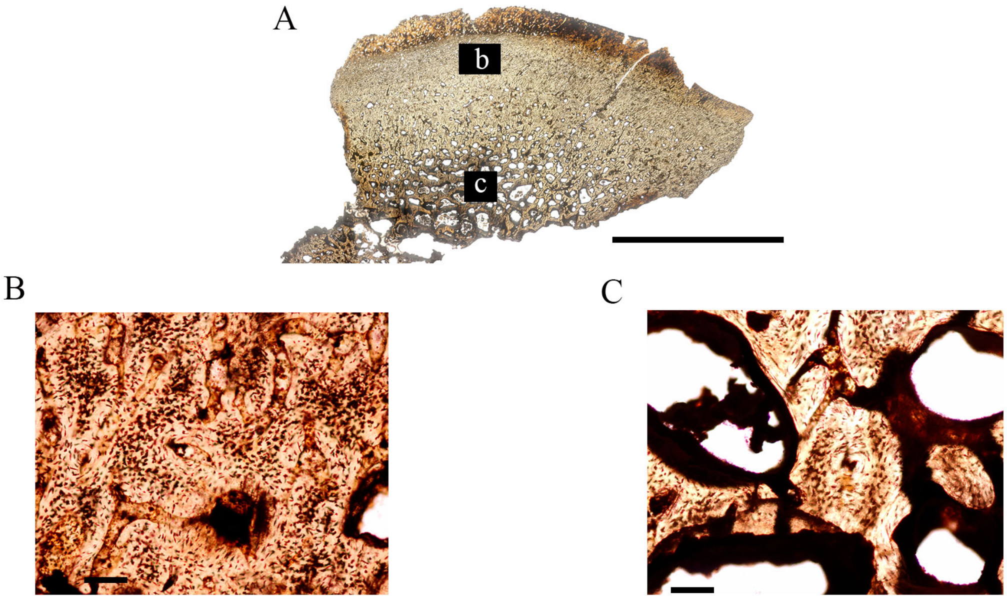

Figure 2.4. UALVP 49545 ceratopsian horncore (A). Microscope images locations (b, c), microscope images (B, C). Scale bars equal 1 cm (A) and 0.1 mm (B, C).

TMP 1981.16.499

Similar to UALVP 49545, the orbital horncore of TMP 1981.16.499 (Figure 2.5) shows differentiation between the core and cortex. The specimen is composed of fibrolamellar bone and also has dense osteocyte lacunae. The core is composed of more trabecular bone than the cortex, which is compact with smaller vascular spaces.

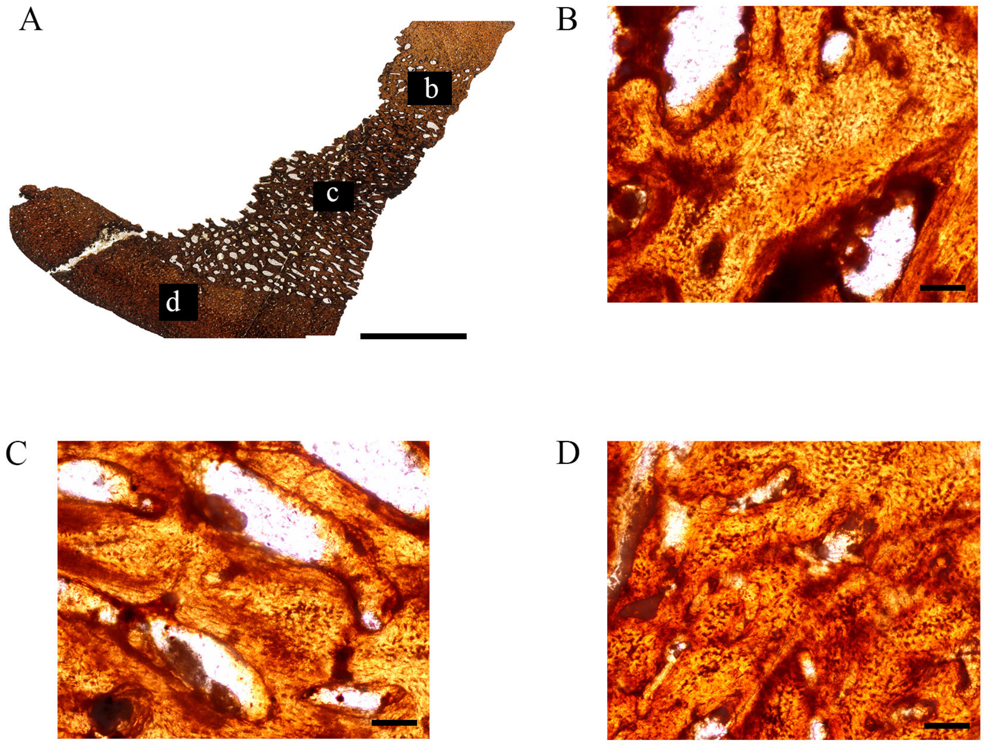

Figure 2.5. TMP 1981.16.499 (*Chasmosaurus sp.*) horncore (A). Microscope image locations (b, c, d) and microscope images (B, C, D). Scale bars equal 1 cm (A) and 0.1 mm (B, C, D).

UALVP 52526

The *Pachyrhinosaurus* frill (UALVP 52526, Fig. 2.6) is poorly vascularized in comparison to horncores, but is also composed of fibrolamellar bone that secondarily remodels as the animal ages. There is secondary remodeling seen in the core of the frill.

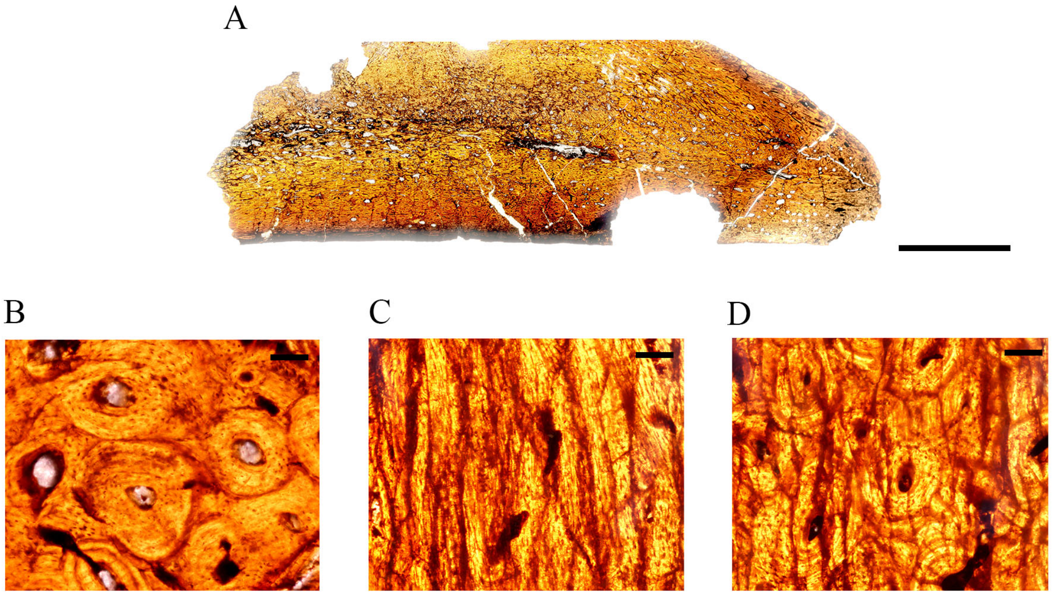

Figure 2.6. UALVP 52526 (*Pachyrhinosaurus sp.*) frill, thin section (A) and microscope images (B, C, D). Scale bars equal 1 cm (A) and 0.1 mm (B, C, D).

TMP 2000.57.009

The *Anchiceratops* squamosal (TMP 2000.57.09, Fig 2.7) is a slightly more vascular in comparison to UALVP 52526. However, it is still composed of fibrolamellar bone and has evidence of secondary remodeling.

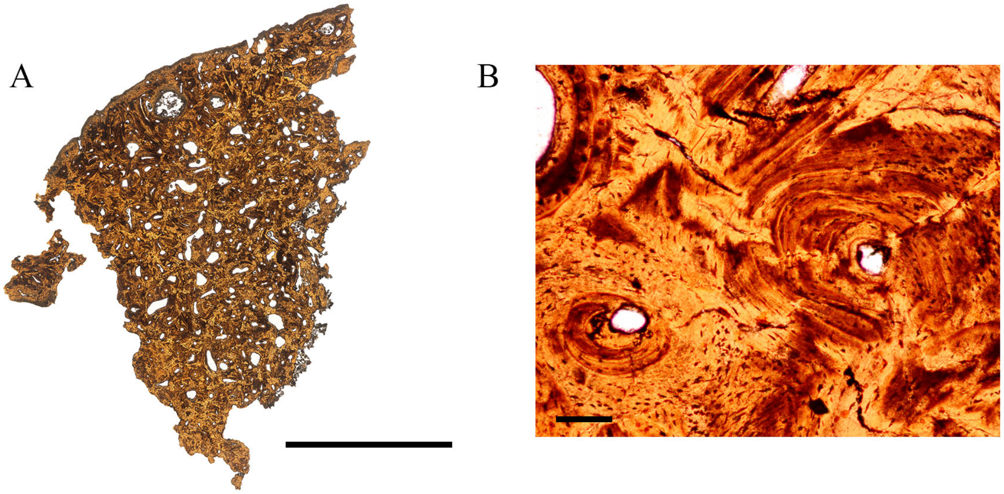

Figure 2.7. TMP 2000.57.09 (*Anchiceratops*) squamosal, thin section (A) and microscope image (B). Scale bars equal 1 cm (A) and 0.1 mm (B).

UALVP 54165

The *Pachyrhinosaurus* parietal horn (UALVP 54165, Fig. 2.8) has large trabeculae and is mostly secondarily remodeled fibrolamellar bone, with several generations of secondary osteons. It also have a spongy appearance similar to nasal bosses. No metaplastic bone is visible.

