Osteology and variation of Brachylophosaurus canadensis (Dinousauria, Hadrosauridae) from the Upper Cretaceous Judith River formation of Montana
by Albert Prieto-Marquez

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Earth Sciences
Montana State University

Abstract:
The recovery of an adult articulated, complete skeleton and more than 1,300 specimens from a bonebed of the hadrosaurid dinosaur Brachylophosaurus canadensis allowed a reexamination of the morphologic features of this taxon. The fossils were recovered from Upper Cretaceous (Campanian) Judith River of northeastern Montana. The bones were first described element by element in order to produce a complete redescription of the whole skeleton. Secondly, a systematic analysis of the morphological variation present in each element was conducted. Finally, a revision of the systematic position of this taxon was undertaken.

B. canadensis is rediagnosed on the basis of a subrectangular skull with a relatively deep snout; nasals greatly developed into a paddle-like solid crest that extends caudodorsally overhanging the dorsal region of the skull; nasals possessing an anteroposteriorly-oriented groove terminating in an elongated foramen, located medial to the prefrontal; prefrontal projected posteriorly, resting dorsomedially over the anterior process of postorbital and, more posteriorly, extending ventromedially underlying the nasal; jugal with a ventrally projected semicircular flange, being deeper element than in Maias aura; depressed dorsal surface of the frontal between the nasal joint and the postorbital suture; anteroposteriorly short exoccipital-supraoccipital roof posterior and dorsal to the foramen magnum; sternals with a compressed, oval “paddle”; and very elongated, slender forearm due to elongation of radii and ulnae. The species B. goodwini is considered a junior synonym of B. canadensis. The completeness of the new specimens from Malta complements our knowledge on hadrosaur anatomy.

The available specimens of B. canadensis show individual, ontogenetic, and dimorphic variation. At least four subadults and two adults are represented in the bonebed as deduced from the maximum number of specimens of the same side of a single element. Most remarkable is the dimorphic variation, which is here explained either as sexual dimorphism or size and ontogenetic changes.

The phylogenetic analysis agrees with previous hypothesis that placed B. canadensis as the sister taxon of Maiasaura peeblesorum. Both taxa form a relatively basal clade in relation to the successive more derived Gryposaurus, Prosaurolophus, and Edmontosaurus.

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APPROVAL

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Albert Prieto-Marquez

This thesis (dissertation) has been read by each member of the thesis (dissertation) committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

The recovery of an adult articulated, complete skeleton and more than 1,300 specimens from a bonebed of the hadrosaurid dinosaur *Brachylophosaurus canadensis* allowed a reexamination of the morphologic features of this taxon. The fossils were recovered from Upper Cretaceous (Campanian) Judith River of northeastern Montana. The bones were first described element by element in order to produce a complete redescription of the whole skeleton. Secondly, a systematic analysis of the morphological variation present in each element was conducted. Finally, a revision of the systematic position of this taxon was undertaken.

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The phylogenetic analysis agrees with previous hypothesis that placed *B. canadensis* as the sister taxon of *Maiasaura peeblesorum*. Both taxa form a relatively basal clade in relation to the successive more derived *Gryposaurus*, *Prosaurolophus*, and *Edmontosaurus*.

CHAPTER 1

INTRODUCTION

The dinosaurs of the family Hadrosauridae have been more intensely studied and we possess more fossil evidence about them than on any other dinosaur group. Yet, despite the current amount of data available, there are still gaps concerning the current knowledge of these creatures. For example, relatively little attention has been paid to their postcrania (Brett-Surman, 1976; Maryañska and Osmolska, 1983; Maryañska and Osmolska, 1984) in relation to the amount of work carried out on their cranial material. Thus, most diagnosis and studies have been focused on the skull (Ostrom, 1961; Heaton, 1972; Hopson, 1975; Maryañska and Osmolska, 1979; Weishampel, 1981b; Horner, 1992), plus some features of the appendicular skeleton (Chapman and Brett-Surman, 1990; Weishampel and Horner, 1990), probably because it is the most easily distinctive part of their anatomy. Likewise, a detailed morphological description of all the skeleton elements is not common in the literature, in spite of the vast quantity of specimens collected since the middle of the nineteen-century (Lull and Wright, 1942; Colbert, 1984). Abundant hadrosaurid remains, including complete and partial skeletons, eggs, nests, babies and even integument (Horner, 1984) remains have been collected during the past hundred and fifty years in North and South America (Lull and Wright, 1942; Dodson, 1971; Horner, 1983; Bonaparte et al., 1984; Head, 1998), Europe (Weishampel et al., 1993; Laurent et al., 1997; Company et al., 1998; Casanovas et al., 1999) and Asia (Maryañska and Osmolska, 1982; Buffetaut and Tong-Buffetaut, 1993). Thus, we not only have information on hadrosaur anatomy and evolutionary history (Hopson, 1975; Weishampel, 1981b; Horner, 1990), but also on behavior and life strategies (Horner and Makela, 1979; Horner, 1982; Horner and Currie, 1994; Cooper and Horner, 1999), functional morphology (Galton, 1970; Weishampel, 1981a; Norman and Weishampel, 1985), paleoecology (Weishampel and Norman, 1989; Chin and Gill, 1996) and taphonomy and sedimentology of its fossil occurrences (Dodson, 1971).

Morphological differences in some areas of the hadrosaurid skeleton are so subtle that preservational effects can easily obliterate them. Hence it is usually difficult to use some skeletal elements (especially those that are evolutionary conservative) for diagnosis, variation and generally any study emphasizing fine morphological observation, in the hadrosaurid material available.

In 1996 a practically complete, fully articulated skeleton of an adult "duck-billed" dinosaur of the genus *Brachylophosaurus,* was excavated from Judith River Formation strata near Malta, northeastern Montana (Harmon, 1997; Horner and Dobb, 1997). Posteriorly, the articulated hindquarters of a subadult were uncovered, but never prepared. In the summers of 1998 and 1999, a paucispecific, multiindivual bone bed was excavated in the vicinity of the other two sites (LaRock, 2000). Detailed sedimentologic and taphonomic studies were conducted on the bonebed (LaRock, 2000).

The purpose of this study is first to redescribe *Brachylophosaurus* on the basis of the new material. Specific goals of this research include: (1) to provide a descriptive model of a hadrosaurid dinosaur, (2) determine the degree and type of morphologic variation existing among the available specimens, and (3) reassess the phylogenetic position of this taxon, as well as the characters useful for hadrosaurid phylogenetic systematics. It is hoped that the osteology and variation presented in this thesis will contribute to the detailed undertanding of hadrosaur anatomy, providing a complete description to be used in further anatomical studies on "duck-billed" dinosaurs.

General Geologic Context

The Judith River Formation forms a terrigenous wedge west of the front of the Rocky Mountains with its contemporaneous counterpart, the western Two Medicine Formation. The Two Medicine Formation - Judith River clastic wedge (fig. 1), located in the Western Interior of the United States and the southern Western Canada sedimentary basin, has been a major source of dinosaur and other Late Cretaceous fossil remains and information for the past century (Currie, 1987; Eberth, 1997). The sites to be studied in project belong to this clastic wedge.

These nonmarine sediments are interpreted as the remains of an extensive alluvial plain that stretched from the west rising front of the Cordilleran thrust belt to the western shoreline of the Western Interior Seaway. The lowest deposits may be Santonian in the westernmost outcrops and the youngest are early Maastrichtian (Rogers et al., 1993). The wedge formed as the result of the deposition of terrigenous material shed from the thrust belt front into its foreland basin, during a major regressive-transgressive cycle of the Western Interior Seaway (Kauffman and Caldwell, 1993). The wedge thins eastwards and interfingers up section with the transgressive, marine Bearpaw Formation, and down section with the marine, regressive Clagget Formation (Montana) and the Pakowki-Lea

Park Formation (southern Alberta). Below the lower nonmarine sandstones of the Eagle Formation in Montana and the Milk River Group in southern Alberta are present (Eberth, 1997). The middle portion of that broad alluvial plain is lost due to the erosion of strata from the Sweetgrass Arch. In fact, this post-Cretaceous erosional event isolated the Two Medicine Formation in western Montana from its correlative strata to the east, the marine Clagget Formation, nonmarine Judith River Formation and the marine Bearpaw Formation (Rogers, 1994). The Two Medicine-Judith River wedge and its interfingered marine correlatives are overlaid by the Maastrichtian Saint Mary River Formation in the west and the Hell Creek Formation in the east.

Stratal packages range from mudstones to litharenites and volcanic litharenites, and represent a wide array of paleonvironments – beach and barrier island complexes, deltas, lakes, floodplains and fluvial channel systems (Eberth, 1997).

The strata of the Judith River Formation represent the more distal portion of the alluvial plain and thin eastwards towards the Cretaceous shoreline of the Western Interior Seaway. The deposits formed as the result of an eustatic fall of the sea level during Campanian time. The formation correlates in southern Alberta with the Belly River Group and the Judith River Group (Foremost, Oldman and Dinosaur Park Formations) (fig. 2) (Eberth, 1997). The outcrops of the Judith River Formation can be found in central Montana and south Alberta, and represent a coastal plain with fluvial, lacustrine and deltaic environments developed under a subtropical to temperate climate (Horner, 1989). The terrigenous material is chiefly composed of grayish to brownish siltstone and mudstones interbedded with medium-grained sandstone (Rogers, 1993).

Hadrosaur remains from the Judith River Formation are rather fragmentary in Montana, in contrast to the more complete and articulated specimens found in Alberta (Waldman, 1969; Horner, 1988; Currie, 1987; Weishampel, 1990). The material described here, recovered from Malta, may well be among the most complete and beautifully preserved hadrosaurid remains ever collected.

Location and taphonomy of the bone-bearing strata

The specimens herein studied were recovered from sites located in Phillips County, about 15 miles north of Malta, and 50 miles south of the Canadian border. The strata correspond to the lower portion of the Judith River Formation, in the Upper Cretaceous (Campanian). The Malta bonebed lies stratigraphically close to the underlying marine Clagget Shale, suggesting that these dinosaurs may have lived relatively near the shore of the Western Interior Seaway (LaRock, 2000).

In this area, the Judith River Formation outcrops are exposed in badlands located on the Bureau of Land Management lands. The tan-colored sandstones that entombed the Malta hadrosaurs are medium grained and well sorted. In the field area the Judith River Formation is composed by interbedded quartz rich, fine to medium grained sandstones and mudstones (LaRock, 2000). Fossil plant material is common and consists of isolated wood fragments, and interbedded plant material and sand layers (LaRock, 2000).

The taphonomy and sedimentology of the Malta bonebed,conducted by Jeff LaRock (2000), indicates that the deposit accumulated in a shallow sandy meandering channel under lower flow regime conditions. Likewise, the channel, which is of rather small scale and nine meters from the underlying shoreface Parkman Sandstone, may have been a distributary one close to the paleoshoreline (LaRock, 2000). A tree trunk was found lying across the bonebed. The high degree of association coupled with the lack of hydraulic equivalence between the bones and the grain size of the sediment led LaRock to suggest that "the hadrosaurs arrived in the quarry as bloated carcasses and accumulated on the unpstream portion of a fallen tree" (LaRock, 2000). This logjam was subsequently scavenged, disarticulated and slightly weathered. The accumulation of the hadrosaur remains probably represents a period not surpassing five years, based on the presence of bark on the tree (LaRock, 2000). The bonebed represents the remains of at least four subadults and two adult *Brachylophosaurus*. No evidence suggests herding behavior or that the animals were together at the moment of death.

Material and Methods

The complete list of the specimens studied can be found in Appendix A. In brief, the redescription, variation, and taxonomy of *Brachylophosaurus canadensis* is based on complete adult, articulated skeleton MOR 794, the more than 1,000 prepared specimens from the Malta bonebed (MOR 1071), a few cranial elements collected in the early twentieth century in Alberta, Canada (PB 862), and a fragmentary nasal UCB 130139.

The bone material of MOR 1071 and MOR 794 shows minimal weathering, none or very slight abrasion, some fractures, crushing, and a few tooth marks. MOR 794 is mediolaterally compressed due to lithostatic pressure probably, but otherwise is exquisitely preserved.

MOR 1071 includes complete and partial cranial elements such as premaxilla, nasal, prefrontal, frontal, lacrimal, postorbital, jugal, maxilla, pterygoid, ectopterygoid, palatine, predentary, dentary, quadratojugal surangular, splenial, squamosal, including two articulated braincases in partial skulls (nearly complete roof skulls); and either complete or partial postcranial elements including cervical, dorsal, sacral and caudal vertebrae, sternals, scapula, coracoid, humerus, ulna, radius, pubis, ilium, ischium, femur, tibia, fibula, carpals, tarsals, metacarpals, metatarsals, manual and pedal phalanges, including unguals.

The MOR 794 and 1071 specimens were hardened with vinac and were prepared duting the last five years. In fact, as this manuscript is written, more jackets are still being opened providing more elements from the Malta bonebed that will not be included here due to the limitations of time.

