



Osteology and variation of *Brachylophosaurus canadensis* (Dinosauria, 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
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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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by

Albert Prieto-Márquez

A thesis submitted in partial fulfillment
of the requirements for the degree

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in

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MONTANA STATE UNIVERSITY
Bozeman, Montana

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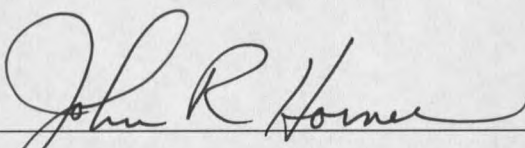
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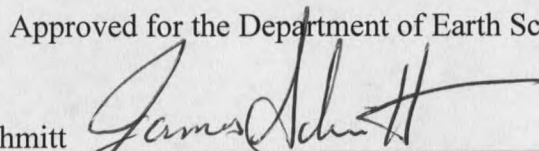
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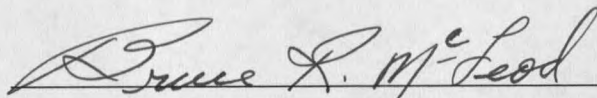
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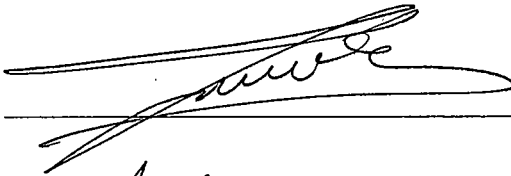

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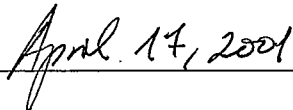
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ABSTRACT

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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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; Maryańska and Osmolska, 1983; Maryańska 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; Maryańska 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 (Maryańska 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, multiindividual 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 understanding 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 interfingering 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 paleoenvironments – 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 unstream 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, prementary, 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 during 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 neurocranial 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 *Maiaasaura*, 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 paucispecific 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 prementary, splenials, surangular, angulars, articulars, pterygoids, ectopterygoids, 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,

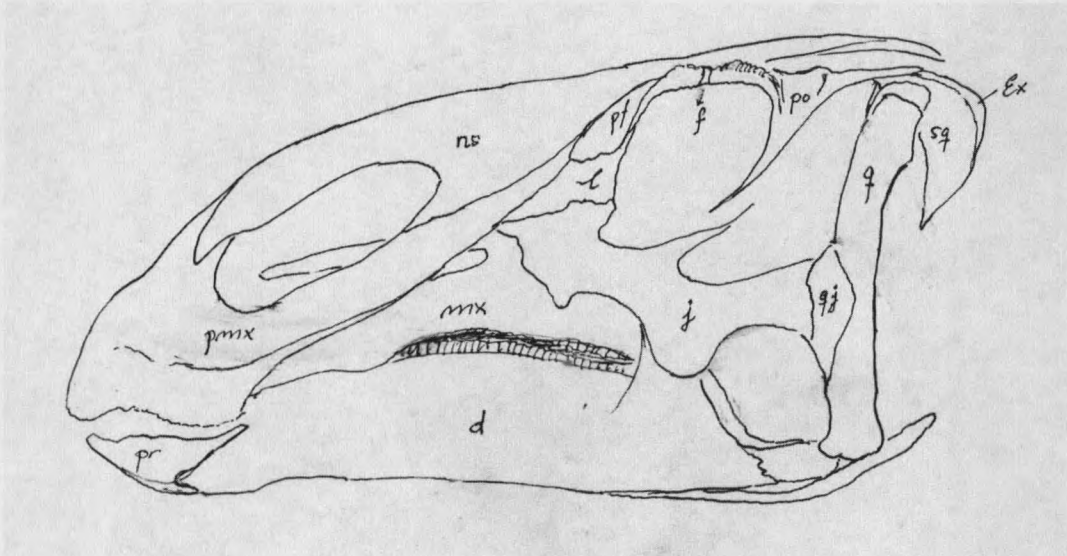


Figure 1. Skull MOR 794 in left lateral view. Pmx: premaxilla, pr: premaxilla, ns: nasal, d: dentary, mx: maxilla, l: lacrimal, j: jugal, pf: prefrontal, f: frontal, po: postorbital, qj: quadratojugal, q: quadrate, sq: squamosal, ex: exoccipital, sa: surangular, h: hyoid.

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 supratemporal 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 prementary. The greatest prementary width is reached at the ventrally deflected corners of the element. Posterior to the prementary, the dentaries draw an anteroposteriorly 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 prementary. 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 antero-caudally. Dorsomedial from this, there is the other foramen, which is located near 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 antero-caudal 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.

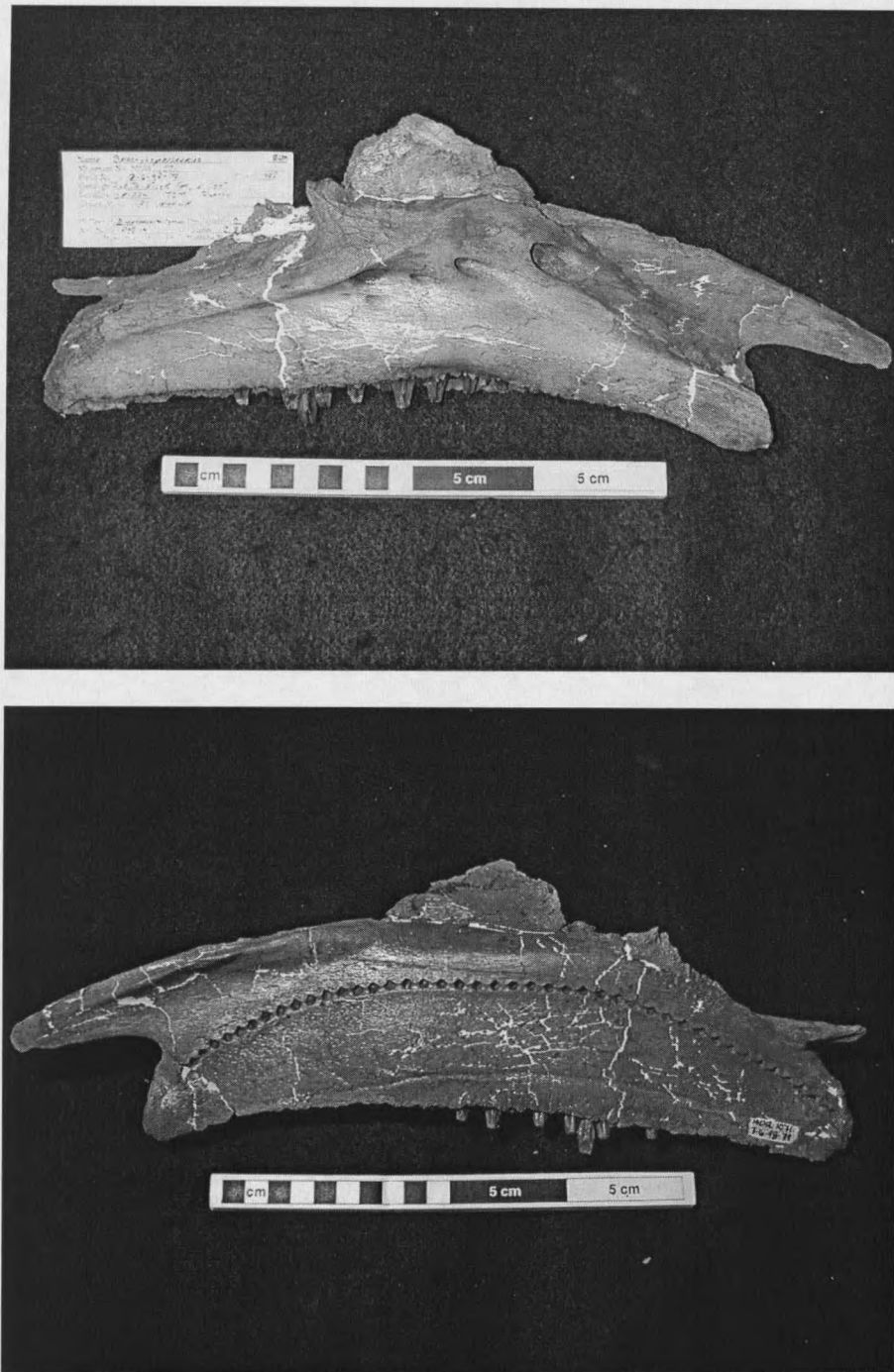


Figure 3. Left maxilla MOR 1071-7-6-98-79 in lateral (top) and medial (bottom) views.

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 antero-caudal length of the maxillary cavity. The anterodorsal process of the maxilla mediolaterally compressed, rod-like, and 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 jugular 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 jugular 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 jugular 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 is located on under of the jugular 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 occlusal 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-like 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 joining 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.

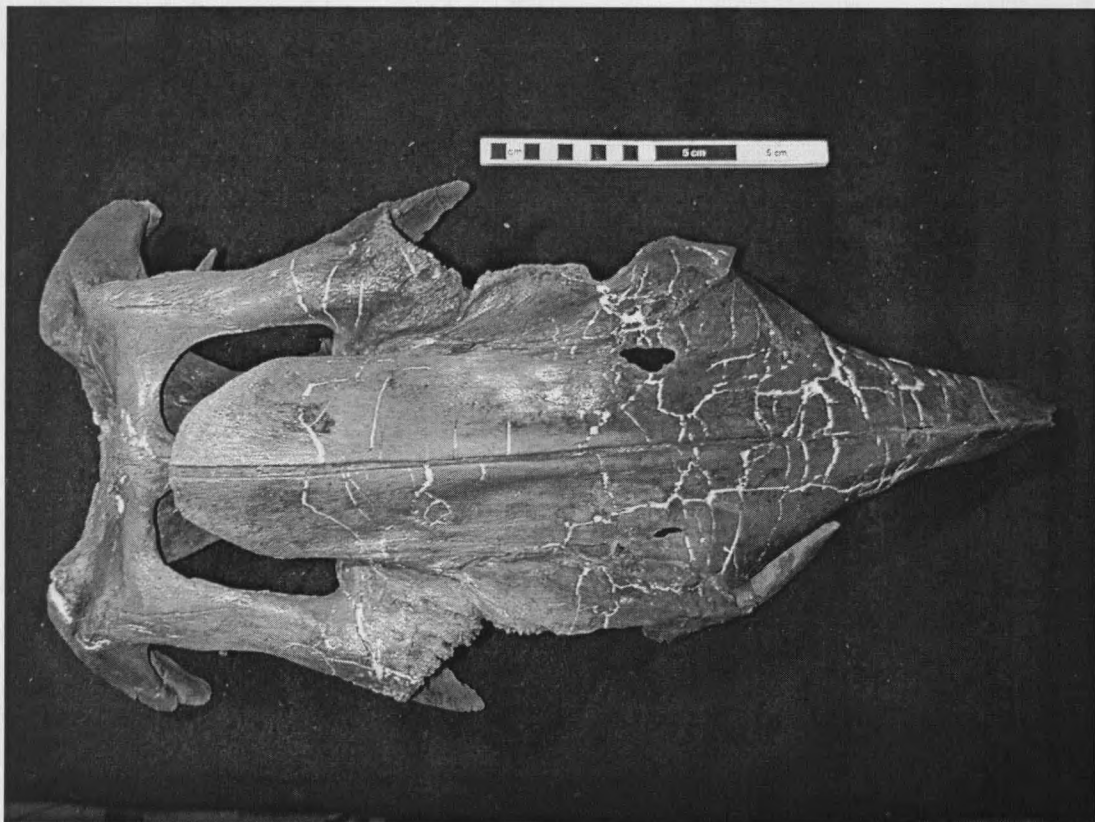
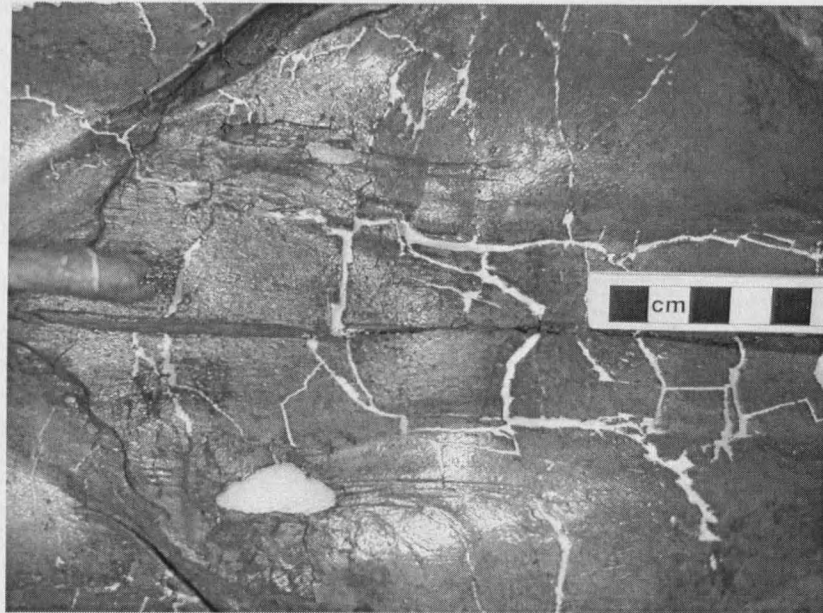


Figure 4. Articulated nasals MOR 1071-7-7-86-98. Ventral detail showing foramina and grooves (top). Dorsal view showing solid crest projecting caudodorsally (bottom).

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 prefrontals. 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 jugular 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

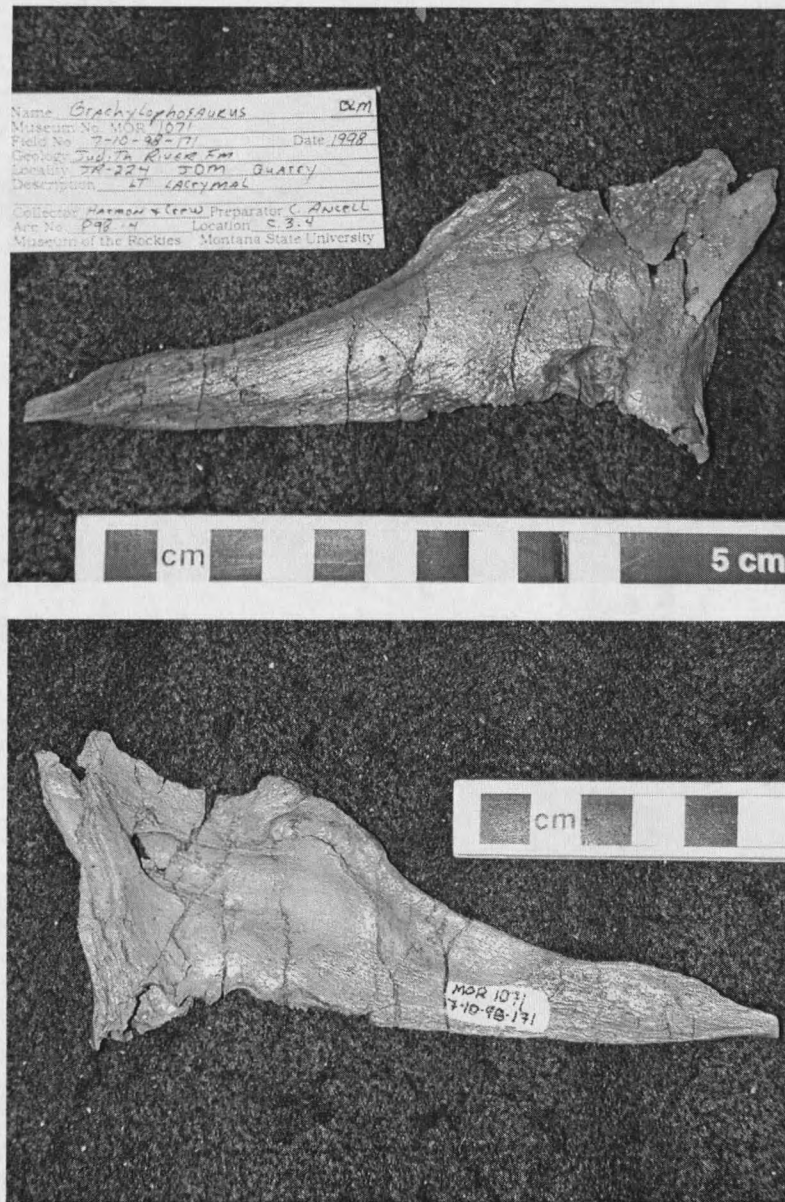


Figure 6. Right lacrimal MOR 1071-7-10-98-171 in lateral (top) and medial (bottom) views.

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 foramen. 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 foramen (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 antero-caudally 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.

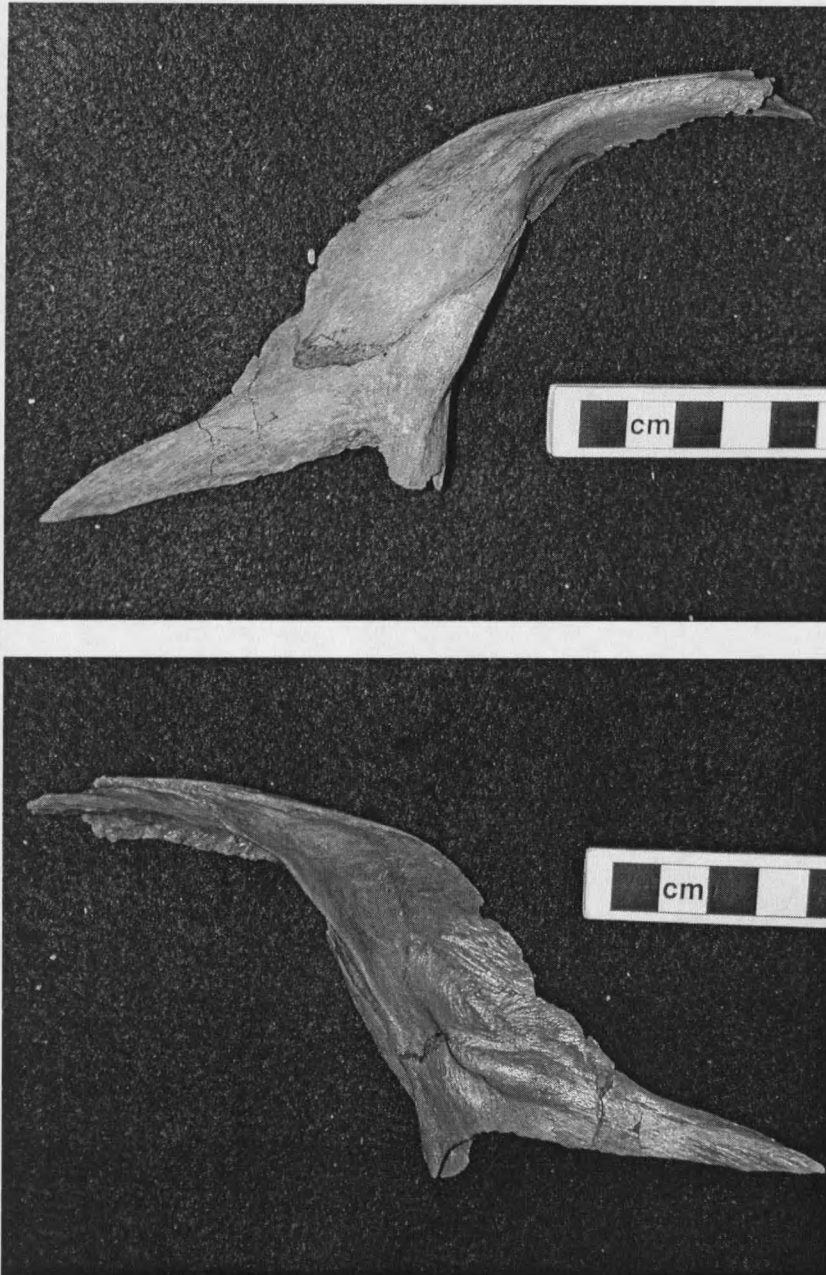


Figure 7. Left prefrontal articulated to lacrimal, in lateral (top) and medial (bottom) views. Subadult specimen MOR1071-8-5-99-447G.

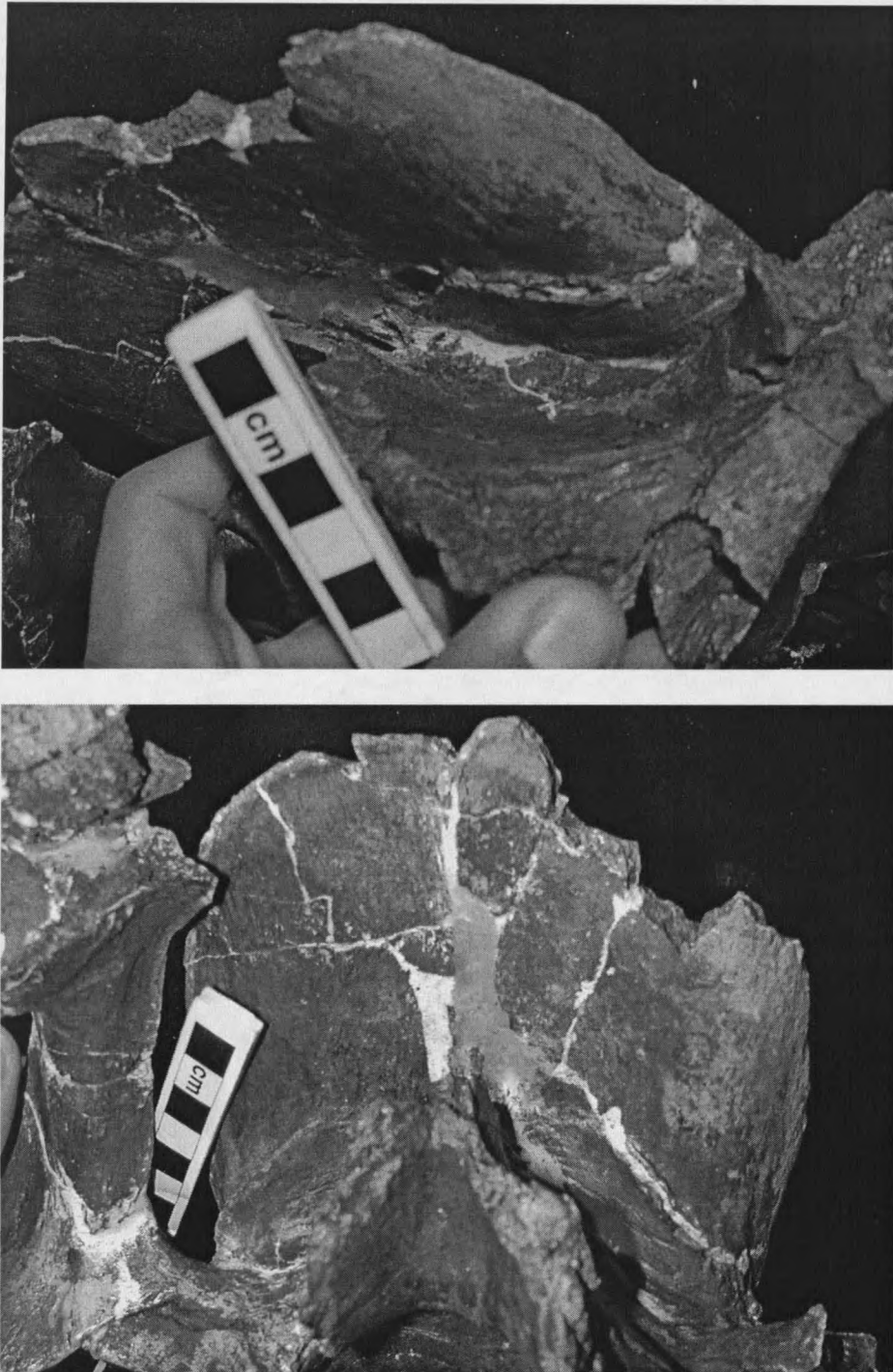


Figure 8. Adult frontals underlying (arrow) the nasal crest in PR 862. Ventrolaterocaudal view (top); ventral view (bottom).

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 dorsoventrally 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 possess more than one foramen. MOR 1071-7-10-98-171 has three foramina 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 (jugular 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

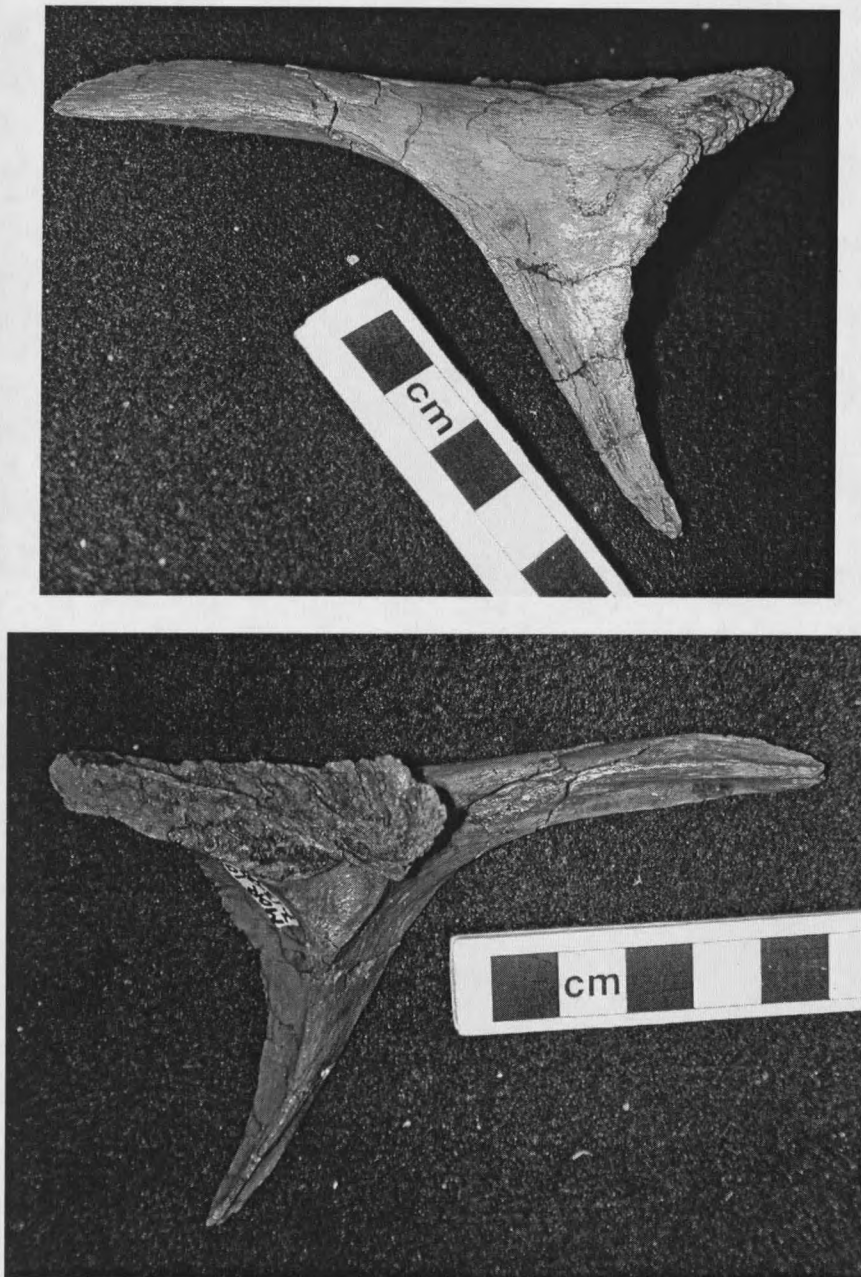


Figure 9. Right subadult postorbital MOR 1071-7-13-99-87-L in lateral (top) and medial (bottom) views.

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 antero-caudally. 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 antero-caudally thicker and concave. Dorsally, the lateral border widens antero-caudally 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 find them merging with the indentations that form the rugose rim of the orbit. Posteriorly, on the laterodorsal 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*.

Quadratojugal

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 posterior 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.

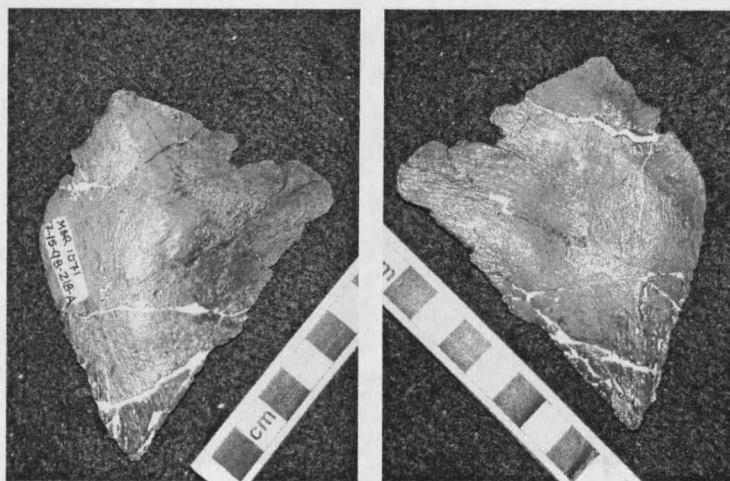


Figure 11. Right quadratojugal MOR 1071-7-15-98-28A in lateral (left) and medial (right) views.

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 lateroventrally. 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 antero-caudally. 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.

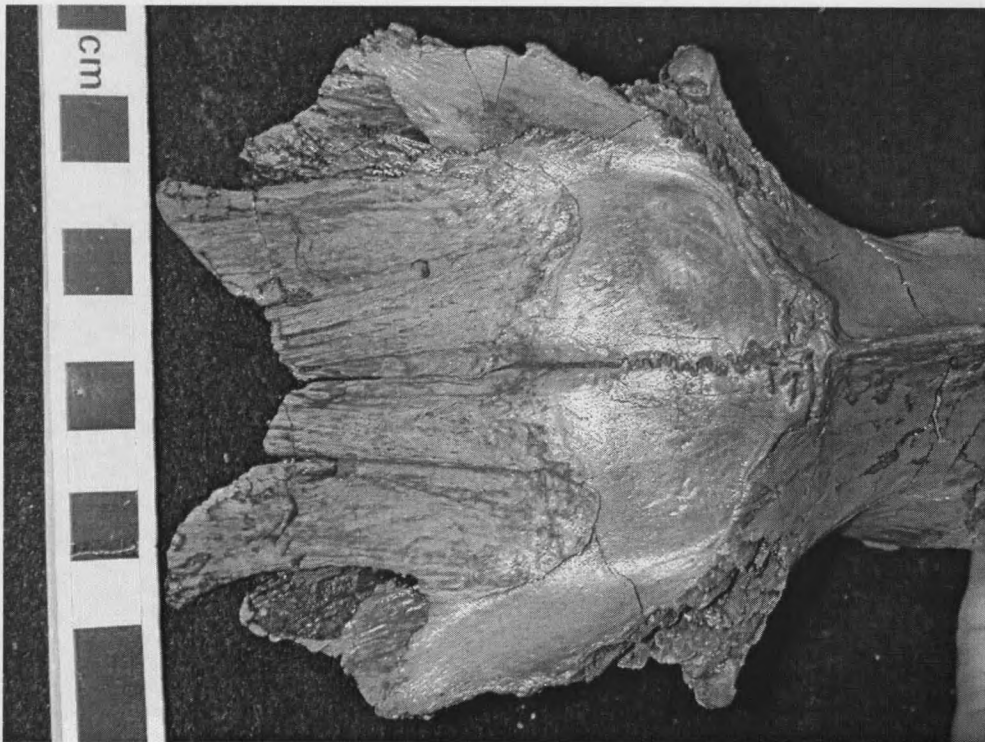


Figure 14. Subadult prefrontals in dorsal view, MOR 1071-7-13-99-87I.

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 antero-caudally-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

from the observation of disarticulated subadults. Both parietals are already fused in juveniles, as already noted elsewhere (Horner, 1992). The parietal articulates with the frontals anteriorly, the postorbitals anterolaterally, the laterosphenoids lateroventrally and anteriorly, the supraoccipital posteroventrally, and the squamosals caudolaterally. As suggested by Horner (1992), the parietal is excluded from contacting the prootic lateroventrally due to an anteriorly directed, wedge-like intervening portion of the supraoccipital towards the dorsolateral border of the laterosphenoid.



Figure 15. Subadult parietal MOR 1071-7-13-99-87I in dorsal view.

The parietal is mediolaterally expanded anteriorly, where it sends two anterolateral processes at each side. The bone becomes progressively narrower caudally. The ventral side of the parietal is extremely concave, since the bone encloses the caudal exit of the cerebral cavity posterior and adjacent to the frontals, a large canal that connects with the foramen magnum. Perhaps the most distinctive feature of the parietal is the possession of a high parasagittal crest that runs throughout all the anteroposterior length of the element. The crest is taller and mediolaterally thicker posteriorly, at the squamosal articulation. From the sharp edge of the parasagittal crest the parietal slopes ventrolaterally, forming a dorsolaterally facing side. The ventrolateral surfaces of the parietal are convex at the middle, while being slightly concave anteriorly and posteriorly.

The parietal sends three processes anteriorly, two anterolaterally and one at the center, and two caudolaterally. The two anterolateral processes are curved in that direction and meet the postorbital. The joint for the postorbital is crenulated. The anterolateral processes of the parietal meet the caudomedially-projecting process of the postorbital. The central, anterior process is located medial to the anterolateral processes and is triangular in ventral view. Its anterior border is crenulated and forms a triangular wedge that fits between the mediocaudal corners of the frontals, separating the interfrontal suture. The ventral surface of the anterior, central process of the parietal is concave and ascends anterodorsally towards the cerebral cavity enclosed by the frontals. In ventral view there is smooth, convexity between the cerebral cavity and the canal enclosed by the ventral surface of the parietal. At the level of that convexity the concave ventral side of the parietal reaches its maximum mediolateral width. Caudal to the

convexity there is a longitudinal channel-like concavity of the ventral side of the parietal. Its width decreases gradually until disappearing in front of the ventral joint for the supraoccipitals. That canal is bordered by the mediolaterally thick ventral, lateral articulation for the laterosphenoids and the supraoccipital. The attachment surface for the laterosphenoid and part of the supraoccipital is very rugose. Even in adults it is possible to see the suture between these elements. In lateral view, the contact between these elements draws a line that ascends caudodorsally towards the occipital region of the skull. The laterosphenoids are contacted along little more than the anterior longitudinal half of the parietal. Adjacent and caudal to that articulation, the parietal lateral, ventral border articulates with a wedge-shaped portion of the supraoccipital, which thickens posteriorly. The prootic contacts the ventral, lateral border of the supraoccipital, posterior to the laterosphenoid, but not contacting the parietal. The parietal-supraoccipital articulation extends medially from the lateral, ventral border of the parietal, so that more than the caudal third of the ventral side of the element contacts the supraoccipital. In this union the ventral side of the parietal is deeply concave to receive the convex dorsal, grooved face of the supraoccipital. The two posterior processes of the parietal participate in the parietal-supraoccipital joint. These processes arch posterolaterally in a similar way than the anterolateral processes. However, the posterolateral processes are mediolaterally narrower than the anterolateral ones. While the ventral border of these processes sits on the laterodorsal sides of the supraoccipital, their caudolateral borders converge towards the center of the element to form the posterior edge of the parasagittal crest of the

parietal. The caudolateral border of the caudal processes show a crenulated texture for receiving the medial, parietal process of the squamosals.

Braincase. General Description and Neurovascular System

The braincase (Fig. 16 through 20) is a complex structure located caudally and ventromedially in the skull. The frontals and parietal contribute to encase dorsally the neurocranial cavity. The braincase is formed by fused elements that constitute a unit perforated by numerous foramina for blood vessels. Mediodorsally to the crista prootica, within the supratemporal fenestra, the braincase abuts dorsally against the parietal.

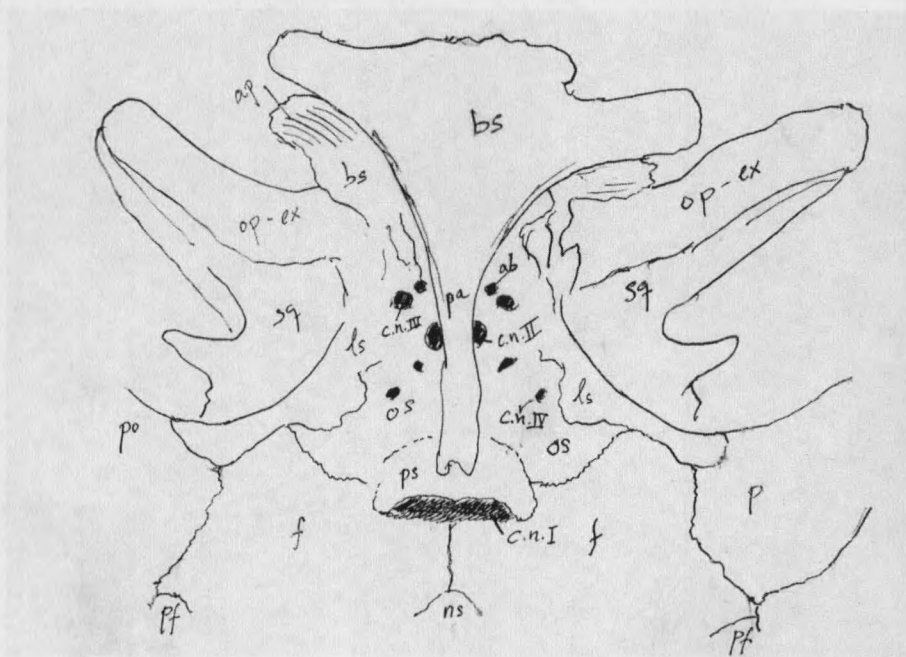


Figure 16. Braincase MOR 1071-7-7-98-86 in anterior view. Bs: basisphenoid, ap: alar process, op-ex: opisthotic-exoccipital, sq: squamosal, ls: laterosphenoid, po: postorbital, f: frontal, ns: nasal, pf: prefrontal, os: orbitosphenoid, ps: presphenoid, pa: parasphenoid, c.n.I: olfactory canal, c.n.II: optic foramen, c.n.III: oculomotor foramen, c.n.IV: trochlear foramina, ab: abducens foramen.

Anterocaudally and dorsally, the lateral view exposes the presphenoid, orbitosphenoid, laterosphenoid, prootic, opisthotic and exoccipital. Ventrally, the parasphenoid, basisphenoid, and basioccipital are also exposed. The ventral elements form a posterior rectangular region as seen ventrally and laterally, which ends anteriorly into the pair of laterally salient and expanded pterygoid processes and the cranially long cultriform process, which are part of the basisphenoid. The pterygoid processes and the cultriform process form a T-shaped structure as seen anteroventrally. The dorsal elements of the braincase that articulate with the frontals and the parietal form a subconical anterior portion that exits into the olfactory foramen, then expand mediolaterally to bound caudally the orbit at the level of the laterosphenoids, and curve to become concave laterally along the caudalmost region. This last curvature contains a ridge, the crista prootica, which links with the paroccipital process of the exoccipitals.

Most of the foramina for transmitting the cranial nerves are located on the dorsal and ventral elements of the braincase. The largest **olfactory** foramen (c.n. I) exits anterodorsally in front of the neurocranium, ventral to the frontals, and around the parasagittal plane of the skull. Posteroventrally from c.n. I there is a relatively large foramen for the **optic** nerves (c.n. II), limited by the orbitosphenoid (dorsally) and the basisphenoid (ventrally), and centered around the dorsoventral midline of the skull, as c.n. I. The optic foramen is mediolaterally elongated and dorsoventrally compressed. Laterodorsally from the optic foramen there are two small foramina on the anterolateral surface of the orbitosphenoid for the **trochlear** nerves (c.n. IV). Caudal and lateral, and slightly ventral to the optic foramen there is the **oculomotor** foramen (c.n. III), which

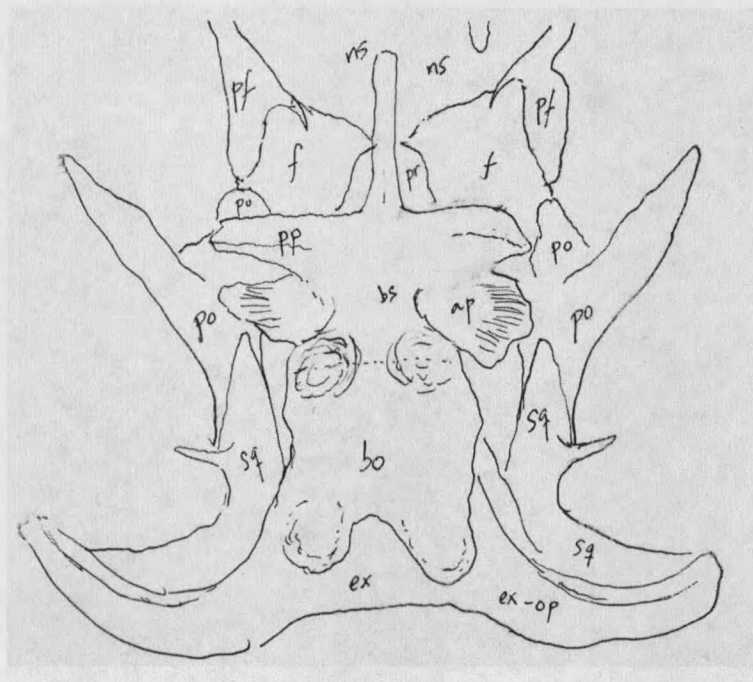


Figure 17. Braincase of MOR 1071-7-7-98-86 in ventral view. Pf: prefrontal, ns: nasal, f: frontal, po: postorbital., pp: pterygoid process, bs: basisphenoid, ap: alar process, bo: basioccipital, sq: squamosal, ex-op: exoccipital-opisthotic, pr: presphenoid.

following Ostrom (1961) would transmit also c.n. VI. The oculomotor foramen is circular and relatively large, although smaller than the optic foramen. The **abducens** foramen is seen ventral and adjacent to the oculomotor. Both foramina are separated by a thin strip of bone. All these foramina for the trochlear, oculomotor and abducens nerves are located on the anteriolaterally facing side of the dorsal half of the braincase, anterior to the caudal boundary of the orbital cavity marked by the laterosphenoid. The **pituitary fossa** is completely surrounded by bone in MOR 1071-7-7-98-86 and MOR 1071-7-16-98-248. The remaining exposed foramina are located caudal to the posterior boundary of the orbital cavity, as seen in lateral view. The **trigeminal** foramen (c.n. V), mainly formed by the prootic, is a major and circular opening located adjacent and dorsal to the caudal edge of the alar process of the basisphenoid. C.n. V is the largest foramen in the braincase after the olfactory foramen. Anteriorly, the trigeminal foramen is open for allowing the passage of the oftalmic and maxillary divisions. The mandibular part of the trigeminal nerve would be transmitted anteroventrally through a narrow groove on the basisphenoid, anterodorsal to the alar process (Weishampel, personal communication). Caudal to the large trigeminal foramen there is the **facial** foramen (c.n. VII), which is contained in the prootic. The facial foramen is the smallest on the lateral side of the braincase, caudal to the orbit, and is encased in a long, oblique groove that runs anteroventrally ventral to the base of the alar process of the basisphenoid. This is the carotid groove, which transmits carotid division of the facial nerve. The groove ends in a large and ellipsoidal, anteroventral to caudocranially elongated foramen. This foramen is located medial and ventral to the alar process, and lateral to the mediolateral narrowing of the basisphenoid

before the beginning of the pterygoid processes. A second division of the facial nerve would run caudodorsally. Posterior to c.n. VII there is the fenestra **ovalis** (c.n. VIII), which is separated from the facial foramen by a ridge coming from the crista prootica, near the suture between the prootic and the opisthotic. The fenestra ovalis is formed by the prootic dorsocranially and the opisthotic caudoventrally. The fenestra ovalis is smaller than the trigeminal foramen. The fenestra ovalis is composed by two foramina, only partially separated interiorly by a sharp and slender triangular lamina of bone in the prootic. The fenestra ovalis is encased between the boundaries of a wide groove, which is formed between the cristal prootica and, ventrally, a ridge that links with the paroccipital process. Following Trexler (1995), the fenestra transmits c.n. VIII. Part of the **glossopharyngeal** nerve (c.n. IX) is also transmitted, which exits dorsocaudally within a groove that pierces the fenestra in the same direction. A thin membrane would cover the ventral part of the fenestra ovalis for the movement of the stapes (Weishampel, personal communication). Caudoventrally from the fenestra ovalis, there are a series of three foramina located ventral and caudal to the ridge that bounds caudoventrally the fenestra ovalis, on the ventral and lateral side of the opisthotic. The two anterior-most of these foramina are adjacent to each other and distributed anteroposteriorly, separated by a dorsoventral thin strip of bone. Each one of these foramina is about half the size of the fenestra ovalis. In MOR 1071-7-16-98-248 only one foramen, instead of these paired foramina, can be seen in that area of the braincase. These foramina serve for transmitting a portion of the **glossopharyngeal** nerve (c.n. IX), along with the **vagus** (c.n. X), **spinal accessory** (c.n. XI), and **hypoglossal** (c.n. XII) nerves. The third foramina, as seen in

MOR 1071-7-7-98-86 is located slightly more ventral and caudal to the paired foramina, being slightly larger. This foramen serves for the exit of part of the hypoglossal nerve.

Presphenoid

This element is located anteriorly and dorsally on the braincase, abutting the ventral surface of the olfactory depression of the frontal. The presphenoid is the most anterior element of the neurocranium along with the more dorsal cultriform process of the basisphenoid. Besides meeting the frontal, the presphenoid attaches caudally to the orbitosphenoid, medially with its counterpart, but not with the parasphenoid (in contrast to the condition observed by Horner in 1992 for *P. blackfeetensis*). The paired presphenoids limit lateroventrally the **olfactory** canal (c.n. I). This canal is a very large exit that faces dorsocranially allowing the passage of the olfactory nerves. The presphenoid consists in a lateroventrally convex wall of bone that projects anteroventrally a short distance. Anteromedially, near the articulation with its counterpart, the presphenoid contains a small excavation, which produces a salient, small and slightly more anteroventral process formed by the joint of both elements. The ventral edge of the presphenoids along its juncture is a sharp keel that ends anteriorly in the described small process.

Orbitosphenoid

The orbitosphenoid resembles the presphenoid in being an anterolaterally facing and convex thick sheet of bone. The paired orbitosphenoids extend caudally encasing the

olfactory foramen. The orbitosphenoid is slightly rounded anteriorly and larger than the presphenoid. The caudal half of the orbitosphenoid extends caudoventrally, wedging

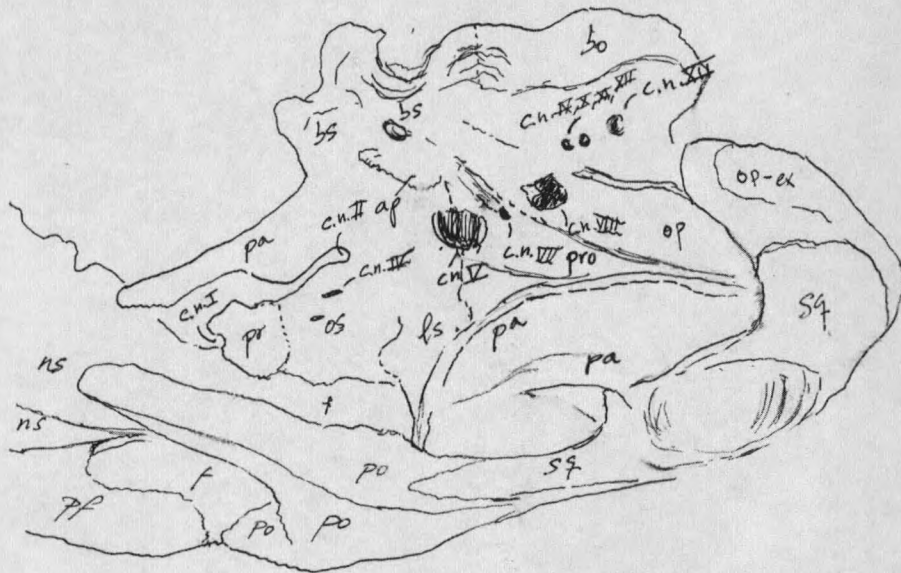


Figure 18. Braincase MOR 1071-7-7-98-86 in lateral view. Bs: basisphenoid, ap: alar process, op-ex: opisthotic-exoccipital, sq: squamosal, ls: laterosphenoid, po: postorbital, f: frontal, ns: nasal, pf: prefrontal, os: orbitosphenoid, ps: presphenoid, par: parasphenoid, pa: parietal, c.n.I: olfactory canal, c.n.II: optic foramen, c.n.IV: trochlear foramina, c.n.V: trigeminal foramen, c.n. VI: facial foramen, c.n. VIII, fenestra ovalis.

under the anteroventral border of the laterosphenoid. The outline of the edge of the caudal half of the orbitosphenoid is rather irregular, in order to accommodate the joining laterosphenoid. A crescentic concave lateral profile on the caudal edge of the orbitosphenoid form a suture with a corresponding rounded anterior tongue on the anterior edge of the laterosphenoid. Besides fusing caudally with the laterosphenoid, the orbitosphenoid attaches anteriorly with the presphenoid, ventrally with the basisphenoid, dorsolaterally with the oftalmic depression of the frontal, and medially with its counterpart along the midline of the braincase. The frontal-orbitosphenoid joint is visible even in the adult specimens, in the form of a crenulated line that also includes caudally the laterosphenoid-frontal suture. The presphenoid is medially recessed in respect to the lateroventral surface of the Orbitosphenoid. Posteriorly the orbitosphenoid forms a continuous surface with the laterosphenoid. The laterosphenoid-orbitosphenoid suture is slightly visible. Its crenulated line is convex anteriorly, where it draws an oval outline against the orbitosphenoid. Ventrally the orbitosphenoid is fused to the basisphenoid, and is not clear if that is also the case with the parasphenoid more anteriorly, since the basisphenoid and parasphenoid are very well fused. Two relatively small trochlear foramina can be observed on the lateroventral surface formed by the orbitosphenoid and laterosphenoid. These foramina look like deep punctures on the bone surface. The foramina are dorsoventrally arranged and face anterolaterally. The dorsal trochlear foramen is located in the laterosphenoid, caudal to the rounded termination for joining the orbitosphenoid, as observed on the unfused braincase of the subadult MOR 1071-7-13-99-87. That foramen is more rounded and slightly smaller in MOR 1071-7-7-98-86 than

the other trochlear foramen. Ventrally, the second foramen is more elongated and contained in the orbitosphenoid, near its ventral surface, where it forms the dorsal roof of the optic foramen. The caudal wedge-like extension of the orbitosphenoid contributes to form the anterior and dorsal inner face of the oculomotor foramen.

Laterosphenoid

The laterosphenoid is located posterior to the orbitosphenoid, with which it articulates. The laterosphenoid joins also the postorbital laterodorsally, the prootic caudally, the basisphenoid ventrally, the frontal anterolaterally and dorsally, the parietal dorsally and its counterpart medially. The laterosphenoid consists of four processes, a prootic, postorbital, orbitosphenoid and basisphenoid process. The prootic process is caudally directed and attaches to the prootic. The postorbital process projects laterodorsally to meet the postorbital. The basisphenoid process directs ventrally to articulate with the basisphenoid. The orbitosphenoid process is small, roughly rounded, and is mediocranially-directed. Its surface faces lateroventrally. The prootic and the postorbital processes form a characteristic and extensive arched, concave and caudolaterally-facing surface, located adjacent and caudal to the posterior limit of the orbital cavity anterior to the crista prootica. The laterosphenoid is mediolaterally compressed. While the described concave curvature occurs caudolaterally, its medial and anteromedial sides are dorsoventrally concave and longitudinally convex. The orbitosphenoid process forms a tongue-like expansion anteromedial to the ventral ridge of the postorbital process. Its edge is crenulated for joining the caudal border of the orbitosphenoid. In adults that suture is obscured by the fusion of both elements.

The postorbital process is a transversally compressed and moderately elongated branch. The process is laterodorsally-directed and fits into a smooth depression on the medial, central body of the postorbital. The laterodorsal end of the postorbital processes has rounded corners and its articulation surface is convex. Weishampel (personal communication) considers this articulation as a possible synovial joint. The rest of articulation surfaces of the laterosphenoid are grooved and crenulated, as noted by Horner (1992) in *P. blackfeetensis*. Ventrally the postorbital process forms a ridge that divides the caudal boundary of the orbit from the arched, concave smooth posterior surface of the element.

The prootic process is dorsoventrally deep and projects caudally to meet the prootic. The process is mediolaterally compressed and forms a crenulated suture with the prootic, which fuses in the adult stage. As in the postorbital process, the lateral surface is smooth. A triangular groove coming from the trigeminal foramen separates the prootic process from the basisphenoid process. That groove is anteroposterioly elongated, relatively wide dorsoventrally and projects anteroventrally, thinning slightly. It transmits the ophthalmic and maxillary divisions of the trigeminal nerve (Weishampel, personal communication). This groove represents an anterior opening of the lateral side of the trigeminal foramen. Internally (medially) the foramen does not exit anteriorly. Dorsal and adjacent to the dorsal edge of the groove the lateral surface of the laterosphenoid is depressed. That depression is triangular in outline and extends along the whole anteroposterior area of the ventral portion lateral surface of the laterosphenoid, caudal and adjacent to the posterior boundary of the orbit.

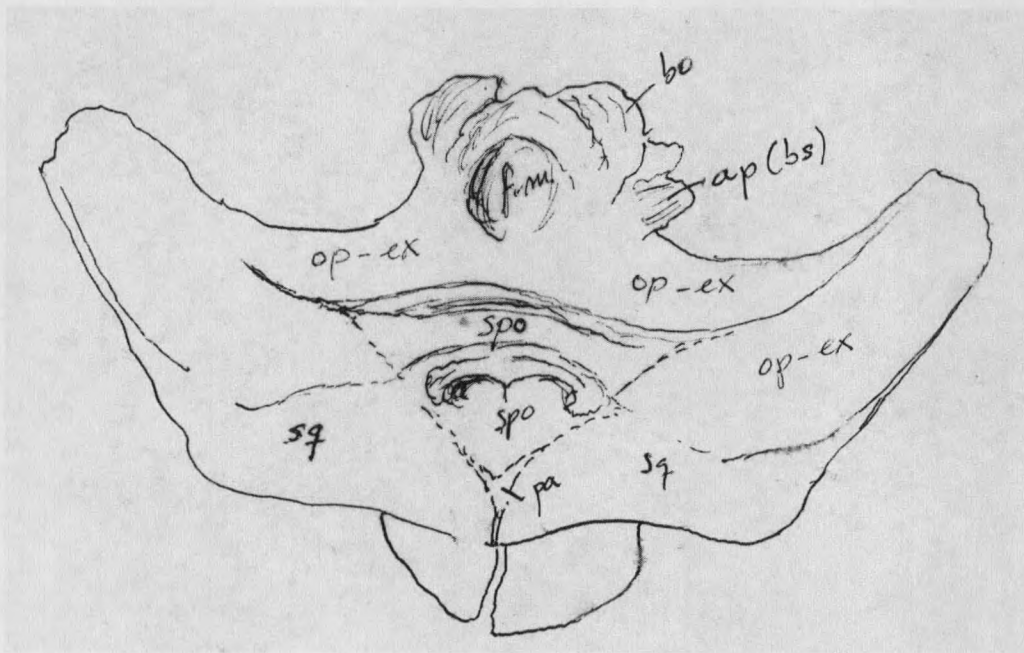


Figure 19. Braincase of MOR 1071-7-7-98-86 in occipital view. Sq: squamosal, pa: parietal, bo: basioccipital, f.m.: foramen magnum, spo: supraoccipital, op-ex: opisthotic-exoccipital, ap: alar process, bs: basisphenoid.

Comprising the trigeminal groove and extending ventrally, the basisphenoid process is roughly subrectangular and relatively expanded mediolaterally. The basisphenoid process forms the anterior boundary of the trigeminal foramen. The ventral surface of the process is deeply grooved, forming a medioventrally-facing articulating surface for the basisphenoid. The process meets its counterpart along the medial edge, while the rest of the ventromedial surface formed by both laterosphenoids is devoted to join the basisphenoid. The caudal border of the basisphenoid process attaches to the prootic, also by means of a crenulated contact. The basisphenoid process-prootic contact forms the anteroventral limit of the trigeminal foramen.

Prootic

The prootic follows caudally the laterosphenoid along the dorsal half of the braincase, ventral to the frontals and the parietals. The long axis of the prootic is obliquely (anteroventrally to caudodorsally) oriented. The prootic fuses with the laterosphenoid anteriorly, the basisphenoid ventrally, the basioccipital caudoventrally, the opisthotic-exoccipital mediocaudally, and the supraoccipital dorsomedially. The prootic is excluded from contacting the parietal due to the intervening supraoccipital, as Horner (1992) noted in *P. blackfeetensis*. In MOR 1071-7-13-99-87-I the supraoccipital wedges anteriorly between the parietal above and the prootic below. Because the opisthotic is completely fused with the exoccipital already in the early ontogenetic stages (exemplified here by MOR 1071-7-13-99-87-I), it is not possible to concrete where or whether the prootic attaches to the exoccipital, the opisthotic or both. Here the opisthotic is considered to be located adjacent and caudal to the prootic, so that both elements would

constitute the otic vestibule (Romer, 1956). A large and subtriangular process projects caudodorsally from the region opposite to the anterodorsal laterosphenoid process. This caudodorsal process, which comprises more than half of the longitudinal length of the prootic, wedges mediolaterally and thins dorsoventrally near its caudodorsal end. A ridge, the crista prootica, divides longitudinally the lateral side of the process in two concave smooth surfaces. One of these surfaces faces lateroventrally and the other laterodorsally. The process attaches to the opisthotic-exoccipital complex through its medial side. The medial face of the caudodorsal process of the prootic is flattened and shows a series of longitudinal narrow grooves and sharp ridges. A similar pattern is seen in the corresponding articulating surface of the opisthotic-exoccipital, anteroventral to the squamosal join surface. The rest of the prootic consists on a laterally and medially concave and crescentic. The prootic forms most of the trigeminal foramen. The prootic contributes to the foramen dorsally, and forms most of its the ventral rim, as well as its caudal boundary by means of a sharp edge. The trigeminal foramen in the prootic forms two anterior processes, one dorsal and another ventral, both of which articulate with the laterosphenoid through crenulated sutures. The anteroventral laterosphenoid process is subrectangular, mediolaterally expanded and strongly concave on its lateral side. Caudally, the process includes a portion of the alar process that grows mostly from the basisphenoid. The anterodorsal process is larger and curves dorsomedially to join the laterosphenoid along all its caudolateral and caudodorsal edge, except for the more mediodorsal extreme, where a wedge-like extreme of the intervening supraoccipital is joined. The anterior portion of the crista prootica begins along the lateral surface of the

anterodorsal process of the prootic. The facial foramen for c.n. VII is also included in the prootic and penetrates mediolaterally the central, ventral body of the element. The foramen is much smaller than both the trigeminal foramen and the fenestra ovalis. The facial foramen is located just ventral to the crista prootica and the anterodorsal process of the prootic. The foramen is obliquely elongated in the same direction than the prootic and located anteroposterioly between the trigeminal and the fenestra ovalis. A groove runs caudoventrally from and around (enclosing) the facial nerve, which transmitted one of the divisions of this nerve. The caudal central border of the prootic contributes to form the anterior half of the fenestra ovalis. A small triangular process protrudes caudally from the inner portion of the lateral wall.

The medial side of the foramen-bearing region of the prootic, ventral to the caudodorsal process, is concave and encloses the otic vestibule. Numerous foramina perforate the medial surface of the prootic. There are three small foramina located adjacent and dorsal to the medial exit of the facial foramen. The facial plus these other foramina are concentrated together at the center of the bone, between the trigeminal and the fenestra ovalis. Two of them are located anteriorly within a larger depression. The other small foramen exits internally into the fenestra ovalis, perforating its medial wall.

The mediolaterally compressed posterior side of the prootic is contains several foramina and depressions, the contribution to the fenestra ovalis, and the caudoventral join surface for the basioccipital and, more ventrally and anteriorly, the basisphenoid. A large and circular foramen deepens anteriorly into the caudal side of the prootic, dorsally

displaced from the lateral opening of the fenestra ovalis and located adjacent and ventral to the caudodorsal process of the element. Ventrally, this large foramen is separated from a shallower depression by a smooth ridge. This depression is ventrally located in respect to the lateral opening of the fenestra ovalis.

Opisthotic-Exoccipital

No suture can be recognized between the opisthotic and the exoccipital in any of the available specimens, independently of the ontogenetic stage of development. Therefore, both elements are herein described together as a single unity. Probably, the anterolateral, dorsal that joins caudodorsal process of the prootic would correspond to the opisthotic, in agreement to Ostrom (1961). Weishampel (personal communication) considers the extremes of the paroccipital processes as pertaining to the opisthotic. The exoccipital-opisthotic complex joins the caudodorsal process of the prootic anterolaterally and the basioccipital ventrally. The supraoccipital is met dorsally and the squamosal caudally. Most of the complex is formed by the crescentic large paroccipital process, which arches lateroventrally producing a "horn-like" structure. The paroccipital process is anteroposteriorly compressed. There is a change in the orientation of its anterior and caudal sides. Proximally its anterior side faces anterodorsally, while distally towards the tip the anterior side faces anteroventrally and that wedges lateroventrally. The anterior surface of the paroccipital process forms an extensive, flat surface for the reception of the posterior surface of the postquadratic process of the squamosal. The caudoventrally-facing side of the paroccipital process is convex. Anterior to the proximal

end of the paroccipital process is the attachment surface for the caudodorsal process of the prootic, formed by longitudinal ridges and grooves.

Two more processes are located ventral and medial to the paroccipital process, respectively. The medial, wing-like supraoccipital process is medially projected and strongly compressed dorsoventrally. In dorsal view, the wing has the outline of a parallelogram. Its anterior and caudal sides converge medially. Its anterodorsal surface is full of grooves and ridges similar to the prootic joint. The caudoventral side of the supraoccipital sits over the wing-like medial process of the exoccipital-opisthotic complex and abuts the medial side of the proximal area of the paroccipital process. The medial edge of this wing-like process meets its counterpart, forming a sharp but low ridge on the ventral side. A sharp and narrow ridge bisects longitudinally the medial edge of the wing-like process. At the anterior extreme of the wing-like supraoccipital process there is a ridge that connects it with the medial surface of the basioccipital process. This ridge is medially salient and caudoventrally directed. Caudally and between this ridge and the supraoccipital process there is a smooth triangular depression. When both exoccipitals are articulated, these are a pair of depressions that bound the dorsal portion of the foramen magnum. These depressions held muscles that aid the supporting function of nuchal ligament (Weishampel, personal communication).

The basioccipital process forms the ventral part of the exoccipital-opisthotic complex. The process is subrectangular, mediolaterally compressed, and expanded antero-caudally. The process is also slightly expanded mediolaterally across its ventral border. Dorsally, the caudal border of the process links with the proximal and

caudoventral, lateral border of the paroccipital process through a continuous semicircular arch. The caudal end of the basioccipital process is rounded and slightly hooked. This end contributes with the basioccipital to form the paired occipital condyles around the ventral region of the foramen magnum. Most of the ventral surface of the basioccipital process fuses with the basioccipital. The joint surface is rugose and carved pits and short ridges. The basioccipital process includes several cranial foramina. Anteriorly, it contributes to the fenestra ovalis, forming its caudal half. The fenestra ovalis is dorsoventrally elongated and narrowed in the middle by a triangular small process that points caudally coming from the prootic. As observed in *M. peeblesorum* (Trexler, 1995), there is no additional foramen for the fenestra rotundum. Posterodorsally the caudal border of the fenestra ovalis is bounded by a strongly marked ridge, which runs parallel and dorsally to the crista prootica, and links smoothly with the ventral border of the proximal area of the paroccipital process. The area between this ridge and the crista prootica is concave and includes the prootic-opisthotic suture. The remaining foramina that are exposed laterally are located ventral to that ridge. Ventral and caudal to the fenestra ovalis there is a pair of rounded foramina. There is a third, larger foramen located caudally and more ventrally near the basioccipital, and relatively more separated from that pair of foramina. The relatively more anterior paired foramina served as the exit of parts of the glossopharyngeal (c.n. IX) and the hypoglossal (c.n. XII) nerves, plus the vagus (c.n. X) and spinal accessory (c.n. XI) nerves. The third, caudoventral-most foramen transmitted a part of the hypoglossal nerve.

Basioccipital

The basioccipital has been removed from the available braincases and only an eroded remnant can be seen fusing with the opisthotic-exoccipital complex and the basisphenoid. The basioccipital is subrectangular, being anteroposteriorly longer than mediolaterally wide. The element would form a little more than the caudal half of the floor of the braincase and the ventral portion of the occipital condyles. Anteriorly the element fuses with the basisphenoid, forming probably the caudoventral portion of the spheno-occipital tubercles. In MOR 1071-7-7-98-86, which displays the best-preserved tubercles, a basisphenoid-basioccipital joint is insinuated. This joint would be oblique, anteroventrally directed. Less than the caudal half of the tubercles would be part of the basioccipital as seen laterally. The basioccipital contribution to the tubercles would just form their caudoventral portion. The tubercles are fairly rugose, narrow mediolaterally, and longer anterioposteriorly. The lateral side of the tubercles plus a portion of the lateral ventral surface of the basisphenoid, anteroventral to the fenestra ovalis, is also rather rugose. Laterally and dorsally to the spheno-occipital tubercles, at the level of the edge between the ventral and the lateral side of the braincase, there is an excavation at each side of the braincase. Considered here as part of the basisphenoid, this excavation is anteroposteriorly elongated and narrow dorsoventrally, like a small incision into the bone. Medially between the two tubercles the ventral surface of the braincase is concave and forms a passage as wide mediolaterally as each individual tubercle. Posterior to the tubercles the ventral surface of the basioccipital is swollen dorsally. The caudal third of

the ventral floor of the braincase (the caudal half of the basioccipitals) is progressively convex until reaching the ventral end of the occipital condyles.

Anterolaterally, the basioccipital probably fuses with the prootic along a small portion of the ventrolateral border the prootic, between the basisphenoid-prootic and the opisthotic-prootic joints. Caudally, the basioccipital articulates with the opisthotic, ventral to the line of foramina for cranial nerves IX, X, XI and XII. Caudoventrally the basioccipital joins the exoccipitals to contribute ventrally to the occipital condyles. The occipital condyles are medioventrally compressed and medioventrally inclined about 30-40 degrees from the parasagittal plane of the skull.

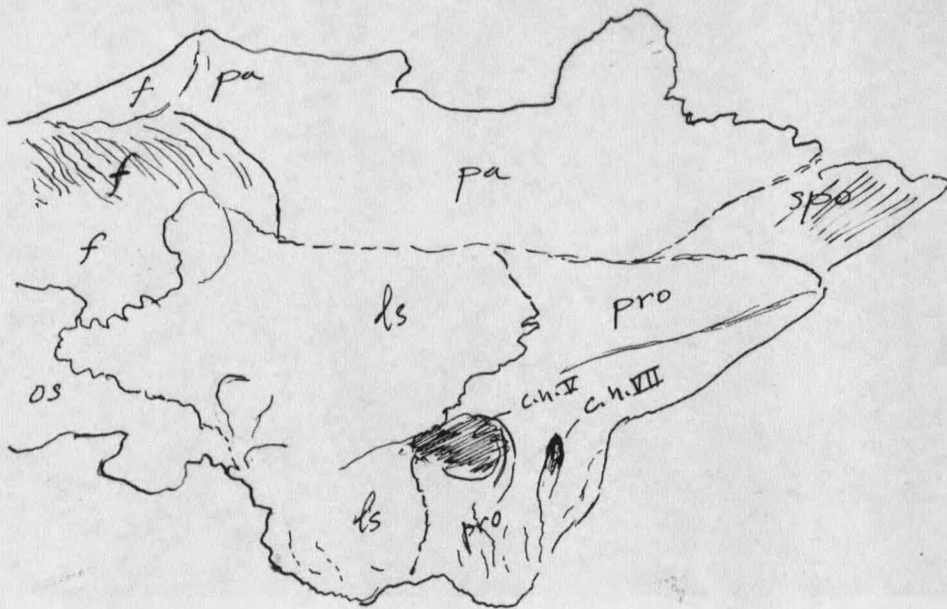


Figure 20. Subadult braincase of MOR 1071-7-13-99-87I in left lateral view. Os: orbitosphenoid, f: frontal, pa: parietal, ls: laterosphenoid, pa: parietal, spo: supraoccipital, pro: prootic, c.n. V: trigeminal foramen, c.n. VII, facial foramen.

Basisphenoid

The basisphenoid is the most complex element of the braincase in terms of structural design. The element forms the anteroventral portion of the neurocranium, and the ventral region along with the basioccipital. The basisphenoid articulates with a number of bones: the basioccipital caudoventrally, the prootic caudally and dorsally, the parasphenoid anteriorly, the orbitosphenoid anterodorsally, the laterosphenoid dorsally, and the pterygoid anterolaterally. The basisphenoid consists of two pair of laterally expanded and large process, the pterygoid and alar paired processes, and a ventral and caudal "neck" or constricted area anterior and adjacent to the contribution to the spheno-occipital tubercles. The basisphenoid "neck" area is fairly smooth and strongly compressed dorsoventrally. It represents a mediolateral narrowing of the ventral side of the basisphenoid, comprised between the tubercles posteriorly and the pterygoid process rostrally. The "neck" bounds ventrally the large and ellipsoidal foramen that transmits the internal carotid artery through the carotid canal, a division of the facial nerve (Weishampel, personal communication). The smooth texture of the "neck" contrasts with the rugose surface of the caudally adjacent spheno-occipital tubercles.

Dorsal to the carotid foramen and forming its dorsal border is the beginning of the alar process. The prootic also participates in the formation of this process, but its contribution is minimal compared to that of the basisphenoid. In *B. canadensis* the alar processes are relatively large and well developed, as in *M. peeblesorum*. The process consists on a lamina of bone of that expands laterally anteroventral to the trigeminal foramen. The alar process is tilted in respect to a horizontal plane, being roughly parallel

to the crista prootica and the large ridge of the anteromedial segment of the opisthotic-exoccipital complex. Both the ventrocaudal and dorsocranial surfaces of the process exhibit radial and coarse striations concentrated in the area near the lateral edge of the process.

The paired pterygoid processes form the rostral portion of the basisphenoid, anterior and adjacent to the alar processes and the "neck-like" region. They constitute a conspicuous feature of the whole braincase, as they form two large salient and stout lateral expansions. Anterodorsally and medially, the processes converge into a concave triangular and extensive area ventral to the long cultriform process of the parasphenoid. In MOR 1071-7-7-98-86 there is a small, broken, but salient process projecting caudoventrally from that ventral edge, centered on the parasagittal plane between both pterygoid processes. At the lateral end the cross section of the pterygoid processes is triangular. Anterodorsal to the alar processes and caudodorsal to the pterygoid processes, ventral and adjacent to the orbitosphenoid and the laterosphenoid, there is the basisphenoid suture with the orbitosphenoid anteriorly and the laterosphenoid posteriorly. Immediately dorsal to the medial segment of the pterygoid processes there is a deep circular depression. Two triangular, rough, rugose and anteriorly directed, relatively small process are contained in the area anterodorsal to the alar and pterygoid processes of the basisphenoid. The processes are aligned dorsoventrally. The ventral process links caudodorsally with the caudal boundary of the orbit defined by a ridge in the laterosphenoid. This process has been identified in *M. peeblesorum* (Trexler, 1995, p. 86, fig. 38, J). The other process is ventrally located, anterolaterally directed and more

salient. It is anteriorly adjacent to the circular depression that exists dorsal to the beginning of the pterygoid process.

The pterygoid-basisphenoid joint is inferred from the relative position of these elements in the skull, the features of distal portion of the pterygoid processes, and comparison with other taxa such as *Gryposaurus* (MOR CAST 068 RTMP 80-22-1) and *Edmontosaurus* cf. *annectens* (MOR 003). The lateral-most segment of the pterygoid process in *B. canadensis* is relatively thick and shows an anterodorsal flat surface.

Parasphenoid

The parasphenoid is fused to the basisphenoid. In MOR 1071-7-7-98-86 and MOR 1071-7-16-98-248 there is a vertical trace of a possible suture between the long cultriform process and the triangular concave anterior face of the basisphenoid. This coincides with the possible suture observed by Ostrom (1961) in *Corythosaurus casuarius*. The parasphenoid probably consists of the cultriform process. This process is an elongated rod-like extension of bone that projects anterodorsally at the front of the braincase. The cultriform process links caudally and laterally with the medial segment of the pterygoid processes. As in *M. peeblesorum* (Trexler, 1995), the anterior tip of the cultriform process is U-shaped, concave dorsally. This is due to the presence of a longitudinal and deep groove that excavates the process anteroposteriorly along most of its length. The ventral border of the process is smooth and convex. The cultriform process is slightly arched longitudinally so that its ventral border is concave ventrally. Posteriorly the cultriform process is fairly expanded dorsally, possessing a mediolaterally-compressed sheet of bone.