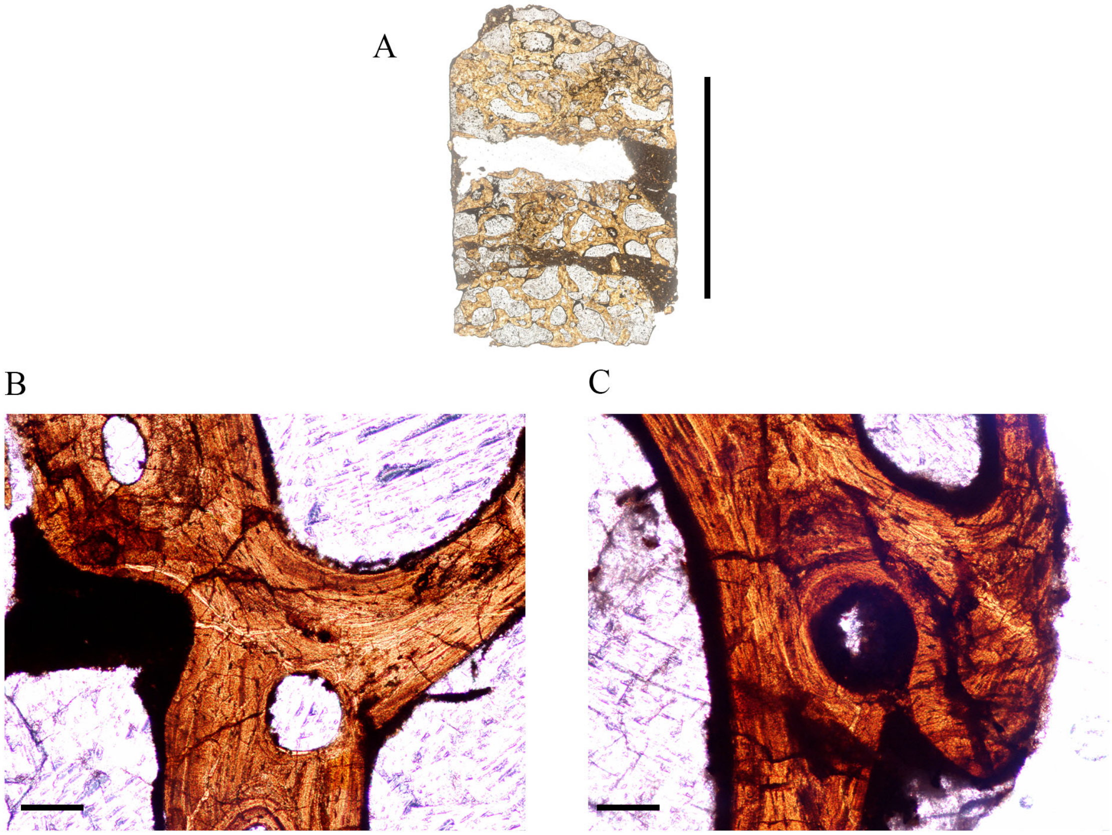

Figure 2.8. UALVP 54165 (*Pachyrhinosaurus*) parietal P3 horn, thin section (A), and microscope images (B, C). Scale bars equal 1 cm (A) and 0.1 mm (B, C).

TMP 1989.55.1240, UALVP 55138, UALVP 53300, TMP 1985.112.119

Pachyrhinosaurus nasal bosses are exceptionally spongy with rather thick trabeculae and all specimens show several generations of secondary remodeling (Figure 2.9). However, unlike other ceratopsian horncores there is no differentiation of bone compactness between the core and cortex. Vascularity and the relative amount of remodeling increases with age same with the appearance of absorption pits. Juvenile nasal bosses (TMP 1989.55.1240, Fig. 2.9 A; see also Chapter 1) initially look more like nasal horns than bosses before they morph into their more rugose counterparts.

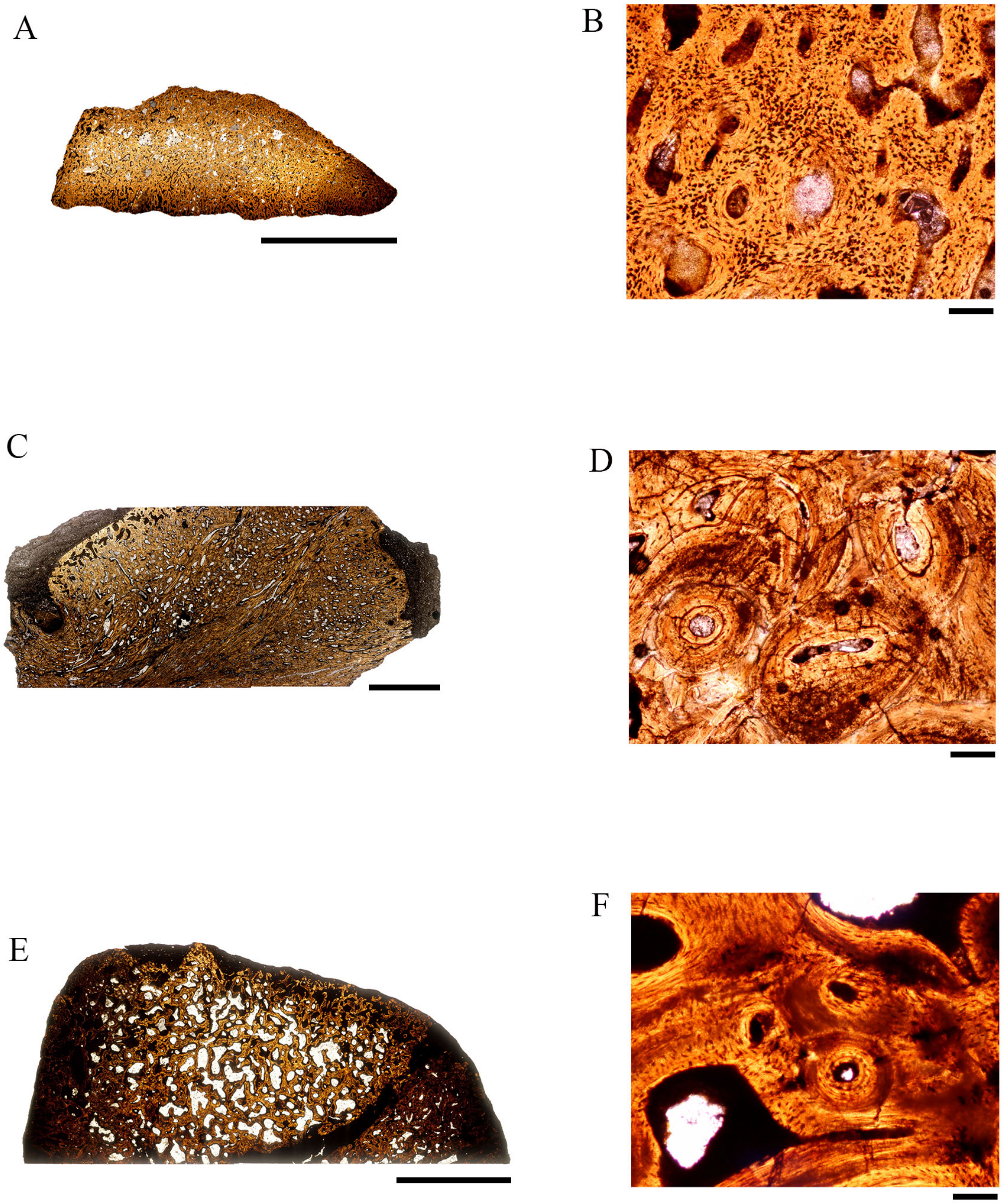

Figure 2.9. *Pachyrhinosaurus* nasal bosses. TMP 1989.55.1240, juvenile (A, B); UALVP 55138, subadult (C, D); and TMP 1985.112.119, adult (E, F). Scale bars equal 1 cm (A, C, E) and 0.1 mm (B, D, F).

UALVP 54894

In contrast to the other cranial elaborations, the epoccipital (UALVP 54894, Fig. 2.10) demonstrates metaplastic bone, which is described as interwoven structural fiber bundles. The bone is not particularly vascular and there are several generations of secondary osteons. Near the anterior portion of the specimen, is a pit representing a neurovascular groove running across the specimen.

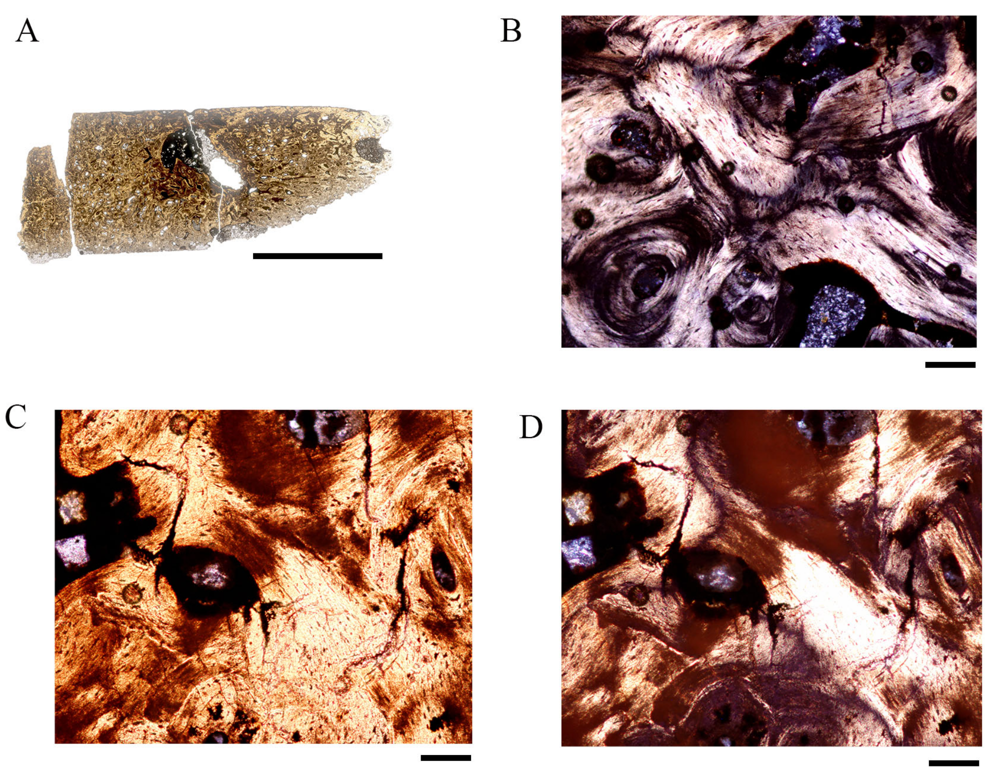

Figure 2.10. UALVP 54894 (ceratopsian) epoccipital, thin section (A), microscope images (B, C, D). Cross polarized light (B), plain polarized light (C), cross polarized light of B (D). Scale bars equal 1 cm (A) and 0.1 mm (B, C, D).

Discussion

With the exception of epoccipitals, the cranial elaborations of ceratopsians are formed intramembranously, and thus are outgrowths of the dermatocranium. It is interesting to see how the formation of various elaborations on the frill differ so much. Because we often find isolated epoccipitals that have a sutural-like surface instead of a break, it would be plausible that epoccipitals form within the skin on the frill and fuse to the frill bones later in ontogeny. Before fusing to the frill margins, epoccipitals remodel after initially laying down woven bone, which forms quickly but is more disorganized than Haversian bone. The one ceratopsian that may be an exception to this hypothesis is *Triceratops*, where its epinasal and epoccipitals can be found in isolation before fusing to the skull later in ontogeny. Furthermore, nasal bosses look unlike any other cranial elaboration sampled here. For a greater histological analysis of *Pachyrhinosaurus* nasal bosses see Chapter 1. However, across the taxa that were sampled in this study, it can be postulated that the cranial elaborations of ceratopsians all form in similar manners.

The only other comparable histological study focuses on the ontogeny of the parietal of *Triceratops* (Horner and Lamm, 2011). The results of Horner and Lamm (2011) agree with those presented here, in the sense that parietals are composed of fibrolamellar bone. This suggests that all ceratopsian parietals are composed of fibrolamellar bone. Otherwise there has been no comprehensive study of ceratopsian cranial elaborations.

This study does not have wider implications for all of Marginocephalia, which possess bizarre cranial ornamentations that form as outgrowths of the skull, pachycephalosaurs form their elaborations through metaplasia. Horner and Goodwin (2009) sectioned the cranial dome and squamosal horns of various pachycephalosaurs and determined that they formed through metaplasia. The sweeping conclusion states that marginocephalian dinosaurs utilize metaplasia to grow their cranial ornamentations, which this study disagrees with that assumption. Based on the presence of osteocytes in many of these specimens, it is shown that these ornamentations grow out of the skull, with the exception of the epoccipitals, instead of forming through metaplasia. How the formation of cranial ornamentation differs between the two major groups of Marginocephalia is interesting, and further investigation of this could prove to be enlightening. Five different species were sampled in this study (*Anchiceratops, Centrosaurus, Chasmosaurus, Pachyrhinosaurus,* and *Styracosaurus*), two chasmosaurines and three centrosaurines. Future research would include a more comprehensive study of ceratopsian cranial elaborations of more species and across a greater span of time.