The bones are characteristically tan-colored and show minimal permineralization or infilling. The immense majority of specimens fall in the 0 and 1 weathering stages of Behrensmeyer (1978). The stage 1 of weathering is seen in the form of mosaic-cracking patterns on the articular surface of mostly vertebrae (especially caudals) and distal limb elements such as phalanges and unguals (LaRock, 2000, fig. 10A). Spiral fractures are also present in some specimens and are interpreted by LaRock (2000) as prefossilization breakage. A few specimens, dentary (MOR 1071-8-15-98-574), a partial nasal (MOR 1071-7-12-99-76), and two vertebrae, show deep grooves possibly indicative of tooth marks. The case of the dentary is very compelling, as it includes two deep and sharp grooves plus a puncture mark in its vicinity. Eight bones from the bonebed show pathologies (Hanna et al., 1999). Perhaps the most remarkable is a subadult metacarpal II with a bone overgrown.

This work was accomplished by first describing the skeleton of *Brachylophosaurus* in a rather systematic way, starting for the postcrania and ending up in the braincase. For organization purposes, the description is arranged in cranial and postcranial (appendicular and axial) osteology. Within the cranial description, the skull is organized in facial, palatal, mandibular and neurocranial segments or regions. The facial elements are those exposed externally and around the maxilla, a major bone in the skull. The neucranial complex includes the braincase and the frontal and parietal, which are intimately related to the former.

Once the dinosaur was fully described, attention was paid to the analysis of the variation present among the fossil material. The two age classes found in the bonebed represent ontogenetic variation. Individual and, possibly dimorphic, variations were also studied and described.

Finally, a new diagnosis of the taxon was established, along with a revision of the systematic position of *Brachylophosaurus*. It should be emphasized that the phylogeny here presented is rather limited by the time and taxonomic sample size available to me, and is intended only as a way to provide a phylogenetic context to *Brachylophosaurus*. Most of the characters employed were taken from a recent list by Horner, Weishampel and Forster (personal communication). Some characters were modified, several others deleted, and a few ones added to the list used here. The resulting matrix was input into MacClade 3.0 and PAUP, to obtain the tree herein presented.

The hadrosaur fossil material is here assigned to the species *Brachylophosaurus canadensis*. All the hadrosaur non-diagnostic elements from the Malta sites are also placed in this taxon, assuming that they follow the diagnosis suggested by the other elements. This is considered here the most parsimonious and probable hypothesis on the taxonomic precedence of these remains.

Numerous measurements were taken of several dimensions and features of the osteologic elements, whenever the landmark was complete enough. Linear measurements were taken with a caliper, while a few angular measures were taken with a conventional protractor. The measurements are intended to provide an idea of the dimensions of the different features of the skeletal elements. Although very precise figures are given, they should not be taken as the actual measures of the features, since breakage, abrasion, crushing, concealing by articulation and other preservational artifacts commonly affect the remains.

CHAPTER 2

SYSTEMATIC PALEONTOLOGY

Ornithopoda Marsh, 1871

Iguanodontia Dollo, 1888

Hadrosauridae Cope, 1869

Brachylophosaurus Sternberg, 1953

Brachylophosaurus canadensis (Sternberg, 1953)

(= *B. goodwini* Horner, 1988)

Revised Diagnosis

Hadrosaurid possessing a subrectangular skull, with a relatively deep snout; nasals greatly developed into a paddle-like solid crest that extends caudodorsally overhanging the dorsal region of the skull; nasals possessing an anteroposteriorly-oriented groove terminating in an elongated foramen, located medial to the prefrontal; prefrontal projected posteriorly, resting dorsomedially over the anterior process of postorbital and, more posteriorly, extending ventromedially underlying the nasal; jugal with a ventrally projected semicircular flange, in overall a deeper element than in *Maiasaura*, but more lightly built than in gryposaurs, saurolophs and edmontosaurs; extremely elongated, rod-like anterodorsal process of the maxilla projecting medial to the narial cavity along most of the anteroposterior length of the external naris; depressed dorsal surface of the frontal between the nasal joint and the postorbital suture; anteroposteriorly short exoccipital-supraoccipital roof posterior and dorsal to the foramen magnum; sternals with a compressed, oval "paddle"; and very elongated, slender forearm due to elongation of radii and ulnae.

Referred Specimens

MOR 794, a complete adult articulated skeleton lacking only the distal part of the tail; MOR 1071, more than 800 subadult and adult specimens from a paucispecifc bonebed, including disarticulated or partially articulated and/or associated coracoids, scapulae, sternals, ilia, pubes, ischia, cervical, dorsal, sacral and caudal vertebrae, ribs, humeri, radii, ulnae, carpals, metacarpals, phalanges, femora, tibiae, fibulae, tarsals, metatarsals, pedal phalanges, premaxillae, maxillae, a partial nasal, prefrontals, postorbitals, jugals, quadratojugals, quadrates, dentaries, a predentary, splenials, surangular, angulars, articulars, pterygoids, ectopteyrgoids, palatines, frontals, and two articulated skull roofs with preserved braincases, plus an articulated partial subadult skull. PR 862 is a partial skull roof with associated jugals, dentaries, pterygoid, nasals, right surangular, angulars, and left quadrate. UCB 130139, a partial nasal from the holotype of *B. goodwini* (Horner, 1988).

Locality

The adult quarry of MOR 794 (MOR locality JR-168) and the bonebed of MOR 1071 (MOR locality JR-224) correspond to two sites located in Phillips County, about 17 miles north of Malta, northeastern Montana, 54 miles from the Canadian Border (LaRock, 2000). PR 862 was found in 1922 by the Elmer S. Riggs expedition, in the Red Deer River area, north of Medicine Hat, Alberta, Canada. The nasal UCB 130139 is part of the material found by Mark Goodwin in 1981 in the Judith River Formation, UCMP locality no. V83125, Canadian Creek, Hill County, Montana.

Horizon

MOR 794 and MOR 1071 correspond to the Judith River Formation. PR 862 was unearthed from strata pertaining to the Two Medicine Formation. Both formations are Campanian in age.

Discussion

Sternberg (1953) originally named and described briefly *Brachylophosaurus canadensis* on the basis of a complete skull, cervical and anterior dorsal vertebrae, ribs, scapulae, coracoids, humeri, left ulna, and radius. These specimens came from the Oldman (Judith River) Formation of southern Alberta. In 1988 Horner emended Sternberg's diagnosis, characterizing *Brachylophosaurus* by the possession of a solid and low, sheet-like, nasal crest caudally directed, a nasal depression that do not extends to the crest, lightly constructed jugal with a ventrally projecting boss and an craniocaudally short supraoccipital-exoccipital roof caudal to the foramen magnum (Horner 1988, emended diagnosis). This diagnosis is here enhanced to accommodate a few more characters.

In the same 1988 paper, Horner described and named a new species of *Brachylophosaurus*, *B. goodwini*, from fragmentary cranial elements from the Judith River Fm. of Montana. This taxon is here considered invalid and a junior synonym of *B. canadensis*. Horner diagnosed *B. goodwini* on the basis of a deep and rounded dorsal depression or pit at or near the junction of the frontal and postorbital, dorsally concave upper process of the nasal, posterolateral surface of nasal reaching orbital rim, and quadratojugal process of the jugal parallel with postorbital process (Horner, 1988).

The depression on the dorsal surface of the frontal near the postorbital joint has been also found in the Malta specimens. The subadults MOR 1071-7-13-99-87-I and MOR 1071-6-30-98-4 show depressed areas near the postorbital suture. These depressions are elongated, but individual and/or ontogenetic variation might account for that discrepancy with Horner's observation.

The nasal characters are probably resulting from the wrong reconstruction of the fragmentary remains of this element studied by Horner. Horner interpreted the nasal UCB 130139 as having a concave relief, in contrast to the arched relief of the holotype and the other specimens of *Brachylophosaurus canadensis*. However, a closer comparison with the MOR 794 and MOR 1071 specimens shows that the UCB nasal was oriented in the opposite direction. When correctly oriented, the UCB nasal fragment corresponds probably to the supra to preorbital region of the skull and follows the outline of the typical *Brachylophosaurus* skull. The only difference is the large size of the UCB specimen. The parallel quadratojugal and postorbital process of the jugal is a case of individual variation. MOR 794 shows jugals with postorbital processes only slightly divergent. Among the bonebed specimens of available there is a degree of variation in the divergence between the postorbital and quadratojugal processes, coupled with a remarkable variation in the size and shape of the quadratojugal process (but see variation).

CHAPTER 3

OSTEOLOGIC DESCRIPTION

This chapter, the major section of this project, is intended as a redescription, as detailed as possible, of *Brachylophosaurus canadensis*. It revises and enhances the account given by Sternberg in his original paper in 1953, in the light of the new, more diverse and complete specimens. The text is organized in cranial and postcranial osteologies. The postcrania is split into appendicular and axial skeletons. The appendicular skeleton includes all the elements excluding the vertebral column and the ribs, being more or less related to the limbs. The cranial section is mainly divided into mandibular, facial, palatal, and neurocranial complexes, in a similar, but not exact, way of Ostrom (1961). Facial complex is preferred here instead of maxillary complex (Ostrom, 1961; Horner, 1992), since, although the maxilla is the major element in that segment of the skull, not all the elements included in that area contact the maxilla. Facial complex elements here are those exposed externally on the skull, exception made of the ones associated with the braincase and the mandibular segment. The other cranial complexes considered here follow the organization of Ostrom (1961).

General Description of the Skull

The skull of *Brachylophosaurus canadensis*, as exemplified by MOR 794 (Fig. 1) and the MOR 1071 specimens, is about two and half times longer than deep. The skull is relatively broad mediolaterally, especially across the postorbital width and the paroccipital processes, where the skull is one third as wide as it is long. In lateral view, the dorsal border of the skull is anteriorly arched and sloping along the anterior third, close and from the nasal-premaxilla joint. Along the posterior two thirds of the dorsal border the skull is rather straight, only rising posterodorsally very gently due to the projection of the nasal crest. The ventral border of the skull is also rather straight and mainly formed by the ventral edge of the dentary, the anteroventral deflection of which is slight in MOR 794, but much more remarkable in PR 862.

Brachylophosaurus shows a ellipsoidal, anteroposteriorly elongated and large external naris. The premaxilla forms the anterior edge of the narial cavity, while the nasal forms a lunate posterior border. The ventral border of the external naris is formed by the dorsal edge of the posteroventral process of the premaxilla. The dorsal border of the narial cavity is mostly formed by a laterally convex anterodorsal process of the nasal. The anterodorsal process of the maxilla can be seen crossing almost all the narial cavity anteroventrally as a narrow and long rod-like projection. A relatively large maxillary foramen opens anterolaterally, its anterior edge bounded by the lateral border of the posteroventral process of the premaxilla. The orbit is oval, relatively more elongated dorsoventrally. The longest axis of the orbital cavity extends in a dorsoposterior to anteroventral direction, about 20-25 degrees from a vertical line. The orbit is relatively very large and its anterodorsal edge is sharp and rugose, formed by a prefrontal that overlaps the dorsal face of the anterior process of the postorbital to underlie the nasal. Likewise, the posterodorsal and posterior edges of the orbit, formed by the postorbital, are still more rugose, notched and mediolaterally expanded at the dorsal area of the jugal process. The infratemporal fenestra is triangular in MOR 794, with a rather acute dorsal apex. However, other specimens, such the MOR 1071 and the holotype, NMC 8893,