Palatal Complex

Palatine

The palatine (Fig. 21) articulates with the maxilla ventrally, the jugal anterolaterally, and the pterygoid dorsally. Horner (1992) indicates that the palatine of *P. blackfeetensis* meets the lacrimal, which is not observed in *B. canadensis*. Probably the palatine also contacts the vomer, but this articulation cannot be described given the lack of vomers among the available material and the fragmentary state of the palatines. The palatine is composed of three branches, or a ventral, elongated segment that sends two processes, one anterolaterally, and the other anterodorsally and medially. The ventral long segment sits on the dorsomedial ridge of the posterior half of the maxilla. The ventral side of the palatine contains a longitudinal and deep groove, which embraces the maxillary ridge. The internal (ventral) surface of that groove is very rugose, showing small and sharp ridges. At its anterior extreme, there is a sharp ridge that divides the ventral side of the palatine into a narrow, lateral, and deep cleft, and a shallow, medial and rugose surface. The ventral grooved side of the palatine is asymmetrical. The medial wall of that groove overlaps the medial side of the maxilla that lies dorsal to the row of maxillary special foramina. The lateral side of the ventral palatine abuts the maxillary ridge, dorsally elevating the former in respect to the medial wall of the groove. A mediolaterally compressed pyramidal, rugose and sharp elevation of the dorsomedial ridge of the maxilla fits into a corresponding concavity on the ventral, grooved side of the palatine. The ventral long segment of the palatine gradually tapers caudoventrally, becoming a mediolaterally thin sheet that continues to be applied to the medial side of the

posterior end of the maxilla, dorsal to the special foramina of the dental battery. The lateral side of the ventral groove ascends dorsocaudally forming an acute angle with the ventral border of the element. Probably the lateral side of the groove contacted a portion on the lateral side of the anteroventral border of the palatine ramus of the pterygoid.

Two processes form the anterior third of the palatine. The anterolateral process is antero-caudally compressed, and is slightly expanded distally dorsoventrally. The anterolateral end contains an ellipsoidal surface for articulating with a short process of the medial side of the anterior process of the jugal. The anterodorsal process of the palatine is a mediolaterally-compressed, fan-shaped flange of bone. This flange gradually becomes more compressed near its dorsal border, where it is antero-caudally expanded. The medial side of the anterodorsal flange is concave while the lateral side is slightly convex. Although broken in the available specimens, probably the anterodorsal flange would be linked to the rest of the dorsocaudal edge by means of a thin sheet of bone, as deduced from comparisons with the articulated skull of *Edmontosaurus* cf. *annectens* (MOR 003). The palatine ramus of the pterygoid would contact it including the fan-like flange. The medial and lateral sides of the dorsal border of the flange shows short striations oriented perpendicular to the edge. The dorsal border of the anterodorsal flange is indented, showing break in the profile of the dorsal edge. And anterior half is dorsally more elevated in relation to the caudal half of the arch described by the dorsal border of the flange. In dorsal view the caudal half of the border has been medially displaced a few millimeters from the anterior half.

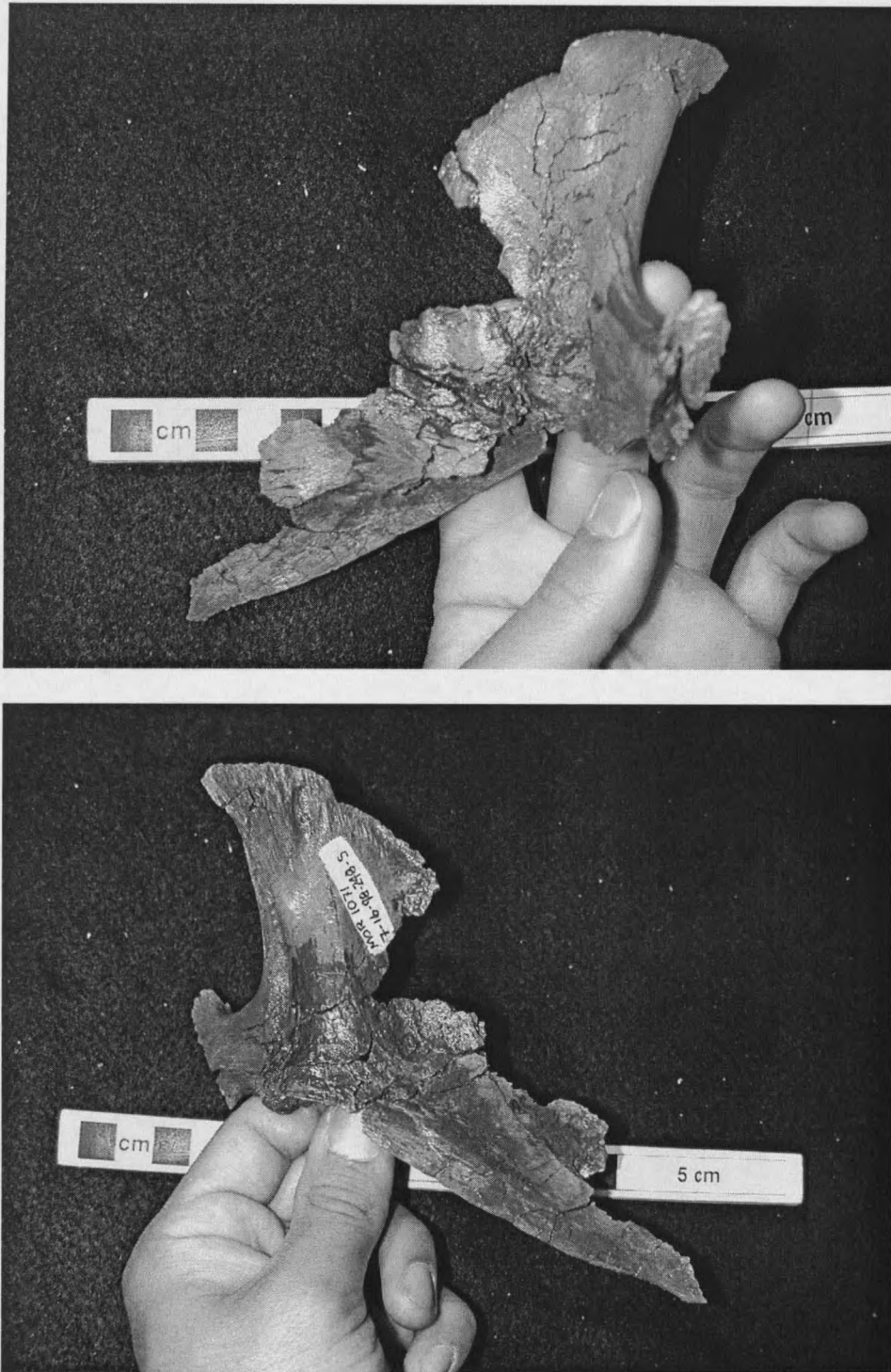


Figure 21. Right palatine MOR 1071-7-16-98-248-S in lateral (top) and medial (bottom) view.

Pterygoid

The pterygoid (Fig. 22) is the largest and most complex element in the palate. The element is composed of a central body from which radiate four large processes, each at about 90 degrees from the other. Anteriorly, a vaulted, folded palatine ramus projects anterodorsally to meet the element of the same name. Its anteroventrally-facing space forms the palatal arch. A shorter process projects ventrally to contact the caudal end of the maxilla and the ectopterygoid laterally. Expanding posterocaudally there are two quadrate processes, which articulate with the pterygoid flange of the quadrate. One of these processes is the dorsal quadrate wing, a triangular lamina of bone that projects caudodorsally and laterally. The ventral quadrate ramus is caudoventrally and laterally projected. The dorsal quadrate wing plus the palatine ramus are larger than the other two ventral processes. On the medial side there is a strongly buttressed process that projects caudomedially from the center of the element. The palatine ramus links with this buttress, which is also linked with to the ventral quadrate and ectopterygoid processes through two thin flanges.

The dorsal quadrate wing is a thin lamina of bone. It has the shape of an isosceles triangle, with a sharp apex projecting caudodorsally and laterally to articulate with the pterygoid flange of the quadrate. In that contact the pterygoid wing inserts its distal, sharp tip in a triangular excavation located dorsally on the medial surface of the pterygoid flange of the quadrate. The quadrate flange laterally overlaps more than half of the lateral surface of the pterygoid wing. The lateral side of the dorsal quadrate wing is rugose, showing an array of small and sharp ridges. Near the central, medial buttress of the

pterygoid the anteroventral wide base of the caudodorsal wing is strongly vaulted, rolled to form a subcylindrical fold that applies to the dorsomedial side of the palatine ramus. This fold would wrap the lateral portion of the pterygoid process of the basisphenoid. Its rugose texture indicates the area where the basisphenoid was contacted.

The ventral quadrate process projects posterolaterally and is a relatively shorter process. It abuts a small depression adjacent to the medial border of the quadrate. The process contacts the quadrate by means of a mediolaterally compressed end, which has a dorsoventrally elongated and narrow, rugose surface. Except for the extreme that contacts the quadrate, the ventral quadrate process of the pterygoid is V-shaped in transversal section, as it consists of a folded thick sheet of bone. That folding produces a concave dorsal surface and a ventral keel-like border. The dorsal concavity continues becoming even deeper into the central area of the medial side of the pterygoid. In contrast to the flat lateral surface, the medial side of the quadrate ventral process is convex and dorsally expanded to become a thin flange that links with the medial central buttress of the element.

The ventrally directed ectopterygoid process is the shortest of the four radial expansions of the pterygoid. The process is mediolaterally compressed and antero-caudally expanded. Its ventral edge is arched, ventrally convex as seen anteriorly, and anteroventrally directed. Medially, the ventral border ascends mediodorsally forming a flange that, as in the case of the ventral quadrate process, ascends until the central, medial buttress of the pterygoid. In the case of the ectopterygoid process, the flange does

not link with the buttress, but fuses into its ventral side. On the lateral side, dorsal to the ventral edge of the ectopterygoid process there is a D-shaped rugose area. This area

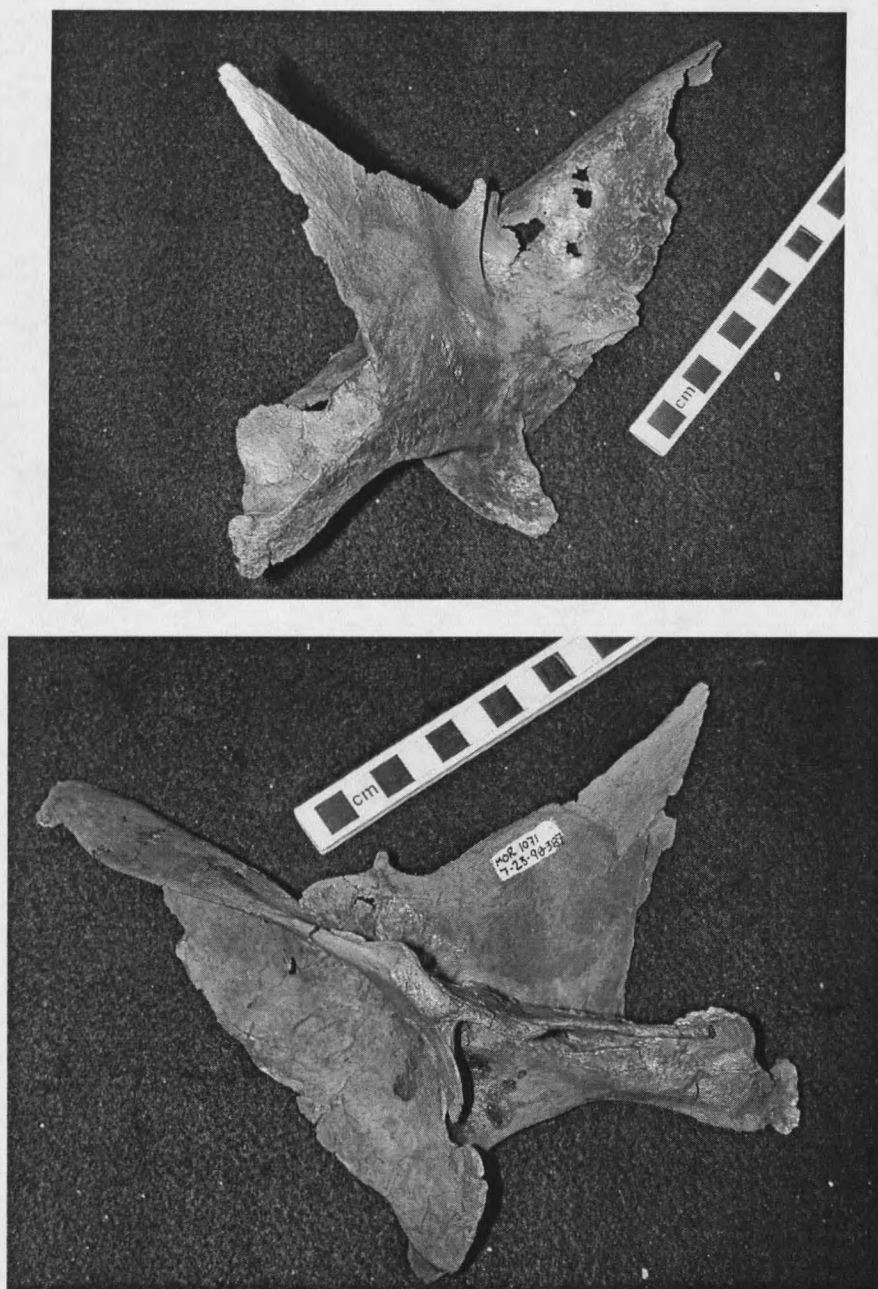


Figure 22. Right pterygoid MOR 1071-7-23-98-387 in lateral (top) and mediocaudal (bottom) views.

contacts the posterior, ventrocaudal process of the ectopterygoid. This articulation extends along the anterior surface of the ectopterygoid process of the pterygoid, well until its ventral border. Dorsally, the articulation is bounded by a sharp edge, the ventral border of a salient, anteriorly projected process. The maxilla is contacted along the anterior border, which follows the convex relief of the caudal border of the maxilla. This lateral, anteriorly-salient process of the palatine ramus has been described by Trexler (1995) in *Maiasaura peeblesorum*. As he pointed out, the process "appears as a thin strip of bone applied to the lateral surface of the pterygoid" (Trexler, 1995, page 55). Heaton (1972) also described this process in *Edmontosaurus regalis*. This process is mediolaterally compressed and in projecting anteriorly leaves a narrow, but deep concavity ventrally.

The palatine ramus is the longest branch of the pterygoid. The ramus is a medioventrally-vaulted sheet of bone that projects anterodorsally to articulate with the dorsal border of the palatine. The vaulting increases as the ramus ascends anterodorsally. The incompleteness of the available palatines prevents a detailed description of its articulation with the pterygoid. However, anterodorsally to the articulation for the ectopterygoid, and dorsal to the strip-like process described above, the lateral surface near the ventral border of the palatine ramus shows a rugose surface that most probably indicates the area where the palatine joined. The palatine ramus ends dorsally into a sharp, dorsoventrally compressed, delicate extreme. The longitudinal length of the palatine ramus is about one third longer than in the dorsal quadrate wing. As in *M. peeblesorum* (Trexler, 1995), the lateral border of the palatine ramus possesses a dorsal expansion in

the form of a small flange, near of its anterodorsal sharp tip. That flange extends only a few millimeters dorsally, is very thin and D-shaped, and rather gentle in profile as seen medially and laterally. Ventrally the medial edge of the palatine ramus connects with the central, medial buttress of the pterygoid.

The center of the medial side of the pterygoid shows a medially-projected buttress made of the convergence of the medial edges of the palatine ramus, the ventral quadrate and the ectopterygoid processes. The buttress is anteroventrally to dorsocaudally compressed. Its narrow medial edge is very rugose. A triangular, deep and large cavity is formed below (lateral and ventral to) the buttress, between the ectopterygoid and ventral quadrate processes. This triangular cavity includes a deep and oval fossa.

Anteromedially to the buttress, there is another medial large space made the vaulting of the palatine ramus. This ramus leaves a concave arched area between it and the anteromedial side of the of the ectopteygoid process, the palatal arch (described by Horner in 1992 in *P. blackfeetensis*). The ptergyoid is mediolaterally wider across the palatine ramus than across its posterolateral half.

Ectopterygoid

The ectopterygoid (Fig. 23 and 24) is an L-shaped sheet of bone that articulates with the maxilla medioventrally and the pterygoid posteriorly. The element is anteroposteriorly elongated and dorsoventrally compressed. In *B. canadensis* the ectopterygoid is much longer than in *M. peeblesorum*. However, in *Edmontosaurus* the element is even longer than in *B. canadensis*. In *M. peeblesorum* the ectopterygoid is triangular, not L-shaped as in *B. canadensis*. In *B. canadensis* the anterior, long segment

thins more gradually, being less wedge-like as in *M. peeblesorum*. The ectopterygoid is gradually expanded mediolaterally near its posterior border. In lateral view, the ectopterygoid is arched, with a concave ventral profile. Its dorsolateral surface slopes ventrolaterally. The medioventral surface of the ectopterygoid forms an extensive contact over the dorsolaterally facing shelf of the posterior half of the maxilla. The ventrolateral edge is ventrocaudally curved in order to accommodate the relief of the caudal border of the ectopterygoid shelf of the maxilla. The dorsomedial edge expands dorsally into a recessed surface. This recess fits underneath the medioventral surface of the salient caudodorsal process of the maxilla.

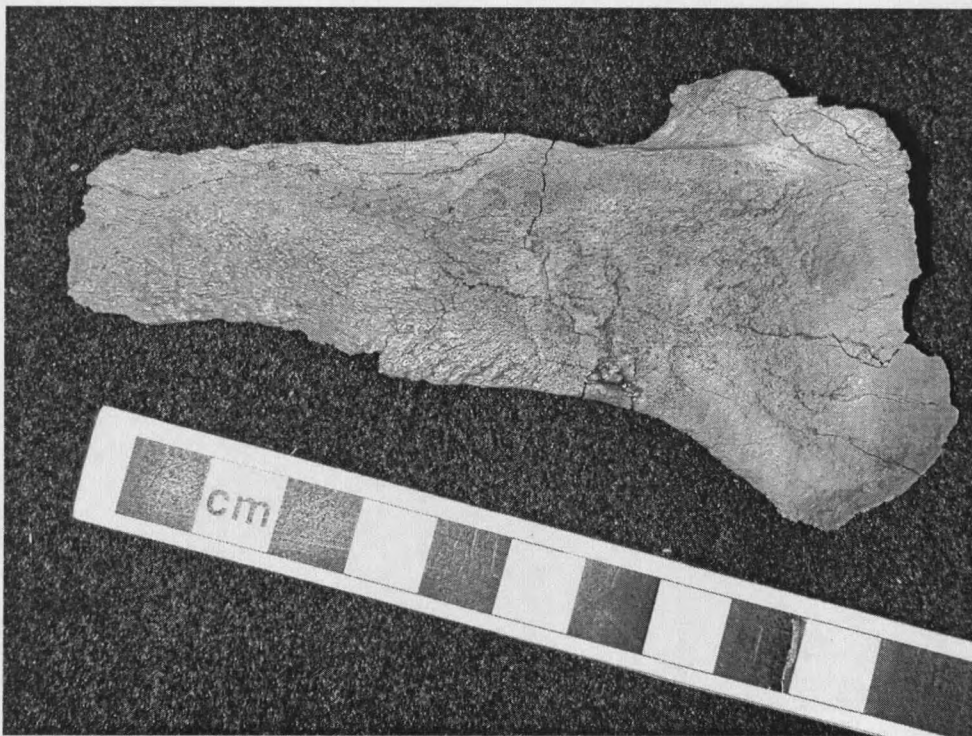


Figure 23. Right ectopterygoid MOR 1071-8-13-98-559-E in dorsolateral view.

The dorsocaudal corner of the ectopterygoid is dorsoventrally thickened because of the presence of a mediocaudally-facing process (the triangular, ventrally-projecting process of Trexler, 1995). The process rises caudomedially as a small expansion and its posterior edge is blended into the caudodorsal corner of the ectopterygoid. The process is anteroventrally bounded by sharp edges. In *M. peeblesorum*, this triangular process is more elongated and its posterodorsal edge is not blended into the medial side of the bone. In contrast, in *B. canadensis* the process has only a ventral apex and an anteroventral sharp edge, being less defined and less triangular.



Figure 24. Right ectopterygoid MOR 1071-8-13-98-559-E in medioventral view.

Anterior and adjacent to the anteroventral edge, the medial surface of the ectopterygoid is strongly concave. The ventral apex of the triangular process links with a sharp and irregular ridge that runs ventrally. Both the triangular ventral process and the ridge have been described by Trexler (1995) in *M. peeblesorum*. The ridge separates a small and concave caudoventral corner from the rest of the medial surface of the ectopterygoid. The mediocaudal side of the process is triangular and more vertical than the medial surface of the rest of the ectopterygoid. This surface is rather rugose and contacts the lateral side of the anteroventral border of pterygoid, anterodorsal to the maxillary process. The pterygoid-ectopterygoid articulation continues ventrally along the caudal border of the ectopterygoid and its medial surface overlaps the lateral side of the maxillary process of the pterygoid. This joint produces an anteromedial concavity where the caudal, ventrally deflected end of the maxilla fits in.

The orientation of the dorsolateral surface of the ectopterygoid changes gradually posteriorly, as it faces more laterally. At the posterior end the dorsolateral face is concave. Anteriorly, the dorsoventral thickness of the lateroventral and dorsomedial edges of the ectopterygoid becomes progressively narrower, until being sheet-like at its anterior end.

In MOR 1071-8-15-98-559-E the pterygoid articulation is wider and more equidimensional than in the other specimen, where the facet is more elongated and relatively narrower. On the laterodorsal surface, there is no trace in MOR 1071-7-31-99-281-I of the ridge present in MOR 1071-8-15-98-559-E.

Mandibular Complex

Predentary

The predentary (Fig. 26) is the most anterior bone in the mandible. It is a crescentic, mediolaterally broad bone that articulates with the anterior portion of the dentary. In dorsal view, the predentary is a rectangular bar with two lateral projections. The long transverse segment contains all the features of the element and continues into the shorter processes projecting caudally from its lateral ends. A sharp dorsocaudal keel divides the predentary in two along the midline. The predentary is dorsoventrally higher along its anterior face.



Figure 25. Predentary MOR 1071-7-28-98-299 in dorsocaudolateral view.

The anterodorsal border of the predentary contains a series of very short and dorsally projecting processes. From the parasagittal plane defined by the dorsocaudal keel, there are five of these processes at each side plus a sixth, broader and flatter one, forming and projecting dorsally from the corner of the anterodorsal edge of the element. These processes are evenly distributed, antero-caudally compressed and cone-shaped. A central pair of smaller, mediolaterally narrower processes located on the parasagittal plane separates these two sets of processes. The central pair is more closely spaced than the other processes. The anterodorsal edge and its series of processes are dorsally elevated in respect to a transverse row of foramina. These foramina are symmetrically arranged at both sides of the parasagittal plane. Medially there is a mediolaterally wide foramen that penetrates into the anterior surface of the predentary. Laterally, there are two small and incompletely individualized foramina. Still laterally to this pair of foramina, there are five circular foramina. The last one of these five foramina is located at the corner of the bone.

The caudodorsal region of the transverse bar of the predentary, which contains the foramina, becomes convex dorsoventrally and lies below the level of the anterodorsal border of the bone. This area is caudoventrally sloping and laterally links with the lateral processes of the predentary. A keel-shaped, sharp and relatively large process divides that area in two symmetrical halves. The large ridge that forms the keel-like appearance of the process faces posterodorsally and runs dorsoventrally. This process is parallel to the anterior ventrocaudal bilobate process of the element. The keel-like process is

dorsoventrally deep. At least one third of it projects ventrocaudally beyond the bilobate process.

The cranial face of the anterodorsal border of the predentary is slightly convex dorsoventrally and mostly straight mediolaterally. It forms about the dorsal half of the anterior side of the bone. Ventrally, the dorsal half of the cranial surface of the predentary contains a series of mediolaterally very wide, ventral indentations. That dorsal region is overlapping the ventral half of the anterior side of the bone.

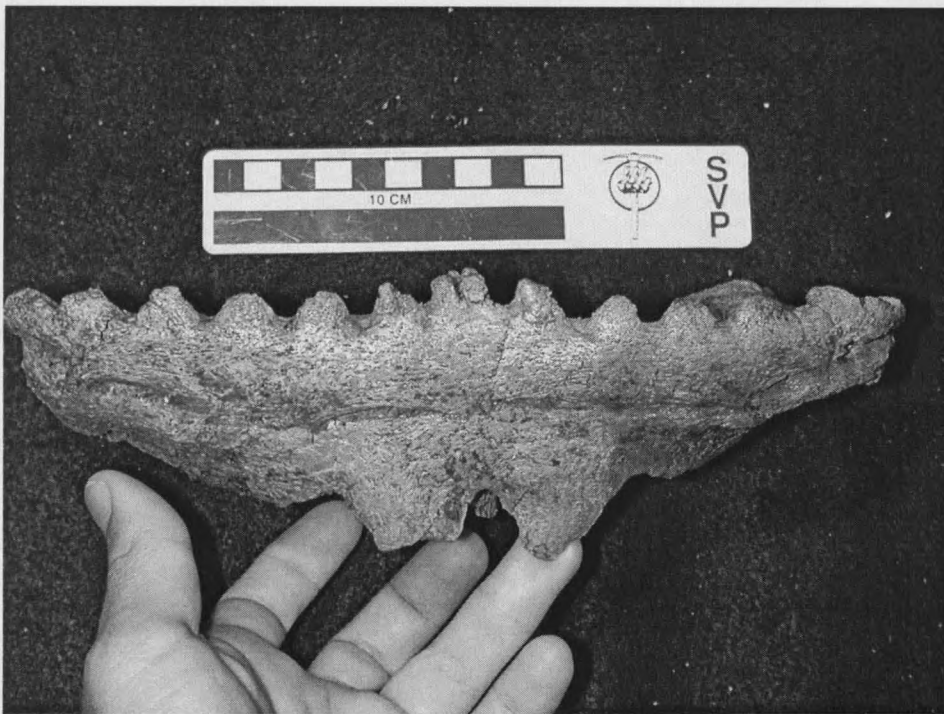


Figure 26. Predentary MOR 1071-7-28-98-299 in anterior view.

The ventral region of the anterior surface of the bone forms a bilobated ventrocaudally projecting processes at the center. This process is linguoid in morphology

and blade-like, strongly compressed craniocaudally. The anteroventral surface of this process is convex, while the opposite side is concave. In *Hypacrosaurus* this process is a single, triangular unit, not split in two lobes like in *Maisaura*, *Prosaurolophus* or *Brachylophosaurus*. Posterior to the bilobate process there are a pair of deep and smooth excavations of oval outline. Each excavation is located behind each lobe of the process, and symmetrical in respect to the parasagittal plane of the predentary.

The major lateral processes of the predentary show a strongly depressed lateral portion, followed by an adjacent convex medial region. Ventromedially, they possess flat surfaces bounded by a ridge that forms the medial edge of the processes. The lateral edge of the lateral processes is also sharp. Like in *Maiasaura*, the lateral process of the predentary of *Brachylophosaurus* are half the length of the transverse bar. In *Prosaurolophus* and *Hypacrosaurus*, the lateral processes are much longer, so that the predentary is more equidimensional in dorsal view.

In the articulated MOR 794 the bilobate process underlie the symphysis of the dentaries, while most probably the keel-like processes fits dorsal to the symphysis of the dentaries. The ventromedial, flattened surfaces of the lateral processes overlie the cranioventrally sloping anterior end of the dentary. Then the concave lateral surfaces of these lateral processes of the predentary would hold the ventral surface of the anterolateral side of the premaxilla, when the animal would close its beak-like mouth extremity.

Dentary

The dentary (Figures 27-28) is the major element in the mandible. It articulates anteriorly with the prementary. At its caudal end, the dentary articulates posteriorly with the surangular, medioventrally with the angular and medially with the splenial. The dentary consists of a dorsoventrally long, laterally offset coronoid process (located posteriorly) and an anteroposteriorly elongated, main body containing all the features of the element. The rostral third is edentulous, while posteriorly the dentary is more expanded dorsoventrally and presents a dental battery of densely packed teeth. The ventral border is rather straight, continuing into the ventrally deflected anterior third. The mandibular symphysis forms a small angle with the parasagittal plane and is anterolaterally directed. Posteroventrally, the medioventral side of the dentary begins to open into a narrow but deep groove that caudally becomes the exit of the Meckelian canal. The lateral side of the dentary is smooth and dorsoventrally convex. A series of foramina are anteroposteriorly spread on the lateral surface until the anterior end of the element. These foramina are obliquely arranged, so that the most posterior ones are the most dorsally located and the more anterior ones are located most ventrally. The medial side of the dentary is convex, but becomes strongly convex at the edentulous region. The teeth are arranged in closely packed vertical rows, forming a dorsoventrally convex mosaic of teeth crowns on the medial side of the element. At the base of the alveoli there are evenly distributed special foramina, bordering all the ventral margin of the medial dental battery, describing a dorsally concave arch. Posteriorly and gradually, the dental battery becomes more and more emarginated from the lateral side.

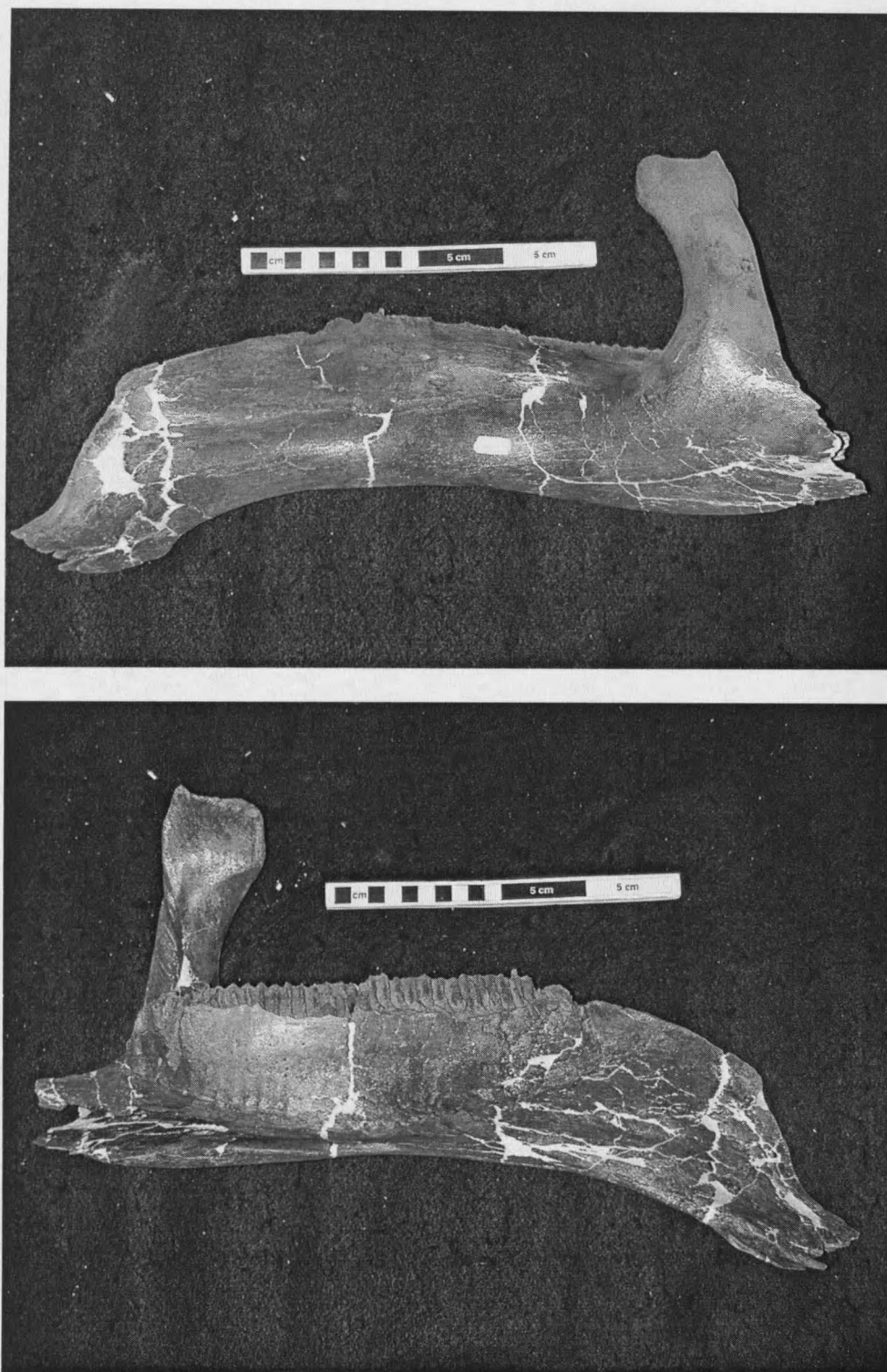


Figure 27. Dentary MOR 1071 in lateral (top) and medial (bottom) views.

In dorsal view, it is possible to see how the occlusal surface runs obliquely from medial to the base of the coronoid process to medially near the rostral third of the dentary.

The edentulous anterior third is mediolaterally compressed. Its dorsal border slopes gently anteroventrally. However, at about one half of the length of the diastema, the dorsal border suddenly changes of slope, being much more steep. At the point of that change of slope the rostral region of the dentary flares laterally, reaching the maximum concavity on the medial surface. Still more anteriorly, the slope changes again becoming much more gentle to form the mandibular symphysis. In *Prosaurolophus blackfeetensis* the diastema is much more gently deflected and straighter. A pair of deep longitudinal grooves carves the symphysis. The longest is the most ventral, a clench carved on the medioventral border of the symphyseal end of the dentary. The other groove is found a few millimeters anterior and dorsal to the other clench, and is much shorter. Where the two dentaries articulate their symphyses, the resulting anterior end is U-shaped in cranial view.

Caudal to the diastema is the dental battery. In this region the dentary is mediolaterally wider. The enameled surface of the dental battery forms a convex surface. A thin sheet of bone, the dental lamina, medially covers the battery. The ventral base of the battery is arched, dorsally concave in medial profile. As is typical in hadrosaurs, there is a line of special foramina following the contour of the ventral base of the dental battery. These foramina are evenly distributed, mostly of equal size and anteroposteriorly elongated. Close to the ventral border of the dental battery, the alveoli direct

ventromedially. The special foramina are located at the interface of that ventromedial offset and the dental lamina. Tiny pits evenly distributed carve the medial surface of the dental lamina. When the dental lamina is removed, it is possible to observe up to five teeth in the vertical section of a single tooth position. The most ventral tooth is still emerging. This maximum count is true for the median area of the battery, where it is dorsoventrally deeper. Posteriorly and anteriorly the depth of the dental battery decreases gradually and so does the number of teeth per position. The minimum count observed is two teeth in the last, posterior-most position. When removing the teeth, what remains are the columnar grooves or alveoli of each vertical tooth row. Thin and sharp-edged ridges separate these grooves. Each alveolus is U-shaped in dorsal view. They are anteroposteriorly wider at along the center of the battery, thinning slightly towards the caudal end and, to a less degree, towards the anterior end. In approaching the anterior end of the battery, the alveoli begin to tilt being anteroventrally inclined, instead of being vertically directed. The last, caudal-most alveolus is bounded by a posterior ridge that is more medially salient than the ridges of the rest of alveoli. There is a minimum of thirty-three teeth positions in the dentary. Posterior and ventral to the dental battery, the medial side of the dentary tapers into a mediolaterally compressed, wedge-shaped process. This process contacts the splenial and shows a longitudinal ridge on its medial side.

In occlusal view, there are as many as three teeth exposed, which are sectioned at different heights. Like in *Maiasaura peeblesorum*, the occlusal surface is concave and faces laterodorsally to meet the medioventrally-oriented occlusal surface of the

maxillary tooth row. In *Prosaurolophus blackfeetensis* and *Hypacrosaurus stebingeri* the occlusal surface is flat, and the section of each tooth position is obliquely directed, not

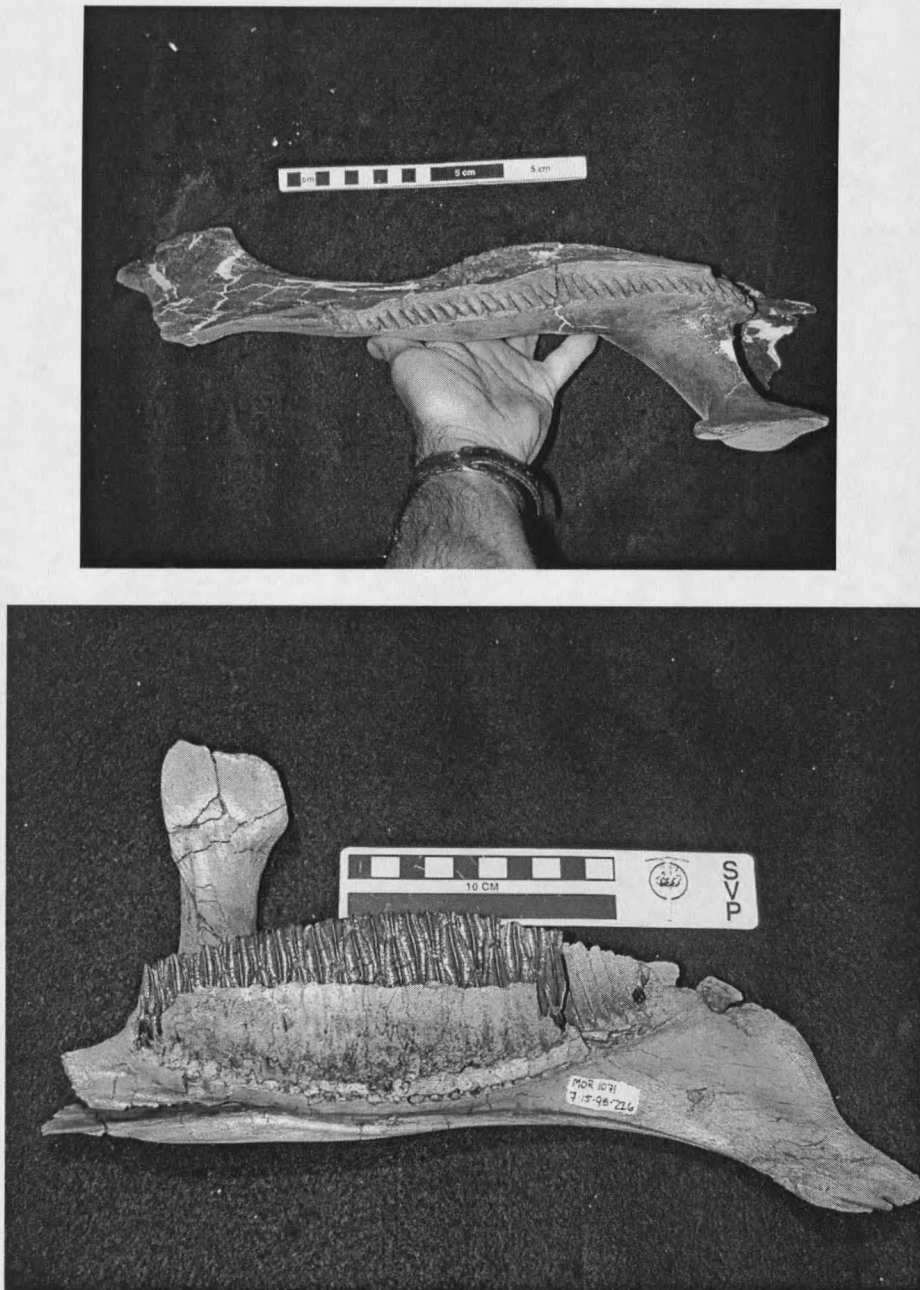


Figure 28. MOR 1071 dentary in dorsal view (top) and subadult dentary MOR 1071-7-15-98-216 in medial view.

mediolaterally straight as in *Brachylophosaurus*. In lateroventral view, only a small fraction of the dorsoventral depth of the dental battery is seen over the dorsal edge of the alveoli.

Medioventrally, near the ventral border of the dentary there is a narrow groove. The groove is shallow and not penetrative along the anterior half of the element. Posteriorly, it becomes gradually deeper until it opens communicating medially into the Meckelian canal, while being craniocaudally wider. The medioventral edge of the dentary is sharp along the posterior half of the dentary and contains oblique striations directed posteroventrally, indicating where the angular was attached.

Interiorly, the posterior dentary contains the Meckelian canal, which exits caudally into a large opening, the Meckelian fossa. This canal is a large conic conduct that tapers anteriorly deep into the interior of the dentary. At the anterior end of the Meckelian canal there is a relatively large foramen. This foramen is very deep and penetrates several millimeters anteriorly. Posteriorly, the lateral wall of the Meckelian fossa is made of a narrow sheet of bone. This delicate sheet possesses a rounded caudal edge and laterally ascends dorsally into the coronoid process. Fine sets of oblique striations are seen on the medial side of the lateral wall of the caudal exit of the Meckelian canal, dorsal to the articulation for the anterodorsal process of the surangular. The anterior portion of the surangular overlaps the inside of the ventrolateral wall of the Meckelian fossa.

The coronoid process is laterally offset from the main body of the dentary and arched towards the medial side of the bone. The process ascends dorsally over the dorsal

border of the dental battery, more than doubling the dorsoventral height of the battery. The dorsal extreme of the coronoid process is expanded and oval, although much expanded anteriorly than caudally. The caudal border of the expanded dorsal portion of the coronoid process runs ventrally to meet the opening of the Meckelian fossa. There, there is a medial, small surface with coarse striations. Caudally, the lateral and medial sides of the coronoid process bound the Meckelian fossa. This last thins dorsally wedging into the caudal edge of the coronoid process, forming a triangular groove. The medial surface of the medial wall of the coronoid process is dorsoventrally concave, being antero-caudally convex in its ventral half, and becoming concave at its dorsal end. The lateral side of the coronoid process is convex. In contrast to *Brachylophosaurus*, the coronoid process in *Prosaurolophus blackfeetensis* tilted anteriorly.

Surangular

The surangular (Fig. 29-30) is the second largest element in the mandible. It is located posteriorly, articulating with the caudal end of the dentary. The surangular articulates medially with the splenial, medioventrally with the angular, and posteromedially with the articular. The bone is anteroposteriorly elongated and arched longitudinally so that the ventral side is strongly convex. The lateral border is rather convex anterior to the quadrate articulation. Anteriorly, the surangular is expanded mediolaterally. In *P. blackfeetensis* the surangular is still more expanded than in *B. canadensis*. In *B. canadensis* the anterior region is dorsally concave and sheet-like, similar to the lateroventral wall of the caudal end of the dentary with which it articulates. Anteriorly, the lateral side sends dorsally a long, mediolaterally compressed process that

continues the craniocaudal arching of the element. This process is anterolaterally directed and nearly as long as the main body of the surangular. Near its dorsal end, the process shows a slightly rugose thickening. There is a narrow surface that slopes anteroventrally formed on that thickening. The dorsal end of the anterolateral process of the surangular is again mediolaterally thin and truncated at its top. The sheet-like anterior expanded region of the surangular overlies the medioventral wall of the posterior end of the dentary. Laterally, the anterolateral process of the surangular ascends applied over the inner (medial) surface of the lateral wall of the dentary and its ascending coronoid process. The anterior region of the surangular contributes to limit the Mackelian fossa of the dentary.

Posteriorly the surangular narrows mediolaterally. The lateral side will then articulate with the quadrate, while the medial surface articulates with the splenial and the angular. The caudal end will articulate with the articular. The medial border of the surangular is mostly divided by a longitudinal and medially projected, low ridge. This ridge separates two grooves. The wider groove located dorsally houses the ventral border of the splenial. The ventral, narrower groove holds the articular. The dorsal border of the surangular along the upper groove for the splenial is dorsally expanded in the form of a sharp ridge. In that area, this ridge separates the medial region of the bone from the lateral one. Posterolaterally from that ridge there is a concave, laterodorsally-facing depression for the reception of the quadrate. That surface is slightly rugose, covered with smooth and small bumps and ridges.

From the quadrate joint the surangular elongates posteriorly into an almost obliquely compressed, caudally projected process. This process wedges posteriorly into a

sharp edge. That edge is laterodorsally to medioventrally oriented, and sinusoidal or arched (dorsally convex) in caudal view, depending on the specimen. An anterior cross-section of the posterior process of the surangular produces a triangular outline that wedges ventromedially. The caudal process of the surangular houses the articulation for the articular bone on its dorsomedial face. Along its posterior-most end the process is convex for the reception of the corresponding concave lateral side of the articular. Along with the articular, the caudal process of the surangular forms the retroarticular process of the mandible. On the opposite, ventrolateral side, the posterior process of the surangular contains a series of coarse striations directed antero-caudally. The ventrolateral surface of the posterior process is concave, as opposed to the flatter, slightly convex dorsomedial surface where the articular sits on.



Figure 29. MOR 1071 surangular in dorsal view.

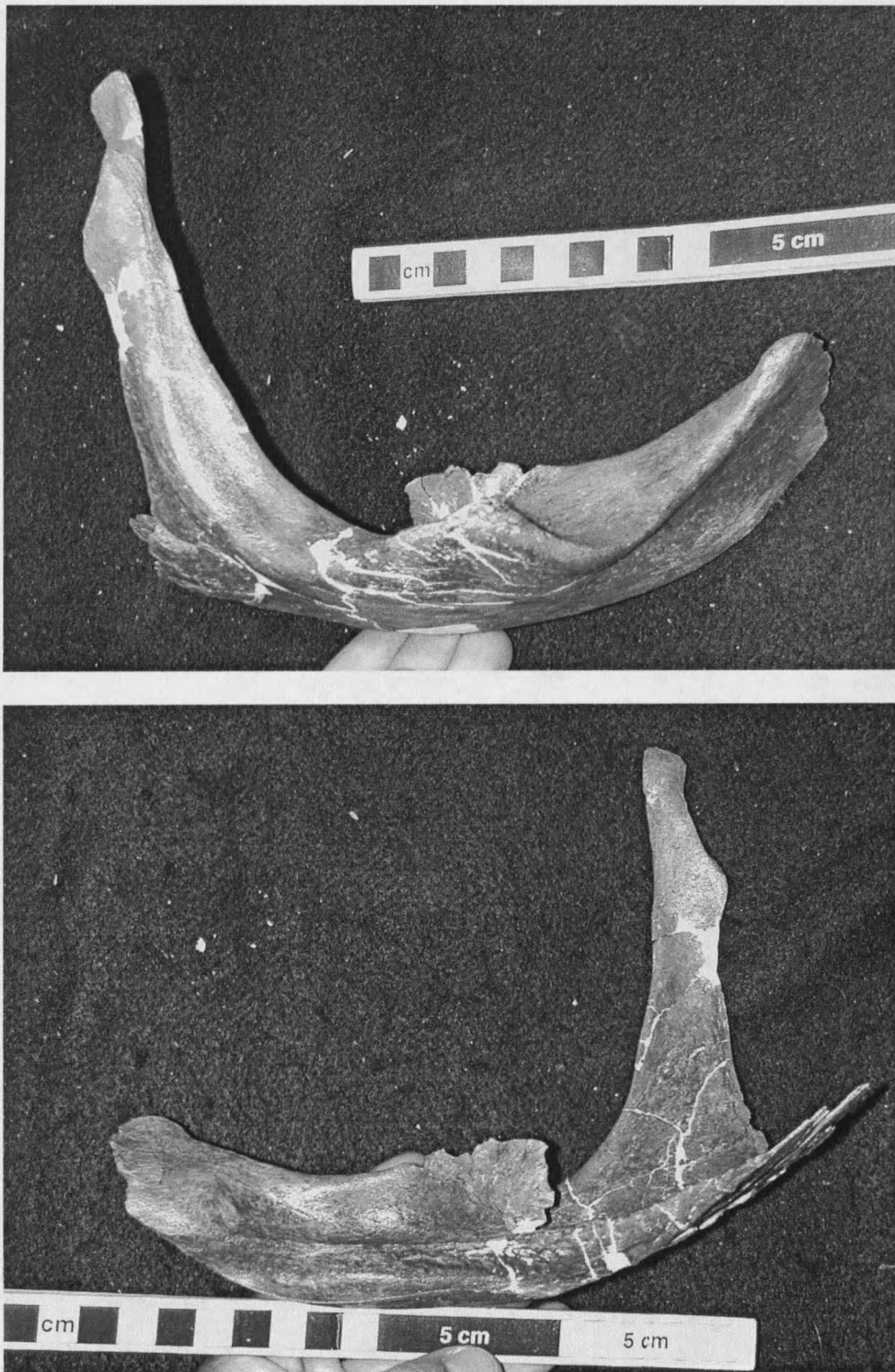


Figure 30. Left surangular MOR 1071 in lateral (top) and medial (bottom) views.

Angular

The angular (Fig. 31) is a rod-like, long bone located on the medial side of the mandible. Posteriorly, the element is mediolaterally compressed and extends all the way along the ventromedial margin of the mandible. The angular articulates anteriorly and laterally with the dentary. Laterally and more posteriorly it joins the surangular. Dorsally the angular underlies the splenial, and caudally joins the articular. In *B. canadensis* the angular is a slender element in relation to the one in *P. blackfeetensis*. In *P. blackfeetensis*, the angular is mediolaterally thicker, more constant in thickness and less irregular in morphology.

The angular is relatively smooth laterally, in contrast to its medial side, which shows an array of longitudinal grooves and ridges, especially along the posterior segment. The posterior segment is mediolaterally compressed, while anteriorly the bone becomes gradually thicker, nearly cylindrical. Ventrally, the bone presents a sharp border along its length, while dorsally the edge is only sharp posteriorly. The mediolaterally compressed posterior segment includes the deepest region. Posteriorly from this, the bone shallows towards the caudal end forming a semicircular profile as seen laterally. That semicircular profile is straight dorsally, while arched ventrally. Anterior to this, the angular becomes shallower, but more gradually, whereas the bone thickens mediolaterally. In dorsal view, the angular is not straight, but slightly sinuous, so that the posterior segment is concave towards the medial side. The grooves on the lateral side indicate the articulations for the other elements of the mandible. A sharp ridge runs longitudinally along the deeper posterior segment of the lateral side of the angular. This

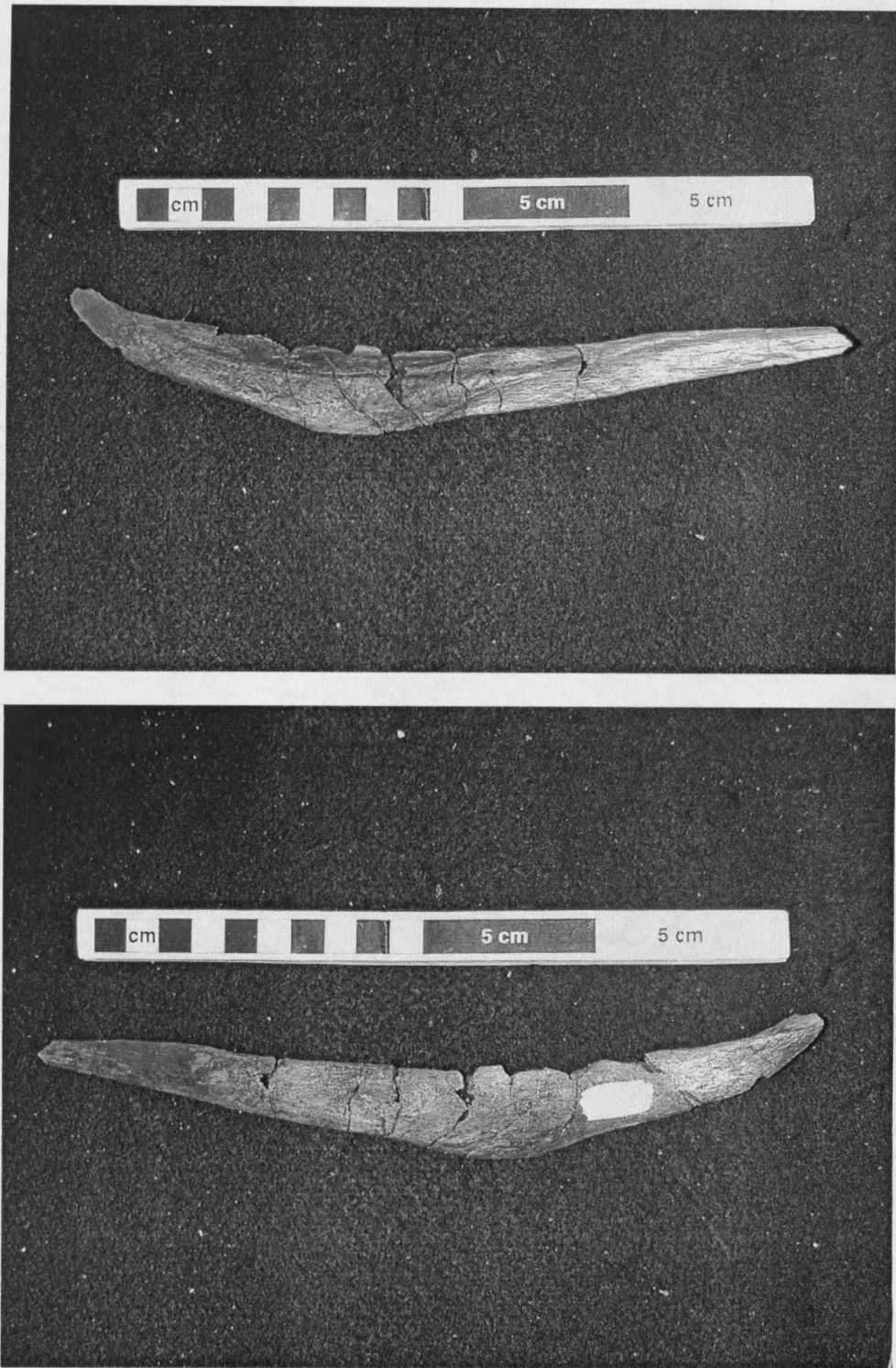


Figure 31. MOR 1071 right angular in lateral (top) and medial (bottom) views.

ridge separates the site for the splenial joint above from the surangular articulation below. The surface for the surangular is rather irregular, because it includes a deep groove filled with oblique and fine striations. The groove is lenticular in outline and accommodates a flattened surface of the medial side of the surangular. In the angular, the posterior convex portion of the surangular joint fits into a longitudinal groove of the surangular. Thus, the lateral surface of the posterior segment of the angular becomes attached to the medial, ventral side of the surangular. There the angular becomes mediolaterally compressed and antero-caudally concave. Its semicircular ventral edge fits into the semicircular medioventral edge of the surangular.

Coming from the ventral edge of the posterior segment of the angular, another sharp ridge ascends anterodorsally on the lateral side of the bone. This ridge converges anterodorsally with the anterior tip of the longitudinal groove described above. At that convergence the angular is mediolaterally thick and triangular in cross section. From this convergence, a single longitudinal ridge runs along the anterior segment of the angular. There, the lateral side of the anterior half of the angular meets the medial border of the dentary, ventral to the medial overture of the Meckelian canal. Medial and ventral to Meckelian canal the groove for the angular extends anteriorly until reaching two thirds of the antero-caudal length of the dentary.

The main longitudinal ridge on the lateral side of the angular serves as the ventral limit of the articulation for the splenial. This joint is dorsoventrally narrow, about half of the width of the surangular articulation facet, and faces laterodorsally. Like the articulation surface for the surangular, the joint surface for the splenial is anteriorly

concave and becomes posteriorly convex. The articular is met along a short segment of the dorsal edge at the caudal end of the angular. There, the dorsal border of the angular is slightly flattened and probably contacts only small portion of the ventral border of the articular. The external, medial surface of the posterior end of the angular shows longitudinal and fine striations. Posteriorly, the medial side of the element presents more striations, but oriented anteroventrally.

Splénial

The splénial (Fig. 32) is mediolaterally thin and antero-caudally elongated. It is located posteriorly on the medial side of the mandible. It articulates with the medial side of the surangular along most of its length, with the articular caudally, with the dentary anteriorly, and the angular along its ventromedial border.

The splénial is arched longitudinally, both antero-caudally and mediolaterally. The bone is dorsally convex when observed in medial view, and medially concave when viewed in dorsal and ventral profile. The articular is dorsoventrally convex on its medial side, while being concave on its lateral surface. Anteriorly the bone becomes deeper near its articulation with the dentary. There, the splénial bifurcates anteriorly into a deeper ventral expansion and a dorsal, shallower one. The anterodorsal border of the splénial probably wrapped around the posterodorsally end of the dental battery, as in other hadrosaurs (Horner, 1992). Along its anterior half of the element, the medial side contains a triangular and wide groove for the reception of the splénial process of the dentary. A central and shallow ridge longitudinally bisects this groove. Dorsally the

groove is well limited by a rounded, laterally curl border. Ventrally and posteriorly the splenial is mediolaterally very thin and blade-like. Anteriorly the lateral groove, the

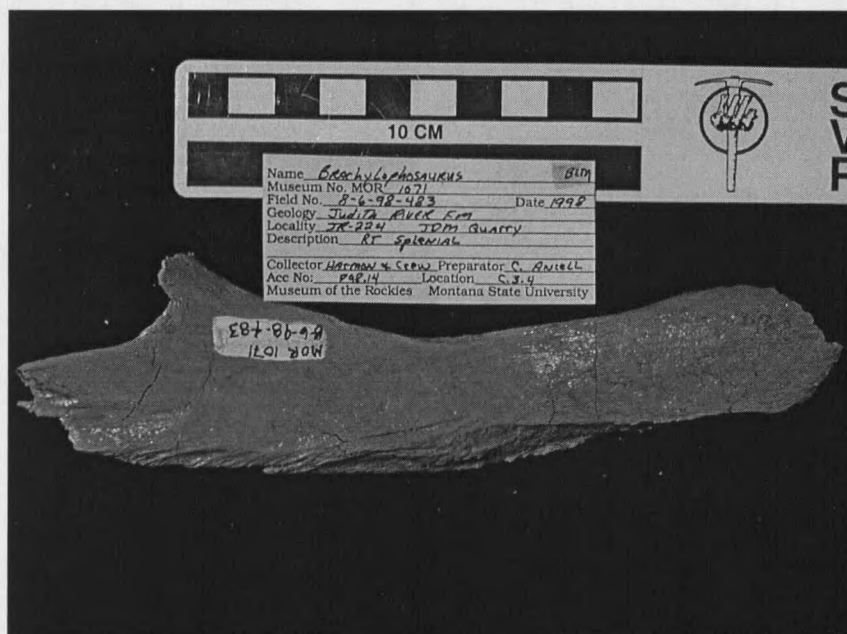


Figure 32. Right splenial MOR 1071-8-6-98-483 in lateral (top) and medial (bottom) views.

medial face of the splenial is concave. Adjacent to the dorsal border, there are two rugose small areas. One is located at the posterior end of the articular joint, while the other one is found near of the beginning of the groove. The surface that houses the medial side of the articular is concave and mediolaterally thin, including the posterior end of the splenial.

The ventral border of the splenial exhibits the articulation surface for the angular. That area is narrow and faces ventromedially. The ventral border is convex along its posterior half, but anteriorly becomes concave. It is ventrally recessed and oriented at the posterior end of the bone. Sets of oblique, anteroventrally directed striations can be seen on the articulation surface for the angular.

In *Prosaurolophus blackfeetensis*, the splenial is deeper, especially along the central and the posterior regions. The triangular groove for the splenial process of the dentary is limited ventrally by a sharp edge in *P. blackfeetensis*, but not in *B. canadensis*. The splenial of *B. canadensis* is more elongated and slender than in *P. blackfeetensis*.

Articular

The articular (Fig. 33) is a small, saddle-shaped element. It is located posteriorly on the medial side of the mandible, contributing with the caudal process of the surangular to form the retroarticular process. The bone is very compressed mediolaterally and antero-caudally than dorsoventrally. The articular is arched, leaving a dorsally concave profile as seen laterally. In contrast, its ventral edge is convex and narrower mediolaterally than the dorsal border. The lateral side is concave and articulates with the convex medial face of the caudal process of the surangular. The medial side contains two surfaces separated by a diagonal, ventrocaudally directed low ridge.



Figure 33. Right articular MOR 1071-8-13-98-554-A in lateral (top) and medial (bottom) views.

The area cranial to that ridge is convex and overlapped by the caudal end of the splenial. More ventrally, a small portion of the posterior tip of the angular would contact the articular. The remaining, dorsocaudal surface of the medial side of the articular is slightly concave and instead of facing medially, faces nearly dorsally, like the mediodorsal surface of the caudal process of the surangular. The dorsolateral border of the articular thickens along the anterior half of the element into a narrow, concave area that articulates with a small medial process of the ventral end of the quadrate.

Horner (1992) discuss the possible presence of a prearticular bone anterior to the anterior border of the articular, based on the rugose anterior surface of this last. As the disarticulated specimens available for *Brachylophosaurus* are broken anteriorly, it is not possible to proof or disproof that claim. And the articulated MOR 794 does not allow an observation of most of the medial and anterior regions of the articular. In contrast to *P. blackfeetensis*, in *B. canadensis* the articular has a flatter concave posterior, dorsomedial face. The articular of *B. canadensis* shows a narrower caudal half of its dorsal border and a narrower quadrate facet. In *P. blackfeetensis* the laterally bent process that contacts the convex medial side of the caudal process of the surangular is more curl, not just inclined laterally as in *B. canadensis*.

The subadult articular is much more compressed mediolaterally, as shown in MOR 1071-7-18-98-282-B. In the subadult, the majority of the body of the articular is a thin blade of bone, which becomes at least three times thicker in the adult. The quadrate facet, while relatively narrow in the adults, is further reduced in the subadult due to the mediolateral compression of the element.

Dentition

Dentary teeth are formed by a long, cone-like root and a diamond-shaped enameled crown. At least four teeth per position have been observed in *B. canadensis* and a maximum of 33 row positions. A maximum of three teeth are seen forming the occlusal surface of a given vertical row. This number descends to two along the caudal and anterior ends of the dental battery. When removing the dental lamina, a convex mosaic of diamond-like teeth crowns forms the medial face of the dental battery. The conic root deepens and curves ventrolaterally into the dentary, tapering gradually into an acute end. The roots of the four tooth of single family apply to each other in mediolateral sucession. The ventral half of the roots is hollow. The anterior and posterior walls of the roots are flat along the hollow ventral segment. Dorsally the root expands mediolaterally, and to a lesser extent anteroposteriorly to support the crown. The crown is dorsoventrally elongated, diamond-shaped and faces medially forming an angle of 35 degrees with the long axis of the root. The crown is enameled on its medial side and is longitudinally bisected by a median carina. The surface of the crown is enameled and strongly concave at each side of the keel. The edge of the crown contains smooth and small papillae. This edge is slightly thicker along the dorsal half of the crown. The crowns of the different teeth of the dental battery are sectioned at different levels by the occlusal plane, depending on the degree of wear and eruption. Figure 34 shows several examples of dentary teeth from the bonebed specimens.

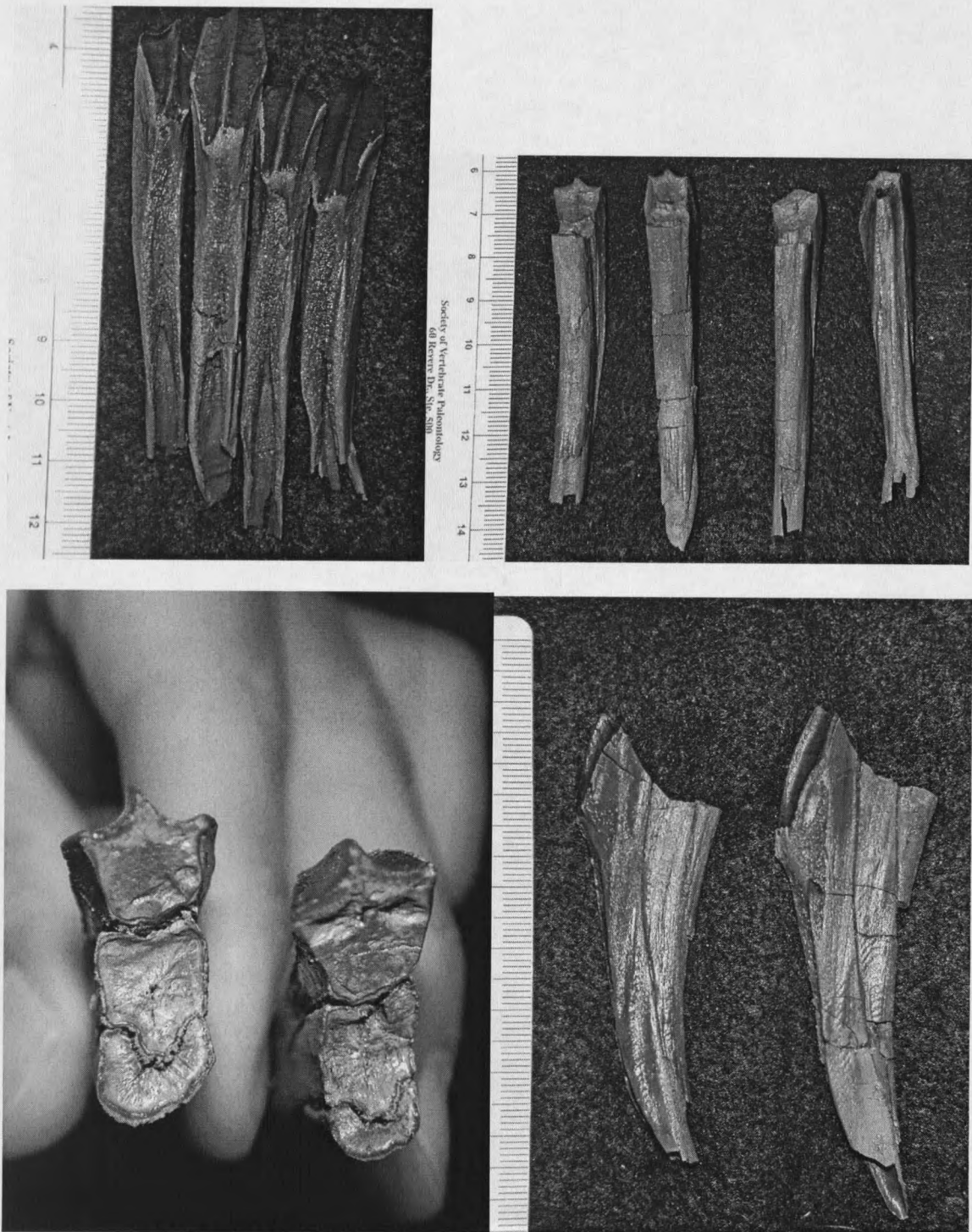


Figure 34. MOR 1071 dentary teeth in labial (top, left), labial (top, right), occlusal (bottom, left) and side (bottom, right) views.

Maxillary teeth (Fig. 35) are slightly different in morphology. They are composed by a rod-like, thin root that expands abruptly to support the crown. There are a minimum of 40 and maximum of 43 vertical rows among the available maxillae, each showing two teeth on the occlusal plane. A minimum of three teeth are present in a single family (i.e. MOR 1071-8-15-98-573), but this figure is probably too conservative, given the depth of the dental battery which might provide room for at least four teeth (as described for *P. blackfeetensis*, Horner, 1992). The arched long roots are relatively thin both antero-caudally and mediolaterally. Internally, the roots are hollow and thin-walled, and open medially, where they join to the succeeding tooth of a single vertical row concealing the enameled lateral side, as already noted by Ostrom (1961). There the roots are semitubular to provide room for the median carina of the lateral side of the crown. Ventrally, the roots expand abruptly, thickening the tooth medially to form the crowns, more than doubling the lateromedial width of the former. The lateral enameled side is not restricted to the diamond-shaped crown, but extends further dorsally into the root. As in the case of the dentary teeth, there is a median carina bisecting longitudinally the lateral, enameled and diamond-shaped side of the crown. This carina does not reach the apical end of the crown, unlike the dentary teeth. The apex of the maxillary crowns is much more blunt and gently curved and rounded as seen anteriorly. The margins contain evenly distributed papillae. The medial, opposite face of the crown is not enameled and varies from being flattened to convex. The anterior and posterior sides of the expanded crowns are concave dorsally. One more difference, previously observed by Ostrom (1961), between the dentary and the maxillary dental battery concerns to the amount and location

of the enamel on the occlusal surface. In the dentary, the enamel is restricted to a rim that corresponds to the sectioned medial side. In contrast, the maxillary occlusal surface shows rims of enamel on the lateral edge of the successive teeth of a single family.

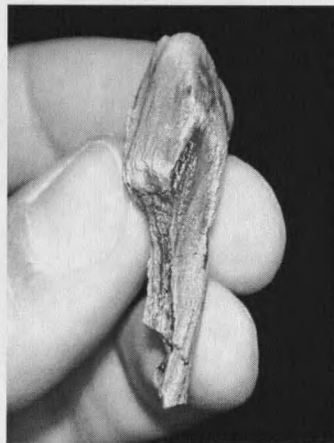


Figure 35. Maxillary teeth MOR 1071 in lingual and side views (top) and labial (bottom) view.

Accessory Elements

Hyoids

The hyoids (Fig. 36 and 37) are long and arched, paired elements located ventral and posterior to the mandible. They are found medioventrally, running parallel to the posterior region of the dentary, the angular, surangular and the retroarticular process. The hyoids are commonly interpreted as the first ceratobranchials (Ostrom, 1961; Trexler, 1995). The elements are composed by a compressed and narrow posterior shaft curved dorsocaudally. In *Corythosaurus* the hyoids are not so arched caudodorsally (Ostrom, 1961, p. 78). Anteriorly the shaft gradually becomes more mediolaterally compressed and expands dorsoventrally having the morphology of an isosceles triangle as seen laterally. The anterior end is slightly expanded mediolaterally. Along the anterior expanded third the lateral surface contains a triangular concavity (contra Trexler, 1995). The hyoids of *B. canadensis* are relatively longer and have a more expanded rostral end than in *M. peeblesorum*. The longitudinal axis of the anterior portion is anterocaudally directed, while the posterior shaft arches projecting dorsocaudally. In ventral view the hyoids are posterolaterally directed. The dorsoventral axis of the hyoids is tilted medially a few degrees from the parasagittal plane. In the articulated skull of MOR 794, the left and right hyoids form a V-shaped structure along the ventromedial, posterior half of the mandible. The expanded anterior portion of the hyoids converges anteriorly to form the apex of the "V", but do not articulate or attach each other. The crescentic anterior end of the hyoids possesses a rugose and mediolaterally expanded surface that faces cranially, side by side

with its counterpart. It is not clear to what structure this anterior surface articulated or attached, but most probably was not to its counterpart.



Figure 36. Articulated hyoids on MOR 794, ventral view of the skull.

Posteriorly the progressively thinner median segment of the hyoids still runs applied to the ventromedial border of the caudal end of the dentary and the ventral portion of the angular. But along the most caudal region of the mandible the hyoid shaft ascends posteriorly overlapping the lateral border of the caudal process of the surangular. The hyoid shaft begins to twist medially so that what would be the lateral side of caudal

end is in fact a dorsolateral face. At that level, the caudal process of the surangular shows a well-developed, striated groove. On the medial side of the hyoid, there is an oblique and short ridge coming from the narrow dorsal border of the caudal shaft. This ridge is sinusoidal in dorsal view and crosses the bone craniolaterally. This feature has been described for the left hyoid of *M. peeblesorum* (Trexler, 1995). The caudal end of the hyoids is more compressed than the rest of the shaft, as the anterior expanded region, and is rather rectangular.



Figure 37. Left subadult hyoid MOR 1071-8-20-98-597-B in medial view.

Sclerotic Plates

Only two disarticulated sclerotic elements have been recovered. These elements are delicate, saddle-shaped small plates that formed a ring around the eyeball (Romer, 1956). The determination of the lateral and medial sides is tentative, until better

preserved and/or articulated material is available. The sclerotic plates exhibit a slightly arched border, probably the one that faced to the internal diameter of the eye. What is here interpreted as the lateral side is transversely convex, but longitudinally concave. About half of the medial side is depressed in the form of a tongue-shaped concavity, presumably for being overlapped by an adjacent sclerotic plate in the actual ring. A ridge separates an external recessed area from a concave inner area and longitudinally divides the lateral surface. That recessed area is covered by short striations perpendicular to the external border, and occupies at least one third of the transversal width of the plate. The non-recessed portion is also cut by an oblique ridge that links with the one previously described, and limits another, still more recessed area. This last recess is tongue-like, salient, and is located at the opposite extreme in relation to the excavation on the medial side. Probably, the tongue-like recess of the lateral side fitted into the depression of the medial side of an adjacent plate.



Figure 38. Pair of disarticulated sclerotic plates from the bonebed.

Axial Skeleton

The vertebral column of the articulated MOR 794 is composed of 31 presacral vertebrae (13 cervicals, 18 dorsals), 9 sacrals (including a dorsosacral and a sacrocaudal contribution), and an indeterminate number of caudals, of which the 32 anterior-most elements are preserved. The neck (Fig. 39) describes a gentle dorsal concave curvature. Posteriorly into the sacral region, the dorsals stretch straight anteroposteriorly into the sacrals and the anterior elements of the tail. A rhomboidal mesh of ossified tendons attaches to the neural spines and the diapophyses from the anterior dorsals through the rest of the vertebral column.

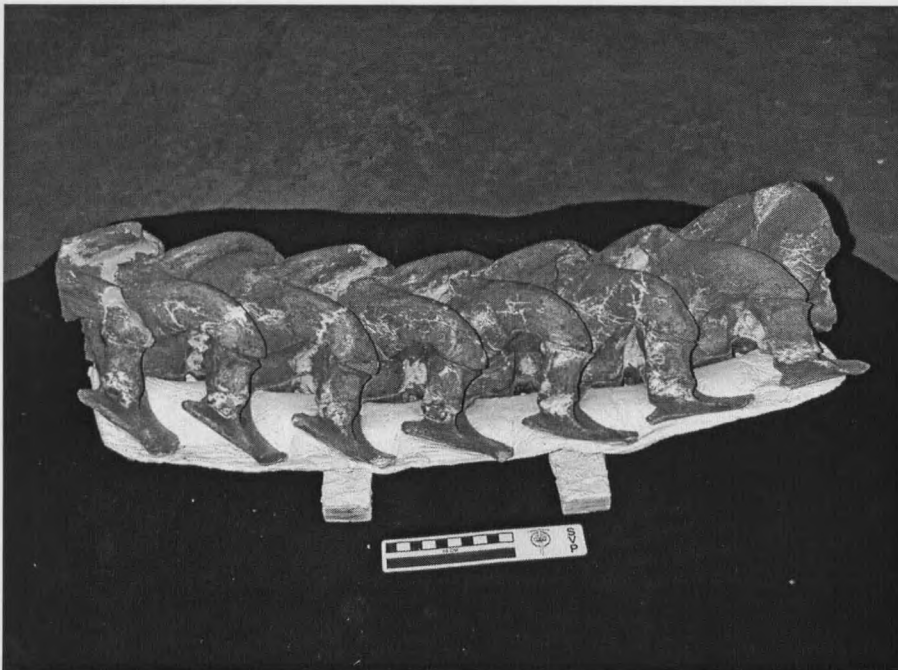


Figure 39. Neck of MOR 794 in left laterodorsal view.