Conclusions

Prior to this study, it was unknown if the horns and spikes on the frills of ceratopsians were formed through metaplasia (similar to ankylosaur osteoderms) or as outgrowths of the dermatocranium. This chapter demonstrates that in centrosaurine and chasmosaurine (with the exception of *Triceratops*) cranial elaborations are outgrowths of the skull, with the exception of epoccipitals (i.e. epiparietals and episquamosals), which are formed through metaplasia. *Triceratops* differs partially in this aspect. Its nasal horn is not formed from the nasals, but instead derives from a bone known as the epinasal that fuses onto the nasal bones during ontogeny; it is derived from a separate center of ossification (Horner and Goodwin, 2008). It is quite possible that the epinasal of *Triceratops* is a trait found only in chasmosaurines. However, little has been done on the cranial ontogeny of chasmosaurines other than *Triceratops*, so it is uncertain whether the epinasal is a feature found just in *Triceratops*. Additionally, if the epinasal is a feature found only in chasmosaurines that could be used as a character to further distinguish chasmosaurines from centrosaurines. Conversely, a mostly complete juvenile *Chasmosaurus* (UALVP 52613) from the Dinosaur Park Formation has been found and has a nasal bump with no evidence of an epinasal. Instead the epinasal could be a feature unique to *Triceratops*.

Overall, a more comprehensive histological study of ceratopsian cranial elaborations needs to be performed. There is still much to be discovered about ceratopsians and their obscure ornamentations.

Chapter 3

“A new species of *Pachyrhinosaurus* from the Wapiti Formation (upper Campanian) of Alberta”

This chapter will be submitted to PLoS ONE for publication.

Introduction

The upper Cretaceous strata of the Grande Prairie region (Alberta, Canada) are exceptionally rich in their record of prehistoric Alberta. Here the taxon from the Wapiti River Bonebed, a recently described multi-taxic ceratopsian bonebed, is described as a new species of horned dinosaur. The bonebed is located 150 meters stratigraphically higher than the well-known Pipestone Creek Bonebed that produces *Pachyrhinosaurus lakustai* specimens. *Pachyrhinosaurus youngi* sp. nov. exhibits an apomorphic parietal horn and wide, raised separation between its supraorbital bosses. A phylogenetic analysis of seventeen taxa of ceratopsians produced a weakly supported resolution of the relationships between the *Pachyrhinosaurus* species, resulting in a polytomic crown group composed of *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi*. The Wapiti River Bonebed represents one of the most inland occurrences of centrosaurines in North America.

Geologic Setting

The Wapiti River Bonebed is a multi-taxic ceratopsian dominated bonebed within the Wapiti Formation (Fanti, Currie, and Burns, in press). The bonebed can be traced linearly 107 m and has been systematically excavated over an area of 40 m^2 during annual field expeditions from 2007 to 2014. The Wapiti River Bonebed occurs 660 meters above the base of the Wapiti Formation and 300 meters above a coaly interval, that is correlative to the lower tongue maximum flooding surface of the Bearpaw (Fanti and Catuenau, 2010; Fanti et al., in press). The lithography of the bonebed is composed of a lower mudstone layer (up to 40 cm thick) comprised of a large amount of oxides that form a light-colored ironstone layer. The overlying mudstone layer exhibits disorganized and folded laminae and is then overlain by parallel and undisturbed layers (Fanti et al., in press). Larger bones are encased within the ironstone layer, whereas the upper laminated layer preserves smaller elements. The depositional setting was an oxbow lake or marshy/swampy, water-saturated area, or a lacustrine setting within an alluvial plain (Fanti et al., in press). Other identified fossils have been identified as toissible ornithomimid elements and dromeosaurid, troodontid, and tyrannosaurid teeth; there are several elements from hadrosaurids (Fanti et al., in press).

Several elements demonstrate evidence of pre-burial exposure (fragmentation and breakage) that indicate some degree of sub-aerial exposure and fluvial transport prior to burial

(Fanti et al., in press). Tooth marks are only visible on five specimens. No bones have been found articulated. The minimum number of *Pachyrhinosaurus* individuals is eight and is based on partial skulls and occipital condyles. ^{40}Ar/^{39}Ar dating provides an age of 71.89±0.14 million years, based on a 25 cm thick, altered volcanic ash 180 cm below the bonebed layer (Figure 3.1; Fanti et al., in press). The Wapiti River Bonebed represents one of the most inland occurrences of centrosaurines in North America.

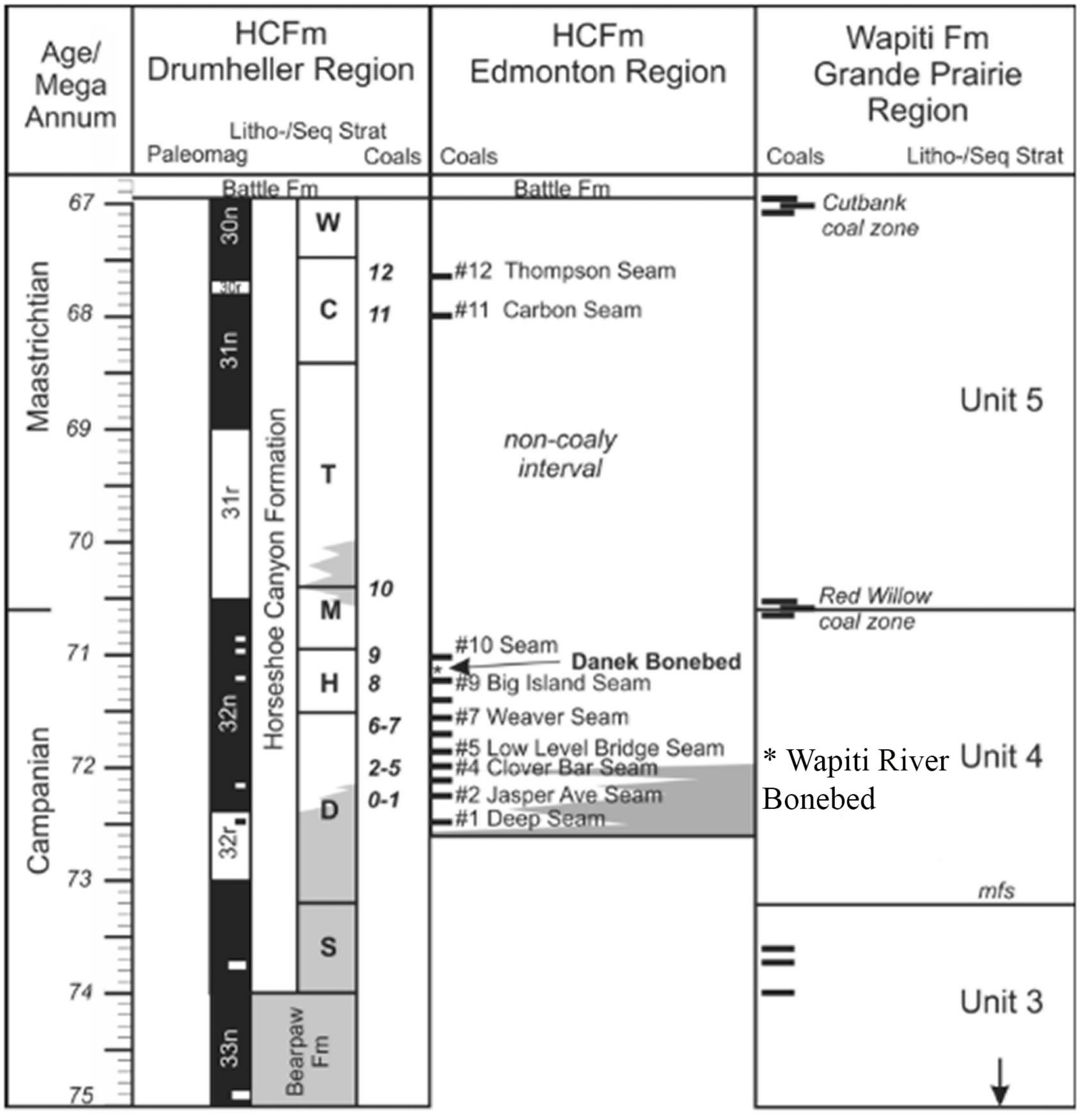

Figure 3.1. Chronostratigraphic correlation chart for the Horseshoe Canyon Formation in Drumheller and Edmonton, and the Wapiti Formation in Grande Prairie. Modified from Eberth and Bell (2014). Abbreviations: C, Carbon Member; D, Drumheller Member; H, Horsethief Member; Litho-/Seq Strat, Lithostratigraphy and Sequence-Stratigraphy; M, Morrin Member; S, Strathmore Member; T, Tolman Member; W, Whitemud Member.

Abbreviations: UALVP, University of Alberta Laboratory for Vertebrate Paleontology; Edmonton, Alberta, Canada.

Systematic Paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1888

Ceratopsidae Marsh, 1888

Centrosaurinae Lambe, 1915

Pachyrhinosaurus Sternberg, 1950

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

Pachyrhinosaurus youngi sp. nov.

Figs. 3.2-3.5

Etymology: In recognition of the Young family who have allowed the University of Alberta to excavate the Wapiti River Bonebed on their land.

Type Material: Holotype: UALVP 53300, partial skull missing parietals, squamosals, and right cheek region. Paratypes: UALVP 54165, automorphic parietal P3 horn; UALVP 50652, parietal bar and horn (P2); UALVP 55805 (originally catalogued as GPRC/RH 03.06.03.01.02.015) partial skull missing rostrum, parietals, squamosals, and cheek regions.

Type Locality: All specimens collected from the Wapiti River Bonebed along the Wapiti River, near Grande Prairie, Alberta, Canada.

Type Horizon: The specimens were collected from upper Campanian rocks (71.89±0.14 Ma) within the Wapiti River Formation (Fanti et al., in press).

Diagnosis: *Pachyrhinosaurus youngi* is distinguished from other pachyrhinosaurs by its dorsolaterally curved parietal horns and a distinctive tall separation between supraorbital bosses. It differs from *Pachyrhinosaurus lakustai* by lack of a rostral comb and an anteriorly protruding "pommel." *Pachyrhinosaurus youngi* is also differentiated from *Pachyrhinosaurus canadensis* by the absence of a "supranasal boss" and "fist-sized knobs;" however the new species is united with *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus perotorum* based on the nasal and supraorbital bosses that are nearly in contact and only separated from each other by a narrow grooves.