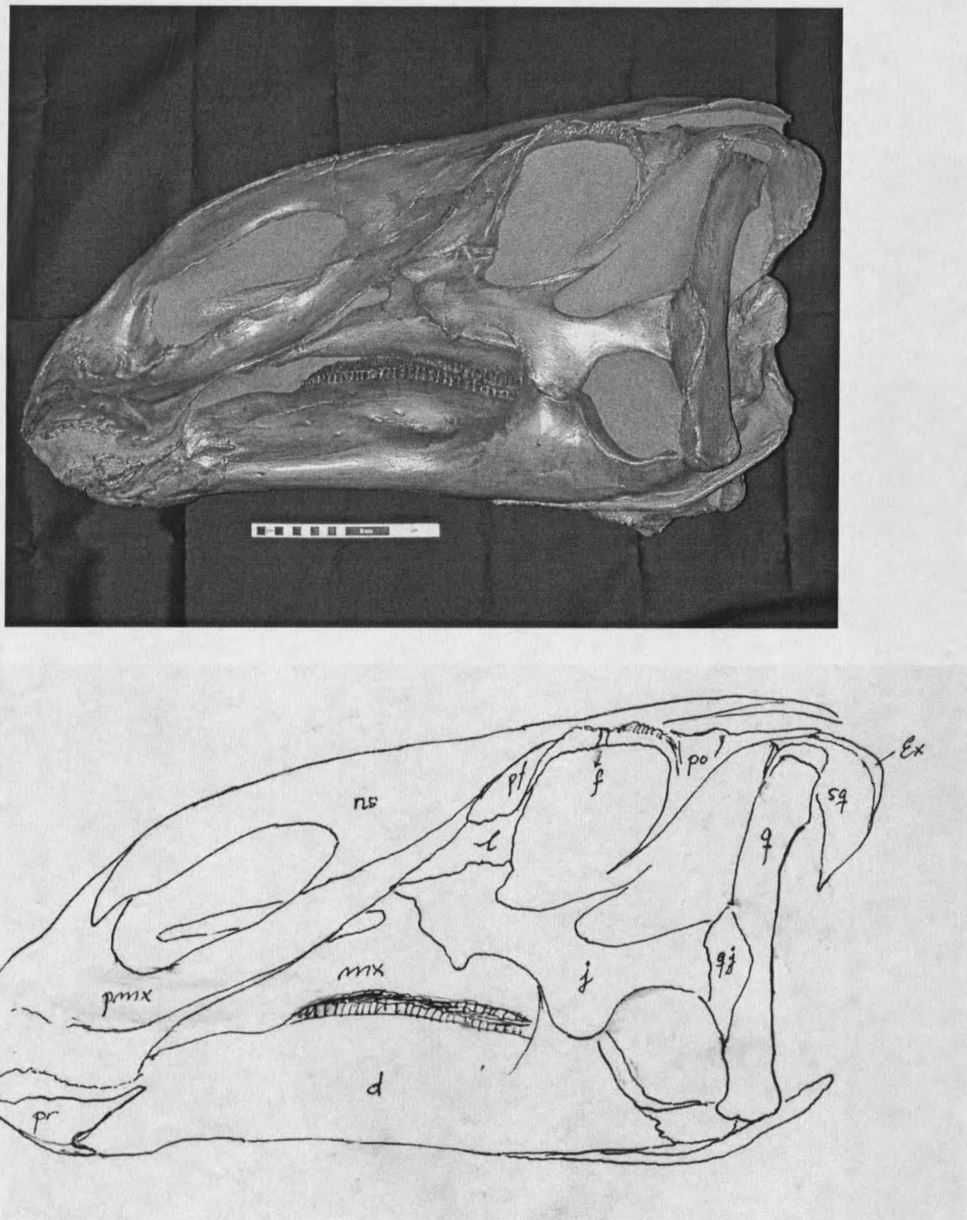

Figure 1. Skull MOR 794 in left lateral virew. Pmx: premaxilla, pr: predentary, ns: nasal, d: dentary, mx: maxilla, l: lacrimal, j: jugal, pf: prefrontal, f: frontal, po: postorbital, qj: quadratojugal, q: quadrate, sq: squamosal, ex: exoccipital, sa: surangular, h: hyoid.

exhibit differences in the outline of the infratemporal fenestra, being less triangular and less narrow dorsally. The infratemporal fenestra is not larger than the orbit and the external naris. Ventrally, a circular opening exists formed by the jugal, quadratojugal, quadrate and the surangular. This opening is about two thirds as large as the orbital cavity. The supratemporal fenestra is ellipsoidal, about twice as long anteroposteriorly than mediolaterally. The fenestra is slightly narrower posteriorly, where it is medially inclined due to the relative mediolateral narrowing across the level of the quadrates.

The oral cavity is relatively broad mediolaterally, rather expanded in relation to the mediolateral narrowing of the dorsal and antorbital region of the nasals. From about the level of the orbit the nasals expand mediolaterally to form the solid crest. The crest conceals most or completely the supratempral fenestrae, depending on the specimen. The premaxilla and the nasal form the exposed dorsolateral and dorsal region of the skull. The dentary is a massive element, as occurs commonly in hadrosaurs, and forms most of the mandible. The lateroventral and laterodorsal zone of the maxilla and dentary, respectively, are medially indented, placing the teeth rows medial in respect to the lateral side of the surrounding elements. This is especially true posteriorly, where the occlusal plane is medially sunk in respect to the jugal ventral edge and the posteroventral dentary lateral face. Anteriorly, a sharp and thin reflected rim of the posteroventral process of the premaxilla overlies the anterodorsal maxilla, being laterally offset in respect to the anterior occlusal plane of the dental batteries.

In ventral view, the skull is greatly expanded across the predentary. The greatest predentary width is reached at the ventrally deflected corners of the element. Posterior to the predentary, the dentaries draw an anteroposterioly long and mediolaterally narrow "U" from their symphysis. At the posterior third of the skull, the dentaries diverge laterally, bearing a pair of hyoids attached to their medial sides.

Maxillary Complex

Premaxilla

The premaxilla (Fig. 2) is one of the major and more complex elements in the skull of *Brachylophosaurus*. It is a paired element that forms the upper half of the "duck bill" so characteristic in hadrosaurs. The bone articulates medially with its counterpart, posteroventrally with the maxilla, lacrimal and prefrontal (dorsocaudally in this order), and posterodorsally with the nasal. The premaxilla probably also articulates with the vomer posteroventrally (Horner, 1992). The anterior portion of the premaxilla is strongly concave, "pocket-like" dorsally, and expanded laterally. It is flattened medially for contacting its counterpart. Posteriorly the element quickly diverges into two long dorsocaudal and ventrocaudal, projecting processes. The anterior edge of the narial cavity is mostly formed by the space enclosed by these processes. Posteriorly the lateral rim of the posteroventral process of the maxilla is reflected.

The anterior border of the premaxilla is ventrally deflected, as in *Maiasaura*, but unlike the reflected anterior rims of *P. blackfeetensis* and *Gryposaurus*. That deflection forms a triangular and rounded corner. The anterior edge of the premaxillas contains a series of small ventral processes. These processes are interpreted by various authors (Ostrom, 1961; Weishampel and Horner, 1990) as holding in life a ramphoteca that would meet a counterpart in the predentary. Small circular foramina are found distributed among these ventral processes of the anterior rim of the premaxilla. Posteriorly, and ascending anterodorsally, there is a semicircular border parallel to the anterior edge of the maxilla. This border separates the anterior deflection of the premaxilla from a small depression. This depression is anterior to the pocket-like region of the premaxilla, the anterior beginning of the circumnarial depression. At least two relatively large foramina are located anteromedially. One foramen is located near the anterior border of the anterior depression. This foramen is oval and slightly elongated anterocaudally. Dorsomedial from this, there is the other foramen, which is located near of the base of the posterodorsal process of the premaxilla. This foramen exits ventrally perforating the premaxilla, and may correspond to the ventral premaxillary foramen described in *P. blackfeetensis* (Horner, 1992). Dorsocaudal and adjacent to this foramen there is a semicircular, small and shallow concavity. A sharp semicircular rim anteriorly bounds this concavity.

Figure 2. Subadult premaxilla MOR 1071-7-7-98-84 in anterodorsal view.

The ventrocaudal process is mediolaterally thin. Its laterodorsal surface is strongly concave longitudinally, containing the circumnarial depression. The process is mediolaterally expanded anteriorly but gradually narrows while ascending posterodorsally. Posteriorly the process becomes gradually less concave, and faces more laterally. The lateral edge of the ventrocaudal processes of the maxilla forms a reflected and sharp rim over the anterior region of the maxilla and beyond anteroventrally, posterior to the deflected anterior area of the premaxilla. Where the process is most concave, anterior to the deflection of the premaxilla, the bone forms a ventral bulge. This bulge, also found in *M. peeblesorum* (Trexler, 1995), probably fits on a concavity on the dorsal face of the anteroventral process of the maxilla. The bulge is more prominent in *P.*

blackfeetensis. Medial to this bulge, there is a indentation on the dorsal side of the medial border of the ventrocaudal process. This indentation receives the posterior portion of the anterodorsal process of the maxilla. The medial border of that indentation is formed by a flattened surface for contacting the medial side of the ventrocaudal process of the other premaxilla. Due to the proximity of the maxillary indentions when the two premaxillae articulate medially, it is probable than the anterior portions of the anterodorsal processes of the maxillae meet each other medially. Posteriorly, the ventrocaudal process thins progressively and wedges between the dorsal border of the lacrimal and the ventral border of the anteroventral process of the nasal. The dorsal end of the ventrocaudal process of the premaxilla tapers contacting the anterodorsal rim of the prefrontal.

The dorsocaudal process of the premaxilla is mediolaterally compressed and ascends posterodorsally with a steeper angle than the ventrocaudal process. The posterodorsal process thins and arches progressively over the anterior portion of the skull. The medial side is flat and meets the medial side of its counterpart in the skull. The lateral side is also flattened and contains the articulating surface for the anterodorsal process of the nasal. The dorsocaudal process of the premaxilla forms the anterior boundary of the narial cavity, while most of the dorsal bounday is formed by the ventral edge of the anterodorsal process of the nasal. A series of oblique striations can be found on the nasal contact. Posteriorly over the dorsal border of the snout, the posterior segment of the anterodorsal process thins extremely, wedging between the anterodorsal process of the nasal. The posterior end of the posterodorsal process of the premaxilla is located posterior to the level of the posterior border of the external naris.

Maxilla

The maxilla (Fig. 3) occupies a central, ventral position in the skull, and bears the upper dental battery. It is triangular in lateral view, anteroposteriorly elongated and mediolaterally compressed. In *P. blackfeetensis* the maxilla is more elongated than in both *B. canadensis* and *M. peeblesorum*. In contrast, *Gryposaurus* exhibits the shortest observed maxilla. Posteriorly, the maxilla of *B. canadensis* presents a dorsal shelf along little less than the anterocaudal length of the bone. This is the ectopterygoid shelf, which attaches to the element of the same name. There is a thin and crest-like dorsal flange, the apex of the maxilla, mainly for joining the lacrimal. The anterior end of the maxilla bifurcates into two processes, a long anterodorsal process, and a short and stout anteroventral process. Ventrally, the lateral side of the maxilla is dorsoventrally convex. In contrast, the medial surface of the element is flat and composed mainly by the dental lamina that, as in the dentary, covers the dental battery. The maxilla articulates with the premaxilla anteroventrally, with the jugal posterodorsally, the lacrimal dorsally, the ectopterygoid posterolaterally and caudally, the pterygoid posterodorsally, the vomer anterodorsally and medially, and is perhaps with the nasal dorsally.

The anterior end of the maxilla is bifurcated into the anteroventral and anterodorsal processes, which are separated in lateral profile by a crescentic notch. The anteroventral process is relatively short and wedges anteroventrally. It presents a concave surface that faces anteriorly and dorsolaterally. This surface contains a number of small foramina of different sizes and supports the middle region of the medioventral surface of the ventral process of the premaxilla.

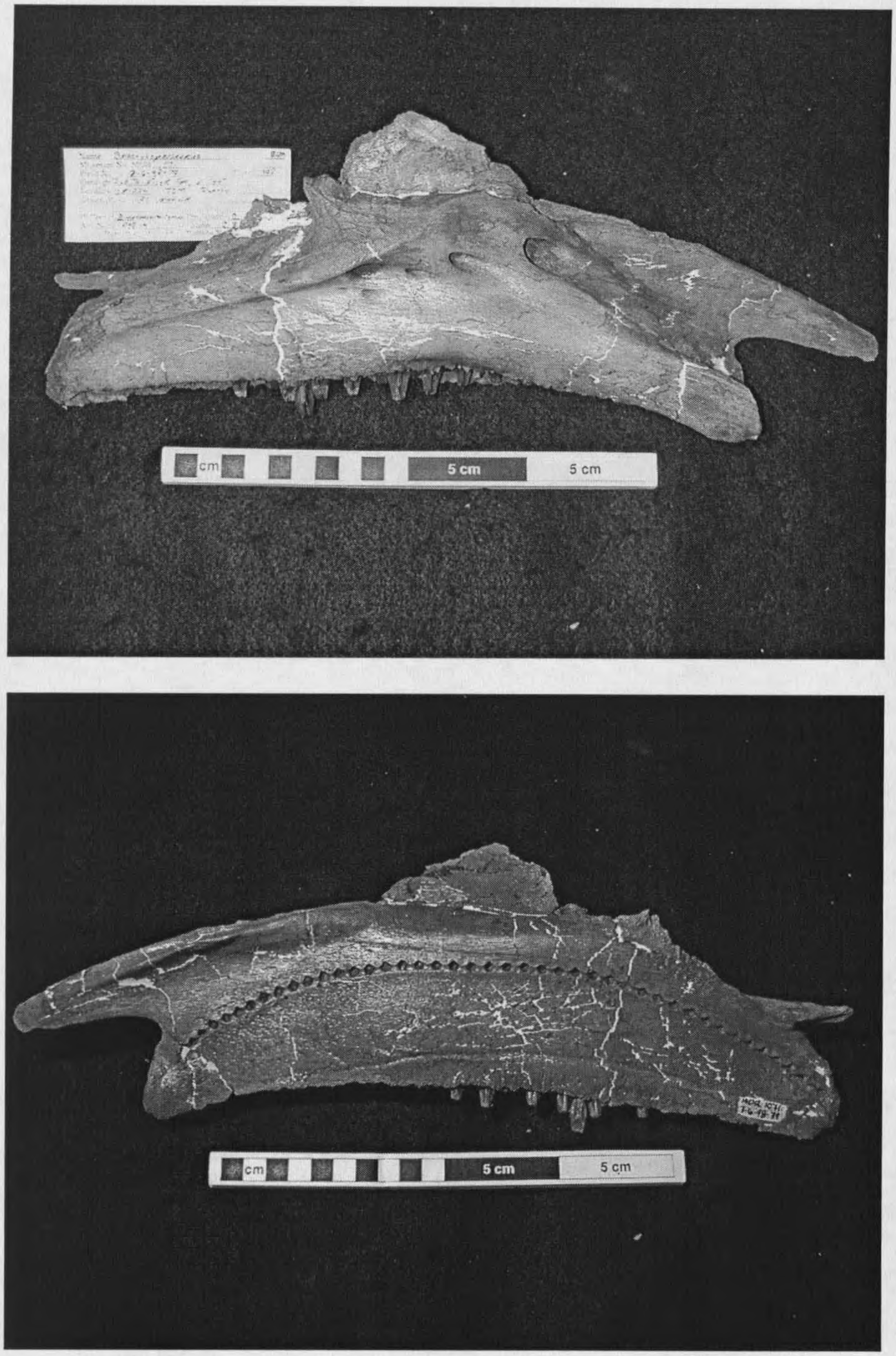

Figure 3. Left maxilla MOR 1071-7-6-98-79 in lateral (top)l and medial (bottom) views.