Cervical vertebrae

The atlas (Fig. 40 and 41) of *Brachylophosaurus* is a ring-shaped structure composed of a toroidal intercentrum and a neural arch. The intercentrum is fused to the neural arch through an irregular and inclined facet. The lateral extremities of the intercentrum meet the two halves of the neural arch. The dorsal surface of the intercentrum contains a longitudinal and wide groove. The anterior side of the intercentrum wedges anteroventrally. In contrast, the posterior surface is nearly vertical and convex dorsoventrally. The ventral side of the intercentrum is more expanded anteroposteriorly than the dorsal surface.



Figure 40. Atlas of MOR 794 in right lateral view.

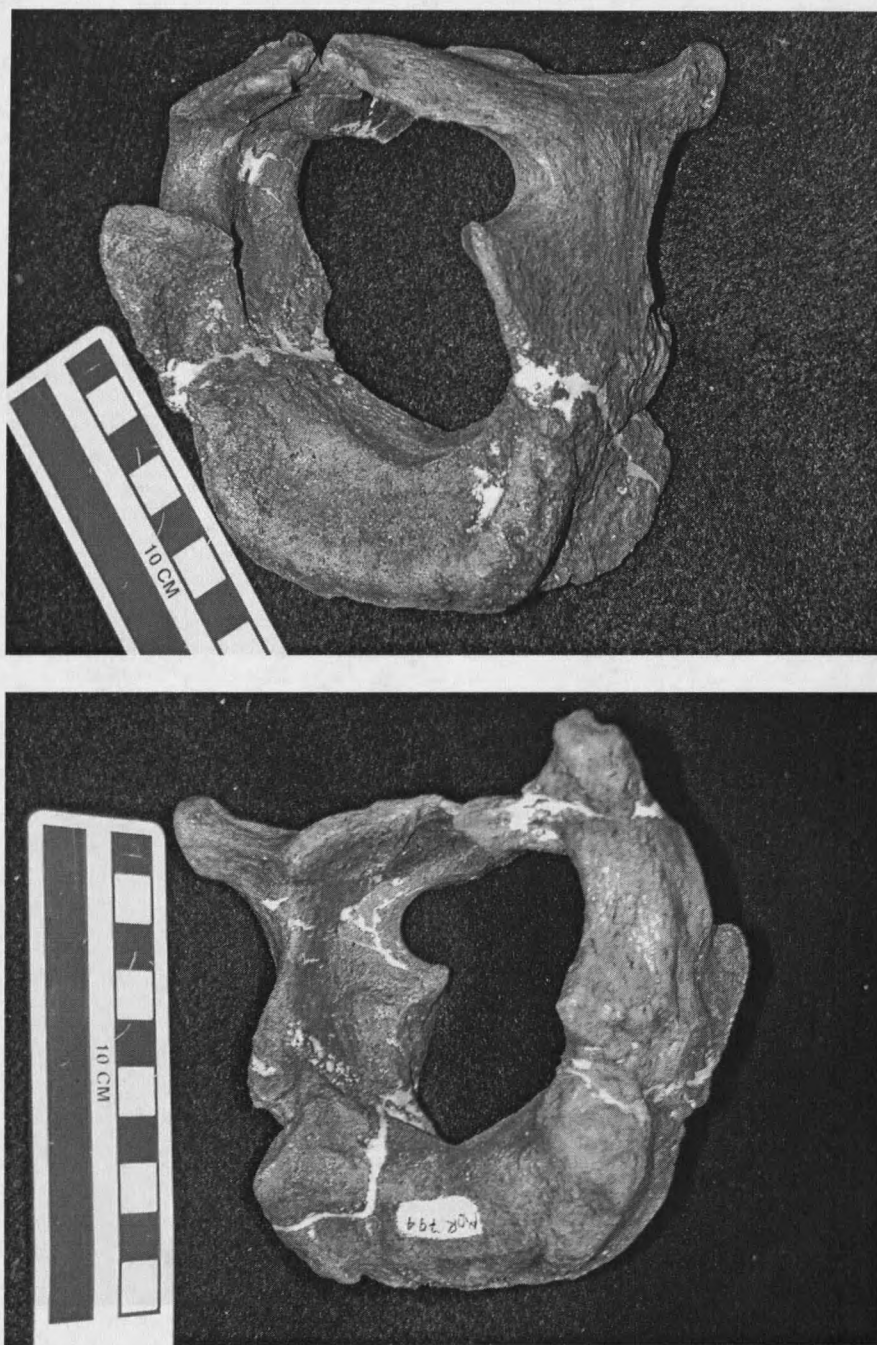


Figure 41. Atlas of MOR 794 in anterolateral (top) and posterolateral (bottom) views.

The lateral sides of the intercentrum are concave and anteroposteriorly expanded, the widest dimension of the intercentrum. The lateral concave side of the intercentrum, below its joint with the neural arch, shows a rugose texture. The neural arch is composed of two halves that do not fuse at the top, leaving posteriorly space for the insertion anterodorsal flange of the neural spine of the axis. Two short posterodorsal, lateral process project from the laterodorsal corner of each half of the neural arch. These processes end caudally into a rounded extreme. The processes are compressed mediolaterally. Medially from those processes, the dorsal surface of the neural arch is concave and sends a pointed and short process posteroventrally. On the ventromedial side of these pointed projections there is the ellipsoidal facet of the postzygapophysis. In lateral view, the neural arch is craniocaudally expanded in the ventral and dorsal regions. The lateral side of the neural arch that joins the intercentrum is slightly convex. Ventrally there is a triangular anterodorsal projection. Dorsal to this the lateral wall of the neural arch is anteroposteriorly constricted. Dorsally the laterodorsal side of the neural arch expands again anteroposteriorly into an anteromedial blade. Posteriorly there are the rounded processes of the laterodorsal corner already described. Medially the walls of the neural arch are excavated.

The centrum of the axis (Fig. 42 and 43) is strongly opisthocoelous and elongated craniocaudally. The cranioventral end is sharp and wedge-shaped. In ventral view the centrum is hourglass-like in shape because the element is mediolaterally constricted in the middle region. There is a median ridge running craniocaudally on the mid ventral region of the centrum.



Figure 42. Axis of MOR 794 in anterolateral (top) and left lateral (bottom) views.



Figure 43. Axis of MOR 794 in caudal view. Note the deformation of the element.

Craniodorsally, the centrum shows an odontoid process, ventral to the prezygapophyses. The odontoid process is spoon-shaped and thicker along its cranial border. Laterally it becomes thinner posteriorly, ending in a narrow ridge. The dorsal surface of the process is concave deepening posteriorly towards the neural canal. Ventrally the odontoid process is concave, showing a ventrally salient anteroventral edge. The odontoid process is wider mediolaterally than anteroposteriorly. The neural arch supports neural spine and the zygapophyses. The neural spine is strongly compressed mediolaterally. It shows forms an arched flange that occupies the anterior half of the

neural spine. The flange ends in a hooked anterior tip. The lateral surfaces of this flange are carved with a small, dorsally radiating framework of ridges. Posterior to the flange, the postzygapophyseal processes are two massive, well-developed structures that expand caudally. The processes and diverge laterocaudally, so that in dorsal view, the flange plus the postzygapophyseal processes describe a "Y". The postzygapophyses have ellipsoidal surfaces and face lateroventrally. A laterocaudally directed flange that ends posteriorly in a small, sharp epiphysis forms the top of the postzygapophyseal processes. The prezygapophyses are located over the craniolateral portion of the neural arch. They have elongated facets that face laterodorsally. The diapophyses and parapophyses are short processes fused to the cervical ribs. These ribs are also short elements that extend caudally parallel to the centrum. The medial side of these ribs is concave and is bisected by a longitudinal ridge. The ribs are very thin-walled and have convex lateral surfaces. The dorsoventral width of the ribs thins caudally until they end in a truncated extreme.

Cervical vertebrae (Fig. 44 and 45) are very broad mediolaterally, more as progressing caudally through the series into the dorsals. While all the cervicals exhibit huge postzygapophyseal processes, low neural arches and tiny neural spines, the last one is notably different, in possessing a relatively high neural arch, shorter postzygapophyses, and a D-shaped neural spine. The cervical centrum is strongly opisthocoelous, craniocaudally elongated and wider than high, dorsoventrally compressed. In caudal view the centrum kidney-shaped in outline, concave along the dorsal border and convex along the ventral one. The craniocaudal length of the centrum gradually decreases posteriorly.



Figure 44. MOR 1071--15-98-221, cervical vertebra in dorsal (top) and anterior (bottom) views.



Figure 45. Cervical vertebra MOR 1071--15-98-221 in right lateral view.

In cervicals 3, 4 and 5 the lateral outline of the caudal end of the centra is cranially tilted, so that the dorsal border is more anteriorly positioned than the ventral one. More posterior cervicals (mostly from the ninth vertebra) have a more vertical, lateral profile of the caudal edge of their centra. Ventrolaterally the centrum is compressed below the parapophyses, having an oval, extensive depression. There are two longitudinal grooves on the ventral face. These features are best expressed in the anterior cervicals. The anterior side of the centra is formed by a hemispherical convexity. The dorsal surface of the centra is longitudinally depressed. The centra are more expanded mediolaterally in its caudal section. The neural arch is anteroposteriorly elongated. Their walls have a constant thickness in the more anterior cervicals. In more posterior cervicals

the walls thicken caudally, probably associated with the more developed postzygapophyseal processes. In the anterior cervicals the neural canal is rounded as seen anteriorly, but in the more caudal cervicals it becomes more triangular, concave ventrally and A-shaped dorsally. Posteriorly the dorsal, anteroposterior length of the neural arch decreases in length. The slope of the roof of the neural arch becomes more vertical posteriorly along the neck. In cervicals 12 and 13 the neural arch becomes almost vertical, higher, expanded dorsoventrally and relatively shorter anteroposteriorly, as in the first dorsal vertebrae. The anterior, dorsal edge is thicker in the last two cervicals. In cervicals 12 and 13 the neural spine decreases gradually in size until it leaves a smooth, non-salient surface dorsal to the roof of the neural arch.

The postzygapophyses are supported by large, massive postzygapophyseal processes that arch caudoventrally to meet the prezygapophyseal facets of the following vertebra. In the more anterior cervicals the cranial portion of the postzygapophyseal processes is longer than its caudal segment. These processes remain large and massive throughout the series, although they are relatively less massive and craniocaudally shorter in the anterior and last two cervicals. The articular facet of the postzygapophyses is a large, ellipsoidal surface that faces ventrolaterally. In the more anterior cervicals this facet is more rhomboidal in shape, caudally pointed and more individualized from the body of the postzygapophyses. Dorsally each postzygapophyseal process describes a V-shaped morphology. This "V" opens posteriorly along the series until reaching a maximum in cervical eleven. Cervical twelve has shorter postzygapophyseal processes. Its postzygapophyseal facets face more ventrally than laterally. It is in cervical twelve,

thirteen, and in the anterior dorsals where the neural arch increases in height. A peculiar feature of the postzygapophyseal process in the cervicals is a salient and pointed, V-shaped process located where the processes reach its maximum curvature. The apex of that "V" points laterally. The prezygapophyses are oval and cranially pointed in the anterior cervicals but become more subrectangular and mediolaterally elongated towards the posterior cervicals. There is a shift in the position of the prezygapophyses between cervical four and five. In cervicals three and four the prezygapophyses are located craniolaterally as in the axis. From the fifth vertebra the prezygapophyses are located laterally from the neural arch. The neural spine of the cervical vertebrae is small and only partially preserved. The neural spine was probably extended along most of the craniocaudal extent of the neural arch in the anterior cervicals, except on the cranialmost edge of it. The neural spine was shorter in the more anterior cervicals to gradually increase in size and thickness posteriorly. The diapophyses root throughout the lateral side of the neural arch, but only at the cranioateral half in the more anterior cervicals. They are fused to the prezygapophyses and are lateromedially short in the more anterior cervicals. Posteriorly the diapophyses increase gradually in mediolateral length, becoming as long as the dorsoventral height of the caudal. The diapophyses are located ventral to the prezygapophyses in the middle and posterior cervicals, and caudoventral in the axis and vertebrae three and four. The diapophyses are ventrally arched and articulate lateroventrally with the tuberculum of the cervical rib. The parapophyses protrude from the lateral side of the centrum and anteriorly abut its anterior hemispherical convexity. They are short processes and show an oval facet that is craniocaudally elongated.

Dorsal vertebrae

There are 18 dorsal vertebrae in *B. canadensis* (Fig. 46-49) Posterior to the last cervical, the zygapophyses become reduced in size, especially the postzygapophyses, which become smaller and dorsoventrally thinner, especially between dorsal two and three, and from the third to the fourth. The centra become heart-shaped in caudal view and are less opisthocelous in relation to the cervicals. The transverse processes increase in length and are located dorsolaterally and caudolaterally. The neural spine gradually becomes more rectangular, dorsoventrally higher and moderately tilted caudally.



Figure 46. Anterior dorsal vertebra MOR 1071 in anterolateral view.



Figure 47. Anterior dorsal vertebra depicted in figure 46, here seen in right lateral view.

In ventral view, the centrum is hourglass-shaped, possessing a keel formed as a result of the mediolateral compression of its ventral portion. Proximodistally oriented striations radiate from the caudal and cranial borders. The neural canal is oval, slightly wider medilaterally. The first dorsal vertebrae is similar to the last cervical. The postzygapophyses are still massive, but short and stocky elements. However the postzygapophyses of the first dorsal are slightly more caudally directed. Its transverse processes is still laterally and horizontally directed, but antero-caudally wider than in the last cervical. The neural spine is larger than in the last cervical and is more dorsally located. It is a D-shaped blade, longer and strongly directed caudally. The second dorsal still resembles the first one in its stocky postzygapophyses, and the thin, blade-like D-shaped neural spine. In this second element the neural spine is larger, the

postzygapophyses are thinner and more caudally directed. The transverse processes are subrectangular in dorsal view and thicker. These diapophyses begin to tilt dorsally and caudally. Dorsal vertebra three is already rather different from the previous two. The neural spine is much sharper and ends caudally in a triangular apex. The postzygapophyses are suddenly reduced in size, being much thinner dorsoventrally and anterocudally shorter. The transverse processes are dorsolaterally and caudolaterally, oriented and become longer. The fourth dorsal possesses still more dorsocaudally-directed transverse processes. The diapophyses are trapezoidal in lateral view, with concave cranial, dorsal and especially ventral, sides. The tuberculum articulates with its head fitting in a caudoventrally-facing concavity of the diapophyses. Dorsally the diapophyses begin to be anteroposteriorly wider proximally, a trend that will continue caudally in the series. The neural spine is similar to the third dorsal, in being a long caudally curved, thin blade of bone. It is nearly as long as the third one, but the tip is not so sharp, but flattened. The fifth dorsal initiates a big change in the series, which consists in the possession of flat-topped, subrectangular neural spines. Dorsal six and seven posses a neural spine that is taller and more rectangular, although still caudally inclined. Dorsal eight shows the widest neural spine. Gradually and caudally along the series the neural spines become more dorsoventrally oriented and less caudally tilted. This is achieved by dorsals ten and eleven. Along the middle dorsals the lateral sides are concave and converge ventrally into a narrow edge. There are several deep, parallel foramina on the lateral sides of the centrum. These are proximodistally elongated and lenticular in profile. The parapophyses consitute an oval excavation located under the base of the

diapophyses, dorsally on the lateral side of the neural arch. The postzygapophyses are two ellipsoidal, smooth facets, larger than in the more anterior dorsals. They face lateroventrally. The prezygapophyses are similar in size, shape and texture than the postzygapophyses. These facets are located dorsocranially over the neural arch and face craniodorsally. The neural spine is a subrectangular, dorsally elongated, and thick.



Figure 48. Dorsal vertebra MOR 1071 in anterolateral view.

Posteriorly from dorsal twelve, the neuroapophyses are rather straight proximodistally, and are less flattened caudolaterally, slightly less proximodistally wide and slightly convex, lenticular in cross-section.



Figure 49. Dorsal vertebra shown in figure 48, seen here in left lateral view.

Sets of striations can be seen near of the dorsal edge of the neural spines. In the middle dorsals the diapophyses are triangular and strongly back-turned. In the most posterior dorsals the diapophyses stretch laterally horizontally, not dorsolaterally as in the median and anterior dorsal vertebrae. The centrum of posterior dorsals is more oval and less heart-shaped. The ventral portion less mediolaterally constricted into a keel, although is still compressed. The centrum is higher, being equally long proximodistally than mediolaterally width. The centrum of the more posterior dorsals is anteroposteriorly short in relation to the middle and anterior dorsals. The parapophyses are reduced in size. They form two oval excavations facing cranio-laterally adjacent to the craniodorsal border of the medial segment of the diapophyses. Laterally, the parapophyses continue under the craniodorsal border of the diapophyses in the form of a groove, which disappears

gradually towards the lateral end of the transverse processes. The neural spine is widest at the base and near the dorsal end. The diapophyses are not dorsocaudally projected, as in the middle and anterior dorsals, but stretch horizontally. However, they maintain a dorsal lift of no more than 25 or 30 degrees from the horizontal, less than in the preceding dorsals.

Sacral vertebrae

The sacrum (Fig. 50) is composed of nine fused vertebrae, including a last dorsal fused to the first sacral and a last sacral fusing with the first caudal. The centrum of the dorsosacral vertebra is relatively robust. The next seven sacrals are ventrally united along the longitudinal iliac blade. This blade is ventrally made of the parapophyses. Dorsally the seven sacral vertebrae are united through their diapophyses, both of which fuse with the central body of the ilium. In ventral view, this iliac bar begins anteriorly rather parallel to the centra to diverge laterally in going posteriorly. The iliac bar fuses with the ventral third of the medial surface of the central body of the ilium. Sacral vertebrae are distinctive from the other vertebrae of the column by the possession of bone laminae linking the ventral side of the transverse process with the lateral side of the neural arch. These laminae attach to the medial side of the ilium.

Sacral neural spines are relatively tall, subrectangular and craniocaudally thicker than anywhere else in the vertebral column. At their dorsal ends they become wider and thicker. The neural spines are slightly arched with the concavity facing anteriorly, while being progressively more caudally tilted. Dorsally the neural spines show striations. The postzygapophyses are elongated and ellipsoidal, facing lateroventrally.

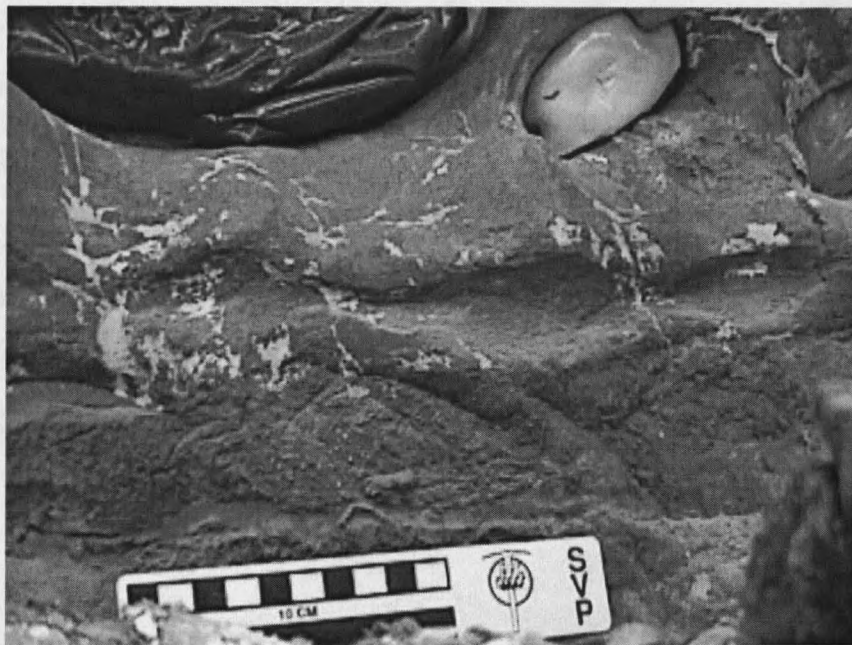


Figure 50. Sacrum of MOR 794 in ventral view (top). Detail of the groove along sacral vertebrae seven to nine.

The prezygapophyses are similar in shape to the postzygapophyses and face dorsomedially. On the lateral sides of the neural arch, on each the caudal and cranial sides of the lateral laminae, there are cone-shaped, deep depressions. The transverse processes are horizontal and stretch laterally. They are relatively narrow craniocaudally and subtriangular in cross-section. The fourth through the sixth sacral centra are relatively slender. Sacral seventh through ninth become larger in size. The neural spines increase gradually in anteroposterior width from the third sacral, being widest on sacra seven and eight. The sacral centra are rather compressed mediolaterally, producing a keel on the ventral surface. The transverse process of the sacrodorsal vertebra is shorter than in the last dorsal and projects laterodorsally to curve ventrally at its distal end.

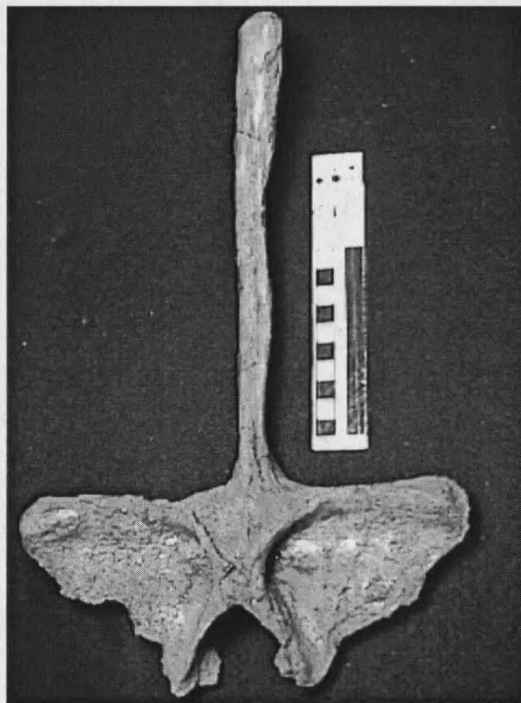


Figure 51. Subadult sacral neural arch and spine, in anterior view (MOR 1071-8-13-98-543).

The pubic peduncle is anteriorly linked to the first three sacrals by means of two sacral ribs. These ribs could well be an overgrowth of the parapophyses, given their relatively ventral position. The first, most anterior of these structures grows from the lateral side of the caudal border of the centrum of the sacrodorsal vertebra. The rib is mediolaterally compressed, and sends two branches, one branch caudodorsally and the other one caudoventrally, which crosses the centrum of the second sacral to meet a short bar of bone. This bar receives also the second rib seen on the lateral side of MOR 794 and connects with the pubic peduncle of the ilium. This second structure is more like a thick ridge that protrudes from the lateral side of the centrum of the third sacral. The transverse processes become horizontally oriented along the last three sacrals. Dorsally and parallel to the iliac bar, from the second until the seventh sacral, the transverse processes are antero-caudally bridged each other from one to the following vertebra. In MOR 794 this is preserved in sacrals two and three, but broken in the other ones. Ventrally the transverse processes fuse with the iliac bar. This union forms a thin wing of bone (Fig. 50 and 51) that stretches in each of these sacrals from the transverse processes ventrally and laterally to the iliac blade. The fused diapophyses attach to the dorsal portion of the medial surface of the ilium, and help to support the element along a longest distance than the iliac bar, from the most anterior portion of the postacetabular blade to the caudal third of the preacetabular process. In this last and along the central body of the ilium, the diapophysis attach to the medial ridge of the ilium. There is a groove running ventrally along the centra of sacrals seventh through nine. The groove appears suddenly after the smooth, but convex ventral side of the sixth sacral. A sacrum of *Hypacrosaurus*

stebingeri (MOR 549) exhibits a ventral groove, indicating that the presence of groove is not diagnostic at subfamily level.

Caudal vertebrae

The nearly complete tail of *Brachylophosaurus* is shown in figure 52. Caudal centra are mediolaterally wide and hexagonal as seen in cranial and caudal views. Anterior caudal central is anteromedially compressed, but become gradually more elongated posteriorly along the series. More posterior caudals show a more perfect hexagonal contour, with more marked edges. The transverse processes are narrow, rod-like, and horizontal. On the anterior dorsals the distal end of the diapophysis is curved ventrally. These transverse processes attach to the dorsal, central border of the centra and to the lateral edge of the neural arch. The neural spine is mediolaterally thick at the central area and ellipsoidal in cross section. The neural spine projects caudodorsally. Longitudinal striations are seen along the dorsal third of the neural spine. The base of the neural spine shows a dorsoventrally wide and straight indentation along the ventral edge, just dorsal to the postzygapophyses. Dorsally this indentation is followed by a thin ridge that continues almost until the dorsal end of the neural spine, decreasing gradually in height. At The cranial edge presents another low ridge that disappears gradually dorsally before reaching half the height of the neural spine. The neural canal is circular and relatively small. The zygapophyses are small and oval facets (Fig. 53). Anteriorly, the prezygapophyses are more circular than the postzygapophyses and are supported and projected craniodorsally by two short prezygapophyseal processes. The space between the prezygapophyses is a U-shaped, concave surface. The postzygapophyses are found

hanging from the caudoventral surface of the base of the neural spine, adjacent to the dorsal border of the neural arch. They are supported by two short postzygapophyseal processes. Chevrons attach to the ventral surface of two successive centra. The anterodorsal portion articulates with the caudal region of the centrum, while the dorsocaudal portion articulates with the cranial region of the caudally adjacent centrum. There are two pairs of rounded and concave excavations, one on the cranioventral and the other pair on the caudoventral border of each centrum. The centra are strongly concave on their lateral sides. They are platycoelic, with show only slightly concave cranial and caudal surfaces. Posteriorly along the series there is a decrease in the length of the transverse processes.

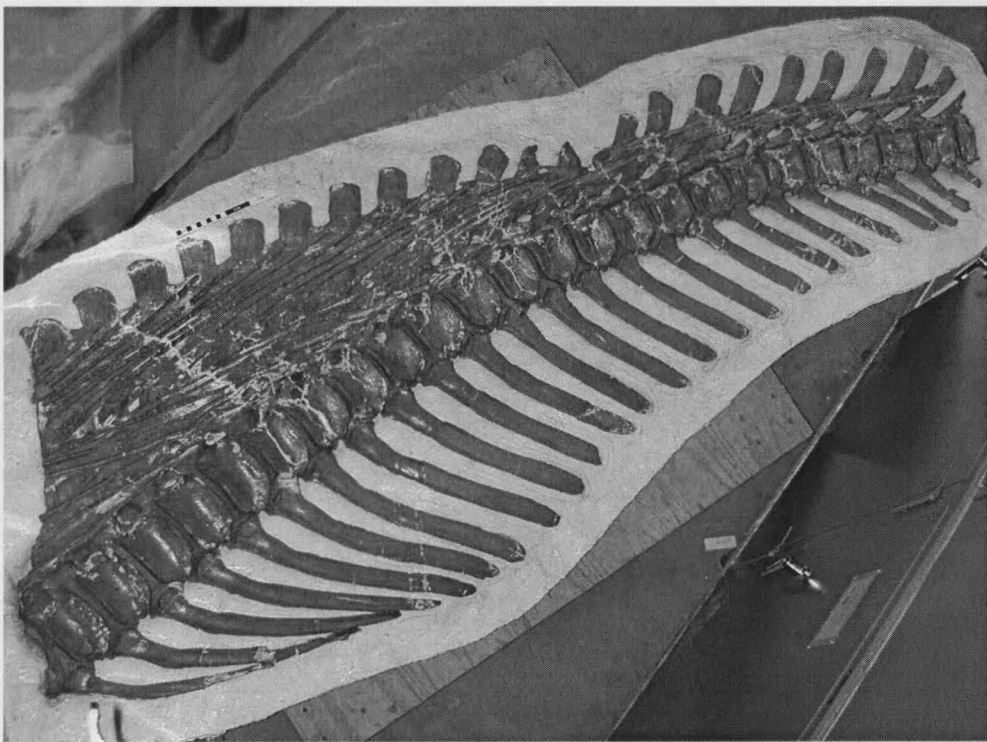


Figure 52. Articulated tail of MOR 794 in left lateral view.

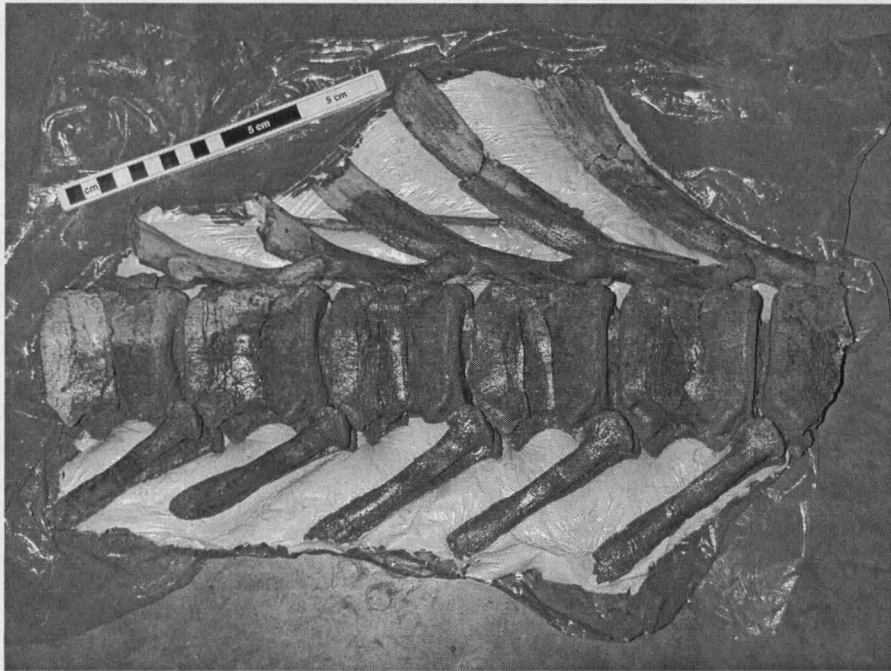
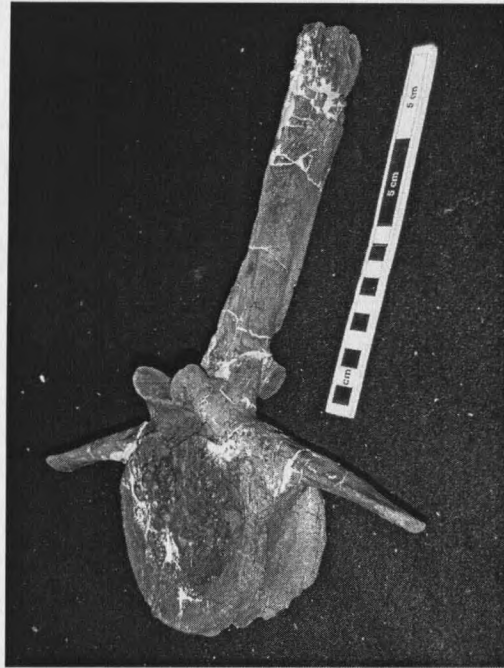


Figure 53. Caudal vertebrae in anterolateral view (MOR 1071-8-4-98-466) (top). Distal portion of the tail of MOR 794 in right lateral view (bottom).

The postzygapophyses shift more dorsocaudally. The neural spine becomes more caudoventrally inclined and there is a decrease of its height (Fig. 53). The transverse processes decrease in length until disappearing from caudal thirty. From caudal vertebra seventeen to nineteen the diapophysis is reduced to a rugose tubercle.

Cervical ribs

All the cervical vertebrae, except the atlas, exhibit ribs (Fig. 42). The ribs show a short and compressed main branch that bifurcates cranially into two more rami, a capitulum and a tuberculum. The medial side of the cervical ribs is concave and bisected by a longitudinal ridge. The lateral side is convex and smooth. The main ramus projects laterocaudally. The tuberculum is the shorterst of the two and projects dorsally to attach with the transverse process. The capitulum projects medially and is longer, articulating with the parapophysis, which is located around the center of the lateral surface of the cervical vertebra. Both the tuberculum and the capitulum are craniocaudally expanded and blade-like. Both processes are expanded at its ends, forming oval, craniocaudally elongated and rugose surfaces for attaching to the diapophyses and the parapophyses. The capitular articular surface is more expanded craniocaudally. The main ramus of the cervical ribs extends a short distance cranially into a tapering end after giving rise to the tuberculum and the capitulum. The ventral surface of the capitulum is smooth and slightly convex, while the lateral side of the tuberculum and the anterior portion of the lateral side of the rib form a strongly concave surface. Posteriorly the main ramus of the cervical ribs shortens craniocaudally and widens mediolaterally. The capitulum becomes longer. In

lateral view the orientation of the main branch of the anterior ribs is caudoventral, but in the more posterior ribs becomes horizontal, parallel to the ventral surface of the centra.

Dorsal ribs

The dorsal ribs form a dorsoventrally deep and anteroposteriorly short rib cage (Fig. 54). The ribs tend to converge together distally, with the only exception of the more posterior elements. The distance between two consecutive ribs increases posteriorly. There is no gradual change between cervical and dorsal ribs. Thus, the first dorsal rib has already a long shaft that bifurcates dorsally into a short capitulum and a shorter tuberculum. The capitulum is at least five times longer than the tuberculum. Most of the dorsal ribs show a mediolaterally flat, tape-like shaft. The shaft is arched dorsoventrally, mostly on the central, larger ones. This shaft becomes mediolaterally thicker mediolaterally the dorsal end, in order to give rise to the capitulum. This is accomplished by the formation of a longitudinal thick and smooth ridge located on the medial surface of the shaft. This ridge arches craniodorsally to form the capitulum, which projects craniolaterally to attach to the parapophysis of the centra. The remaining medial surface of the rib is recessed in respect to that ridge, and the lateral surface is then limited thin caudal and cranial edges along the dorsal third of the shaft. The cross-section of the proximal-most portion of the shaft is a medially concave triangle. The lateral side of the shaft of the rib is convex. The more anterior ribs are mediolaterally more compressed, with the capitulum almost aligned with the main shaft and the median ridge strongly displaced cranially. Thus, the capitulum is almost cranially projected, and the medial side of the head of the rib becomes a concave, smooth surface.



Figure 54. Rib cage of MOR 794, in left lateral view.

The more posterior dorsal vertebrae show parapophyses located also cranial to the diapophyses, but more horizontally projected, so that the capitulum must project medially. The capitulum is rectangular and compressed craniocaudally. It is expanded at its end to form the articular facet for the parapophysis, having an ellipsoidal cross-section. The tuberculum is a very short process that projects dorsally from the lateral surface of the rib. Its caudal edge is thin and continues smoothly into the caudal edge of the shaft. Dorsally the capitulum is expanded, forming an oval articular facet for the diapophysis. The two first dorsal ribs are different from the third and following elements. Dorsal rib one is relatively short, about half the length of the largest ribs, and its shaft tapers ventrally into a pointed end, as in the second rib. However, the second rib is much longer, one fourth shorter than the following larger ribs. The shafts of the first and second

ribs are not medially concave in cranial and caudal profile. The last five ribs are progressively more laterodorsally tilted, opening towards the lateral side. As in the more anterior ribs, the last dorsal ribs are progressively shorter dorsoventrally. The caudal-most ribs exhibit mediolaterally wider shafts and less sharp-pointed distal ends.

Chevrons

The chevrons, or haemal arches, are elongated elements that attach to the ventral side of the centra of the caudal vertebrae. They are composed by a distal shaft that bifurcates dorsally (proximally) into two symmetrical rami. The shaft is mediolaterally compressed, as are the two proximal rami. The two proximal extremes of the chevron, which includes the attachment sites for the centra, are expanded craniocaudally and thicker mediolaterally than the shaft. The proximal rami are more mediolaterally compressed than the shaft. The lateral side of these rami is convex in the more anterior elements. In cranial view, these rami define a U-shaped outline. Posteriorly, that space becomes V-shaped. The chevrons are longer than the neural spines. The chevrons are caudoventrally oriented through the caudal series. Anteriorly, the shaft is at least twice and a half as long as the two proximal rami. It is more cylindrical in cross-section in the most anterior elements. Posteriorly the shaft becomes more mediolaterally compressed and by the fifth chevron it becomes blade-like. The first five or six chevrons are distally sharp-ended and pointed, arching caudally. The chevron located between caudal six and seven becomes rounded at its distal tip, although its shaft is still distally tapering. The next chevron has a more straight and craniocaudally wider, non-tapering shaft and its distal end is wide and rounded. Posteriorly along the series the shaft shortens gradually,

becoming equal in length to the proximal rami. In the most posterior elements of the tail the shaft is lost and only the two rami are present. Thus, last chevrons are small minute, V-shaped elements.

Ossified tendons

A rhomboidal lattice of ossified tendons extends over the lateral surfaces of the neural spines of the dorsal, sacral and caudal vertebrae. The net of tendons is constituted by elements that orient dorsocaudally to anteroventrally crossed by elements arranged in the opposite direction. The number of ossified tendons present in a given neural spine increases with the dorsoventral height of the spines. Individual ossified tendons are rod-like. Some ossified tendons are cylindrical while others are more tape-like and compressed. There is another set of thinner tendons anteroposteriorly oriented and attached to the lateral side of the tuberculum and around the lateroventral area of the diapophyses. This set of tendons runs parallel to the dorsal profile of the rib cage. A fourth set of tendons consists of the ones that attached to the diapophyses. In the caudals these tendons are found in a row of two elements running antero-caudally, attached on the dorsal, proximal portion of the diapophyses, at their junction with the centra and the neural arch. These tendons end about the tenth or thirteenth caudal vertebra, where they are very thin and tapered.

The most anterior ossified tendon attach to the neural spine of the third dorsal vertebra. In the fourth dorsal neural spine another tendon joins ventrally to the first one and possibly there was another one dorsally. The fifth and sixth dorsal neural spines

continue to support three tendons. Two more tendons attach to the caudal portion of the sixth neural spine. More ossified tendons are added in the eighth dorsal neural spine, suddenly thickening mediolaterally the complex of tendons and orienting obliquely about 20 degrees in respect to a plane perpendicular to the parasagittal one.



Figure 55. Hips of MOR 794 showing the ossified tendons; left lateral view.

The lattice properly begins to form at the caudal portion of the ninth dorsal neural spine with the incorporation of tendons oriented in the opposite direction, that is, caudoventrally to anterodorsally. By the tenth dorsal neural spine there are three different

layers of ossified tendons in the mediolateral dimension: two sets running anteroventrally that sandwich another set running caudoventrally. In dorsals tenth to fifteenth the lattice of ossified tendons is mediolaterally thicker. In neural spines tenth to eleven there are about six tendons seen on the lateralmost layer, which are more densely packed. In dorsal fifteen there are up to seven ossified tendons in a single layer, as the height of the neural spine increases caudally and with it the available space for tendon attachment. Along the dorsal vertebrae much thinner tendons are observed running more antero-caudally over the lateral surface of the tuberculum of the ribs and around the laterodistal portion of the transverse processes. This complex of tendons first appears caudal to the fourth dorsal rib and its diapophysis. In the sacral region the arrangement of the ossified is less organized. There is no lattice-like arrangement and the tendons are widely spaced. The tendons are also extremely elongated, each one covering several neural and arranged following an anterodorsal-caudoventral direction. Five long tendons are counted on the anteriormost portion of the sacral area. Sacral tendons are relatively much thicker and flatter. Posteriorly they bifurcate in at least two branches. Caudally, towards the beginning of the tail, the ossified tendons become again more numerous. These first, caudal ossified tendons arise in fact from a relatively massive and poorly organized, caudal spreading of tendons. These tendons emerge from the wide and flat ossified sacral tendons. In MOR 794 the caudal ossified tendons are not forming a rhomboidal lattice on most of the tail, but only over the first fifteenth caudals. From about the sixteenth neural spine the tendons are arranged parallel to the curvature of the tail. Ossified tendons mostly cover the neural spines of the caudal vertebrae until approximately the sixth caudal.

Pectoral Girdle

Coracoid

The coracoid (Fig. 56) is a relatively small element in the pectoral girdle. The element differs from the one described by Lull and Wright (1942) and Brett-Surman (1989) for hadrosaurids. Instead of curving "abruptly downward in a hook-like process" (Lull and Wright, 1942), the coracoid is formed by a quadrangular central body from which two anteromedial processes and two caudolateral articular facets emerge. The morphology described by Lull and Wright, and Bret-Surman is what remains after the coracoid loses its processes by breakage and abrasion. The last include the contribution to the glenoid, for the humerus, and the articulation for the scapula. One of the anteromedial processes consists dorsally on a short projection of bone, rounded in its end and that smoothly follows the dorsal surface of the coracoid, which is concave upwards. The second, rod-like process is longer, at least two and a half times the length of the dorsal one. It projects ventrally with a rounded tip that ends close to the sternal. Ventrally and caudally this process smoothly connects through a strong concave anterolateral profile with the expanded border of the humeral articular surface of the coracoid. The element is perforated by a foramen located at about two-thirds the long axis of the bone, near the articular surfaces. The glenoid is facing caudolaterally. The coracoid is caudolaterally thicker, more than doubling the mediolateral thickness of its distal anteromedial portion. The caudolateral thick region to exposes the scapular and humeral articular surfaces. The scapular facet is very different from the glenoid and it is situated dorsomedially on the proximal end of the bone. It occupies about two thirds of the

proximal, caudolateral-facing surface of the coracoid, making an angle of 115 degrees with the glenoid. The dorsomedial border of the anterior scapula forms a downward slope into the coracoid. The dorsal, cranial-most end of the scapula articulates extensively with the coracoid scapular facet. The articular surface for the scapula is rugose, formed by a series of grooves and pits of variable size. The humeral facet faces caudolateroventrally. It is an oval and deep depression surrounded by a thick, D-shaped rim. The semicircular border of this rim is located ventrally. The rim is strikingly thicker dorsally and becomes gradually thinner ventrally. In its thicker region, rounded pits and other small excavations cover its surface.



Figure 56. Left coracoid of MOR 794 in articulation with scapula and humerus. Anterolateral view.

Scapula

The scapula (Fig. 57 and 58) is a blade-like, very elongated bone that projects caudally from its articulation with the coracoid and the humerus, in the anterior region of the thorax. The proximal end is mediolaterally thicker, showing the articular facets for the coracoid and the humerus. In lateral view the scapula is convex laterally, slightly arched to adapt to the relief of the rib cage. The medial surface is rather flat, particularly along the long blade, while the lateral side is convex. The scapula has a narrow neck or anterior strangulation of its dorsoventral width near the proximal region. This neck is half the width of the maximum dorsoventral length of the scapula in MOR 794. The narrowness of this neck is ontogenetically and individually variable.



Figure 57. Right scapula MOR 1071-7-18-98-298 in lateral view.



Figure 58. Left subadult scapula, MOR 1071-7-8-98-115

The average anteroposterior length in MOR 794, measured from the dorsocaudal corner of the blade to the cranial-most point of the coracoid facet, is 89 cm, longer than the longest bone in the forelimb, the ulna (76.25 cm versus the 57.5 cm of the much shorter humerus). The scapular neck occurs anteriorly and adjacent to the first dorsal rib. The acromion process is located just ventral to the last cervical rib, while the cranial-most point of the scapula lies ventral to the last cervical centrum. The scapula overlaps and crosses seven dorsal ribs to stop covering a small portion of the anterior edge of the eighth dorsal rib. In lateral view the mediolaterally thick proximal region is facing cranioventrally. A thin rim draws the anteroventral contour of both the coracoid facet and the glenoid. The glenoid and the coracoid articular facet meet at an angle of 140 degrees. The acromion process is shallow and elongated. It projects laterally from the

anterodorsal border of the scapula. In cranioventral view the proximal end is U-shaped. The dorsal border of the anteroventral portion of the scapula describes a gentle sigmoid, concave in its path along the acromion and convex caudal to it. The coracoid facet is mediolaterally wider than the glenoid. It is suboval on average morphology and anteriorly located, medially to the glenoid. Its surface is concave and surrounded by thick rims. Ventrally to the coracoid facet lies the glenoid. This articular facet for the humerus is elongated. Its long axis has about twice the length of the diameter of the coracoid facet. The glenoidal surface is, as seen anteroventrally, thinner and with parallel edges after its ventral connection with the coracoid facet. Then the glenoid thickens mediolaterally dorsoventrally. Its ventrolateral edge is straight, a line of dorsolateral-ventromedial orientation. The glenoid describes an arch that opens cranioventrally. This arch is more closed on the lateral border of the glenoid than in the medial edge.



Figure 59. Left sternal MOR 1071-7-12-99-71, in anterolateroventral view.

Sternals

The sternals are flattened and elongated bones formed by a paddle-like expanded anterior region located at the end of a long and elongated, handle-like segment (Fig. 59). The medial side of the sternals is slightly concave, particularly on the "paddle". In MOR 794 the long axis of the sternals follows an anteromedial-caudolateral direction, anterior to the rib cage and with the "paddle" below the coracoid. The "handle" of the sternals stops about two centimeters from abutting the third thoracic rib. The ventrocaudal-most end of the sternals is located at the level of the caudal edge of the second thoracic rib. The "paddle" is fan-like, with the dorsal portion being squared and the ventral one decreasing in extension to a tapering and rounded border. Laterally, the distal edge of the "paddle" is finely striated. The "handle" is mediolaterally compressed and ellipsoidal in cross section. The segment is constant in dorsoventral width, except in its caudal-most end, where it becomes slightly expanded.

Only one subadult specimen is available for study, the right sternal MOR 1071-7-18-98-283. The other nearly or fully complete adults are MOR 1071-7-12-99-71, MOR 794, and MOR 1071-7-25-98-406. The handle of the subadult is relatively thinner along all its dimensions in respect to the adults. The paddle is partially preserved in the subadult, but no differences were detected in relation to the adult. MOR 1071-7-25-98-406 is remarkably different in morphology from the other sternals, since it shows a subrectangular and thicker "paddle". Its handle is also much thicker and oval in cross-section, not ellipsoidal as in the other sternals. This sternal might well belong to another hadrosaur taxon, and the element may be useful for diagnosis.

Pelvic Girdle

Ilium

The ilium (Fig. 60) is an elongated and mediolaterally compressed bone. The element is composed of a central, deeper body that sends two long caudal and cranial processes. A long and ventrally deflected preacetabular process projects anteroventrally. A shorter and deeper postacetabular process projects caudodorsally. A ventrally deflected antitrochanter projects laterally from the dorsal edge of the central body of the ilium. Ventrally, the central body exhibits the pubic and ischial peduncles and forms the dorsal boundary of the acetabulum. The dorsoventral width of the preacetabular process is rather constant, except for a slight thickening near the anterior end and the posterior, widest portion that is linked to the central body of the ilium. The tip of the preacetabular process points anteroventrally at the level of the ventral border of the pubic peduncle. On the medial side the preacetabular process there is a large ridge that continues caudally into the anterior portion of the central body of the ilium. Posteriorly the ridge gradually increases in medial extension and dorsoventral thickness. The ridge is wave-like and indented as seen dorsally, for attachment of the sacral vertebrae. Caudally the ridge is more dorsally located, until it unites with the dorsal border of the central body of the medial ilium. The ridge ends in a concave, thin and U-shaped border that faces medially, opposite to the antitrochanter. Anterior to the antitrochanter and through its dorsal border, the ilium describes a sinuous outline. This outline is convex cranial to the antitrochanter and concave along the caudal portion of it. The central body of the ilium is deeper anteriorly at the level of the pubic peduncle.

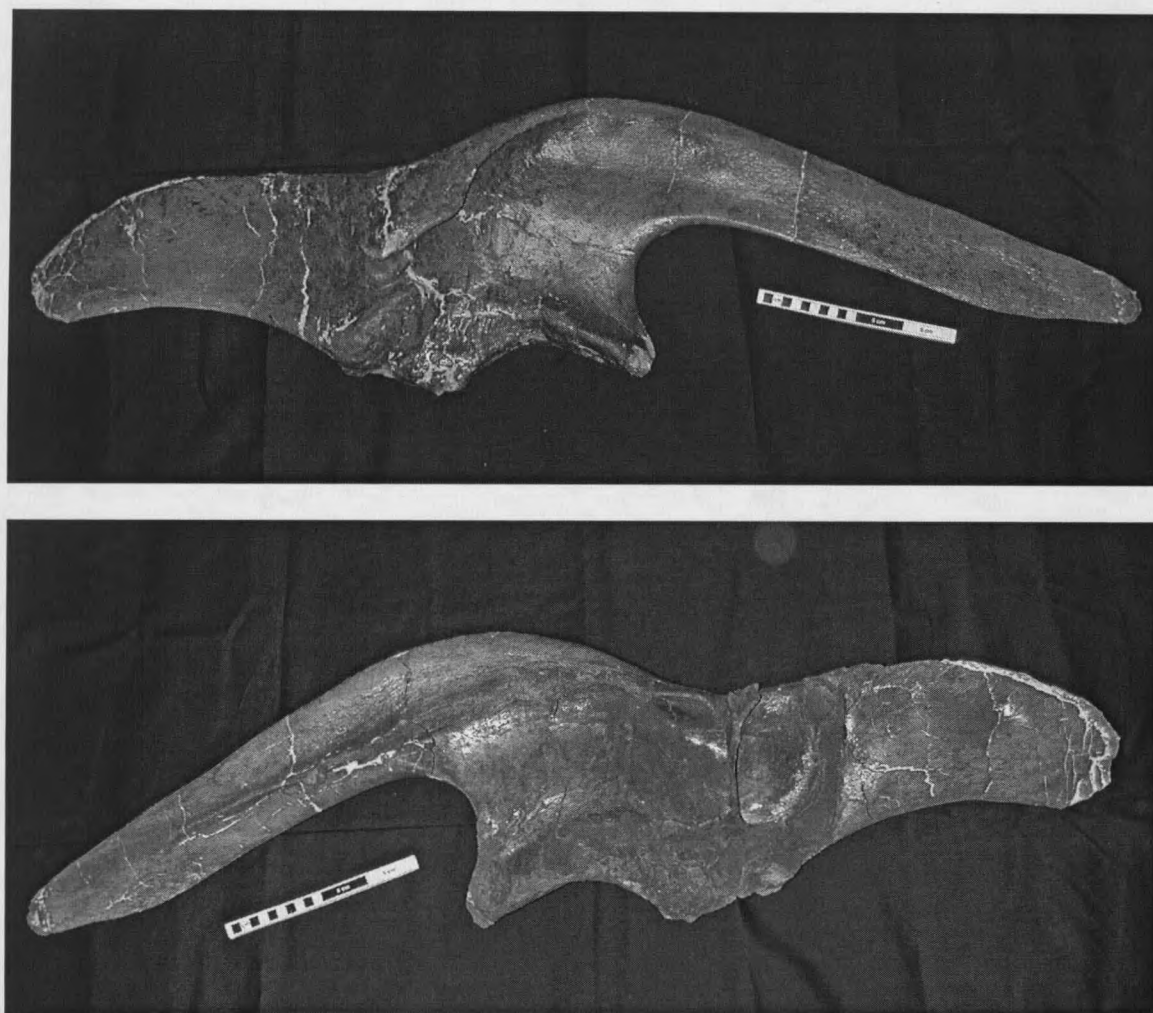


Figure 60. Right ilium of MOR 794 in lateral (top) and medial (bottom) views,

In lateral view, the ventral profile of the central body of the ilium is formed by the gentle arch, the dorsal border of the acetabulum, followed caudally by a dorsocaudally directed profile made of the ventral facet of the ischial peduncle. The central body of the ilium is mediolaterally compressed. Its medial face is slightly concave dorsoventrally, but convex anterocaudally. The medial side is crossed by ventrally-radiating striations that end in the ventromedial edge of the peduncles.

The antitrochanter is a relatively large process that projects lateroventrally from the dorsal, ventrally sloping lateral border of the central body of the ilium. The process overhangs the caudal half of the central body of the ilium, at the level of the ischial peduncle, and is ventrally supported by thickening of bone. The mediolateral width of the dorsal side of the antitrochanter doubles the mediolateral width of the central body of the ilium. In dorsal view the antitrochanter is subrectangular, its shorter sides linked caudal and cranially by concave edges. The anterior border is more elongated and connects with the base of the preacetabular process.

At the anteroventral corner of the central body of the ilium lies the pubic peduncle. This process is cranioventrally directed and sharp, more lightly constructed than the ischial peduncle, as is common in hadrosaurids (Weishampel and Horner, 1990). The surface of the ventral side of the peduncle is rather rugose and forms a very asymmetrical "V" in lateral profile, its shortest side being the cranial one where the pubis articulates. The articular surface for the pubis is small, reduced to the anteroventral portion of the pubic peduncle. In ventral view the pubic peduncle is subtriangular and wedging cranially. Laterally, the ventral border of the pubic peduncle runs caudodorsally into the central body of the ilium, forming a short ridge. On the medial side, the medioventral border of the pubic peduncle connects smoothly with the medial side of the ischial peduncle, so that in ventral view they form a medially convex, crescentic profile.

The ischial peduncle is relatively massive. Its anterior surface forms the caudal half of the roof of the acetabulum. The ventral surface is more mediolaterally compressed than its anteroventral surface and the ventral side of the pubic peduncle. On the lateral b

order of the ischial peduncle there are perpendicular and short indentations. More indentations are found in the ventrolateral portion of the articular facet, which is fairly rugose. A very conspicuous feature of the ilium is a massive, thick overgrowth of bone caudodorsal to the ischial peduncle. This excrescence is only found in the lateral side of the ilium and is very rugose and convex laterally. The feature stretches following an anterodorsal-caudoventral direction, nearly parallel to the antitrochanter as seen in lateral view. Caudoventrally, the overgrowth connects with the caudal end of the ischial peduncle and the ventral border of the base of the postacetabular process. There is a groove over and following the dorsal contour of the excrescence.

Caudally, the central body of the ilium extends into blade of bone, the postacetabular process. The postacetabular process is twice dorsoventrally deep as the preacetabular process, but shows less than two-thirds the antero-caudal length of the preacetabular process. The dorsal and ventral edges are parallel until they converge caudally to form a crescent end. The lateral surface is concave in the cranial two-thirds and more convex in its caudal third. Although mostly convex, the medial surface of the postacetabular process is rather irregular because it is anteroventrally crossed by a pair of indentations. Parallel striations are found following these indentations. Striations are also seen on the medial side of the preacetabular process, running antero-caudally ventral to the medial ridge. Also they are present radiating on the dorsal surface of the antitrochanter and on the medial surface of the central body of the ilium.

Pubis

The pubis (Fig. 61) is a mediolaterally thin element composed of an anterior expanded prepubic blade followed caudally by three bone projections, the iliac and pubic peduncles and an elongated postpubic process. The iliac peduncle is thick, relatively massive, short, and laterally offset. The ischial peduncle is much slender, mediolaterally compressed and caudally projected. The postpubic process is caudomedially offset and projected in respect of the two peduncles. The prepubic blade constitutes half of the antero-caudal length of the element, nearly as much as the postpubic process. The cranial two-thirds of the blade is a subellipsoidal sheet of bone that expands cranially. However, the outline of the blade is variable among different individuals. The blade opens from a narrower portion or neck that links the blade to the area formed by the peduncles and the postpubic process. At its narrower point the neck is about half the maximum dorsoventral width of the prepubic blade. The dorsal edge of the prepubic blade is irregularly, slightly twisted, so that in some specimens it is slightly concave laterally and convex medially in the neck area, while in others is more or less twisted in a mediolateral direction.

The dorsalmost portion of the pubis is constituted by the iliac peduncle. This is the larger and more massive of the peduncles. It extrudes from the lateral face of the pubis. The peduncle projects caudodorsally from an extensive portion of bone that connects cranially with the dorso-caudal portion of the pubic neck and ventrally to the craniodorsal base of the ischial peduncle. The iliac peduncle has the dorsal outline of an equilateral triangle.

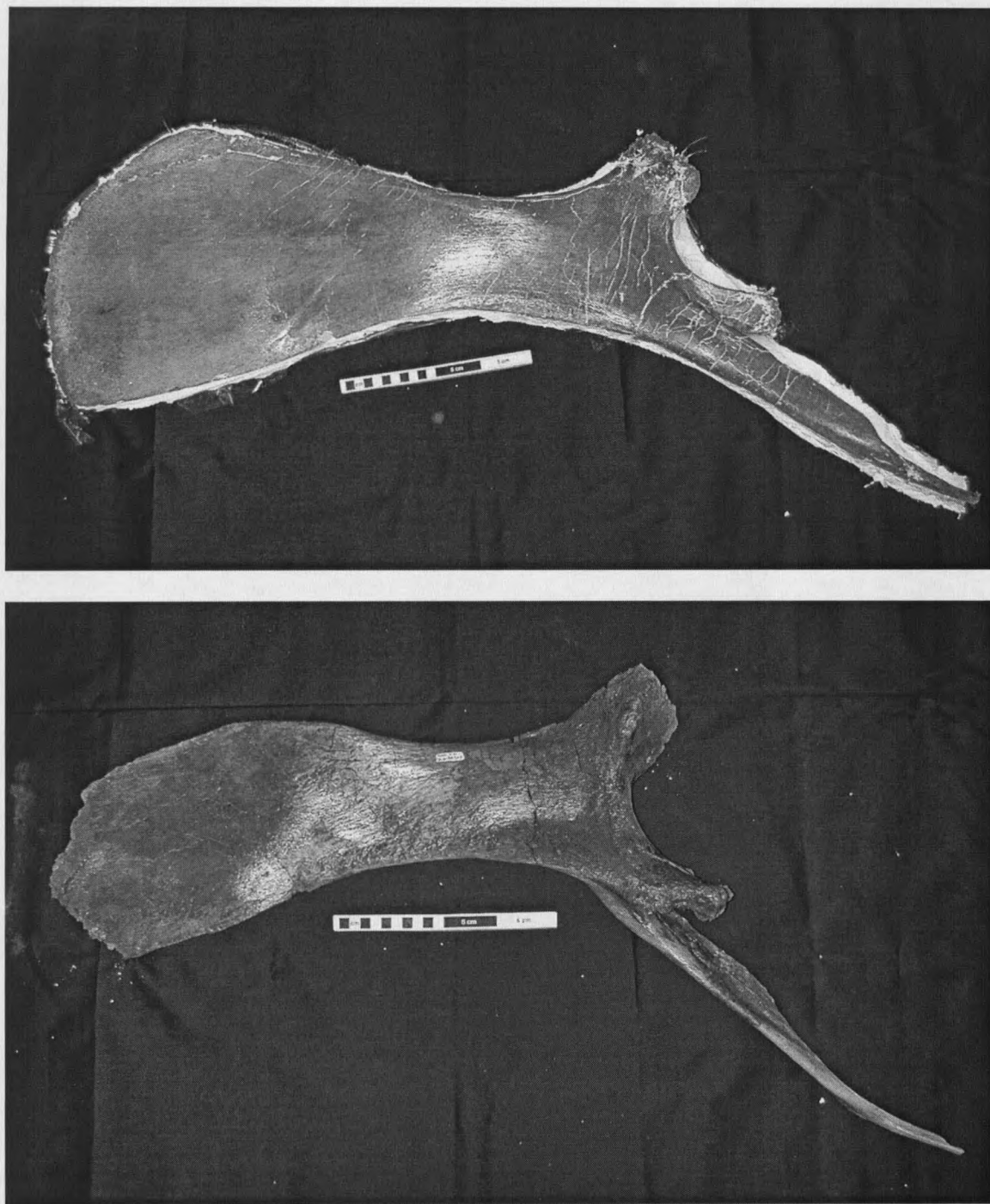


Figure 61. Right pubis of MOR 794 in medial view (top) and left ilium MOR 1071-7-16-98-243 in lateral view (bottom).

The dorsal surface of the peduncle is craniomedially oriented and rather flat. It connects cranially with the dorsocaudal border of the prepubic blade, before the neck. The iliac peduncle may be roughly assimilated to a tetrahedral with the apex pointing downwards, laterally rotated around the dorsoventral axis. The biggest facet is slightly concave, facing caudolaterally about 45 degrees from the mediolateral plane. This surface has the outline of an inverted teardrop and is dorsoventrally crossed by numerous striations. Cranial and adjacent to this face and separated from it by a thick dorsoventrally oriented edge, there is a craniolateral surface. This surface is smooth and irregular in topography where it softly connects with the prepubic blade. The third face of the peduncle is its contribution to the medial wall of the pubis.

The ischial peduncle is a mediolaterally compressed slender process that extends a short distance caudally. Its mediolateral width does not surpass the mediolateral thickness of the iliac blade. In lateral view, the ischial process is subrectangular, although relatively expanded dorsoventrally in its cranialmost portion, where it departs from the main body of the pubis. The ventral border of the ischial peduncle is laterally offset from the dorsoventral plane of the pubis, forming a boss in its anteroventral extreme. The caudal end of the ischial peduncle is slightly expanded dorsoventrally, although much less than its cranial region. In caudal view, the ischial peduncle is subtriangular, with a fairly rounded apex.

The postpubic process is a long, rod-like thin process that projects caudoventrally. It is medially offset at its union with the main body of the pubis, ventral to the ischial peduncle, so that in dorsal view it is possible to see how the postpubic process departs

mediocaudally from the body of the pubis. Caudoventrally the process gradually thins until tapering into a rounded and very thin tip. Near the main body of the pubis, the postpubic process is relatively thick, mediolaterally compressed and widest dorsoventrally, subparallel to the parasagittal plane of the bone. There the process reaches its maximum mediolateral thickness, which is similar to that of the pubic neck. After the first third of its antero-caudal length, the process exhibits an anterior concavity on its dorsocaudal border. After this concavity the process gradually changes from extending dorsoventrally to extend perpendicular to the parasagittal plane. After that transition the postpubic process receives the ventral portion of the ischium surrounding its foramen and including the obturator process.

Ischium

The ischium is made of a long rod-like shaft that expands cranially into an irregular blade that contains the iliac and pubic processes. This expanded anterior region is not parallel to the parasagittal plane, but tilts a few degrees laterally. The shaft is rather straight and projects caudally. At the caudal tip the shaft is slightly bent ventrocaudally. The iliac peduncle is larger than the pubic one. Ventrocaudally in the expanded region there is a foramen formed by the coalescence of the obturator process with the caudoventral portion of the pubic peduncle. The expanded anterior region of the ischium arches dorsally to form the iliac process. Ventrally, it projects cranially into the pubic process. When both ischia are joined the anterior blades diverge a few degrees laterally from each other, while caudally the shafts become united. In cranial view the ventral half of the blade is slightly offset laterally in respect to the parasagittal plane of the ischium.

The dorsal border of the expanded portion of the ischium is twice thicker mediolaterally than the ventral border. Posteriorly, the obturator process is displaced medially from the parasagittal plane of the ischium (Fig. 62)

The iliac process is subrectangular and projects anterodorsally from the dorsal portion of the ischial blade. The anterodorsal end of the iliac process is mediolaterally and dorsoventrally expanded. The articular facet for the ilium is subellipsoidal in cross section. The pubic peduncle is more slender and less differentiated than the iliac peduncle. It projects anteriorly and is more compressed mediolaterally than the iliac one. The articular facet for the pubis is subtriangular in cross section. The pubic process is slightly concave laterally and convex medially. Numerous striations are found running antero-caudally across the lateral side of the pubic peduncle, especially on its ventral portion, extending into the caudoventral process of the ischial blade.



Figure 62. Right ischium with a portion of the distal shaft of the left ischium, medial view.

Cranioventral to the ischial shaft there is a relatively large foramen. This foramen is produced by the coalescence of the obturator process caudally and a caudoventrally projecting process of the ventral border of ischial blade. Medially, the area that surrounds the foramen anteriorly, ventrally and caudally is fairly rugose and is medially offset. The lateral surface, as well as the rest of the ischial blade, is rather smooth. The area surrounding the foramen is slightly convex medially. The antero-caudal length of the obturator process is twice the length of the more anteriorly located caudoventral process of the ischial blade. The obturator process forms a relatively small blade of bone that projects ventrally from the caudoventral border of the anterior expanded blade of the ischium. Dorsocaudally the obturator process connects through a ventromedially directed ridge with the proximal portion of the ischial shaft. The shaft of the ischium is very long, more than three times longer than the anterior expanded blade. At its proximal, lateral side and running caudoventrally, there is a rugose and flattened area. The shaft is ellipsoidal in cross section. The major axis of this ellipse is oriented following a dorsomedial-caudolateral direction. There is an angle of about 60 degrees between the plane that contains the major axis of the shaft and the anterior blade of the ischium. The major axis of the shaft tilts about 40 degrees medially from the parasagittal plane, whereas the anterior blade tilts roughly about 20 degrees laterally from the parasagittal plane. The shaft is thicker along its proximal. The shaft ends in a slightly expanded and ventrally oriented rounded extreme. However, no foot is formed at the end of the ischial shaft. Along the dorsomedial half the shaft contains a series of pronounced longitudinal striations, showing the area where the shaft of both ischia joined. The shafts of both

ischia are dorsomedially attached from their proximal segments. At the caudal end the shafts are slightly separated from each other (Fig. 63).

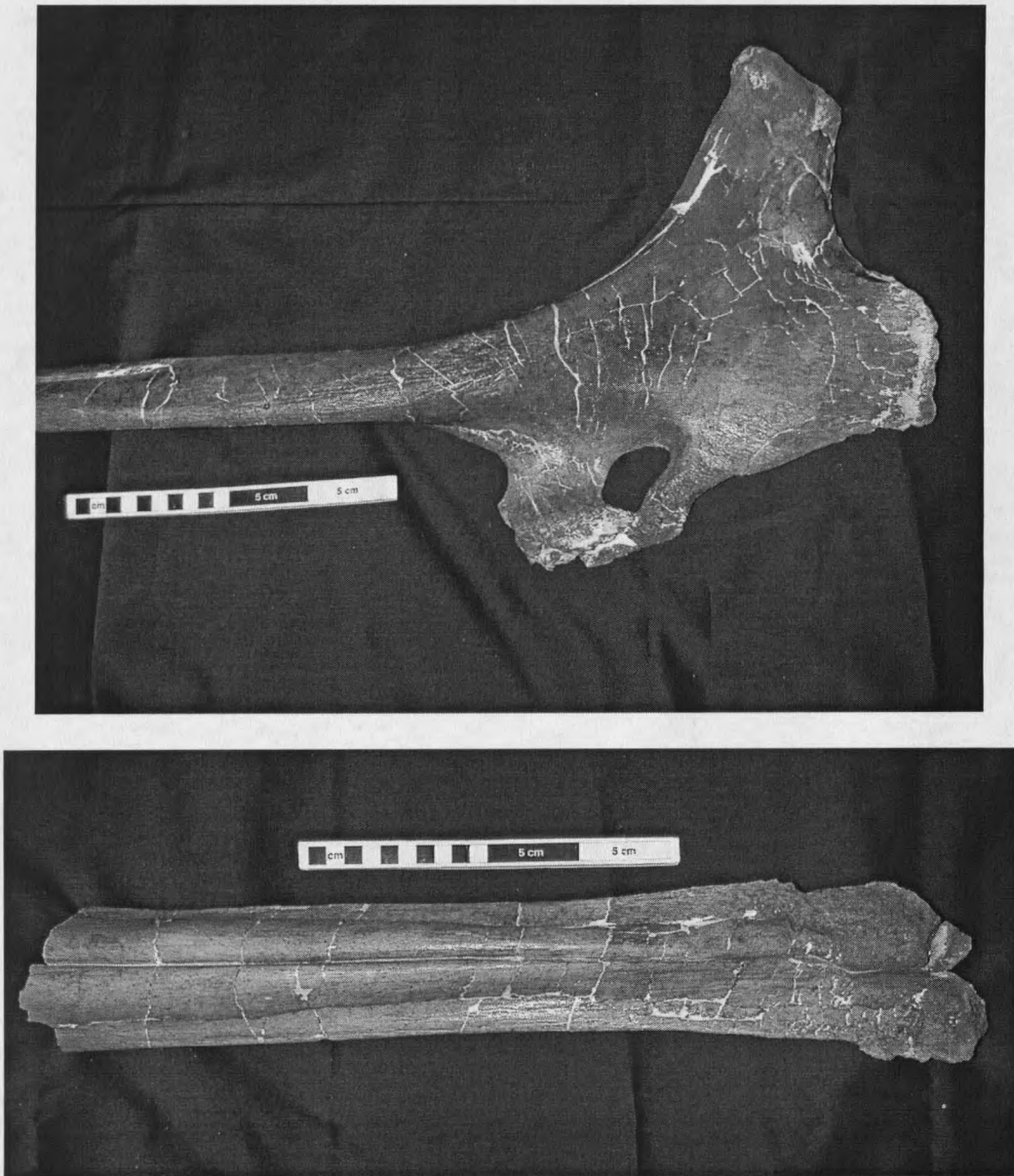


Figure 63. Anterior blade (top, lateral view) and distal shafts (bottom, dorsal view) of the ischia of MOR 794.

ForelimbHumerus

The humerus is a robust element in the forearm. The proximal half is cranioventrally expanded in a prominent deltopectoral crest, as is typical in hadrosaurids. The humerus is expanded in its extremes, but more proximally than distally. The proximal half is medioventrally twisted in respect to the parasagittal plane, which is mostly parallel to the medial surface of the ulnar condyle. In proximal view the humerus describes a triangular outline. The proximal half of the humerus is similar to a slightly folded blade that thickens gradually distally. The head of the humerus is massive, rounded and also triangular in craniodorsal view. Its surface is rugose and carved by small depressions and convexities. It articulates with the glenoid cavity, formed by the coracoid and the proximal scapula. It sends a slight convexity medially, but a relatively large, rugose subconical tuberosity caudolaterally. This tuberosity is subconical with the apex pointing distally, attached to the proximal, laterocaudal face of the humerus. Medially from the tuberosity the humerus expands mediodorsally in a concave and blade-like prominence. On the caudomedial side, at mid length of the proximal half of the bone and immediately distal to the mediodorsal prominence, there is a rugose depression that contains a sharp, thick and rugose ridge running in the middle. This feature begins at mid length of the proximal half and extends proximodistally on the caudal surface. On the other side, ventrolaterally to the head, the humerus begins to expand cranioventrally to form the deltopectoral crest.



Figure 64. Left humerus MOR 794 in lateral (top) and medial (bottom) views.

The medial side of the proximal half of the humerus is concave. Through the craniomedial proximal border, there are a series of thick and short indentations parallel to the long axis of the humerus. The proximal half of the humerus is more open and flattened on the medial side proximally, being gradually narrower and more longitudinally concave near the mid length of the bone. The deltopectoral crest projects anterolaterally from the main shaft of the humerus and covers the proximal half of total length the bone. The blade-shaped deltopectoral crest begins at the proximal end of the humerus and is mediolaterally compressed. There is a rounded corner where distal end of the deltopectoral crest and the distal half of the humerus meet. The thickness of the deltopectoral crest is changing along its length, being relatively thicker at the proximal corner, then narrowing to be thinner along its distal border. The dorsal border of the humerus is not parallel to the ventral edge of the deltopectoral crest. Instead, the width of the humerus perpendicular to its long axis increases gradually distally, being largest at the level of the distal end (ventral corner) of the deltopectoral crest. The deltopectoral crest projects little more than half the diameter of the humerus.

Caudal to the deltopectoral crest and into the distal half of the humerus, the shaft is mediolaterally thick, nearly cylindrical. In lateral view, the ventral border of the distal half of the humerus describes a gentle arch that ends in the cranioventral extreme of the radial condyle. The dorsal profile, as seen in lateral view, is first straight and directed caudodorsally. After this the dorsal profile arches downward to form the medial border of the ulnar condyle. The distal-most portion of the humerus is formed by the radial and ulnar condyles. The ulnar condyle is set medially, while the radial one is placed laterally.

The proximal end of the humerus appears slightly twisted medioventrally in respect to the distal shaft. When viewed in lateral view the ulnar condyle seems to have been displaced dorsally in respect to the radial one. The ulnar condyle is larger than the radial one, although the degree of disparity in condylar size varies among specimens. The condyles are dorsocaudally and ventrocranially separated by deep notches, the deepest being the dorsocaudal one. This notch receives the olecranon process of the ulna. Both condyles are lateromedially compressed and show small concavities in their lateral (the radial) and medial (the ulnar) sides. The condyles are slightly turned and pointed cranioventrally. The distal condyles are antero-caudally directed. The radial condyle is slightly expanded dorsocaudally and ventrocranially, as seen in lateral view, and rounded at the distal border. In distal view, the radial condyle is subtriangular. The rounded articular facet for the radius is rugose. The depressed lateral side of the radial condyle is coplanar with the lateral surface of the deltopectoral crest. The ulnar condyle is subellipsoidal and thicker than the radial one. A sharp ridge crossed the medial side of the ulnar condyle. This ridge disappears gradually and dorsocranially into the shaft of the humerus.

Muscle scars and striations are very conspicuous on the humerus. Besides the conspicuous scar found on the caudomedial surface of the proximal half of the humerus, several areas are finely striated. Short striations trending cranio-caudally are present along the medioventral margin of the deltopectoral crest. A less extensive set of striations is seen on the lateral border of the crest, covering its distal half. Both the distal condyles

and the proximal condyle and border contain radiating sets of striations, more or less parallel to the long axis of the humerus.