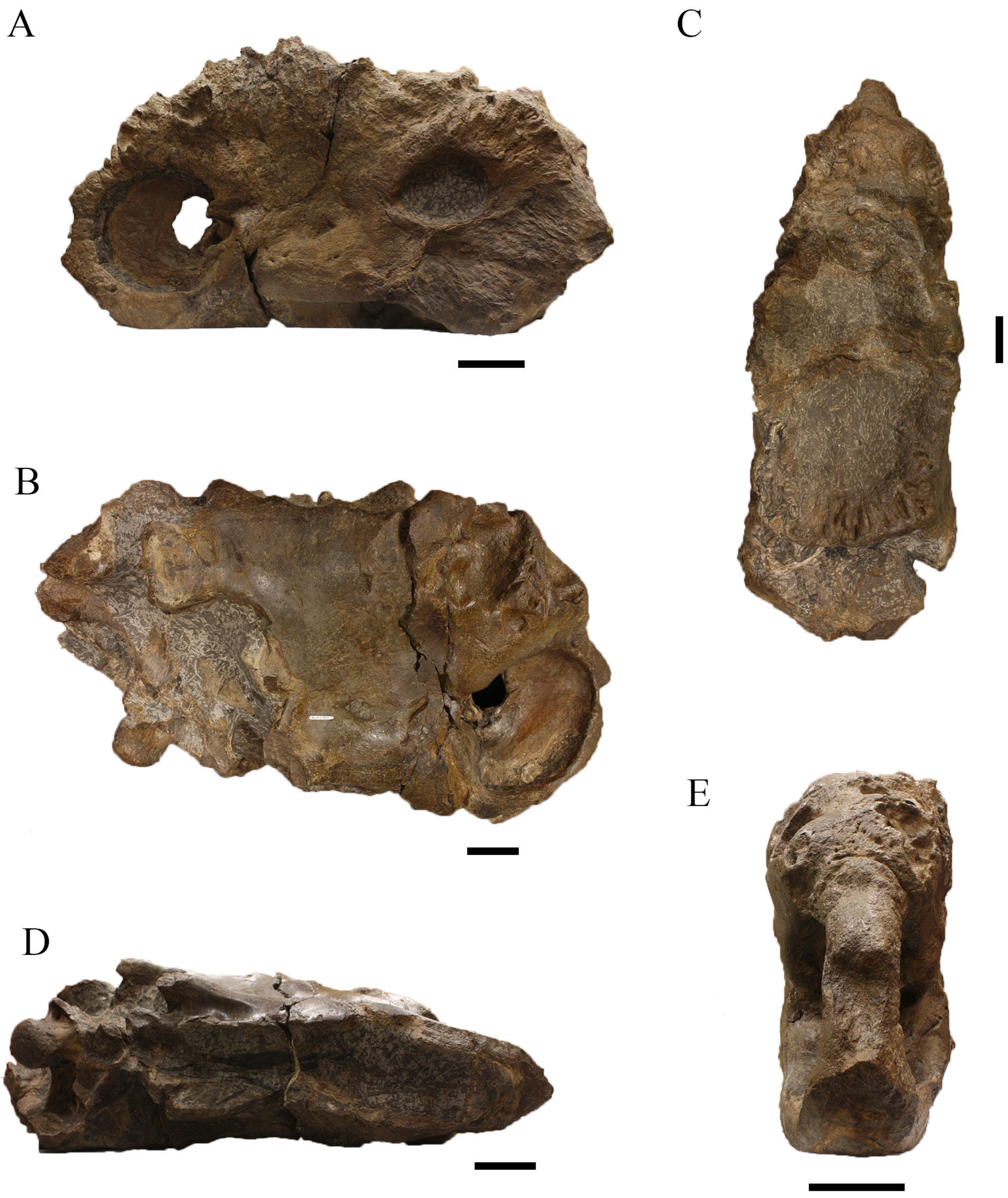

Figure 3.2. Centrosaruine ceratopsid *Pachyrhinosaurus youngi* sp. nov., holotype (UALVP 53300); skull in left lateral (A), right lateral (B), dorsal (C), ventral (D), and anterior (E) views. Scale bars 10 cm.

Table 3.1 Measurements (in mm) of UALVP 53300, *Pachyrhinosaurus youngi* holotype skull. Landmarks used by Langston (1975) and Currie et al. (2008). Lowercase "e" after number signifies an estimate.

A	Top of nasal boss to ventral limit of maxilla	487
B	Vertical height of narial opening in lateral view	101
C	Maximum vertical height	487
D	Vertical height of narial fossa	198
E	Top of orbit to tip of supraorbital boss	69
intrF	Rostrum to posterior edge of naris	331e
G	Posterior edge of naris to anterior margin of orbit	298
H	Anteroposterior length of orbit	157
I	Posterior edge of orbit to supratemporal fenestra	?
J	Antorbital length	582e
K	Height of orbit	127
L	Posterior edge of naris to posterior edge of nasal boss	444
M	Bottom of orbit to bottom of jugal	?
N	Greatest width of expansions behind nares	255
O	Width across lowest flange of premaxilla	126
P	Least transverse width of narial bridge	85
Q	Greatest width of narial aperture	190
R	Greatest width of nasal boss	264
S	Least transverse width of face between nares and orbit	229
T	Length of nasal boss	607
	Length of skull roof (tip of nasal boss to posterior edge supraorbital boss	744e
	Skull length (rostrum to occipital condyle)	875e

Description

Rostral

What remains of the rostral bone (Fig. 3.2) is fused to the premaxillae and is missing the anterior point or beak and posteroventral portions. The rostral bone is rugose in texture. The degree of curvature of the beak could not be determined. There is no evidence for pre-mortem breakage of the rostral bone.

Premaxilla

The premaxillae (Fig 3.2) are fused together with the right side being slightly eroded and smooth, whereas the left side is well preserved and pitted. The premaxillae form the broad narial septum typical of a centrosaurine. The narial septum is mostly smooth; however, there are small cracks in it, most likely due to postmortem compaction. The septum composes the anterior two-thirds of the narial fossa. There is no rostral comb present in *Pachyrhinosaurus youngi*, unlike *Pachyrhinosaurus lakustai* and *Pachyrhinosaurus perotorum*.

Maxilla

The maxilla (Fig. 3.2) has a broad triangular profile, a medial ascending process that contacts the premaxillae anterodorsally, and an ascending lateral process that contacts the jugal. The floor of the antorbital fenestra separates these processes. In left lateral view, the ventral surface of the maxilla has been partially eroded, whereas in the right lateral view the ventral surface has eroded up to the overhanging portion of the maxilla. There are 20 alveoli preserved in the paratype skull (UALVP 55805) (Fig. 3.3), although the tooth count may have had a few more tooth positions. This number is close if not comparable to other similarly sized ceratopsids (25-28 in *Achelousaurus,* 18-30 in *Chasmosaurus*, 16-35 in *Centrosaurus*, 24-28 in *Einiosaurus*) (Currie et al., 2008). The maxilla contacts the ectopterygoid, jugal, lacrimal, palatine, premaxillae, pterygoid, and vomer; however, these contacts are either not visible or not preserved in this specimen.

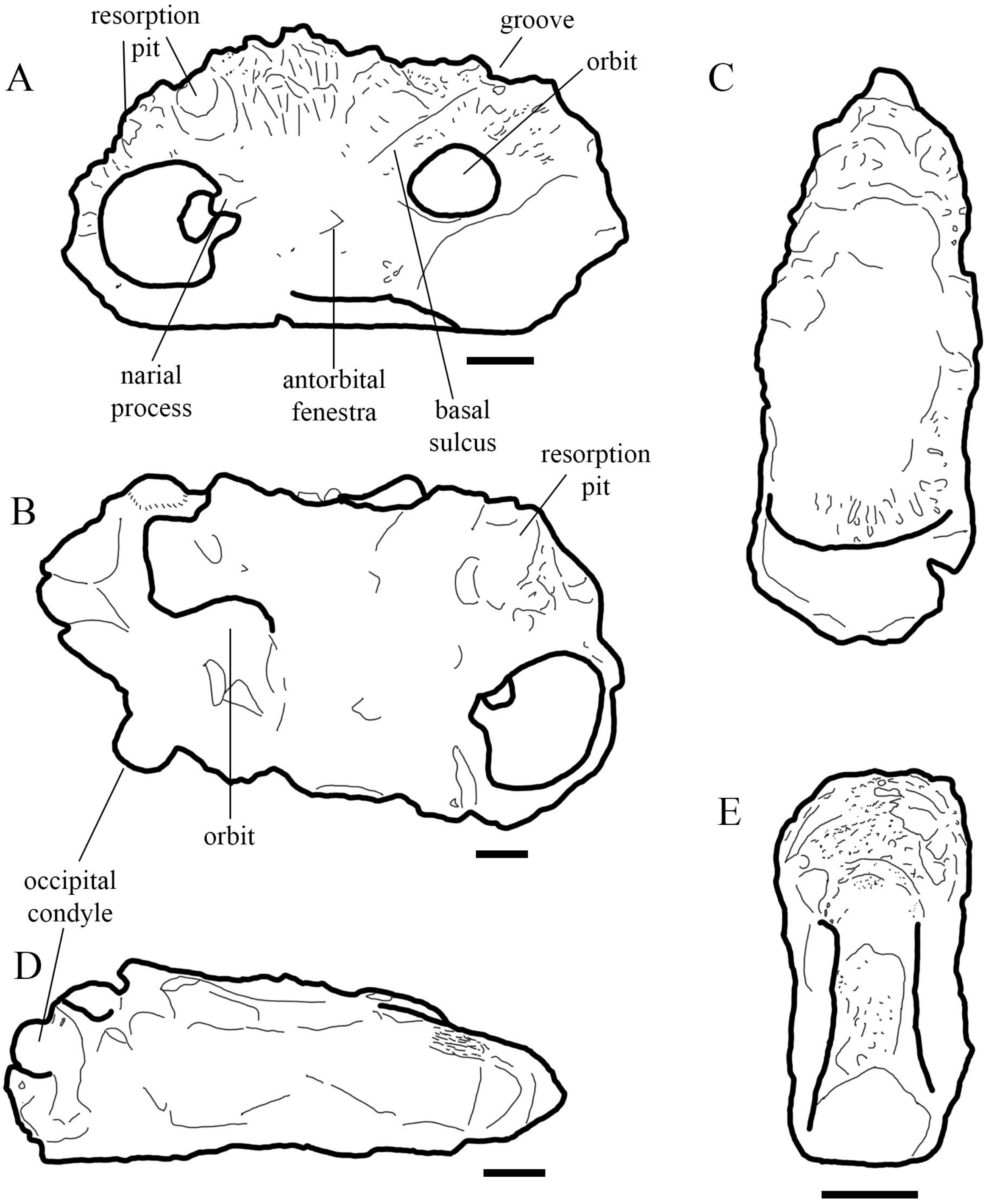

Figure 3.3. Centrosaruine ceratopsid *Pachyrhinosaurus youngi* sp. nov., holotype (UALVP 53300); skull in left lateral (A), right lateral (B), dorsal (C), ventral (D), and anterior (E) views. Scale bars 10 cm.

Nasal

The skull of UALVP 53300 (Fig. 3.2, 3.3) is dominated by a massive nasal boss that extends from the anterodorsal part of the narial fossa to above the middle of the orbit. The boss has no anterior pommel, such as is found in specimens of *Pachyrhinosaurus lakustai*, but instead has several large resorption pits (Fig. 3.3). Resorption pits have not been found on the anterior portion of the nasal boss in any other pachyrhinosaur species, but are common on the supraorbital bosses. There are at least three large pits visible on the anterior nasal boss with two being best seen in anterior view (Fig. 3.2 E) and the other from the left lateral view (Fig. 3.2 A). There is another possible resorption pit seen in right lateral view, but it is well worn from erosion (Fig. 3.2 B). These resorption pits could be considered pathological; however, there is evidence that small resorption pits can form in subadults (Chapter 1) indicating that these pits may not be pathological in origin but are instead common in this species of *Pachyrhinosaurus*. The basal sulcus (Hieronymus et al., 2009) is best seen angling anteroventrally from at the posterior edge of the nasal boss just dorsal to the orbit. Just anterior to the orbit, the basal sulcus becomes difficult to see but most likely continues toward the dorsal rim of the narial fossa. The lateral sides of the nasal boss bear vague dorsoventrally oriented grooves and ridges giving the palisade texture seen in other *Pachyrhinosaurus* bosses. The dorsal edges are relative jagged, instead of smooth.