Medial from the anteroventral process, the anterior maxillary notch forms a crescentic lateral profile into the anterodorsal process. This process is extremely long in *Brachylophosaurus*, nearly extending completely along the anterocaudal length narial cavity. The anterodorsal process of the maxilla mediolaterally compressed, rod-like, sand directed anteriorly. At the base of the process, the dorsal edge of the anterior end of the maxilla is arched. On the medial side, the anterodorsal process shows a large ridge that runs anteroposteriorly well into the body of the maxilla until the level of the seventh special foramen of the dental battery. Anteriorly this ridge extends along the first centimeters of the anterodorsal process. The surface below and above the ridge is concave.

Posterior to the anterodorsal process, the dorsal border of the maxilla is medially offset from the dorsal, crest-like apex of the maxilla. The apex of the maxilla is expanded dorsally in the form of a triangular flange, which is laterally offset from the parasagittal plane. This mediolaterally-compressed flange has rugose lateral and medial surfaces. The medial side of the anterior, wedge-like extreme of the lacrimal articulates on the lateral side of the triangular flange. The remaining, ventral region of the lateral side of the flange contacts the arrow-like anterior process of the jugal. Below the maxillary flange, there is a lateral expansion for the anterior process of the jugal, anterior to the dorsal, posterior shelf of the maxilla. This expansion, the jugalar process, forms an irregular lateral ridge that links posteriorly with the lateral border of the posterior ectopterygoid shelf of the maxilla. The morphology of the jugalar joint surface molds the outline of the ventral border of the arrow-like, anterior process of the jugal. A small portion of the caudal edge of the dorsal (lacrimal) flange fits into a space anteroventral to the palatine articulation of the jugal, on the dorsal area of the medial side of the anterior process of this last element.

The posterior half of the maxilla is mainly devoted to contact the palatine, ectopterygoid and pterygoid bones of the palate. Posterior to the jugalar process, there is the ectopterygoid shelf, a flat surface that deflects ventrally at the posterior end of the maxilla. On that platform rests the medioventral side of the ectopterygoid, forming a relatively extensive joint. Medially offset at the caudal end of the maxilla there is a salient, thin, rod-like, and posteriorly projected process for the reception of the maxillary process of the pterygoid (Horner, 1992). The medioventral side of the process rests on a recess on the mediodorsal border of the ectopterygoid. Anterior and mediodorsal to that short process there is a narrow and rugose ridge that receives the ventral groove of the palatine. This ridge runs anteriorly to end medial and at the level of the posterior border of the lacrimal flange. The lateral surface of the palatine ridge slopes ventrolaterally to link smoothly with the posterior ectopterygoid shelf. The medial side of the dorsal edge for the palatine contains oblique striations.

The remaining lateral side of the maxilla forms the lateral surface of the dental battery. This surface is dorsoventrally convex and curves ventromedially along its ventral half, producing a space for the hypothetical fleshy cheeks. This lateral surface contains up to six foramina dorsally located along the anterior half. Two of them are relatively large. The largest, major maxillary foramen faces anterolaterally. It is located posterior to the beginning of the anterodorsal process and anteroventral to the lacrimal flange. The second large foramen in located on under of the jugalar process. This foramen communicates with another large foramen located posteromedial to the lacrimal flange ridge. Anterior to this posteromedial foramen, there is another foramen of similar size and depth. Posterior to the maxillary foramen there are several smaller foramina scattered on the lateral side of the maxilla. The number and arrangement of these foramina varies among the specimens. Otherwise, the lateral surface of the dental battery is fairly smooth and triangular in lateral view.

The medial side of the maxilla is rather flat and formed by the dental lamina that covers the dental battery. In medial view, the medial surface of the maxilla is semicircular in profile (excluding the anterodorsal process), straight horizontally along the alveolar margin and arched dorsally, and convex. As the medial side of the dentary, the medial maxilla also contains a line of special dental foramina that arch drawing a semicircular contour. These special foramina are dorsally located and form the dorsal boundary of the thin sheet that is the dental lamina. There are between 40 and 43 of these special foramina, each corresponding to a dental alveolus. The row of special foramina does not reach the anterior extreme of the maxilla, but they nearly reach the posterior end. At a short distance from the ventral edge of the dental lamina, there is a shallow groove on the medial side of the dental lamina. This narrow groove runs parallel to the ventral edge of the dental lamina. The maxillary dental battery is narrower mediolaterally than the dentary one. In the maxilla, there are as much as two teeth per position forming the occlusal surface. The teeth occlussal plane faces medioventrally to meet the occlusal plane of the dentary teeth. Maxillary teeth are described in its own entry. The alveoli are located on the opposite side of the dental lamina, carved on the internal (medial) face of the lateral wall of the maxilla. These alveoli are dorsoventrally long, tubular grooves. Sharp ridges, as in the case of the dentary, separate the grooves. The inner (lateral) surface of the medial, dental lamina is also grooved. However these grooves are less defined and bounded by less sharp ridges. The grooves on the lateral side of the dental lamina face its counterparts on the medial side of the lateral surface of the maxilla. In the maxillary battery, the teeth curve medially, in contrast to laterally as in the dentary. Then, the enameled sides of the crowns are exposed along the lateral (labial) side, in contrast to lingually (medially) as in the dentary battery.

Nasal

The nasal of *Brachylophosaurus* is the longest and most derived bone in the skull. It is found forming most of the dorsal exposed region of the skull, from the anterior area of the external naris to the caudal-most end, where it partially covers the supratemporal fenestra in the form of a flat, "paddle-like" solid crest (Fig. 4). The bone is mediolaterally compressed into a sheet of bone along most of its surface, except for the crest. The element is convex laterally throughout the laterodorsal, middle region and the anterodorsal rostral portion of the skull. The nasal consists of a central subtriangular body from which three processes emerge. Two of them project anteroventrally, articulating with the two processes of the premaxilla to enclose the external naris. The third projection of the nasal extends dorsocaudally over the skull, contacting the prefrontal and the frontal, and forming the nasal crest that projects dorsocaudally over the parietal after leaving the articulation with the frontal.

The hook-like anterodorsal process of the nasal is very long and arches anteroventrally to form nearly all the dorsal rim of the external naris. The medial face of that process articulates with the lateral side of the posterodorsal process of the premaxilla. The anterodorsal process of the nasal overlaps laterally the posterodorsal process of the premaxilla, except for the anterior-most region of this last, over which the nasal process wedges anteroventrally into a hook-like end. The anterodorsal process of the nasals do not contact each other because they are separated by the dorsocaudal processes of premaxilla, which contact forming the midline of the rostrum as far as posterior to the external nares. Posterior to this, the parasagittal plane of the skull is formed by the articulation of the nasals. There anterodorsal process of the nasal is deepest at its hook-lie anterior end. There the process is laterally convex. Posteriorly the ventral edge of the anterodorsal process curves anteroventrally to form the caudal rim of the external naris and connect with the anteroventral process.

The anteroventral process of the nasal is very short and it is reduced to a triangular wedge. The ventral portion of this process is medially recessed for joning the ventrocaudal process of the premaxilla. The anterior sharp, wedge-like end of the anteroventral process of the nasal forms the posteroventral border of the external naris.

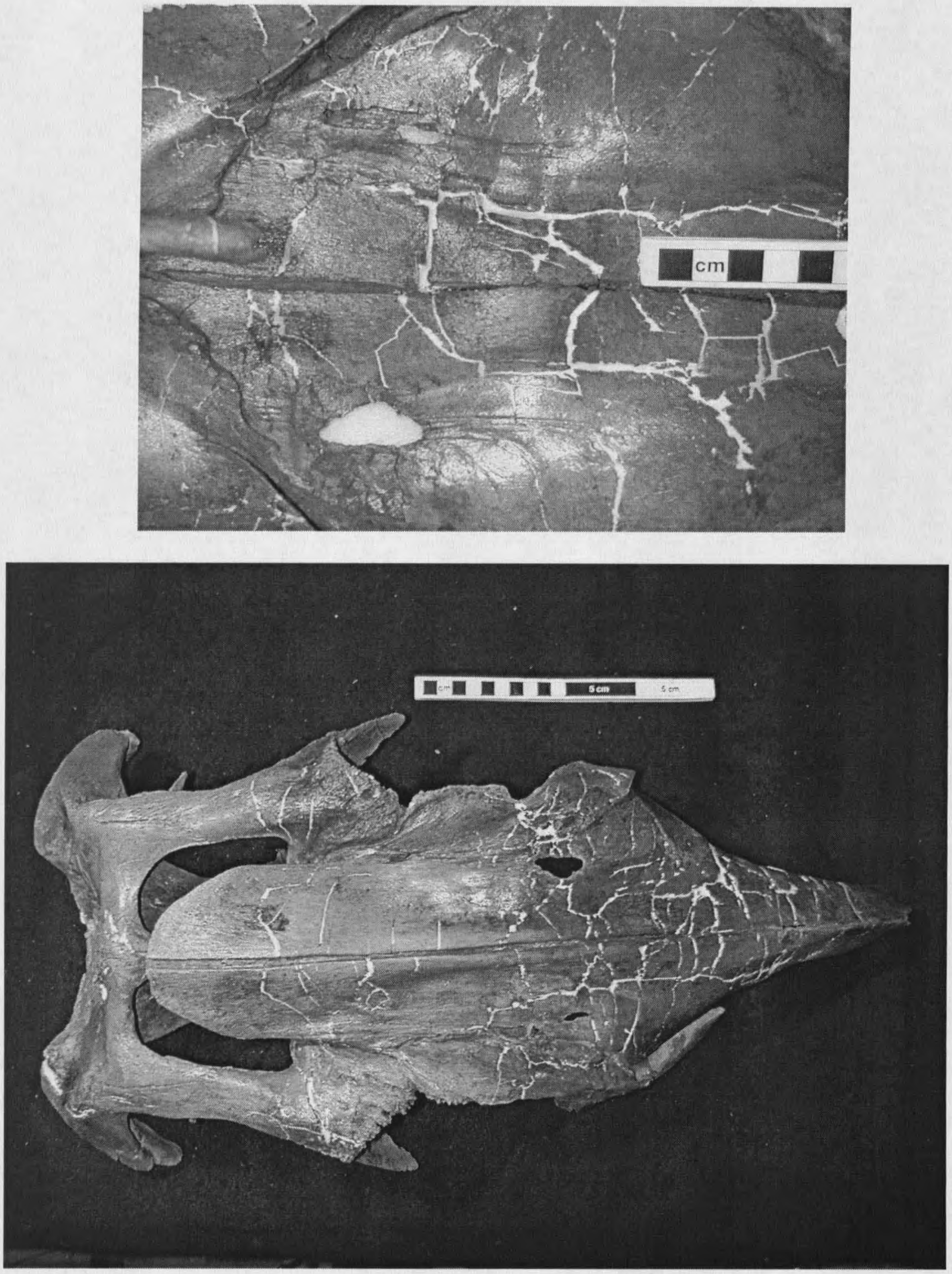

Figure 4. Articulated nasals MOR 1071-7-7-86-98. Ventral detail showing foramina and grooves (top). Dorsal view showing solid crest projecting caudodorsally (bottom).

The central body of the nasal articulates with the prefrontal posteroventrally. Along that articulation, the lateral, convex wall of the nasal changes in orientation, becoming a dorsal sheet of bone that extends caudally forming the crest. At the beginning of the crest the nasal forms a sharp lateral edge over the prefrontal and postorbital. The nasal overlaps dorsally only the mediodorsal border of the prefrontal. This fits into an excavation on the ventral side of the roof of the nasal. Internally (medially) the central body of the nasal overlaps a portion of the anterodorsal region of the concave medial face of the lacrimal. Probably the nasal also abuts the dorsal border of the lacrimal flange of the maxilla.