Radius

The radius (Fig. 65) is a long, subcylindrical bone that occupies a dorsomedial position over the ulna. It is nearly as long as the ulna and rather constant in thickness along its proximodistal length. The element expands suddenly at its proximal end, and is more gradually and less expanded at its distal extreme. The proximal extreme is cup-like and has a flattened proximal surface. In proximal view, the radius is subrectangular in outline. The outline of this section varies from trapezoidal to more rounded and/or squared depending on the specimen and its preservation. Ventrally, the proximal end is expanded in a thick, keel-like prominence that fits into a U-shaped concavity on the dorsomedial surface of the ulna. Proximal to that prominence the ventral surface is concave. The proximal region of the radius contains perpendicular striations.

Distally from the proximal end the radius thins quickly and becomes a subcylindrical long shaft. However the mid third of the radius is compressed in a lateroventral-mediiodorsal direction. Along the last third, the shaft becomes subtriangular in cross section and flattened on the lateroventral side that articulates with the ulna. The surface of the distal, flattened surface of the radius contains the longest and deeper striations. Gradually the radius expands dorsoventral and mediolaterally until the distal end. The distal end (Fig. 66) is subtriangular, with rounded corners. There, there is a laterodorsal, flattened and smooth surface, adjacent to the lateroventral, striated articular surface for the ulna. At the contact between the articular, lateroventral surface for the

ulna and the laterodorsal side, there is a sharp edge running on the lateral side along the distal fourth of the length of the element. Dorsally, the laterodorsal smooth surface arches medially, giving rise to a medial, rounded surface that forms the medial, ventrally sloping side of the subtriangular distal outline. In the articulated specimens the radius is centered on the dorsal, proximal surface of the ulna. However, immediately distal to the proximal, expanded end, the radius is diagonally set in respect of the shaft of the ulna, so that the former is anteromedially directed crossing the shaft of the ulna, dorsolaterally over the distal end of the ulna.

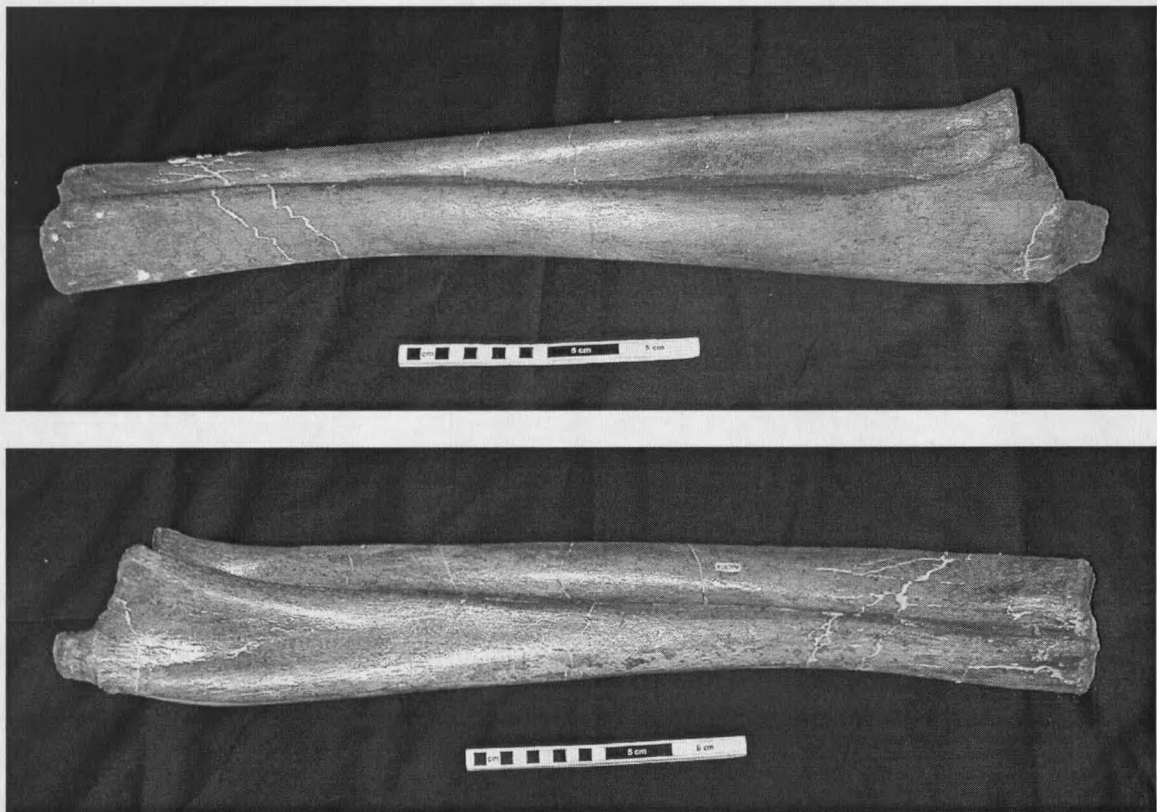


Figure 65. Left radius and ulna of MOR 794 in lateral (top) and medial (bottom) views.

Ulna

The ulna (Fig. 65) is the longest bone in the forelimb. It is a relatively slender and very elongated element. It expands slightly distally, but mostly proximally. Proximally there are two dorsally directed flanges for reception of the proximal expanded portion of the radius. Distally the ulna becomes a subtriangular, long shaft that ends curving slightly medioventrally in a flat surface for reception of the distal, flattened distal face of the radius. As seen in lateral view, the ulna describes a slight sinusoidal profile, concave upwards along the proximal half and downwards along the distal one. Proximally and throughout most of the shaft its triangular section has the vertex of the triangle pointing ventrally, while a more or less horizontal side of that triangle would constitute the dorsal side. The olecranon is proximally pointing and subconical. The ulna thins progressively distally, slightly as seen laterally, but more remarkably in medial perspective. At the distal end (Fig. 66) the ulna further expands slightly.

The proximal third of the ulna is the most dorsoventrally expanded region. As introduced before, it is formed by two flanges that enclose a U-shaped concavity for reception of the proximal, ventral prominence of the radius. This groove is deepest at the proximal border of the ulna and becomes distally shallower, until disappearing into the flat dorsal surface of the element. The medial flange is dorsomedially directed and is the largest, while the lateral one opens laterodorsally. In proximal view, these flanges plus the proximally pointing olecranon produce crescentic outline. The medial face of the medial flange is concave and carved by a wide, proximodistally-directed groove. The groove becomes distally shallower disappearing into the mid shaft. The lateral flange is

less dorsally pointed and its surface is convex dorsoventrally. This flange is thickest at its base and less uniform in thickness than the medial flange. In lateral profile, the proximal end of the ulna is wedge-shaped. Both the lateral and medial faces of the proximal flanges are longitudinally crossed by deep striations that fade away distally. The ventral side is convex. The olecranon process is subconical and located caudoventrally at the proximal end of the ulna. The process projects straight caudally and is received by a deep notch in the humerus located between its radial and distal condyles. This process is flattened on its dorsal surface in some specimens and expands ventrally in a rounded and thick convex morphology.

The mid third of the ulna is a shaft as dorsoventrally deep as it is mediolaterally thick. Its cross-section is triangular. The dorsal face is subhorizontal, flat and smooth. Along the mid third, the ulna initiates its slight medial bending, about ten degrees from the proximodistal direction of the long axis of proximal third of the element. The distal third of the ulna continues having the equal proportions of the mid shaft although it is slightly expanded towards the distal end of the element, where it curves medioventrally. Although the distal third of the ulna also shows a triangular cross section, this time the apex of that triangle points dorsolaterally instead of ventrally. The dorsomedial face serves for the articulation of the distal, lateroventrally-oriented face of the radius. Sets of deep, proximodistally directed striations carve the distal portion of the ulna on its three surfaces. These striations are deepest in the articular facet, relatively less pervasive on the lateral surface, and distally limited in the ventromedial face.

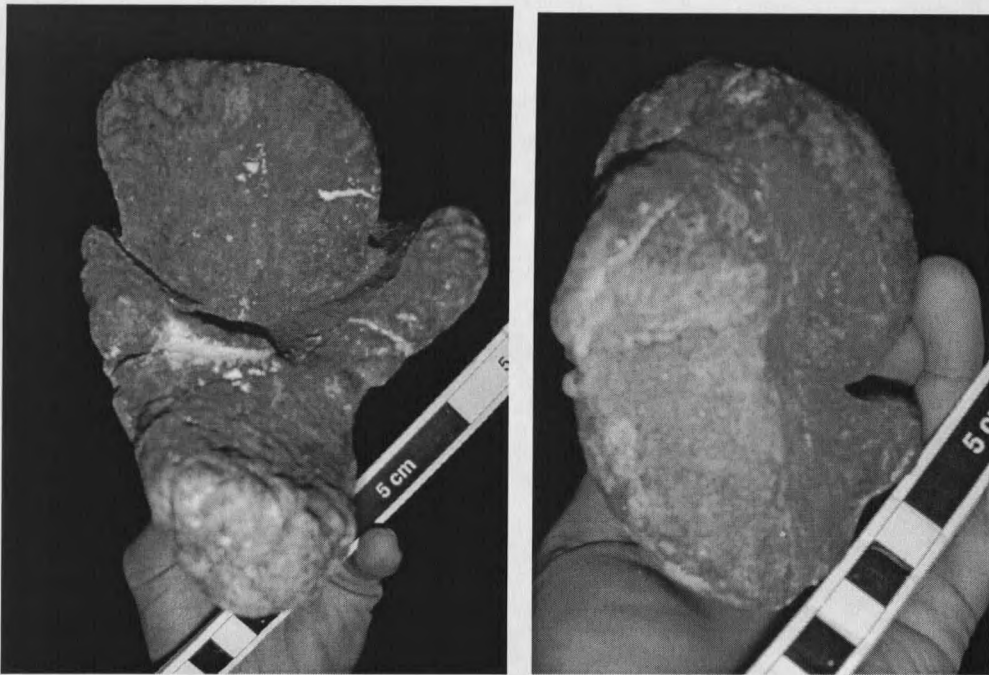


Figure 66. Ulna and radius in proximal (left) and distal (right) views. Note a carpal attached on the distal surface. The left photo is from the left forearm and the right image from the right forearm of MOR 794.

Carpals

The hand of *B. canadensis* is relatively slender and rather elongated. A maximum of two carpals are observed in the right articulated forearm of MOR 794, a tiny, spherical piece of bone and a much larger element. The larger carpal (Fig. 67) is a tetrahedral bone encased between the distal ends of the ulna and radius, and the proximal ends of the metacarpals. Its minute companion (Fig. 67) is located laterally, between the ventrolateral side of the larger carpal and the laterodistal border of the ulna. It is a pebble-like bone that floats on the sandy matrix of the carpus of MOR 794. Measuring just a few millimeters in diameter, the element is easily overlooked, as well as removable, and is in fact missing in the left carpus of MOR 794. No disarticulated carpals like this are known

from the bonebed. The element is perforated in the center by a minute foramen. The large carpal is proximally wedged between the distal ends of the radius and ulna in the right wrist of MOR 794, while just contacting the radius in the left wrist.



Figure 67. Right carpus of MOR 794 in laterodistal view.

The tetrahedral carpal is formed by an asymmetrical, scalene, and triangular face and three isosceles triangular sides that meet in an apex that is medially deflected. The scalene side faces dorsolaterally, while the isosceles three surfaces project in the direction

of the bone, dorsolaterally to ventromedially. The long axis of the carpal is oriented in a dorsolateral-ventromedial direction. The dorsolateral face is the visible surface in the articulated forelimbs. This face is asymmetrical and shows an inscribed shallow, centered excavation. This excavation is oval and its extension differs depending on the specimen. It is relatively small in the disarticulated MOR 1071-8-12-98-537A, while it occupies most of the surface of that side of the carpal in MOR 794. The borders or boundaries of the excavation are rather sharp and well defined. Near the center of this excavation there is a small but distinctive foramen. A relatively large, shallow, and oval foramen is located on the lateroventral face.

General Description of the Hand

The hand (Fig. 68-69) is composed of four digits, corresponding to II, III, IV and V. Metacarpals II, III and IV are elongated and roughly subcylindrical. Metacarpal III is the longest and more robust, followed by metacarpal IV in proximodistal length, although this last bone is mediolaterally thicker. Metacarpal II is the shortest and most slender of the three. In contrast to metacarpals II to IV, metacarpal V is a proximodistally short and robust element that projects towards the lateral side of the hand. Proximally, the extreme of metacarpal V is distally displaced in respect to the proximal extremes of metacarpals II-IV, so that digit V roots relatively more distally along the proximodistal length of metacarpal IV. Metacarpals II-IV form a rather tight and compact unit. Metacarpal II articulates lying medioventrally rather than completely medially in respect to metacarpal III. And metacarpal IV articulates being lateroventrally located instead of laterally in

relation to metacarpal III. The articulation between metacarpals III and IV is made through two flat surfaces, the lateral one of the former with the medial one of the last.

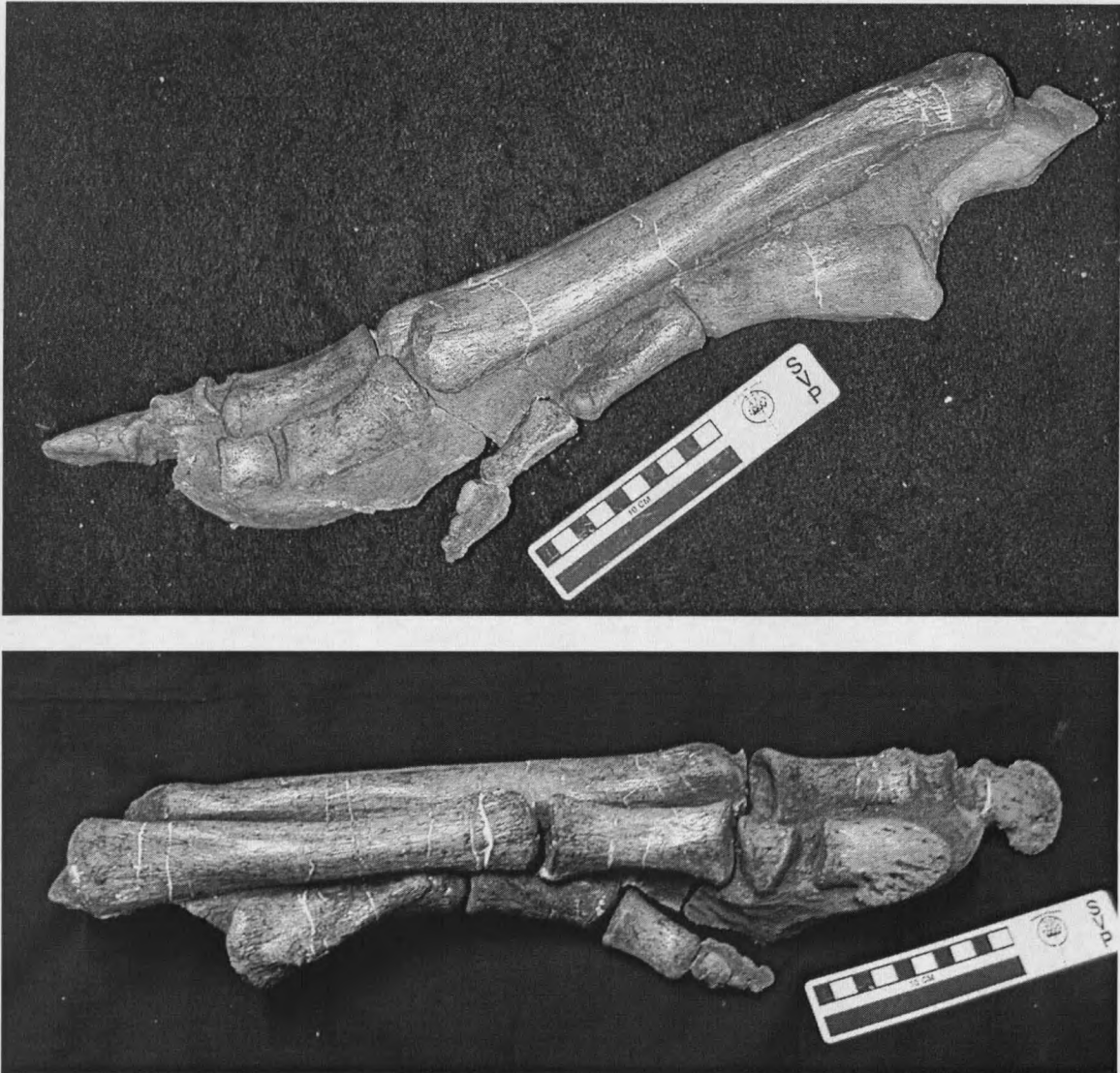


Figure 68. Left manus of MOR 794 in lateral (top) and medial (bottom) views.

The phalangeal formula is 3, 3, 3?, 4. Digits II to IV are supported by the long metacarpals and project proximodistally. In contrast to digits II to IV, digit V is the relatively small and short. The morphology of its metacarpal offsets the finger laterally from the proximodistal axis of the hand, as has been reflected in many artistic renditions. The phalanges of digit V are progressively smaller, proximodistally shorter, and mediolaterally narrower distally, with roughly the morphology of truncated cones. Digits II and III are similarly constructed in that they both begin proximally with a subrectangular, slightly hourglass-shaped first phalange (II1 and III1), then possess a wedge-shaped, distinctive phalange II2 and III2 respectively, to finally end distally with a hoof-shaped ungual each. Digit IV shows proximally a mediolaterally twisted subrectangular phalange IV1. Phalange IV2 is a stocky, relatively small subrectangular bone, in contrast to the wedge-shaped phalanges II2 and III2. The ungual (phalange II3) on digit II is different from any ungual of both the manus and the pes. It is asymmetrical and has a coarsely indented lateral border that is attached to the main body of the bone, instead of being laterally projected as in all other unguals. Ungual III (phalange III3) is symmetrical, but differs from the pedals in having a relatively less sharp and less medially and laterally projected arrow-shaped borders. Unguals are preserved in digits II and III. No ungual IV is present on the left articulated manus of MOR 794, but there is an unprepared element on the right manus that might be phalange IV3. The distal surface of phalange IV2 does not differ from the one on the second phalanges of digits II and III, where there are a mediolateral concavity and a saddle-shaped morphology.

Metacarpals (Fig. 68-70).

Metacarpal II. Like metacarpals III and IV, this is an elongate and narrow, stick-like element. The bone is expanded in its proximal and distal ends. The proximal border is more expanded dorsally, while the distal extreme is more expanded ventrally.

Metacarpal II is mediolaterally compressed, possessing ellipsoidal proximal and distal sides. The long axes of the ellipsoidal proximal and distal sides are parallel each other. The medial side is concave near the proximal edge, after which it quickly becomes convex along the 60 % of the longitudinal length of the element, to distally become concave again along the distal end. The proximal concavity shows shallow pits and broad proximodistal striations. In contrast, the distal concavity is very shallow and less rugose, although also striated. The lateral surface is flattened and articulates with the medial side of the metacarpal III. For that purpose there is an extensive scar running along the distal half of the lateral face of the metacarpal, although confined to the dorsal, longitudinal half. The scar ends distally producing a sharp edge at the border between the dorsal and lateral side of the bone.

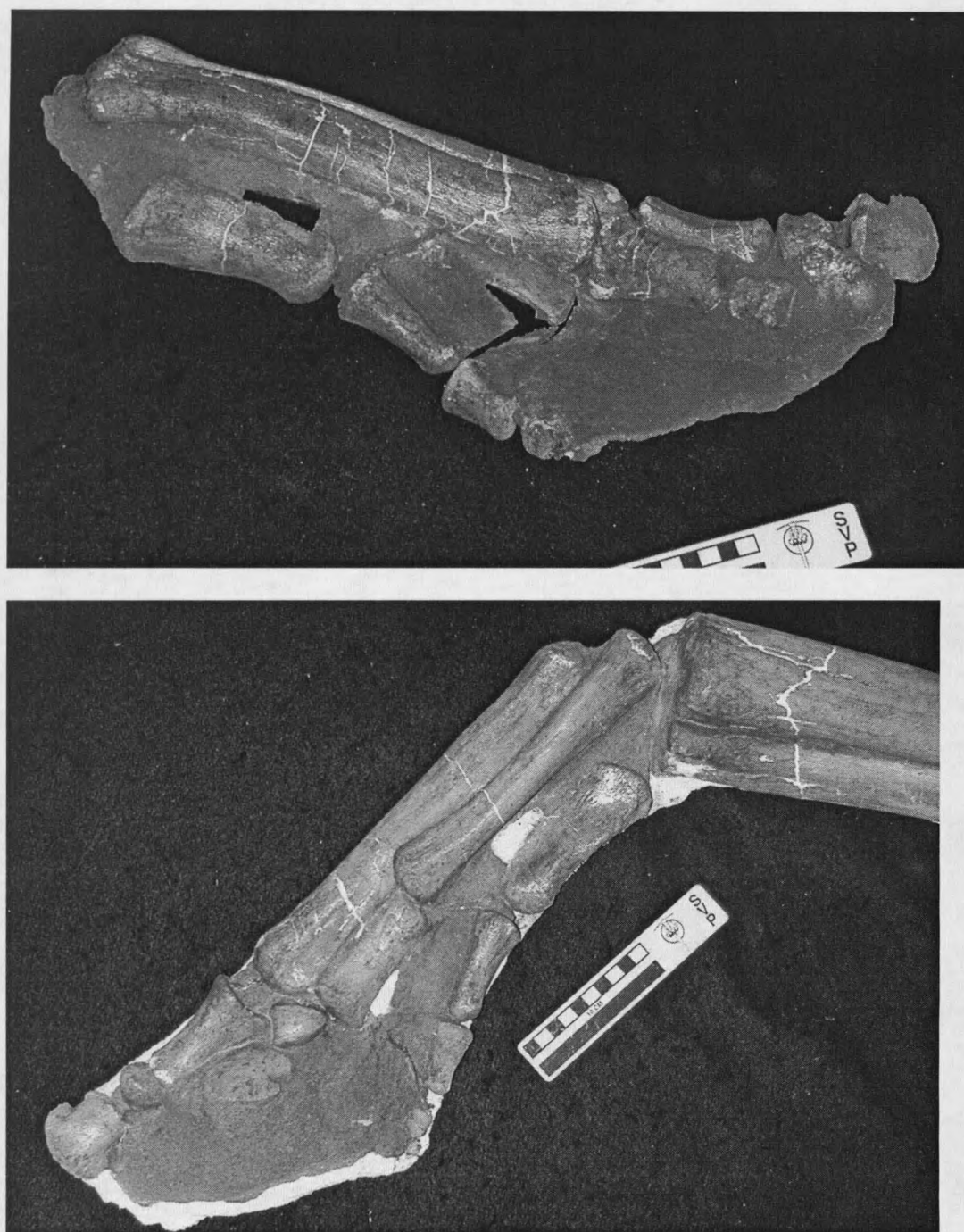


Figure 69. Right manus of MOR 794 in lateral (top) and medial (bottom) views.

Metacarpal III. This is a subcylindrical element, stouter than metacarpal II. It is expanded in its extremes, but more in its distal end, especially in the mediolaterally. However, the bone is less mediolaterally compressed than metacarpal II and narrower along one third of its total length. Proximally metacarpal III is subtriangular in cross-section. Distally it becomes more subsquared in cross section towards the distal end. The mediodorsal corner of the distal surface is more medially salient than the laterodorsal corner. The mediodorsal corner is slightly curved ventrally due to a concavity on the medial face adjacent to the distal edge of the element. The dorsal edge of the distal border is quite perpendicular to a parasagittal plane. The triangular cross-section of the proximal facet shows an arch than covers the dorsal and the dorsomedial half of the medial face of the bone. The proximal and distal surfaces are convex. The lateral side is flattened and striated for the articulation with the medial surface of metacarpal IV. Proximally the lateral side is slightly concave and deeply, proximodistally striated. Distally, the lateral face is slightly concave. The mediodistal face is slightly concave, but less deeply striated. A small scar can be seen centered at the mid length of the lateral side of the metacarpal. The edge between the lateral and dorsal surfaces is rather sharp and well defined from the proximal extreme of the bone and distally until most of the proximodistal length of the element, except along the distal quarter, where it becomes more rounded and smoothed. The medial side is convex except for the distal and proximal ends, where it is ventrally deflected and concave. A scar, larger than the one on the lateral side, is visible along the proximal third of the bone, separated by a few centimeters from the proximal border, for articulation with the lateral side of metacarpal II. The distal convexity articulates on the

lateral side of phalange II1. The dorsal surface is rather smooth and convex, mediolaterally arched. Near to the distal end there are two sharply defined grooves, oriented proximodistally. The dorsal side is more expanded proximally, reaching its maximum mediolateral width at the proximal border of the metacarpal. The ventral side is relatively narrow, especially proximally, and rounded. Distally it flattens and becomes concave at the border.



Figure 70. Proximal view of the metacarpals of the left manus of MOR 794, with a carpal attached. In clockwise sense, proximal views of metacarpals IV, III, II and V.

Metacarpal IV. This element is distinctive in possessing a mediolaterally expanded and laterally deflected proximal end. The bone narrows progressively along the distal portion. Dorsoventrally the bone is rather constant in thickness, except for a slight proximal expansion and a much remarkable expansion of the distal end. The bone is dorsoventrally compressed along most of its proximodistal length, except at the distal end, where it is mediolaterally compressed. The medial side of metacarpal IV is flattened and striated as the lateral side of metacarpals II and III. In metacarpal IV the central portion of the longitudinal length of the medial face is slightly convex. Only the distal extreme of that side is concave. The dorsal face is slightly convex except for the proximal extreme, where it is concave and mediolaterally expanded, as well as laterally curved in a sharp corner. Proximodistally oriented striations can be seen at both distal and proximal portions of the dorsal side of the metacarpal. The lateral side is convex and rounded, but flattened and striated at the distal end and striated and laterally projected at the proximal end. Proximally there is a sharp and proximodistally elongated concavity for the reception of a rough projection of metacarpal V. The ventral side is, like the dorsal face, expanded and laterally deflected proximally and progressively thinner mediolaterally near the distal end. As seen laterally, the ventral surface is sinusoidal, describing a concave profile at the proximal end, followed distally by a gentle convexity, then another concavity, and ending distally in a dorsoventrally expanded distal extreme. A set of proximodistal striations carves both the proximal and distal ends. The proximal surface describes an isosceles triangular outline, with the apex pointing laterally and the base of the triangle forming the proximal outline of the medial surface. The surface of the

proximal face contains, like in metacarpal III, an irregular and labyrinthic series of grooves and pits. The distal surface describes a dorsoventrally elongated trapezoidal outline, similar to the distal side of metacarpal II. As in metacarpal II, the dorsal side, as seen in distal view, terminates laterally in a salient and slightly curled corner.

Metacarpal V. Metacarpal V is a short, compact and dorsoventrally compressed, subconical element. The distal portion is dorsolaterally twisted in respect to the proximal region. A striking feature is a bulge protruding laterally from the lateral side of the element. The dorsal and ventral (plantar) surfaces are the largest and most exposed ones. The dorsal side is proximodistally concave, reaching its maximum concavity at the mid longitudinal length of the bone, and is rather smooth. Mediolaterally the dorsal surface is convex on the distal (especially) and the proximal portions, and flat at the center. There are short striations near the proximal end, while the proximal area adjacent to the proximal border is more rugose rather than striated. The ventral face is, like the dorsal one, proximodistally concave, reaching its maximum concavity at the center. Mediolaterally, the ventral side is convex proximally, but in contrast to the dorsal face, it becomes flatter distally until being slightly concave at the area adjacent to the distal end of the bone. Both the medial and lateral side are equally thinner, at least half of the mediolateral width of the dorsal and ventral sides, as a result of the dorsoventral compression. The medial and lateral sides are hourglass-shaped in profile due to the concavities on the dorsal and ventral faces. Metacarpal V contains two conspicuous and extensive rugosities. One of them is located on the lateral side, on the lateral protrusion of that surface. The other rugosity is located on the medial side, at mid proximodistal length

of the bone, and fits in a groove on the lateral face of metacarpal IV. This scar continues proximally invading the ventral surface of the metacarpal. The proximal surface is oval in outline, dorsoventrally thicker medially and narrower distally. The long axis of the oval, ellipsoidal profile is quite perpendicular to a parasagittal plane. A maze-like pattern of sinusoidal grooves carves the proximal, articular surface of the metacarpal. In contrast with other metacarpals, the proximal surface is flat and formed by two faces, a large one, which forms most of the proximal side of the element, and a small, lateral one, which faces more caudally. The larger surface is facing proximomedially and offsets laterally the fifth digit of the manus. The distal face is subtriangular, having the outline of a scalene triangle.

Phalanges on Manual Digit II

Phalange II1. All the phalanges of the manus of *B. canadensis* are illustrated in figures 68 and 69. Phalange II1 is hourglass-shaped and mediolaterally compressed. The lateral side is convex and dorsoventrally arched. The medial side is convex distally and includes a triangular, striated and shallow depression distally. The distal portion of the bone is mediodorsally twisted in respect to the proximal area, which is roughly parallel to the parasagittal plane. This twist, along with a mediolaterall thickening, allows the distal half of the medial side of the phalange to articulate in a concavity on the medial, distal side of metacarpal II. The proximal side of phalange II1 is convex and slopes proximodistally. The distal surface is strongly concave. Both the proximal and distal

Surfaces are ellipsoidal in outline, though the distal one is more mediolaterally compressed and rounded, while the proximal face is more crescentic due to a slightly concave medial side. An elongated and deep foramen can be observed on the medial surface of the right phalange II1 of MOR 794. There is a rugose area running proximodistally on the center of the lateral side of the phalange, entering into the triangular concavity and adjacent to that foramen. The concave proximal surface of the phalange holds the convex distal surface of metacarpal II, while the convex distal face articulates with the proximal side of the wedge-shaped phalange II2.

Phalange II2. This is a wedge-shaped bone that wedges towards the medial side until the distal face meets the proximal side forming a rounded border. The ventral (plantar) side is proximodistally higher than the dorsal one. The bone is characterized by possessing a concave zone that runs through the dorsal, lateral and plantar side, in a continuous band of lighter color. This region is proximodistally wider on the plantar side, where it is subrectangular, while on the dorsal side it is wedge-shaped, following the profile of the element. The texture of this distinct area is also different in the dorsal side, where it is rather smooth and contains unevenly distributed, small foramina. In contrast, the plantar side is slightly more rugose and contains radiating striations and tiny foramina. A relatively large and rounded foramen can be observed on the dorsolateral portion of the concave band of the phalange. The distal face of the element is convex and rather smooth, well delineated from the concave band by a rim. That convexity fits on the concave proximal facet of ungual II.

Manual Ungual II. This element differs from all other types of pedal and manual unguals. The medial edge is not medially expanded, but attached to the main body of the Bone (Fig. 71). The ungual is asymmetrical when viewed dorsally and proximodistally elongated. Only the lateral edge is mediolaterally expanded. The medial border bears a series of indentations, as is the case of the other unguals, but these are deeper proximally. The plantar side of the ungual bears several foramina. The biggest of them is medially located, deepening cranially at the end of a longitudinal groove. Another elongated and lateroventrally deep foramen is present on the lateral side, proximal to the expanded region. No plantar keel is observed on manual unguals II. The proximoventral border is sinusoidal. The proximal surface is subellipsoidal and the major axis of the ellipse is mediolaterally oriented. The dorsal edge of that proximal profile describes an arch.

Phalanges on Manual Digit III

Phalange III1. This is a rather symmetrical, hourglass-shaped bone, but more robust than phalange II1. The morphology of phalange III1 is similar to phalange II1, being also dorsoventrally compressed, but the former differs in being more robust and proximodistally short. Phalange III1 more dorsoventrally expanded at its proximal end. The dorsal surface is mediolaterally convex and, at the same time, proximodistally concave and flat. The plantar surface is proximodistally concave and mediolaterally convex. It contains a triangular groove running from the distal border to the center of the plantar surface. The distal surface is kidney-shaped, thicker dorsoventrally and ventrally

curved at the border side. The proximal surface is dorsoventrally enlarged to articulate with the distal end of metacarpal III. The proximal profile of phalange III1 is pentagonal, with a very short ventral side, two symmetrical medial and lateral sides sloping ventrally, and a dorsal side that arches to form the two upper sides of the pentagon. The distal surface is mediolaterally concave and dorsoventrally convex. The proximal surface is concave.



Figure 71. From left to right, manual ungual III and II in dorsal view.

Phalange III2. Like phalange II2, phalange III2 is a wedge-shaped and compact bone. Also in this case the element wedges towards the lateral side. In contrast to phalange II2, phalange III3 is proximodistally compressed instead of dorsoventrally. As a result, the proximal surface of phalange III2 is oval, dorsoventrally concave, and mediolaterally convex. The distal face is smooth and convex, to fit on the concave proximal surface of ungual III. As in phalange II2, there is a distinctive, slightly concave

band running around the dorsoplantar perimeter of the phalange, except for the acute edge of the wedge. The texture of the dorsal region of that concave band is smoother than the plantar area. The plantar region of the band is rather rugose and extends further distally invading a small fraction of the distal surface of the bone. The ventral surface is dorsally deflected, giving an asymmetrical aspect to the element. Small foramina are dispersed on the dorsal region of the concave band. There is also a larger foramen near the lateral border of the phalange. A striking feature is the invasion of the distal surface attached into the concave, lateral surface of the phalange. This invasion is ventrally deflected and made of a curved and proximally projected portion of the lateral rim of the distal surface of the element.

Manual Ungual III. This element is hoof-shaped like the other ones unguals, but it is not so acute and less expanded mediolaterally (Fig. 71). In dorsal view the distal border describes an open semicircle instead of the pointed, arrow-shaped edge of manual ungual II and the pedal unguals. The edges of the expanded medial and lateral sides are relatively rounded. No plantar keel is observed on the available specimens. Like in the pedal unguals, a deep foramen is present on both lateral sides, located on the posterior edge of

the lateral corner. Like in manual ungual II, the proximoverbal border, as seen on plantar view, is sinusoidal.

Phalanges on Manual Digit IV

Phalange IV1. Phalange IV1 is a robust and subrectangular bone. Its medial side is proximodistally. The proximal side is slightly concave. The laterodorsal surface is convex and smooth. The distal facet is proximodistally convex and mediolaterally concave. The distal portion is medioventrally twisted. The bone is dorsoventrally higher at its proximal end, to conform the morphology of the distal facet of metacarpal IV. In contrast, the distal end of phalange IV1 is dorsoventrally compressed and expanded mediolaterally. The medial side is covered by short striations adjacent to the proximal border. A few foramina are dispersed on the medial side. Proximally, the ventral side is slightly concave due to a shallow groove, then flattens at the center, and distally is again carved by another deeper and wider groove at the distal end. Sets of proximodistal striations are seen adjacent to the proximal border. The phalange is convex along the lateral and dorsal faces, forming a continuous dorsolateral surface. Laterovertrally there is a proximodistally elongated rugose area. The border between the medial and dorsal surfaces is proximodistally concave, while the edge between the ventral and lateral faces is proximodistally straight. The proximal surface is D-shaped, the vertical side forming the medial side and being parallel to the parasagittal plane. The distal facet of phalange IV is kidney-shaped, but less than in phalange III1, because the medial side is thicker than the lateral one. The dorsal profile of the distal side is arched and slopes laterovertrally. The distal surface is dorsoventrally convex and mediolaterally concave,

while the proximal surface is rather flat. The distal portion is faces ventromedially, while the proximal end is expanded parallel to the parasagittal plane (dorsoventrally).

Phalange IV2. This is a small, squared, and proximodistally short bone. The element is dorsoventrally expanded at its proximal end and relatively less expanded along the distal portion. The dorsal surface is slightly concave and contains several small foramina. The orientation of this face changes from facing dorsolaterally at the proximal region of the bone to face dorsally distally. This is reflected in the fact that the proximal end is laterodorsally twisted in respect to the more horizontal position of the distal extreme. The medial, ventral and lateral surfaces of phalange IV are relatively rugose, especially the ventral one. Both the medial and lateral sides are proximodistally concave and dorsoventrally convex, while the ventral face is flat and shows a rounded foramen. The medial surface is dorsoventrally thicker than the lateral side, and slopes lateroventrally. The proximal facet is rather oval. It is dorsomedially to lateroventrally convex and concave along the perpendicular direction. The distal surface is subrectangular, mediolaterally concave and dorsoventrally convex. Part of the rugose texture of the ventral side of the phalange invades the distal face, forming a large semicircular indentation that is displaced towards the lateral two thirds of the distal side. The lateral corner overhangs proximally invading one third of the proximodistal length of the lateral side.

Phalanges on Manual Digit V (Fig. 72)

Phalange V1. This is a subrectangular and moderately elongated phalange. The bone is only slightly expanded at its proximal and distal ends. The proximal end is relatively more expanded than the distal one. The element is mediolaterally thinner distally, although the thinnest point is reached near of the center of its longitudinal length. Phalange V1 is dorsoventrally compressed. The dorsal surface is proximodistally concave and mediolaterally convex. The ventral side is flat, and its medial and lateral faces are concave. The dorsal surface is smooth and striated at the very distal and proximal ends. The ventral surface is more rugose and irregular in texture. The medial side is dorsoventrally thinner than the lateral one. The proximal side is oval, dorsoventrally higher laterally than medially. In contrast, the distal surface is semicircular, but also higher laterally than wide medially. The distal surface is smooth and a portion of its medial corner is proximally projected, attached over a tiny portion of the medial side of the bone. The distal surface is dorsoventrally convex and slopes into the dorsal side of the bone. The proximal facet is moderately concave.

Phalange V2. Like phalange V1, this element is subrectangular, but relatively smaller and proximodistally shorter. The proximodistal length of phalange V2 is less than double mediolateral width of its proximal end. All the medial, lateral, dorsal and ventral surfaces of phalange V2 are proximodistally concave. The bone is slightly expanded both dorsoventrally and mediolaterally at its proximal and distal ends. However, the phalange is more mediolaterally expanded than it is dorsoventrally high due to the dorsoventral

compression of the element. Like in other phalanges, the dorsal face is smoother and mediolaterally convex. The ventral surface is rugose and contains one or two small foramina located near the center. Both the distal and proximal surfaces are oval, but the proximal one is dorsoventrally thicker. At the distal end there is a sharp rim around the whole perimeter of the bone. The proximal surface is concave at the center and flatter near the perimeter.

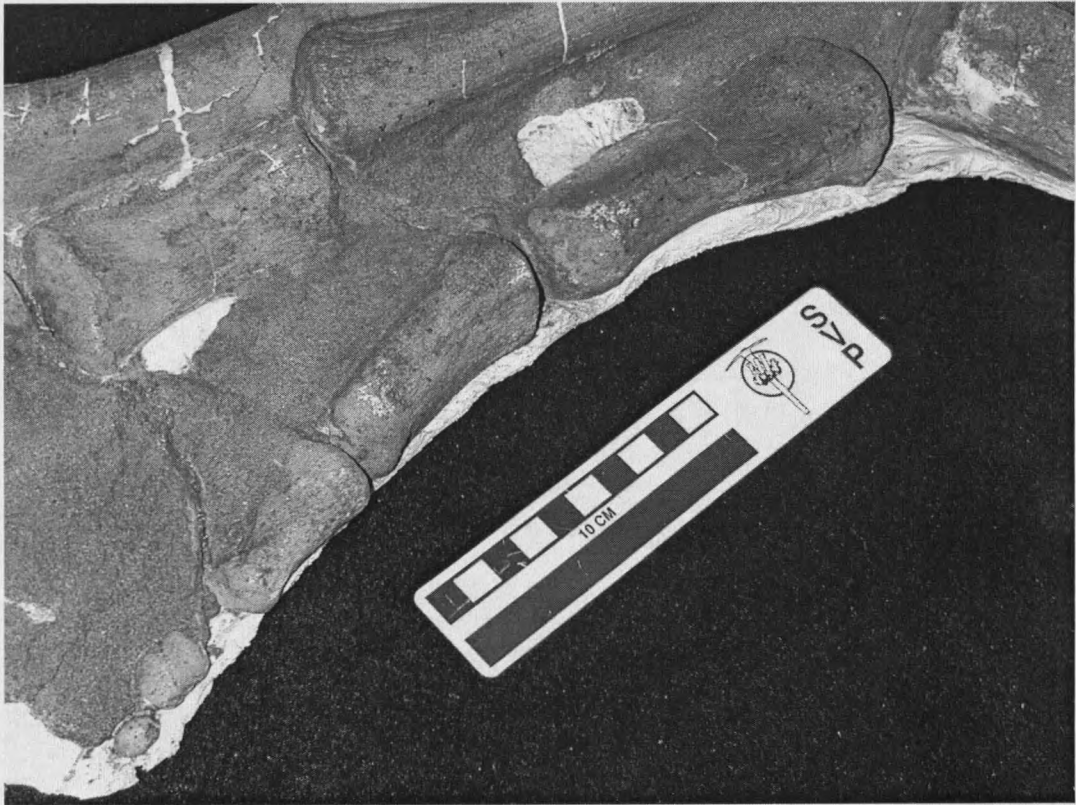


Figure 72. Right manual digit V, lateral view of the manus of MOR 794.

Phalange V3. This is a very small, subtriangular to oval element. The bone is dorsoventrally compressed. The dorsal surface is proximodistally concave and dorsomedially convex. The ventral side is convex and has a rough texture, especially near the lateral and medial sides. Both the dorsal and ventral surfaces can include several small foramina. The proximal and distal faces are distinct smooth, convex, and mediolaterally expanded. However, the proximal face is less convex than the distal one and more expanded both mediolaterally and dorsoventrally. In MOR 794 and MOR 1071-162-A the distal and proximal surfaces expand over the medial and lateral faces, so that they contact each other at the mid length of those sides. In other specimens the distal surface expands over a small distance into either the lateral or medial surface, and the proximal and distal surfaces are much less expanded into the dorsal and ventral sides.

Phalange V4. This is a pebble-like, tiny element. The bone is ellipsoidal in shape, dorsoventrally compressed, and relatively thinner distally. This element has only been preserved on the articulated MOR 794.

The possession of a fourth phalange on digit V contradicts the general condition of the manual phalangeal formula of the Hadrosauridae, 0-3-3-3-3 as stated by Weishampel and Horner (1990). It would be interesting to search for the number of phalanges on digit V in other hadrosaur taxa. *Maiaasaura peeblesorum*, the sister taxon of *Brachylophosaurus canadensis*, has three phalanges on digit V (David Dilkes, personal communication). However, given the small size of phalange V4, it is difficult to know whether its absence in other taxa is due to a real morphological condition or to a taphonomic bias.

Hindlimb

Femur

The femur (Fig. 73) is a columnar and robust element, the largest and longest bone in the skeleton. The femur is straight along its proximodistal length and mediolaterally compressed. Proximally the femur is expanded to form the head and the greater trochanter. Distally the bone expands into the distal condyles. The femur is rather constant in thickness along its longitudinal length. In caudal view it is possible to see how the femur curves slightly medially. As is typical in hadrosaurids, there is a relatively large, subtriangular fourth trochanter that projects caudally from roughly the middle of the shaft. The distal condyles project and curl caudally. The massive head projects medially about 90 degrees from the laterally located greater trochanter.

The proximal segment of the shaft is more mediolaterally expanded and craniocaudally wide than the distal portion of the femur. The portion of the shaft that expands into the head is more convex and cylindrical, separated by a shallow longitudinal groove that connects proximally with the lesser trochanter. The femoral head is a subcylindrical portion of bone that projects medially from the proximal end of the shaft. It is rather individualized by a laterally located constriction or neck. This neck separates the head from the medial surface of the greater trochanter, which forms the lateral side of the proximal end of the femur. The head is oval and more expanded mediolaterally than proximodistally, but less than craniocaudally. Laterally the large greater trochanter is much more expanded craniocaudally and proximodistally than the head, but mediolaterally compressed. Its proximal border is convex mediolaterally. Anteriorly and

proximally to the greater trochanter there is a deep cleft that separates it from the lesser trochanter. The lesser trochanter is a proximodistally elongated feature, thinner proximally and thickening distally. The trochanter is wedge-shaped and curves towards the proximal end of the greater trochanter, being also mediolaterally compressed.

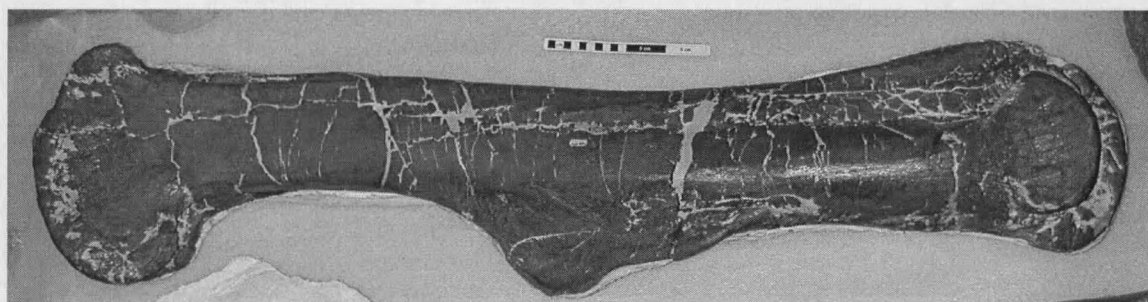


Figure 73. Right femur of MOR 794 in medial view.

The fourth trochanter comprises little less than one third of the total proximodistal length of the femur. It is slightly proximally located, so that its distal edge ends just a bit beyond the middle point of the proximodistal length of the femur. Its proximal end stops a few centimeters before the shaft begins to expand to form the proximal end of the element. In caudal view, the trochanter shifts from being centered on the caudal surface to be proximally near the medial side of the femur. The fourth trochanter is slightly sinusoidal and mediolaterally very compressed into a gentle triangular blade. Proximally the triangular profile includes a gentle outline followed by a deeper and more angulose, D-shaped distal summit. On its medial side, the fourth trochanter shows two deep muscle scars separated by a diagonally oriented ridge. One comprises most of the medial side and the border the angulose, D-shaped distal portion of

the fourth trochanter. In this area the bone surface is covered by a series of small and relatively sharp ridges oriented craniocaudally. The other large scar is a groove that lies proximally, cranial to the proximal, gentle outline of the trochanter. This groove is deeper than the distal rugosity and proximodistally oriented. Its surface contains small depressions, bumps and ridges. As the groove becomes deeper proximally its surface becomes less carved and smoother.



Figure 74. Right femur of MOR 794 in proximal (left) and distal (right) views.

Distally to the fourth trochanter the shaft of the femur remains constant in thickness for some distance, until it begins to expand slightly near the distal end. Distally the femur is relatively more expanded antero-caudally. The cross section of the shaft is subrectangular, the short sides being the caudal and cranial ones. The four sides of the

shaft are rather flattened. The lateral side contains two remarkable, proximodistally-elongated scars. One of them, the less pronounced, is located about the mid proximodistal length of the femur, parallel to the fourth trochanter. The other lateral scar is deeper and runs proximodistally parallel to the fourth trochanter, but more distally located than the other lateral scar. Craniocaudally, the feature extends covering the anterior half of the lateral side, until very near of the cranial border. Similarly to the other scar, it shows a rugose texture, but relatively sharper. The distal extreme of the femur is formed by the two condyles for articulation with the tibia.

The distal condyles describe an H-shaped outline in distal view. (Fig. 74). The condyles are mediolaterally compressed and expand antero-caudally, although more caudally than cranially. The condyles curl caudodorsally, forming thick, rounded caudodorsal and caudoventral borders. They mediolaterally thicker caudoventrally than they are caudodorsally. The distal condyles are separated by a deep and wide groove. This groove runs following the proximal and caudal contour of the distal end of the femur. That groove is very deep distally, to gradually become shallower proximally until disappearing into the anterior face of the distal femoral shaft, adjacent to a bony, rugose portion of bone that bridges the anteroproximal corner of the distal condyles. The medial condyle is larger and mediolaterally thicker, especially proximocaudally. It is more cranially and caudally salient than the lateral condyle, but more caudally than anteriorly. Its medial face is slightly concave and crossed by striations that radiate proximodistally towards the proximal border of the condyle. There, the edge of the condyle is carved by

proximodistally oriented, evenly spaced, narrow and deep indentations. Cranially, the distal condyle is much less expanded than caudally and forms a triangular, mediolaterally thin projection. The caudal portion of the condyle is proportionally more extensive proximodistally as well as craniocaudally than the anterior portion. The lateral distal condyle is smaller than the medial condyle. It is cranially thick mediolaterally and, like the medial condyle, the lateral condyle is much more expanded caudally than cranially. The curved, caudal portion of the lateral condyle is slightly concave on the lateral face and separated from the rest of the lateral surface by a ridge. The lateral surface of the lateral condyle is full of proximodistally radiating striations. Near to the border there are narrow and relatively deep indentations.

Tibia

Like the femur, the tibia (Fig. 75) is a long and robust element in the hindlimb. It is made of a rather straight, cylindrical central shaft that expands proximally and distally. The central portion is proximodistally brief and most of the longitudinal length of the tibia is devoted to the proximal and distal expanded areas. The tibia is compressed at its distal and proximal ends, but in different directions. The distal end is anteromedially to mediocaudally expanded, its face being craniolaterally oriented in respect to the parasagittal plane. In contrast, the proximal portion is laterocaudally facing and the cnemial crest curves laterally. The proximal tibia contains two condyles caudally oriented and relatively small compared to the well-developed cnemial crest, which is set anteriorly to the condyles. Anteriorly to the condyles, the lateral face, mostly part of the cnemial crest, is depressed for the reception of the proximal portion of the fibula. The distal end

of the tibia articulates in the two medial thirds with the astragalus. Anterolaterally it is excavated for the reception of the ascending process of the astragalus, and laterally articulates with the calcaneum. That excavation divides the craniolateral face of the distal end of the tibia in two different regions. The larger region is more anteriorly located, less distally salient, and receives the astragalus. The other, more lateral excavation is less extensive, more distally projected, and receives the calcaneum.

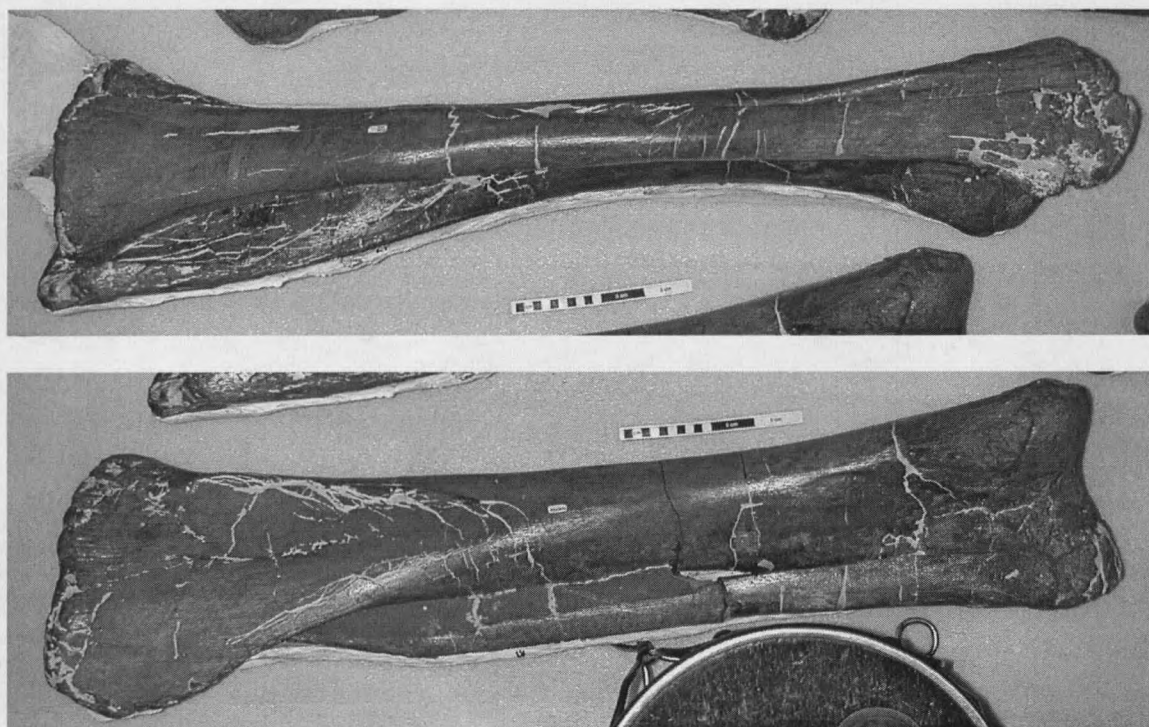


Figure 75. MOR 794, left tibia in lateral view (top) and right tibia in medial view (bottom).

The expanded proximal third of the tibia is cup-like in medial outline. The proximal end is more expanded than the distal end and at least doubles the diameter of

the central shaft. The proximal tibia expands following an anterolateral-caudomedial line and is strongly compressed. In proximal view, the tibia is arched leaving a concavity on the lateral surface. This concavity receives the proximal end of the fibula and is located between the proximal pair of condyles and the cnemial crest. The medial or anteromedial surface of the proximal tibia is slightly convex, a large and thick, cup-like blade as seen medially. Sets of proximodistally-oriented striations are seen ending against the proximal edge. The two condyles are located caudally and near each other, occupying the caudomedial portion of the proximal tibia. Anteriorly to the proximal border of the condyles the proximal edge thins to form the cnemial crest. One of the condyles borders the caudomedial corner of the proximal tibia. The other one is found anteriorly to this, attached to the lateral face of the tibia. The more anterior condyle projects caudally parallel to the medial face of the fibula, while the more caudal condyle is curled anterolaterally. The caudal condyle is at least twice as thick mediolaterally as the other condyle. The condyles are separated by a narrow cleft. This cleft is parallel to them and deepens distally into the tibia a few centimeters. The proximal surface of the condyles is rugose, carved with small pits and bumps (Fig. 76).

The cnemial crest expands anterolaterally forming the anterolateral side of the proximal end of the tibia. The crest is prominent and well developed. It is slightly arched laterally to partially embrace the proximal portion of the fibula. The crest begins to rise from the central shaft as a sharp ridge. This ridge quickly thickens and becomes wider proximally until forming the cnemial crest. The edge of that ridge and that of the crest along the anterolateral border shows sharp and minute ridges proximodistally-oriented.

The surface around the central shaft is smooth, except for a low ridge that rises on the anterolateral face. Distally, the ridge increases its prominence to form the laterodistal edge of the articulation facet for the calcaneum. There is an ellipsoidal foramen at the proximal terminus of the ridge. Before arriving to the expanded distal end there is a small, rugose area that rises over a surrounding and depressed region. The feature is similar to a rugosity located on the caudal surface of the humerus and both are about the same absolute size. The rugose area is relatively sharp and proximodistally elongated.



Figure 76. Proximal view of the right tibia and fibula of MOR 794.

The distal end of the tibia is not coplanar with the proximal extreme of the bone, but faces craniolaterally. This portion of the tibia is anteroposteriorly compressed. The

distal end of the tibia is asymmetrical and includes a flat and striated craniolateral face, a caudal, flattened and antero-caudally narrow surface, and a convex caudomedial surface. The laterocranial face is divided in two areas, one more craniomedially expanded and another relatively more lateral one that is more caudolaterally salient. The craniomedial border opens in a fan-like way. The laterocaudal third of the distal extreme of the tibia is more distally extended than the two anteromedial thirds, which are separated by a subtriangular groove for the ascending process of the astragalus. The distal border of the craniolateral face is more extended distally than the edge of the caudomedial border, so that there is a slope between both edges that forms the distal surface. The anterolateral surface of the distal end of the tibia is flat and strongly striated. The anterolateral face extends proximally into the shaft and has the outline of a narrow isosceles triangle. Its base forms the medial third of the distal, anterolateral border of the tibia. This triangular, elongated and striated surface serves for articulation of the distal fibula and, more distally at the border of the bone, of the calcaneum. The medial two thirds of the anterolateral surface of the distal tibia include a subtriangular groove that narrows proximally for reception of the ascending process of the astragalus.

Fibula

The fibula (Fig. 75) is a very long and slender element. It is very compressed mediolaterally, particularly on its proximal portion, and antero-caudally narrow. The bone is distally and proximally expanded to join the tibia medially and the calcaneum distally. The fibula is located along the lateral side of the tibia. The element is proximodistally elongated and parallel to the parasagittal plane until it twists medially along the distal

third. Proximally, the fibula is so mediolaterally compressed that it can be described as a long and craniocaudally narrow blade. The mediolateral thickness is greater at the proximal edge, gradually decreasing distally. The proximal border is straight, antero-caudally directed and slightly arched medially. The medial surface of the proximal end is concave and rather rugose. A shallow ridge that thins proximodistally bisects the medial face. The caudal half, separated by that ridge, is proximodistally crossed by coarse striations. The concavity of the medial surface of the proximal tibia deepens distally into a subtriangular, elongated groove that thins gradually until reaching two thirds of the proximodistal length of the bone. At the mid proximodistal length of this groove there is a rugose area. The proximal border of the tibia is very rugose and coarsely indented. It projects cranially, while forming a 90 degrees angle with the caudal border of the element.

The central third of the fibula is laterally smooth and antero-caudally convex on the lateral side. As the fibula expands mediolaterally distally from the proximal region, the central shaft is mediolaterally thicker distally. The medial side is concave. It contains the distal end of the central groove initiated from the concavity of the proximal portion of the bone. Near the end of the groove and anteriorly there is a relatively small, ellipsoidal, elongated, and shallow foramen. Distally to the groove, the medial surface of the central fibula is slightly concave. More distally, approaching the distal third of the bone, the surface becomes flat and smooth. Approximately at the level of the scar that lies within the groove described before, there is the beginning of a gradual twist of the distal half of the fibula. The shaft progressively twists medially as we approach the distal end of the

element. The cross section of the fibula changes from crescentic to a scalene subtriangular section. Distally the fibula is composed of three flattened faces. One is smooth and forms the lateral side of the element. Another one forms the anterior face and is also smooth. Finally, a third surface constitutes the articulating surface for the tibia. This is a mediocaudally facing surface that contains a proximodistally elongated, slight concavity. There the bone is coarsely striated proximodistally, especially medially.

The fibula is mediolaterally thickest before arriving to the distal ending, where the articulating surface for the tibia and the cranial, flat and smooth face meet in a medially projected border. This border is the more medially salient region of the tibia and is rugose, as well as thickened and flattened anterocaudally.

The distal extreme of the fibula is slightly expanded, although much less than the proximal region. In spite the twisting of the fibula above described, the distal end is expanded producing a distal surface that is almost parallel to the proximal border of the bone or to the parasagittal plane. The distal end is a rather straight. The lateral surface of the distal end of the fibula is, like the other sides, very rugose and deeply carved with proximodistal striations that meet the edge of the bone. The distal surface of the fibula is very rugose and slightly rounded.

Astragalus

The astragalus (Fig. 78) is the major bone in the tarsus. It is subtriangular in anterior view, and at least twice more extensive mediolaterally than proximodistally. The astragalus articulates laterally with the calcaneum to form the proximal tarsus of the hadrosaur, and proximally with the more proximally retracted border of the tibia. The

astragalus is proximodistally shallow, convex on its distal face and concave on its proximal side. The subtriangular profile is asymmetrical, laterally skewed, and the ascending process of the astragalus forms the apex of the triangle. This process projects proximally from the anterior face. The caudal face is much shorter proximodistally. The distal side is a broad saddle-shaped surface. In distal view, the astragalus is subrectangular laterocaudally, but then narrows towards the medial side, ending medially in a rounded border parallel to the tibia. The astragalus is oriented with its long axis trending anterolaterally, parallel to the anterolateral, distal end of the tibia with which articulates. It covers the distal end of the ulna along the medial two thirds, the medial side, and little more than half of the caudal one, where the bone thins proximodistally towards the lateral side of the tibia. On the distal face of the tibia, the astragalus never becomes more salient than the last, extending only until the border of the tibia. The ascending process constitutes at the same time the lateral border of the astragalus. The element reaches its maximum proximal extent in a cusp-like point of the ascending process and then gradually becomes proximodistally shallower medially until the medial border of the tibia, in a concave upwards profile.

The medial face of the astragalus is rather flattened and parallel to the medial side of the distal tibia. The medial side of the astragalus contains proximodistal striations. The medial side constitutes the antero-caudally most expanded portion of the astragalus, which becomes progressively narrower laterally. The medial face is proximodistally deeper than the lateral side, but much shallower than the anterolateral face. The caudal surface thins laterally from the thickness of the medial face, and becomes wedge-shaped in thinning

laterally and distally. In laterocaudal view the lateral side of the astragalus is, like the medial, arched distally. The anterior half of the lateral surface articulates with the medial border of the calcaneum, while the caudal half articulates with the tibia. For that purpose the lateral side of the astragalus is rather irregular. Its caudal half forms a border that expands proximodistally towards the anterolateral side, to form the lateral edge of the ascending process of the astragalus. It is indented along the edge to articulate with the calcaneum and its face "sinks" inwards, that is, medially. There are a few foramina of different sizes and located near the anterodistal border of the tibia. On its anterior, distal and caudal surfaces, the astragalus shows small and rounded pits, which are rather evenly distributed. They are deeper on the more central, proximally depressed area, near the ascending process. There is a sharp boundary in the surface features between the proximal area of the ascending process and the adjacent, anterior surface. The strongly carved anterolateral surface of the ascending process lies in a scalene, triangular area. The ascending process shows an irregular network of small pits and sharp, short ridges. These last are found on the anterior face of the distal half of the process. The proximal portion of the process contains a rugose surface with less sharp ridges. There is a relatively large and rounded foramen located in a proximal-central position on the triangular cusp of the ascending process, on its anterolateral face. The ascending process of the astragalus is caudally tilted, towards the distal part of the groove on the distal end of the anterolateral face of the tibia. This groove is not totally filled by the process, but about one half of its proximodistal length is left exposed proximally.



Figure 77. Right proximal tarsals of MOR 794 in anterior view.

Calcaneum

The calcaneum (Fig. 77-79) is a crescentic and compact bone. It is the smaller of the proximal tarsals and is located laterally. It articulates with the astragalus medially, the fibula proximally and the tibia caudally. The overall morphology of the bone is similar to a quarter from a hypothetical, short cylinder. The lateral face is flat. There is an anterodistal surface that is convex and rounded. Two strongly concave, caudal and proximal surfaces are separated by a sharp ridge, and a medial, narrow border. The calcaneum covers about one third of the total mediolateral width of the articulated tibia

and fibula. Both the lateral side and the medial border of the calcaneum are rather parallel. The calcaneum is proximodistally deeper laterally and gradually becomes shallower medially, until being shallowest at the medial border. The calcaneum is indented along the cranial, medial and caudal borders. The lateral side describes the quadrant of a circumference and is relatively smooth. There are a few foramina on the lateral face of the calcaneum. The larger is located distally, near to the distal border and at mid length of the arch. The dorsal edge is longer than the caudal border and these two meet in a straight angle at a very sharp corner located proximocaudally. Near the distal border of the calcaneum there is another circular foramen located anteriorly. The anterodistal side is a strongly convex, arched and rounded. It is the more extensive surface of the calcaneum and is rather rugose, showing shallow, oval and small pits. In anterior and caudal view, it is possible to see how the anterodistal face of the calcaneum is gradually shallower medially, and forms about twenty degrees with a horizontal line.



Figure 78. Distal view of the proximal tarsals of the right hindlimb of MOR 794.

The proximal surface of the astragalus articulates with the distal end of the fibula. It is a strongly concave facet and D-shaped in proximal view, the arch of the "D" being cranially directed. This surface is rugose and carved with circular and minute pits. The margins around all the contour of the face are very sharp. The caudal surface of the calcaneum articulates with the anterodistal area of the tibia. It is more salient distally than the distal end of the tibia element. This surface is still more strongly concave than the proximal one, giving a crescentic profile in lateral and medial views. The concavity slopes proximodistally. It is rather smooth and contains a relatively large foramen located medially, proximodistally located at the level of the maximum concavity. The caudolateral surface is gradually most concave medially. Cranially, this concavity ascends proximally forming a vertical area that ends in a very sharp edge. Cranially to the ridge extends the proximal, concave surface of the calcaneum. Thus, the proximal terminus of the caudal surface and that sharp ridge constitutes the boundary between the two concave surfaces of the calcaneum, the caudomedial and the proximal. The ridge is directed following a laterocaudal- anteromedial line, as seen in proximal view. The medial side of the calcaneum articulates with the lateral side of the astragalus. This side of the calcaneum is proximodistally very shallow, a rugose and indented, arched border. Proximally on the medial side of the calcaneum there is the medial terminus of the sharp ridge that results from the union of the caudolateral and proximal faces of the bone. Proximally over the medial border of the calcaneum the ridge forms an sharp triangular apex.

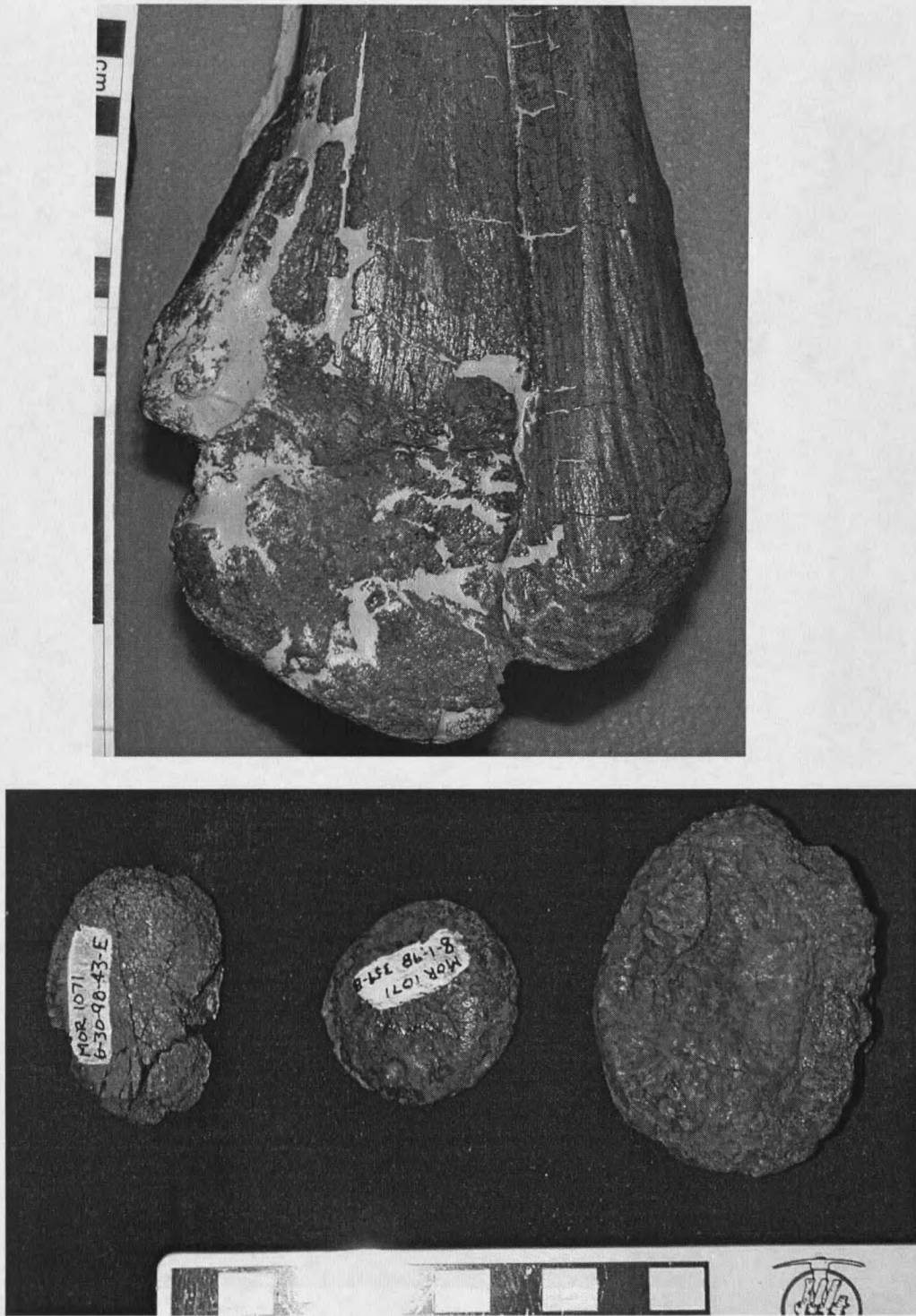


Figure 79. Left calcaneum of MOR 794 in lateral view (top); distal tarsals in distal (far left and far right) and proximal view (center).

The Foot and the Distal Tarsal

The foot of *B. canadensis* is a robust and compact structure (Fig. 80-83). There are three digits that have a phalangeal formula of 3-4-5. The metatarsals are large and stout elements, proximodistally elongated and expanded at its distal and proximal ends. In contrast, the phalanges are compact and proximodistally short elements. Only one distal tarsal is preserved both in the feet of the articulated MOR 794 and among the bonebed specimens. The element is discoidal and relatively small. It is extremely compressed proximodistally and the major axis of its proximal and distal ellipsoidal profile extends dorsoventrally. The element is slightly concave on its proximal side. The distal surface is proximodistally expanded on its lateral half. The lateral border is much thicker than the thin, sheet-like medial edge. The bone texture in the available specimens is very rugose and uneven. The proximal, concave area is indented in respect to a wide rim that surrounds it following the contour of the bone at the periphery. The ventral border is slightly more pointed than the relatively more rounded dorsal edge. This more pointing ventral border is slightly displaced laterally. The element is attached to the medioventral area of the proximal surface of metatarsal IV, abutting the lateroventral border of the proximal surface of metatarsal III, as will be described below.

The metatarsals form a tightly unit. This is reflected, for example, in the extensive articulation surface between metatarsal II and III, in which the whole lateral side of the former is employed in the articulation. Metatarsal II is shorter than metatarsal III, but longer than metatarsal IV. Metatarsal III is the longest and most robust of the metatarsals.

In proximal view, its articulation with metatarsal II describes an oval outline when considering the proximal outline of this last. Metatarsal IV is only slightly shorter than metatarsal II, and its morphology is roughly a spectral image of metatarsal II. Whereas metatarsal II and III form tight articulation, metatarsal IV forms a less extensive articulation with metatarsal III. Only little more than the proximal third of the medial side of metatarsal IV is articulated with the lateral face of metatarsal III. The proximal surface of metatarsal IV does not articulate at the same level as the one of metatarsal III, but the bone is slightly displaced distally. This arrangement provides space for the insertion of the distal tarsal, which fits on the proximomedial, concave surface of metatarsal IV contacting the proximoventral, lateral edge of metatarsal III. The addition of the distal tarsal fills that space until the level of the proximal border of metatarsals III and II.

The toes are proximally supported by a relatively larger, very robust and broad phalange. Phalange III1 is the largest of them, being subrectangular and dorsoventrally compressed. Phalange II1 and IV1 are similar in morphology, but the last is proximodistally shorter. Phalange II1 and IV1 are shaped roughly as spectral images of each other. While phalange III1 has bilateral symmetry, phalanges II1 and IV1 are asymmetrical and convex towards the medial and lateral sides of the foot, respectively. The remaining phalanges are proximodistally very short and compact. The phalanges become more proximodistally compressed from digit II to digit IV. Thus, for example, phalange II2 is almost twice as proximodistally long as phalange III2, and this last is proximodistally longer than phalange IV2. Successive, more distal phalanges become also more proximodistally short within each toe. Each digit terminates in a spade, hoof-

like ungual. Ungual III has bilateral symmetry, while unguals II and IV are asymmetrical. Pedal unguals II and IV are spectral images each other, to the point that is difficult to distinguish between, for example, a left ungual IV and a right ungual II. Pedal unguals are very different from the manual ones, in being much more arrow-shaped, with more expanded distal portions. The described arrangement of the metatarsals and that of phalanges III1, III1 and IV spreads the toes in a fan-like pattern. Pedal digit III is more dorsally salient, while digits II and IV surround it at a slightly lower level. Probably this is reflected in the asymmetry of unguals II and IV.

Metatarsals

Metatarsal II. Metatarsal II is a mediolaterally-compressed element. The bone becomes wider distally. It is expanded proximally, but less distally. The metatarsal is medially arched. The medial face is proximodistally concave, while the articulating lateral surface is more proximodistally convex. The proximal surface is trapezoidal, while the distal face is strongly compressed mediolaterally and dorsoventrally elongated, lenticular in outline. The distal surface is medially inclined and faces mediodistally, while the proximal side is facing proximolaterally. Sets of coarse striations radiate proximodistally from the proximal edge of the medial surface. A large flange is found along the distal half of the laterodorsal edge of the metacarpal. There, the medial side of the element is dorsolaterally oriented and ascends dorsally to merge with the flange. The lateral side of metatarsal II continues ventrally into the ventrolateral face of the bone. The lateral surface fits tightly into a large concavity on the medial face of metatarsal III. That

surface is proximodistally and dorsoventrally convex. Sets of striations are located on the proximal and distal ends of the lateral side of the bone. The lateral surface of the flange is rugose and contains a scar that extends distally. There is an ellipsoidal foramen adjacent to the ventral border within the proximal third of the lateral surface. Properly speaking, there is no continuous dorsal side, but instead a ridge that results from the meeting of the mediodorsally oriented dorsal half of the medial surface and the more vertical (parasagittal) lateral surface. The ventral side is in fact a ventral ridge along the proximal third of the metacarpal. Distally, the ridge thickens gradually and becomes a ventrolateral face. The lenticular proximal surface is concave at its center and rugose and bumpy. The margin of the proximal face shows a series of deep indentations. The distal surface is trapezoid in outline and represents the mediolaterally widest area of the metatarsal. In contrast to the vertical orientation of the proximal face, the medial and lateral sides of the distal surface are laterally tilted, producing the trapezoidal profile. There is a groove that runs from the distal end of the ventrolateral surface of the metatarsal into the ventral portion of the distal face. That groove separates two mediolaterally-compressed condyles. The medial one is medially oriented ventrally and its lateral face is slightly concave. The lateral condyle is laterally directed into a sharp and curled point. The lateral face of that condyle is strongly concave. The perimeter of the distal face is carved by deep indentations that continue also into the medial, lateral and dorsal sides. The texture of the distal surface of metatarsal II consists of a pattern of grooves that define small and isolated polygons of bone in between.