The nasal boss is roughly rectangular in dorsal view (Fig. 3.2 C), with rounded anterior and posterior margins. The edges of the nasal boss are raised whereas the middle of the dorsal surface has a dished out concavity, similar to specimens of *Pachyrhinosaurus lakustai* (Currie et al., 2008). There is only sediment visible in the medial portion of the nasal boss preparation was not completed because the nature of the preservation makes it difficult to determine where the ironstone stops and bone begins. In dorsal view (Fig. 3.2 C) the widest point of the boss is above the center of the maxilla, which is normal in pachyrhinosaurs. Along the posterior and posterolateral edges of the dorsal surface of the boss are a series of short grooves oriented anteroposteriorly. The median ridge that defines the fusion of the two nasals is not visible in this specimen. The nasal boss continues posteriorly where it stops dorsal to the middle of the orbit as a ridge. Behind this ridge is a wide transverse groove.

Within the narial fossa, the narial process is only preserved on the left side (Fig. 3.2 A, 3.3 A). The process is sizeable and is triangular in profile with a slight hook oriented ventrally.

The bulbous anterior portion of the nasal boss where the resorption pits are located is in the same position as the "supranasal boss" of *Pachyrhinosaurus canadensis* (Langston 1967, 1975). However, there is no "fist-sized knob" posterodorsal to the narial fossa also seen in *Pachyrhinosaurus canadensis* (Sternberg 1950). Neither the "supranasal boss" nor the "fist-sized knob" is seen in *Pachyrhinosaurus lakustai* (Currie et al., 2008).

Supraorbital bosses

The supraorbital bosses of UALVP 53300 are mostly eroded (Fig. 3.2); however, part of the right boss is preserved as a nondescript lump (Fig. 3.2 B). There is a discernable transverse groove between the nasal and supraorbital bosses. Although the supraorbital bosses are eroded, based on the left lateral view (Fig. 3.2 A) it can be seen that the nasal and supraorbital bosses were not separated as much as they are in *Pachyrhinosaurus lakustai*, due to the continuation of the rugosity along the dorsal edge of the skull.

The supraorbital bosses are preserved in the paratype skull (UALVP 55805) (Fig. 3.4). These are deeply excavated bosses that may connect with the sinus cavity below; however, small bones were deposited in these pits during burial, and they obscure the extent of the pits (Fig. 3.4 C). These pits are a result of resorption that occurs at an advanced age and are also seen in other centrosaurines such as *Centrosaurus* and *Styracosaurus* (Sampson et al., 1997). Separating the two supraorbital bosses is a thick longitudinal ridge (Fig. 3.4 C) that sits flush with the walls of the excavated boss and is a feature not seen in other pachyrhinosaurs where the bone typically dips down between the supraorbital bosses even when they are exceptionally resorbed. Therefore, this can be considered a diagnostic character.

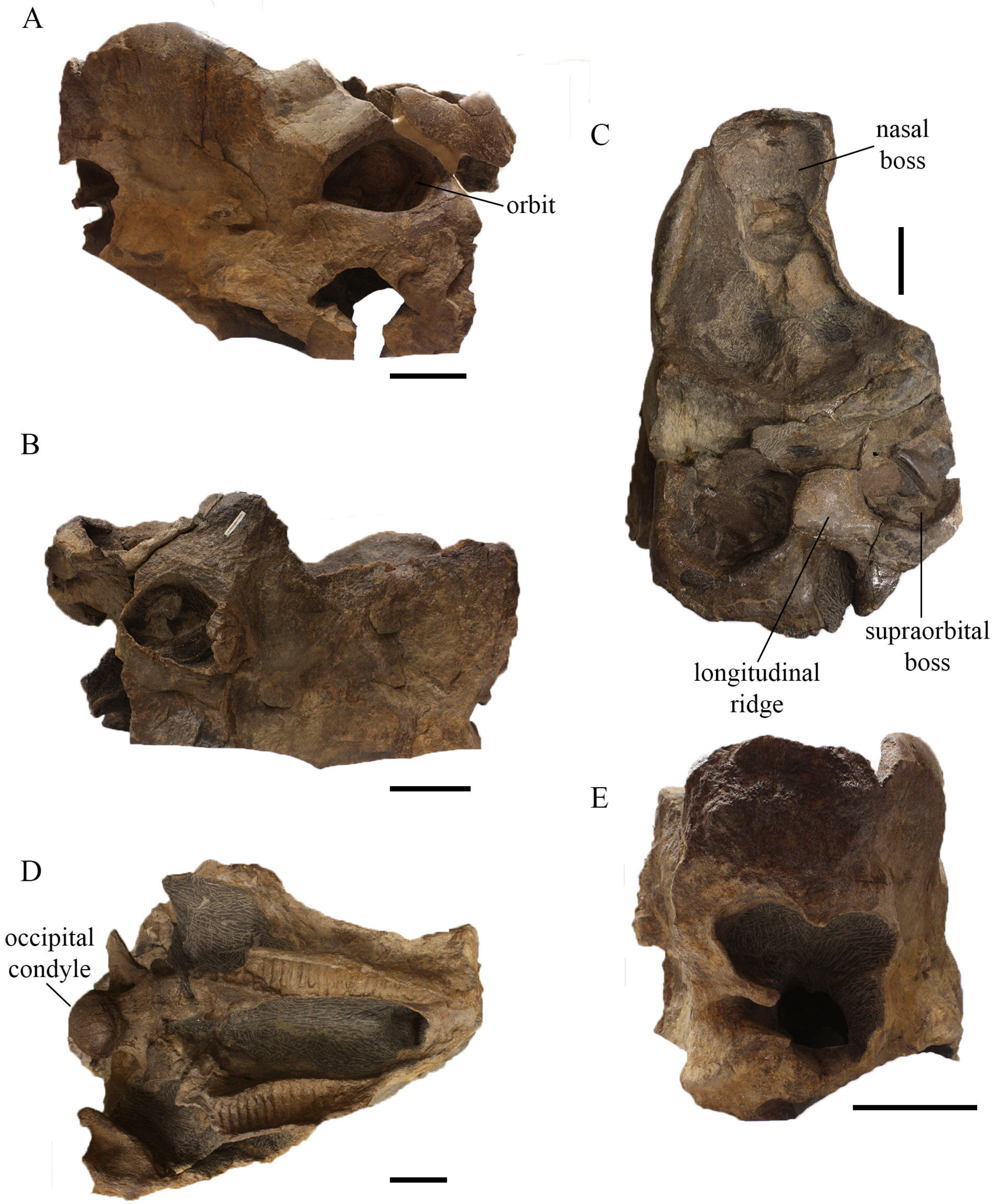

Fig. 3.4. Centrosaurine ceratopsid *Pachyrhinosaurus youngi* sp. nov., paratype (UALVP 55805); skull in left lateral (A), right lateral (B), dorsal (C), ventral (D), and anterior (E) views. Scale bars equal 10 cm.

Fig. 3.5. Centrosaurine ceratopsid *Pachyrhinosaurus youngi* sp. nov., parietals. Paratype (UALVP 54165) right parietal horn, P3 (A) and (UALVP 50652) parietal bar with P2 horn in anterior view. Scale bars equal 5 cm.

Parietal

The paratype parietals of *Pachyrhinosaurus youngi* consist of a single right parietal horn (UALVP 54165) (Fig. 3.5 A), and a partial parietal bar and horn (UALVP 50652) (Fig. 3.5 B). The convention of referencing parietal horns and processes laid out in Sampson (1995) (Fig. 3.6) will be used here. The median paratype parietal bar (UALVP 50652) (Fig. 3.5 B) is generally triangular in section and its ventral side is vaulted. The bar flattens dorsoventrally towards the back and the ventral surface becomes relatively flat. This vaulting is similar to that of *Pachyrhinosaurus lakustai* (Currie et al., 2008) that also differs from other large ceratopsians in that their median parietal bars are broadly convex in ventral view. Visible on the dorsal surface of the median parietal bar are numerous neurovascular grooves. Near the posterior end of the parietal bar, the bar widens laterally and a deeply excavated pit is visible on the left lateral side of the bar; (Fig. 3.5 B) there is a shallower pit on the right lateral side of the bar in line with the other pit. These pits are of unknown origin and could represent resorption pits due to advanced age or pathology.

At the posterior edge of the parietal bar is the dorsomedially hooked P2. *Pachyrhinosaurus youngi* lacks Process 1 near the midline, which is consistent with *Achelousaurus*, *Einiosaurus*, *Pachyrhinosaurus canadensis*, and *Pachyrhinosaurus lakustai*. The posterodorsal region experienced some erosion that allows the inner striations of the bone texture to become visible. There is a drop in topography moving from the resorption pits on the parietal bar toward the Process 2 horn, this is also most likely due to erosion. The dorsal and ventral surface textures alternate between smooth and striated bone.

Neurovascular grooves are visible on both sides of the paratype parietal horn (UALVP 54165) (Fig. 3.5 A). This specimen has been designated as a P3 horn based on its similarity to the P3 horns of *Pachyrhinosaurus lakustai*. However, unlike *Pachyrhinosaurus lakustai*, the P3 horn of this specimen is not twisted dorsally, but instead it is curves laterally. The specimen also does not have the grooves extending along its length like those seen in *Pachyrhinosaurus lakustai* (Currie et al., 2008). The distal tip of the P3 horn is broken and thus would have been slightly longer in life. Although the P3 horns of *Pachyrhinosaurus lakustai* can be quite variable, and the horns of *Pachyrhinosaurus canadensis* are mostly straight, the curvature of the process 3 horn of *Pachyrhinosaurus youngi* is distinct enough to be considered a diagnostic feature. Furthermore Currie et al. (2008) are uncertain as to the origin of the hooks and spikes on the pachyrhinosaur frill, whether they are osteodermal or outgrowths of the parietal. Based on preliminary studies (Kruk et al., 2013) it has been determined that parietal horns are simply outgrowths of the parietal as they do not show metaplastic bone typically found in osteoderms (Chapter 2).

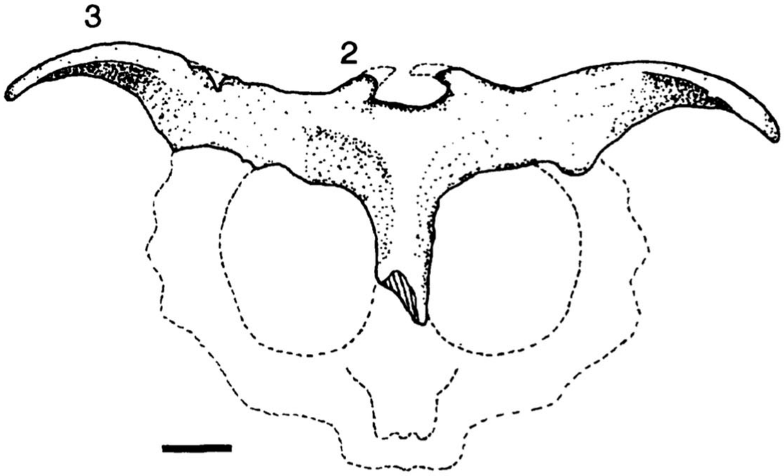

Fig. 3.6. Modified from Sampson (1995) demonstrating the convention of referencing parietal horns and processes. Scale bar equals 20 cm.