The articulation with the frontal occurs ventrally, where the nasals overlie the posterodorsal surface of the skull. The surface of the nasofrontal suture could not be observed in adults. In the observed subadult specimens, the dorsal surface of the frontal shows a series of craniocaudally-directed grooves and ridges. The nasal articulation extends over two thirds of the anteroposterior length of the frontals. Mediolaterally, that articulation is also limited to the two medial thirds of the frontal. The posterior end of the nasal-frontal articulation is M-shaped in outline across both frontals and bounded by a sharp rim of bone. Posterior to the frontal joint, the nasals, already in the form of a solid crest, are supported ventrally by the expanded mediocaudal portion of the prefrontals. Posteriorly, the nasal crest projects posterodorsally over the top of the skull overhanging the parietals. The crest is solid, tongue-like and contains the parasagittal plane of the skull, contained along the suture between both nasals. The joint between both nasals forms a low ridge along the crest. Lateral from that ridge, the dorsal surface of the crest is slightly concave and slopes lateroventrally.

There is a foramen located medial to the prefontals. On the ventral surface of the nasal, there is a anteroposterioly-directed groove emerging anteriorly from the foramen (Fig. 4, top). This groove is very narrow, but delimited by well-defined edges. On the dorsal surface of the nasal, there is another groove of similar proportions, but running posteriorly from the foramen. The foramen was probably at least as wide as those grooves. Anteromedial to the nasal foramina, the ventral surface of the element contains a shallow bulge. The bulge is formed around the nasal joint and protrudes ventrally.

Jugal

The jugal (Fig. 5) is a mediolaterally-compressed sheet of bone that forms the ventral borders of the orbit and the infratemporal fenestra on the lateral face of the skull. The bone is W-shaped in lateral view, with an arrow-like cranial end. The posterior end of the jugal is dorsoventrally expanded into a flange, the quadratojugal process that meets the bone of the same name. The jugal is slightly arched, so that the medial side is concave. Anteriorly the jugal articulates with the lacrimal dorsally, the palatine medially and anterodorsally, and the maxilla ventrally. Posteriorly the jugal meets the postorbital to form the caudoventral border of the orbit. Caudally, the jugal articulates with the quadratojugal. The jugal is expanded in four directions. Besides the arrow-like anterior process, the dorsal edge sends at the middle a long, slender and rod-like postorbital process. This process joins the jugal process of the postorbital to form the posterior border of the orbit. Posteroventrally from this the jugal expands into an oval boss. This boss is also found in *M. peeblesorum*, and to a lesser extent in *Gryposaurus*, but is very reduced in more derived hadrosaurs, such as *P. blackfeetensis*, *Edmontosaurus*, and *H. stebingeri*.

The arrow-like, anterior maxillary process wedges anteriorly into a sharp, pointed end that arches anteroventrally. The posterior end of the process is mediolaterally thicker and limited by a medial ridge. The medial surface of the anterior process of the jugal is full of grooves and ridges. It is convex and anteroposterioly bisected by a ridge. In contrast, the lateral side is fairly smooth, except for the dorsolateral border, which shows a series of fine, short and oblique striations. The dorsal edge of the anterior process of the jugal molds the ventral relief of the ventral border of the lacrimal, with which it articulates. Posteriorly on the anterior process of the jugal there are forms two small process. The more anterior is mediolaterally compressed, rounded and fits into a circular indentation on the lateral, ventral border of the posterior region of the lacrimal. The other process, which is located adjacent to the rounded one, is a short, dorsal projection that fits into a deep excavation on the caudoventral corner of the lacrimal. The contact maxilla-lacrimal excludes de jugal from reaching the nasal. Posterior and ventral to these two small processes, on the medial side of the anterior process of the jugal, there is the articulation for the palatine. The joint is an elongated, oblique and rugose convexity that contacts an anterolateral process on the palatine, which shows the same ellipsoidal, but concave, outline. Heaton (1971) mentioned that the lacrimal flange of the maxilla participates in the articulation with the anterolateral process of the palatine. In *Brachylophosaurus* it seems improbable, given the distance separating the posterior edge of the lacrimal flange and the jugal-palatine articulation. The ventral border of the anterior process of the jugal sits on the laterally salient jugalar process of the maxilla.

Figure 5. Left jugal MOR 1071 7-16-98-248G in lateral view.

Posterior to the anterior process, the jugal thins dorsoventrally, showing concave lateral profiles on both its dorsal and ventral edges. The dorsal border projects caudodorsally to form the long postorbital process, while the ventral border links caudoventrally with the ventral boss. The postorbital process is triangular at its base on the dorsal border of the jugal. Dorsally, the postorbital process gradually twists, changing form being mediolaterally compressed to anteroposteriorly compressed. This twist and change in orientation allows the process to receive the jugal process of the postorbital, forming a not very tight joint. After twisting, the postorbital process expands mediolaterally for a short distance. Along its dorsal half, the anterior side of the postorbital process is concave.

The posterior, ventral boss of the jugal is an oval process that is found overlapping the lateral side of the coronoid process of the dentary. The lateral side of that boss is flat, while the medial side is convex. On the lateral side, along the ventrocaudal border, there are sets of short striations oriented ventrocaudally.

The quadratojugal process forms the posterior end of the jugal. This process is dorsoventrally expanded, forming a flared sheet of bone that is gradually more compressed mediolaterally near of its posterior, sharp edge. The medial side of that process is concave, except for the convex dorsal border. The concavity received the anterior portion of the lateral side of the quadratojugal, which is overlapped by this process of the jugal. The medial surface for the quadratojugal is slightly rugose, with oblique striations near the dorsal border. The caudal edge of the quadratojugal process is irregular in outline, made of an uneven set of small indentations. The dorsal border of the quadratojugal process forms most of the ventral border of the infratemporal fenestra.

Lacrimal

The lacrimal (Fig. 6) is a triangular, wedge-shaped, mediolaterally-compressed element. The anterodorsal border articulates with the ventrocaudal process of the premaxilla. The dorsal and caudodorsal borders contact the prefrontal. The ventral side meets the jugal, while the medial surface articulates with the dorsal flange of the maxilla. The caudal edge contributes to form the anterior border of the orbit. The posterior half of the lacrimal is caudodorsally projected, while the anterior portion consists in an

elongated, sharp and

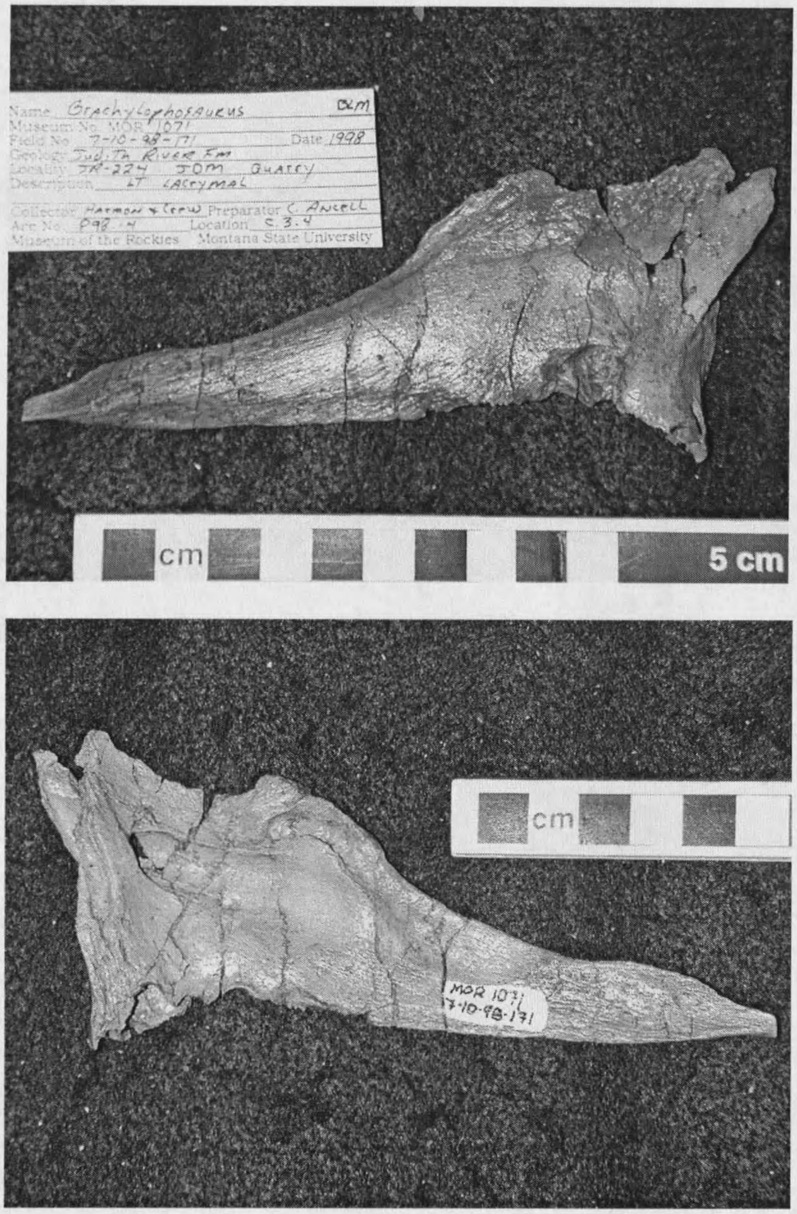

Figure 6. Right lacrimal MOR 1071-7-10-98-171 in lateral (top) and medial (bottom) views.

pointed extreme. The ventral border is rather straight, as the posterior border. The lateral surface of the lacrimal is slightly convex, while the medial side is concave.

The anterodorsal border of the lacrimal is overlapped when receiving the medioventral border of the ventrocaudal process of the premaxilla. Posterodorsally that border becomes progressively concave, being excavated by a groove until reaching the dorsally ascending, more posterior edge of the lacrimal. The ventral border of the anteroventral region of the prefrontal overlaps the posterodorsal area of the lateral side of the lacrimal. However, on the medial side the lacrimal shows a triangular process on its posterodorsal region that indents into the prefrontal. Posteriorly the lacrimal still meets the prefrontal at two more spots. The caudal border of the lacrimal sends a dorsally projecting process. This process borders the caudoventral edge of the prefrontal and inserts into a deep cleft in the posterior side of the element. This process of the lacrimal arches dorsomedially, being convex laterally. In *P. blackfeetensis* (Horner, 1992) that process does not arch, but projects straight dorsally. Its caudal side is flat and forms the lateral wall of the lacrimal formen. Forming the medial wall of the lacrimal foramen is a dorsally-projecting, shorter posteromedial process. The dorsal surface of this process is very rugose and receives a ventrocaudal process of the prefrontal. The medial face of the caudomedial process of the lacrimal is concave.

The ventral border of the lacrimal is joins the dorsal border of the anterior process of the jugal. At the posterior end of that border, the lacrimal is mediolaterally wider. Ventrally, there is a distinctive circular and deep excavation. This is followed anteriorly by a semicircular indentation, deep into the lateral side, at the ventral and posterior corner of the lacrimal. While most of the ventral border of the lacrimal abuts the dorsal border anterior end of the jugal, the posterior lateral indentation and the excavation are penetrated by two corresponding short processes of the posterodorsal corner of the anterior process of the jugal.

The concave medial side of the element contains the lacrimal foramen or canal. This foramen begins anteriorly as a wide depression. Gradually, this depression deepens caudodorsally, until penetrating the bone to exit through the dorsal third of the caudal border of the bone. Besides containing the lacrimal foramen, the medial side of the element articulates with the lacrimal flange of the maxilla and receives a portion of the ventral region of the nasal. In the maxillary articulation, there is a space between the medial side of the lacrimal and maxillary flange, which is aligned with the long axis of the lacrimal formen (or canal). Probably, the lacrimal canal would continue anteriorly along the space between the lacrimal-maxilla joint. On the medial side of the lacrimal, there are striations along the dorsal border, as well as throughout the anteriorly pointed, elongated segment. Anteroventrally adjacent to the dorsal crescentic groove there is a shallower concavity that might hold a ventral extension of the nasal, since it is located where the nasal would reach the medial side of the lacrimal.

Prefrontal

The prefrontal (Fig. 7) is an arched bone that forms the anterodorsal rim of the orbit. It articulates with the lacrimal ventrally and the nasal mediodorsally. The prefrontal contacts the premaxilla anteroventrally and the frontal medially and posteriorly. Anteroventrally, the prefrontal faces laterally, being anterocaudally expanded and mediolaterally compressed. Posterodorsally the bone gradually twists to face dorsally, so that its lateral edge forms the anterodorsal corner of the orbit. In *B. canadensis* the prefrontal is especially developed, as it extends caudomedially to underlie the nasal crest (Fig 8).