Metatarsal III. This is longest and most robust metatarsal. It is composed of a thick, fairly straight, cylindrical and stout shaft. The proximal end is mediolaterally expanded, whereas the distal end expands dorsoventrally. The shaft is distally flattened dorsoventrally. The medial face is concave proximally to articulate with the lateral, convex topography of metatarsal II, and at the same time, is more dorsoventrally expanded in that area than the lateral side. Proximally there is a mediolaterally compressed flange that protrudes ventrally, similar to the dorsal flange of metatarsal II. The proximal surface is crescentic and holds the convex lateral side of the proximal surface of metatarsal II. The distal surface is subrectangular, mediolaterally concave and dorsoventrally convex. Distally the medial side is slightly concave, then proximally becomes convex and contains a scar at the mid proximodistal length of the metatarsal. More proximally, the medial surface flattens and is proximodistally crossed, roughly bisected, by a groove that is deeper nearest to the proximal edge of the element. This groove holds a corresponding ridge on the lateral proximal side of metatarsal II. Where the medial side describes a ventral flange, near the proximal end, the texture of the bone features an elongated scar. Both the distal and proximal ends show sets of striations radiating close to the border. However, these are far more notorious at the proximal end. The lateral side of metatarsal III is dorsoventrally convex, especially proximally, where the element becomes dorsoventrally expanded. The distal end is more dorsoventrally compressed on its lateral side than it is on the medial face. The distal end is strongly concave by means of a wide groove that contains a scar on its ventral wall. Dorsally, at the level of end of that groove, the bone forms a conspicuous lateral projection, as

happens more distally on the ventral portion. These projections are very rugose.

Proximally the lateral surface becomes notably convex dorsoventrally. At the proximal end there are sets of proximodistally oriented, deep striations that continue into the dorsal and ventral sides. There is an extensive scar near the proximal fourth of the bone. Along the proximal half of the metatarsal, the meeting between the medial and the ventral sides form a sharp ridge. Both the ventral and dorsal faces are quite constant in mediolateral width. And both sides share flat distal and middle regions, while being more convex proximally. As in metatarsal II, the proximal outline of metatarsal III is crescentic, being concave on the medial edge. The proximal end is dorsally pointed, while being mediolaterally thicker and nearly straight on its ventral edge.



Figure 80. Distal view of the left pes of MOR 794.

The proximal surface is bumpy and rugose in texture, as in metatarsal II. The distal end is more dorsoventrally compressed on the lateral border, and more mediolaterally concave on its ventral side. The texture is, like in metatarsal II, a maze-like pattern of grooves and convex patches of bone. This pattern ends at the lateral and medial borders in deep indentations. These indentations are evenly distributed and continue into the lateral and medial edges of the metatarsal.

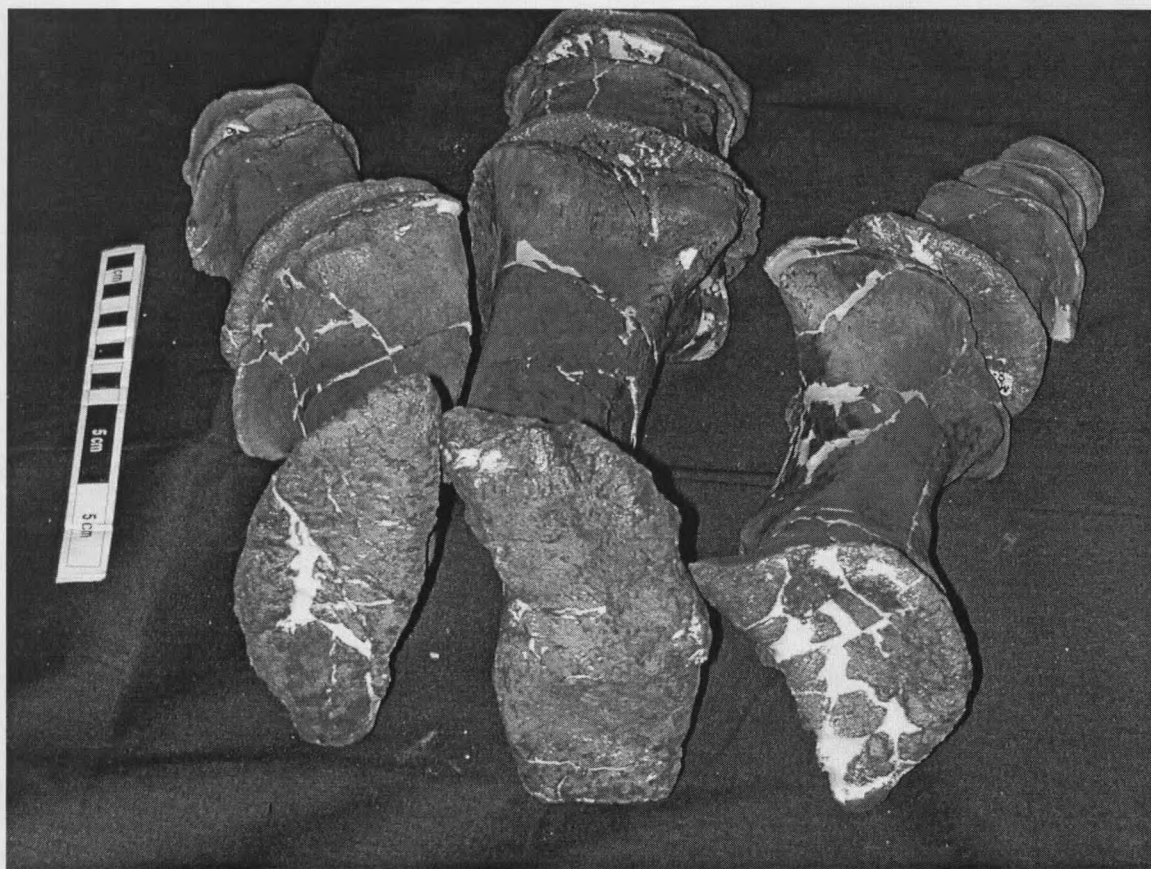


Figure 81. Subadult composite pes in dorsodistal view.

Metatarsal IV. Metatarsal IV is the shortest of the three metatarsals. While metatarsal II diverges medially distally from metatarsal III, metatarsal IV diverges laterally. The lateral surface of metatarsal IV is proximodistally concave. The shaft of metatarsal IV is as robust as in metatarsal III, but in mediolaterally compressed. As in all the metatarsals, the IV element is expanded at its proximal and distal ends. A distinctive feature of metatarsal IV is a dorsoventrally thick and large flange that projects on the medial surface. The proximal surface is D-shaped. The distal face is subtrapezoidal, as in metatarsal II, but in contrast to this last, it is more mediolaterally expanded. At the same time, the distal surface of metatarsal IV is lateroventrally rotated a few degrees in respect to the more parasagittal orientation of the proximal surface. Both the dorsal and ventral surfaces are proximodistally concave. The medial flange of the metatarsal occupies all the dorsoventral thickness of the shaft and extends proximodistally until a few centimeters beyond the mid proximodistal length of the bone. The medial surface of that flange is very rugose. The maximum dorsoventral thickness of the flange is reached at the proximal third of the proximodistal length of the bone. The distal end the medial face is strongly concave, including a dorsoventrally wide groove. There the bone expands dorsoventrally, although much less than in the proximal end. The distal end contains a circular concavity. Besides the medial flange, there is a scar crossing the lateral and ventral surfaces along the distal third of the bone, arising from the proximal rim of the distal circular, concave surface. The dorsal surface is proximodistally concave and mediolaterally convex. Its texture is rather smooth. The ventral face is more flattened than the dorsal one, but still also proximodistally concave. As in the other two

metatarsals, the proximal side is cranially tilted dorsally. The curvature of the "D" constitutes the dorsal, lateral and ventral sides of that outline. The medial edge is concave and projects dorsally. The ventromedial corner is slightly more rounded, but still forms a rather sharp area, rather symmetrically in respect to the dorsomedial one. The proximal surface is concave and rugose, showing pattern of elongated pits, which are more defined at the periphery. The lateral and medial borders of the distal face are medially tilted, while the dorsal and ventral sides are rather horizontal. This last is symmetrically opposite on the trapezoidal distal outline on metatarsal II. The dorsal border of the distal surface of metatarsal IV is curved, lateroventrally sloping. The ventral border is concave at the middle because of a wide and shallow groove that splits the distal, ventral end in two, incompletely differentiated, condyle-like lateral and medial regions. This condition is also found in metatarsal II. The lateral condyle projects ventrolaterally and is mediolaterally more compressed and sharper than the medial one. The medial condyle projects medioventrally. The distal surface of metatarsal IV is convex, slightly flattened dorsoventrally until connecting ventrodistally with the described groove. The texture of the distal surface is, like in the other metatarsals, a labyrinth of grooves mixed with convex patches of bone.

Phalanges on Pedal Digit II

Phalange II1. Phalange II1 is the largest phalange of pedal digit II. It is moderately elongated proximodistally. The bone is expanded proximally and distally, but much more proximodistally. The phalange is mediolaterally compressed proximally.



Figure 82. Subadult composite pes in dorsal view.

Phalange II1 has flattened lateral and ventral surfaces, while the dorsal and medial faces form in fact a convex dorsomedial face. The dorsal surface is proximodistally concave in relief and mediolaterally convex. The dorsal surface presents a descending slope towards the distal end. The proximal half is medially sloping, near the proximal end. The dorsal side flows medially into the medial surface. There the bone is distally more concave, but also proximodistally concave in relief. The ventral side of phalange II1 is hourglass-shaped, being more mediolaterally compressed than the dorsal surface. The ventral face is concave distally, but convex proximally with a scar on the lateroproximal corner. The proximal surface describes the outline of a quadrant of a circle. The arch of this quadrant forms the dorsal and medial sides. The straight proximal borders of the ventral and lateral sides form an angle of 110 degrees. The proximal side is concave, containing circular, small pits concentrated around the central depressed region. Outside this region, the proximal side of the phalange is rather smooth, having only very short striations near the edge. The distal surface of phalange II1 is crescentic and ventrally concave. It is asymmetrical, with the lateral side being shorter and steeper than the longer medial edge. The distal surface is mediolaterally concave and dorsoventrally convex. Ventrally, the surface is concave and splits the distal border into two narrow, condyle-like portions. The lateral one projects ventrolaterally and the medial one does so medioventrally. This last is more projected than the lateral one. The texture of the distal side is rather smooth. There are a series of circular pits located evenly around the center. The ventrolateral and ventromedial edges extend further proximally along the medioventral and lateroventral borders. This last feature is more developed on the medial

side. The medial and lateral edges of the distal surface are indented. Sets of proximodistally-oriented striations are found along the proximal end, on the dorsomedial, lateral and ventral sides.

Phalange II2. Phalange II2 is the most equidimensional element in the foot. It is considerably reduced in proximodistal length in respect to phalange II1, being a very compact bone, and much more smaller than the preceding element. Phalange II2 is less asymmetrical than phalange II1, but still the medial side is less steep in slope and longer than the lateral one. The element is mediolaterally compressed and subrectangular in cross section. The dorsal side is flattened, being slightly concave. Laterally and medially, the dorsal side curves (more gently medially) to link with the lateral and medial surfaces of the bone. The ventral surface is concave. Proximally, the ventral side is convex at the medial and lateral corners. These are slight ventral expansions of the proximal border. Similarly, the ventral side is concave at the center and convex lateral and medially due to the ventrally projecting corners of the distal end. This condition is more developed at the distal end than at the proximal one. Near the distal end both the lateral and medial sides are concave, especially the lateral side. Like in phalange II1, the distal surface is crescentic. However, phalange II2 differs in having a more symmetrical profile and a slightly concave dorsal border. The distal side is mediolaterally concave, but dorsoventrally convex at the center. As in phalange II1, the ventrolateral and ventromedial borders project proximally, especially the medial one, which is also thicker. The proximal surface is more oval than in phalange II1, though still possesses a deeper

medial side. The surface is concave, except for a convexity near the center and the ventral border. The proximal surface is much more extensive than the distal one. Several foramina are unevenly distributed mostly through the dorsal, lateral and medial surfaces of the phalange. Among these, there are two relatively large foramina on the dorsal surface.



Phalanges on Pedal Digit III

Phalange III1. As happens with the other first phalanges on digits II and IV, phalange III1 is the largest element among the phalanges of pedal digit III. However, phalange III is also the largest and more robust of all pedal phalanges. It has bilateral symmetry, except for the slightly more dorsoventrally compressed lateral, proximal border. Phalange III1 is subrectangular in dorsal view and is slightly elongated proximodistally. It is expanded at its distal and proximal ends, but more proximally and more mediolaterally than dorsoventrally. The dorsal and ventral surfaces are the most extensive. They are proximodistally concave. The dorsal surface is flattened, slightly concave with a gentle lateroproximal slope. The ventral surface is slightly concave mediolaterally, except for the proximal region, where it becomes convex. The bone texture is quite smooth on both the dorsal and ventral sides. However, the convex area in the proximal region of the ventral surface is rugose around the center. Both surfaces are proximodistally concave, especially towards the distal end. At the proximal border, the lateral and medial faces become dorsoventrally convex. Proximally, the lateral and medial sides become dorsally more salient in respect to the ventral area. The distal end is circular in lateral and medial view, as in the case of phalanges II1, II2 and IV1. Sets of striations arranged proximodistally surround the proximal end of phalange III1. There is large, proximodistally-elongated foramen on the lateral face of the subadult MOR 1071-7-98-216. Another one appears on the ventral side of the right phalange III1 of MOR 794,

laterally displaced. The proximal surface is subellipsoidal in outline, with a more dorsomedially compressed lateral arch in respect to the deeper medial side. The ventral edge is slightly concave at the center. The proximal face is concave, with a deep, mediolaterally elongated excavation at the center. Numerous circular pits are found on the central region of the proximal surface of the phalange. The distal surface is semicircular and slightly crescentic, with a flat dorsal border and a concave ventral side. The surface is smooth and differentiated from the rest of the bone by a sharp rim that surrounds it along its entire perimeter. The distal side is dorsoventrally convex and slightly concave mediolaterally. Ventrally the bone projects slightly laterally and medially into two mediolaterally compressed corners.

Phalanges III2 and III3. These elements are similar in morphology. They are strongly proximodistally-compressed elements. These elements are much wider mediolaterally than proximodistally and dorsoventrally thick. Phalange III3 is twice as dorsoventrally high as it is proximodistally long. In contrast, the proximal surface of phalange III2 is only slightly higher dorsoventrally than proximodistally long. The proximal surface of phalanges III2 and III3 is D-shaped, with the straight side of the "D" forming the ventral border. The dorsal border is gently arched, but more arched towards the lateral and medial edges. The proximal surfaces are dorsoventrally concave, but mediolaterally convex at the center. Isolated foramina can be found on those faces. The convex central portions contain a few small and circular depressions. The proximal outline of phalange III3 is dorsoventrally shorter at the lateral border. The distal surface

differs in outline between phalange III2 and III3. In phalange III3 it is similar to the profile of the proximal side, while in phalange III2 it is bell-shaped. The bell-shape distal profile is due to open indentations on the dorsal portions of both the lateral and medial borders. In phalange III2, the lateroventral corner of the distal end is more laterally projected and salient than the medioventral one. In phalange III3 these are more equally projected. The distal outline of phalange III2 is dorsoventrally shorter at the lateral edge, a feature much less expressed in phalange III3. The distal surfaces of both phalanges are mediolaterally concave and dorsoventrally convex. Sharp rims mark the boundary between the distal surface and the other surrounding four sides of the bones. As in other phalanges, the medioventral and lateroventral corners of phalanges III2 and III3 project and thin proximally invading a portion of the lateral and medial sides. The dorsolateral, dorsomedial and ventral surfaces are recessed in respect to the proximal and dorsal sides. The dorsal surface forms a continuous surface with the medial and lateral surfaces. These sides are proximodistally concave and mediolaterally flattened. They are not so smooth as the proximal and distal faces, and contain numerous foramina. The ventral surface is relatively rugose, flatter and slightly convex at the center.

Phalanges on Pedal Digit IV

Phalange IV1. It is the largest element of pedal digit IV. The bone is morphologically similar to phalange II1, nearly a mirror image of this last. Phalange IV1 is proximodistally shorter, and mediolaterally and dorsoventrally more compressed than phalange II1. The distal surface is mediolaterally wider. On the proximal side, the

proximomedial border is as high dorsoventrally as the one in phalange II1, but the ventral border is mediolaterally wider. The bone has rather flattened medial and ventral surfaces, while the dorsal and lateral faces form convex dorsolateral face. The dorsal surface is proximodistally concave and mediolaterally convex. The dorsal surface presents a descending slope towards the distal end. The medial surface is more flattened than the dorsal side, but also proximodistally concave in relief. The ventral side of phalange IV1 is more mediolaterally compressed than the dorsal surface. The ventral face is concave distally, but convex proximally showing a scar on the proximomedial corner. The ventral side of phalange IV1 is mediolaterally wider than in phalange II1. The proximal surface describes the outline of the quadrant of a circle. This is mediolaterally wider than in phalange II1, so that in phalange IV1 the ventral side is almost as wide as the medial one. The arch of this quadrant forms the dorsal and lateral sides. The straight proximal borders of the ventral and medial side form an angle of 110 degrees. The proximal surface is concave, containing circular, small pits concentrated around the central, relatively depressed region. Outside this region, the proximal side of the phalange is rather smooth and presents short striations and indentations near the edge. The distal surface of phalange IV1 is crescentic, ventrally concave and dorsally flat. This flat dorsal border is mediolaterally more extensive than in phalange II1. The distal side is asymmetrical, so that the medial side is shorter and steeper than the longer lateral edge. The distal surface is mediolaterally concave and dorsoventrally convex. Ventrally, the surface is concave and splits the distal side in two narrow corners. The medial one projects ventromedially and the lateral one does so mediolaterally. This last is more projected than the medial

one. The perimeter of the distal surface is well differentiated from the surrounding sides of the element by means of distinctive rims. The texture of the distal side is rather smooth. The ventrolateral and ventromedial edges further extend proximally along the medioventral and lateroventral borders for some distance. This feature is more developed on the lateral side. The medial and lateral edges of the distal surface have only minute and short indentations, in contrast to the deeper and larger ones on phalange II1. Sets of proximodistally-oriented striations are found along the proximal end, on the dorsolateral, lateral and ventral sides.

Phalanges IV2, IV3 and IV4. These elements are very compressed proximodistally, as in the case of phalanges III2 and III3. But in contrast to these, phalanges IV2 through IV4 are much more expanded dorsoventrally, producing a discoid overall appearance. This discoid morphology is slightly folded, so that the central portion of the bones are convex towards the proximal direction, while having distally projecting medial and lateral sides. The most extensive surfaces are the distal and proximal ones. The dorsal, lateral, medial and ventral sides form a concave, recessed ring in between the distal and proximal surfaces. The proximal surface is, like in other phalanges, dorsoventrally more expanded than the distal one. It is dorsoventrally concave and mediolaterally convex. The texture of the proximal side of the phalanges is smooth, like the on the distal side. The distal side of these bones is crescentic, mediolaterally concave and dorsoventrally convex, especially on the central area. Ventrally, the concavity becomes slightly deeper between the medioventral and lateroventral corners. Like in

other phalanges of the foot, these corners project proximally some distance invading the lateral and medial sides. The lateroventral corner is relatively more expanded, both lateroventrally and proximally. The lateral border is dorsoventrally shorter than the medial one, in conjunction with a less steep slope towards the lateroventral side. This feature is also present on the whole lateral and proximolateral outline of the phalanges. The dorsal, lateral, medial and ventral surfaces are proximodistally concave and proximodistally striated, containing a few small foramina. The ventral surface is gradually less extensive, both mediolaterally and dorsomedially, from phalange IV2 to IV4. Phalanges IV2 to IV4 differ mainly in their relative size, proximodistal thickness, and distal and proximal outline. The overall size and dorsoventral height decrease from phalange IV2 to phalange IV4. Phalange IV2 is the dorsoventrally highest and the proximodistally thickest of all three phalanges. It has the proximal outline of a dorsally truncated triangle. The dorsal and ventral sides of the proximal surface are horizontal, while the medial and lateral sides slope medially and laterally. The medial slope is steeper. The dorsal rim of the distal surface is also horizontal, in contrast to phalanges IV3 and IV4. Phalange IV3 has more crescentic distal surface, with a rounded dorsal border and a concave ventral edge. The lateroventral corner of the distal side is dorsoventrally more expanded than in phalange IV2. In proximal view, the dorsal edge is also rounded, slightly pointed dorsomedially. The ventral edge of the proximal side is less concave than the one of the distal surface, but more than the one of the proximal side of phalange IV2. Phalange IV4 is most similar to phalange IV3, but is smaller, dorsoventrally thinner and more oval in distal and proximal outline. The dorsal border of

the proximal surface is relatively more rounded. The ventral border is concave, but the lateroventral corner is less salient than in the other phalanges.

Pedal Unguals

The pedal unguals are arrow or spade-shaped bones as seen in dorsal and plantar views. The distal border show a series of indentations proximodistally arranged, connecting with elongated grooves. Two deep trenches or grooves run parallel at some distance from the craniolateral distal edges of the unguals. The bone thins distally producing a wedge-shaped lateral profile. All pedal unguals show a median longitudinal plantar keel, a condition shared with *Maiasaura peeblesorum* (Weishampel and Horner, 1990). A set of plantar foramina is relatively randomly scattered around and over that keel. The distal portion of the “arrow” describes a wide arch that stretches lateromedially beyond the mediolateral width of the proximal half.



Figure 84. Pedal unguals in dorsal view.

This contrasts with the mediolaterally narrower unguals of *Prosaurolophus blackfeetensis* (for example, MOR 454 7-27-6-6). The proximal, concave articular face of unguals III show a dorsoventrally compressed hexagonal contour, with the upper and lower sides of the hexagon doubling the length of the rest of lateral sides. This condition differs from unguals II and IV. In ungual II the proximal surface is mediolaterally more compressed in respect to the other two unguals, more oval and showing a wider dorsal edge. In ungual II the maximum mediolateral width of the proximal surface is nearly equal to its dorsoventral height. In ungual IV the proximal surface is not hexagonal, like in ungual II, but in the former this side is mediolaterally wider, especially the dorsal border in respect to the shorter and ventrally pointed ventral edge. Another difference concerns to the orientation of the ventral border of the proximal surface. In ungual II and III it is rather centered, but in ungual IV it is laterally displaced. Ungual III is both mediolaterally more expanded and broad in overall proportions than unguals II and IV. In contrast to ungual III, unguals II and IV are asymmetrical as seen dorsally, with one side more expanded than the other (the lateral in ungual IV and the medial in ungual II). All unguals have a deep foramen located on the medial and lateral side of the central portion, near the proximal, straight border of the lateral expansions of the unguals. This foramen is ventrally directed and positioned. The proximal region of the unguals is only slightly expanded, but much less than the distal, arrow-like half of the bone. The dorsal and ventral borders of the proximal surface describe a gentle semicircular contour.



Figure 85. Pedal ungual III showing a plantar keel (MOR 1071-7-31-99-273). Anterior view.

CHAPTER 4

VARIATION

Individual Variation

Individual variation is concerned with the morphological changes observed between elements of the same size, which are considered specimens corresponding to individuals of the same stage of ontogenetic development. Those features are separated from the autapomorphies of the taxon in that they only occur in one or a few specimens of the same element, but not in all the available specimens.

Skull

Predentary. Only one predentary, the adult specimen MOR 1071-7-28-98-299, is available for comparison with the articulated MOR 794. No subadults were found. Little variation was observed between the two specimens. The distribution and shape of the anteroventral foramina changes, so that in MOR 1071-7-28-98-299 these foramina are mediolaterally elongated, while being circular in MOR 794. The lateral processes are proportionally longer in MOR 794, but the mediolateral compression suffered by this specimen during taphonomy probably affected this observation.

Dentary. The sample of dentaries is relatively large, and besides MOR 794, it includes two left and two right adult specimens, and four left plus one right subadult specimens. The number of tooth positions is rather constant, being 33 in most specimens,

subadults and adults. A remarkable exception is the subadult MOR 1071-8-1-99-313, which has 26 tooth positions. The mediolateral width of the Meckelian fossa (or the caudal exit of the Meckelian canal) is proportionately wider in the subadult MOR 1071-7-10-98-179 in respect to the rest of dentaries, both subadults and adults.

But perhaps the most remarkable difference exists between the MOR 1071 specimens from the bonebed, and MOR 794 and PB 862. Both the left and right dentaries of PB 862 correspond to material collected in 1922 by Elmer S. Riggs from the Belly River (Two Medicine) Formation of Alberta (Canada), in the Red Deer River area. MOR 794 and PB 862 have more robust dentaries. In these specimens the dorsoventral dimension of the dentary from the alveolar edge to the ventral border, as well as that of the diastema, is about 20-25 % deeper than in the bonebed specimens (including subadults). Otherwise, the overall size, such as their anteroposterior length, is equal in all the adult specimens.

The dentaries of PB 862 have anterior ends that are relatively more downturned than the MOR 1071 and MOR 794 specimens. The degree of anteroventral deflection of the diastema is rather variable. For example, between the bonebed adults, MOR 1071-7-13-99-93 is relatively less downturned than MOR 1071-8-15-98-574. And among the subadults, MOR 1071-7-15-98-226 is slightly more deflected than MOR 1071-8-1-99-313.

Surangular. The medial ridge of the surangular is much thinner in the subadult MOR 1071-7-24-99-192-A, and thicker in the other subadult and the adults. MOR 1071-

7-27-99-230 has a mediolaterally thinner anterodorsal process than PR 862. The subadult MOR 1071-8-8-99-484-B has a strongly marked lateral border of the ascending anterolateral process of the surangular, in contrast to all the other specimens, both adults and subadult.

Splenial. Two adult specimens from the bonebed, MOR 1071-7-31-99-281-R and MOR 1071-8-6-98-483, are equal in size and proportions. However, MOR 1071-8-6-98-483 has a wider medioventral articulation facet for the angular. On the lateral side of the splenial, MOR 1071-8-6-98-483 shows a thicker ridge than MOR 1071-7-31-99-281-R within the triangular groove. Dorsal to that ridge and close to the short anterodorsal process of the element, MOR 1071-8-6-98-483 exhibits another well-developed, longitudinally short ridge, which is nearly absent in MOR 1071-7-31-99-281-R. The splenials of MOR 794 are concealed by articulation.

Premaxilla. The three subadults are too damaged for comparison and taphonomically modified in different ways. MOR 1071-7-7-98-84 has been compressed dorsoventrally, so that its narial cavity is narrower than was in life. MOR 1071-7-5-98-66 has been compacted and crashed mediolaterally. MOR 1071-7-23-99-179 is anteriorly broken, exposing a concave, excavated anterior rim; this specimen lacks most of its posterior region and processes.

Maxilla. Among the three adult disarticulated maxillae, MOR 1071-7-6-98-79 is relatively shallower dorsoventrally than the other two maxillae, especially MOR 1071-8-

13-98-559. MOR 1071-8-13-98-559 shows a relatively more developed (i.e. mediolaterally wider) medial ridge on the anterodorsal process than the other two specimens. Besides the position of the anterolateral, major foramen, the other lateral foramina are irregularly arranged among the maxillae, both in number and distribution

Jugal. All the available jugals are here attributed to adult specimens. Two jugals, a left and right one, possibly from the same individual, come from the PB 862 specimen. MOR 794 and four specimens from the bone bed complete the sample. MOR 794, MOR 1071-7-16-98-248-Q and PB 862 have distinctive deeper anterior processes, wider bosses and deeper segments between the anterior, postorbital and quadratojugal processes. Those jugals are also relatively more robust than the other specimens, MOR 1071-7-27-98-453, MOR 1071-7-31-99-281 and MOR 1071-6-30-98-3. In MOR 1071-7-16-98-248-Q the ventral border of the quadratojugal process is curved inwards, not straight, like the other jugals, and is more expanded dorsoventrally. The quadratojugal processes are variable in width and morphology among the available jugals, ranging from relatively narrow and long (PR 862) to wide and flared (MOR 1071-7-16-98-248-Q).

Lacrima. Adult lacrimals are well represented by five articulated specimens (two in MOR 794, two in MOR 1071-7-16-98-248, and the other one in MOR 1071-7-7-98-86) plus a disarticulated specimen. Subadults comprise three specimens from the bonebed. In MOR 1071-7-10-98-171 the anterior end tapers being sharp and pointed, while in MOR 1071-7-16-98-248 that end is deeper and rounded, having parallel borders. The adult MOR 1071-7-10-98-171 and subadults MOR 1071-6-30-98-9 and MOR 1071-

8-5-99-447-G possess a less expanded lacrimal groove on the medial side. This groove is further expanded dorsoventrally in the subadult MOR 1071-8-3-99-378 and the adult MOR 1071-7-16-98-248. MOR 1071-8-5-99-447-G has a smaller secondary, dorsal excavation on the medial side of the lacrimal and, probably, also MOR 1071-8-3-99-378. In contrast, MOR 1071-7-10-98-171, MOR 1071-7-16-98-248, and MOR 1071-6-30-98-9 have a deeper excavation dorsal to the lacrimal groove. The dorsal edge of the lacrimal groove itself is sharper and more defined in MOR 1071-7-10-98-171 and MOR 1071-8-3-99-378, in contrast to MOR 1071-8-5-99-447-G and MOR 1071-6-30-98-9.

Nasal. Most of the available nasals are found articulated in MOR 794, PB 862, and the skull roofs MOR 1071-7-16-98-248 and MOR 1071-7-7-98-86. Two additional adult fragmentary nasals are MOR 1071-7-12-99-76 and UCB 130139 (which is part of the material on which *B. goodwini* was erected by Horner (1988)). No subadults are known.

Two morphs are distinguished based on the crest morphology. On one hand, MOR 794 and PB 862 are characterized by nasal crests that are further extended caudally and mediolaterally, reaching the posterior end of the squamosals, and concealing the supratemporal fenestra. On the other hand, MOR 1071-7-7-98-86 and MOR 1071-7-16-98-248 exhibit nasal crests that do not reach the posterior bar of the squamosal and are much narrower mediolaterally, covering just the medial half of each supratemporal fenestra. In MOR 1071-7-16-98-248 there is a thin, stick-like bone or piece of bone emerging from the olfactory canal, and incised right along the suture between both nasals

along the parasagittal plane as seen ventrally. This feature has not been observed in the other specimens.

Postorbital. Among the adults, the postorbital is more ornamented in MOR 794 and PB 862. In MOR 794 there is a ridge running dorsoventrally between the central body of the element and the posterior squamosal process. The dorsal surface of the central portion of the postorbital is depressed, as the lateral surface, and anteriorly followed by rugose dorsolateral area that connects with the orbital rim. In MOR 794 the infratemporal fenestra is relatively narrow dorsally, due to the straighter posterior border of the jugular process. In the MOR 1071 skull roofs the posterior border of the jugular process is more rounded and concave, producing a dorsally wider infratemporal fenestra. The MOR 1071 skulls have postorbitals with jugular process more anteriorly inclined than in MOR 794.

Prefrontal. In the adults PR 862, and probably also in MOR 794, the prefrontals, when being under the nasals supporting the crest, are posterolaterally more expanded than in the two roofs skulls (MOR 1071-7-7-16-98-248 and MOR 1071-7-7-98-86). Thus, in PR 862 that portion of the prefrontal contacts the parietal medially and overhangs its caudal region, being closely applied to the ventral surface of the crest. In contrast, in the roof skulls, that region of the prefrontals does not extend caudally beyond the level of the laterosphenoid-postorbital joint. In MOR 794 and MOR 1071-7-16-98-248 the lateral edge of the prefrontal extends further caudally over the orbit, ending posterior to its caudal border. That caudal extension of the prefrontal continues

contacting the lateral edge of the nasal and is partially overlapped by this last. This is not observed in the subadult disarticulated specimens or in the roof skull MOR 1071-7-7-98-86, where the posterior expansion of the prefrontal is found squeezed below the lateral border of nasal dorsal to the orbit.

In MOR 1071-7-16-98-248 there is a deep groove running parallel to the lateral border of the nasal, on the dorsal surface of the expanded posterior region of the prefrontal. This groove plunges anteriorly into a deep foramen. In MOR 794 the mediolateral compression of the specimen may have obscured that feature. The other roof skull, MOR 1071-7-7-98-86, exhibits a depression instead of a groove. However, all the specimens possess a foramen on the dorsal surface of the prefrontal, over the orbital rim. In the subadult MOR 1071-8-1-99-346 there are three foramina arranged in a triangular pattern over the dorsolateral surface of the bone, while in the other subadult MOR 1071-8-5-99-447-G there is only a foramen in that area as in the adults. In some specimens the foramen that lies on the ventral surface of the medial ridge does not penetrate dorsally that ridge (for example, the case of the subadult MOR 1071-7-10-98-171 and the adult MOR 1071-7-16-98-248), while in others it does (MOR 1071-7-7-98-86, right prefrontal).

Quadrates. The two nearly complete disarticulated adults, MOR 1071-8-13-98-559-D and PB 862 differ in that the former has a mediolaterally narrower dorsal head, while being equally wide anteroposteriorly. In MOR 1071-8-13-98-559-D the quadratojugal notch has a relatively wider surface on its ventral portion.

Quadratojugal. The adult MOR 1071-8-9-98-509 has a larger and deeper excavation, limited by sharp edges, on the medial quadrate articulation surface, along the posteroventral border. In MOR 1071-7-15-98-218-A and MOR 1071-8-3-99-366 (subadult) this depression is much narrower and shallower.

Squamosal. The observed individual differences are mainly associated to differences in size. Thus, the skull roof MOR 1071-7-16-98-248 is slightly larger than MOR 1071-7-7-98-86, and so, for example, the postorbital process of the squamosal of the former is mediolaterally wider.

Pterygoid. The size and shape of the ectopterygoid joint surface is variable among the specimens, either subadults or adults. In MOR 1071-8-14-99-A and MOR 1071-7-23-98-387 the ectopterygoid joint is semicircular in outline, being relatively wider. In contrast, the joint is relatively narrower in MOR 1071-8-1-99-315. The ectopterygoid process is anteroposteriorly thicker in PB 862 than in MOR 1071-7-23-98-387.

Palatine. Only adult specimens have been collected from this element. The only nearly complete palatine is MOR 1071-7-16-98-248-S. All other specimens are anterodorsal fragments with jugular process or portions of the ventral maxillary joint. The jugal articulation facet is dorsoventrally longer in MOR 1071-7-16-98-248-S and wider than in other specimens. The length of the jugular process is longer in those specimens with shorter and narrower jugal facets. The mediolateral width of the concave ventral maxillary joint is variable in all the specimens, being narrower in MOR 1071-7-16-98-248-S and wider in 1071-8-15-98-567.

Ectopterygoid. Only two disarticulated specimens are available for comparison, the nearly complete MOR 1071-8-15-98-559-E and a posterior fragment, MOR 1071-7-31-99-281-I. No adults were found. Given the incompleteness of the sample, only the posterior region of the element was compared. In MOR 1071-8-15-98-559-E the pterygoid articulation is wider and more equidimensional than in the other specimen, where the facet is more elongated and relatively narrower. On the laterodorsal surface, there is no trace in MOR 1071-7-31-99-281-I of the ridge present in MOR 1071-8-15-98-559-E.

Frontal. The frontals in MOR 794, PB 862, and the skull roofs MOR 1071 constitute the adult sample, all of which are articulated and therefore concealed by other cranial elements. In MOR 794 and PB 862, where the nasal crest is more expanded posteriorly and mediolaterally, the frontal appears to underlie completely the nasal. In the bonebed skull roofs the nasal seems to be posterodorsally elevated and leaving the dorsal surface of the frontal before reaching the parietal-frontal joint. Concerning the two disarticulated subadults, in MOR 1071-6-30-98-4 the posterior edge of the nasal contact is mediolaterally straight and curved at the corners. In MOR 1071-7-13-99-87-I the border defines a sinusoid, being anteriorly concave at the center and convex at the lateral extremes. In MOR 1071-7-13-99-87-I the region lateral and posterior to the nasal contact is strongly depressed, while in the other subadult it is shallower.

Braincase. Individual differences in braincase morphology were derived mostly from comparison of the adult articulated braincases MOR 1071-7-16-98-248 and MOR 1071-7-7-98-86. Most of the observed variation concerns to the number and arrangement of some foramina. Posteriorly, in MOR 1071-7-7-98-86 there are three foramina on the lateral surface of the opisthotic. A larger posterior-most foramen for the exit of part of the hypoglossal nerve (c.n. XII), and two smaller foramina anteriorly for cranial nerves IX to part of XII. In MOR 1071-7-16-98-248 only a large, elongate and anteriorly deepening foramen is exposed. The configuration of the foramina on this area of the braincase is also different in the subadult (see ontogenetic variation). In MOR 1071-7-7-98-86 the trigeminal foramen is relatively larger than in MOR 1071-7-16-98-248. In contrast, the facial nerve foramen is slightly larger in MOR 1071-7-16-98-248. However, even in a single individual, the size and outline of the foramina can be variable. Thus for example, in MOR 1071-7-16-98-248 the fenestra ovalis is relatively larger and rounded on its left side. The olfactory foramen is less dorsoventrally compressed in MOR 1071-7-16-98-248 and relatively larger.

The mediolateral width of the basioccipitals and the basal tubera is larger in MOR 1071-7-16-98-248 than in MOR 1071-7-7-98-86. In MOR 1071-7-16-98-248 the braincase is relatively more expanded mediolaterally at the level of the basal tubera. The ventral ridge on the laterosphenoid lateral process, which defines the posterior limit of the orbit, is smoother in MOR 1071-7-7-98-86. In MOR 1071-7-16-98-248 that ridge is sharper and continues further medially into the ventrolateral surface of the laterosphenoid. The cultriform process of the parasphenoid is longer in MOR 1071-7-7-

98-86 and straighter, more projected anterodorsally. In MOR 1071-7-16-98-248 the presphenoids are mediolaterally wider than in the other roof skull.

Axial Skeleton

Vertebrae. The atlas is only completely represented in MOR 794. In the bonebed, an isolated intercentrum (MOR 1071-6-24-99-18) and a recently prepared, crushed atlas are the only remain of this element besides a very fragmentary, possible neural arch. The incompleteness of the remains does not allow an observation of the variation. The rest of cervical, dorsal, sacral and caudal vertebrae, as well as their chevrons, most ribs and ossified tendons, comprise the articulated MOR 794 and isolated adult and subadult specimens from the bonebed. No morphological variation was observed between the specimens. Furthermore, it is difficult to know whether two vertebrae correspond to different individual animals (except for cervicals 12 and 13 and the very first dorsals, which are most distinctive along the series). Most probably, as deduced from comparisons between individual specimens of the same size and state of development, the axial skeleton of hadrosaurs is the less variable part of their anatomy.

Ribs. Some individuals have anterior cervical ribs with main ramus that nearly bifurcate caudally (for example, MOR 1071-7-16-98-248-H). Other specimens have main ramus with mediolaterally narrow caudal portions. More remarkable is the recovery from the bonebed of a certain number of cervical ribs that quite differ from the morphology described here for *B. canadensis*. Specimens such as MOR 1071-7-23-99-183 and MOR 1071-7-23-99-185 represent those ribs. They are characterized by a long

capitulum, a caudal end of the main ramus that caudally tapers into a sharp point, and a ventral curvature of the caudal end of the main ramus. The dorsal rib MOR 1071-7-16-98-248-T has a pathological craniocaudal thickening of the capitulum.

Appendicular Skeleton

Scapula. MOR 794 includes both articulated scapulae. MOR 1071-7-18-98-298 represents the right scapula of an adult. Both scapulae differ in the narrowness of their necks in relation to the dorsoventral expansion of the distal portion of the blade. In MOR 794 the scapular blade is not continuously and gradually expanded caudally, but it reaches a maximum dorsoventral width before its caudal end (concretely ventral to the gap between the 5th and 6th dorsal rib), to gradually decrease in depth near the caudal edge. This condition had been observed in the five available subadults, as described below. In contrast, in the adult MOR 1071-7-18-98-298 the scapular blade is progressively and gradually wider dorsoventrally to reach its maximum width in its caudal edge, although this specimen lacks some bits on the dorsal border and the caudal end.

Coracoid. Only one adult coracoid, MOR 1071-7-31-99-281-W, is available besides MOR 794. The specimen is too damaged proximally to assess what appears to be a mediolaterally narrower humeral facet than MOR 794. Both adults are about the same size, and no other differences are appreciated.

Sternals. Besides MOR 794, two more adult specimens were recovered from the bonebed: MOR 1071-7-12-99-71 and MOR 1071-25-98-406. MOR 794 shows a wider, much more robust handle and anterolateral region than the other morphologically equivalent adult sternal from the bonebed, MOR 1071-7-12-99-71. MOR 1071-25-98-406 is so distinct morphologically from all the other sternals that it might actually belong to another taxon. MOR 1071-25-98-406 shows the following distinct features in respect to the other sternals from *Brachylophosaurus*: 1) the extreme of the handle is much more circular, not flat and compressed as in the other specimens; 2) the specimen is much more arched, longitudinally; 3) the proximal, "paddle-like" portion is much shorter and squared than in the rest of specimens; 4) the anterodorsal, shorter border of the paddle, is relatively longest and the anteroventral border is relatively shorter; 5) the anterodorsal border is relatively much thicker; 6) the curvature of the ventral anterior end of the handle, towards its ventral origin from the anteroventral border of the sternal, is relatively more open and gentle in curvature; 7) the distal border of the handle is relatively less expanded (hence, being thicker mediolaterally); and 8) the handle is mediolaterally thicker.

Ilium. MOR 794 and MOR 1071-8-2-98-469 are practically identical, except for the dorsoventral thickness of the preacetabular process. Both ilia of the articulated MOR 794 possess a wider and more robust preacetabular process than the specimen from the bonebed. The subadult MOR 1071-7-10-99-50 shows the following differences in respect to MOR 794, MOR 1071-7-15-98-215 and MOR 1071-8-2-98-469: 1) much shallower dorsoventral depth of the central body; even though bits of the ventral region of the

central body are missing due to breakage and abrasion, the acetabular ventral surface is not missing and is taken as reference to compare the dorsoventral depth of the ilium; 2) relatively greater development of the antitrochanter, both in its antero-caudal extension and lateroventral projection; 3) ventrally projected, U-shaped process caudal to the medial ridge (where in the rest of specimens the ridge ends in a slight concavity) and immediately cranial to the dorsal border of the beginning of the postacetabular process; 4) dorsoventrally shallower and less ventrally projected peduncles (might be caused by preservation); 5) dorsoventrally shallower and longer postacetabular process; and 6) the dorsal and ventral borders of the postacetabular process are parallel, while in the other available specimens both borders tend to converge towards the caudal edge of the ilium.

Among the subadults, it is remarkable the dorsoventrally thinner preacetabular process of MOR 1071-7-31-99-285, although this specimen is about the same size as the other specimens. In MOR 1071-7-31-99-285 the antitrochanter is relatively reduced, both mediolaterally, antero-caudally and dorsoventrally. Although this process is broken and damaged, it is clear that it is less developed because the lateral surface of the central body of the ilium is already much less projected laterally at that level. The acetabular region is mediolaterally much thinner than in the other specimens, but mediolateral compression of the specimen may have affected this observation.

Pubis. The adult pubes of MOR 794 were compared to two adult pubes from the bonebed, the left MOR 1071-7-16-98-243, and the right MOR 1071-8-20-98-597. MOR 794 possesses much more robust pubes than the MOR 1071 specimens. While the postpubic process shows the same length in all three specimens, the prepubic blade of

MOR 794 and the subadult MOR 1071-13-99-86 is much deeper dorsoventrally and longer antero-caudally. In particular, the blade is MOR 794 and MOR 1071-13-99-86 is much more flared, especially along the dorsal edge. While the other (both adult and subadult) pubes possess a dorsal edge with a profile that curves downward, in MOR 794 and MOR 1071-13-99-86 the lateral profile of the dorsal edge continues ascending anterodorsally more cranially, to curve ventrally nearer the cranial border of the blade than in the bonebed specimens. The neck of the pubes, the transition between the blade and the acetabular region, is dorsoventrally deeper in MOR 794. Among subadults, MOR 1071-7-20-98-300 shows a narrower neck than the other subadults, MOR 1071-8-17-98-586 and MOR 1071-13-99-86. The postpubes are very similar, except for their thickness, which again is greater in MOR 794. The ischial peduncle in MOR 794 is strongly compressed mediolaterally, while being thicker, subcylindrical in cross-section in the MOR 1071 specimens. Mediolateral compression of MOR 794 might account for this difference. In MOR 794 the ventral border more opened, so that the ventral edge of the prepubic blade forms a wider angle with the ventral border of the postpubic process. In the MOR 1071 specimens, the anteroventral border of the postpubis is slightly more arched cranially. That difference has been also noted between the subadult MOR 1071-7-20-98-300, and both MOR 1071-8-17-98-586 and MOR 1071-13-99-86. In MOR 1071-7-20-98-300 the ventral border of the pubis forms a wider, more gentle profile than in MOR 1071-8-17-98-586. Thus, in this aspect, as well as concerning the depth of the pubic neck, MOR 1071-8-17-98-586 and MOR 1071-13-99-86 are closer to the adult specimens from the bone bed, while the other subadult, MOR 1071-7-20-98-300, is similar to MOR 794.

Ischium. Individual variation was assessed among the subadults, since only one adult ischium (MOR 794) has been recovered; all other five specimens are subadults from the bonebed (MOR 1071). The subadults exhibit little variation. Only the obturator foramen shows slightly different ellipsoidal contours, but the presence of taphonomic cracking and compression might account for or exaggerate this differences. The maximum width of the ischial shaft changes only slightly among those ischia.

Humerus. The humeri of MOR 794 and a right humerus, MOR 1071-7-20-89-325, represent the adult specimens. In MOR 1071-7-20-89-325 the ulnar condyle is larger in relation to the radial condyle than in MOR 794. In MOR 1071-7-20-89-325 the ulnar condyle is mediolaterally wider and more massive in overall construction. In MOR 1071-7-20-89-325 the distal shaft is slightly thicker than in MOR 794. In MOR 1071-7-20-89-325 the deltopectoral crest is thicker and its thickness changes more gradually proximally than in MOR 794. The muscle scar on the anteromedial border of the deltopectoral crest is rather continuous in both humeri of MOR 794, while in MOR 1071-7-20-89-325 the scar is well developed proximally and distally along the border, leaving a central smooth area.

Radius. Three subadult radii and an adult radius from the bonebed, plus the articulated radii of MOR 794 constitute the available sample for this element. As in the case of the ulna, the MOR 794 radii are about 20% longer proximodistally than the adult radius from the bonebed, MOR 1071-7-15-98-257. Both adults show the same mediolateral and dorsoventral thickness, as in the case of the ulnae. Individual subadult

radii change in the relative proximodistal length and the size of the proximal and distal length. Slightly longer radii, like MOR 1071-7-8-98-126, have mediolaterally and dorsoventrally thicker proximal and distal ends.

In proximal view two of the subadults and the MOR 1071 radii are more dorsoventrally compressed in relation to the adult MOR 794. The third subadult, MOR 1071-7-14-98-204, shows a more squared proximal outline, closer to MOR 794. However, MOR 1071-7-14-98-204 is considerably abraded proximally, so this feature should be taken with caution. The slightly longer subadult MOR 1071-7-8-98-126 possesses a rather circular distal outline, in contrast to the rest of adult and subadult specimens.

Ulna. The ulna is among the most abundant elements collected. Besides the articulated ulnae of the complete skeleton MOR 794, there are two adult specimens and at least six subadults, with a possible seventh one (MOR 1071-7-12-99-77). It is remarkable the difference in length between the adults MOR 794 and MOR 1071-8-1-99-359-J, where the former is about 20 % longer proximodistally than the specimen from the bonebed, even though both ulnae exhibit the same mediolateral and dorsoventral thickness. The other adult, MOR 1071-7-2-99-36, is not complete distally. Among the subadults, some specimens are proximodistally longer than others, whereas all the specimens show the same mediolateral and dorsoventral width and size. Among the five complete subadults, one of them, MOR 1071-8-13-99-557 is relatively long, while the other four are shorter and similar in length.

Metacarpal II. Apart from the articulated adult MOR 794, one more adult metacarpal II has been recovered from the bonebed, MOR 1071-8-16-98-578. Both specimens show the same robustness, mediolateral and dorsoventral thickness, but as in the case of the ulna and the radius, the bonebed adult is about 15 % shorter proximodistally. Four subadult metacarpals II are available for comparison. Three of these specimens are mostly equal in length, while a fourth one is a bit shorter and more slender. MOR 1071-7-20-98-317 is a pathological metacarpal II. This specimen shows a massive bone thickening of the proximal area. The bone is overgrown mediolaterally and especially dorsoventrally.

Metacarpal III. MOR 794 and MOR 1071-8-1-98-359-A are the two adults available. Again, MOR 794 is about 1/6 proximodistally longer than the MOR 1071 specimens, even though both specimens are equally thick mediolaterally and dorsoventrally. From the five collected subadult metacarpals III, three are complete and differ in their relative proximodistal length. Subadult metacarpals III also differ in their relative mediolateral width and dorsoventral height of their proximal and distal surfaces.

Metacarpal IV. Adult metacarpals IV are represented by MOR 794 and two specimens from the bonebed. The MOR 1071 specimens are about 1/8 shorter proximodistally than MOR 794, while having the same degree of robustness, mediolateral and dorsoventral thickness.

Metacarpal V. MOR 794, and one adult and three subadults from the bonebed compose the sample. There is a high degree of variation among these specimens, especially among the subadults. MOR 794 is 1/8 longer than the adult MOR 1071-7-21-98-340. In MOR 794 the proximal surface is more oval in outline. The medial and lateral ridges are sharper and more developed in MOR 794. The subadult MOR 1071-7-7-98-87 is relative thin and slender mediolaterally in respect to all other adult and subadult specimens. The distal and proximal surfaces of MOR 1071-7-21-98-340 are relatively reduced. The other two subadults, MOR 1071-8-2-98-464 and MOR 1071-8-5-98-481, are relatively more compressed dorsoventrally. MOR 1071-8-2-98-464 differs in number of features from the other metacarpals. It is proportionally wider mediolaterally, the small surface of the proximal face is more acute and narrower, the proximal surface is more subrectangular, not oval like in the other specimens, and the distal surface is lateroventrally deflected and asymmetrical as a result in respect to the more equidimensional distal face of the other metacarpals.

Manual Digit II. Only one disarticulated adult phalange II1 (MOR 1071-7-27-99-223) is available for comparison against MOR 794; both specimens are practically identical. The only adult specimens of phalange II2 are those of MOR 794. The bonebed produced three subadults. The phalanges differ mainly in the outline of the recessed middle area and in the distribution and size of its foramina. Ungual II is represented by three adult and two subadult specimens from the bonebed, and MOR 794. Two of the bonebed adult unguals (the right MOR1071-8-12-98-533 and the left MOR 1071-7-27-99-225) are basically identical in morphology and differ from the third specimen in the

non-horizontal position of the caudal border of the medial expansion. This border is roughly horizontal in MOR 1071-8-3-99-374 and caudally pointed and more extensive proximodistally in MOR 794. MOR1071-8-12-98-533 and MOR 1071-7-27-99-225 are proximodistally longer and proportionately thinner mediolaterally than MOR 1071-8-3-99-374. MOR1071-8-12-98-533 and MOR 1071-7-27-99-225 are dorsoventrally thicker than MOR 1071-8-3-99-374.

Manual Digit III. Three subadult phalanges III1 are the only remains of this element from the bonebed. MOR 1071-7-30-99-256 is mediolaterally and dorsoventrally thinner and more slender than the other subadults. Phalanges III2 differ in that some of them are dorsoventrally wider, possessing more oval proximal surfaces. Thus, for example two adult specimens from the bonebed, MOR 1071-8-16-98-579 and MOR 1071-7-27-98-427 have oval proximal surfaces, while the other specimens (adults and subadults) exhibit more ellipsoidal proximal faces. Part of the morphology of MOR 794 is concealed by its articulated state. MOR 1071-8-13-98-554-B is the only adult manual ungual III recovered besides MOR 794 at the time of writing this paper. The former may be slightly shorter proximodistally than MOR 794, although this might be influenced by the abraded and partial state of the former.

Manual Digit IV. Phalange IV1 is represented by the adult MOR 794 and two adult specimens from the bonebed, plus two subadults. One the adults, MOR 1071-8-12-98-534, is more robust, has relatively more expanded proximal and distal faces, and is proximodistally longer than the other adult from the bonebed, MOR 1071-8-1-99-321.

The same occurs between the two subadults, where MOR 1071-8-9-99-523-D is longer and shows more expanded distal and proximal ends. The shorter specimens are relatively thicker mediolaterally along their middle portions. There is a notable difference between the adult phalanges IV2 of MOR 794 and MOR 1071-8-13-98-559 in respect to MOR 1071-8-11-525. This last specimen is proximodistally shorter, so that its mediolateral dimension is wider than in proximodistal length, while the other specimens are roughly squared as seen dorsally. Likewise, MOR 1071-8-11-525 is much thicker dorsoventrally. Given these differences, is not clear if MOR 1071-8-11-525 should be assigned to the same taxon.

Manual digit V. The only adult phalange V1 besides MOR 794, MOR 1071-7-27-99-227, is relatively shorter proximodistally and less expanded mediolaterally along its distal region. The four-sized adult specimens (including MOR 794) of phalange IV2 show a high degree of variation among themselves. This concerns the dorsoventral and mediolateral thickness of the bones, as well as their relative proximodistal length. MOR 794 is slightly longest proximodistally, while MOR 1071-7-21-98-341 is thinner distally being the narrowest both dorsoventrally and mediolaterally. The same occurs between the two subadults, where one of them is mediolaterally wider and proximodistally longer. The specimens of Phalanges V3 are rather variable from each other. MOR 794, MOR 1071-7-27-98-452 and MOR 1071-162-A are the three available adults. They differ in the extension and outline of the dorsal and ventral recessed surfaces. In MOR 794 and MOR 1071-162-A the recessed faces are ellipsoidal in outline and the whole phalange is oval in dorsal and ventral views. In contrast, MOR 1071-7-27-98-452 is more subtriangular in

outline and the recessed area wraps the bone having more parallel proximal and distal boundaries.

Femur. Two adults, including MOR 794, and four subadults are available for comparison. The main differences concern the size of the lesser trochanter, the proximodistal length and mediolateral thickness of the femur, the mediolateral thickness of the greater trochanter, the antero-caudal width of the distal condyles, and the prominence and length of the fourth trochanter. MOR 794 shows the larger femur within the adult sample, in contrast to MOR 1071-7-21-98-331. Among the four subadults, two of them are complete, MOR 1071-7-31-99-282 and MOR 1071-8-1-99-327. MOR 1071-7-31-99-282 is about 10% shorter than MOR 1071-7-31-99-282. Both specimens have shafts of equal mediolateral thickness. However, the shorter femur shows also antero-caudally thinner distal condyles and shaft. Probably related to these differences, MOR 1071-7-31-99-282 has a proximodistally shortest and less prominent fourth trochanter, while MOR 1071-8-1-99-327 exhibits a longest and more acute trochanter. The lesser trochanter of MOR 1071-7-31-99-282 is antero-caudally thinner than in MOR 1071-8-1-99-327.

Tibia. Individual differences in the available tibiae are mainly size-related, as in the case of the femur. MOR 794 is the only adult collected. Five subadult specimens are known from the bonebed. Two of the subadults, left and right specimens, are relatively shorter proximally (about a 15 %) and are slightly more slender than another pair of subadults, also a right and left tibiae. The cnemial crest of the larger pair of tibiae is more

developed and the proximal and distal ends are more expanded. However, the thickness and stoutness of the shaft is rather equal in these four specimens.

Fibula. The adult MOR 794 is about 10 % longer proximodistally than the other adult from the bonebed, MOR 1071-7-7-98-88, although both specimens are equally thick antero-caudally and mediolaterally. Both specimens are equally expanded proximally and distally. Something similar occurs between the subadults MOR 1071-8-1-99-329 and MOR 1071-8-5-99-430, where the former is a bit shorter, but otherwise equally robust.

Astragalus. MOR 794 and MOR 1071-7-3-99-270 are two available adults. MOR 794 is mediolaterally shorter, but proximodistally higher than the specimen from the bonebed. Although MOR 1071-7-3-99-270 lacks its caudal portion, it is clear that MOR 794 has a more antero-caudally compressed middle region and a more antero-caudally expanded medial side.

Calcaneum. There are six calcanei collected from the bonebed (two adults and four subadults), plus the articulated elements of MOR 794. The adult MOR 1071-7-16-98-261 is narrow mediolaterally in respect to the wider adult MOR 1071-7-30-99-257, which, at the same time, is antero-caudally longer. These differences are also present among the four available subadults, where, for example, MOR 1071-8-5-99-447-E is mediolaterally narrower than the other specimens. Proximodistally, some calcanei are slightly deeper than others. Only one calcaneum, MOR 1071-7-15-98-215-A lacks the large and deep foramen on the caudal face, present on all other specimens of both adults

and subadults. The number and distribution of foramina on the lateral surface of the calcaneum is also variable. The diagonal sharp edge that separates the articular fibular concave surface from the tibial face reaches more anterolaterally in the adult MOR 1071-7-16-98-261 than in the adult MOR 1071-7-30-99-257. Thus, in lateral view the anterolateral corner of MOR 1071-7-16-98-261 is anteriorly salient.

Distal Tarsal. The two available adults, MOR 794 and MOR 1071-7-20-99-158 differ in outline. The right distal tarsal of MOR 794 shows a more circular shape, while the bonebed specimen is ellipsoidal. Among the three subadults, there are differences in proximodistal thickness and also in outline. Thus, the subadults MOR 1071-8-1-98-359-B and MOR 1071-8-1-99-328-D are circular and relatively thin proximodistally, while MOR 1071-8-5-99-447-A is laterally thick proximodistally as is usual in adults.

Metatarsal II. The only adult recovered from the bonebed appears to be dorsoventrally thinner at the middle, although breakage of the specimen may account for this difference. The mediodorsal flange is less developed in some specimens (for example, the subadult MOR 1071-8-1-99-330), where it forms a gentle elevation in contrast to the higher arched ridge found in adults and in the subadult MOR 1071-8-7-99-470.

Metatarsal III. MOR 1071-7-8-98-411, the only adult besides MOR 794, differs from this last in a number of features. MOR 1071-7-8-98-411 has a mediolaterally much broader and much less dorsoventrally expanded proximal end. Remarkably, the dorsomedial corner of the proximal end of MOR 1071-7-8-98-411 is not dorsally pointed

as in MOR 794 and the two subadults, but instead it is medially directed. Thus, in proximal view MOR 1071-7-8-98-411 is subsquared rather than crescentic. MOR 1071-7-8-98-411 is also slightly shorter proximodistally than MOR 794. Dorsally both specimens are equally wide mediolaterally, but ventrally MOR 1071-7-8-98-411 is much narrower. The proximal portion of the ventral side of MOR 1071-7-8-98-411 contains a large elongated concavity lateral to the ventromedial flange of the metatarsal. Some of these changes are also found between the two subadults. MOR 1071-8-1-99-332 is mediolaterally narrower across the ventral side and its proximal end is relatively more expanded dorsoventrally than in the other subadult, MOR 1071-7-26-98-425. The ventromedial flange of metatarsal III is further developed in the specimens with dorsoventrally expanded and mediolaterally narrower proximal ends.

Metatarsal IV. MOR 1071-7-22-98-173, an adult specimen from the bonebed, has a proximal end that is dorsoventrally compressed and mediolaterally wider than in MOR 794. However, in some cases, like in the subadult MOR 1071-7-7-89-98, dorsoventral compression due to preservation may have altered the original shape of the specimen. No such deformation is observed in the adult specimen from the bonebed.

Pedal Digit II. Individual differences in pedal phalange II1 concern to the mediolateral and dorsoventral width of the proximal and distal ends. For example, the right phalange II1 of MOR 794 has a distal surface that is mediolaterally wider but dorsoventrally shallower than in the other only available adult, MOR 1071-8-5-99-421. The same is observed between the proximal faces of both specimens. In phalange II2

specimens of approximately the same size vary in their relative proximodistal length in relation to its mediolateral and dorsoventral thickness.

Pedal Digit III. No adults of phalange III1 are available for comparison with MOR 794. Among the subadults, two of them, MOR 1071-7-98-216 and MOR 1071-8-1-99-333, are similar in size. MOR 1071-8-1-99-333 is relatively longer proximodistally, but mediolaterally narrower than MOR 1071-7-98-216. Individual changes on phalanges III2 and III3 concern slight variations in the proximodistal and dorsoventral thickness that, when observed in specimens of different sizes, are here related to ontogeny.

Pedal Digit IV. The phalange IV1 of MOR 794 is a proximodistally longer adult specimen than MOR 1071-7-8-98-124. The proximal, medial border of MOR 794 is dorsoventrally deeper than in the bonebed specimen. However, MOR 1071-7-8-98-124 has a dorsoventrally deeper distal, medial border than MOR 794. The three subadults are similar in size. MOR 1071-7-25-98-419 is mediolaterally narrower than the other two and its laterodistal border is slightly shallower. MOR 1071-8-1-99-328-C is the mediolaterally widest of the three subadults, although is as long proximodistally as the other two.

Pedal Unguals. Individual changes in the unguals involve the more or less accentuated caudal projection of the corners of the arrow-shaped distal ends. For example, in MOR 794 those corners are relatively more caudally directed than in MOR 1071-8-10-98-515, a pedal ungual III. The distribution of the numerous foramina on these elements is rather variable and does not follow a regular pattern.

Ontogenetic Variation

This kind of morphological variation concerns to that existing among elements between the two age classes available. "Subadult" here is used to refer to individuals that did not reach the adult stage at the moment of death, as represented in the Malta bonebed. At least four subadult individuals are present, and all of them have roughly the same size and proportions, about 50 to 60 % de size of the adults. At least two adults are present in the same bonebed, and the articulated skeleton MOR 794 plus the other non-MOR specimens are the other available adult specimens.

Skull

Dentary. The enameled surfaces of the dentary teeth are similar in length and width in both the subadults and the adults. However, in the adults the anteroposterior and mediolateral width of the occlusal surface occupied by each tooth is larger, as well as the anteroposterior width of the roots as seen laterally coming out of the alveoli. The edentulous diastema is proportionally longer in the adults. The oblique striations located on the medial side of the caudal border of the coronoid process become coarser in the adults.

Surangular. In subadults the caudal end of the surangular is thinner in respect to the adults, and the ventral surface is less concave and shows finer striations. The medial ridge separating the dorsal groove for the splenial from the ventral one for the angular is

slightly less continuous in the subadults. The articular surface for the angular tapers anteriorly in the subadults and is dorsoventrally deeper in adults. The facet for the quadrate contains relatively coarser and more developed striations and rugosities on the adults.

Splénial. A single subadult splénial is available, MOR 1071-8-8-99-484-A. This specimen is dorsoventrally more compressed at its mid anteroposterior length than the adults. The subadult lacks a median ridge along the anterior, lateral surface of the triangular groove. This lateral groove is deeper and not so long as in adults, and its apex is bilobated. In the two disarticulated adult specimens, the apex of the groove is not bilobated, but tapers in a pointed end. Another remarkable difference is that the angular articular facet in the subadult is grooved longitudinally.

Angular. In the subadults the angular is mediolaterally thinner and more slender than in adults, as shown for example in PB 862 and MOR 1071-7-31-99-276. The groove on the lateral surface of the element, between the two ridges, is deeply carved in the adult. The ridges have sharper edges, especially the ventral one. Oblique striations are found in the adults anterior to the point where the lateral ridges converge; those striations are much finer in the subadults.

Articular. The subadult articular is much more compressed mediolaterally, as shown in MOR 1071-7-18-98-282-B, the only available subadult. In the subadult, the majority of the body of the articular is a thin blade of bone, which becomes at least three

times thicker in the adult. The quadrate facet, while relatively narrow in the adults, is further reduced in the subadult due to the mediolateral compression of the element. The posterodorsal region points more dorsally in the subadult than dorsolaterally as in the adult.

Hyoids. The adult hyoids of MOR 794 are dorsoventrally more expanded along their posterior halves than the subadults MOR 1071-7-15-98-209 and MOR 1071-8-20-98-597-B. Subadult hyoids are more rod-like and relatively slender.

Premaxilla. MOR 794 shows the only adult premaxilla, while the other three specimens from the bonebed are subadults. In the adult, the posteroventral process is mediolaterally wider than in the subadult MOR 1071-7-7-98-84, where process is less crashed. In MOR 794 the anterior region is wider than in the subadults. As deduced from comparing the subadult MOR 1071-7-5-98-66 with MOR 794, the space for the external naris provided by the posterodorsal process of the premaxilla is larger and deeper in the adult. Although concealed by the anterodorsal process of the nasal, probably the posterodorsal process is dorsoventrally thicker in MOR 794 than in the subadults.

Maxilla. Three adult and two subadult maxillae from the bonebed, plus MOR 794, constitute the sample for the maxilla. Subadult maxillae are characterized by being mediolaterally wider and dorsoventrally shallower than the adults. In particular, the dorsoventral depth of the subadults (disregarding the dorsal apex for the jugal) is practically equal to the mediolateral width. In contrast, in adults the element is twice as deep as thick mediolaterally. The region posterior to the jugal articulation, which contains

the palatine joint, is relatively thicker mediolaterally in subadults. Proportionally, the dorsoventral distance between the lateral border of the ectopterygoid shelf and the dental alveoli is shallower in the subadults. The anterior region of the maxilla is also dorsoventrally shallower in the subadults and concave in lateral profile, while in the adults the profile is convex. The number of tooth positions in subadults is 35, in contrast to the 41-43 count in the adults. Maxillary teeth are similar in size in both adults and subadults when concerning to the enameled surface. However, as in the case of the dentary teeth, the occlusal section is smaller in each individual subadult tooth. In subadults, the longitudinal ridge on the medial face of the anterodorsal process is much less developed and medially expanded than in the adults. The proximal area of the anterodorsal process is shallower in subadults. The articulation for the jugal is larger in the subadults in relation to the proportions and size of the maxilla, although it is taller on adults. The rugosities and striations on the jugal, palatine and premaxilla articulations are further developed and coarser in adults.

Lacrima. Subadult lacrimals are proportionately less elongated anteroposteriorly than adults. In adults, the long anterior segment is longer than the dorsoventrally deeper posterior region, while in subadults both areas of the bone are mostly equal in length. In subadults the anterior elongated segment tapers gradually, its dorsal edge sloping anteroventrally, while in adults the dorsal edge becomes more irregular and high in profile. In adults the medial excavation dorsal to the lacrimal groove is more developed in size and depth.

Postorbital. All the adult postorbitals are articulated in their respective skulls, MOR 794, PR 862, MOR 1071-7-16-98-248 and MOR 1071-7-7-98-86. The four available paired subadult postorbitals, probably belonging to two individuals, are disarticulated. Adult postorbitals are much more ornamented on their lateral and laterodorsal surfaces. The orbital rim contains deeper and thicker incisions in the adults, and the central body of the postorbital is more concave on the lateral side. The frontal joint surface is proportionately larger in the subadults, especially concerning the anteroposterior length of the suture. Among the subadults, the thickness of the frontal suture is wider in MOR 1071-6-30-98-4 than in MOR 1071-7-13-99-87-G. The mediolateral width of the jugular process is also wider in MOR 1071-6-30-98-4.\

In subadults the orbit is huge, as exemplified by MOR 1071-7-13-99-87 in contrast to the adult skulls.

Prefrontal. The main difference between the adult and subadult prefrontal is that in the former, in relation to the further development of the nasal crest, the element is posteromedially expanded in order to underlie the nasal and overlie the orbital rim of the postorbital. In the subadult, the prefrontal terminates posteriorly in a sharp projection for joining the frontal. The relative size of the subadult prefrontal is close to the size in the adult, contributing to form a relatively larger orbit in the subadult.

Quadrate. In subadults the dorsal head of the quadrate is relatively narrower mediolaterally, so that the dorsal end is at least four times anteroposteriorly long as mediolaterally thick. In the adults, the narrowest observed head is about three times wider

anteroposteriorly than thick mediolaterally. The quadratojugal notch in the subadults has a relatively narrower area for the quadratojugal, especially dorsally. The striations and rugosities of the different areas on the quadrate surface are less developed and finer in the subadults. The pterygoid flange is proportionately thinner and more sheet-like in the subadults. In subadults, the pterygoid flange and the lateral wall that supports the quadratojugal notch are less divergent than in the adults.

Quadratojugal. The subadult MOR 1071-8-3-99-366, the only one recovered, is dorsoventrally less expanded than the adults. Whereas the adult quadratojugal is longer dorsoventrally than anteroposteriorly, the subadult is only slightly deeper than wider anteroposteriorly. The subadult is mediolaterally thinner and the rugosities found on the medial face are finer and less marked than in the adults.

Squamosal. As in the case of the postorbital, nasal and prefrontal, the adult squamosals are found in articulated skulls. Here the subadults form the disarticulated sample. The prequadratic process is more robust and longer in the adults. The postquadratic process is more robust in the adults, especially its caudolateral corner, which is antero-caudally thicker. The postorbital process is mediolaterally wider in the adults.

Pterygoid. Most differences are concentrated on the palatine ramus. In adults the palatine ramus is more vaulted than in the subadults, so that for example in the adult MOR 1071-7-23-98-387 the dorsal border of the ramus is further rolled ventrally than in the subadult MOR 1071-8-1-99-315. In fact, the whole palatine ramus is mediolaterally

and anteroposteriorly much wider than in the subadults. The ectopterygoid process is mediolaterally more expanded in adults. The rugosities on the lateral surface of the ectopterygoid joint are coarser and more developed in adults. In adults the lateral surface of the pterygoid is more rugose and contains oval, shallow pits not seen in the subadults.

Frontal and Nasal. Most of the variation of the frontal is probably related to the variation in development of the overlying nasal crest. The only adult specimens are articulated so that it is not possible to observe directly the morphology of the element. The nasal attaches to the dorsal surface of the frontal and this joint is observable in two subadult disarticulated specimens, MOR 1071-6-30-98-4 and MOR 1071-7-13-99-87-I. In the subadults, the nasal articulation surface extends anteroposteriorly covering two thirds of the frontal longitudinal length. It not known how developed was the nasal crest in subadults, but it seems reasonable to think that it was less developed than in adults. In PB 862 the nasal crest appears to rest on the frontal further posteriorly. In the MOR 1071 skull roofs some sediment is present in a narrow space located between the ventral surface of the nasal crest and the parietal-nasal joint, suggesting that in those specimens at least, the nasal might not cover the whole dorsal surface of the frontals. Adult disarticulated frontals are needed in order to clarify what differences exist between the nasal-frontal joint between subadults and adults.

Parietal. The only observed difference is the relative thickening of the walls of the bone and the dorsal ridge in the adults, but otherwise the adults are larger-scale versions

of the disarticulated subadults. Adult disarticulated specimens are needed to look for further differences in ontogeny.

Braincase. The adult braincase is observed in the articulated skull roofs MOR 1071-7-7-98-86 and MOR 1071-7-16-98-248, and in a fragmentary state in PB 862. MOR 1071-6-30-98-4 and MOR 1071-7-13-99-87-I represent subadult specimens. MOR 1071-7-13-99-87-I is a well-preserved and articulated, but lacks the ventral portion of the braincase, including the presphenoids, parasphenoid, basisphenoid, and basioccipitals. Most of the elements that form these adult braincases are fused. However, sutures can be seen between the orbitosphenoids and the frontals, and between these and the prefrontals and postorbitals. In subadults the prootic, supraoccipital, basioccipital, laterosphenoid, basisphenoid, presphenoid and orbitosphenoid are not fused each other. The parietals are already fused into a single element, as also happens with the opisthotic and exoccipital.

In adults, the laterodorsal process of the laterosphenoid is proportionately thicker at the joint with the postorbital. In adults the ridge from the basioccipital process to the paroccipital process on the exoccipitals, parallel to the crista prootica, is very well developed, but poorly marked in subadults. This is evident when comparing MOR 1071-7-13-99-87-K with MOR 1071-7-7-98-86. The paroccipital process is relatively small in subadults, where it tapers quickly before reaching the development seen in adults. In contrast, the foramina-bearing portion of the opisthotic is comparatively large in the subadult. In the adult braincases the pituitary fossa is enclosed by bone, while in MOR 1071-7-13-99-87-I the fossa is opened and separated by a strip of bone from the foramen for the optic nerves. The trigeminal foramen is proportionately larger in the subadult

MOR 1071-7-13-99-87-I than in the adults, where the foramen is only slightly bigger. The groove for the maxillary and ophthalmic divisions of the trigeminal foramen is much deeper and irregularly excavated in adults. In subadults this is just a groove with a smooth surface. The foramen for the facial nerve (c.n. VII) is similar in absolute size in both adults and subadults. The olfactory foramen is relatively larger in subadults in relation to the mediolateral width of both frontals. In adults, the frontals are more expanded mediolaterally, but the olfactory canal is only a bit more expanded than in subadults at the level of the orbitosphenoids. The brain cavity in adults doubles the size of the one in the subadults. The prootic is a proportionately larger in the subadults than in the adults, and probably the same can be said for the fenestra ovalis. The opisthotic-exoccipital of MOR 1071-7-13-99-87-I shows foramina for cranial nerves X through XII that are also relatively larger in size than in the adults. The posterior-most foramen, for a portion of the hypoglossal nerve (c.n. XII), is only slightly smaller in the subadult. Anteriorly to this foramen, there is a single lateral foramen that interiorly includes three divisions separated by thin strips of bone, probably for the exit of the glossopharyngeal (c.n. IX), vagus (c.n. X), spinal accessory (c.n. XI), and hypoglossal (c.n. XII) nerves, since anterior to it there is the fenestra ovalis (c.n. VIII). The basioccipital processes are not much smaller in the subadult in respect to the adult.