Neurocranium

The braincase is only seen in the paratype skull (UALVP 55805) (Fig 3.4 D). The articular surfaces of the occipital condyle in both the holotype and paratype skulls are nearly round, which is common in ceratopsids. The exoccipitals surround the foramen magnum and are broken laterally. Two foramina exit near the base of the condyle and the exoccipitals, the large one is the jugular foramen carrying cranial nerves IX-XI and the smaller one is the hypoglossal formen (XII). The basioccipital and basipterygoid processes are visible and intact.

Phylogenetic Analysis

To determine the relationship between *Pachyrhinosaurus youngi* and other centrosaurines a phylogenetic analysis was performed. This analysis was based on that of Fiorillo and Tykoski (2012), which derived from Currie et al. (2008) based on previous works by Sampson (1995), Dodson et al. (2004), and Ryan (2007). The entire character list and data matrix can be found in Appendix 1. Non-applicable characters were coded as missing data, all multistate characters were considered unordered, and two taxa had two polymorphic characters that were treated as such. The taxon-character matrix was created in Mesquite 2.75 (Maddison and Maddison, 2011) and analyzed in TNT 1.1 (Goloboff et al., 2008). Bremer support, Bootstrap (1000 replicates), and Jackknife (1000 replicates) values were calculated for the resulting trees.

The analysis initially produced three equally parsimonious trees. These trees differed in the position of *Pachyrhinosaurus lakustai*, which is determined as either the sister taxon to a clade consisting of *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi*; or *Pachyrhinosaurus* is a pair of sister species relationships with *Pachyrhinosaurus lakustai* being more closely related to *Pachyrhinosaurus perotorum* with *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus youngi* being more closely related to each other; or *Pachyrhinosaurus lakustai* forms a clade with TMP 2002.76.1 and is sister taxon to a clade comprising of *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi*. A majority rule consensus produced one parsimonious tree (Fig 3.7) with a length of 110, consistency index (C.I.) of 0.7909, and a retention index (R.I.) of 0.8231.

Diabloceratops eatoni is the most basal of the centrosaurine monophyly and is followed by *Albertaceratops nesmoi*. A weakly supported clade of *Coronosaurus brinkmani*, *Centrosaurus apertus*, and *Styracosaurus albertensis* is the sister clade to the group consisting of

Rubeosaurus ovatus and *Einiosaurus procurvicornis*, and the Pachyrostra (*Achelousaurus* + *Pachyrhinosaurus)*. These results are consistent with prior analyses (Sampson, 1995; Dodson et al., 2004; McDonald and Horner, 2010).

Achelousaurus horneri forms the base of the nasal-boss bearing taxa; it is a clade supported by the presence of nasal and supraorbital bosses in place of more typical nasal ornamentations. There is weak support for the placement of TMP 2002.76.1 as basal to the clade composed of *Pachyrhinosaurus lakustai*, *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi* due to the presence of a reduced antorbital fenestra, or its outright loss.

There is also weak support for *Pachyrhinosaurus lakustai* falling basal to the clade formed by *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi* (Fig. 3.7). These three *Pachyrhinosaurus* species are most likely united by having nasal and supraorbital bosses that are nearly in contact, separated by a narrow groove as well as the loss of the anterior protruding "pommel" typically seen in specimens of *Pachyrhinosaurus lakustai* and TMP 2002.76.1.

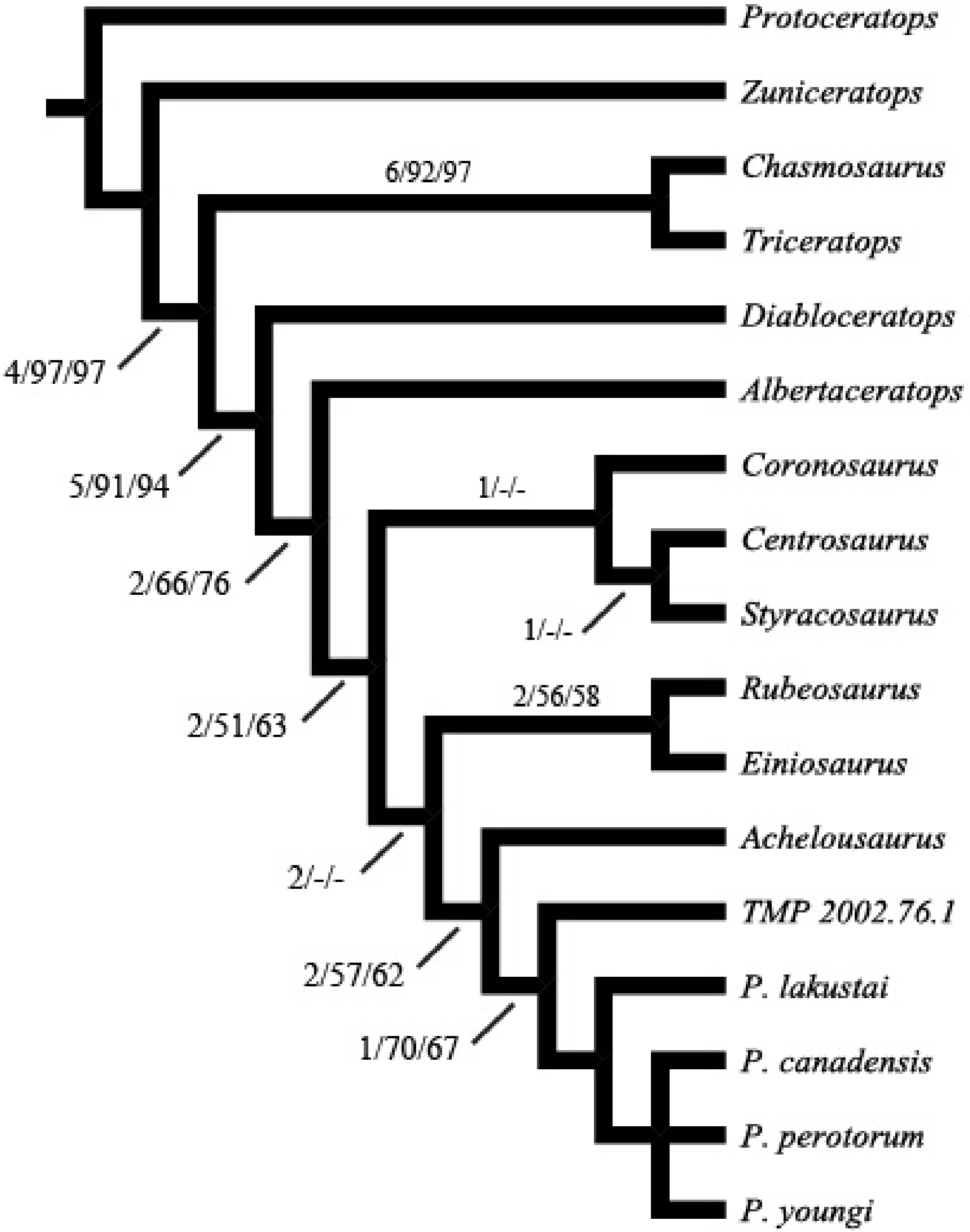

Figure 3.7. Results of phylogenetic analysis. Majority Rule consensus of the three equally parsimonious tree generated by the analysis (length = 110, C.I. (consistency index) = 0.7909, R.I. (retention index) = 0.8231). Numbers at nodes are Bremer support / Bootstrap percentages / Jackknife percentages recovered from 1000 replicates.

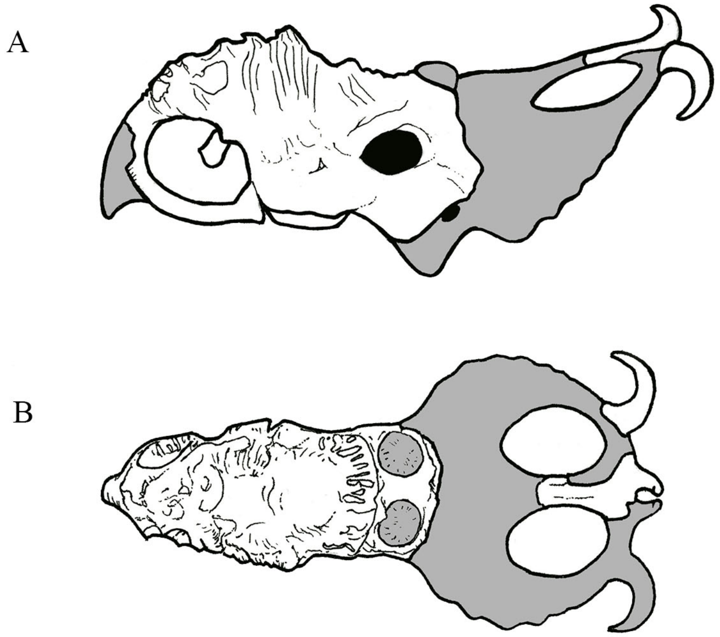

Figure 3.8. Line drawing reconstruction of the skull of *Pachyrhinosaurus youngi* (UALVP 53300, UALVP 54165, UALVP 50652) in left lateral (A) and dorsal (B) views.

Discussion

The phylogenetic analysis was unable to fully resolve the polytomy between *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi*. There is very weak support for *Pachyrhinosaurus lakustai* being basal to that group and even weaker support for TMP 2002.76.1 being basal to the other *Pachyrhinosaurus*. Some features uniting TMP 2002.76.1 and *Pachyrhinosaurus lakustai* are an anteriorly directed pommel and a separation between the nasal and supraorbital bosses. Uniting *Pachyrhinosaurus lakustai* and *Pachyrhinosaurus perotorum* is the presence of a rostral comb; however, this is not seen in either *Pachyrhinosaurus canadensis* or *Pachyrhinosaurus youngi*. Having nasal and supraorbital bosses that are nearly in contact unite *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi*. The diagnostic P3 process of *Pachyrhinosaurus youngi* resembles those of *Pachyrhinosaurus lakustai*, but it lacks the anterolateral twist seen in the latter, and the new species P3 is not as long or large as it is in *Pachyrhinosaurus lakustai*. Furthermore, the differences in degree of separation between the supraorbital bosses are unique among the pachyrhinosaurs.

The diversity of ceratopsians, especially centrosaurines, exploded in the Late Cretaceous and the group also had a fairly rapid turnover. The Pachyrostra (*Achelousaurus* + *Pachyrhinosaurus*) are the last centrosaurine clade to appear in the fossil record (Ryan et al., 2010) and recently have become much more diverse than previously thought. The temporal ranges of *Pachyrhinosaurus youngi* and *Pachyrhinosaurus canadensis* overlapped for the full existence of the former. However the new species is not *Pachyrhinosaurus canadensis* based on their differing frill ornamentations and overall skull size, with *Pachyrhinosaurus canadensis* being significantly bigger.

A possible fifth species of *Pachyrhinosaurus* has been reported from Dinosaur Park (Alberta, Canada) (Ryan et al., 2010). The authors describe a *Pachyrhinosaurus*-like ceratopsian from the top of the Dinosaur Park Formation (71.5 million years). However, it lacks the diagnostic parietal and therefore has not been named yet as a new species. When this fossil is placed into a phylogenetic matrix larger than performed by Ryan et al. (2010), it is recovered as basal to the other described *Pachyrhinosaurus* species but as more derived than *Achelousaurus* (Fiorillo and Tykoski, 2012). This placement at the base of *Pachyrhinosaurus* is supported by a large separation between the nasal and supraorbital bosses and a reduced antorbital fenestra. It is excluded from *Achelousaurus* based on the presence of an overhanging pommel on the anterior portion of the nasal boss similar to *Pachyrhinosaurus lakustai*, and a nasal boss without the fin-like texture, which is characteristic of the dorsal view of *Achelousaurus*.