The anteroventral region of the prefrontal is a thin lamina with a concave medial surface and a convex lateral side. The medial side is separated from the ventral surface (the anterodorsal roof of the orbit) by a large and sharp ridge. The articulation with the lacrimal is complex. The medial surface of the prefrontal rests on the dorsal, lateral side of the lacrimal. The medial side of the prefrontal shows a triangular groove that receives the posterodorsal process of the lacrimal. Ventrally, on the caudal border of the prefrontal, there is a narrow and long, blade-like indentation that receives the caudodorsal, lateral process of the lacrimal. The caudomedial border of the prefrontal projects ventrally to contact a short, dorsally directed process on the posteromedial edge of the lacrimal. The anterior edge of the prefrontal overlaps a small portion of the caudodorsal end of the ventrocaudal process of the premaxilla. The medial surface of that border of the prefrontal shows striations heading anteroventrally, indicating where the premaxilla is contacted.

The lateral edge of the dorsal region of the prefrontal, the anterodorsal rim of the orbit, is dorsally deflected. It lies dorsally higher than the dorsal surface of the skull, with the exception of the parasagittal plane of the nasal crest. That border contains small indentations and bumps that form a crenulated profile, as in the postorbital. Medially the anteroventral concave side of the prefrontal wedges posterodorsally, due the posterodorsal convergence of the medial border of the anterodorsal region and the posteromedial edge.

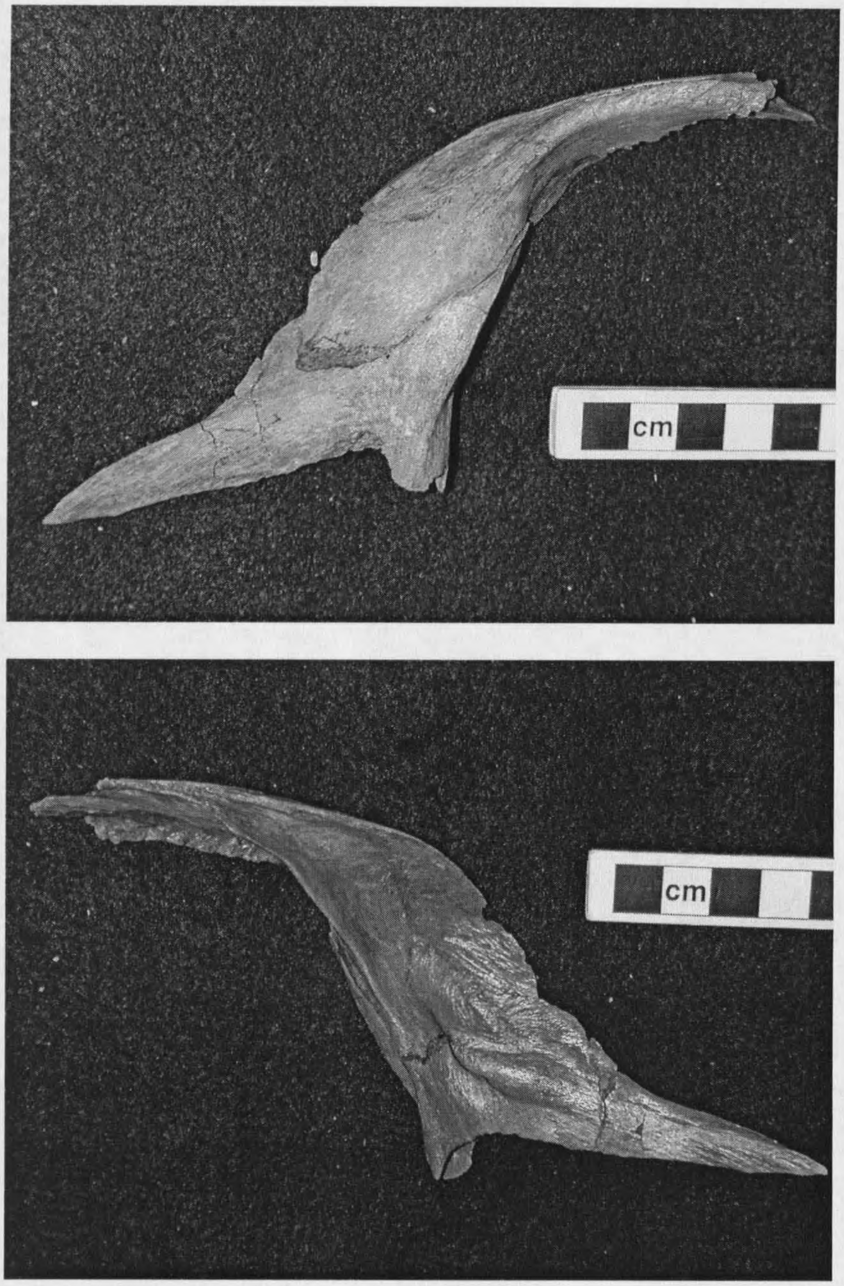

Figure 7. Left prefrontal articulated to lacrimal, in lateral (top) and medial (bottom) views. Subadult specimen MOR1071-8-5-99-447G.

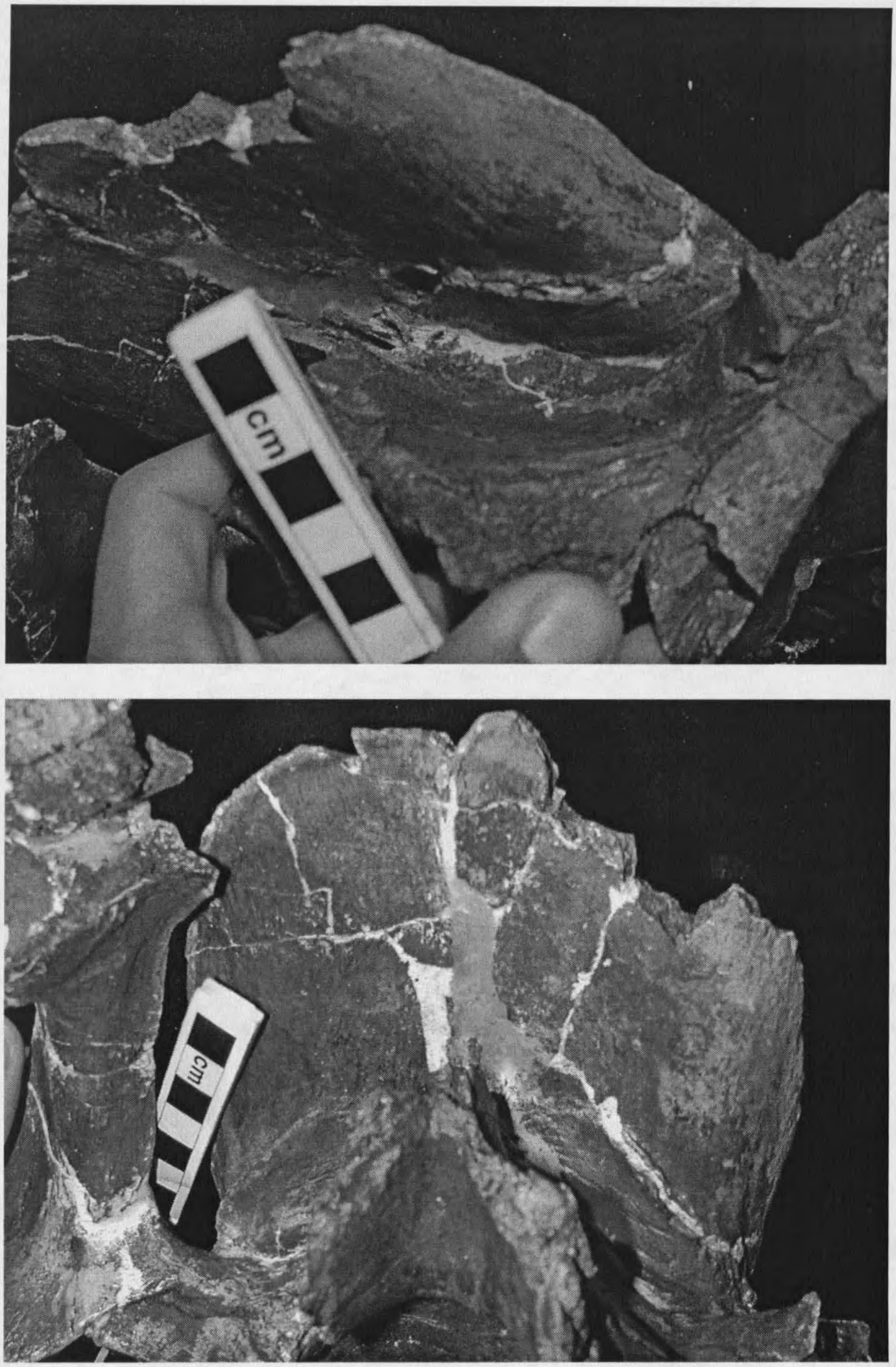

Figure 8. Adult frontals underlying (arrow) the nasal crest in PR 862. Ventrolaterocaudal view (top); ventral view (bottom).

The medial and caudal borders of the caudodorsal region of the prefrontal are devoted to the articulations with the nasal and, mainly, the frontal. A distinctive triangular process projects caudomedially from the posteromedial edge of the prefrontal. This process is dosoventrally compressed and its ventral and dorsal surfaces show deep grooves and ridges longitudinally arranged. This process fits into a narrow cavity within the anterolateral border of the frontal. Anterodorsal to the frontal articulation, the mediodorsal border of the prefrontal is medioventrally tilted, showing a smooth and narrow surface for the lateral border of the nasal. The lateral edge of the prefrontal extends further posteriorly over the orbit and overlying the frontal, running parallel to the nasals. Along that posterior segment the prefrontal wedges as seen in dorsal view, tapering posteriorly and then deepening medioventrally to fit underneath the nasal. There the prefrontal forms a sheet that closely applies to the ventral surface of the nasal crest.

The dorsal side of the prefrontal contains a longitudinal groove that shallows disappearing posteriorly after comprising most of the anteroposterior length of the dorsal portion of the prefrontal. That groove, which runs parallel to the lateral border of the nasal, is deep and ends anteriorly into a relatively large foramen, caudal to the level of the supraorbital foramen. On the anterodorsal surface of the prefrontal, in front of the anterodorsal corner of the orbit, there is a deep foramen, the supraorbital foramen. In that area some specimens posses more than one foramen. MOR 1071-7-10-98-171 has three formaina arranged in a triangular distribution in the same area. More consistent in morphology and location is another foramen, found on the ventral side of the medial ridge of the prefrontal, perforating the anteroventral corner of the roof of the orbit. This foramen has the same shape and size than the supraorbital one, but is more medially displaced on the ventral side of the element.

Postorbital

The postorbital (Fog. 9) forms the posterodorsal border of the orbit. The element is composed of four processes that radiate from a common central body. Two of them form, respectively, the anterior and the posteromedial tip of an oblique border that articulates with the frontal medially and the parietal posteromedially through a crenulated suture. A long branch (squamosal process) projects posteriorly to articulate with the squamosal. A second ramus (jugalar process) arches and projects anteroventrally to meet the postorbital process of the jugal. Medially, and ventral to the oblique medial sutural edge, the central body of the postorbital articulates with the laterosphenoid by means of a possible synovial joint (Weishampel, 1984).

The anterior, triangular, anteriorly pointed process of the postorbital has a very rugose lateral border. This border shows a series of indentations and bumps, similar to those on the lateral border of the posterodorsal region of the prefrontal. Some of these indentations continue posteriorly over the dorsal border in the form of deep grooves. This anterior process of the postorbital is the prefrontal process of Horner (1992). But since in *B. canadensis* it meets the frontal, it is here simply called anterior process. The frontal is contacted anteriorly through a crenulated suture. Most of that anteromedial border is devoted to joining the frontal through a thick crenulated suture. Ventrally and caudally the laterosphenoid joint bounds the frontal suture. The parietal is contacted posteromedial to the frontal articulation. The same crenulated border that joins the frontal projects caudomedially, forming a process that meets the anterodorsal, lateral and crenulated