Axial Skeleton

Cervical Vertebrae. No subadult atlas has been collected for comparison. And it is not clear if the partial axis MOR 1071-7-21-98-331-A represents a subadult (see

individual variation for a discussion on the specimen). In adults the postzygapophyseal processes of the cervicals are mediolaterally wider towards their caudal ends, as well as their postzygapophyseal facets. In adults the neural arch is wider at the point where the postzygapophyseal processes begin to project caudodorsally. The prezygapophyseal facets are antero-caudally more enlarged in adults. Comparing the subadult MOR 1071-7-26-99-216, which has the most complete centrum among the subadults, with the adult specimens, it is observed that in the former the centrum is not so elongated antero-caudally as in adults. Subadult centra are relatively less expanded mediolaterally along their caudal rims than in the case of adults. MOR 1071-7-8-98-110 is a posterior subadult cervical, probably the number 12 or 13 in the series. The same position represents the adult MOR 1071-7-10-98-189, which exhibits a relatively higher neural arch than the subadult.

Dorsal Vertebrae. Among the anterior dorsal vertebrae, the blade-shaped neural spine is proportionately larger in the subadults in relation to the rest of the vertebra (for example, in MOR 1071-8-1-99-402). Concretely, the antero-caudal width of the spine in subadults is similar to that in the adults. In more posterior dorsals, the mediolateral thickness of the neural spine increases relatively in the adults (for example, between the adult MOR 1071-7-6-99-45 and the subadult MOR 1071-7-15-98-219). The postzygapophyseal facet becomes relatively enlarged in adults. The centrum of MOR 1071-7-6-99-45 is antero-caudally longer than in MOR 1071-7-15-98-219, but this may be due to the more anterior axial position of the subadult specimen. The diapophyses are proportionately thicker in the adults.

Sacral Vertebrae. Apart from MOR 794, sacral vertebrae are very poorly represented. Only a partial vertebra and a few fragmentary sacral have been recovered from the bonebed. Those specimens are probably subadult, but since articulation and part of the sediment concealed the sacral region in MOR 794, no comparison was possible.

Caudal Vertebrae. Caudal vertebrae are among the most abundant remains in the bonebed. Most specimens probably correspond to subadults. A still uncataloged anterior caudal unquestionably corresponds to an adult. This specimen allows comparison with a relatively anterior subadult caudal, MOR 1071-8-4-98-466. The adult has excavations at the anterior region of the diapophyses where these attach to the centrum. The subadult MOR 1071-8-4-98-466 lacks such excavations and no other subadult vertebra have been found having them. The adult has relatively larger zygapophyseal facets, its neural spine is mediolaterally wider and thicker near the neural arch, and the centrum has more expanded anterior and posterior edges.

Cervical and Dorsal Ribs. The absolute thickness of the tuberculum and capitulum of the cervical ribs is similar in both subadults and adults. The probable subadult dorsal ribs MOR 1071-8-12-98-506 and MOR 1071-7-14-98-191 have long, but relatively more slender ribs. The capitulum is relatively more slender in the subadults.

Chevrons. Adult chevrons show mediolaterally and antero-caudally thicker shafts, and their proximal articular facets are relatively larger in surface and supported by stouter branches.

Appendicular Skeleton

Coracoid. MOR-1071-7-30-99-258-A and MOR 1071-8-9-99-523-B represent respectively the left and right coracoids of two subadults. These two specimens show a mediolaterally more compressed humeral facet than the adult 794. While in MOR 794 the humeral facet is twice mediolaterally longer than is dorsoventrally, in MOR-1071-7-30-99-258-A and MOR 1071-8-9-99-523-B the facet is mediolaterally thick as it is dorsoventrally wide. In MOR 794 the oval depression of the humeral facet is displaced medially, but this is centered in the subadult.

Scapula. Besides the two larger adult specimens, the rest of the material corresponds subadults. Subadult scapulae are characterized by possessing a relatively narrow neck and a proportionally distally expanded blade. Good examples are MOR 1071-MOR 1071-7-8-98-115, MOR 1071-7-9-98-153 and MOR 1071-8-4-99-411. The ratio between the maximum dorsoventral width of the blade and the minimum dorsoventral width of the neck ranges from about 1.5 to 1.7. Another difference is the overall stouter morphology of the adult morphs, in contrast to the more gracile subadult scapulae. This is reflected in that the subadult morphs are relatively more elongated craniocaudally and proportionally narrower mediolaterally, but also dorsoventrally along

all the scapular length. The proximal region and the acromion process are stouter and thicker in the adult morphs. A third difference refers to the articular facets. In the adult scapula the coracoid facet has a more square-shaped contour. Indeed, this is D-shaped in MOR 1071-7-18-98-298. In contrast, in the subadults the coracoid facet is more oval.

Sternals. Only one subadult specimen is available for study, the right sternal MOR 1071-7-18-98-283. The other nearly or fully complete adults are MOR 1071-7-12-99-71, MOR 794, and MOR 1071-7-25-98-406. MOR 1071-7-25-98-406 is left aside because of its remarkable different features (see individual variation). The handle of the subadult is relatively thinner along all its dimensions in respect to the adults. The paddle is partially preserved in the subadult, but no differences were detected in relation to the adult.

Ilium. Three subadult ilia, MOR 1071-7-15-98-215, MOR 1071-7-10-99-50, and MOR 1071-7-31-99-285 were recovered from the bonebed. The adult ilium is more robust, as expected. In adults the central body of the ilium is deeper proportionately, and so is the postacetabular process. Especially, the concave lateral profile of the dorsal border of the ilium along the transition between the central body and the postacetabular process is much more marked in the subadult. Otherwise the subadult ilium is a small-sized version of the adult.

Pubis. Two right subadult pubes of the same size were recovered from the bonebed, the complete MOR 1071-7-20-98-300, and the partial MOR 1071-8-17-98-586. Since there is variation between the two subadults themselves, and only one of them is complete, most of the ontogenetic variation is made by comparing MOR 1071-7-20-98-

300 with the MOR 794 and MOR 1071 adults. MOR 1071-7-20-98-300 differs from adults in the possession of a dorsoventrally shallower prepubic blade, a narrower neck, and a more slender overall construction. The angle between the ventral border of the postpubic process and the ventral edge of the prepubic blade is the most open of all the specimens.

Ischium. The main difference between the adult and the subadult stage concerns the mediolateral thickness of the iliac peduncle. In MOR 794 this process is more mediolaterally compressed, while in the subadults the peduncle is mediolaterally thicker. It is however possible that the general mediolateral compression of MOR 794 produced this difference. Nevertheless, the iliac peduncle in the adult is relatively more developed and massive in the adult than in the subadults, in relationship to the proportions of the anterior expanded region of the ischium.

Humerus. The three available subadults, the left MOR 1071-7-14-98-202, and the rights 1071-7-23-99-178 and MOR 1071-7-14-98-192, are about 50 % the size of the adults. In the subadults the proximal end is less expanded than in the adults, where the proximal end is rather flared. The muscular scar located on the caudal surface of the proximal half of the humerus is comparatively larger in the subadults. In the subadults the scar is about 15 % smaller than those of the adults. At the same time, the sharp convexity of the scar is much more developed in the adults, being rather shallow in the subadults. The scar on the anteromedial border of the deltopectoral crest is slightly less developed in

the subadults, and as such easily abraded. The shaft of the distal half of the subadult humeri is relatively more slender, compared to the robustness of the adults.

Radius. Subadult radii are relatively more slender than the adults, especially along their shafts. Distally, subadult radii are only slightly less expanded than the adults. Otherwise, subadult radii do not differ much from the adult specimens.

Ulna. In the subadults, the size of the olecranon approaches that of the adults. The proximodistal length of the olecranon is practically equal in both adults and subadults. This is exemplified when comparing the subadult MOR 1071-8-14-99-B with the adults MOR 794 and MOR 1071-8-1-98-359-J. MOR 794 possesses a mediolaterally wide olecranon, doubling the mediolateral width of the olecranon in the other specimens. However, the MOR 1071 specimens show severely abraded olecranons. In subadults, the ulnar shaft is very slender and gracile, in contrast to the much more stout adult shafts. The proximal end of the ulna is relatively shallow in the subadults, whereas in the adults the medial and lateral sides of the proximal region of the element become relatively deeper.

Carpals. Besides the articulated MOR 794, only a right, adult tetrahedral carpal (MOR 1071-8-12-98-537A) and a left subadult tetrahedral carpal (MOR 1071-7-8-98-130) are available for comparison. The adult is more pointed ventrally (the long axis of the tetrahedron) and more expanded proximodistally on the laterodistal side of the dorsal face than the subadult.

Metacarpal II. Subadult specimens are mediolaterally thinner than adults. This is exemplified when comparing the proximal and distal outlines of MOR 1071-8-16-98-578 with those of the subadults. The rough scar on the medial side of the metacarpal is much more developed in the adults (for example, compare any subadult with MOR 1071-8-16-98-578).

Metacarpal III. Besides the expected increase in robustness of the adults in respect to the subadults, the proximal surface of the adults is mediolaterally wider than in the subadults. In the subadults, the outline of the proximal surface is more triangular and pointed ventrally. The distal face keeps the same proportion and shape than in the adults. In relation to that, in adults the proximal region of the metacarpal is mediolaterally wider. The distal regions and surfaces in the adults do not differ from those of the subadults. The mediodorsal scar that exists at the distal end of the proximal half of the element is much more developed in the adults and probably more easily abraded in the subadults.

Metacarpal IV. Two right subadults are available for comparison. In the adults the shaft of metacarpal IV is mediolaterally more robust and relatively thicker than in the subadults. These specimens lack the scar located on the middle of the medial surface of the adults.

Metacarpal V. Adult metacarpals possess more developed lateral and medial ridges and scars. The middle portion of the adult elements is dorsoventrally thickened in respect to the subadults.

Manual Digit II. The subadult phalanges II1 are mediolaterally compressed, hourglass-like in relation to the thicker adults MOR 1071-7-27-99-223 and MOR 794. The phalange II2 of the adult MOR 794 is proximodistally more expanded along the medial side than in the subadults, producing in the former a better developed triangular morphology as seen dorsally and ventrally. Two subadult unguals II are available. They are proportionately thinner mediolaterally and the medial expansion only occupies the proximal half of the proximodistal length of the medial side of the bone.

Manual Digit III. The adult phalange III1 of MOR 794 is mediolaterally thicker than in subadults, especially near the proximal border, which is more expanded than in the subadults. In the subadult phalanges III2 the lateral corner of the proximal surface is less laterally overhanging or invading the lateral side. In the subadult phalanges III2 is less proximodorsally shortened, less expanded dorsoventrally, that is, the proximal side is less oval and more subrectangular or ellipsoidal. Like in the case of phalange II2, the subadult phalanges III2 have are less wedge-shaped than the adults. The only recovered subadult manual ungual III (MOR 1071-8-1-99-303) is less expanded mediolaterally along its arrow-like distal region than in the case of the adults.

Manual Digit IV. Subadult phalanges IV1 are mediolaterally thinner along their middle portions and dorsoventrally thinner distally in respect to the adult specimens. The ventral rugose surface of the adult phalange IV2 is rougher and more developed in the adult than in the only available subadult (MOR 1071-7-9-98-159-A). The subadult is slightly shorter proximodistally than the adult form.

Manual Digit V. Subadult phalanges V1 are mediolaterally much thinner and dorsoventrally compressed in relation to the adult. The subadult phalanges V2 are proportionately shorter proximodistally than the adults. Whereas in the adults the mediolateral width equals to half the proximodistal length of the bone, in the subadults the bone is only one half more longer than wide. MOR 1071-8-2-99-354 is the only subadult specimen of phalange V3 recovered. This bone is mediolaterally thinner and more pointed distally, closer to the subtriangular morphology of MOR 1071-7-27-98-452. The recessed rough surface that wraps the element in the adult is forming the entire surface of the bone in the subadult. These differences suggest that older specimens might exhibit a more oval morphology along with a reduction of the recessed roughened surface. Phalange V4 is too featureless and too few specimens are available for comparison.

Femur. In the subadults the lesser trochanter, as seen laterally, is slightly larger proportionally in respect to the adults, especially concerning to its anterocaudal thickness. In the adult femur the fourth trochanter is anterocaudally much more prominent. In subadults, the D-shaped outline of the fourth trochanter is gentler than in adults. The muscle scars on the sides of the fourth trochanter are more deeply carved and coarser in the adult form. The femoral head is mediolaterally more expanded in adults. In overall proportions, the head is more massive and proportionately larger in the adults. The shaft of the femur is more robust and anterocaudally thicker in the adults.

Tibia. In subadults the cnemial crest is not so well developed and does not expand so much anteriorly to partially wrap the proximal fibula. The shaft of the tibia is thickest in the adults and the oval scar located further distally is also relatively larger and more developed in adults.

Fibula. Six subadult fibulae are collected. These specimens show a thinner distal shaft as compared to the adults. Even among the subadults, the relatively smaller MOR 1071-7-23-99-181 has a thinner distal shaft in respect to the other, slightly larger subadults. In the adults there is a well-developed, rough scar along the distal segment of the anteromedial ridge of the fibula. This scar is practically absent in subadults.

Astragalus. The astragalus in subadults has a less depressed distal surface than in the case of the adults. The anterior, triangular surface of the ascending process is relatively less rugose in subadults. In adults, the astragalus is more compressed antero-caudally at the middle, coinciding with a more developed distal depression.

Distal Tarsal. Subadult distal tarsals are proximodistally thinner than adults, especially along their lateral sides where adults show a relatively thicker. Otherwise, distal tarsals in both adults and subadults are rather rugose elements with variable outlines (see individual variation).

Metatarsal II. The three subadult collected specimens have less mediolaterally compressed and less ventrally elongated proximal borders. Smaller and younger subadults, show less dorsoventrally expanded proximal ends. This is the case of MOR

1071-8-7-99-470, as opposed to the other two, larger subadults. In contrast, the adults show even more dorsoventrally expanded proximal regions. The medial side of the distal end is dorsoventrally shallower in the relatively smaller MOR 1071-8-7-99-470, being deeper in the other two subadults. The smaller individual exhibits a dorsoventrally thinner shaft proximal to the mediodorsal flange.

Metatarsal III. Two subadult elements are available for comparison with the adult specimens. Subadults have proportionately narrower, less stout shafts. The ventromedial flange is not so developed as in adults (though see individual variation). The scar on the middle of the medial side is more developed and more rugose in the adults.

Metatarsal IV. In the adult specimens the scar on the medial surface of the flange is much more rugose and developed. The shaft is dorsoventrally thinner in subadults.

Pedal Digit II. In subadults, the proximal surface of phalange II1 has more equilateral lateral and ventral sides, while in adults the lateral border is higher than the ventral one. In adults the lateral side of phalange II1 shows a more extensive and rugose scar than in subadults. Phalange II2 grows increasing its mediolateral width and shows more expanded proximal and distal ends. This variation is observed in the progressively more mediolaterally expanded specimens that range from the smaller MOR 1071-8-9-99-410-A, to the larger subadult MOR 1071-8-1-99-334 and to the adult MOR 794. The bone widens mediolaterally with age through the subadults. The adult shows a deeper middle portion of the phalange. The size of the five available subadults changes rather continuously and is variable among the sample.

Pedal Digit III. Adults have phalanges III1 with a relatively more dorsoventrally and mediolaterally expanded proximal surfaces. The distal end of adults is also mediolaterally wider. As in the pedal phalanges of digit II, the middle portions of phalange III2 are mostly equally thick dorsoventrally among subadults of different sizes. However, larger specimens possess mediolaterally wider middle regions. Among subadults of different sizes, the distal surface is mediolaterally wider in larger specimens, but equally deep. In adults phalanges III2 and III3 become proximodistally and dorsoventrally thicker, and their distal and proximal facets are more expanded.

Pedal Digit IV. The changes found in phalange IV1 are similar than those in phalanges II1 and III1: larger individuals are mediolaterally wider and their proximal and distal surfaces become relatively more expanded dorsoventrally and mediolaterally. The scar located on the ventromedial region of the element is more developed and extensive in the adults. The same changes observed for phalanges III2 and III3 are valid for phalanges IV2, IV3 and IV4.

Pedal Unguals. In adults, the pedal unguals are more mediolaterally expanded in its distal, arrow-shaped ends, which are also dorsoventrally thicker than in subadults. Adults exhibit a further development of a pair of grooves located distally and laterally on the dorsal surface of unguals III.

Dimorphic Variation

I will consider here dimorphic variation to explain the observed variation that occurs in two different, discrete morphs between at least more than two specimens for the same element. No intermedial states of variation are found between the two morphs.

Following this criterion, the following two morphs are recognized:

Morph A (Fig. 86)

Referred specimens. MOR 794 (complete skeleton), MOR 1071-7-16-98-248-Q (jugal), PR 862 (partial skull roof).

Distinct features. Nasal crest extends until the dorsal border of the squamosals, covering the supratemporal fenestrae, and widens slightly posteriorly. Aiding in the support of the nasal crest, the prefrontals extend further caudally and medially underlying the nasal, forming a sharp lateral border along the dorsolateral edge of the skull, which ends caudal to the orbit. The following features are found in correlation to MOR 794 and PR 862: (1) relatively more massive and deeper dentary, (2) deeper jugals, with distinctive deeper anterior processes, wider bosses and less dorsoventrally narrowed segments between the anterior and postorbital and quadratojugal processes (3), relative increase in the ornamentation of the postorbitals.

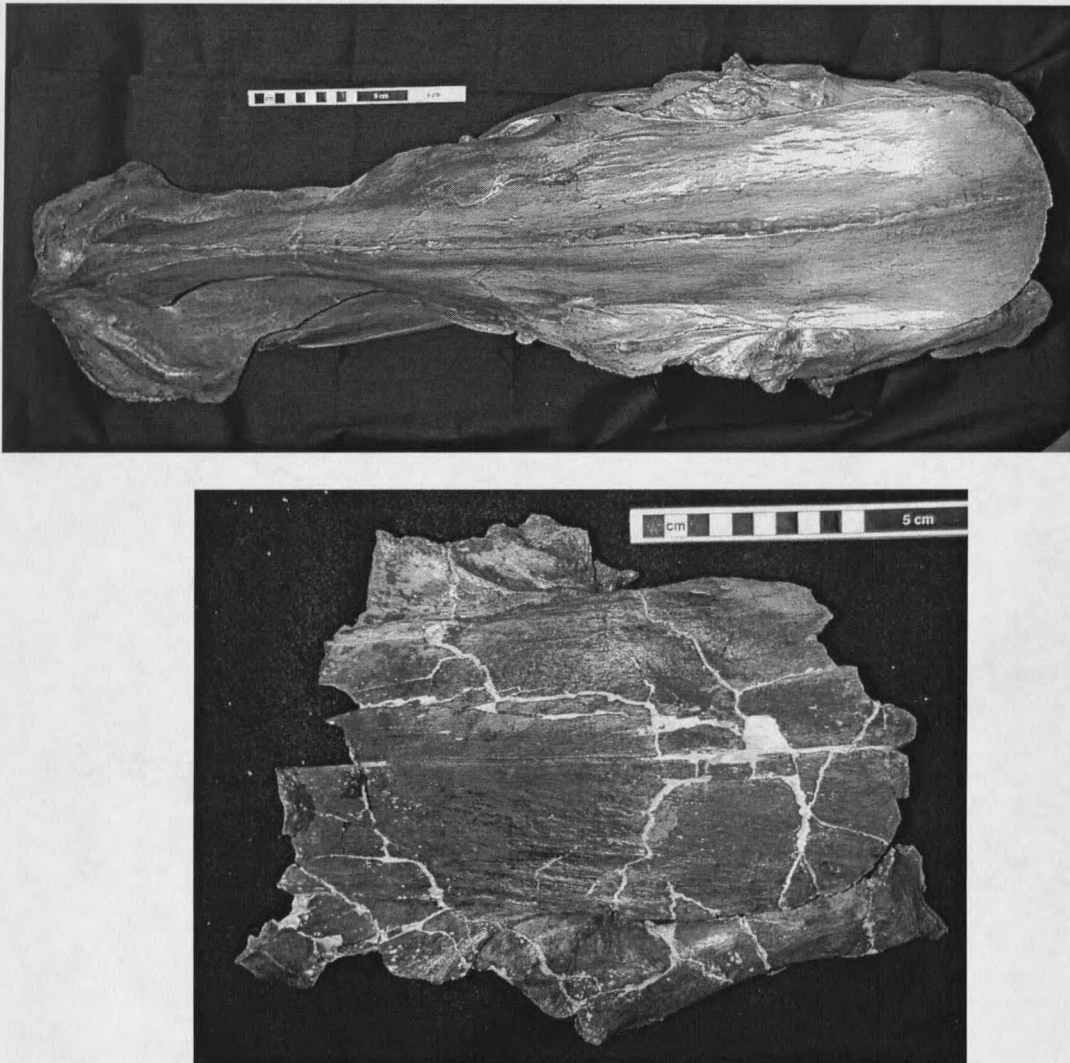


Figure 86. Nasal crest in morph A. Dorsal views of MOR 794 (top) and PR 862 (bottom).

Morph B (Fig. 87 and 88).

Referred specimens. MOR 1071-7-16-98-248 (skull roof), MOR 1071-7-7-98-86 (skull roof), and cranial material from the bonebed associated to those skull roofs in contrast to those associated to MOR 794 and PR 862.

Distinct features. The nasal crest does not reach the squamosals and is mediolaterally narrower. The crest covers little more than half the width of the supratemporal fenestra. Posteriorly the crest thins mediolaterally. Prefrontals do not extend posterior to the orbit. Other features, found by contrast with morph A, include: (1) dorsoventrally shallower and relative more gracile dentary, (2) dorsoventrally shallower and more lightly built jugals, (3) postorbital ornamentation relatively reduced.

Interpretation

Two hypotheses are formulated to explain this dichotomy. The first hypothesis is that these specimens represent two sexual dimorphs. This is based on of the presence of this variation in the same adult size, with no continuous variability - only two discrete forms. All the specimens show the autapomorphies of this taxon, while at the same time exhibit those variable features listed above. Sexual dimorphism on hadrosaurs shown in the shape of the crests has previously been pointed out by Dodson (1975) concerning lambeosaurines.

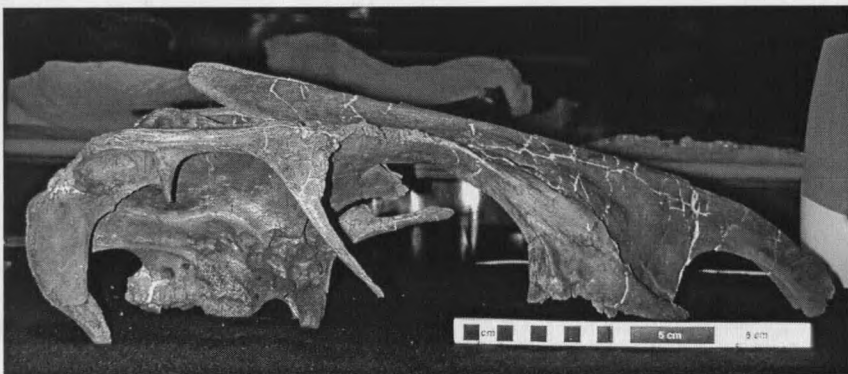


Figure 87. Right lateral view of the skull roof MOR 1071-7-7-98-86.



Figure 88. Nasal crest in morph B. Dorsal views of MOR 1071-7-7-98-86 (top) and MOR 1071-7-16-98-248 (bottom).

The other hypothesis implies that the adult size is reached before the crest is fully developed, so that the short-crested forms correspond to large subadults or to relatively young adults. The small sample does not represent other states of variation that were present among individuals of *Brachylophosaurus*. MOR 794 shows more robust and longer appendicular elements. Older adults and/or simply older individuals would also exhibit longer and more robust appendicular elements, mostly limb bones.

CHAPTER 5

PHYLOGENETIC POSITION OF *BRACHYLOPHOSAURUS CANADENSIS*

The purpose of this section is to provide a phylogenetic context for *Brachylophosaurus*. Eighty-three characters of the cranial and postcranial anatomy of hadrosaurids and two iguanodontian dinosaurs were chosen. *Tenontosaurus tilleti* and *Iguanodon* were used as successive outgroup taxa. In addition to *Brachylophosaurus canadensis*, the other hadrosaurines included in this analysis are *Maiaasaura peeblesorum*, *Gryposaurus*, *Prosaurolophus blackfeetensis*, and *Edmontosaurus*. The lambeosaurine *Hypacrosaurus stebingeri* was also included. The data matrix was processed using PAUP 3.0 and MacClade 3.03 software.

The author started from a recent character list provided by Horner, Weishampel and Forster. This list included 129 characters. Some of them were eliminated because of lack of accuracy or clarity, relevancy to the problem of this project, and specimen availability. A few characters were added by the author. It is remarkable that Horner, Weishampel, and Forster included no character from the braincase. This is probably due to the absence of available braincases for most hadrosaurs. I included one character from the braincase and it is hoped that further descriptions and studies will allow a better understanding of this region of the skull. Other elements of the skull, such as the predentary, might show a greater degree of variability and phylogenetic use than previously thought. In preparing this phylogeny, the author realized that an exhaustive survey of hadrosaur elements on virtually all the taxa and specimens known is needed in

order to be able to better understand hadrosaur phylogeny. Needless to say, such a survey is beyond the scope of this thesis.

The resulting tree consists of 138 steps and has a consistency index of 0.83.

Within the Hadrosauridae, the Hadrosaurinae is supported by seven characters in this analysis (see Appendix C). Two clades within the hadrosaurines were found (Fig. 1). The less derived is formed by *Brachylophosaurus* and *Maiasaura*. In this sense the present analysis agree with previous hypothesis that place *Maiasaura peeblesorum* as the sister taxon of *Brachylophosaurus* (Horner, 1992). *Maiasaura* and *Brachylophosaurus* share an anterior mediolateral width of prementary that doubles the anteroposterior length of the lateral processes, a posterior margin of circumnarial fossa that does not excavate the side of nasal/nasofrontal solid crest, a posteriorly reflected, anteriorly deflected premaxillary rim, a pointed anterior process of jugal centered on the anterior region of the element, being triangular and symmetrical in shape, a relatively large and very expanded alar process of basisphenoid, and the presence of a plantar keel on the pedal unguals.

The second clade within the hadrosaurines is formed by *Gryposaurus* and a dichotomy that includes *Prosaurolophus* and *Edmontosaurus*. The clade is supported only by a few characters. These are the presence of a flange posteroventral to the postorbital process and individualized from quadratojugal process, so that the dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange is less than double the minimum dorsoventral depth of anterior segment of jugal

between anterior and postorbital process, a squamosal prequadratic process equal or longer than anteroposterior width of quadrate cotylus, and a anteriorly and posteriorly reflected

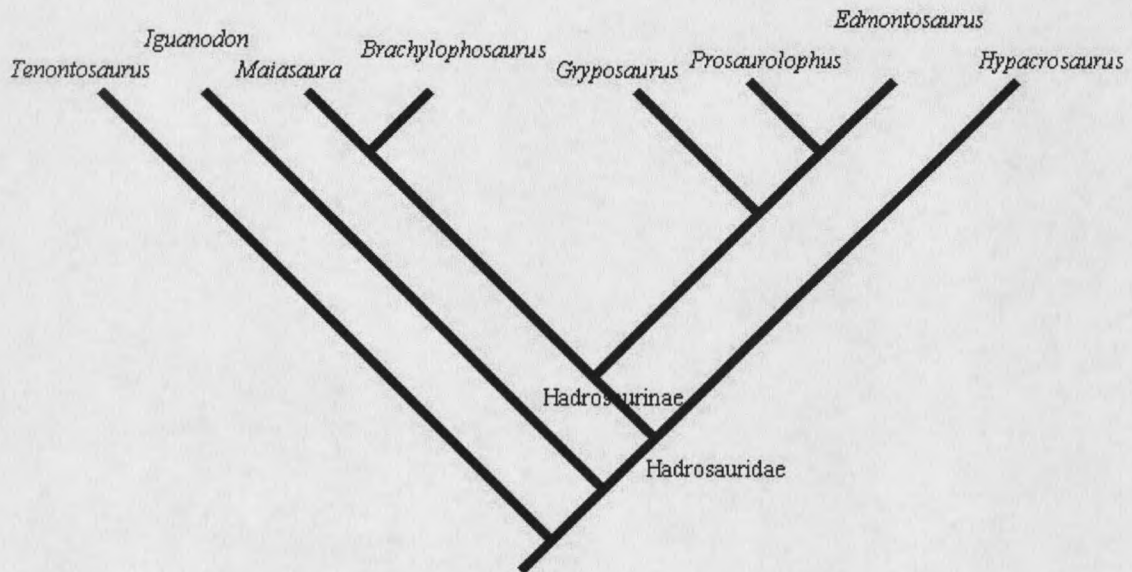


Figure 89. Cladogram showing the phylogenetic position of *Brachylophosaurus* within a few selected taxa, two outgroup iguanodontians, four hadrosaurines, and one lambeosaurine hadrosaur.

premaxillary rim. *Prosaurolophus* and *Edmontosaurus* are united by only having a well demarcated, deeply incised, and invaginated posterior margin of the circumnarial fossa, and a posterior-most apex of external nares formed by the nasal dorsally and the premaxilla ventrally. It must be emphasized that this analysis is very limited by the number of taxa, specimens, and a more comprehensive assessment of the characters to be used in future phylogenies.

CHAPTER 6

CONCLUSIONS

The hadrosaurid dinosaur *Brachylophosaurus canadensis* is redescribed on the basis of new specimens recovered from the Upper Cretaceous (lower Campanian) Judith River Formation of Malta, northeastern Montana. A new diagnosis is erected for the genus and species. The species *B. goodwini* is found to be invalid. Some of the characters included in the diagnosis of *B. goodwini* are here explained as misplacement of the nasal and individual variation. Other characters are found also in the Malta specimens and added to the diagnosis of *B. canadensis*.

The completeness of the MOR 794 and MOR 1071 specimens allowed a detailed and exhaustive description, as well as the observation of some morphological features relevant for hadrosaur anatomy in general. Among these, the carpus has been preserved in place, showing a minute and a larger, tetrahedral element, unlike the "one or two subrounded carpals" described by Weishampel and Horner (1990). The phalangeal formula of *Brachylophosaurus* is not 0-3-3-3-3 as has been postulated for the Hadrosauridae, but 0-3-3-3?-4. The presence of a fourth, minute phalange on digit IV might be a feature more widespread among other hadrosaurs, since the bone is easily removed by taphonomic processes and/or overlooked during or after collection of the fossils. A third phalange on digit four may be present in the right manus of MOR 794, although it is unprepared. The hadrosaur coracoid has been described as showing a

caudoventral hook below the glenoid (Lull and Wright, 1942; Weishampel and Horner, 1990). The coracoid of the bonebed specimens of *Brachylophosaurus* follows that description, but not the one of MOR 794. In MOR 794 the coracoid exhibits to rod-like processes, an anterior short process and a longer ventral one. Probably these processes were present on the bonebed specimens as well as on other hadrosaurs. The hook-like morphology is probably produced by breakage and abrasion of the processes. The variation observed in the narrowness of the scapular neck in relation to the dorsoventral width of the distal blade casts doubts about using this relationship for separating hadrosaurines from lambeosaurines. The subadult scapulae of hadrosaurs such as *Brachylophosaurus* and *Maiasaura* show a relatively narrow neck. MOR 794 scapula shows a relatively narrower neck than the adult specimen from the bonebed. The morphology of the sternals is found to be variable among the observed genus *Brachylophosaurus*, *Prosaurolophus*, and *Hypacrosaurus*, and it might be of diagnostic use in hadrosaurs. In the skull, two nasal foramina are here described for the first time in hadrosaurs.

The study of the morphologic variation present on the available specimens shows individual, ontogenetic, and dimorphic variations. Individual variations are mostly detailed features found among individual elements. MOR 794 is a more robust and slightly larger individual, as compared to the larger elements recovered from the bonebed. This is exemplified in numerous elements such as the sternals, radius, ulna, metatarsals, pubis, and ilium. It is not known if this difference is correlated with the further development of the nasal crest.

The most remarkable variations are the ontogenetic and the dimorphic. As deduced from counting the number of elements of the same side of the most abundant elements, there are at least four subadults and two adults represented in the bonebed. This is shown, for example, in the presence of four left ulnae and four left dentaries of 50 to 60 % the adult size, and the two articulated skull roofs of adult size. Different elements show particular ontogenetic variations. The preorbital region of the subadult skull is probably shorter anteroposteriorly. The subadult skull shows larger openings, and proportionately larger foramina on the braincase. In particular the subadult orbital cavity is very large, and so are the elements surrounding it. The postorbital and prefrontal are not much smaller in the subadults than in the adults. The braincase is relatively narrow in the brain cavity and the mediolateral width of the laterosphenoids. The neurocranial foramina are relatively large, in contrast. It is not known how developed the nasal crest was in subadults, since no subadult nasal is available. However, the prefrontal is not extended caudally and medially in subadults, probably associated to a lesser development of the nasal crest. The nasofrontal articulation is visible in two subadult specimens, but is concealed in the adults due to their articulation state. The most generalized changes in the postcrania between these two age classes relate to the more developed muscle scars and rugosities, and the increase in robustness and thickness of the adult bones. The scapular neck is relatively narrow in subadult hadrosaurs. All these changes contrast to the ones observed by Horner and Currie (1994) in the embryonic and nestling *Hypacrosaurus stebingeri*. The subadults of *Brachylophosaurus* show, as in the baby *Hypacrosaurus*, shorter preorbital regions and large orbits. However, in contrast to *Hypacrosaurus*, the

subadults of *Brachylophosaurus* exhibit a similar dentary tooth count and size, and more slender appendicular elements and less developed muscle scars. The opposite was found in the babies of *Hypacrosaurus*.

The dimorphic variation separates two forms, mainly on the basis of the nasal crest morphology. One morph shows a wide and long crest, while the other exhibits much narrower and shorter crest. No middle form is found among the available specimens. There are just these two variations. The wide-crested morph shows deeper and more robust dentaries, jugals, and more ornamented postorbitals and slightly more developed prefrontals. This dimorphic variation may indicate sexual dimorphism, or simply age-related changes. Further specimens are needed before choosing between these two hypotheses.

Finally, *Brachylophosaurus canadensis* is found to be the sister taxa of *Maiasaura peeblesorum*. Both taxa form a relatively basal clade within hadrosaurine hadrosaurs, in agreement with the current state of knowledge (Weishampel and Horner, 1990; Horner, 1992). Although the present cladistic analysis is too much simple, it has shown that an exhaustive reassessment of hadrosaur characters should be conducted in order to produce a robust phylogeny of the group.

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APPENDICES

APPENDIX A

LIST OF SPECIMENS

Specimens used for description, variation and taxonomy (in alphabetic order and listed by taxon).

Brachylophosaurus canadensis

Cranial Material (in alphabetic order)

Angular

MOR 794 (articulated angulars)
MOR 1071-7-31-99-276 (right, subadult)
MOR 1071-7-20-99-146 (left, subadult)
PR 862 (left and right angulars, adult)
MOR 1071-8-20-96-597-C (left fragment, subadult)

Articular

MOR 794 (articulated articulars)
MOR 1071-8-13-98-554-A (right, adult)
MOR 1071-7-18-98-282-B (left, subadult)

Braincase

MOR 794 (not exposed)
MOR 1071-7-7-98-86 (adult, articulated presphenoids, orbitosphenoids, laterosphenoids, prootics, opisthotics, exoccipitals, supraoccipitals, basioccipitals (mostly ripped off), basisphenoid, and parasphenoid).
MOR 1071-7-16-98-248 (adult, articulated presphenoids, orbitosphenoids, laterosphenoids, prootics, opisthotics, exoccipitals, supraoccipitals, basioccipitals (mostly ripped off), basisphenoid, parasphenoid).
MOR 1071-6-30-98-4 (subadult associated fragments of frontals, supraoccipitals, parietal and opisthotic-exoccipital).
PR 862 braincase (adult partial, but articulated braincase with laterosphenoid, orbitosphenoids, parietal and frontals)

MOR 1071-7-13-99-87-I (subadult articulated, incomplete braincase with supraoccipital, opisthotic, exoccipital, parietal, frontal, orbitosphenoid, prootic, and laterosphenoids)

Dentary

MOR 794 (articulated dentaries)

MOR 1071-8-15-98-574 (right, adult; no teeth)

MOR 1071-7-13-99-93 (left, adult; no teeth)

MOR 1071-7-25-98-405 (left, subadult; no teeth)

MOR 1071-7-15-98-226 (left, subadult; w/teeth)

MOR 1071-10-98-179 (left, subadult; no teeth)

MOR 1071-8-1-99-313 (right, subadult; w/teeth)

MOR 1071-8-8-44-484-E (left dentary (partial); subadult, w/teeth)

PB 862 (left and right dentaries, adult, w/teeth)

Ectopterygoid

MOR 794

MOR 1071-8-13-98-559E (left, dult)

MOR 1071-7-31-99-281-I (right, adult, posterior end)

Frontal

MOR 794

MOR 1071-7-7-98-86 (both frontals, articulated, adult)

MOR 1071-7-16-98-248 (both frontals, articulated, adult)

MOR 1071-6-30-98-4 (both frontals, incomplete and associated to subadult braincase fragments)

PR 862 (both frontals, articulated, adult)

MOR 1071-7-13-99-87-I (both frontals, articulated, subadult)

Hyoids

MOR 794

MOR 1071-7-16-98-248-K (right hyoid, subadult)

MOR 1071-8-20-98-597-B (left? partial, subadult)

MOR 1071-7-15-98-209 (right? partial, subadult)

Jugal

MOR 794

MOR 1071-7-16-98-248-Q (right, adult)

MOR 1071-7-27-98-453 (left, adult)

MOR 1071-6-30-98-3 (left, subadult)

MOR 1071-7-31-99-281-O (right, adult)

PR 862 (left and partial right jugals, adult)

Lacrima

MOR 794

MOR 1071-7-7-98-86 (right, adult and articulated)

MOR 1071-7-16-98-248 (both lacrimals, adult and articulated)

MOR 1071-7-10-98-171 (left, adult)

MOR 1071-8-3-99-378 (left, subadult)

MOR 1071-6-30-98-9 (left, subadult)

MOR 1071-8-5-99-447-G (left, subadult, articulated to the prefrontal)

Maxilla

MOR 794

MOR 1071-8-13-98-559 (right, adult)

MOR 1071-8-13-98-554 (left, subadult)

MOR 1071-8-5-99-447-N (left, subadult)

MOR 1071-8-15-98-573 (left, adult)

MOR 1071-7-6-98-79 (right, adult)

Nasal

MOR 794

MOR 1071-7-12-99-76 (right, adult, partial fragment)

MOR 1071-7-7-98-86 (both nasals, adult, lacking anterodorsal processes)

MOR 1071-7-16-98-248 (both nasals, adult, lacking anterodorsal processes)

UCB 130139 (right, particularly large adult, partial central body)

PR 862 (both nasals: fragment of anterodorsal process and articulated crest, adult)

Palatine

MOR 794

MOR 1071-7-16-98-248-S (right, adult, almost complete)

MOR 1071-7-26-99-221 (left, adult, anterodorsal portion)

MOR 1071-7-19-99-139 (right, anterior and middle portion of ventral segment)

MOR 1071-8-13-98-559-G (right, adult, fragment of ventral segment)

MOR 1071-8-15-98-568 (left, adult, fragment of ventral segment)

MOR 1071-8-15-98-567 (right, adult, anterodorsal portion)

Parietal

MOR 794

MOR 1071-7-7-98-86 (articulated, adult)

MOR 1071-7-16-98-248 (articulated, adult)

MOR 1071-6-30-98-4 (anterior fragment, attached to frontals, subadult)

MOR 1071-7-13-99-87-I (articulated, subadult)

PR 862 (partial, articulated, adult)

Postorbital

MOR 794

MOR 1071-7-7-98-86 (both postorbitals, adult, articulated)

MOR 1071-7-16-98-248 (both postorbitals, adult, articulated)

MOR 1071-6-30-98-4 (right & partial left postorbital with associated braincase fragments, subadult)

MOR 1071-7-13-99-87-L (right, subadult, articulated w/ squamosal MOR 1071-7-13-99-87-H and MOR 1071-7-13-99-87-I skull roof and braincase)

MOR 1071-7-13-99-87-G (left, subadult, articulated w/MOR 1071-7-13-99-87-I skull roof and braincase)

PR 862 (left, adult, articulated).

Predentary

MOR 794 (articulated adult)

MOR 1071-7-28-98-299 (adult and complete)

Prefrontal

MOR 794

MOR 1071-7-7-98-86 (both prefrontals, adult, articulated)

MOR 1071-7-16-98-248 (both prefrontals, adult, articulated)

MOR 1071-8-2-99-346 (right, subadult)

MOR 1071-8-5-99-447-G (left, subadult, articulated to lacrimal)

MOR 1071-? (right, subadult, crashed)

Premaxilla

MOR 794

MOR 1071-7-7-98-84 (left, subadult)

MOR 1071-7-5-98-66 (right, subadult)

MOR 1071-7-23-99-179 (right, subadult, partial)

Pterygoid

MOR 794

MOR 1071-8-1-99-315 (left, subadult, attached to quadrate)

MOR 1071-8-14-99-A (left, subadult, ventral fragment)

MOR 1071-7-23-98-387 (right, adult)

PR 862 pterygoid (right, adult, partial, ventral portion)

Quadrate

MOR 794

MOR 1071-8-13-98-559D (right, adult)

MOR 1071-6-30-98-1 (left, subadult)

MOR 1071-8-1-99-315 (left, subadult, articulated to the pterygoid)

MOR 1071-7-6-99-44C (left, adult, ventral fragment)

MOR 1071-8-8-99-484-O (left, subadult, incomplete)

PR 862 (right, adult)

Quadratojugal

MOR 794

MOR 1071-7-15-98-218-A (right; adult)

MOR 1071-8-9-98-509 (right; adult)

MOR 1071-8-3-99-366 (right, subadult)

Sclerotic plates

MOR 1071-8-6-98-484-A (pair of disarticulated sclerotic plates)

Splénial

MOR 794

MOR 1071-8-6-98-483 (right, adult)

MOR 1071-8-8-99-484-A (left, subadult)

MOR 1071-7-31-99-281-R (left, adult)

Squamosal

MOR 794

MOR 1071-7-7-98-86 (both squamosals, adult, articulated)

MOR 1071-7-16-98-248 (both squamosals, adult, articulated)

MOR 1071-7-13-99-87H (left, subadult, in articulation)

MOR 1071-8-5-99-458 (left, subadult)

MOR 1071-6-30-98-4 (right, partial squamosal, associated to fragments of braincase, subadult)

Surangular

MOR 794

MOR 1071-7-25-98-405-A (right, adult)

MOR 1071-7-27-99-230 (left, adult)

MOR 1071-7-24-99-192-A (right, subadult)

MOR 1071-8-8-99-484-B (left, subadult)

MOR 1071-8-7-99-460-L (left, subadult, crashed)

Axial Skeleton (in alphabetic order)**Atlas**

MOR 794 (complete and articulated, adult)

MOR 1071-7-21-98-350 (right neural arch half, rostral and caudal portions preserved)

MOR 1071-6-24-99-18 (intercentrum, adult)

Axis

MOR 794 (axis, complete and articulated, adult)

MOR 1071-7-21-98-331-A (partial neural arch, w/left prezygapophysis and cranial flange; crushed and deformed)

Haemal arches

MOR 794 (articulated chevrons on tail)

MOR 1071-7-23-99-186 (anterior)

MOR 1071-7-19-99-119

MOR 1701-7-15-98-215 (proximal fragment)

MOR 1071-8-2-99-351 (anterior?)

MOR 1071-7-19-99-138 (proximal fragment)

MOR 1071-8-13-98-559-B

MOR 1071-7-18-98-298-A

MOR 1071-7-9-98-165

MOR 1071-8-1-98-359-D

MOR 1071-7-18-98-359-E (partial chevron)

MOR 1071-8-1-98-359-F

MOR 1071-8-1-98-359-G (partial chevron)

MOR 1071-8-13-98-556

MOR 1071-7-16-98-248-I

MOR 1071-6-30-98-13

MOR 1071-7-16-98-248-E

MOR 1071-7-16-98-248-J (posterior)

MOR 1071-7-16-98-248-B (posterior)

MOR 1071-278-A (posterior)
MOR 1071-248-G (posterior)
MOR 1071-8-11-98-526 (partial chevron)
MOR 1071-7-16-98-259 (partial chevron)
MOR 1071-7-18-98-289 (proximal end fragment)
MOR 1071-7-20-98-305 (proximal end fragment)
MOR 1071-21-98-339 (anterior)
MOR 1071-7-26-98-437
MOR 1071-7-21-98-343
MOR 1071-7-18-98-297 (anterior)
MOR 1071-7-18-98-284 (posterior)
MOR 1071-7-1-98-42 (anterior)
MOR 1071-7-16-98-245
MOR 1071-7-19-99-138 (posterior)

Ribs - cervicals

MOR 794
MOR 1071-8-15-98-561 (left, attached to a partial centrum, adult)
MOR 1071-7-19-99-126 (left, adult)
MOR 1071-7-12-99-81-A (right, subadult)
MOR 1071-8-3-99-379 (left, subadult)
MOR 1071-7-31-99-280 (caudal tip, adult)
MOR 1071-7-31-99-279 (left, subadult)
MOR 1071-7-16-98-248-M (right, adult)
MOR 1071-7-16-98-248-LL (left, adult)
MOR 1071-7-16-98-248-H (left, adult)
MOR 1071-? (left, adult)

Ribs-dorsals

MOR 794
MOR 1071-7-11-99-68 (right, anterior, subadult)

MOR 1071-7-10-99-53 (left, adult)
MOR 1071-7-12-99-81 (right, adult)
MOR 1071-7-15-98-218 (right, adult; only dorsal end)
MOR 1071-7-20-99-155 (left, anterior?; only main shaft)
MOR 1071-7-15-98-231 (left, subadult?)
MOR 1071-7-27-98-448 (right)
MOR 1071-7-21-98-349 (right)
MOR 1071-7-28-98-446 (left)
MOR 1071-7-17-98-274 (right)
MOR 1071-6-30-98-17 (1st or 2nd?; only shaft)
MOR 1071-6-30-98-16 (shaft)
MOR 1071-6-30-98-18 (shaft)
MOR 1071-8-20-98-597-A (1st?; right, only shaft)
MOR 1071-7-20-99-155-A (1st?, only shaft)
MOR 1071-7-16-98-248-R (capitulum and tuberculum, right, adult)
MOR 1071-7-16-98-248-T (capitulum and tuberculum, left adult; pathological craniocaudal thickening of the capitulum)
MOR 1071-7-3-98-61 (right, adult?)
MOR 1071-7-6-98-78 (right, subadult?)
MOR 1071-7-22-98-327 (shaft, adult)
MOR 1071-8-12-98-506 (right, subadult?)
MOR 1071-7-14-98-191 (right, subadult?)
MOR 1071-7-6-98-69 (right, adult?)
MOR 1071-7-19-99-153 (anterior, adult)

Vertebrae - caudals

MOR 794 (articulated tail, lacking distal region; adult)
MOR 1071-8-4-98-466 (anterior, subadult)
MOR 1071-8-4-98-465 (middle caudal, subadult)
MOR 1071-8-15-98-564 (middle caudal, subadult)
MOR 1071-8-1-98-359-H (posterior caudal)
MOR 1071-7-15-98-218-B (posterior caudal)

MOR 1071-8-1-98-359-I (posterior caudal)
MOR 1071-7-15-98-218-D (posterior caudal centrum)
MOR 1071-7-15-98-218-C (ending caudal)
MOR 1071-8-3-99-388-V (posterior caudal, subadult)
MOR 1071-7-98-215-B (ending caudal)
MOR 1071-8-2-99-356 (ending caudal)
MOR 1071-7-30-99-294 (ending caudal)
MOR 1071-7-10-98-173-A (ending caudal)
MOR 1071-7-19-98-295 (ending caudal)
MOR 1071-7-10-98-173-B (ending caudal)
MOR 1071-7-30-99-241 (ending caudal)
MOR 1071-7-30-99-242 (ending caudal)
MOR 1071-7-31-99-277 (ending caudal centrum)
MOR 1071-7-21-98-347 (ending caudal centrum)
MOR 1071-7-30-99-239 (ending caudal)
MOR 1071-7-30-99-240 (ending caudal)
MOR 1071-7-16-98-248-A (ending caudal adult)
MOR 1071-7-1-98-25 (ending caudal)
MOR 1071-7-16-98-248-N (ending caudal adult?)
MOR 1071-7-25-98-411 (ending caudal)
MOR 1071-7-16-98-248-O (ending caudal)
MOR 1071-7-21-98-337 (ending caudal)
MOR 1071-7-16-98-248-F (ending caudal)
MOR 1071-7-17-98-266 (ending caudal)
MOR 1071-7-9-98-165-A (ending caudal)
MOR 1071-7-20-98-312 (ending caudal)
MOR 1071-7-26-98-426 (ending caudal centrum)
MOR 1071-8-13-98-560 (ending caudal)
MOR 1071-7-26-98-447 (ending caudal)
MOR 1071-7-21-98-348 (ending caudal centrum)
MOR 1071-7-18-98-290 (ending caudal centrum)
MOR 1071-8-2-98-462 (anterior caudal centrum, subadult)

MOR 1071-9-18-98-296 (anterior caudal, subadult)
 MOR 1071-8-13-98-559-C (posterior caudal)
 MOR 1071-7-6-98-77 (anterior caudal, subadult; lacks left diapophysis)
 MOR 1071-7-18-98-282 (anterior caudal centrum)
 MOR 1071-7-15-98-230 (posterior caudal)
 MOR 1071-7-25-98-412 (ending caudal, crushed)
 MOR 1071-7-9-98-163 (ending caudal, pathology on chevron facet)
 MOR 1071-7-10-98-177 (ending caudal)
 MOR 1071-7-9-98-143 (ending caudal, subadult)
 MOR 1071-7-9-98-149 (anterior caudal, subadult)
 MOR 1071-7-6-98-78-C (median caudal, subadult)
 MOR 1071-7-9-98-145 (middle caudal)
 MOR 1071-7-9-98-147 (middle caudal)
 MOR 1071-7-6-98-78-D (middle caudal, subadult)
 MOR 1071-7-6-98-78-B (ending caudal)
 MOR 1071-7-6-98-78-A (ending caudal)
 MOR 1071-6-30-98-20 (caudal neural arch and spine)
 MOR 1071-6-30-98-11-B (caudal neural spine)
 MOR 1071-8-7-98-493 (caudal neural arch and spine)
 MOR 1071-6-30-98-12 (caudal neural arch and spine)
 MOR 1071-6-30-98-11 (caudal neural spine)
 MOR 1071-6-30-98-19 (caudal neural arch and spine)

Vertebrae – cervicals

MOR 794 (complete and articulated adult neck)
 MOR 1071-6-30-98-14 (complete subadult cervical)
 MOR 1071-7-10-98-189 (complete cervical 12 or 13?)
 MOR 1071-7-15-98-221 (nearly complete, adult)
 MOR 1071-7-15-98-223 (nearly complete, adult)
 MOR 1071-7-23-98-368 (nearly complete, adult)
 MOR 1071-7-26-98-436 (nearly complete, adult)
 MOR 1071-7-8-98-118 (almost complete, subadult, 12th or 13th)

MOR 1071-8-19-98-588 (nearly complete, adult)
 MOR 1071-8-12-98-519-A (nearly complete, adult)
 MOR 1071-8-12-98-519-B (nearly complete, adult)
 MOR 1071-8-8-99-484-F (cervical, subadult)
 MOR 1071-7-26-99-216 (middle cervical, subadult)

Vertebrae - Dorsals

MOR 794 (complete and articulated rib cage)
 MOR 1071-7-6-99-45 (middle-posterior dorsal)
 MOR 1071-7-13-99-85 (posterior dorsal, probably subadult)
 MOR 1071-7-3-98-65 (almost complete, broken diapophyses and neural spine, subadult)
 MOR 1071-8-1-99-402 (anterior, probably 3rd or 4th; subadult)
 MOR 1071-7-15-98-219 (anterior-middle dorsal, subadult)
 MOR 1071-8-18-98-593 (middle-posterior dorsal; pathologic)
 MOR 1071-7-17-99-111 (adult centrum)
 MOR 1071-7-15-98-218-E (centrum from anterior dorsal, subadult?)
 MOR 1071-7-16-98-255 (centrum from posterior dorsal, adult)
 MOR 1071-7-3-98-56 (partial anterior dorsal)
 MOR 1071-7-17-98-278 (neural arch and spine, subadult; from anterior dorsal)

Vertebrae – Sacrals

MOR 794 (complete and articulated sacrum)
 MOR 1071-8-13-98-543 (neural spine and arch, and diapophyses, adult)
 MOR 1071-7-10-99-51 (sacral rib)
 MOR 1071-8-5-99-452 (sacral rib)
 MOR 1071-7-13-99-87-M (sacral diapophysis?)
 MOR 1071-7-18-98-282 (sacral centrum?, subadult)
 MOR 1071-7-3-98-55 (sacral rib)

Appendicular Skeleton (in alphabetic order)

Carpals

- MOR 794 (articulated carpal set, adult)
MOR 1071-8-12-98-537 (right "radial" carpal)
MOR 1071-7-8-98-130 (possible carpal, probably subadult)

Coracoid

- MOR 794
MOR 1071-6-30-98-11C right coracoid, subadult
MOR 1071-8-9-99-523-B right coracoid, subadult
MOR 1071-7-30-99-258-A left coracoid, subadult
MOR 1071-7-31-99-281-W right coracoid, adult

Femur

- MOR 794
MOR 1071-7-21-98-331 (left, adult)
MOR 1071-7-1-98-? (left, subadult)
MOR 1071-8-5-99-451 (left, subadult)
MOR 1071-8-1-99-327 (right, subadult)
MOR 1071-7-31-99-282 (right, subadult)

Fibula

- MOR 794
MOR 1071-8-12-98-519 (left, subadult)
MOR 1071-7-23-99-181 (right, subadult)
MOR 1071-8-10-98-516-A (left, subadult)
MOR 1071-7-7-98-88 (left, adult)
MOR 1071-7-23-98-374 (right, subadult)
MOR 1071-8-1-99-329 (right, subadult)
MOR 1071-8-5-99-430 (left, subadult)

Humerus

MOR 794 complete articulated, adult humeri
MOR 1071-7-23-99-178 (right, subadult)
MOR 1071-7-14-98-202 (left, subadult)
MOR 1071-7-20-98-325 (right, adult)
MOR 1071-7-14-98-192 (right, subadult)

Ilium

MOR 794
MOR 1071-8-2-98-469 left ilium, subadult
MOR 1071-7-15-98-215 right ilium, subadult
MOR 1071-7-10-99-50 left ilium, subadult
MOR 1071-7-31-99-285 right ilium, subadult

Ischium

MOR 794
MOR 1071-7-19-99-154B left ischium, partial, mostly just shaft, subadult
MOR 1071-7-14-98-200 left ischium, partial, subadult
MOR 1071-7-15-98-207 right ischium, subadult, partial
MOR 1071-7-12-98-182 right ischium, subadult, partial
MOR 1071-8-9-99-522 left ischium, subadult

Metacarpals

MOR 794 (complete and articulated metacarpals II, III and IV, right and left).
MOR 1071-8-16-98-578 (metacarpal II (right), adult)
MOR 1071-7-23-98-386 (metacarpal II (left), subadult, crushed)
MOR 1071-7-20-98-317 (metacarpal II (right), subadult and pathological)
MOR 1071-8-2-99-363 (metacarpal II (left), subadult)
MOR 1071-7-8-98-110 (metacarpal II (right), subadult)
MOR 1071-7-31-99-294 (metacarpal III (right), subadult)
MOR 1071-8-1-98-359-A (metacarpal III (right), adult)
MOR 1071-7-9-98-128 metacarpal III (right), subadult)

MOR 1071-7-1-98-48 metacarpal III (left, subadult)
 MOR 1071-7-14-98-193 metacarpal III (right, subadult, lacks distal end, crushed)
 MOR 1071-7-5-98-67 metacarpal III (right, subadult, lacks distal end, crushed)
 MOR 1071-7-19-99-137 metacarpal IV (left, adult)
 MOR 1071-8-13-98-547 metacarpal IV (right, adult)
 MOR 1071-7-7-98-96 metacarpal IV (right, subadult)
 MOR 1071-8-13-98-548 metacarpal IV (right, subadult)
 MOR 1071-8-5-98-481 metacarpal V (left, subadult)
 MOR 1071-7-21-98-340 metacarpal V (right, adult)
 MOR 1071-7-7-98-87 metacarpal V (right, subadult)
 MOR 1071-8-2-98-464 metacarpal V (right, subadult)

Metatarsals

MOR 794 complete articulated metatarsals
 MOR 1071-7-10-98-104 metatarsal II (left, adult; crushed)
 MOR 1071-8-7-99-470 metatarsal II (right, subadult)
 MOR 1071-8-16-98-577 metatarsal II (left, subadult)
 MOR 1071-8-1-99-330 metatarsal II (right, subadult)
 MOR 1071-7-8-98-114 metatarsal III (left, adult)
 MOR 1071-7-26-98-425 metatarsal III (left, subadult)
 MOR 1071-8-1-99-332 metatarsal III (right, subadult)
 MOR 1071-7-22-98-173 metatarsal IV (right, adult)
 MOR 1071-7-16-98-246 metatarsal IV (right, subadult)
 MOR 1071-8-7-99-467 metatarsal IV (right, subadult)
 MOR 1071-7-7-98-89 metatarsal IV (left, subadult)
 MOR 1071-8-1-99-328-B metatarsal IV (right, subadult)

Manual Phalanges

MOR 794 complete pair of articulated hands
 MOR 1071-7-27-99-223 phalange II1 (right, adult)
 MOR 1071-7-6-98-81 phalange II1 (right, subadult)
 MOR 1071-8-2-99-364 phalange II1 (left, subadult)

MOR 1071-7-21-98-330 phalange II2 (left, large subadult)
MOR 1071-8-2-99-353 phalange II2 (left, subadult)
MOR 1071-8-1-99-310 phalange II2 (right, subadult)
MOR 1071-7-30-99-256 phalange III1 (right, subadult)
MOR 1071-7-9-98-125 phalange III1 (right, subadult)
MOR 1071-8-1-99-361 phalange III1 (left, subadult)
MOR 1071-6-30-98-11-A phalange III2 (left, subadult)
MOR 1071-7-27-98-427 phalange III2 (left, adult)
MOR 1071-8-12-98-537 phalange III2 (left, adult)
MOR 1071-8-3-99-365 phalange III2 (left, subadult)
MOR 1071-7-31-99-268 phalange III2 (right, large subadult)
MOR 1071-8-12-98-534 phalange IV1 (left, adult)
MOR 1071-? phalange IV1 (right, juvenile)
MOR 1071-8-1-99-321 phalange IV1 (right, adult)
MOR 1071-8-9-99-523-D phalange IV1 (left, subadult)
MOR 1071-7-8-98-159-A phalange IV2 (right, subadult)
MOR 1071-8-13-98-559-F phalange IV2 (right, adult)
MOR 1071-8-11-98-525 phalange IV2 (left, adult)
MOR 1071-7-30-99-237 phalange V1 (right, subadult)
MOR 1071-8-3-99-376 phalange V1 (left, subadult)
MOR 1071-7-27-99-227 phalange V1 (left, adult)
MOR 1071-7-17-99-108 phalange V2 (left, subadult)
MOR 1071-8-5-98-478 phalange V2 (left, subadult)
MOR 1071-7-21-98-341 phalange V2 (right, subadult)
MOR 1071-8-12-98-538 phalange V2 (left, small adult)
MOR 1071-7-20-98-519-L phalange V2 (right, subadult)
MOR 1071-8-7-99-460-C phalange V2 (right, adult)
MOR 1071-162-A phalange V3 (adult)
MOR 1071-7-27-98-452 phalange V3 (adult)
MOR 1071-8-2-99-354 phalange V3 (subadult)
MOR 1071-8-3-99-374 manual ungual II (right, adult)
MOR 1071-8-12-98-533 manual ungual II (right, adult)

MOR 1071-8-1-99-304 manual ungual II (right, subadult)
 MOR 1071-8-3-99-377 manual ungual II (left, subadult)
 MOR 1071-7-27-99-225 manual ungual II (left, adult)
 MOR 1071-8-13-98-554-B manual ungual III (left, adult)
 MOR 1071-8-1-99-303 manual ungual III (right, subadult)

Pedal Phalanges

MOR 794 complete articulated feet
 MOR 1071-8-25-99-421 phalange II1 (left, adult)
 MOR 1071-7-6-98-75 phalange II1 (right, subadult)
 MOR 1071-7-31-99-264 phalange II1 (left, subadult)
 MOR 1071-8-5-99-453 phalange II1 (left, subadult)
 MOR 1071-8-1-99-328-A phalange II1 (right, subadult)
 MOR 1071-7-16-98-213 phalange II2 (left, subadult)
 MOR 1071-7-8-98-127 phalange II2 (right, subadult)
 MOR 1071-8-98-561-A phalange II2 (right, subadult)
 MOR 1071-8-1-99-334 phalange II2 (right, subadult)
 MOR 1071-8-4-99-410-A phalange II2 (left, subadult)
 MOR 1071-7-20-98-324 pedal ungual II (right, subadult)
 MOR 1071-7-98-216 phalange III1 (left, subadult)
 MOR 1071-8-5-99-454 phalange III1 (right, subadult)
 MOR 1071-8-1-99-333 phalange III1 (right, subadult)
 MOR 1071-7-17-98-271 phalange III2 (right, subadult)
 MOR 1071-7-8-98-129 phalange III2 (left, subadult)
 MOR 1071-7-27-98-456 phalange III2 (left, subadult)
 MOR 1071-7-21-98-331-B phalange III2 (left, subadult)
 MOR 1071-7-22-98-294 phalange III2 (left, subadult)
 MOR 1071-7-17-98-270 phalange III3 (left, adult; pathologic)
 MOR 1071-8-4-98-475 phalange III3 (right, adult)
 MOR 1071-8-12-98-535 phalange III3 (left, subadult)
 MOR 1071-8-1-99-345 phalange III3 (right, subadult)
 MOR 1071-7-16-98-24 B-C pedal ungual III, uvenile

MOR 1071-7-31-99-273 pedal ungual III, subadult
MOR 1071-7-22-98-345 pedal ungual III, subadult
MOR 1071-7-26-98-439 pedal ungual III, subadult
MOR 1071-7-8-98-132 pedal ungual III, subadult
MOR 1071-8-10-98-515 pedal ungual III, adult
MOR 1071-7-8-98-124 phalange IV1 (left, adult)
MOR 1071-7-25-98-419 phalange IV1 (left, subadult)
MOR 1071-7-26-98-444 phalange IV1 (left, subadult)
MOR 1071-8-1-99-328-C phalange IV1 (right, subadult)
MOR 1071-7-10-98-166 phalange IV2 (left, adult)
MOR 1071-8-5-99-422 phalange IV2 (left, adult)
MOR 1071-8-12-98-532 phalange IV2 (left, subadult)
MOR 1071-8-3-99-382 phalange IV2 (left, subadult)
MOR 1071-8-1-99-336 phalange IV2 (right, subadult; articulated w/ MOR 1071-8-1-99-337)
MOR 1071-8-1-99-335 phalange IV2 (right, subadult)
MOR 1071-7-31-99-271 phalange IV2 (right, subadult)
MOR 1071-7-10-98-168 phalange IV2 (left, adult)
MOR 1071-8-1-99-337 phalange IV2 (right, subadult; articulated w/ MOR 1071-8-1-99-336)
MOR 1071-7-9-98-159 phalange IV2 (right, subadult)
MOR 1071-7-15-98-233-A phalange IV2 (left, subadult)
MOR 1071-7-18-98-282-A phalange IV2 (left, subadult)
MOR 1071-7-21-98-335 phalange IV2? (left, subadult)
MOR 1071-7-15-98-233-B phalange IV2 (right, subadult)
MOR 1071-7-10-98-168 phalange IV3 (left, adult)
MOR 1071-8-1-99-337 phalange IV3 (right, subadult, articulated w/ MOR 1071-8-1-99-336)
MOR 1071-7-9-98-159 phalange IV3 (right, subadult)
MOR 1071-7-15-98-233-A phalange IV3 (left, subadult)
MOR 1071-7-18-98-282-A phalange IV3 (left, subadult)
MOR 1071-7-21-98-335 phalange IV3? (left, subadult)
MOR 1071-7-15-98-233-B phalange IV3 (right, subadult)
MOR 1071-8-3-99-381 phalange IV4 (right, subadult)
MOR 1071-8-1-99-343 pedal ungual IV (right, subadult; broken right border)

MOR 1071-7-10-98-169 pedal ungual IV (right, subadult)
MOR 1071-8-1-98-460 pedal ungual IV (right, subadult)
MOR 1071-7-20-98-322 pedal ungual IV (right, subadult)
MOR 1071-7-17-98-279 pedal ungual IV (left, subadult)
MOR 1071-8-4-98-473 pedal ungual IV (left, subadult)
MOR 1071-6-23-99-9 pedal ungual IV (right, subadult)
MOR 1071-7-25-99-208-A pedal ungual IV (right, subadult)

Pubis

MOR 794
MOR 1071-7-16-98-243 left pubis, adult
MOR 1071-7-20-98-300 right pubis, subadult
MOR 1071-8-17-98-586 right pubis, partial, subadult
MOR 1071-8-20-98-597 right pubis, adult
MOR 1071-7-13-99-86 right pubis, subadult

Radius

MOR 794 articulated radii
MOR 1071-7-8-98-126 (left, subadult)
MOR 1071-7-14-98-204 (left, subadult)
MOR 1071-6-29-99-34 (left, subadult)
MOR 1071-7-15-98-257 (right, adult)

Scapula

MOR 794
MOR 1071-7-18-98-298 right scapula, adult
MOR 1071-7-8-98-115 left scapula, subadult
MOR 1071-7-9-98-153 left scapula, subadult
MOR 1071-7-15-98-233 right scapula, subadult
MOR 1071-8-9-99-523 left scapula, subadult, incomplete and broken blade
MOR 1071-8-4-99-411 right scapula, subadult

Sternals

MOR 794 articulated adult sternals

MOR 1071-7-12-99-71 left sternal, almost complete, and adult

MOR 1071-7-18-98-283 right sternal, subadult

MOR 1071-7-25-98-406 right sternal

MOR 1071-7-15-99-102B left sternal, fragment of the handle, subadult

Tarsals

MOR 794 articulated tarsals, adult

MOR 1071-6-30-98-43-E distal tarsal (large subadult or partial adult)

MOR 1071-7-20-99-158 right distal tarsal, adult

MOR 1071-8-1-98-359-B distal tarsal, subadult

MOR 1071-8-5-99-447-A distal tarsal, subadult

MOR 1071-8-1-99-328-D distal tarsal, subadult

MOR 1071-7-23-98-375 right astragalus, articulated w/ tibia; subadult

MOR 1071-8-10-98-516 left astragalus, subadult; crushed tibia with astragalus articulated

MOR 1071-7-13-99-270 right astragalus, adult

MOR 1071-8-1-99-331 right astragalus, subadult

MOR 1071-7-15-98-215-A left calcaneum, subadult

MOR 1071-7-30-99-257 right calcaneum, adult

MOR 1071-8-1-99-312 right calcaneum, subadult

MOR 1071-7-16-98-261 left calcaneum, adult

MOR 1071-8-5-99-447-E right calcaneum, subadult

MOR 1071-7-13-99-88 right calcaneum, subadult

Tibia

MOR 794 articulated adult tibiae

MOR 1071-8-10-98-516 left tibia, subadult; crushed w/ astragalus articulated

MOR 1071-7-23-98-375 right tibia, subadult; has articulated astragalus.

MOR 1071-8-10-98-514 left tibia, subadult

MOR 1071-8-1-99-328 right tibia, subadult

MOR 1071-8-5-99-445 left tibia, subadult

Ulna

MOR 794 articulated ulnae

MOR 1071-7-12-99-77 (left, subadult)

MOR 1071-8-1-98-359-J (right, adult)

MOR 1071-7-2-99-36 (left, adult)

MOR 1071-9-14-99-B (right, subadult)

MOR 1071-8-16-98-576 (left, subadult)

MOR 1071-6-17-99-4 (right, subadult)

MOR 1071-8-14-99-564 (right, subadult)

MOR 1071-8-13-99-557 (left, subadult)

MOR 1071-7-21-98-363 (left, subadult)

Specimens from a few other ornithopods other than *Brachylophosaurus*, available for comparison include material and casts housed in the Museum of the Rockies from other hadrosaurines, lambeosaurines, and iguanodontoids. The following were used for comparison and systematics:

Tenontosaurus tiletti

MOR 682. Complete articulated skull with articulated associated postcrania.

Iguanodon

Casts from the prementary, dentary, premaxilla, maxilla and neurocranium, plus several isolated teeth casts.

Maiasaura peeblesorum

MOR 547: Disarticulated appendicular, axial and a few cranial elements from several subadults. MOR 758 and MOR 005: Disarticulated cranial and postcranial elements from a bonebed.

Gryposaurus

MOR CAST 068 (RTMP 80.22.1). Articulated, partial skull. MOR 478: Several cranial and postcranial disarticulated elements.

Prosaurolophus blackfeetensis

MOR 454: Includes disarticulated cranial and postcranial material from several individuals, including mandibular, neurocranial and other elements of the skull, and appendicular and axial elements.

Edmontosaurus cf. annectens

MOR 003: Articulated skull.

Hypacrosaurus stebingeri

MOR 355: A few cranial and axial elements, and several appendicular elements, including subadults. MOR 549: Numerous cranial and postcranial elements.

APPENDIX B

MEASUREMENTS

Measurements

All measurements are taken in millimeters. Angles are given in degrees.

* Abrasion, breakage and/or other preservational defects affect the measure. In MOR 794

the symbol means preservational mediolateral compression (deformation).

~ Articulation of the specimen does not allow an accurate measurement, if any.

CRANIAL MEASUREMENTS (In alphabetical order)

Angular

<i>Specimens</i>	<i>L</i>	<i>H</i>	<i>W_c</i>	<i>W_r</i>
MOR 794 (left)	~	~	~	~
MOR 794 (right)	~	~	~	~
MOR 1071-7-31-99-276	130*	15	2.5	6
MOR 1071-7-20-99-146	120*	18	3	6
MOR 1071-8-20-96-597-C	*	14*	2.5	5*
PR 862 (left)	240*	22*	6	11
PR 862 (right)	*	24	6	12

L: Craniocaudal maximum length of the angular.

H_m: Maximum dorsoventral width of the angular (along the posterior segment).

W_c: Mediolateral minimum width of the angular along the caudal portion where the bone is dorsoventrally higher.

W_r: Mediolateral width of the angular at the convergence point of the two longitudinal ridges on the lateral surface.

Articular

<i>Specimens</i>	<i>L</i>	<i>H</i>	<i>W_q</i>	<i>W_c</i>
MOR 794 (left)	~	~	~	~
MOR 794 (right)	~	~	~	~
MOR 1071-8-13-98-554-A	47	25*	10	6
MOR 1071-7-18-98-282-B	31	17	5	2

L: Craniocaudal maximum length of the articular.

H: Dorsoventral depth of the of the articular, taken at the level of the maximum point of concavity of the dorsal border.

W_q: Mediolateral maximum width of the articulation surface for the quadrate.

W_c: Mediolateral maximum width of the caudal border of the articular.

Dentary

<i>Specimens</i>	<i>L</i>	<i>L_b</i>	<i>H_c</i>	<i>H_d</i>	<i>S</i>	<i>C_w</i>	<i>M_w</i>
MOR 794 (left)	515	~228	~	109	~	~	~
MOR 794 (right)	515	~205	~	103	~	~	~
MOR 1071-8-15-98-574	465*	267	200*	89	82	61	48
MOR 1071-7-13-99-93	435*	265	220*	93	70*	53*	48
MOR 1071-7-25-98-405	268*	190	135	62	47*	35*	30
MOR 1071-7-15-98-226	290*	173	136	63	53	42	34
MOR 1071-10-98-179	235*	170	144	55*	*	36*	41
MOR 1071-8-1-99-313	295*	179	137*	66	51	41	26
MOR 1071-8-8-44-484-E	*	*	102*	*	*	37	27*
PB 862 (left)	465	250	193*	107	75*	58	53
PB 862 (right)	435*	250	200	102	76*	60	52

Number of Tooth Positions

MOR 7-13-99-93 (adult) = 33

MOR 8-15-98-574 (adult) = 33

MOR 7-15-98-226 (subadult) = 33 probably (31-32 at least)

MOR 8-1-99-313 subadult = 26

MOR 7-10-98-179 (subadult) = 33 probably (30 at least)

MOR 7-25-98-405 (subadult) = 33.

MOR 794 left (adult) = 33-34.

MOR 794 = ~

PB 862 left (adult) = 35

PB 862 right (adult) = 35

L: Craniocaudal length of the dentary, from the caudal edge of the lateroventral face to the anterior border of the ventrally deflected rostral extreme. (Except in MOR 1071-8-8-44-484-E, which lacks most of the anterior half, the asterisk refers to the breakage of a small portion of the lateroventral, caudal sheet).