Characters shared between TMP 2002.076.0001 and *Pachyrhinosaurus lakustai* include an anteriorly directed pommel on the nasal boss and a distinct separation between the nasal and supraorbital bosses. The presence of a rostral comb is shared by *Pachyrhinosaurus lakustai* and *Pachyrhinosaurus perotorum*, but is absent in *Pachyrhinosaurus canadensis* or *Pachyrhinosaurus youngi*. Furthermore, nasal and supraorbital bosses that are practically in contact unite *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus youngi*. The distinct parietal Process 3 of *Pachyrhinosaurus youngi* resembles that of *Pachyrhinosaurus lakustai*, although it lacks the anterolateral twist seen in the latter, and the P3 process of *Pachyrhinosaurus youngi* is not as long or large as *Pachyrhinosaurus lakustai*. Also, the thick longitudinal ridge separating the supraorbital bosses in *Pachyrhinosaurus youngi* is unique among pachyrhinosaurs.

In their phylogenetic analysis including the proposed fifth pachyrhinosaur, Ryan et al. (2010) modifies Character 3 from Sampson (1995); nasal horncore base (subadult): short-based, restricted in length anteroposteriorly (0); long-based, extends over virtually entire length of nasal (1). Ryan et al. (2010) modifies this character to: nasal ornamentation, basal length (adult): short-based, less than 5% basal skull length (0); long-based, between 10% and 20% basal skull length (1); long-based, greater than 25% basal skull length. However, these percentages do not seem to work, assuming that basal skull length is measured from rostrum to occipital condyle. *Achelousaurus* species and *Pachyrhinosaurus lakustai* are given a character state of 1 by Ryan et al. (2010), but when comparing the nasal ornamentation to basal skull length, their average percentages are 27% and 58% respectively. *Einiosaurus* is given a character state of 0 but has a base ornamentation length to basal skull length percentage of 36%. However, there may be phylogenetic value to this character. Nasal ornamentation length should be plotted against basal skull length and on the resulting graph there may be natural groupings, which could be used to improve this character.

Conclusions

With the addition of a fourth, and possibly fifth, described species of *Pachyrhinosaurus*, this genus is now the most diverse of any of the ceratopsians. All other ceratopsian genera typically have one and at most two species representing them This potentially could be due to preservational biases, the fact that morphological differences are not pronounced or because only fragmentary remains represent most species. With each of the *Pachyrhinosaurus* species (excluding TMP 2002.76.1) their remains have been discovered in bonebeds from which multiple specimens were recovered. It is curious to note that the last of the centrosaurines were the most specious and that all had nasal bosses. New species of ceratopsids are continuing to be described across western North America, and it is evident that this group was diversifying at an explosive rate.

It is entirely plausible for there to be multiple species of the same genus coexisting in the same temporal range, such as *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus youngi*, as there is modern evidence to support this situation. The genus *Equus* is comprised of seven extant species: horse, *Equus ferus;* ass or donkey, *Equus asinus*; mountain zebra, *Equus zebra*; plains zebra, *Equus quagga*; Grévy's zebra, *Equus grevyi*; the kiang, *Equus kiang*; and the onager, *Equus hemionus* (Rubenstein, 2001). There is little difference in the skeletal morphology of each of these extant species, although they occupy slightly different ecological niches. The diversity of the genus *Pachyrhinosaurus* within any single bonebed can be explained by ontogenetic or sexual dimorphism, but the taxonomic diversity of synchronous species (*P. canadensis*, *perotorum*, and *youngi*) may represent geographically or ecologically separated genetic populations.

The amount of speciation, rate of faunal turnover, and diversity in cranial ornamentation in the ceratopsians is unlike any other group within the Ornithischia. Within the Hadrosauridae, the lambosaurines have the elaborate crests but there is little other variation between them. For the most part, the differences are either a posteriorly elongated crest or a more dorsally oriented crest. In the Thyreophora, the Stegosauria only differ slightly in the placement of their dorsal osteoderms, shoulder spikes, and neural spines (*Kentrosaurus*; Mallison, 2011). The only group that comes close to the diversity of ornamentation seen in ceratopsids is the Ankylosauridae displaying a wide variety of dermal armor with spikes and tail clubs (Hayashi et al., 2010). The other group within Marginocephalia is the Pachycephalosauria, which is the least specious of the groups previously mentioned. While all members have cranial ornamentations and do exhibit extreme ontogenetic changes (Horner and Goodwin, 2009), the variation between species is not as dramatic as the ceratopsids. Overall, ceratopsians are amongst some of the most interesting dinosaurs and their diversity only continues to grow as more species are discovered.

CONCLUSIONS

Pachyrhinosaurus is a peculiar clade of ceratopsians, known only from the Upper Cretaceous (upper Campanian to lower Maastrichtian) of North America. Three species have been reported only from Alberta, Canada and one from Alaska. These species include the previously described *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus lakustai*, *Pachyrhinosaurus perotorum*, as well as *Pachyrhinosaurus youngi* first described here. These species are distinguished from one another based on characteristics of the skull, including parietal horn shape and orientation, absence/presence of a rostral comb, median parietal bar horns, and profile of the nasal boss. The ceratopsian diversity in the Late Cretaceous is surprising considering the high and fast rate of faunal turnover (Ryan et al., 2010).

The description of the new species *Pachyrhinosaurus youngi* has increased the diversity of ceratopsians. The genus *Pachyrhinosaurus* has more individual species than any other ceratopsian genus. Furthermore, this implies that it is completely possible for there to be multiple species of the same genus often coexisting at the same time, such as *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus youngi*. This is fitting because there are modern examples of multiple species of the same genus with overlapping temporal, ecological, or geographic ranges; one example is the genus *Equus* (Mallison, 2001). Ceratopsians had quite possibly one of the most explosive radiations seen during the Mesozoic; they were able to diversify immensely in a short time within a limited geographic range (namely Laramidia).

One focus of this thesis was to investigate the ontogeny of *Pachyrhinosaurus* from a histological perspective. Historically, the focus of histological workers has been on long bone histology and understanding the growth of an individual species of dinosaurs. Studies investigating cranial histology are rare but have included studies of *Triceratops* (Horner and Goodwin, 2008; Horner and Lamm, 2011), possible centrosaurine integumentary structures (Hieronymus, et al., 2009), and surface textures of *Centrosaurus* frills (Tumarkin-Deratzian, 2010). These last two studies are the only histological investigations of centrosaurines.

This is the second comprehensive histological study of the ontogeny of a ceratopsian cranial elaborations and is the first one to examine the growth of the nasal ornamentations; the previous study was an investigation of the parietal of *Triceratops* (Horner and Lamm, 2011). The *Pachyrhinosaurus* nasal bosses starts off as a horn-like structure that is more similar to the nasal horns of other juvenile centrosaurines than it is to an the adult nasal boss. These “demihorns” are composed of compact fibrolamellar bone that continues to resorb and remodel through out the lifetime of a Pachyrhinosaurus unti it has a spongy microstructure. No other cranial elaboration examined in this thesis resembles the histology of a nasal boss. Furthermore, *Pachyrhinosaurus* undergoes one of the more extreme ontogenetic changes with regards to cranial ornamentations of the frill.

Studying the ontogeny of nasal bosses has added to the histological work on ceratopsians and has provided a better understanding of the growth of their elaborations. Nasal boss histology can provide an ontogenetic stage (juvenile, subadult, adult) to a given specimen; this will be helpful when only a partial nasal boss is found because it will allow the specimen to be "aged." This discovery can be extrapolated to other ceratopsians whose nasal ornamentation derives from the nasal bones themselves. Calculated osteocyte lacunar density for each stage will be performed prior to the publication of the chapter, it will give a quantitative value to the study and better aid in inferring the ontogenetic stage of the nasal ornamentations in other ceratopsians. It is my belief that more than just long bones deserve to be thin sectioned, there is much more information to be gained from these animals.

Chapter 2 represents the first study comparing the histology of ceratopsian cranial elaborations. Prior to this study, other authors focused on only single species (Tumarkin-Deratzian, 2010; Horner and Lamm, 2011) and this study expanded to include ceratopsians found in Alberta. At least across the species examined all cranial elaborations (except epoccipitals) were found to have been derived from the dermatocranium. Epoccipitals, on the other hand, were formed initially through metaplasia and later fused onto the edges of the frill. *Triceratops* is strange in that its nasal horn derived from an epinasal instead of from the nasal horns. It is uncertain whether this feature is unique to chasmosaurines or *Triceratops* alone. Further investigation into the histology of these structures would clarify this discrepancy. At the very least it can be said that all centrosaurine cranial elaborations, minus epoccipitals, form intramembranously and are composed of fibrolamellar bone that remodels throughout ontogeny. Epoccipitals are composed of metaplastic bone that remodels and eventually fuses onto the frill margin.

Pachyrhinosaurus is the most derived of the centrosaurines, which raises the question of what advantage nasal bosses had over nasal horns and what drove the replacement of the latter by the former. Regardless, we now have a better understanding of the histological ontogeny of

Pachyrhinosaurus nasal bosses, as well as the diversity in *Pachyrhinosaurus*. Furthermore, there is a deeper understanding of the microstructure of ceratopsian cranial elaborations, which has implications on their development. Overall, future work will include expanding the study of ceratopsian cranial elaborations as well as a revision of the ceratopsian character matrix.

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Appendix

Character List – List of characters used in the phylogenetic analysis. Characters 47 through 54 are intended to clarify pachyrhinosaur relationships (Fiorillo and Tykoski, 2012). Characters 55 through 57 are for further pachyrhinosaur clarification (Ryan et al., 2010). Character list is based mainly upon that of Currie, et al. (2008).

1. Rostral, size and shape: triangular in lateral view with short dorsal and ventral processes (0); elongate with deeply concave posterior margin and hypertrophied processes (1) (Sereno, 1986).

2. Premaxilla, septum shape: absent (0); present and subcircular (1); present and anteriorly elongate (2) (Ryan, 2007).

3. Premaxilla, septum within narial chamber: absent (0); thick and has simple, plate-like construction (1); thin, often with transverse perforations (2) (Langston, 1967; Forster, 1996; Holmes et al., 2001).

4. Premaxilla, premaxillary (narial) process extending into the external naris from the caudoventral margin of the premaxillary septum: absent (0); present (1) (Forster, 1990).

5. Premaxilla, thickened narial strut (separating fenestra through septum from narial opening) along posterior border of premaxillary septum: absent (0); present, anteriorly inclined (1); present, caudally inclined (2) (Forster et al., 1993; Holmes et a

6. Premaxilla, ventral expansion of posteroventral margin: absent, posteroventral margin of premaxilla unexpanded and level with alveolar margin of maxilla (1); present, expanded ventrally well below alveolar margin of maxilla (1) (Sereno, 1986; Penkas

7. Premaxilla, posterior tip of posteroventral process inserts into embayment in nasal and is surrounded by the nasal: yes (0); no (1) (Forster et al. 1993; Holmes et al. 2001)

8. Premaxilla contact with lacrimal: separated by nasal and maxilla (0); in contact (1) (Lull, 1933; Makovicky 2002).

9. External antorbital fenestra size: large, 20% or more length of body of maxilla (0); greatly

reduced to <10% length of body of maxilla (1); reduced to a foramen or absent (2) (Granger and Gregory 1923; Chinnery and Weishampel 1998).