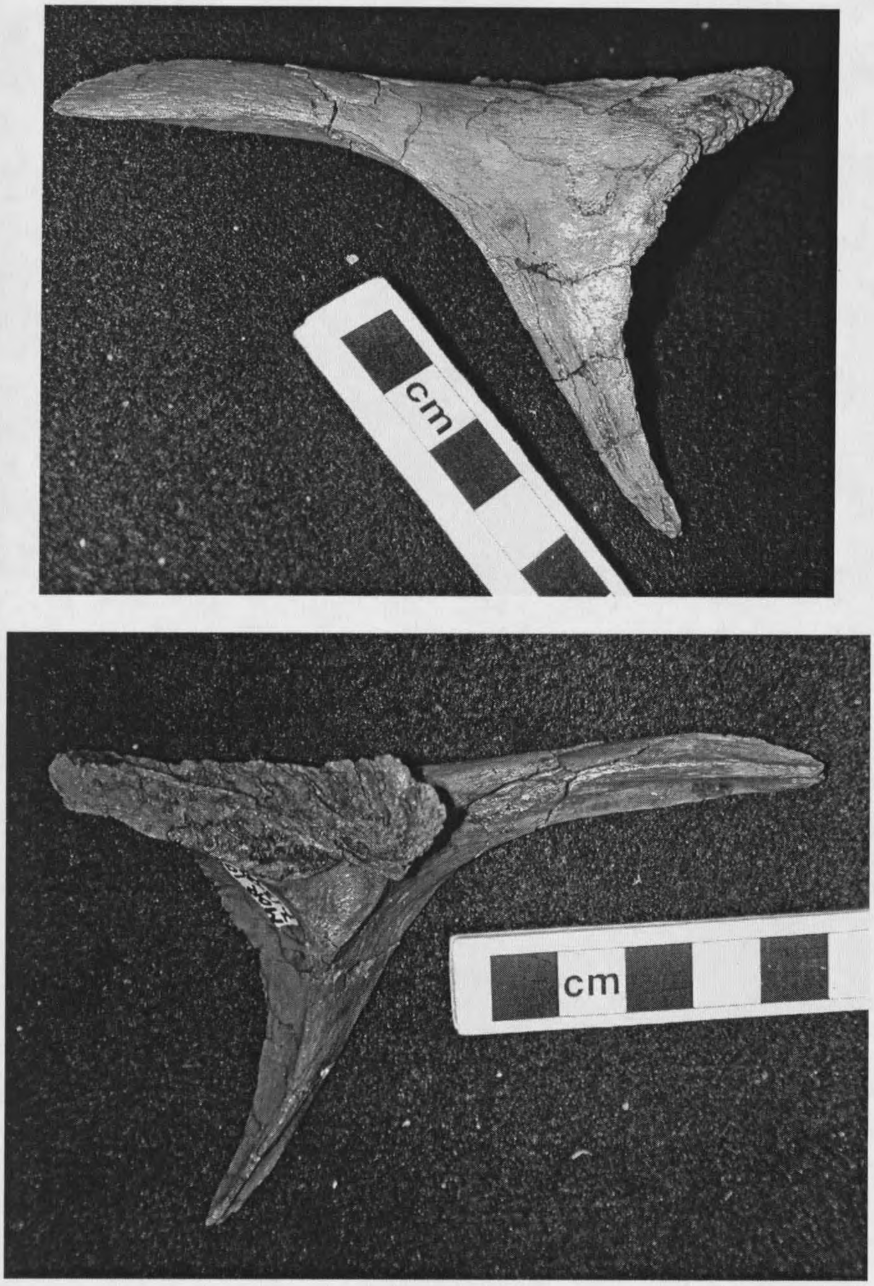

Figure 9. Right subadult postorbital MOR 1071-7-13-99-87-L in lateral (top) and medial (bottom) views.

border of the parietal, located dorsal and adjacent to the laterosphenoid. The postorbital-parietal suture contributes anteriorly to the cranial limit of the supratemporal fenestra.

The squamosal process is dorsoventrally compressed. It shows a laterodorsal convex surface and a concave medioventral side. The medioventral surface of the caudal process of the postorbital articulates with the squamosal, overlapping most of the length of the laterodorsal surface of its anterior process. The medioventral face of the squamosal process of the postorbital has a longitudinal triangular indentation, the apex of which points anteriorly. A longitudinal ridge bisects that indentation. The medial edge of the squamosal process of the postorbital forms the lateral boundary of the supratemporal fenestra

The ventral borders of the squamosal and anterior processes converge at the center of the element to form the jugal process. This process projects anteroventrally and shows a caudal convex and a concave anterior profiles. The process is slightly offset lateroventrally from the parasagittal plane. The anterior surface is strongly concave along its dorsal segment. That process meets the anterodorsal, concave surface of the dorsal part of the postorbital process of the jugal. Both processes form the posterior border of the orbit and the anterior rim of the infratemporal fenestra. Dorsally the jugal process is gradually expanded both mediolaterally and anterocaudally. Anteroventrally towards the jugal articulation the process becomes very thin. The medial edge of the jugal process is thin and sharp, while the lateral border is anterocaudally thicker and concave. Dorsally, the lateral border widens anterocaudally into the lateral side of the central body of the element, which is slightly concave.

On the medial side of the postorbital, at the convergence of the three processes described above, there is the articulation for the laterosphenoid. This is a triangular and smooth concavity that receives the laterodorsal process of the laterosphenoid.

Near the anterodorsal rim of the orbit, there is the supraorbital foramen (Horner, 1992), which penetrates the postorbital dorsoventrally. Additional foramina can be found near this foramen and is not uncommon to found them merging with the indentations that form the rugose rim of the orbit. Posteriorly, on the laterodoral surface of the central body of the postorbital, there is another foramen. There is a sharp, small promontory located on the dorsal surface of the posterior central region, where the squamosal process begins to extend posteriorly. In MOR 794 there is a ridge running dorsoventrally, surrounding the element anterior to the squamosal process and containing the promontory.

Quadrate

Forming the posterior border of the infraorbital fenestra, the quadrate (Fig. 10) is a dorsoventrally elongated element located at the posterior end of the lateral side of the skull. The quadrate articulates with the surangular ventrally, the articular ventromedially, the quadratojugal anterolaterally, the pterygoid anteromedially and the squamosal dorsally.

The quadrate is made of a dorsoventrally elongated shaft that gently curves longitudinally along its dorsal half, being slightly concave posteriorly as seen laterally. The quadrate is also slightly curved along the medial side, so that the lateral side is slightly convex while the medial side is concave in anterior and caudal views. The quadrate is expanded mediolaterally and, to a lesser extent, anteroposteriorly at its ventral end. In contrast, the element is mediolaterally thinner at its dorsal end. The quadrate presents a strongly concave anterior side formed by an anteromedial and a anterolateral sheet. The posterior border of the quadrate is a smooth ridge running along the dorsoventral length of the quadrate.

The ventral end of the quadrate is rounded and rests on a lateral depression of the posterior half of the surangular. Medially and dorsally displaced from the ventral end of the element there is a medial, short process. This process meets a small concavity on the anterior, dorsal border of the articular. In ventral view, the ventral border and the short medial process form a triangular cross section. At the ventral end, the laterocaudal side of the quadrate is slightly concave, while the anterior and mediocaudal sides are relatively more depressed. The anterior surface is mediolaterally concave, showing a few small foramina. Oblique striations are found more dorsally, at the anterolateral border, near of the quadratojugal articulation. The mediocaudal side of the ventral includes two deeper concavities separated by a thick ridge. A small concavity lies dorsal to the medial process. More caudally, a larger and oval concavity is found occupying the remaining surface of the mediocaudal side of the ventral end of the quadrate.

The central region of the quadrate is formed by the two anterolaterally and anteromedially projecting sheets. The anterolateral lamina is relatively short and contains a wide indentation, the quadratojugal notch, which receives the posteromedial border of the quadratojugal. The quadratojugal notch is medially recessed from the rest of the anterolateral edge of the anterolateral sheet. Dorsally the surface of the notch is rugose, concave and terminated in small indentations, while ventrally it becomes smoother and more convex. Ventral to the quadratojugal notch the anterolateral border of the quadrate shows short and oblique striations until the ventral end of the element.

Figure 10.Right quadrate MOR 1071-8-13-98-559D in lateral view.

The other anteromedial sheet of the quadrate is a very expanded wing of bone. This wing is pterygoid flange that contacts the element of the same name. The pterygoid flange is trapezoidal, and slightly curved medially. Its medial surface is strongly concave, where the posterodorsal and posteroventral wings of the pterygoid articulate. The caudodorsal tip of the posterodorsal wing of the pterygoid fits into an elongate groove on the medial side of the anteromedial flange, a few centimeters below the dorsal end of the quadrate. The groove can be followed running ventrally along the anteromedial quadrate flange. The caudoventral end of the posteroventral wing of the pterygoid joins a rugose, concave scar adjacent to the caudomedial border of the quadrate, at the level of the maximum projection of the flange. Anterior to the scar, the anteromedial surface of the flange is rugose and was extensively attached to the lateral surface of the posteroventral wing of the pterygoid. The medial and lateral surfaces of the pterygoid flange are full of radial striations anteromedially directed.

The dorsal end of the quadrate is mediolaterally compressed and ellipsoidal in dorsal view. The medial and lateral surfaces are densely striated. The dorsal border fits into the cotylus of the squamosal, between the anterior, prequadratic and the posterior, postquadratic processes of the squamosal. A small, buttress-like process hangs a short distance caudoventrally and laterally from the posterior border of the dorsal extreme of the quadrate. This process is mediolaterally compressed and meets a scar on the anterior side of the posteroventral process of the squamosal, as noted by Horner (1992) in *P. blackfeetensis*.

<u>Quadratojugal</u>

The quadratojugal (Fig. 11) is a rhomboidal, small blade of bone located posteriorly on the lateral side of the skull, between the jugal and the quadrate. The bone is dorsoventrally deeper posteriorly, near the caudal edge. The quadratojugal is mediolaterally thicker near the posterior edge. In lateral view the element shows sharp and pointed dorsal, ventral and anterior corners. The posterior edge of the quadratojugal is convex and arched in lateral outline. Posteriorly the medial side overlaps a narrow and dorsoventrally wide notch on the lateral side of the quadrate. On the medial side of the element and attached to the porterior edge there are two depressions. One is located posterodorsally and is relatively narrow. The other depression is deeper and located posteroventrally. The quadratojugal is anteriorly projected into a triangular edge that is overlapped by the concave medial surface of the quadratojugal process of the jugal. The anteroventral edge of the quadratojugal is probably longer. The lateral, convex surface of the quadratojugal contains fine sets of striations radiating towards the edges of the bone. Radial striations like these are also present on the medial surface of the element and on the quadrate articulation.

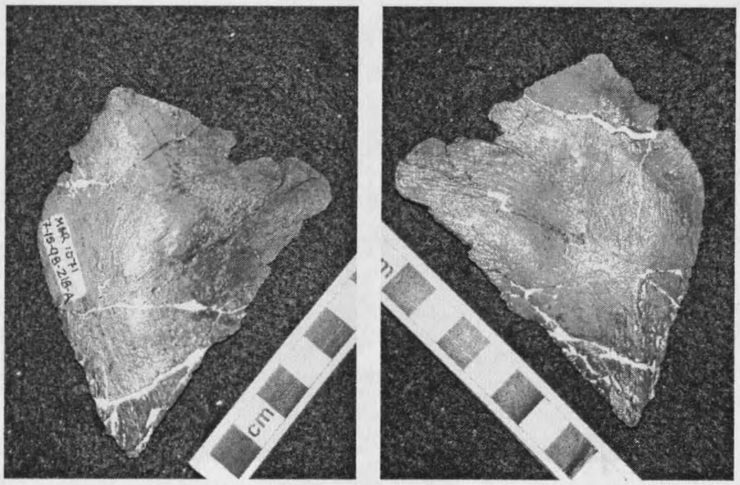

Figure 11. Right quadratojugal MOR 1071-7-15-98-28A in lateral (left) and medial (right) views.

Squamosal

The squamosal (fig. 12 and 13) forms the dorsal, posterolateral corner of the skull. The bone articulates with the postorbital anteroventrally and medially, with the quadrate ventrally and laterally, the parietal medially, the supraoccipital caudomedially, and the exoccipital caudally to form the paroccipital process. The squamosal is excluded from contacting its counterpart by the parasagittal crest of the parietal. The anterior border of the parietal process and the medial edge of the postorbital process form the posterolateral rim of the supratemporal fenestra.

A central body from which four processes radiate composes the squamosal. Two of them are long and pointed, the postorbital process that is anteriorly projected and the postquadratic process that projects lateroventrally. A short prequadratic process is located about midway between the postquadratic and the anterior tip of the postorbital process. The parietal process projects medially from the posterior corner of the element.

The postorbital process is dorsoventrally compressed and thins mediolaterally while extending anteriorly. Its anterior-most segment tilts ventrally. The dorsal surface contains a deep groove that deepens laterally and receives the squamosal process of the postorbital. The postorbital process of the squamosal underlies a triangular excavation on the ventral side of the squamosal process of the postorbital.

The prequadratic process is a salient spike-like feature. It is lateroventrally-directed and slightly anteriorly oriented. The prequadratic process is anteroposteriorly compressed and triangular as seen anteriorly and posteriorly. A thin ridge bisects its laterodorsal border. The anterior side of this process forms the caudodorsal corner of the infratemporal fenestra. Its posterior surface contacts the anterior side of the dorsal head of the quadrate. Both the anterior and caudal faces of the process are striated. The prequadratic process is relatively short in *B. canadensis*. The process is the longer and more robust in *P. blackfeetensis*, *Gryposaurus*, *Edmontosaurus*, and *H. stebingeri*.

Posterior and adjacent to the prequadratic process there is a hemispheric concavity, the quadrate cotylus. This cotylus receives the quadrate head. Is this a not very tight joint, as the dorsal head of quadrate would have some degree of movement, although limited by the prequadrate process in opinion of Horner (1992) and Weishampel (1984). The cotylus faces lateroveñrtally. The anterodorsal side of the postquadratic process forms the posterior surface of the quadrate cotylus.