L_b: Craniocaudal maximum length of the dental battery, taken along the medial side and from the anterior edge of the anterior-most alveolus to the caudal border of the posterior-most one. (In the articulated MOR 794 the measure is incomplete and taken through the visible portion of the lateral tooth row).

H_c: Dorsoventral height of the dentary from the dorsal edge of the coronoid process of the ventral border of the bone.

H_d: Maximum dorsoventral depth of the dentary from the laterodorsal edge of the alveoli to the ventral border of the element.

S: Longitudinal length of the symphysis.

H_d: Maximum antero-caudal width of the expanded, dorsal portion of the coronoid process.

C_w: Maximum mediolateral width of the dorsal expanded portion of the coronoid process.

M_w: Maximum mediolateral width of the caudal exit of the Meckelian canal, measured between the internal sides of its medial and lateral walls.

Ectopterygoid

<i>Specimens</i>	<i>L</i>	<i>L_d</i>	<i>W</i>	<i>H_p</i>	<i>L_p</i>
MOR 794 (left)	~	~	~	~	~
MOR 794 (right)	~	~	~	~	~
MOR 1071-8-13-98-559E	114*	117*	59*	28	31*
MOR 1071-7-31-99-281-I	*	*	57*	26	24*

L: Anterolateral maximum length of the ectopterygoid, from its cranial edge to its posterior border, taken parallel to its dorsomedial edge.

L_d: Diagonal (oblique) maximum length of the ectopterygoid, from the dorsomedial corner of its cranial edge to the ventrocaudal corner of its posterior border.

W: Transversal (roughly mediolateral, with some dorsoventral component, perpendicular to L) maximum width of the caudal portion of the ectopterygoid (= width of the pterygoid contact).

L_p: Anterocaudal length of the dorsomedial border of the triangular, medial process of the ectopterygoid.

H_p: Dorsoventral (with a mediolateral component) extension of the triangular, medial process of the ectopterygoid, from its ventral apex to its dorsomedial edge.

Hvoids

<i>Specimens</i>	<i>L</i>	<i>L_a</i>	<i>H_m</i>	<i>H_c</i>	<i>W_a</i>	<i>W_c</i>
MOR 794 (left)	~	322	~	~15	~	6
MOR 794 (right)	~	310	~	~	~22	*
MOR 1071-7-16-98-248-K	285*	300*	57	15.5*	18*	7
MOR 1071-8-20-98-597-B	120*	127*	*	*	*	*
MOR 1071-7-15-98-209	95*	98*	*	*	*	*

L: Maximum craniocaudal length of the hyoid, from the ventral corner of the anterior end of the caudal extreme.

L_a: Craniocaudal length of the hyoids taken following the ventral curvature.

H_a: Dorsoventral maximum depth of the cranial end of the hyoids.

H_c: Maximum depth of the caudal end of the hyoids.

W_a: Maximum mediolateral thickness of the anterior end of the hyoids. (MOR 1071-7-16-98-248-K is affected by preservational mediolateral compression).

W_c: Maximum thickness of the caudal end of the hyoids.

Jugal

<i>Specimens</i>	<i>L</i>	<i>L_a</i>	<i>H_a</i>	<i>H₁</i>	<i>H_{po}</i>	<i>H₂</i>	<i>H_{qi}</i>
MOR 794 (left)	~295	~	92.5	41	188	80	66
MOR 794 (right)	320	~	93	41	~152*	79	65
MOR 1071-7-16-98-248-Q	270*	89*	87*	39	175	80	89*
MOR 1071-7-27-98-453	267*	73*	74	34	102*	76	64
MOR 1071-6-30-98-3	165*	42*	47*	29	*	*	*
MOR 1071-7-31-99-281-O	234*	56*	84	36	95*	76	64
PB 862 (left)	232*	51*	94	40	150*	86	72*
PB 862 (right)	200*	58*	76*	40	113*	*	*

L: Longitudinal anteroposterior length of the jugal, from the anterior tip to the caudal edge of the quadratojugal process.

L_a: Anteroposterior length of the anterior arrow-like process of the jugal, taken along its medial side, from the posterior border to the anterior tip.

H_a: Dorsoventral maximum depth of the anterior process of the jugal, taken across its posterior region.

H₁: Dorsoventral minimum depth of the segment comprised between the postorbital and the anterior processes.

H₂: Dorsoventral minimum depth of the segment comprised between the postorbital and the quadratojugal processes, from the dorsal edge to the ventral border of the boss.

H_{po}: Dorsoventral maximum height of the jugal from the dorsal tip of the postorbital process to its ventral edge.

H_{qj}: Dorsoventral maximum height of the jugal across the caudal edge of the quadratojugal process.

Lacrima

<i>Specimens</i>	<i>L</i>	<i>H_{md}</i>	<i>H_{cd}</i>	<i>W_c</i>	<i>W_a</i>
MOR 794 (left)	~121	~	~	~	~
MOR 794 (right)	~123	~	78	~	~
MOR 1071-7-7-98-86 (right)	132	~58	80	19	~5
MOR 1071-7-16-98-248 (left)	130*	60	~78	18	6*
MOR 1071-7-16-98-248 (right)	126*	~	~79	19	*
MOR 1071-7-10-98-171	133	*	58*	17	5
MOR 1071-6-30-98-9	54*	35*	*	14	*
MOR 1071-8-3-99-378	51*	*	54*	14	*
MOR 1071-8-5-99-447-G	80	40	54	15	3

L: Longitudinal (roughly craniocaudal) length of the lacrimal, from the caudal border to the anterior tip, measured along the ventral border.

H_{md}: Dorsoventral height of the lacrimal from the dorsal tip of the medial, dorsal process to the its ventral border.

H_{cd}: Dorsoventral height of the lacrimal from the dorsal tip of the caudal, dorsal process to the its ventral border.

W_c: Medirolateral maximum width of the caudal border of the lacrimal.

W_a: Medirolateral maximum width of the anterior, elongated segment of the lacrimal.

Maxilla

<i>Specimens</i>	<i>L</i>	<i>L_t</i>	<i>L_s</i>	<i>L_b</i>	<i>H</i>	<i>H_i</i>	<i>H_b</i>	<i>W</i>
MOR 794 (left)	~	~	~	~	~	~	~	~
MOR 794 (right)	~	~	~	~	~	~	~	~
MOR 1071-8-15-98-573	302	350*	113	270	105*	40	54	64
MOR 1071-8-13-98-559	305	365*	112	270	113*	41	54	60
MOR 1071-7-6-98-79	308	370*	115	284	114*	40	54	59
MOR 1071-8-13-98-554	180*	212*	84	174*	67*	21	34*	48
MOR 1071-8-5-99-447-N	234*	198	85	178	64*	20	30*	49

L: Craniocaudal length of the maxilla, from the blunt caudal border to the anterior tip of the anteroventral process.

L_t: Craniocaudal total maximum length of the maxilla, from the blunt caudal border to the anterior tip of the anterodorsal process.

L_s: Craniocaudal maximum length of the caudal, maxillary shelf, from the caudal edge of the lacrimal flange to the blunt caudal border of the maxilla.

L_b: Craniocaudal maximum length of the dental battery, measured along the ventral margin of the alveolar cavity.

H: Dorsoventral height of the maxilla, from the dorsal edge of the lacrimal flange to the ventral border of the dental battery (dental lamina).

H_j: Dorsoventral height from the ventral-most edge of the jugular process to the ventral border of the dental battery (dental lamina).

H_b: Dorsoventral maximum depth of the dental battery, from the dorsal border of the special foramina to the ventral border of the dental lamina.

W: Maximum mediolateral width of the maxilla, taken from the lateral-most salient point of the jugular process to the mediodorsal border of the element.

Nasal

<i>Specimens</i>	<i>L</i>	<i>L_c</i>	<i>W_c</i>	<i>H_s</i>	<i>H_n</i>
MOR 794 (left)	740	270	148	~	47*
MOR 794 (right)	746	270	148	~	46*
MOR 1071-7-7-98-86 (left)	510*	202	95	~	32
MOR 1071-7-7-98-86 (right)	515*	202	95	~	33
MOR 1071-7-16-98-248 (left)	556*	212	113	~	36*
MOR 1071-7-16-98-248 (right)	514*	212	113	~	40*
MOR 1071-7-12-99-76	*	*	*	28	*
PR 862	*	268	142	~	*

L: Longitudinal length of the nasals. Taken along a straight line through the laterodorsal side, from the anteroventral tip of the anterodorsal process to the caudal end of the crest.

L_c: Craniocaudal length of the nasal crest. The anterior, reference point is taken at the level of the caudal border of the dorsal foramen of the prefrontal.

W_c: Mediolateral width of the nasal crest, at the level of the anterior border of the supratemporal fenestra.

H_s: Maximum dorsoventral thickness of the medial border of the nasal (counterpart suture). (Taken in the partial disarticulated specimen, where it corresponds to the central body of the nasal).

H_n: Maximum dorsoventral thickness of the anterodorsal process of the nasal, caudal to the lateral bowl-shaped bulge. (MOR 794 is affected by mediolateral distortion).

D_f: Mediolateral maximum separation between the dorsal nasal groove and the lateral edge of the element. (MOR 794 is affected by mediolateral preservational compression).

Neurocranial complex (braincase, frontals and parietal)

<i>Specimens</i>	<i>FL</i>	<i>FW</i>	<i>FL_n</i>	<i>FW_n</i>	<i>P_l</i>	<i>P_w</i>	<i>W_{p-o}</i>	<i>C_l</i>	<i>Pt_w</i>	<i>B_w</i>	<i>B_l</i>	<i>L_l</i>
MOR 794	~	~	~	~	~	~	~	~	~	~	~	~
MOR 1071-7-7-98-86	~98	73	~	~	~	~	38	99	120*	65	95	66
MOR 1071-7-16-98-248	~96	73	~	~	~	~	42	76	124	85	94	65
MOR 1071-7-13-99-87-I	100	50	70	63	82	35	36	~	~	~	~	48
MOR 1071-6-30-98-4	*	60*	*	85*	*	*	*	*	*	*	*	*
PR 862	~108	90	~	~	~	~	47*	*	*	*	*	72*

FL: Maximum anteroposterior length of one frontal (in MOR 1071-7-13-99-87-I is taken from the parietal joint to the anterior tip of the prefrontal processes. *: in articulated specimens only the exposed surface is measured, not the prefrontal process).

FW: Maximum mediolateral width of one frontal; taken on the ventral side, from the frontal suture to the orbital margin.

FL_n: Maximum anteroposterior length of the striated articulation surface for the nasal.

FW_n: Maximum mediolateral width of the nasal articulation surface, taken across both frontals.

P_l: Maximum anteroposterior length of the parietal.

P_w: Minimum mediolateral width of the parietal.

W_{p-o}: Mediolateral width across the presphenoids-orbitosphenoids contact, around the olfactory canal.

C_l: Anteroposterior length of the cultriform process of the parasphenoid.

Pt_w: Mediolateral width across both pterygoid processes of the basisphenoid.

B_w: Mediolateral maximum width across basal tubera of the basioccipital-basisphenoid.

B_l: Anteroposterior length of the posteroventral region of the braincase, from the posterior border of the occipital condyles to the anterior border of the basal tubera.

L_l: Mediolateral length of one of the laterosphenoids, from the dorsal border of the trigeminal foramen to the postorbital joint.

Palatine

<i>Specimens</i>	<i>L</i>	<i>L_f</i>	<i>H_v</i>	<i>H_l</i>	<i>W</i>	<i>J</i>
MOR 794 (left)	~	~	~	~	~	~
MOR 794 (right)	~	~	~	~	~	~
MOR 1071-7-16-98-248-S	153*	61*	81	82	17	31
MOR 1071-7-26-99-221	*	42*	83	82	18	25*
MOR 1071-7-19-99-139	*	*	*	*	16	*
MOR 1071-8-13-98-559-G	*	*	*	*	18	*
MOR 1071-8-15-98-568	*	*	*	*	*	*
MOR 1071-8-15-98-567	*	*	83*	73*	19	26

L: Anteroposterior maximum length of the palatine, from the tapering caudoventral end to the anterodorsal edge of the anterolateral process.

L_r: Anteroposterior length of the dorsal border of the anterodorsal flange of the palatine.

H_v: Dorsoventral maximum depth of the palatine, taken from the dorsal border of the anterodorsal flange to the ventral edge of the element.

H_j: Dorsoventral maximum depth of the palatine, taken from the dorsal border of the anterodorsal flange to the ventral corner of the anterolateral process.

W: Mediolateral maximum width of the ventral grooved border of the palatine (which occurs at its anterior end).

J: Length of the long axis of the ellipsoidal section of the jugular articulating surface of the anterolateral process.

Postorbital

<i>Specimens</i>	<i>L</i>	<i>H_j</i>	<i>W_m</i>	<i>W_j</i>	<i>H_m</i>
MOR 794 (left)	~195	160	~	~	~
MOR 794 (right)	~190	158	~	~	~
MOR 1071-7-7-98-86 (left)	172	145	55	26	~
MOR 1071-7-7-98-86 (right)	175	140	54*	25	~
MOR 1071-7-16-98-248 (left)	180	153	48	26	~
MOR 1071-7-16-98-248 (right)	180	160	46	26	~
MOR 1071-6-30-98-4 (left)	*	*	51*	*	20
MOR 1071-6-30-98-4 (right)	106*	53*	57	16	20
MOR 1071-7-13-99-87-L	110	64*	55*	10.5	15
MOR 1071-7-13-99-87-G	108	64*	58	11	16
PR 862	173	*	57	*	~

L: Anterocaudal length of the postorbital, from the caudal border of the squamosal process to the anterior edge of the prefrontal process.

H_j: Dorsoventral (longitudinal) length of the postorbital along the jugal process, from the dorsal border of the element to the anteroventral tip of the process.

W_m: Distance from the anterior end of the prefrontal process to the medial end of the parietal articulation, along the frontal joint border.

W_j: Mediolateral width of the jugal process at the level ventral to the synovial articulation for laterosphenoid.

H_m: Dorsoventral maximum depth of the frontal articulation (medial side).

Predentary

<i>Specimens</i>	<i>M</i>	<i>Lp_l</i>	<i>Lp_h</i>	<i>Lp_w</i>	<i>L</i>	<i>H</i>	<i>K_h</i>	<i>K_w</i>	<i>P_h</i>	<i>P_w</i>	<i>P_l</i>
MOR 794	200*	122*	~29	~	~	~	~	~	56	50*	~
MOR 1071-7-28-98-299	215	102	28	41	35	49	67*	6	40*	55*	2

M: Mediolateral width of the predentary, taken along the anterodorsal border.

Lp_l: Craniocaudal maximum length of the lateral processes of the predentary.

Lp_h: Dorsoventral maximum depth of the lateral processes of the predentary.

Lp_w: Mediolateral maximum width of the lateral processes of the predentary.

L: Craniocaudal maximum width of the main (mediolateral) body of the predentary.

H: Dorsoventral depth of the main (mediolateral) body of the predentary, taken at the center (parasagittal plane), from the ventral border, at a point between the two linguoid processes to the dorsal edge of the central pair of smallest, cone-like processes.

K_h: Dorsoventral depth of the keel-like process of the posterior side of the predentary.

K_w: Mediobasal width of the ventral third of the keel-like process, on the posterior side of the predentary.

P_h: Dorsoventral length of the linguoid, anteroventral processes of the predentary. The dorsal (upper) limit is taken at the boundary between the overlapping (attached) dorsal border and the ventral half of the anterior face of the predentary.

P_w: Mediobasal width of the linguoid, anteroventral processes of the predentary, taken between the lateral edges of both processes.

P_t: Craniocaudal thickness of the linguoid, anteroventral processes of the predentary.

Prefrontal

<i>Specimens</i>	<i>L</i>	<i>L_{al}</i>	<i>L_{am}</i>	<i>W_v</i>
MOR 794 (left)	238	~58	~	~
MOR 794 (right)	231	~50	~	~
MOR 1071-7-7-98-86 (left)	183	60	~	*
MOR 1071-7-7-98-86 (right)	186	37*	*~	15
MOR 1071-7-16-98-248 (left)	198	55*	50	16*
MOR 1071-7-16-98-248 (right)	205	60	~	23*
MOR 1071-8-2-99-346	101*	30*	28*	12
MOR 1071-8-5-99-447-G	113	33	33	15

L: Maximum longitudinal length of the prefrontal, from the anteroventral to the caudal edge (excluding the caudomedial process). The value is taken along the dorsal surface and following the curvature of the element.

L_{al}: Anterocaudal maximum width of the anteroventral end of the prefrontal, taken along the lateral side.

L_{am}: Anterocaudal maximum width of the anteroventral end of the prefrontal, taken along the medial side (from the caudal border of the posteromedial, dorsally-projecting process to the anterior edge).

W_c: Mediobasal width of the caudal border of the prefrontal, taken across the dorsal surface (excluding the nasal and frontal articulation areas, as well as the caudomedial process).

W_v: Mediobasal width of the ventral end of the prefrontal, taken across the caudal end.

Premaxilla

<i>Specimens</i>	<i>L_d</i>	<i>L_v</i>	<i>W</i>	<i>H</i>	<i>W_d</i>	<i>W_v</i>
MOR 794 (left)	480^	524	210	~	~	~
MOR 794 (right)	~470^	535	185*	~	~	~
MOR 1071-7-7-98-84	200*	236*	120	26	7	47
MOR 1071-7-5-98-66	190*	217*	*	44	7	*
MOR 1071-7-23-99-179	*	*	110*	*	7*	40*

L_d: Longitudinal length of the premaxilla along the dorsocaudal process, taken from the anteromedial corner of the bone to the caudodorsal tip of the process. (^ In MOR 794, the complete specimen is measured following the dorsal curvature).

L_t : Longitudinal length of the premaxilla taken from the anteromedial corner to the caudal edge of the ventrocaudal process, above the dorsal surface of the element.

W : Medirolateral maximum width of the anterior edge of the premaxilla, from the anteromedial corner to the lateroventral one.

H : Maximum height or distance between the ventral border of the dorsocaudal process and the medial, dorsal border of the ventrocaudal process. (~ in MOR 794 makes reference to the obscuring of the lateral side of the dorsocaudal process by the articulating nasal).

W_d : Maximum mediolateral thickness of the dorsocaudal process of the premaxilla

W_v : Medirolateral width of the ventrocaudal process at the level of the indentation for the reception of the anterodorsal process of the maxilla. Taken from the caudomedial corner of the indentation to the lateral edge of the ventrocaudal process.

* In MOR 794 the symbol means preservational mediolateral compression (deformation).

MOR 1071-7-7-98-84 is dorsoventrally crashed (i.e. compressed by deformation).

MOR 1071-7-5-98-66 is mediolaterally crashed (compressed by deformation).

Pterygoid

<i>Specimens</i>	L_{pl-dq}	L_{dq-vq}	L_{vq-e}	L_{e-pl}	D_{b-pl}	D_{e-dq}	D_{b-vq}	D_{b-e}	W_e	L_{dq}	L_{pl}
MOR 794 (left)	~	~	~	~	~	~	~	~	~	~	~
MOR 794 (right)	~	~	~	~	~	~	~	~	~	~	~
MOR 1071-7-23-98-387	201*	140	125	185*	154*	155	134	101	53	130	120*
MOR 1071-8-1-99-315	164*	99*	72*	153	138	80	78*	81	33*	~	~128
MOR 1071-8-14-99-A	*	*	87*	*	*	*	92	79	37	*	*
PB 862	*	*	123*	*	*	*	115*	80*	*	*	*

L_{pl-dq} : Distance from the tip of the palatine ramus to the tip of the dorsal quadrate wing of the pterygoid.

L_{dq-vq} : Distance from the tip of the dorsal quadrate wing to the articulating extreme of the ventral quadrate process of the pterygoid.

L_{vq-e} : Distance from the articulating extreme of the ventral quadrate process to the tip of the anteroventrolateral end of the ectopterygoid process.

L_{e-pl} : Distance from the anteroventrolateral end of the ectopterygoid process to the tip of the palatine ramus of the pterygoid.

D_{b-pl} : Distance from the medial, central buttress to the tip of the palatine ramus.

D_{b-dq} : Distance from the medial, central buttress to the tip of the dorsal quadrate wing.

D_{b-vq} : Distance from the medial, central buttress to the articulating extreme of the ventral quadrate process.

D_{b-e} : Distance from the medial, central buttress to the anteroventrolateral end of the ectopterygoid process.

W_e : Medirolateral width of the pterygoid at its center, from the medial buttress to the center of the lateral side of the element at the same level than the former.

L_{dq} : Length of the dorsal quadrate wing, from the ventral end of the small lateral ridge (that terminates in a small anterodorsal salient process) on the lateral side of the pterygoid to the articulating dorsolaterocaudal tip of the wing.

L_{pt} : Length of the palatine ramus, from the ventral end of the small lateral ridge (that terminates in a small anterodorsal salient process) on the lateral side of the pterygoid to the anterodorsal tip of the ramus.

Quadrate

<i>Specimens</i>	<i>H</i>	<i>H_{qi}</i>	<i>L_f</i>	<i>D_l</i>	<i>D_m</i>	<i>V_l</i>	<i>V_m</i>
MOR 794 (left)	~320	102	~	39	~	53	~
MOR 794 (right)	~324	105	~	39	~	49	~
MOR 1071-8-13-98-559D	325	107	92	40	19	49	55
MOR 1071-6-30-98-1	215*	71	62	26	11	31*	30*
MOR 1071-8-1-99-315	207*	67*	73*	27*	11*	20*	23*
MOR 1071-7-6-99-44C	*	*	*	*	*	46	58
MOR 1071-8-8-99-484O?D?	217*	61*	*	20*	12*	21*	29*
PB 862 (right)	310*	105	110*	39	24	*	*

H: Dorsoventral maximum length of the quadrate, from the ventral to the dorsal border.

H_{qi}: Dorsoventral width of the quadratojugal notch.

L_f: Anterocaudal maximum length of the pterygoid flange.

D_l: Anterocaudal width of the dorsal end of the quadrate.

D_m: Mediolateral width of the dorsal end of the quadrate.

V_l: Anterocaudal width of the ventral end of the quadrate.

V_m: Mediolateral width of the ventral portion of the quadrate, from its laterocaudal side to the mediocaudal border of the process for the articular.

Quadratojugal

<i>Specimens</i>	<i>H</i>	<i>L_{av}</i>	<i>L_{ad}</i>	<i>W</i>
MOR 794 (left)	106	~	~	~
MOR 794 (right)	100	~	~	~
MOR 1071-7-15-98-218-A	97	65	90	9
MOR 1071-8-9-98-509	98*	51*	88*	10
MOR 1071-8-3-99-366	60	45	53	5

H: Dorsoventral maximum length of the quadratojugal.

L_{av}: Length of the anteroventral edge of the quadratojugal.

L_{ad}: Length of the anterodorsal edge of the quadratojugal.

W: Mediolateral maximum thickness of the quadratojugal.

Sclerotic plates

<i>Specimens</i>	<i>L</i>	<i>T</i>	<i>T_r</i>	<i>T_h</i>
MOR 1071-8-98-484-A—a	24*	12*	4*	8
MOR 1071-8-98-484-A—b	20*	13*	3*	10

L: Longitudinal length of the sclerotic plate.

T: Transversal (perpendicular to L) maximum width of the sclerotic plates.

T_r: Transversal (perpendicular to L) maximum width of the recessed area of the medial side.

T_h: Transversal (perpendicular to L) maximum width of the mediolaterally higher (non-recessed) area of the medial side.

Skull general measurements

<i>Specimens</i>	<i>L</i>	<i>L_b</i>	<i>H</i>	<i>W</i>	<i>L_n</i>	<i>H_n</i>	<i>L_o</i>	<i>H_o</i>	<i>H_{if}</i>	<i>W_{if}</i>	<i>M_l</i>	<i>L_{sf}</i>
MOR 794	830	710	390	230*	240	70	130	190	243	80	102	~
MOR 1071-7-7-98-86	590*	*	*	250	*	*	132	*	*	*	*	90
MOR 1071-7-16-98-248	610*	*	*	250	*	*	128	*	*	*	*	100
PR 862	*	*	*	250*	*	*	125*	*	*	*	*	*

L: Anteroposterior length of the skull, from the anterior border of the premaxilla to the level of the posterior edge of the paroccipital process. (The MOR 1071 skull roofs are missing the premaxillae and the anterior nasals).

L_b: Basal length of the skull, from the anterior edge of the prementary to the posterior end of the articular.

H: Dorsoventral height of the skull from the top of the parasagittal plane of the nasal crest to the ventral border of the dentary, following a vertical line that bisects the coronoid process.

W: Mediolateral width of the skull, at the level of the posterodorsal edge of the orbits (In PR 862 the measurement is estimated).

L_n: Length of the longest axis of the external naris.

H_n: Length of the shorterst dimension of the external naris, perpendicular to L_n.

L_o: Anteroposterior interior diameter of the orbital cavity, along a bisecting horizontal line.

H_o: Length of the longest axis of the orbital cavity.

H_{if}: Length of the long side of the infratemporal fenestra (from its anterodorsal apex to the anteroventral edge).

W_{if}: Width of the infratemporal fenestra perpendicular to the length of its long axis, from the apex formed by quadratojugal-quadratoquadrate joint.

M: Dorsoventral maximum diameter of the opening formed by the jugal, quadratojugal, quadratoquadrate and the surangular.

L_{sf}: Maximum length of the longitudinal axis of the supratemporal fenestra.

* In MOR 794, that symbol indicates that the skull is mediolaterally compressed by sedimentary compaction.

Splénial

<i>Specimens</i>	<i>L</i>	<i>H_a</i>	<i>H_m</i>	<i>H_c</i>
MOR 794 (left)	~	~	~	~
MOR 794 (right)	~	~	~	~
MOR 1071-8-8-99-484-A	101*	30	15	18*
MOR 1071-8-6-98-483	175*	45	27	25*
MOR 1071-7-31-99-281-R	175*	44	27	26

L: Maximum craniocaudal length of the splénial.

H_a : Dorsoventral maximum depth of the anterior region of the splenial.

H_m : Dorsoventral maximum depth of the splenial at its middle craniocaudal length.

H_c : Dorsoventral maximum depth of the caudal border of the splenial.

Squamosal

<i>Specimens</i>	L_{po}	W_{pa}	L_{prq}	L_{poq}	L_{spr}	L_{qc}	H_{qc}	H_{pa}
MOR 794 (left)	~	~	41	108*	~	55	~	~
MOR 794 (right)	~	~	~	114*	~	~	~	~
MOR 1071-7-7-98-86 (left)	~113	~85	33	92*	~	50	32	~
MOR 1071-7-7-98-86 (right)	~115	~87	32	110*	~	48	32	~
MOR 1071-7-16-98-248 (left)	~118	~88	35	104*	~	51	37*	~
MOR 1071-7-16-98-248 (right)	~117	~84	32*	104*	~	52	34	~
MOR 1071-7-13-99-87H	77	50	17	56*	29	31	19	26*
MOR 1071-8-5-99-458	77	50	16	67	26	31	20	28
MOR 1071-6-30-98-4	*	*	*	*	23*	31*	21*	29*
PR 862 (left)	~114	*	36	*	*	52	32*	*

L_{po} : Anterocaudal, longitudinal length of the postorbital process, from the posterolateral corner of the squamosal to the anterior tip of the process.

W_{pa} : Mediolateral width of the squamosal, including the parietal process, taken from the laterodorsal border of the element to the medial border of the process.

L_{prq} : Longitudinal length of the prequadratic process, taken from its ventrolateral tip to the lateral edge of the dorsal surface of the postorbital process. (* MOR 794 is distorted by mediolateral compression of the specimen.)

L_{poq} : Longitudinal length of the postquadratic process, taken from its ventrolateral tip to the lateral edge of the posterodorsal corner of the squamosal.

L_{spr} : Longitudinal (anteromedial to laterocaudal) length of the supraoccipital articulation border of the squamosal.

L_{qc} : Anterocaudal width of the quadrate cotylus, taken from the posterodorsal side of the postquadratic process to the dorsolateral edge of the bisecting ridge of the prequadratic process. (As The postquadratic process is more robust in the adults, especially its caudolateral corner, which is anterocaudally thicker, the measure in them does not extend until the caudolateral border, but until a mid point of it thickness).

H_{qc} : Dorsoventral height of the quadrate cotylus, from its dorsolateral border to its ventrolateral edge.

H_{pa} : Dorsoventral height of the crescentic parietal articulation.

Surangular

<i>Specimens</i>	L	W_a	W_m	H_a	C_w	R_h	H_m
MOR 794 (left)	~	~	~	~	~	~	~
MOR 794 (right)	~	~	~	~	~	~	~
MOR 1071-7-25-98-405-A	178*	71*	55*	98	32	20*	32
MOR 1071-7-27-99-230	170*	69*	59	96	27*	18*	34
MOR 1071-8-8-99-484-B	125*	59*	35	55*	24	15	23*
MOR 1071-7-24-99-192-A	109*	39*	33	*	28	17	26

L : Craniocaudal length of the surangular, from the anterior expanded border to the posterior edge of its caudal process.

W_a : Maximum mediolateral width of the anterior expanded region of the surangular.

W_m: Maximum mediolateral width at a point anterior and adjacent to the quadrate articulation, where the lateral border of the surangular becomes convex in dorsal and ventral views.

H_a: Dorsoventral height of the anterior, ascending process of the surangular, from its dorsal border to the ventral surface of the element (this last, horizontal surface, is taken at the medial ventral border of the articulation, medial surface for the angular).

R_h: Maximum dorsoventral height of the medial ridge of the surangular.

H_m: Dorsoventral depth of the surangular across the ridge medial to the angular articulation and that contributes to the medial side of the splenial articulation.

C_w: Maximum (not mediolateral, but oblique) width of the caudal process of the surangular.

AXIAL MEASUREMENTS (In alphabetical order)

Atlas

<i>Specimens</i>	<i>C_{lc}</i>	<i>C_{ll}</i>	<i>C_w</i>	<i>C_h</i>	<i>PO_l</i>	<i>PO_w</i>	<i>A_w</i>	<i>A_h</i>	<i>H</i>
MOR 794	32	50	82	28	30/31	15/15	83	67	105
MOR 1071-7-21-98-350	*	*	*	*	*/33	*/19	*	66*	*
MOR 1071-6-24-99-18	34	36*	89*	24	*	*	*	*	*

C_{lc}: Proximodistal length of the intercentrum, taken along the ventral side following a bisecting line.

C_{ll}: Proximodistal maximum length of the lateral sides of the intercentrum (taking the highest value of the two sides).

C_w: Mediobasolateral maximum width of the intercentrum.

C_h: Dorsoventral thickness of the intercentrum, taken at the center, at mid mediobasolateral width.

PO_l: Proximodistal length of the facet of the postzygapophyses, taken along the major, longitudinal axis of the "ellipse". The value at the left side of the bar corresponds to the left postzygapophysis and the right to the right one.

PO_w: Mediobasolateral width of the facet of the postzygapophyses, taken along the minor, transversal (perpendicular to PO_l) axis of the "ellipse". The value at the left side of the bar corresponds to the left postzygapophysis and the right to the right one.

A_w: Mediobasolateral maximum width of the neural arch.

A_h: Dorsoventral height of the neural arch, from its lateral suture with the intercentrum to the craniodorsal border.

H: Dorsoventral height of the atlas, taken from the ventral side of the centra to the dorsal surface of the neural arch.

Axis

<i>Specimen</i>	<i>C_l</i>	<i>C_h</i>	<i>C_w</i>	<i>PO_l</i>	<i>PO_w</i>	<i>PO_h</i>	<i>Pr_l</i>	<i>Pr_w</i>	<i>A_l</i>	<i>A_w</i>	<i>H</i>	<i>F</i>
MOR 794	84	56*	58*	75	72*	54*	35/38	19/15	65	32*	133	79
MOR 1071-7-21-98-331-A	*	*	*	*	*	*	*	*	65*	*	*	63

C_l: Proximodistal maximum length of the centrum, taken along the lateral sides.

C_h: Dorsoventral maximum height of the caudal end of the centrum.

C_w: Mediolateral maximum width of the caudal end of the centrum.

Po_l: Proximodistal length of the postzygapophyseal process, taken along its major, longitudinal axis, from their caudoventral end of the articular facet to the caudal edge of the flange of the neural spine (the largest value of the two).

Po_w: Mediolateral maximum width between the lateral borders of the postzygapophyseal processes.

Po_h: Dorsoventral maximum thickness of the postzygapophyseal processes (the largest value of the two), including the epipophyses.

Pr_l: Maximum proximodistal length of the prezygapophyses, across the articular facet. The value at left of the bar corresponds to the left prezygapophysis and the right to the right one.

Pr_w: Maximum mediolateral width of the prezygapophyses, across the articular facet. The value at left of the bar corresponds to the left prezygapophysis and the right to the right one.

A_l: Proximodistal length of dorsal "roof" the neural arch, measured laterally.

A_w: Mediolateral width between the caudolateral borders of the neural arch, taken at its mid dorsoventral height.

H: Dorsoventral height of the vertebra, taken from the caudoventral edge of the centrum to the caudodorsal point where the postzygapophyses converge.

F: Proximodistal length of the flange of the neural spine.

Ribs - Dorsals

<i>Specimens</i>	<i>R</i>	<i>R_{wh}</i>	<i>R_{wm}</i>	<i>R_{wd}</i>
MOR 794 - 1 st	420	28.5	22	10
MOR 794 - 2 nd	635	37	33	11
MOR 794 - 3 rd	845	44	35	26
MOR 794 - 4 th	995	52	37	32
MOR 794 - 5 th	1090	49	34	40
MOR 794 - 6 th	1194	52	36	44
MOR 794 - 7 th	1185	56	38	42*
MOR 794 - 8 th	1090*	54	33	44*
MOR 794 - 9 th	1015	50	33	32
MOR 794 - 10 th	888	37	30	24
MOR 794 - 11 th	645	35	30	16
MOR 794 - 12 th	410	34	33	17
MOR 794 - 13 th	325	35	33	20
MOR 794 - 14 th	>240*	24	22	~
MOR 794 - 15 th	242	22	22	~
MOR 794 - 16 th	217	21.5	22	~
MOR 794 - 17 th	198	21	17	~
MOR 794 - 18 th	173	19	13	~

(Only the left elements are measured, since the right side of the body of MOR 794 was not accessible at that time.)

R: Longitudinal length of the rib, from the ventral tip to the proximal, articulating extreme of the tuberculum.

R_{wh}: Proximodistal width of the rib shaft at a level just distal to the head, perpendicular to R.

R_{wm}: Width of the rib shaft at mid R and perpendicular to this last dimension.

R_{wd}: Proximodistal width of the distal end of the rib.

Bonebed ribs:

R: Longitudinal length of the rib, from the ventral tip to the proximal, articulating extreme of the tuberculum.

S_{wm}: Width of the rib shaft at mid R and perpendicular to this last dimension.

S_{tp}: Mediobasal thickness of the proximal portion of the rib shaft at a level just distal to the head, perpendicular to R and S_{wm}.

S_{tm}: Mediobasal thickness of the rib shaft at mid R, perpendicular to R and S_{wm}.

S_{td}: Mediobasal thickness of the rib shaft at its distal end, perpendicular to R and S_{wm}.

C: Mediobasal (longitudinal) length of the capitulum, from the lateral side of the rib to the articular surface for the parapophysis. The measure is taken along a longitudinal bisecting line of the capitulum.

C_w: Dorsoventral (transversal) width of the capitulum near the mid longitudinal length.

C_t: Mediobasal thickness of the capitulum, taken at its mid longitudinal length and perpendicular to C_w.

T: Dorsoventral maximum height of the tuberculum, taken from its dorsal end to the level of the dorsal border of the capitulum (not perpendicular to the articular surface).

*Breakage and other effects of preservation does not allow or affect the measure. In **R** and **S_{td}** it refers to the incompleteness of the distal end, and sometimes, also of the proximal portion.

^ Pathological thickening.

<i>Specimens</i>	<i>R</i>	<i>S_{wm}</i>	<i>S_{tp}</i>	<i>S_{tm}</i>	<i>S_{td}</i>	<i>C</i>	<i>C_w</i>	<i>C_t</i>	<i>T</i>
MOR 1071-7-12-99-81	735*	45	52	21	12*	150	42	15	28
MOR 1071-7-15-98-218	*	*	55	*	*	160	45	16	29
MOR 1071-7-10-99-53	776*	39	32	16	5*	153	36	15	22
MOR 1071-7-20-99-155	520*	19	32	14	10*	*	*	*	*
MOR 1071-7-11-99-68	346*	22	21	8	2*	86	17	9	12
MOR 1071-8-20-98-597-A	228*	20	*	13	2*	*	*	*	*
MOR 1071-7-15-98-231	220*	16	22	6	3*	78	15	8	10
MOR 1071-7-27-98-448	174*	18	19	8	4*	78	13	8	10
MOR 1071-7-28-98-446	174*	18	15	6	3	73	13	8	11
MOR 1071-7-17-98-274	153*	13*	12	5	1*	60	10	10	13
MOR 1071-7-21-98-349	172*	16	11	6	1*	58*	10	9	9*
MOR 1071-6-30-98-17	271*	19	*	6	3*	*	*	*	*
MOR 1071-6-30-98-18	262*	18	*	6	4*	*	*	*	*
MOR 1071-7-20-99-155-A	171*	19	*	5	1	*	*	*	*
MOR 1071-7-16-98-248-R	*	*	44	*	*	165*	40	14	14
MOR 1071-7-16-98-248-T	*	*	42	*	*	142*	25	19^	*
MOR 1071-7-3-98-61	482*	16	20	7.5	3*	100*	*	8.5	*
MOR 1071-7-6-98-78	620*	38	48	13	7	146	35	16	22
MOR 1071-7-22-98-327	493*	35	*	11	6*	*	*	*	*
MOR 1071-8-12-98-506	575*	23	26	11	6*	98*	21	7	10
MOR 1071-7-14-98-191	610	20	34	11	3	92*	23	9	12
MOR 1071-7-6-98-69	372*	21	34	22*	*	94*	24	9	10
MOR 1071-7-19-99-153	680*	38	36	20	8*	89*	35	11	*

Vertebrae – Caudals (bonebed specimens)

<i>Specimens</i>	<i>C_l</i>	<i>C_h</i>	<i>C_w</i>	<i>Pr</i>	<i>Po</i>	<i>A_l</i>	<i>A_w</i>	<i>N_h</i>	<i>N_{lb}</i>	<i>N_{ld}</i>	<i>H</i>
MOR 1071-8-4-98-466	54	100*	95	21/20	20/20	42	40	233*	34	46*	342*
MOR 1071-8-4-98-455	54	76	70	20/20	19/18	41	31	212	26	39	255
MOR 1071-8-3-99-388	58	59	65	15/16	*/*	32	33	120	13	17	132
MOR 1071-8-15-98-564	51	65	61	16/15	15/16	35	29	153	20	27*	208
MOR 1071-7-15-99-103	54	64	59	17/17	15/16	31	26	157	15	23*	181
MOR 1071-8-1-98-359-H	52	59	61	16/16	16/16	31	25	150*	16	27*	182*
MOR 1071-8-1-98-359-I	50.5	62	56	16/14*	15/16	29	24	164	13	22*	180
MOR 1071-7-15-98-218-D	47	53	49	*/*	*/*	*	*	*	*	*	*
MOR 1071-7-15-98-218-B	45	48*	47	10/9	9/9	25	20	128*	11	18	153*
MOR 1071-7-15-98-218-C	29	23	28	4/*	-	11	10	19*	3	*	35.5*
MOR 1071-7-10-98-173-B	26	20	23	4/3*	-	10	11	21	2	3	31
MOR 1071-7-15-98-215-B	35.5	35	36	5/5	-	15	14	30*	4	8	54*
MOR 1071-8-2-99-356	35	35	34	4/3	-	13	15	54	6	8	75
MOR 1071-7-30-99-242	31	27	31	3/3	-	12	13	18*	4	*	40*
MOR 1071-7-10-98-173-A	28	24	26	*/*	-	10*	12	32*	3	4*	38*
MOR 1071-7-30-99-294	34	32	31	*/*	-	16	12	41	5	6	55
MOR 1071-7-19-98-295	31	28	32	-	-	12	12	14*	3	*	39*
MOR 1071-7-30-99-240	24	19	22	-	-	9	12	12	3	3	30
MOR 1071-7-30-99-241	32	27	32	-	-	13	13	20*	5	*	43*
MOR 1071-7-21-98-347	28	23	26	*	-	10*	12*	*	*	*	*
MOR 1071-30-99-239	26	22	25	-	-	10	10	24*	3	*	37*
MOR 1071-7-31-99-277	22	19	22	-	-	*	*	*	*	*	*
MOR 1071-7-18-98-296	55	81	75	18/18	18/19	31	33	220*	30	41*	285*
MOR 1071-8-13-98-559-C	52	66	62	12/13	17/15	31	28	163	17	28	210
MOR 1071-7-30-99-247	*	*	*	12/13	*/13	31	28	153*	15	21*	*
MOR 1071-8-2-99-349	*	*	*	16/17	17/20	29	28	136*	21	24*	*
MOR 1071-7-14-99-100-B	*	*	*	*	*	*	*	185*	27	38*	*
MOR 1071-7-19-99-121	*	*	*	15/15	14/14	31	24	146*	21	27*	*
MOR 1071-7-25-98-411	48	57	54	12/12	14/13	23	22	141	11	17	163*
MOR 1071-7-16-98-248-A	41	41	46	6/8	-	18	19	88*	8	10*	94
MOR 1071-7-16-98-248-N	44	48	49	7/6	8/7	20	20	49*	12*	*	87*
MOR 1071-7-16-98-248-F	44	46	45	7/6	-	20	19	91*	8	11*	113*
MOR 1071-7-21-98-337	36	35	39	-	-	16	19	35*	7	*	57*
MOR 1071-7-16-98-248-O	35	34	36	-	-	15	15	56	6	7	67
MOR 1071-7-1-98-25	31	31	34	-	-	14	12	43	4	3	53
MOR 1071-7-26-98-426	33	30	37	-	-	*	*	*	*	*	*
MOR 1071-7-9-98-165-A	32	29	33	-	-	13	13	46	3	7	56
MOR 1071-7-17-98-266	32	27	35	-	-	14*	15	21*	5	*	42*
MOR 1071-7-26-98-447	30	25	31	-	-	11	14	23*	5	*	44*
MOR 1071-7-20-98-312	31	27	31	-	-	11	13	34*	3	5*	41*
MOR 1071-8-13-98-560	26	21.5	27	-	-	7	9	14	3	*	34*
MOR 1071-7-21-98-348	18	12	16	-	-	*	*	*	*	*	*
MOR 1071-7-18-98-290	17	11	17	-	-	*	*	*	*	*	*
MOR 1071-?	10	7	9	-	-	*	*	*	*	*	*
MOR 1071-7-6-98-77	55	91	86	16/18	18/18	39	37	234	34	51	310
MOR 1071-7-9-98-147	54	85	78	16/17	18/20	35	32*	223	32	45	285
MOR 1071-7-9-98-149	54	96	95	19/*	18/19	38	40	230	34	51	338
MOR 1071-7-6-98-78-C	53	78	71	16/16	19/18	36	32	197	26	40	269
MOR 1071-7-9-98-195	53	68	62	17/17	18/18	33	28	175	19	31	208
MOR 1071-7-9-98-143	52	61.5	60	16/16	21*/22*	30	27	143*	15*	22*	150
MOR 1071-7-6-98-78	55	79	71	17/18	18/18	37	34	135*	28	*	206*
MOR 1071-7-6-98-78-B	47	49	52	13/13	12/13	21	21	129	10	15	139
MOR 1071-7-6-98-78-A	32	28	32	*	-	12	14	23*	4	*	47*
MOR 1071-7-15-98-230	51	61	55	18/18*	*	*	24	*	*	*	*

MOR 1071-7-10-98-177	45	51	49	14/14*	8.5/9	25	23	116*	12	18	127*
MOR 1071-7-9-98-163	50	57	54	13/14	12/12	25	22	56*	11	*	114*
MOR 1071-6-30-98-11-B	*	*	*	*	*	*	*	139*	22*	32*	*
MOR 1071-6-30-98-11	*	*	*	*	*	*	*	113*	16*	21*	*
MOR 1071-6-30-98-20	*	*	*	22/22	19/19	37	35	223*	29	35*	*
MOR 1071-6-30-98-19	*	*	*	17/18	18/18	34	27	159*	19	29*	*
MOR 1071-8-7-98-493	*	*	*	15/15	15/17	29	21	142*	19	30*	*
MOR 1071-6-30-98-12	*	*	*	17/17	17/17	30	26	148*	16	22*	*

C_l: Craniocaudal maximum length of the centrum.

C_h: Dorsoventral maximum height of the caudal end of the centrum. Includes the facets for the chevrons.

C_w: Medirolateral maximum width of the caudal end of the centrum.

Po: Maximum diameter of the articular facet of the postzygapophyses. The value on the left of the bar refers to the left postzygapophysis and the right to the right.

Pr: Maximum diameter of the prezygapophyses, across the articular facet. The value at left of the bar corresponds to the left prezygapophysis and the right to the right one.

A_l: Proximodistal length of the neural arch, along the mid dorsoventral height of the lateral sides.

A_w: Medirolateral width of the neural arch, taken at its mid craniocaudal length.

N_h: Longitudinal height of the neural spine, taken from the proximodorsal surface of the transverse process to the dorsocaudal end of the spine.

N_{lb}: Proximodistal extent of the neural spine, taken at just over the level of the postzygapophyses. When no postzygapophysis is present, the taken measure is the minimum of the base of the spine, right over the neural arch.

N_{ld}: Proximodistal extent of the neural spine, taken at its dorsal end.

H: Dorsoventral height of the vertebra, taken from the ventral edge of the centrum to the top of the neural spine, along a vertical line (not parallel to the longitudinal length of the spine).

(-): No such a feature is present in the specimen. In the case of the diapophyses, it is also applied when there is trace, but very reduced, to just a bumpy feature. In the case of the prezygapophyses the symbol is applied when there is not prezygapophyseal facet.

Vertebrae – Caudals (articulated MOR 794)

<i>Specimens</i>	<i>C_l</i>	<i>C_h</i>	<i>N_h</i>	<i>N_{lb}</i>	<i>N_{ld}</i>	<i>D_w</i>	<i>D_l</i>	<i>A_l</i>
MOR 794 – 1 st	74	~76	~42	~	72*	~	~	~
MOR 794 – 2 nd	75	~72*	~395*	~	71*	~	~	~
MOR 794 – 3 rd	*	*	~435	~	62*	~	~	~
MOR 794 – 4 th	80	~132	*	*	*	~90*	42	~
MOR 794 – 5 th	82	~134	~432	~	70	~91*	39	~
MOR 794 – 6 th	79	~130	~410	~	70	~83*	37	~
MOR 794 – 7 th	79	~131	~405	~	68	~75*	34	~
MOR 794 – 8 th	80	~129	~390	~	64	~63*	32	~
MOR 794 – 9 th	81	~128	~376	~	65	~60	32	~
MOR 794 – 10 th	89*	~127	~355	~	63	~57*	33	~
MOR 794 – 11 th	84	~123	~336	~	59	~61	34	~
MOR 794 – 12 th	84	~120	~328	~	59	~52*	32	~
MOR 794 – 13 th	87	~117	~303	~	52	~54	32	~
MOR 794 – 14 th	81	~119	~290	~34	58	~43	32*	~
MOR 794 – 15 th	80	~113	~250*	34	*	~34	30	~

MOR 794 – 16 th	81	108	222*	35	45*	32	29	51
MOR 794 – 17 th	80	108	252	37*	46*	23	26	51
MOR 794 – 18 th	81	106	275	28	48*	12	~21	50
MOR 794 – 19 th	79	100	275	~29	45	-	-	50
MOR 794 – 20 th	80	94	280	~31	46	-	-	51
MOR 794 – 21 st	80	95	262	27	47*	-	-	54
MOR 794 – 22 nd	79	93	258	26	45	-	-	49
MOR 794 – 23 rd	81	93	250	25	43	-	-	46*
MOR 794 – 24 th	81	89	252	26	42	-	-	50
MOR 794 – 25 th	80	88	205*	25	37*	-	-	46
MOR 794 – 26 th	79	87	*	23	*	-	-	45
MOR 794 – 27 th	~78	87	220*	21	37*	-	-	*
MOR 794 – 28 th	75	85	212*	21	30	-	-	41
MOR 794 – 29 th	74	84	132*	21	27*	-	-	39
MOR 794 – 30 th	72	80	106*	18	26*	-	-	39
MOR 794 – 31 st	74	79	100*	14	*	-	-	39
MOR 794 – 32 nd	72	77	*	*	*	-	-	34*

Only the left side is accessible in vertebrae 4th through 24th, and only the right side from the 1st to the 3rd, and the 25th to the 29th caudal.

C_l: Anterocaudal maximum length of the centrum. (In the fused vertebra of the sacral region, it is taken from the middle of the rim at the junction of two fused centra to the next one.)

C_h: Dorsoventral height of the centrum.

N_h: Longitudinal height of the neural spine, taken from the proximodorsal surface of the transverse process to the dorsocaudal end of the spine.

N_{lb}: Proximodistal extent of the neural spine, taken at just over the level of the postzygapophyses. When no postzygapophysis is present, the taken measure is the minimum of the base of the spine, right over the neural arch.

N_{ld}: Proximodistal extent of the neural spine, taken at its dorsal end.

D_w: Medirolateral length of the transverse processes. Here the measure refers only to the visible portion of the diapophyses, from the lateral side of the dorsal border of the centrum; the base is covered by sand and/or ossified tendons.

D_l: Anteroposterior width of the transverse processes, taken at its mid medirolateral extension.

A_l: Proximodistal length of the neural arch, along the mid dorsoventral height of the lateral sides.

(-): Absence of the feature or extreme reduction.

Vertebrae - Cervicals

<i>Specimens</i>	<i>C_l</i>	<i>PO_l</i>	<i>PR_l</i>	<i>PR_w</i>	<i>A_l</i>	<i>A_w</i>	<i>H</i>	<i>D_l</i>
MOR 794 3 rd	106*	120	40*/36*	26*/28*	72*	38*	122*	37*/35*
MOR 794 4 th	106*	124	43*/48*	20*/25*	61*	46*	117*	38*/43*
MOR 794 5 th	109*	129	37*/39*	26*/30*	54*	54*	121*	45*/47*
MOR 794 6 th	~	~130	37*/35*	~	~	63*	~120*	~
MOR 794 7 th	~	130	32*/33*	~	56*	74*	~130*	~
MOR 794 8 th	~	129	37*/35*	~	55*	78*	~132*	~
MOR 794 9 th	~	129	37*/34*	~	54*	~80*	~136*	~
MOR 794 10 th	~	125	38*/~	~	56*	~	~139*	~

MOR 794 11 th	~	~132	38*/~	~/~	~	~	~143*	~/~
MOR 794 12 th	~	~120	~42	~	~	*	~160	~
MOR 794 13 th	~	~124	~	~	~	~	~	~
MOR 1071-7-15-98-221	107*	135	33/37	33/36	40	88	103*	82*/85*
MOR 1071-7-15-98-223	85*	129	*32	*34	47.5	88	111	*77
MOR 1071-7-23-98-368	107*	145*	30/39	25/26.5	60	53	106	43/43
MOR 1071-7-26-98-436	95	123	34/*	29/*	50	70	126*	*79
MOR 1071-6-30-98-14	56*	87	22/21	23/21	31	52	82*	46*/53
MOR 1071-8-19-98-588	84*	124	31/34	36/35	43	70	132*	62*/94
MOR 1071-8-12-98-519-A	*	124	*28*	*34	48	75*	94	*68
MOR 1071-8-12-98-519-B	103.5	125	38/34	34/34	50	69	117	67*/75
MOR 1071-7-10-98-189	84	101	36/35	40/38	44	63	157	116/108*
MOR 1071-7-8-98-118	47*	82	19/21	30/32	26	45	96	67*/74*

C_i: Proximodistal maximum length of the centrum, taken along the ventral side in the MOR 794 specimens, and laterally in the MOR 1071 specimens.

PO_i: Proximodistal length of the postzygapophyseal process, taken along its major, longitudinal axis, from their caudal end to the craniodorsal edge of the neural arch (the largest value of the two). In cervicals 11 and 12 the length is taken from the caudal end to the cranial edge of the neural spine.

PR_i: Maximum proximodistal length of the prezygapophyses, across the articular facet. The value at left of the bar corresponds to the left prezygapophysis and the right to the right one.

PR_w: Maximum mediolateral width of the prezygapophyses, across the articular facet. The value at left of the bar corresponds to the left prezygapophysis and the right to the right one.

A_i: Proximodistal length of dorsal "roof" the neural arch, along the bisecting mid line described by the neural spine.

A_w: Mediolateral width between the caudolateral borders of the neural arch, taken at its mid dorsoventral height.

H: Dorsoventral height of the vertebra, taken from the caudoventral edge of the centrum to the caudodorsal point where the postzygapophyses converge.

D_i: Mediolateral length of the diapophyses, taken from the craniomedial edge of the neural arch until its articulation with the cervical rib. The value at left of the bar corresponds to the left diapophysis and the right to the right one.

* Mediolateral deformation in MOR 794, crushing mainly in the 1071 specimens, bone missing and other preservational effects affect the measure.

Vertebrae – Dorsals (bonebed)

<i>Specimens</i>	<i>C_i</i>	<i>C_h</i>	<i>C_w</i>	<i>A_i</i>	<i>A_w</i>	<i>N_h</i>	<i>N_i</i>	<i>D_i</i>	<i>D_h</i>	<i>H</i>
MOR 1071-7-6-99-45	82	80	81	61	55	190*	70	114*/90*	25/26	340*
MOR 1071-7-13-99-85	63	85	73	48	43	177	48	77/81	12/11	300
MOR 1071-7-3-98-65	65	53	49	47	29*	80*	45	71*/58*	15/14	185*
MOR 1071-8-1-99-402	72*	45*	43*	48	40	92*	46	53*/61*	15/16	145*
MOR 1071-7-15-98-219	70	58	57	47	36	104*	50	50*/64*	15/15	200*
MOR 1071-8-18-98-593	91	93	79	70	53*	202*	81	82*/100	22/24	350*
MOR 1071-7-17-99-111	67	64*	75*	*	*	*	*	*	*	*
MOR 1071-7-15-98-218E	57	99	72*	*	*	*	*	*	*	*
MOR 1071-7-3-98-56	71	57*	56*	47	39	*	*	64*/*	15/*	*
MOR 1071-7-16-98-255	60	44	40	*	*	*	*	*	*	*

C_j : Proximodistal maximum length of the centrum.

C_h : Dorsoventral maximum height of the caudal end of the centrum.

C_w : Medirolateral maximum width of the caudal end of the centrum.

A_j : Proximodistal length of the neural arch, along the mid dorsoventral height of the lateral sides.

A_w : Medirolateral width of the neural arch, taken near the proximal end.

N_h : Dorsoventral height of the neural spine, taken from the proximodorsal surface of the transverse process to the dorsal end of the spine.

N_l : Proximodistal extent of the neural spine, taken at a point located at mid N_h .

D_l : Medirolateral length of the diapophyses, taken from the lateral side of the base of the neural spine to the lateral end of the transverse process. The value at left of the bar corresponds to the left diapophysis and the right to the right one.

D_h : Dorsoventral thickness of the diapophyses, taken at a point located at mid D_l . The value at left of the bar corresponds to the left diapophysis and the right to the right one.

H : Dorsoventral height of the vertebra, taken from the ventral edge of the centrum to the dorsal end of the neural spine.

Vertebrae – Dorsals (MOR 794)

<i>Specimens</i>	<i>L</i>	<i>L_{nsp}</i>	<i>H_c</i>	<i>H_{nsp}</i>	<i>M_a</i>	<i>M_b</i>	<i>T</i>
MOR 794 – 1 st	~	17*	~	78*	~	~	39
MOR 794 – 2 nd	~	21*	~	116	~	~	41
MOR 794 – 3 rd	~	24	~	~180	~	~	40
MOR 794 – 4 th	~	29	~	~185	~	~	42
MOR 794 – 5 th	~	41''	~	~125	~	~	47
MOR 794 – 6 th	~	84	~	~183	~	~	49
MOR 794 – 7 th	~	87*	~	~	~	~	~45
MOR 794 – 8 th	~	80*	~	~	~	~	~
MOR 794 – 9 th	~	94	~	~	~	~	~
MOR 794 – 10 th	~	86	~	~	~	~	~
MOR 794 – 11 th	~	86	~	~>195	~	~	~
MOR 794 – 12 th	~	93	~	~>215	~	~	~
MOR 794 – 13 th	~	82*	~	~>215	~	~	~
MOR 794 – 14 th	*	*	~	~260	~	~	42
MOR 794 – 15 th	82	82	~	~265	~	~	40.5
MOR 794 – 16 th	86	82	~115	~270	~	~	36
MOR 794 – 17 th	85	83	~120	~280	~	~	35
MOR 794 – 18 th	84	78	~121	~285	~	~63	36

L : Anterocaudal maximum length of the centrum. In fused vertebra, it is taken from the middle of the rim at the junction of two fused centra to the next one.

L_{nsp} : Proximodistal length of the dorsal border of the neural spines.

H_c : Dorsoventral height of the centrum.

H_{nsp} : Dorsoventral, longitudinal height of the neural spines. In caudally inclined neural spines the measure is not dorsoventral, but along its longitudinal dimension, parallel to its cranial and caudal borders.

M_a : Medirolateral thickness of the centra taken along their anterior rim.

M_p : Medirolateral thickness of the centra taken along their posterior rim.

T : Craniocaudal width of the transverse process, taken at its mid medirolateral projection.

From dorsals 5th to the 1st, the antero-caudal dimension of the neural spine is taken in a line parallel to the parasagittal plane, because those spines are not squared at the top, but blade. D-shaped; so in fact, the dorsal rim in this spines is a point.

Vertebrae - Sacrals

<i>Specimens</i>	<i>L</i>	<i>L_{nsp}</i>	<i>M_a</i>	<i>M_b</i>	<i>H</i>	<i>H_{nsp}</i>	<i>T</i>
MOR 794 – 1 st	84	~74	~44	~50	132	295	38*
MOR 794 – 2 nd	88	87	~50	~108	~122	~300	36
MOR 794 – 3 rd	87	89	~108	~47	~75	~303	35
MOR 794 – 4 th	74	89	~47	~46	~75	~	36
MOR 794 – 5 th	70	94	~46	~48	~65	~	44
MOR 794 – 6 th	70	96	~48	~	~69	~37.7	37
MOR 794 – 7 th	89	97	~	~76	~70	~39	35
MOR 794 – 8 th	94	~96	~76	~63	~73	~40.5	27
MOR 794 – 9 th	92	91*	~63	~95	~71	~41	21

Other Measurements:

ANTEROCAUDAL LENGTH of the SACRUM: 780 mm.

MEDIOLATERAL OPERTURE OF THE VENTRAL GROOVE AT JUNCTION OF SACRALS 7th & 8th: 32.5 mm.

ANTEROCAUDAL LENGTH of the GROOVE: 230 mm. W/shallow end: 285 mm.

ANTEROCAUDAL length of the ILIAC BLADE through the ventral border: 460 mm.

DORSOVENTRAL height of the iliac blade: 81 mm.*

ANTEROCAUDAL thickness of the overgrowth rim at junction of sacra 1st and 2nd: 77 mm.

MEDIOLATERAL dimension of the overgrowth rim at junction of sacra 2nd and 3rd: ~108 mm.

L: Antero-caudal maximum length of the centrum. In fused vertebra, it is taken from the middle of the rim at the junction of two fused centra to the next one.

L_{nsp}: Antero-caudal length of the dorsal border of the neural spines.

M_a: Medi-lateral thickness of the centra taken along their anterior rim.

M_p: Medi-lateral thickness of the centra taken along their posterior rim.

H: Dorso-ventral height of the centrum.

H_{nsp}: Dorso-ventral height of the centrum.

T: Antero-posterior width of the transverse process, taken at its mid medi-lateral projection.

APPENDICULAR MEASUREMENTS (In alphabetical order)

Carpals

Pebble-like carpal

<i>Specimen</i>	<i>D</i>
MOR 794 right	2

Tetrahedral carpal

<i>Specimens</i>	<i>H</i>	<i>P</i>	<i>MD</i>	<i>LD</i>
MOR 794 left	~	34	34	27.5
MOR 794 right	~	37	34	28
MOR 1071-8-12-98-537A	43	36	34	29
MOR 1071-7-8-98-130	23*	21	20.5	12

H: Dorsoventral (approx.) height of the carpal, from the base (dorsal face) to the ventral tip of the tetrahedron constituted by the element morphology.

P: Mediolateral (approx.) length of the proximal border of the dorsal face of the carpal.

MD: Length of the mediodistal side of the dorsal face of the carpal.

LD: Length of the laterodistal side of the dorsal face of the carpal.

Coracoid

<i>Specimens</i>	<i>L</i>	<i>L'</i>	<i>A</i>	<i>W_s</i>	<i>W_g</i>	<i>W_p</i>	<i>S</i>	<i>G</i>	<i>F</i>
MOR 794 (left)	~105	177	100	~	82	88	80	61	14
MOR 1071-7-30-99- 258A	98*	*	66*	43	40	46	53*	42*	10
MOR 1071-6-30-98-11-C	83*	*	*	*	*	*	*	*	10*
MOR 1071-8-9-99-523-B	86*	*	63*	45*	32*	42*	49*	40*	10
MOR 1071-7-31-99-281W	129*	145*	95*	*	60*	*	*	60*	18*

L: Dorsoventral length from the lateral border of the scapular facet to the distal (ventral) edge of the bone (anterior to the projection of the ventral process), perpendicular to the border of the facet for the scapula.

L': Dorsoventral length from the lateral border of the scapular facet to the distal extreme of the ventral process of the coracoid.

A: Length of the coracoid from the lateral border of the glenoid facet to the anterior extreme of the cranial process of the bone, perpendicular to the former.

W_s: Mediolateral thickness of the scapular facet, at a mid point of its antero-caudal (longitudinal) length.

W_g: Mediolateral thickness of the humeral facet, at a mid point of its longitudinal length.

W_p: Mediolateral thickness of the proximal edge of the coracoid, taken along the meeting border between the glenoid and the scapular facets.

S: Antero-caudal length of the scapular facet, along a bisecting line.

G: Longitudinal (perpendicular to mediolateral) length of the humeral facet or glenoid, along a bisecting line.

F: Diameter of the foramen of the coracoid. (In more elliptical foramens, the given value is the length intermedial between the major and the minor axis of the ellipse).

Femur

<i>Specimens</i>	<i>L</i>	<i>L₄</i>	<i>L_h</i>	<i>H₄</i>	<i>H_{mdc}</i>	<i>H_{ldc}</i>	<i>H_h</i>	<i>H_g</i>	<i>W_p</i>	<i>W_d</i>	<i>L_l</i>
MOR 794 left	~1120	435	95	255	285	~250	145	~	~	160	~
MOR 794 right	1290	440	95	250*	290	282	150	225	180	135	89
MOR 1071-7-21-98-331	1140	310	65	~230	230	160*	112*	145*	212	197	105
									*	*	
MOR 1071-7-1-98-??	750	225	70*	138	180*	171	80*	165*	135	95	90*
									*		
MOR 1071-8-5-99-451	825	210	58	146	200	192	79	137*	144	133	73*
MOR 1071-8-1-99-327	825	230	64	151	205	201	84	135	148	135	76
MOR 1071-7-31-99-282	750	230	50*	135	190	170	69*	120*	156	132	75

L: Proximodistal length of the femur, from the distal border of the medial distal condyle to the proximal edge of the greater trochanter (projected on the medial side if taken on that view).

L₄: Proximodistal length of the fourth trochanter, along the medial side.

L_h: Proximodistal length the medial face of the head (excluding any medial projection of the ventromedial slope).

H₄: Anterocaudal length of the distal, D-shaped portion of the fourth trochanter plus the shaft; taken from the caudal tip of the apex of the D shape to the anterior border of the shaft, in a straight line perpendicular to the proximodistal axis..

H_{mdc}: Maximum anterocaudal length of the medial condyle, along the medial face.

H_{ldc}: Maximum anterocaudal length of the lateral condyle.

H_h: Maximum anterocaudal length of the femoral head.

H_g: Maximum anterocaudal length of the greater trochanter.

W_p: Maximum mediolateral width of the proximal end of the femur, from the medial border of the head to the lateral border of the greater trochanter.

W_d: Maximum mediolateral width of the distal end of the femur, from the medial border of the medial condyle to the lateral border of the lateral condyle.

L_l: Maximum proximodistal length of the lesser trochanter. This is taken measuring the proximodistal length of the cleft separating the lesser from the anterior border of the greater trochanter along the lateral side.

~ In the case of *L*, measure taken from proximal border on medial head to distal border of medial condyle, because of articulation of the specimen does not allow observation of the lateral side (obscured by the ischium).

Fibula

<i>Specimens</i>	<i>L</i>	<i>W_p</i>	<i>W_d</i>	<i>W_s</i>	<i>M_p</i>	<i>M_d</i>	<i>M_s</i>
MOR 794 left	1020	173	115	63	50	~	~48
MOR 794 right	1030	~150	105	~	45	67	~48
MOR 1071-8-12-98-519	635	107*	65*	40*	26	42	28
MOR 1071-7-23-99-181	642	100	61	38	36	45	27
MOR 1071-8-10-98-516-A	>540*	>95*	60*	42*	28*	38*	25*
MOR 1071-7-7-98-88	945	155	106*	58	43	53	44
MOR 1071-7-23-98-374	610*	>90*	69	36*	32	42	30
MOR 1071-8-1-99-329	683	105	72*	38	43	46	35
MOR 1071-8-5-99-430	690	103*	76	39	42	48	33

L: Proximodistal length of the fibula, from the proximal border to the distal one.

W_p: Anterocaudal length of the proximal border of the fibula.

W_d: Anterocaudal length of the distal border of the fibula, taken on the lateral side.

W_s: Anterocaudal length of the shaft, at mid length of *L*, taken on the lateral side.

M_p: Maximum mediolateral thickness of the proximal border of the fibula, taken on proximal view.

M_d: Maximum mediolateral thickness of the distal border of the fibula, taken on distal view (if articulated, measured on lateral side).

M_s: Medirolateral length of the mid shaft of the fibula, taken at a point located at mid length of *L*.

Humerus

<i>Specimens</i>	<i>L</i>	<i>L_d</i>	<i>W_d</i>	<i>W_s</i>	<i>P[^]D</i>	<i>W_p</i>	<i>W_{ds}</i>
MOR 794 left	590	300	110	78	129	157	113
MOR 794 right	600	300	113	79	132	144	112
MOR 1071-7-20-98-325	550	280	103	76	133	158	121
MOR 1071-7-23-99-178	350	175	60	40	123	86	71
MOR 1071-7-14-98-202	368	170	58	42	132	78	70
MOR 1071-7-14-98-192	365	167	60	43	130	92	77

L: Length of the long axis of the humerus, perpendicular to the lines defined by the termini of the proximal and ulnar (the slightly more distally salient) condyles.

L_d: Length of the deltopectoral crest, as used by Trexler (1995), measured between the bisectors of the curvatures. Equivalent to the *L₁* of Trexler (1995).

W_d: Proximal width of Trexler (1995), the minimum transverse distance at the midpoint of *L_d*.

W_s: Lateral distal shaft diameter, the minimum distance between the cranioventral and dorsocaudal borders of the shaft in the distal half of the humerus.

P[^]D: Angle between the proximal and distal halves of the humerus, that is, the angle described by the distal corner of the deltopectoral crest in passing to the distal shaft of the bone, along the cranioventral border.

W_p: Proximalmost, maximum width of the humerus, taken on the cranioventral view of the element and from the cranioventral corner of the deltopectoral crest to the dorsocaudal opposite corner of the bone.

W_{ds} : Width of the humerus distal end, this is, the transversal in craniomedial view distance from the medialmost profile of the ulnar condyle to the lateralmost profile of the radial condyle.

Ilium

<i>Specimens</i>	<i>L</i>	<i>L_{pr}</i>	<i>L_{po}</i>	<i>L_c</i>	<i>H</i>	<i>H'</i>	<i>H''</i>	<i>h1</i>	<i>h2</i>	<i>A</i>	<i>B</i>	<i>C</i>
MOR 1071-8-2-98-469	1050*	560*	340*	300	192	237	172	80	130	130*	~	~
MOR 1071-7-15-98-215	730*	340*	236*	205	148	175	136	63	92	93	80*	92
MOR 794 (left)	1153	520	380	330	225	285	200	102	145	98	90*	97
MOR 794 (right)	1156	520	360	315	230	300	225	98	145	93	89*	103
MOR 1071-7-10-99-50	762	354	230	220	120	127	104	69	86	117	80	35
MOR 1071-7-31-99-285	615*	260*	287*	189*	145	165	160	45	83	56	90*	120*

L: Anteroposterior length; taken from the cranialmost tip of the preacetabular process to the caudalmost edge of the postacetabular one, as defined by Trexler (1995).

L_{pr}: Length of the preacetabular process following its anteroventral slope, along the dorsal border, from the level of the cranialmost tip to the inflexion point where that slope changes of tilt into the central body of the ilium.

L_{po}: Length of the postacetabular process, from the caudoventral corner of the ischial peduncle to the caudoventral projection of the caudalmost point of the caudal edge of the process.

L_c: Anteroposterior length of the central body of the ilium, from the anteroventral corner of the pubic peduncle to the caudoventral one in the ischial peduncle.

H: Distance between the dorsalmost point of the acetabular arch (roof) and the dorsal border of the ilium, in a perpendicular line to *L*.

H': Distance between the cranioventral corner of the pubic peduncle and the dorsal border of the ilium, in a normal line to *L*.

H'': Distance between the caudoventral corner of the ischial peduncle and the dorsal border of the ilium, in a normal line to *L*.

h1: Width of the preacetabular process, taken at mid length, perpendicular to *L_{pr}*.

h2: Width of the postacetabular process, taken at mid length, perpendicular to *L_{po}*.

A: Dorsolateral extension of the antitrochanter (from the medialmost boundary of the ilium), taken perpendicular to *L* through a bisecting line.

B: Anteroposterior length of the lateral edge of the antitrochanter.

C: Minimum distance between the lateral edge of the antitrochanter and the ventral border of the ilium (laterally projected).

Ischium

<i>Specimens</i>	<i>L</i>	<i>L_b</i>	<i>L_s</i>	<i>W_{ip}</i>	<i>W_s</i>	<i>W_d</i>	<i>S[^]IP</i>	<i>W_i</i>	<i>W_p</i>
MOR 794	1120	261	859	280	68	370	150	82	66
MOR 1071-8-9-99-522	530*	141	389*	168	40	200	145	~50	~
MOR 1071-7-14-98-200	556*	144	412*	157	36	210	145	60	50
MOR 1071-7-15-98-207	470*	~120	350*	~164	~34	~165	140	~	~
MOR 1071-7-12-98-182	564*	145	419*	~	36	212	150	62	~
MOR 1071-7-19-99-154B	~460	~120	340*	~	40	~	140	~	~

L: Anteroposterior length; taken from the anterior edge of the pubic peduncle to the caudalmost end of the shaft.

L_b: Anterocaudal length of the ischial expanded region (blade), taken from the anterior edge of the pubic peduncle caudally to a point perpendicular to the caudodorsal edge of the obturator process.

L_s: Anterocaudal length of the ischial shaft, taken from a point perpendicular to the caudodorsal edge of the obturator process to the caudal end of the shaft.

W_{ip}: Perpendicular (to the anterocaudal direction of the ischial shaft) distance from the caudodorsal corner of the iliac process to the ventral edge of the pubic peduncle.

W_s: Maximum width of the shaft, that is, the maximum dorsomedial-ventrolateral length of the major axis of the ellipse described by the shaft cross section.

W_d: Diagonal distance: the length from the anterodorsal edge of the iliac process to the caudoventral edge of the obturator process.

S[^]IP: Angle between the stright caudoventral projection of the slope of the iliac peduncle and the stright anterodorsal projection of the slope of the proximal portion of the ischial shaft (from the level of the caudal edge of the obturator process).

W_i: Length of the anterodorsal border of the iliac process.

W_p: Length of the dorsoventral border of the pubic peduncle.

Metacarpal II

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sp}</i>	<i>H_{sc}</i>	<i>H_{sd}</i>	<i>W_{sp}</i>	<i>W_{sc}</i>	<i>W_{sd}</i>	<i>L</i>
MOR 794 left	39	21	33	~	34	24	30	~14	~20	~12	207
MOR 794 right	38	20	32	~	33	25	26	~	~20	~13	208
MOR 1071-8-16-98-578	38	23	33	18	30	27	25	16	22	15.5	180
MOR 1071-7-23-98-386	24	12	18	10	22	17	18	10	11	10	122*
MOR 1071-7-20-98-317	30	18	22	11	32	21	19	19	17	10	129
MOR 1071-8-2-99-363	22	12	19*	9	22	12	20	10	11	8	124
MOR 1071-7-8-98-110	22	10	18	8	21	13	15	9	10	8	116

P_h: Dorsoventral maximum height of the proximal end of metacarpal II.

P_w: Medirolateral maximum width of the proximal end of metacarpal II.

D_h: Dorsoventral maximum height of the distal end of metacarpal II.

D_w: Medirolateral maximum width of the distal end of metacarpal II.

H_{sp}: Dorsoventral height of the shaft of metacarpal II, at a mid point of the proximal third of the bone.

H_{sc}: Dorsoventral height of the shaft of metacarpal II, at a mid point of the proximodistal length of the bone (L).

H_{sd}: Dorsoventral height of the shaft of metacarpal II, at a mid point of the distal third of the bone.