10. Nasal, (subadult) basal length of horn or boss: short based, restricted in length anteroposteriorly (0); long-based, ornamentation covers almost entire length of nasal (1) (Sampson et al. 1997).

11. Nasal, (adult) ornamentation type: absent or poorly developed, <15% basal skull length (0); elongated horn >20% basal skull length (1); long based, low thickened ridge (2); boss (3) (Forster et al. 1993; Sampson 1995; Ryan 2007).

12. Nasal, posterior margin of external naris: concave (0); pronounced tab-like process projecting anteriorly into nasal vestibule (1) (Langston 1975; Sereno 1986).

13. Jugal, infratemporal flange (adult): absent (0); present, contacts jugal flange of squamosal under infratemproal fenestra (1) (Brown and Schlaikjer 1940; Lehman 1996; Forster 1996; Ryan 2007).

14. Prefrontal, separated by frontals and excluded from margins of frontal fontenalle (0); contact each other on midline, separate nasals from frontals and form anterior margin of frontal fontenalle (1) (Lambe 1915; Forster 19990; Ryan 2003).

15. Prefrontal and lacrimal: form prominent antorbital buttress (0); do not form antorbital buttress (1) (Currie et al. 2008).

16. Postorbital, (subadult) postorbital ornamentation horn core: conical, at least 3X taller than anteroposterior basal length, rounded base and pointed apex (0); pyramidal, approx. 1:1 ratio length to height (1); longer than high, rounded (2) (Sampson 199

17. Supraorbital (adult) ornamentation type: absent (0); present, horn (1); present, boss (2) (Sampson 1995).

18. Postorbital, horn core shape (unmodified adult): elongate, pointed apex, rounded base (0); pyramidal, rounded apex, at least as tall as base length (1); rounded apex, base longer than horn tall (2) (Sampson 1995; Ryan 2007).

19. Postorbital, horn core height (unmodified adult): long, >60% length of face (0); short, <40% length of face (1) (Forster 1990; Holmes et al. 2001; Ryan 2007).

20. Postorbital, position of horn core (adult): posterior to orbit (0); over or anterior to orbit (1) (Lehman 1996).

21. Postorbital horn core curvature (adult): no horn, absent (0); straight, dorsally, anteriorly, anterodorsally, or anterolaterally curved (1); posteriorly curved (2) (modified from Forster et al., 1993; Lehman, 1996; Holmes et al., 2001)

22. Parietosquamosal frill, length relative to basal skull length: elongate, 0.80 or more (0); shortened, 0.70 or less (1) (Hatcher et al. 1907; Lehman 1996).

23. Squamosal, length relative to parietal: equal or sub-equal in lenth (0); squamosal <60% total parietal length (1) (Sereno 1986).

24. Squamosal, shape of posterodorsal (medial) margin: straight (0); posterior portion stepped-up relative to anterior portion, transition where quadrate groove passes from ventral dorsal surface of bone (1) (Dodson 1986; Penklaski and Dodson 19999; Ryan

25. Squamosal, anteromedial lamina forming posterolateral floor of dorsotemproal fossa: absent (0); present (1) (Dodson 1986).

26. Parietal, dorsal surface of medial bar: smooth and flat (0); small rounded midline bumps (1); large spikes (2) (Sampson 1995).

27. Parietal, posterior surface on midline: posteriorly convex or straight (0); deep, U- shaped emargination (1) (Currie et al. 2008)

28. Epoccipital, profile shape of epoccipitals on squamosal: not present (0); crescentic to lozenge shaped (1); triangular (2) (Holmes et al. 2001).

29. Epoccipital, number of loci on parietal rami lateral to midline margin: none (0); three to five (1); six to eight (2) (Ryan 2007).

30. Epoccipital, most medial process (P1): absent (0); unelaborated, posterior margin (1); short

(length=base diameter) procurving hook on dorsal margin (2); long (length 2x base diameter) procurving hook on dorsal side (3); triangular on dorsal side of parietal (4) (Currie et al., 2008).

31. Epoccipital, P1 orientation: absent (0); posteriorly directed (1); dorsally directed (2); anteriorly directed in pronounced anterior curl (3) (Sampson 1995; Ryan 2007).

32. Epoccipital, P2: absent (0); unelaborated on posterior margin (1); small medially directed hook (2); large medially curled hook (3); multipronged posteriorly directed (4); large triangular profile (5) (Sampson 1995; Ryan and Russell 2005; Ryan 2007)

33. Epoccipital, P3 length compared to base width: absent (0); small unelaborated on posterior margin (1); length 1-3x base diameter (2); length >4X basal diameter (3) (modified from Sampson 1995; Ryan and Russel1, 2005)

34. Epoccipital, P3 orientation: absent or small (0); posteriorly directed (1); posterolaterally directed (2); laterally or anterolaterally directed (3); dorsolaterally directed (4); posteromedially directed (5) (modified from Sampson, 1995; Ryan and Russell, 2005; Ryan, 2007).

35. Epoccipitals, pattern of fusion to frill margin: occurs from rostral to caudal (0); occurs from caudal to rostral (1) (Lehman 1996).

36. Parietal process P4-P6: absent (0); present (1) (modified from Sampson, 1995).

37. Epoccipital, imbrication of lateral marginal undulations of parietal: absent (0); present (1) (Sampson et al. 1997).

38. Predentary, orientation of triturating surface relative to horizontal plane of element: nearly horizontal (0); steeply inclined laterally (1) (Lehman 1990; Forster 1996).

39. Dentary, coronoid process: incipient process with gently convex apex and no neck (0); well developed but lacks anterior extension distally (1); high, powerful and expands anteriorly at the distal end (2) (Lull, 1933).

40. Dentary, posterior extent of tooth row: terminates medial to coronoid process (0); termiantes posterior to coronoid process (1) (Brown and Schlaikjer 1940).

41. Teeth, roots: single (0); double (1) (Brown and Schlaikjer 1940).

42. Teeth, number of vertically stacked replacement teeth per tooth family: one or two (0); more than two (1) (Brown and Schlaikjer 1940).

43. Tooth ornamentation: subsidiary ridges present, extending from margin to base of tooh (0); subsidiary ridges reduced, present only at margin of teeth (1) (Dodson et al. 2004).

44. Sacrum, deep longitudinal channel on ventral surface: present (0); absent (1) (Lambe 1915; Lehman 1990).

45. Ischium, cross-sectional shape of shaft: ovoid (0); laterally compressed and blade like, narrow along dorsal margin (1) (Dodson et al. 2004).

46. Ischium, orientation of shaft: nearly stright (0); slightly decurved (1)l broad and continuously curved (2) (Brown and Schlaikjer 1940).

47. Premaxilla, anterior surface of narial bar between nasal and rostral bears: shallow transverse grooves and ridges (0); two or more large transversely-oriented protrusions that contribute to a rostral comb (1).

48. Nasal ornamentation or boss anterior end in mature individuals: a nearly continuous curved profile from nasal to premaxilla (0); nasal with distinct anteriorly protruding, overhanging 'pommel' in some individuals (1).

49. Nasal ornamentation or boss posterior edge: stops anterior to orbit (0); stops dorsal to orbit (1).

50. Nasal ornamentation or boss mediolateral width in mature individuals: much narrower than underlying rostrum (0); approximately equal width to underlying rostrum (1); widest part of antorbital region of skull (2).

51. Nasal and supraorbital ornamentation separation on dorsal skull surface of mature individuals: widely separated (0); nearly in contact or contacting, separated only by narrow groove (1).

52. Elongate parietal process P3 lateral and medial margins: curved (0); straight (1) (McDonald and Horner, 2010).

53. Parietal process P4: absent (0); small, unmodified epoccipital (1); small spike (2); elongate spike (3) (derived from Sampson, 1995; McDonald and Horner, 2010).

54. Parietal process P5: absent (0); small, unmodified epoccipital (1); small spike (2); elongate spike (3) (derived from Sampson, 1995; McDonald and Horner, 2010).

Character Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Protoceratops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0
Zuniceratops	?	0	0	?	?	0	1	?	1	?	0	?	?	?	0	0	1	0	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0	?	?	1	0	0	0	0	0	?	0	0
Chasmosaurus	1	2	2	1	1	0	0	0	1	0	1	0	1	0	0	?	1	0	0	1	2	0	0	0	0	0	1	2	1	1	2	1	1	0	0	0	0	0	2	1	1	1	1	1	1	2	0	0	0	0	0	?	?	?
Triceratops	1	2	2	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	2	1	1	1	1	1	0	0	0	0	0	2	1	1	1	1	1	1	2	0	0	0	0	0	?	?	?
Diabloceratops	0	1	1	0	0	0	1	0	1	0	0	1	1	?	0	0	1	0	0	0	2	1	0	1	1	0	1	1	2	0	0	0	3	2	?	1	1	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1
Albertaceratops	?	?	?	?	?	1	?	?	1	1	2	1	1	?	0	0	1	0	0	0	2	?	1	1	?	1	1	1	2	0	0	0	3	3	?	1	1	1	2	1	1	1	1	?	?	?	0	0	0	0	0	0	1	1
Centrosaurus	0	1	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	2	1	1	1	1	1	1	1	2	3	3	3	1	0	1	1	1	1	2	1	1	1	1	0	0	1	0	0	0	0	0	?	1	1
Coronosaurus	0	1	1	0	0	1	1	?	1	0	1	1	1	0	0	1	1	1	1	0	2	?	1	1	?	1	1	1	2	3	3	4	2	4	?	1	1	1	2	1	1	?	1	0	0	1	0	0	0	0	0	?	1	0
Styracosaurus	0	1	1	0	0	1	1	?	1	0	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	2	2	3	2	2	2	1	1	1	1	2	1	1	1	1	0	0	1	0	0	0	0	0	0	3	2,3
Rubeosaurus	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	1	2	1	0	0	?	?	?	?	?	?	1	2	0	0	1	2	5	?	1	1	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	3	1,2
Einiosaurus	0	0	1	0	0	1	1	1	1	0	1	1	1	0	1	2	1	2	1	0	0	1	1	1	?	1	1	1	2	0	0	1	2	1	1	1	1	1	2	1	1	1	1	0	0	1	0	0	0	0	0	1	1,2	1
Achelousaurus	0	0	1	0	0	1	1	1	1	1	3	1	1	0	1	2	2	?	1	0	0	1	1	1	1	1	1	1	2	0	0	2	2	2	1	1	1	1	2	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1
TMP 2002.76.1	0	0	1	0	0	1	1	?	2	?	3	1	1	?	1	?	2	?	1	0	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	2	1	1	?	?	?	?	?	0	1	0	1	0	?	?	?
P. lakustai	0	0	1	0	0	1	1	1	2	1	3	1	1	0	1	2	2	?	1	0	0	1	1	1	1	2	1	1	2	0	0	3	3	3	?	1	1	1	2	1	1	?	1	0	0	1	1	1	1	2	0	0	1	1
P. canadensis	0	0	1	0	0	1	1	1	2	1	3	1	1	?	1	2	2	?	1	0	0	1	1	1	1	?	1	1	2	0	0	3	2	3	1	1	1	1	2	1	1	1	1	0	0	1	0	0	1	2	1	0	1	1
P. perotorum	0	0	1	0	0	1	1	1	2	?	3	1	1	?	1	?	2	?	1	0	0	?	?	?	?	?	1	?	?	0	0	?	2	3	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	2	1	0	?	?
P. youngi	?	0	1	0	0	1	1	1	2	1	3	1	1	?	1	?	2	?	1	0	0	?	?	?	?	0	1	?	?	0	0	3	2	3	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	2	1	0	?	?