The postquadratic process projects lateroventrally and posteriorly from the laterocaudal corner of the squamosal. Distally the process is anteriorly curved forming a pointed tip and acquires a crescentic morphology that follows the curvature of the paroccipital process of the exoccipital. The process is anteroposteriorly compressed and faces anterodorsally. The anteroposterior compression increases gradually towards its distal end. The postquadratic process is dorsoventrally deeper than the postorbital process is mediolaterally wide. The posterior surface of the postquadratic process is attached to the anterior side of the paroccipital process of then exoccipital. However, the postquadratic process is not closely attached along the whole extent of the exoccipital. Proximally both elements are separated by a triangular space. The lateroventral half of the postquadratic process shows oblique striations.

Medial to the postquadratic process there is the main body of the squamosal. Medially and adjacent to the caudal concavity on the postquadratic process for the exoccipital there is a shallow and smooth depression. That depression faces caudodorsally and contains unevenly distributed small foramina. Its surface is fairly smooth. Medial to this depression, the main body of the squamosal is mediodorsally expanded into the parietal process. This process is relatively short mediolaterally and wide anterocaudally. The process curves caudally and then anteriorly, producing a crescentic surface for articulating the parietal dorsally and the supraoccipital ventrally. That joint surface is very rugose and forms a tight union with the supraoccipital. Due to that curvature, a pocket-like concavity is formed interiorly, on the cranial side of the main body of the squamosal. The caudolateral corner of the squamosal shows a series of ridges that contain a few small bumpy excrescences each. The postquadratic process shows oblique striations on the exposed lateral side along the crescentic distal tip.

Figure 12. Subadult right squamosal MOR 1071-7-13-99-87-H in lateral view.

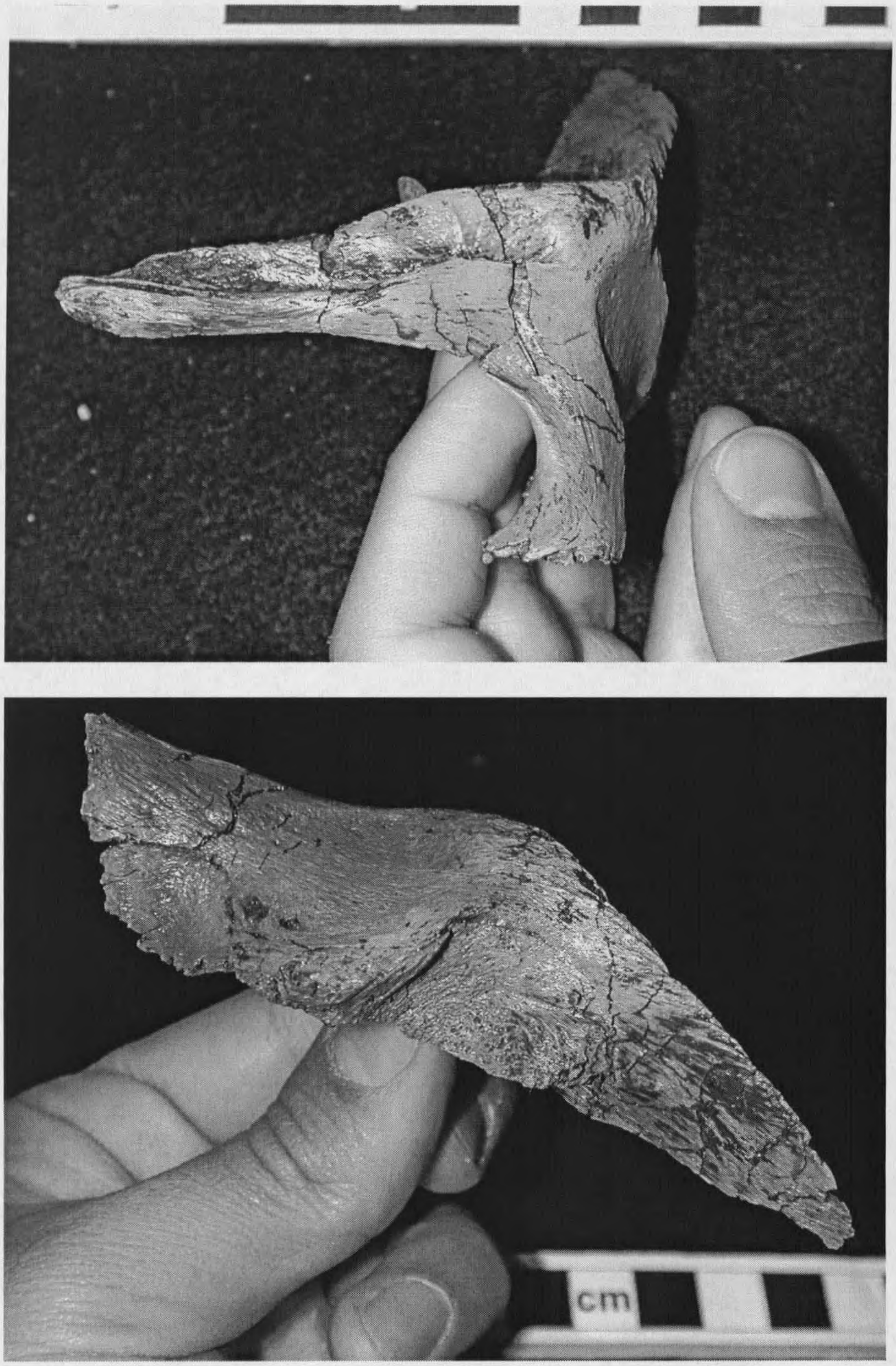

Figure 13. Subadult right squamosal MOR 1071-7-13-99-87-H in dorsal (top) and caudal (bottom) views.

Neurocranial Complex

Frontal

The frontals (Fig. 14) contribute to form the roof of the posterior half of the skull, including the medial, internal side of the orbital cavity, and the olfactory and cerebral cavities. The frontal articulates tightly by means of crenulated joints with the prefrontal anteriorly, anterolaterally, and posteriorly, the postorbital posterolaterally, the parietal posteriorly, the orbitosphenoid and laterosphenoid ventrocaudomedially, and the presphenoid anteromedioventrally. The nasal is contacted dorsally and is the only joint of the frontal that is not crenulated. The frontal meets its counterpart along its anteroposteriorly straight medial border, containing the parasagittal plane. On the ventral side, the posterior third of the interfrontal suture is posterolaterally directed, so that both frontals provide room for the insertion of the triangular anterior extreme of the parietal. The interfrontal articulation is dorsocaudally elevated at the parietal contact. Dorsally, the posterior and lateral edges of the frontals form a semicircular posterolateral border. After meeting the parietals caudally, this posterolateral border articulates with the anteromedially-facing border of the postorbital. Anteriorly the frontal is dorsoventrally thinner. As in *M. peeblesorum*, but unlike *P. blackfeetensis* and other more derived hadrosaurs, the frontal sends a lateral, small tongue that forms a small portion of the dorsal rim of the orbit, between the prefrontal and the postorbital. This condition was already noted by Sternberg (1953). In *P. blackfeetensis* and *H. stebingeri* the prefrontal meets the postorbital excluding the frontal from the orbital rim.

Anterior to the frontal contribution to the orbital rim there is the articulation for the prefrontal. There the dorsal surface of the frontal is ventrally recessed and slightly curved ventrally. The ventral recession deepens caudally within the body of the frontal, forming a deep cavity for the reception of the posteromedial triangular process of the prefrontal. Ventrally there is a notch bounded by the anterolateral hook-like projection of the frontal, which receives the caudomedial extreme of the posteromedial ridge of the prefrontal.

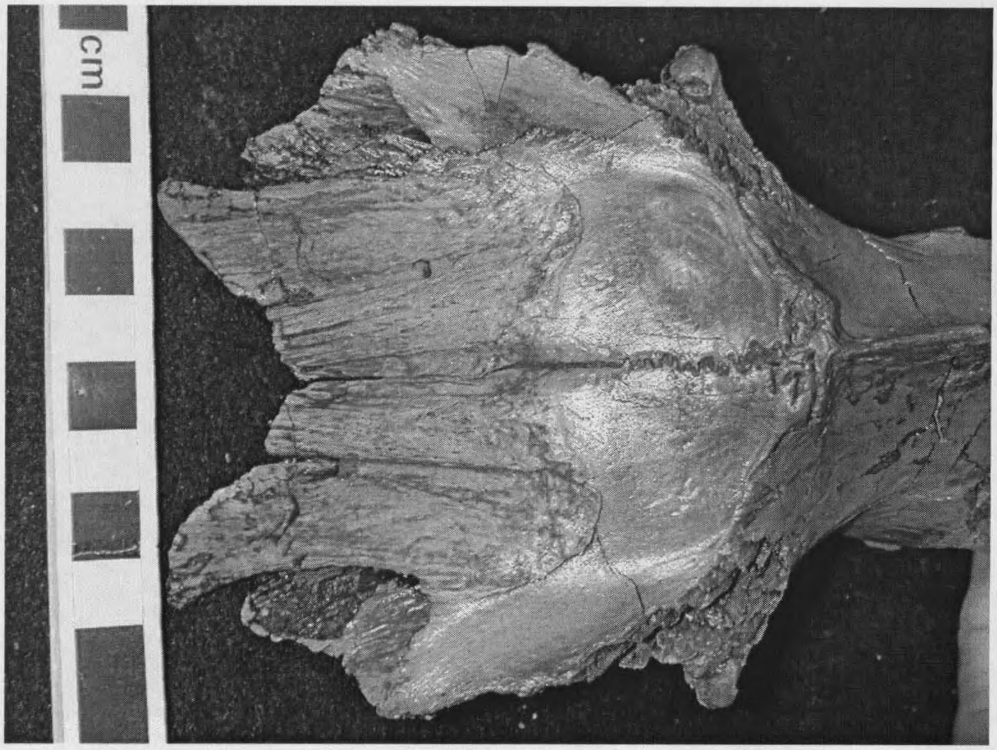

Figure 14. Subadult prefrontals in dorsal view, MOR 1071-7-13-99-87I.

The area of the nasal articulation extends over the dorsal surface of the frontal. This joint forms an M-shaped dorsal outline between both frontals. The anterior end of the nasal joint is also the anterior end of the dorsal surface frontal, where it projects anterolaterally into a triangular, hook-like process. Anteroposteriorly the nasal joint extends at least along the two thirds of the frontal dorsal surface. The adult specimens are articulated and concealed by the nasal crest and the described features of the nasofrontal joint were observed on subadult disarticulated specimens. The surface of the nasofrontal joint is very distinctive, containing anterocaudally-directed long and coarse striations. In each frontal these striations are found in two longitudinal zones separated by a deep and narrow groove. The M-shaped posterior edge of the nasofrontal articulation is sharp and elevated a few millimeters from the dorsal surface of the frontal. Adjacent and posterior to the nasal articulation, forming the dorsal surface of the cerebral cavity, the dorsal surface of the frontals is slightly convex. There is a depressed and smooth area posterolateral to the nasofrontal joint and medial to the postorbital articulation. This depression was described by Horner (1988) in erecting *B. goodwini,* and is not present in other hadrosaurs.

The ventral side of the frontal is composed of three areas, the cerebral cavity, and the olfactory and orbital depressions, as already pointed out by Horner (1992) when describing the frontals of *P. blackfeetensis*. The orbital depression faces lateroventrally, while the olfactory cavity faces anteromedially. The cerebral cavity is subspheric and its (ventral) surface is fairly smooth. It is located along the posterior portion of the frontal. The roof of that cavity is formed by the ventral posteromedial surface of the frontals. Posteriorly the wedge-like triangular anterior end of the parietal fits between both frontals. The medial, anterior half of the cavity in each frontal is bounded by the interfrontal articulation, whereas its posterior, caudomedially-facing half is limited by the parietal joint. Anteriorly, the cavity is limited by the narrow presphenoid contact, anterolaterally and adjacent to this by the extensive orbitosphenoid joint, and laterocaudally by the laterosphenoid contact. A short ridge separates the presphenoid from the orbitosphenoid articulation. That ridge continues anteriorly to separate the olfactory from the orbital depressions. The cerebral cavity exits anteriorly and medially around the zone of the interfrontal joint into the olfactory depression, through the space enclosed by the paired presphenoids. The orbital depression faces lateroventrally and is only slightly concave. The depression is bordered posteromedially by the presphenoid, orbitosphenoid and laterosphenoid joints in this order, the postorbital contact laterally and the prefrontal joint anterolaterally. The low ridge before described separates the orbital from the olfactory depression. A few small and unevenly distributed foramina can be observed on the ventral surface of the orbital depression. The olfactory depression occupies the anterior and medial, relatively smaller area of the ventral side of the frontal, anterior to the cerebral cavity. Its surface is more rugose than the rather smooth orbital depression. The olfactory depression is laterally bounded by the low ridge, posteriorly and laterally by the presphenoid joint, posteriorly and medially by a smooth convexity at the anterior end of the cerebral cavity, medially by the interfrontal joint and anteriorly by the anterior, medial edge of the frontal.

Parietal

Since all the available parietals (Fig. 15) are articulated and the nasal crest and other elements in the skull conceal the adult specimens, most of this description comes