W_{sp}: Medirolateral width of the shaft of metacarpal II, at a mid point of the proximal third of the bone.

W_{sc}: Medirolateral width of the shaft of metacarpal II, at a mid point of the proximodistal length of the bone (L).

W_{sd}: Medirolateral width of the shaft of metacarpal II, at a mid point of the distal third of the bone.

L: Proximodistal length of metacarpal II

Metacarpal III

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sp}</i>	<i>H_{sc}</i>	<i>H_{sd}</i>	<i>W_{sp}</i>	<i>W_{sc}</i>	<i>W_{sd}</i>	<i>L</i>
MOR 794 left	~	~34	~	44	~	~	~	30	28	39	280
MOR 794 right	~	35	~42	42	~30	~	32	29	24	36	280
MOR 1071-7-31-99-294	27	20	26	29	21	21	19	17.5	17	25	170
MOR 1071-7-8-98-128	26	24	28	31	18	19	20	19	20	26	176
MOR 1071-8-1-98-359A	41	38	45	48	31	32	29	29	28	41	250
MOR 1071-7-1-98-48	30	25	29	35	25	25	24	19	19	27	191
MOR 1071-7-5-98-67	26*	28	*	*	23*	22*	23*	21*	*	*	168*
MOR 1071-7-14-98-193	28	23	*	*	24	26	*	20	15	*	145*

P_h: Dorsoventral maximum height of the proximal end of metacarpal III.

P_w: Mediolateral maximum width of the proximal end of metacarpal III.

D_h: Dorsoventral maximum height of the distal end of metacarpal III.

D_w: Mediolateral maximum width of the distal end of metacarpal III.

H_{sp}: Dorsoventral height of the shaft of metacarpal III, at a mid point of the proximal third of the bone.

H_{sc}: Dorsoventral height of the shaft of metacarpal III, at a mid point of the proximodistal length of the bone (*L*).

H_{sd}: Dorsoventral height of the shaft of metacarpal III, at a mid point of the distal third of the bone.

W_{sp}: Mediolateral width of the shaft of metacarpal III, at a mid point of the proximal third of the bone.

W_{sc}: Mediolateral width of the shaft of metacarpal III, at a mid point of the proximodistal length of the bone (*L*).

W_{sd}: Mediolateral width of the shaft of metacarpal III, at a mid point of the distal third of the bone.

L: Proximodistal length of metacarpal III.

Metacarpal IV

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sp}</i>	<i>H_{sc}</i>	<i>H_{sd}</i>	<i>W_{sp}</i>	<i>W_{sc}</i>	<i>W_{sd}</i>	<i>L</i>
MOR 794 left	~	49	41	~	~33	36	34	36	~32	~24	273
MOR 794 right	~	~50	39	~	~34	35	37	36	33	~24	265
MOR 1071-7-19-99-137	38	51	37	25	33	29	26	36	30	26	260
MOR 1071-8-13-98-547	33	53	34*	23*	28	24*	31	42	35*	26	248*
MOR 1071-8-13-98-548	22*	29*	23*	13*	17	20*	18*	28*	17*	15*	165
MOR 1071-7-7-98-96	24	34	25*	16*	17	18	19	30	20	17	174*

P_h: Dorsoventral maximum height of the proximal end of metacarpal IV.

P_w: Mediolateral maximum width of the proximal end of metacarpal IV.

D_h: Dorsoventral maximum height of the distal end of metacarpal IV.

D_w: Mediolateral maximum width of the distal end of metacarpal IV.

H_{sp}: Dorsoventral height of the shaft of metacarpal IV, at a mid point of the proximal third of the bone.

H_{sc}: Dorsoventral height of the shaft of metacarpal IV, at a mid point of the proximodistal length of the bone (*L*).

H_{sd}: Dorsoventral height of the shaft of metacarpal IV, at a mid point of the distal third of the bone.

W_{sp}: Mediolateral width of the shaft of metacarpal IV, at a mid point of the proximal third of the bone.

W_{sc}: Mediolateral width of the shaft of metacarpal IV, at a mid point of the proximodistal length of the bone (*L*).

W_{sd} : Mediolateral width of the shaft of metacarpal IV, at a mid point of the distal third of the bone.

L : Proximodistal length of metacarpal IV along its medial side.

Metacarpal V

<i>Specimens</i>	P_h	P_w	D_h	D_w	H_{sp}	H_{sc}	H_{sd}	W_{sp}	W_{sc}	W_{sd}	L
MOR 794 left	40	~50	~26	~33	33	22	~26	43	40	~32	105
MOR 794 right	38	~50	27	35	31	23	25	43	41	33	106
MOR 1071-7-21-48-340	37	52	29	30	32	22	26	43	39	29	99
MOR 1071-8-5-98-481	27	36	15*	24*	22	13	15	30	27	22	60*
MOR 1071-7-7-98-87	18*	24*	13*	15*	17	13	13	21	18	14	56
MOR 1071-8-2-98-464	22	29	14*	19*	19	13	14	26	21	20	57

P_h : Dorsoventral maximum height of the proximal end of metacarpal V.

P_w : Mediolateral maximum width of the proximal end of metacarpal V.

D_h : Dorsoventral maximum height of the distal end of metacarpal V.

D_w : Mediolateral maximum width of the distal end of metacarpal V.

H_{sp} : Dorsoventral height of the shaft of metacarpal V, at a mid point of the proximal third of the bone.

H_{sc} : Dorsoventral height of the shaft of metacarpal V, at a mid point of the proximodistal length of the bone (L).

H_{sd} : Dorsoventral height of the shaft of metacarpal V, at a mid point of the distal third of the bone.

W_{sp} : Mediolateral width of the shaft of metacarpal V, at a mid point of the proximal third of the bone.

W_{sc} : Mediolateral width of the shaft of metacarpal V, at a mid point of the proximodistal length of the bone (L).

W_{sd} : Mediolateral width of the shaft of metacarpal V, at a mid point of the distal third of the bone.

L : Proximodistal length of metacarpal V, along the longest, longitudinal axis of the bone; from the more salient, dorsal point to the inflexion point between the major, proximomedial surface and the lesser, proximolateral facet, of the proximal side.

Metatarsal II

<i>Specimens</i>	L	H_p	H_{dl}	H_{dm}	H_f	H_n	W_p	W_{dv}	W_{dd}	W_s	F
MOR 794 left	367	197	~	122*	114*	94	75.5	~	57*	~	93
MOR 794 right	370	193	96	103	109	84	75.5	98	72	47	96
MOR 1071- 7-10-98-104	335	192	98	104	97*	78*	70*	75*	64*	47	88
MOR 1071- 8-7-99-470	237	94	59	55	60	41	48	59	46	29	51
MOR 1071-8-16-98-577	235	126	64	69	57	50	49	67	51	39	51
MOR 1071-8-1-99-330	232	127	63	66	62	49	50	67	52	40	52

L : Maximum proximodistal length of metatarsal II.

H_p : Maximum dorsoventral height of the proximal surface of the metatarsal.

H_{dl} : Dorsoventral height of the lateral border of the distal surface of the metatarsal, perpendicular to the horizontal dorsal edge.

H_{dm} : Dorsoventral height of the medial border of the distal surface of the metatarsal, perpendicular to the horizontal dorsal edge.

H_f : Dorsoventral height of the shaft at the level of the dorsal-most point of the flange.

H_n : Dorsoventral height of the shaft at the level of maximum concavity of the dorsal outline of the metatarsal, proximal to the flange.

W_p : Maximum mediolateral width of the proximal surface of the metatarsal.

W_{dv} : Mediolateral maximum width of the ventral edge of the distal surface of the bone.

W_{dd} : Mediolateral maximum width of the dorsal edge of the distal surface of the bone.

W_s : Mediolateral maximum width of the mid shaft, at the level of half L .

F : Proximodistal length of the dorsal flange of metatarsal II. Its proximal and distal end points are set at the inflexion points.

Metatarsal III

<i>Specimens</i>	<i>L</i>	<i>H_p</i>	<i>H_{dl}</i>	<i>H_{dm}</i>	<i>W_p</i>	<i>W_{dv}</i>	<i>W_{dd}</i>	<i>W_s</i>
MOR 794 left	~420	~173	94	110	~	~	126	~70
MOR 794 right	440	171	95	109	91.5	113	129	71
MOR 1071- 7-8-98-114	417	131	96	109	95	116	128	83
MOR 1071-7-26-98-425	310	104*	62	70	74	78	86	54
MOR 1071-8-1-99-332	295	121	67	76	64	86	95	53

L : Maximum proximodistal length of metatarsal III, taken along the medial side.

H_p : Maximum dorsoventral height of the proximal surface of the metatarsal, taken on the medial side.

H_{dl} : Dorsoventral height of the distal surface of the metatarsal, parallel to a parasagittal plane, and taken along the lateral side.

H_{dm} : Dorsoventral height of the distal surface of the metatarsal, parallel to a parasagittal plane, and taken along the medial side.

W_p : Maximum mediolateral width of the proximal surface of the metatarsal.

W_{dv} : Mediolateral maximum width of the ventral edge of the distal surface of the bone.

W_{dd} : Mediolateral maximum width of the dorsal edge of the distal surface of the bone.

W_s : Mediolateral maximum width of the mid shaft, at the level of half L .

(-): no flange observed.

Metatarsal IV

<i>Specimens</i>	<i>L</i>	<i>H_p</i>	<i>H_d</i>	<i>H_f</i>	<i>H_s</i>	<i>W_p</i>	<i>W_{dv}</i>	<i>W_{dd}</i>	<i>W_s</i>	<i>W_f</i>	<i>F</i>
MOR 794 left	~330	135	~	~	58	~	~102	~	~70	~80	160
MOR 794 right	345	130	98	60	56	83	104	80	72	88	162
MOR 1071-7-22-98-173	335	117	98	48	47	82	102	82	74	87	150
MOR 1071-8-7-99-467	230	78	57	31	30	53	67	54	51	62	107
MOR 1071-7-7-98-89	245	65	57	33	28	55	62.5	59	48	63	105
MOR 1071-7-16-98-246	*	92*	*	32	31	54	*	*	52*	63	103
MOR 1071-8-1-99-328-B	235	91	64	34	34	52	73	53	54	67	101

L: Maximum proximodistal length of metatarsal IV, taken along the mediodorsal border.

H_p: Maximum dorsoventral height of the proximal surface of the metatarsal, taken along the medial edge.

H_d: Dorsoventral height of the distal surface of the metatarsal, parallel to a parasagittal plane, and taken along the medial border.

H_f: Dorsoventral maximum height of the medial flange.

H_s: Dorsoventral height of the shaft at the middle of the proximodistal length of the element.

W_p: Maximum mediolateral width of the proximal surface of the metatarsal, taken through a mediolaterally bisecting line.

W_{dv}: Mediolateral maximum width of the ventral edge of the distal surface of the bone.

W_{dd}: Mediolateral maximum width of the dorsal edge of the distal surface of the bone.

W_f: Mediolateral maximum width of metatarsal at the level of maximum medial projection of the medial flange.

W_s: Mediolateral maximum width of the mid shaft, immediately distal to the medial flange.

F: Proximodistal length of the medioventral flange. Its proximal and distal end points are set at the inflexion points.

Manual Phalange III

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sp}</i>	<i>H_{sc}</i>	<i>H_{sd}</i>	<i>W_{sp}</i>	<i>W_{sc}</i>	<i>W_{sd}</i>	<i>L</i>
MOR 794 left	38	~	37	~	33	25	30	~	~	~	80
MOR 794 right	~	~	36	~	~30	23	29	~	~	~	~80
MOR 1071-7-27-99-223	34*	19	37	18	31	26	33	17	19	18	80
MOR 1071-7-6-98-81	19*	9*	22	12	18	13	18	9	10	9	48
MOR 1071-8-2-99-364	22	11	24	12	20	14	20	11	12	11	57

P_h: Dorsoventral maximum height of the proximal end of phalange III.

P_w: Mediolateral maximum width of the proximal end of phalange III.

D_h: Dorsoventral maximum height of the distal end of phalange III.

D_w: Mediolateral maximum width of the distal end of phalange III.

H_{sp}: Dorsoventral height of the shaft of phalange III, at a mid point of the proximal third of the bone.

H_{sc}: Dorsoventral height of the shaft of phalange III, at a mid point of the proximodistal length of the bone (**L**).

Manual Phalange II2

<i>Specimens</i>	<i>L</i>	<i>P</i>	<i>D_p</i>	<i>D_d</i>	<i>D_c</i>
MOR 794 left	33	26	~	~	~
MOR 794 right	31	26	~	~	~
MOR 1071-7-21-98-330	23	17	16	14	13
MOR 1071-8-1-99-310	21	14	15	12	11
MOR 1071-8-2-99-353	21	16	13	12	11

L: Mediolateral length of phalange II2, taken along the mid proximodistal length.

P: Maximum proximodistal length of phalange II2, perpendicular to **L**.

D_p: Dorsoventral maximum width of the proximal surface of phalange II2, perpendicular to **P**.

D_d: Dorsoventral maximum width of the distal surface of phalange II2, perpendicular to **P**.

D_c: Dorsoventral width of the central, concave band of phalange II2, parallel to **P**.

Manual Ungual III1

<i>Specimens</i>	P_h	P_w	D_h	D_w	H_{sc}	W_{sc}	L
MOR 794 left	43	49	~30	49	25	36	68
MOR 794 right	~	52	31	50	23	39	69
MOR 1071-7-8-98-125	25*	29*	21	29	16	24	43*
MOR 1071-7-30-99-256	25	31	17*	29	14	22	42
MOR 1071-8-1-99-361	25	31.5	20.5	30	15	24	42

P_h : Dorsoventral maximum height of the proximal end of phalange III1.

P_w : Mediolateral maximum width of the proximal end of phalange III1.

D_h : Dorsoventral maximum height of the distal end of phalange III1.

D_w : Mediolateral maximum width of the distal end of phalange III1.

H_{sc} : Dorsoventral height of the shaft of phalange III1, at a mid point of the proximodistal length of the bone (L).

W_{sc} : Mediolateral width of the shaft of phalange III1, at a mid point of the proximodistal length of the bone (L).

L : Proximodistal length of phalange III1, along the longest, longitudinal axis of the bone, along the medial side.

Manual Phalanges III2

<i>Specimens</i>	L	P	D_p	D_d	D_c
MOR 794 left	42	26	~	~	~
MOR 794 right	41	25	30	~	22
MOR 1071-8-16-98-579	40	25	29	24	23
MOR 1071-7-27-98-427	40	25	34	27	26
MOR 1071-6-30-98-11A	28	23	20	17	15
MOR 1071-8-12-98-537	42	26	30	25	22
MOR 1071-7-31-99-268	32	23	26	22	18
MOR 1071-8-3-99-365	25	18	19	18	15

L : Mediolateral length of phalange III2, taken along the mid proximodistal length, on the concave, central band.

P : Maximum proximodistal length of phalange III2, perpendicular to L and in dorsoventral direction.

D_p : Dorsoventral maximum width of the proximal surface of phalange III2, perpendicular to P .

D_d : Dorsoventral maximum width of the distal surface of phalange III2, perpendicular to P .

D_c : Dorsoventral width of the central, concave band of phalange III2, parallel to P , and taken at the center.

Manual Phalange IV1

<i>Specimens</i>	P_h	P_w	D_h	D_w	H_{sc}	W_{sc}	L
MOR 794 left	~	~	~	~	~	~	66.5
MOR 794 right	42	~	~	~26	29	~	68
MOR 1071-8-1-99-321	36	24	21	27	27	24	67
MOR 1071-8-12-98-534	41	26	25	32	23	24	59
MOR 1071-?	25	16	12*	18*	17	15	43
MOR 1071-8-9-99-523D	23	15	14	19	15	11	44

P_h : Dorsoventral maximum height of the proximal end of phalange III1.

P_w : Mediolateral maximum width of the proximal end of phalange III1.

D_h : Dorsoventral maximum height of the distal end of phalange III1.

D_w : Mediolateral maximum width of the distal end of phalange III1.

H_{sc} : Dorsoventral height of the shaft of phalange III1, at a mid point of the proximodistal length of the bone (L).

W_{sc} : Mediolateral width of the shaft of phalange III1, at a mid point of the proximodistal length of the bone (L).

L : Proximodistal length of phalange III1, along the longest, longitudinal axis of the bone.

Manual Phalange IV2

<i>Specimens</i>	P_h	P_w	D_h	D_w	H_{sc}	W_{sc}	L
MOR 794 left	~	~22	~	~21	~	~19	24
MOR 794 right	~	22	~	24	~	18	25
MOR 1071-8-13-98-359F	22	20	15*	23	14	19	15
MOR 1071-7-9-98-159A	12	16	19	16	9	14	25
MOR 1071-8-11-98-525	23	25.5	18	29	16	22	23

P_h : Dorsoventral maximum height of the proximal end of phalange IV2.

P_w : Mediolateral maximum width of the proximal end of phalange IV2.

D_h : Dorsoventral maximum height of the distal end of phalange IV2.

D_w : Mediolateral maximum width of the distal end of phalange IV2.

H_{sc} : Dorsoventral height of the shaft of phalange IV2, at a mid point of the proximodistal length of the bone (L).

W_{sc} : Mediolateral width of the shaft of phalange IV2, at a mid point of the proximodistal length of the bone (L).

L : Proximodistal length of phalange IV2, along the longest, longitudinal axis of the bone.

Manual Phalange V1

<i>Specimens</i>	P_h	P_w	D_h	D_w	H_{sc}	W_{sc}	L
MOR 794 left	~25	35.5	18	31	21	28	67
MOR 794 right	24	36	19	32	20.5	30	67
MOR 1071-8-3-99-376	16	21	10	19	10	15	40
MOR 1071-7-30-99-237	13	19	9	17	9	16	40
MOR 1071-7-27-99-227	26	36	16	31	17	32	64

P_h : Dorsoventral maximum height of the proximal end of phalange V1.

P_w : Mediolateral maximum width of the proximal end of phalange V1.

D_h : Dorsoventral maximum height of the distal end of phalange V1.

D_w : Mediolateral maximum width of the distal end of phalange V1.

H_{sc} : Dorsoventral height of the shaft of phalange V1, at a mid point of the proximodistal length of the bone (L).

W_{sc} : Mediolateral width of the shaft of phalange V1, at a mid point of the proximodistal length of the bone (L).

L : Proximodistal length of phalange V1, along the longest, longitudinal axis of the bone.

Manual Phalange V2

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	23	30	15	25	15	23	40
MOR 794 right	20	29	14	22	14	22	40
MOR 1071-8-5-98-478	14	19.5	11	16	10	14	25
MOR 1071-7-17-99-108	12	16	9	14	7.5	13	24
MOR 1071-7-21-98-341	19	21.5	10	18	13	17	36
MOR 1071-8-12-98-538	18	25	13	21	15	20	40
MOR 1071-8-7-99-460-C	17	26	15	22	12	19	40
MOR 1071-7-20-98-519L	12	19	10	16	9.5	15	26

P_h: Dorsoventral maximum height of the proximal end of phalange V2.

P_w: Mediolateral maximum width of the proximal end of phalange V2.

D_h: Dorsoventral maximum height of the distal end of phalange V2.

D_w: Mediolateral maximum width of the distal end of phalange V2.

H_{sc}: Dorsoventral height of the shaft of phalange V2, at a mid point of the proximodistal length of the bone (**L**).

W_{sc}: Mediolateral width of the shaft of phalange V2, at a mid point of the proximodistal length of the bone (**L**).

L: Proximodistal length of phalange V2, along the longest, longitudinal axis of the bone.

Manual Phalange V3

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	10	15	7.5	15	8	16	18
MOR 794 right	10	15	9	16	10.5	16	17
MOR 1071-7-27-98-452	12	17.5	8	13	10	15	20
MOR 1071-162-A	9	16	8	12*	8	17	18
MOR 1071-8-2-99-359	6	12	5	8	5	9	15

P_h: Dorsoventral maximum height of the proximal end of phalange V3.

P_w: Mediolateral maximum width of the proximal end of phalange V3.

D_h: Dorsoventral maximum height of the distal end of phalange V3.

D_w: Mediolateral maximum width of the distal end of phalange V3.

H_{sc}: Dorsoventral height of the shaft of phalange V3, at a mid point of the proximodistal length of the bone (**L**).

W_{sc}: Mediolateral width of the shaft of phalange V3, at a mid point of the proximodistal length of the bone (**L**).

L: Proximodistal length of phalange V3, along the longest, longitudinal axis of the bone.

Manual Phalange V4

<i>Specimens</i>	<i>PD</i>	<i>ML</i>	<i>DV</i>
MOR 794 left	9	5.5	5
MOR 794 right	8	6	5

PD: Proximodistal length of phalange V4.

ML: Mediolateral width of phalange V4.

DV: Dorsoventral thickness of phalange V4.

Manual Ungual II

<i>Specimens</i>	<i>L</i>	<i>L'_l</i>	<i>L'_m</i>	<i>H</i>	<i>W</i>	<i>W_n</i>	<i>W'</i>
MOR 794 left	55	49	38	~	31	26	39
MOR 794 right	54	~47	38.5	~	~33	27	40
MOR 1071-8-12-98-533	61	51	28	23	34	29	43
MOR 1071-8-3-99-374	54	41	32	18	32	28	41
MOR 1071-8-3-99-371	34	25	17	12	19	17	24
MOR 1071-8-1-99-304	32.5	24	17*	11	18.5	17	21*
MOR 1071-7-27-99-225	61	51	29	21	33	29	43

L: Proximodistal length of manual ungual II, from the front of the distal edge to the caudal edge, through a bisecting line.

L'_m: Proximodistal length of the medial expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

L'_l: Proximodistal length of the lateral expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

H: Dorsoventral maximum thickness of the proximal border of the ungual.

W: Mediolateral width of the proximal border of the ungual, perpendicular to *L*.

W_n: Mediolateral width of the "neck" of the ungual, that is, the mediolaterally constricted central portion between the arrow-shaped expanded region and the caudal, somehow less expanded end.

W': Maximum mediolateral width of the arrow-shaped, most mediolaterally expanded portion of the ungual.

H_{sd}: Dorsoventral height of the shaft of phalange III, at a mid point of the distal third of the bone.

W_{sp}: Mediolateral width of the shaft of phalange III, at a mid point of the proximal third of the bone.

W_{sc}: Mediolateral width of the shaft of phalange III, at a mid point of the proximodistal length of the bone (*L*).

W_{sd}: Mediolateral width of the shaft of phalange III, at a mid point of the distal third of the bone.

L: Proximodistal length of phalange III, along the longest, longitudinal axis of the bone, along the ventral side.

Manual Ungual III

<i>Specimens</i>	<i>L</i>	<i>L'_l</i>	<i>L'_r</i>	<i>H</i>	<i>W</i>	<i>W_n</i>	<i>W'</i>
MOR 794 left	46	22	21	24	39	31	47
MOR 794 right	46	23	27	23.5	35	28	47
MOR 1071-8-13-98-554-B	39*	*	*	23*	36*	32	42.5*
MOR 1071-8-1-99-303	26.5	14	11*	13	23	19.5	24*

L: Proximodistal length of manual ungual II, from the front of the distal edge to the caudal edge, through a bisecting line.

L'_l : Proximodistal length of the left (on dorsal view) expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

L'_r : Proximodistal length of the right (as seen on dorsal view) expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

H : Dorsoventral maximum thickness of the proximal border of the ungual.

W : Mediolateral maximum width of the caudal border of the ungual, perpendicular to L .

W_n : Mediolateral width of the "neck" of the ungual, that is, the mediolaterally constricted central portion between the arrow-shaped expanded region and the caudal, somehow less expanded end.

W : Maximum mediolateral width of the arrow-shaped, most mediolaterally expanded portion of the ungual.

Pedal Phalange II1

<i>Specimens</i>	P_h	P_w	D_{hl}	D_w	H_{sc}	W_{sc}	L
MOR 794 left	~	~	~60	~	~60	~	150
MOR 794 right	98	80	61	86	59	53	152
MOR 1071-8-5-99-421	101*	74*	62	78	74*	45*	152
MOR 1071-7-6-98-75	57*	50*	33	52	36	41	102
MOR 1071-7-31-99-264	67	64	41	62	38	46	104
MOR 1071-8-5-99-453	61	52	40	53	32	39	90
MOR 1071-8-1-99-328-A	67	65	45	63	37	45	104

P_h : Maximum dorsoventral height of the proximal end of phalange II1.

P_w : Maximum mediolateral maximum width of the proximal end of phalange II1.

D_{hl} : Dorsoventral maximum height of the lateral border of the distal end of phalange II1.

D_w : Mediolateral maximum width of the distal end of phalange II1.

H_{sc} : Dorsoventral height of the shaft of phalange II1, at a mid point of the proximodistal length of the bone (L).

W_{sc} : Mediolateral width of the shaft of phalange II1, at a mid point of the proximodistal length of the bone (L), and taken along the ventral side.

L : Proximodistal length of phalange II1, along the longest, longitudinal axis of the bone, taken along the dorsomedial area.

Pedal Phalange II2

<i>Specimens</i>	P_h	P_w	D_{hl}	D_w	H_{sc}	W_{sc}	L
MOR 794 left	~	78	42	~	41	~	61.5
MOR 794 right	61	77	42	65	41	64	61.5
MOR 1071-7-16-98-213	37	52	24	52	25	47	40
MOR 1071-8-98-561-A	33	47	25	45	22	45	41
MOR 1071-7-8-98-127	37*	55*	28	54	27	52	41
MOR 1071-8-4-99-410-A	36	45	27	42	25	40	40
MOR 1071-8-1-99-334	43	56	32	52	27	52	45

P_h : Maximum dorsoventral height of the proximal end of phalange II2.

P_w : Maximum mediolateral maximum width of the proximal end of phalange II2.

D_{hl} : Dorsoventral maximum height of the lateral border of the distal end of phalange II2.

D_w : Mediobasal maximum width of the distal end of phalange II2.

H_{sc} : Dorsoventral height of the shaft of phalange II2, at a mid point of the proximodistal length of the bone (L).

W_{sc} : Mediobasal width of the shaft of phalange II2, at a mid point of the proximodistal length of the bone (L).

L : Proximodistal length of phalange II2.

Pedal Phalange III1

<i>Specimens</i>	P_h	P_w	D_{hm}	D_w	H_{sc}	W_{sc}	L
MOR 794 left	99	~140	60	115	51	87	146
MOR 794 right	98	140	59	122	50	93	145
MOR 1071-7-98-216	62	92	44*	86	34	74	97
MOR 1071-8-5-99-454	61	88	43	74	36	70	99
MOR 1071-8-1-99-333	69	105	44	85	36	72	101

P_h : Maximum dorsoventral height of the proximal end of phalange III1.

P_w : Maximum mediolateral maximum width of the proximal end of phalange III1.

D_{hm} : Dorsoventral maximum height of the medial border of the distal end of phalange III1.

D_w : Mediobasal maximum width of the distal end of phalange III1.

H_{sc} : Dorsoventral height of the shaft of phalange III1, at a mid point of the proximodistal length of the bone (L), and taken along the lateral side.

W_{sc} : Mediobasal width of the shaft of phalange III1, at a mid point of the proximodistal length of the bone (L), and taken along the dorsal side.

L : Proximodistal length of phalange III1.

Pedal Phalange III2

<i>Specimens</i>	P_h	P_w	D_{hm} <i>m</i>	D_{hl}	D_w	H_{sc}	W_{sc}	L
MOR 794 left	~67	105	47	44	108	49	~112	~53
MOR 794 right	68	112.5	46	43	115	44	110	53
MOR 1071-7-22-98-294	42	81	34	30	81	30	78	37
MOR 1071-7-21-98-331-B	*	81.5*	34	32	87	30	82	40
MOR 1071-7-27-98-456	42.5	82	32	30	85	29	83	36
MOR 1071-7-8-98-129	42	80	32	30	82	30	80	36
MOR 1071-7-17-98-271	42	81	32	29	81	29	82	36

P_h : Dorsoventral maximum height of the proximal end of phalange III2.

P_w : Mediobasal maximum width of the proximal end of phalange III2.

D_{hm} : Dorsoventral maximum height of the medial border of the distal end of phalange III2.

D_{hl} : Dorsoventral maximum height of the lateral border of the distal end of phalange III2.

D_w : Mediobasal maximum width of the distal end of phalange III2.

H_{sc}: Dorsoventral height of phalange III2, at a mid point of the proximodistal length of the bone (**L**), and taken along the medial side.

W_{sc}: Mediobasal width of phalange III2, at a mid point of the proximodistal length of the bone (**L**), and taken along the ventral side. **L**: Proximodistal length of phalange III2, along a bisecting line along the ventral surface.

Pedal Phalange III3

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_{hm}</i>	<i>D_{hl}</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	~51	84	43	40	76	47	~80	~
MOR 794 right	50	88.5	43	40.5	78	42	84	41
MOR 1071-8-4-98-475	45	95	41	39	84	37	94	41
MOR 1071-8-12-98-535	34	67	31	29	63	28	67	29
MOR 1071-8-1-99-345	29	59	25	24.5	57	23	58	26
MOR 1071-7-17-98-270	44	89	44	43	83	39	89	40

P_h: Dorsoventral maximum height of the proximal end of phalange III3.

P_w: Mediobasal maximum width of the proximal end of phalange III3.

D_{hm}: Dorsoventral maximum height of the medial border of the distal end of phalange III3.

D_{hl}: Dorsoventral maximum height of the lateral border of the distal end of phalange III3.

D_w: Mediobasal maximum width of the distal end of phalange III3.

H_{sc}: Dorsoventral height of phalange III3, at a mid point of the proximodistal length of the bone (**L**), and taken along the medial side.

W_{sc}: Mediobasal width of phalange III3, at a mid point of the proximodistal length of the bone (**L**), and taken along the ventral side.

L: Proximodistal length of phalange III3, along a bisecting line along the ventral surface.

Pedal Phalange IV1

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_{hm}</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	~	~	~	~	~	~	115
MOR 794 right	101	97	62	90	51	71	116
MOR 1071-7-8-98-124	97*	93*	72	90	57	69	113
MOR 1071-7-25-98-419	55*	63*	42	56	37	46	79
MOR 1071-7-26-98-444	63	59	43	53	38	41	79
MOR 1071-7-8-1-99-328C	66	65	44	62	37	49	82

P_h: Maximum dorsoventral height of the proximal end of phalange IV1.

P_w: Maximum mediobasal maximum width of the proximal end of phalange IV1.

D_{hm}: Dorsoventral maximum height of the medial border of the distal end of phalange IV1.

D_w: Mediobasal maximum width of the distal end of phalange IV1.

H_{sc}: Dorsoventral height of phalange IV1, at a mid point of the proximodistal length of the bone (**L**), and taken along the medial side.

W_{sc}: Mediobasal width of phalange IV1, at a mid point of the proximodistal length of the bone (**L**), and taken along the ventral side.

L: Maximum proximodistal length of phalange IV1.

Pedal Phalanges IV2

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	~	~	~	~	~	~	37
MOR 794 right	64	85	54	85	54	85	37
MOR 1071-7-10-98-166	60	84	53	86	52	82	39
MOR 1071-8-5-99-422	60	84	52	85	53	84	36
MOR 1071-8-12-98-532	43	59	35	58	35	58	26
MOR 1071-8-3-99-382	38	55	34	54	34	53	24
MOR 1071-8-1-99-335	31	44*	31*	42*	27	43*	20
MOR 1071-7-31-99-271	33	49	33	49	30	49	22
MOR 1071-8-1-99-336	*	53*	~	~	*	53*	23

P_h: Dorsoventral maximum height of the proximal end of phalange IV2.

P_w: Mediolateral maximum width of the proximal end of phalange IV2.

D_h: Dorsoventral maximum height of the distal end of phalange IV2 (which coincides with the medial edge).

D_w: Mediolateral maximum width of the distal end of phalange IV2.

H_{sc}: Dorsoventral height of phalange IV2, at a mid point of the proximodistal length of the bone (**L**), and taken along the medial side.

W_{sc}: Mediolateral width of phalange IV2, at a mid point of the proximodistal length of the bone (**L**), and taken along the ventral side.

L: Proximodistal length of phalange IV2, along a bisecting line along the dorsal surface.

Pedal Phalanges IV3

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	~	~	~	~	~	~	23
MOR 794 right	55	74	46	78	51	74	22
MOR 1071-7-10-98-168	59	74	52	79	52	75	22
MOR 1071-?	37	50	34	49	35	50	14
MOR 1071-7-9-98-159	36	52	35	52	34	53	13
MOR 1071-7-15-98-233-A	35	50	32	51	32	51	15
MOR-1071-7-18-98-282-A	36	51	32	51	33	50	14
MOR 1071-7-21-98-335	32	45	30	45	29	45	17
MOR 1071-7-15-98-233-B	31	43	30	43	27	44	16
MOR 1071-8-1-99-337	36	58	34	57	34	57	15

P_h: Dorsoventral maximum height of the proximal end of phalange IV3.

P_w: Mediolateral maximum width of the proximal end of phalange IV3.

D_h: Dorsoventral maximum height of the distal end of phalange IV3.

D_w: Mediolateral maximum width of the distal end of phalange IV3.

H_{sc}: Dorsoventral height of phalange IV3, at a mid point of the proximodistal length of the bone (**L**), and taken along the medial side.

W_{sc}: Mediolateral width of phalange IV3, at a mid point of the proximodistal length of the bone (**L**), and taken along the ventral side.

L: Proximodistal length of phalange IV3, along a bisecting line along the dorsal surface.

Pedal Phalange IV4

<i>Specimens</i>	<i>P_h</i>	<i>P_w</i>	<i>D_h</i>	<i>D_w</i>	<i>H_{sc}</i>	<i>W_{sc}</i>	<i>L</i>
MOR 794 left	~	~	~	59	~	~	~20
MOR 794 right	49	68	45	62	42	63	22
MOR 1071-8-3-99-381	27	42	27.5	43	25	42	14

P_h: Dorsoventral maximum height of the proximal end of phalange IV4.

P_w: Mediolateral maximum width of the proximal end of phalange IV4.

D_h: Dorsoventral maximum height of the distal end of phalange IV4.

D_w: Mediolateral maximum width of the distal end of phalange IV4.

H_{sc}: Dorsoventral height of phalange IV4, at a mid point of the proximodistal length of the bone (**L**), and taken along the medial side.

W_{sc}: Mediolateral width of phalange IV4, at a mid point of the proximodistal length of the bone (**L**), and taken along the ventral side.

L: Proximodistal length of phalange IV4, along a bisecting line along the dorsal surface.

Pedal Ungual II

<i>Specimens</i>	<i>L</i>	<i>L'_l</i>	<i>L'_m</i>	<i>H</i>	<i>W</i>	<i>W_n</i>	<i>W'</i>
MOR 794 left	83	55	48	50	58	46	82.5
MOR 794 right	82	54	45	49	56	44	80.5
MOR 1071-7-20-98-324	58	33	29	32	38	29	54

L: Proximodistal length of pedal ungual II, from the front of the distal edge to the caudal edge, through a bisecting line.

L'_l: Proximodistal length of the lateral expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

L'_m: Proximodistal length of the medial expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

H: Dorsoventral maximum thickness of the proximal border of the ungual.

W: Mediolateral maximum width of the caudal border of the ungual, perpendicular to **L**.

W_n: Mediolateral width of the "neck" of the ungual, that is, the mediolaterally constricted central portion between the arrow-shaped expanded region and the caudal, somehow less expanded end.

W': Maximum mediolateral width of the arrow-shaped, most mediolaterally expanded portion of the ungual.

Pedal Ungual III

<i>Specimens</i>	<i>L</i>	<i>L'_l</i>	<i>L'_r</i>	<i>H</i>	<i>W</i>	<i>W_n</i>	<i>W'</i>
MOR 794 left	91	54	49	~53	69	54	103.3
MOR 794 right	85	54	55	46	72	53	107
MOR 1071-8-10-98-515	86	51	50	46	75	53	103
MOR 1071-7-8-98-132	58*	30*	30*	29	46	34	67*
MOR 1071-7-16-98-24B-C	35.5	21*	19*	15	28	23	36*
MOR 1071-7-26-98-439	64	35	34	30	50	37	69*
MOR 1071-7-22-98-345	61	32	34	28	49	37.5	66
MOR 1071-7-31-99-273	60	38	42	28	48	36.5	72

L: Proximodistal length of pedal ungual III, from the front of the distal edge to the caudal edge, through a bisecting line.

L'_l: Proximodistal length of the left (on dorsal view) expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

L'_r: Proximodistal length of the right (as seen on dorsal view) expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

H: Dorsoventral maximum thickness of the proximal border of the ungual.

W: Mediolateral maximum width of the caudal border of the ungual, perpendicular to *L*.

W_n: Mediolateral width of the "neck" of the ungual, that is, the mediolaterally constricted central portion between the arrow-shaped expanded region and the caudal, somehow less expanded end.

W': Maximum mediolateral width of the arrow-shaped, most mediolaterally expanded portion of the ungual.

Pedal Ungual IV

<i>Specimens</i>	<i>L</i>	<i>L'_l</i>	<i>L'_m</i>	<i>H</i>	<i>W</i>	<i>W_n</i>	<i>W'</i>
MOR 794 left	81	52	48	49	64	49	90
MOR 794 right	82	52.5	~	48	~63	48.5	~89
MOR 1071-8-1-99-343	60	38.5	32*	29	45	36	54*
MOR 1071-7-10-98-169	69	47	38	32	50*	38	66
MOR 1071-8-4-98-473	59	33	34	31	41	29	54
MOR 1071-7-17-98-279	58	34	35	31	40	31	61
MOR 1071-8-1-98-460	59	35	31	30*	41	29.5	53
MOR 1071-7-20-98-322	59	38	31	30	40	33	61
MOR 1071-6-23-99-9	59	37	32	28.5	40	32	52.5
MOR 1071-7-25-99-208A	58	41	35	30	39.5	32	59
MOR 1071-7-27-99-229	57.5	34	37	29	40	33	57
MOR 1071-7-20-99-156	84*	54*	*	37*	47*	53*	88*

L: Proximodistal length of pedal ungual IV, from the front of the distal edge to the caudal edge, through a bisecting line.

L'_l: Proximodistal length of the lateral expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

L'_m: Proximodistal length of the medial expanded portion of the ungual, from the front of the distal border to the most expanded caudal extreme.

H: Dorsoventral maximum thickness of the proximal border of the ungual.

W: Mediolateral maximum width of the caudal border of the ungual, perpendicular to L.

W_n: Mediolateral width of the "neck" of the ungual, that is, the mediolaterally constricted central portion between the arrow-shaped expanded region and the caudal, somehow less expanded end.

W': Maximum mediolateral width of the arrow-shaped, most mediolaterally expanded portion of the ungual.

Pubis

<i>Specimens</i>	<i>L</i>	<i>L_{pr}</i>	<i>W_n</i>	<i>L_{po}</i>	<i>P^P</i>	<i>W_{pp}</i>	<i>W_b</i>	<i>W_{il}</i>	<i>W_{is}</i>
MOR 794	910*	675	125	360*	150	~210	248	~	~30
MOR 1071-7-16-98-243	800*	555*	112	415	150	175	192*	85	37*
MOR 1071-8-20-98-597	900*	583*	122	455	150	170	227	90	39
MOR 1071-7-20-98-300	580*	345*	60	290*	160	75*	111*	50	23*
MOR 1071-8-17-98-586	~470	~223	79	261*	155	~	~	~	20*
MOR 1071-7-13-99-86	526*	360*	70	275*	155	155	165	56	26

L: Anteroposterior length, taken from the caudoventral tip of the postpubic process to the anteroventral edge of the prepubic blade.

L_{pr}: As defined by Davis (1983) and used by Trexler (1995), this dimension is defined as the "distance between the maximum rostral extent of the prepubis and the closest corresponding point along the acetabular border" (Trexler, 1995).

W_n: Minimum prepubic neck height, the minimum distance between the dorsal and ventral borders of the prepubic neck (Davis, 1983; Trexler, 1995).

L_{po}: Length of the postpubic process, taken along the medial side of the element, from the point where the postpubis begins to diverge caudomedially from the pubis to its caudoventral tip.

P^P: Angle between the prepubic and the postpubic processes, measured along their ventral borders, projecting the slope of the postpubis stright dorsocranially and that of the prepubis caudally.

W_{pp}: Distance between the dorsomedial corner of the iliac peduncle and the caudomedial corner of the ischial one.

W_b: Maximum dorsoventral width of the prepubic blade.

W_{is}: Maximum mediolateral width of the articular facet of the ischial peduncle.

W_{il}: Maximum mediolateral width of the articular facet of the iliac peduncle.

Radius

<i>Specimens</i>	<i>L</i>	<i>W_p</i>	<i>H_p</i>	<i>H_k</i>	<i>W_m</i>	<i>H_m</i>	<i>W_d</i>
MOR 794 left	710	74	61	50*	39	45	55*
MOR 794 right	707	68	62	51*	40	47	52*
MOR 1071-7-8-98-126	415	59	~35	~32	23	30	41
MOR 1071-7-14-98-204	400	~38	36	33	22	25	32
MOR 1071-6-29-99-34	388	~45	~32	~25	22	24	36
MOR 1071-7-15-98-257	620	79	51	52*	35	42	58*

L: Proximodistal length of the radius, from the proximal to the distal end.

W_p: Maximum mediolateral width of the proximal end of the radius.

H_p : Dorsoventral thickness of the proximal end of the radius at the proximal border.

H_k : Maximum dorsoventral thickness of the proximal portion of the radius, not necessarily at the proximal end, but including the ventral keel-like prominence.

W_m : Maximum mediolateral width of the mid shaft of the radius.

H_m : Dorsoventral thickness of the mid shaft of the radius.

W_d : Maximum mediolateral width of the distal end of the radius.

Scapula

<i>Specimens</i>	<i>L</i>	<i>L'</i>	<i>W_{max}</i>	<i>W_C</i>	<i>W_n</i>	<i>W_{max}/</i>	<i>W_{ag}</i>	<i>G</i>	<i>C</i>	<i>G^C</i>
MOR 794	890	960	230	160	110	2.09	184	100	~	140
MOR 1071-7-18-98-298	770 *	790 *	183	183	120	1.525	161	105	98	140
MOR 1071-7-8-98-115	410*	425*	115	*	67	1.72	103	85	40	140
MOR 1071-7-9-98-153	520	535	107	95*	65	1.65	110	70	62	140
MOR 1071-7-15-98-233	310*	330*	101	*	66	1.53	106	67**	**	140
MOR 1071-8-4-99-411	505*	520*	100	*	61	1.64	99*	66	52	125

L: Anteroposterior length; taken from the dorsocaudal corner of the blade to the cranial-most point of the coracoid facet.

L': Anteroposterior length along the curvature of the dorsal edge.

W_{max}: Maximum width (dorsoventral length). Note that it does not necessarily have to coincide with the caudal width

W_C: Dorsoventral width of the caudal edge of scapula.

W_n: Minimum width, which coincides with the dorsoventral length through the scapular "neck". It is taken through a line normal to both the dorsal and ventral curve edges.

W_{ag}: Proximal length from dorsal-most point of the acromion to ventral-most point of the glenoid.

G: Glenoid length (through long axis):

C: Coracoid facet anterodorsal-caudoventral length.

G^C: Glenoid-coracoid facet angle.

* Missing caudal end.

** Missing coracoid and bit of glenoid.

Sternals

<i>Specimens</i>	<i>L</i>	<i>L_a</i>	<i>L_v</i>	<i>L_h</i>	<i>H_d</i>	<i>H_h</i>	<i>W_d</i>	<i>W_h</i>	<i>W_a</i>
MOR 794 (left)	415	70	225	245	83	52	~	~	~
MOR 1071-7-12-99-71	388	43*	185*	237	61*	43	12	18	32
MOR 1071-7-18-98-283	235*	50*	75*	170*	42*	25	9*	12*	20*
MOR 1071-7-25-98-406	319	66	113*	207	43*	36	30	21	52
MOR 1071-7-15-99-102-B	*	*	*	*	*	27	*	10	*

L: Anterodorsal-caudoventral length of the sternal; taken from the anterior corner that results from the meeting of the proximodorsal (anterodorsal) edge and the anteroventral border, in a straight line until the caudoventral edge of the "handle".

L_a : Craniocaudal length of the anterodorsal border of the sternal.

H_v : Dorsoventral length of the ventral border of the proximal, expanded portion of the sternal.

L_h : Anteroposterior length of the "handle" of the sternal, taken from caudal edge of the posterior end/edge of the expanded portion of the bone, until the distal border, along the ventral edge of the element.

H_d : Width (approx. dorsoventral) length of the distal edge of the "handle".

H_h : Width (approx. dorsoventral) at level located at the mid length (L_h) of the "handle".

W_d : Mediolateral thickness of the distal end of the "handle", taken at mid H_d .

W_h : Mediolateral thickness of the "handle" at a point at mid L_h .

W_a : Maximum mediolateral thickness of the anterodorsal border of the sternal.

Tarsals (Astragalus)

<i>Specimens</i>	<i>L</i>	<i>L_m</i>	<i>L_l</i>	<i>A</i>	<i>A'</i>
MOR 794 left	160	~150	~	97*	*
MOR 794 right	160	150	93	104	61
MOR 1071-7-23-98-375	113	91	69	69	35
MOR 1071-8-10-98-516	102	84*	72	>67*	>32*
MOR 1071-7-3-99-270	180	*	*	77	52
MOR 1071-8-1-99-331	116	100	72	61	36

L : Maximum mediolateral length of the astragalus, along its distal surface.

L_m : Maximum antero-caudal length of the medial side of the astragalus, measured along the medial side itself.

L_l : Maximum antero-caudal length of the lateral side of the astragalus, measured along the medial border with the distal surface of the bone.

A : Maximum proximodistal length of the ascending process of the astragalus, including the distal border of the bone and until the proximal cusp.

A' : Maximum proximodistal extent of the carved, rugose triangular area on the anterior face of the ascending process of the astragalus.

Tarsals (Calcaneum)

<i>Specimens</i>	<i>L</i>	<i>W</i>	<i>W_r</i>	<i>H_l</i>	<i>H_m</i>	<i>L_l</i>	<i>L_m</i>
MOR 794 left	102*	59	~	78	~	88	~
MOR 794 right	120	67	~	76	~	88.5	~
MOR 1071-7-30-99-257	104	64	78.5	58.5	39	83	55
MOR 1071-7-16-98-261	109	58	81	60	43	94	56
MOR 1071-8-1-99-312	74.5	47	59	40	24.5	54	35
MOR 1071-7-15-98-215A	74	47	59	41	32	57	37
MOR 1071-8-5-99-447-E	70	41	48	39	30	51	40
MOR 1071-7-13-99-88	74	47	56	43	34	54	42

NOTE: Being rigorous, the lateral side of the calcaneus should be instead called laterocaudal, following the orientation of the hindlimb and pes. However, for brevity purposes, it has been here called "lateral". Same applies to "medial" instead of "mediocranial").

L: Maximum distance from the anteroproximal edge to the caudodistal border, along the anterodistal surface.

W: Medirolateral distance, taken across the anterodistal surface and perpendicular to L.

W_r: Caudolateral-antromedial distance of the caudal edge (ridge) of the proximal surface of the calcaneum (taken from face to face of the bone).

H_l: Maximum proximodistal thickness of the lateral side of the calcaneum, taken from the caudolateral corner of the proximal face perpendicular until the distal border.

H_m: Maximum proximodistal thickness of the medial side of the calcaneum, taken from the anteromedial corner of the proximal face perpendicular until the distal border.

L_l: Anterocaudal distance of the proximal face along its lateral edge (as seen or projected in lateral view, because the lateral border curves cranially along with the anterior one).

L_m: Anterocaudal distance of the proximal face along its medial edge (as seen or projected in medial view, because caudally the medial border curves along with the caudal one).

Tarsals (Distal Tarsal)

<i>Specimens</i>	<i>DV</i>	<i>ML</i>	<i>L</i>	<i>M</i>
MOR 794 left	~69	~	~27	~
MOR 794 right	68	63	26	8
MOR 1071-7-20-99-158	67*	51*	24	6
MOR 1071-8-1-98-359-B	37	35	9	4
MOR 1071-6-30-98-43-E	46*	31*	12*	*
MOR 1071-8-5-99-447	44	36	16	6
MOR 1071-8-1-99-328-D	35	34	9	4

DV: Dorsoventral maximum height of the distal tarsal.

ML: Medirolateral maximum width of the distal tarsal.

L: Proximodistal maximum thickness of the lateral portion of the distal tarsal.

M: Proximodistal thickness of the medial border of the distal tarsal.

Tibia

<i>Specimens</i>	<i>L</i>	<i>W_p</i>	<i>W_d</i>	<i>W_s</i>	<i>H_s</i>	<i>W_{oc}</i>	<i>W_{ic}</i>	<i>L_{oc}</i>	<i>L_{ic}</i>
MOR 794 left	1105	330	198	~	~	80	30*	70	53
MOR 794 right	1090	335	200	103	84	80	60	60^	50
MOR 1071-8-10-98-516	>585*	198*	137*	79*	69*	*	*	*	*
MOR 1071-7-23-98-375	670	185*	175	60	65	44*	30*	48*	35*
MOR 1071-8-10-98-514	665	160*	177*	65	70	45	35	50	44
MOR 1071-8-1-99-328	725	195*	195	67	73	57	38	62	60
MOR 1071-8-5-99-445	750	210*	190*	68	71	65	40	64	55*

L: Proximodistal length of the tibia, from the most distally salient point to the most proximally salient point on the condyles region.

W_p: Maximum width of the expanded proximal end, from the edge of the cnemial crest to the caudal border of the condyles, taken perpendicular to L.

W_d: Maximum width of the expanded distal end, taken perpendicular to L.

W_s: Mediolateral width of the central shaft (at mid proximodistal length of the tibia).

H_s: Anterocaudal length of the central shaft (at mid proximodistal length of the tibia)

W_{oc}: Maximum width of the "outer" proximal condyle, perpendicular to the direction of its long axis. Taken from the beginning of the cleft that separates the two condyles of the proximal tibia.

W_{ic}: Maximum width of the "inner" proximal condyle, perpendicular to the direction of its long axis. Taken at the level of the cleft that separates the two condyles of the proximal tibia.

L_{oc}: Maximum length of the long axis of the "outer" proximal condyle, parallel to the direction of projection; taken from the level of the cleft that separates the two condyles to the extreme of the condyle.

L_{ic}: Maximum length of the long axis of the "inner" proximal condyle, parallel to the direction of projection; taken from the level of the cleft that separates the two condyles to the extreme of the condyle.

Ulna

<i>Specimens</i>	<i>L</i>	<i>H_{mf}</i>	<i>H_{lf}</i>	<i>H_s</i>	<i>H_d</i>	<i>O</i>	<i>W_p</i>	<i>W_m</i>	<i>W_d</i>
MOR 794 left	785	108	102	50	64	43*	105	48	58
MOR 794 right	782	104	100	52	67	54*	93	48	58
MOR 1071-7-2-99-36	575*	96	90	50	*	39*	79	47	*
MOR 1071-8-1-98-359-J	680	105	87	54	61	44*	81	49	54
MOR 1071-9-14-99-B	315*	530^	550	28	*	39*	62	34	*
MOR 1071-8-16-98-576	415	58	45	26	40	25*	73	30	30
MOR 1071-7-12-99-77	~412	~70	~60	35	~	~	~	42	~
MOR 1071-8-14-99-564	450*	60*	50*	32	36*	26*	51.5*	30	40*
MOR 1071-6-17-99-4	357*	52*	47*	*	*	*	*	31	*
MOR 1071-8-13-99-557	520	75	62	32	35	27*	64	32	42
MOR 1071-7-21-98-363	438	56*	52*	28	31	32*	67	31	38*

L: Craniocaudal length of the long axis of the ulna, from the proximal extreme of the olecranon to the distalmost end of the bone.

H_{mf}: Maximum dorsoventral width of the medial, proximal flange, taken on the medial side from the ventral border to the dorsal rounded corner, perpendicular to L.

H_{lf}: Maximum dorsoventral height of the lateral, proximal flange, taken on the lateral side from the ventral border to the dorsal rounded corner, perpendicular to L.

H_s: Minimum dorsoventral height of the mid third of the ulna, taken at the middle of its proximodistal extension (in partial specimens, the last would be estimated), taken across the lateral surface.

H_d: Dorsoventral height of the distal end of the ulna.

O: Craniocaudal length of the olecranon, taken along its dorsal surface.

W_p: Mediolateral width of the proximal ulna, taken dorsally between the dorsal corners of the flanges.

W_m: Mediolateral width of the midshaft of the ulna, taken at mid distance from the proximal and distal ends.

W_d: Mediolateral width of the distal end of the ulna.

* Lacking distal portion.

^ Medially crushed.

~ Lacking proximal and distal portions.

APPENDIX C

PHYLOGENETIC DATA

Character List for the Hadrosauridae.

Modified from Horner, Weishampel, and Forster (2000)

Dentition

1. Number of tooth positions in dentary tooth rows: 30 or less (0); 34-38 (1); 40-49(2); 50 or more (3).
2. Number of tooth positions in maxillary tooth row: 30 or less (0); 34-38 (1); 40-50 (2); more than 50 (3).
3. Packing along tooth row: slight space between tooth base (0); dental batteries with continuous occlusal surfaces formed from closely packed tooth families, grooves on anterior and posterior sides of the roots of cheek teeth for reception of the crowns of the adjacent teeth (1).
4. Number of replacement teeth per tooth position: two (0); 3-5 (1).
5. Number of functional teeth per tooth position: one (0); up to three, at least two teeth in the vertical series contribute to the occlusal surface (1).
6. Maxillary tooth crown length/width ratio: broad relative to length (0); lanceolate, ratio at least 2.5:1 (1).
7. Dentary tooth crown length/width proportions at the center of tooth row: 3:1 or less (0); 3.2-3.8:1 (1); 4 or more: 1 (2).
8. Dentary teeth, ornamentation on lingual surface: numerous subsidiary ridges present (0); one or two subsidiary ridges present (1); loss of all but primary carina (2).
9. Maxillary teeth, ornamentation on labial surface: numerous subsidiary ridges present (0); one or two subsidiary ridges present (1); loss of all but primary carina (2).
10. Teeth, position of apex: offset (0); central, tooth straight and nearly symmetrical (1).

Lower Jaw

11. Dentary, length of the diastema between 1st dentary tooth and prementary: absent (0); short, no more than width of 3-4 teeth (1); long, equal to one fourth or one third of tooth row (2); very long, more than one third of tooth row, but less than one half (3); extremely long, more than one half tooth row length (4).
12. Dentary tooth row, posterior extent of dentary tooth row relative to apex of coronoid process: even with or anterior to (0); posterior (1).
13. Dentary, anterior portion: straight (0); slightly to moderately downturned (1); strikingly downturned, dorsal margin of anterior dentary extends below the ventral margin of the body of the dentary, premaxillary bill margin extends well below level of maxillary tooth row (2).
14. Dentary tooth row, shape in occlusal view: bowed lingually (0); straight (1).
15. Prementary shape: deep and robust, arcuate anterior margin, nutritive foramina located near center of prementary body (0); gracile and shovel-shaped, straight transverse anterior margin, foramina numerous and located just below anterior (1).
16. Prementary triturating surface: vertical (0); horizontal (1).
17. Prementary relative proportions: anterior mediolateral width is smaller or equal to the anteroposterior length of the lateral processes (0); anterior mediolateral width is larger than the anteroposterior length of the lateral processes (1); anterior mediolateral width doubles the anteroposterior length of the lateral processes (2).
18. Ventral central process on prementary: bilobate (0); triangular, non-bifurcated (1).
19. Angular size: large, deep, broadly exposed in lateral view (0); small, dorsoventrally narrow, exposed only in medial view (1).
20. Coronoid bone: present (0); absent (1).
21. Posterior extent of the posteroventral dentary: ends even with or anterior to apex of coronoid process (0); terminates well posterior to coronoid process (1).
22. Surangular foramen: present (0); absent (1).

23. Surangular: extends above level of tooth row (0); restricted in position below tooth row (1).

Cranium

24. Premaxilla, maxilla width oral margin: narrow, fairly vertical (0); flattened horizontally and expanded transversely to interorbital width or narrower (1); further expanded transversely, subequal to width across jugal arches (2).
25. Premaxilla reflected rim: absent (0); non-reflected, but ventrally deflected at anterolateral corner (1); posteriorly reflected, anteroventrally deflected ventrally (2); reflected all along the whole rim (3).
26. Premaxillary anterior bill margin shape: arcuate (0); horseshoe-shaped (1).
27. Premaxillary foramen: absent (0); present (1).
28. Premaxilla, accessory foramen on anterior narial fossa, located anterior to premaxillary foramen: absent (0); present, empties into common chamber with premaxillary foramen (1).
29. Premaxilla, auxiliary narial fossa anterior to circumnarial fossa: absent (0); present (1).
30. Premaxillary posterior processes (PM1, PM2) and nasal passage: posterodorsal premaxillary process short, processes do not meet posterior to the external nares, nasal passages open ventrally beneath nasals (0); both processes posteriorly elongate, join behind external nares to exclude nasals, nasal passage enclosed ventrally by folded, divided premaxillae (1).
31. External nares/basal skull length ratio: 20% or less (0); 30% or more (1).
32. External nares, composition of posteriormost apex: formed entirely by nasal (0); formed equally by nasal (dorsally) and premaxilla (ventrally) (1); formed by premaxilla (2).
33. Circumnarial fossa, posterior margin: absent (0); presence of light depression incised into nasal and premaxilla (1); well demarcated, deeply incised, and usually invaginated (2).

34. Nasals and anterodorsal premaxilla in adults: flat, restricted to area anterior to braincase, *cavum nasi* small (0); premaxilla extended posteriorly and nasals retracted posteriorly to lie over braincase in adults resulting in a convoluted, complex narial passage and hollow crest, *cavum nasi* enlarged (1).
35. Solid nasal or nasofrontal crest over snout or braincase that does not house a portion of the nasal passage: absent (0); present (1).
36. Solid nasal crest, association with posterior margin of circumnarial fossa: absent, circumnarial fossa does not excavate side of crest (0); present, circumnarial fossa excavates lateral side of crest (1).
37. Nasal, solid crest composition: nasals only (0); frontals and nasals (1).
38. Maxilla, anterodorsal: has a separate anterior process that extends medial to the posteroventral process of premaxilla to form part of medial floor of external naris (0); forms sloping shelf that contacts the posteroventral process of premaxilla (1).
39. Maxillary foramen: opens on anterolateral maxilla (0); opens on dorsal maxilla along maxilla-premaxilla suture, exit of vessels facilitated by a groove across PM1 (1).
40. Maxilla, posterior extent of tooth row: terminated even with or anterior to the posterior end of the maxilla-jugal contact (0); extends posterior to the maxilla-jugal contact and beneath the ectopterygoid (1).
41. Nasal anterodorsal process, short (0); anteroventrally elongated and enlarged (1).
42. Lacrimal-maxilla contact: present (0); extremely reduced, only anterior sharp tip of lacrimal contacts maxilla (1); lost or covered due to jugal-premaxilla contact (2).
43. Apex of maxilla, location: posterior to center (0); at or anterior to center (1).
44. Jugal, anterior shape: with distinct anteriorly-pointed process fitting between the maxilla and lacrimal (0); truncated, rounded (1).
45. Jugal, pointed anterior process: process restricted to dorsal portion of jugal (0); process centered on anterior jugal, anterior jugal appears symmetrically triangular in shape (1); anterior jugal is truncated and rounded (2).

46. Jugal, development of a flange posteroventral to postorbital process and individualized from quadratojugal process: absent (0); slightly developed, the dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange is approximately equal to the minimum dorsoventral depth of anterior segment of jugal between anterior and postorbital process (1); present: dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange is less than double the minimum dorsoventral depth of anterior segment of jugal between anterior and postorbital process (2); strongly projected ventrally into a semicircular boss: dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange is at least double the minimum dorsoventral depth of anterior segment of jugal between anterior and postorbital process (3).
47. Frontal at orbit margin: forms part of margin (0); excluded by prefrontal-postorbital contact (1).
48. Supraorbital articulation: freely articulate on orbit rim in a single ossification (0); fused to orbit rim or absent (1).
49. Squamosals on skull roof, separation: widely separated (0); squamosals approach midline, separated by a narrow band of parietal (1); squamosals have broad contact with each other (2).
50. Squamosal, shape of posteroventral surface: nearly horizontal (0); "folded" down to form a near vertical face in posterior view (1).
51. Squamosal prequadratic process: short, only slightly longer than anteroposterior width of quadrate cotylus or dorsal head of quadrate (0); strikingly longer than anteroposterior width of quadrate cotylus or dorsal head of quadrate (1).
52. Transverse width of the cranium in the posterorbital region in dorsal view: broad, width maintained from orbit to quadrate head (0); distinctly narrowed at quadrate heads (1).
53. Occiput shape in posterior view: square (0); triangular, very narrow dorsally, distal quadrates splay distinctly laterally (1).

- 54. Parietal crest and supratemporal fenestra, length: longer than wide (0); crest very abbreviated, wider than long (1).
- 55. Parietal, midline ridge: straight to slightly downwarped along length (0); strongly downwarped, dorsal margin bends below the level of the postorbital-squamosal bar (1).
- 56. Quadratojugal, participation in lower temporal fenestra: present (0); absent due to jugal-quadrato contact (1).
- 57. Quadrate length relative to basal skull length: quadrate short, about 30-40 % basal skull length (0); quadrate long slightly less than 50 % skull length (1); quadrate very long, about 50 % or more of basal skull length (2).
- 58. Basisphenoid, relative size of alar process: process relatively small (0); process relatively large and very expanded (1).

Axial Column

- 59. Cervical vertebrae, number: 11 or fewer (0); 12-15 (1).
- 60. Cervicals, opisthocoely: absent or weak (0); present, strongly developed (1).
- 61. Sacral vertebrae, ventral surface of posterior sacrals: rounded or crested (0); grooved (1).
- 62. Sacral vertebrae, number: six or less (0); seven (1); eight or more (2).
- 63. Dorsal (posterior) and sacral neural spines: relatively short, less than 3 times centrum height (0); elongate, more than 3 times centrum height (1).
- 64. Caudal vertebrae, length of neural spines relative to respective chevrons: shorter than (0); equal or longer than (1).

Pectoral Girdle and Forelimb

- 65. Sternal plates: kidney shaped (0); hatchet shaped, posteroventral process developed (1).
- 66. Coracoid size: large coracoid/scapula lengths $> .2$ (0); coracoid reduced in length relative to scapula (1).

67. Scapula, proximal portion: dorsoventrally deeper than distal end of blade(0); dorsoventrally as deep as distal blade, acromion process projects horizontally, anteroventral corner notched (1); dorsoventrally narrow (no wider than distal scapula), acromion process projects horizontally, anteroventral corner notched (2).
68. Scapula, shape of dorsal margin of blade: concave or flat (0); convex (1).
69. Scapula, orientation of borders of blade: parallel borders with distal end rectangular (0); divergent (1).
70. Deltopectoral crest: short, much less than half the length of the humerus, narrows distally (0); extends at least to midshaft or longer, distally broad (1).
71. Humerus, deltopectoral crest shape in lateral view: rounded (0); angular (1).
72. Humerus deltopectoral crest, width: not wider than half the width of the shaft (0); wider than half of the shaft width (1).
73. Metacarpal III, relative position of proximal end: aligned with those of MC II and IV (0); offset distally relative to MC II and IV (1).
74. Metacarpal, shape: short and robust (0); slender and elongate (1).

Pelvic Girdle and Hindlimb

75. Ilium, shape of dorsal margin: nearly straight (0); distinctly arched dorsally (1).
76. Ilium, postacetabular process: tapers posteriorly to nearly a point (0); rectangular and moderately deep (1).
77. Ilium, length of postacetabular process relative to total length of ilium: less than or equal to 0.3 (0); more than 0.3 (1).
78. Pubis, distal width of prepubic blade: only slightly dorsoventrally expanded (0); dorsoventrally expanded to no more than two times shaft width (1); greatly expanded to more than twice shaft width (2).
79. Pubis, length of prepubic process: elongate, terminates well in front of iliac preacetabular process (0); short, it does not extend beyond iliac preacetabular process (1).

80. Pubis, length of prepubic shaft: long, dorsoventral expansion restricted to distal process (0); neck short, dorsoventral expansion begins almost at base of process (1).
81. Pubis, length of postpubic rod: extends closer to end of ischium, ending past half way down ischium (0); terminates half way down ischium or less (1).
82. Ischium, mediolateral width of shaft posterior to obturator process: broad, slight foot (0); narrow with virtually no foot or tapered (1); broad, large and pendant foot (2).
83. Femur, shape of fourth trochanter: pendant (0); triangular (1).
84. Fibula shape: narrows quickly distally (0); narrows only slightly distally (1).
85. Pes, distal phalanges of pedal digits II through IV: relatively axially elongate (0); axially shortened to disc-like elements with width at least three times length (1); greatly shortened, width at least four times length (2).
86. Pes, shape of unguals: taper evenly distally, claw-like (0); arrow-like distal edge, not strongly flattened dorsoventrally, twice as wide mediolaterally than thick dorsoventrally, hoof-like (1); dorsoventrally flattened and broadened (more than twice as wide mediolaterally than thick dorsoventrally), semicircular distal border, hoof-like (2).
87. Pes, plantar keel on unguals: absent (0); present (1).

Characters 1, 2, 7, 11, 13, 26, 32, 35, 42, 45, 57, 61, 67, 69, 77, 79, 81 and 86 modified from Horner, Weishampel, and Forster (2000).

Characters 3-6, 8-10, 12, 14-16, 19-24, 27-31, 33, 34, 36-40, 43, 44, 47-50, 52-56, 59, 60, 62-66, 68, 70, 71, 73-76, 78, 80, and 83-85 from Horner, Weishampel, and Forster (2000).

Data Matrix of Character States

[illegible]

	3				3				4				4				5								
	0				5				0				5				0								
<i>Tenontosaurus</i>	0	0	0	0	0	0	0	0	0	0	-	-	?	0	0	0	0	?	0	0	3	0	0	0	0
<i>Iguanodon</i>	0	0	0	0	0	0	1	0	0	0	-	-	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Maisaura</i>	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	1	3	0	1	1	1
<i>Brachylophosaurus</i>	1	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	1	3	0	1	1	1
<i>Gryposaurus</i>	1	1	1	1	0	1	0	1	0	0	-	-	0	0	1	1	0	1	0	0	2	0	1	1	1
<i>Prosaurolophus</i>	1	1	?	1	0	1	1	2	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	1	1
<i>Edmontosaurus</i>	1	1	1	1	0	1	1	2	0	0	-	-	0	0	1	1	2	1	0	0	2	0	1	2	1
<i>Hypacrosaurus</i>	1	?	?	0	1	1	2	-	1	0	-	-	1	1	1	-	2	0	1	2	1	1	1	2	1

[illegible]

	8							8				
	0							5				
<i>Tenontosaurus</i>	0	1	0	0	0	0	1	0	0	0	0	0
<i>Iguanodon</i>	0	0	1	0	0	1	0	0	0	1	0	0
<i>Maisaura</i>	1	0	1	0	0	1	1	1	0	1	2	1
<i>Brachylophosaurus</i>	1	0	1	0	0	1	1	1	0	1	2	1
<i>Gryposaurus</i>	1	1	1	0	0	1	1	1	1	?	2	0
<i>Prosaurolophus</i>	1	1	1	0	0	1	1	1	1	2	1	0
<i>Edmontosaurus</i>	1	0	1	0	0	1	1	1	0	?	2	0
<i>Hypacrosaurus</i>	1	1	2	1	1	1	2	1	1	2	2	0

Phylogenetic Relationships and Synapomorphies

Tenontosaurus + *Iguanodon* + Hadrosauridae

1. Angular small, dorsoventrally narrow, and exposed only in medial view. 19(1)

Iguanodon + Hadrosauridae

1. Posterior extend of maxillary tooth row extends posterior to the maxilla-jugal contact and beneath the ectopterygoid. 40(1)
2. Posteroventral surface of squamosals is "folded" down to form a near vertical face in posterior view. 49(1).
3. Strongly developed opisthocoely on cervical vertebrae. 59(1).
4. Grooved ventral surface of posterior sacral vertebrae. 60(1)
5. Hatchet shaped sternals, with posteroventral process developed. 64(1).
6. Postpubic rod of pubis terminates half way down ischium or less. 80(1).

Hadrosauridae

1. Dental batteries with continuous occlusal surfaces formed from closely packed tooth families, grooves on anterior and posterior sides of the roots of cheek teeth for reception of the crowns of the adjacent teeth. 3(1).
2. From 3 to 5 replacement teeth per tooth position. 4(1).

3. Up to three, and at least two teeth in the vertical series contribute to the occlusal surface. 5 (1).
4. Lanceolate maxillary teeth crown, having crown length/width ratio of at least 2.5:1. 6 (1).
5. Loss of all bur primary carina on labial surface of maxillary teeth. 9(2)
6. Apex on teeth is central, tooth straight and nearly symmetrical. 10(1)
7. Extent of dentary tooth row posterior relative to apex of coronoid process. 12(1)
8. Dentary tooth row is straight in occlusal view. 14(1)
9. Shovel-shaped prementary, straight transverse anterior margin, foramina numerous and located just below anterior. 15(1)
10. Horizontal Prementary triturating surface. 16(1)
11. Absence of coronoid bone. 20(1)
12. Posteroventral dentary terminates well posterior to coronoid process. 21(1)
13. Absence of surangular foramen. 22(1)
14. Surangular restricted in position below tooth row. 23(1)
15. Horse-shaped premaxillary anterior bill margin. 26(1)
16. Supraorbital fused to orbit rim or absent. 47(1)
17. In posterior view, the occiput is triangular, very narrow dorsally, and distal quadrates splay distinctly laterally. 52(1)
18. Eight or more sacral vertebrae. 61(1)
19. Coracoid reduced in length relative to scapula. 65(1)
20. Scapula with convex shape of dorsal margin of blade. 67(1)
21. Metacarpal III is offset distally relative to MC II and IV. 72(1)
22. Slender and elongate metacarpals. 73(1)
23. Dorsal margin of ilium is distinctly arched dorsally. 74(1)
24. Rectangular and moderately deep postacetabular process of ilium. 75(1)
25. Triangular shape of fourth trochanter on femur. 82(1)

Hadrosaurinae

1. Loss of all but primary carina on lingual surface of dentary teeth. 8(2)
2. Presence of circumnarial fossa.
3. Presence of accessory foramen on anterior narial fossa, located anterior to premaxillary foramen and emptying into common chamber with premaxillary foramen. 28(1)
4. Auxiliary narial fossa anterior to circumnarial fossa. 29(1)
5. Apex of maxilla located at or anterior to center. 42(1)
6. Nasal with anteroventrally elongated and enlarged anterodorsal process. 41(1)
7. Scapula with dorsoventrally narrow proximal portion (not wider than distal scapula), acromion process projects horizontally, anteroventral corner notched. 66(2)

Maiasaura + Brachylophosaurus

1. Anterior mediolateral width of prementary doubles the anteroposterior length of the lateral processes. 17(2)
2. Posterior margin of circumnarial fossa does not excavate side of nasal/nasofrontal solid crest. 36(0)
3. Posteriorly reflected, anteriorly deflected premaxillary rim. 25(2)
4. Pointed anterior process of jugal centered on anterior region of the element, being triangular and symmetrical in shape. 44(1)
5. Relatively large and very expanded alar process of basisphenoid. 57(1)
6. Presence of plantar keel on pedal unguals. 86(1)

Gryposaurus + Prosaurolophus + Edmontosaurus

1. Flange posteroventral to postorbital process and individualized from quadratojugal process: dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange is less than double the minimum

dorsoventral depth of anterior segment of jugal between anterior and postorbital process. 45(2)

2. Squamosal prequadratic process is equal or longer than anteroposterior width of quadrate cotylus or dorsal head of quadrate. 50(1)
3. Reflected premaxillary rim, anteriorly and posteriorly. 25(3)

Prosaurolophus + Edmontosaurus

1. Posterior margin of circumnarial fossa present and well demarcated, deeply incised, and usually invaginated. 33(2)
2. Posteriormost apex of external nares formed by nasal (dorsally) and premaxilla (ventrally). 32(1)

Hypacrosaurus

1. Dentary tooth crown length/width proportions at the center of tooth row, 4 or more to 1. 7(2)
2. Triangular, non-bifurcated ventral process on prementary. 18(1)
3. Both posterior processes of premaxilla elongate posteriorly to join behind external nares excluding nasals; nasal passage enclosed ventrally by folded, divided premaxillae. 30(1)
4. Posteriormost apex of external nares formed by premaxilla. 32(2)
5. Anterodorsal region of maxilla forms sloping shelf that contacts the posteroventral process of premaxilla. 38(1)
6. Maxillary foramen opens on dorsal maxilla along maxilla-premaxilla suture, exit of vessels facilitated by a groove across PM1. 39(1)
7. Truncated and rounded anterior jugal. 43(1)
8. Parietal crest very abbreviated, wider than long. 53(1)
9. Dorsal (posterior) and sacral neural spines elongate, more than 3 times centrum height 62(1).
10. Length of caudal neural spines equal or longer than length of chevrons. 63(1)

11. Proximal region of scapula dorsoventrally as deep as distal blade, acromion process projects horizontally, anteroventral corner notched. 66(1)
12. Dorsoventrally greatly expanded prepubic blade of pubis to more than twice shaft width. 77(2)
13. Short prepubic blade, it does not extend beyond iliac preactabular process. 78(1)
14. Pubic neck short, dorsoventral expansion begins almost at base of the blade. 79(1)
15. Presence of broad, large and pendant foot at distal ischium. 81(2)

Tree length: 138; Consistency Index: 0.83; Retention Index: 0.68; Rescaled Index: 0.56.

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