**A redescription of the holotype of *Brachylophosaurus canadensis* (Dinosauria:
Hadrosauridae), with a discussion of chewing in hadrosaurs**

by

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B.Sc. Zoology

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the Faculty of Graduate Studies and Research
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ABSTRACT

The holotype of *Brachylophosaurus canadensis* was collected by C.M. Sternberg in 1936 from the Oldman Formation (Upper Cretaceous) of Alberta, Canada, and a brief description focusing on cranial characters followed in 1953. A redescription of the holotype cranium and postcrania confirms its position as a hadrosaurine dinosaur exhibiting the following derived features: paddle-like solid nasal crest; posteriorly elongated prefrontal; only the anterior tip of the lacrimal contacting maxilla; jugal with ventrally projected semicircular flange that is deeper than *Maiaasaura peeblesorum*, but more lightly built than remaining hadrosaurines; extremely elongated anterior maxillary process; and a quadratojugal with a non-crescentic posterior margin forming a paraquadratic foramen with the quadrate. Also, numerous morphological differences are identified with recently described specimens of *Brachylophosaurus*. Based on cranial joints and their kinematic limitations, the dynamic streptostyly mechanism cannot be recreated in *Brachylophosaurus*. A simplified model with a mandible capable of slight propalinal movement and minimal medial rotation about its long axis cannot be rejected.

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LIST OF ABBREVIATIONS

apu	anterior process of ulna	l	lacrimal
boc	basioccipital	lpu	lateral process of ulna
bsf	basisphenoid flange	ls	laterosphenoid
c	centrum	mc	metacarpal
cap	capitulum	mx	maxilla
cn	cranial nerve	na	nasal
co	cotyle	nc	neural canal
con	condyle	ns	neural spine
cp	coronoid process	od	odontoid
d	diapophysis	op	olecranon process
df	deltoid fossa	ops	opisthotic
dn	dentary	p	parietal
dr	deltoid ridge	par	parapophysis
ect	ectopterygoid	pmx	premaxilla
exo	exoccipital	pmx1	posterolateral premaxillary process
exoc-op	exoccipital-opisthotic	pmx2	posterodorsal premaxillary process
f	frontal	po	postorbital
fm	foramen magnum	poz	postzygapophysis
g	glenoid	pozp	postzygapophyseal process
ic	intercentrum	pozf	postzygapophyseal flange
itf	infratemporal fenestra	ppbs	pterygoid process of basisphenoid
j	jugal	pqf	paraquadratic foramen

prf	prefrontal
prs	presphenoid
prz	prezygapophysis
ps	parasphenoid
pt	pterygoid
pvpbs	posteroventral process of basisphenoid
px	phalanx
q	quadrate
qj	quadratojugal
rs	rib shaft
s	surangular
sb	scapular blade
soc	supraoccipital
spc	sternal process of coracoid
sq	squamosal
stf	supratemporal fenestra
tub	tuberculum

CHAPTER I

INTRODUCTION

The Hadrosauridae is a diverse family of Upper Cretaceous ornithischian dinosaurs (Carroll, 1988). They are derived ornithopods that are most distinctively characterized by their highly specialized dentition. Tooth rows are tightly arranged into grinding dental batteries, with each tooth family consisting of three or more replacement teeth (Horner *et al.*, 2004). This arrangement suggests that hadrosaurs were highly efficient herbivores.

The ancestry of this group has been traced in general terms to the relatively primitive iguanodontids. The family is currently divided into two subfamilies, the Hadrosaurinae and Lambeosaurinae (Horner *et al.*, 2004). The Lambeosaurinae is diagnosed by a well-developed crest that is commonly derived from the premaxillae and nasal bones, as observed in members such as *Corythosaurus*, *Parasaurolophus*, or *Hypacrosaurus* (Horner *et al.*, 2004). Members of the Hadrosaurinae lack a cranial crest, or possess a solid crest that is composed of nasal bone as observed in *Brachylophosaurus canadensis*, or nasal and frontal bone as is the case in *Maiasaura peeblesorum* (Sternberg, 1953; Horner, 1983).

Horner (1988) has hypothesized a diphyletic origin of the family. He argued that the hadrosaurines shared more synapomorphies with *Iguanodon bernissartensis*, and the lambeosaurines were more closely related to *Ouranosaurus nigeriensis*. However, this theory has since been rejected and the monophyly of the Hadrosauridae is now generally accepted.

Fossil evidence suggests an Asian or North American geographic origin for hadrosaurs. However, their true origin and subsequent migration pattern remains a topic of controversy (Head, 1998; You *et al.*, 2003). These dinosaurs first occur in the Late Cenomanian and persist into the Late Maastrichtian, making hadrosaurs one of the last ornithopod groups to appear in the Mesozoic. Hadrosaurs are currently represented by approximately 27 genera and enjoyed a near cosmopolitan distribution throughout their evolution (Forster, 1997). They have been extensively described from North America (Lull and Wright, 1942), most notably from Campanian bone beds of Alberta, Canada and Montana, USA (Horner and Makela, 1979; Horner, 1982). Hadrosaurs have also been documented within Asia and Europe (You *et al.*, 2003; Bolotsky and Godefroit, 2004; Horner *et al.*, 2004), with fewer reports from South America (Brett-Surman, 1979) and Antarctica (Case *et al.*, 2000).

Of all the dinosaurs, hadrosaurs may provide the most complete look into one group's ontogeny, morphology, physiology, and social dynamics. Adult hadrosaurs were large, exhibiting an average body size of 3000 kg and an average length of 7 – 10 m (Horner *et al.*, 2004), with some of the largest hadrosaurs attaining lengths of up to 15 m (Forster, 1997). Hatchlings probably weighed less than 1 kg at birth (Horner *et al.*, 2004). Evidence from long bone histology in *Maiaasaura peeblesorum* indicates that growth was rapid. Study of ontogenetic changes indicates six separate growth stages: early and late nestling, early and late juvenile, and sub-adult and adult (Horner *et al.*, 2000).

Hadrosaurs appear to have exhibited gregarious behaviour with complex group dynamics (Varricchio and Horner, 1993). Work by Horner and Makela (1979) and

Horner (1982; 1984; and 1999) provides evidence of colonial nesting and social structure in *M. peeblesorum*. Fossil remains of fifteen young *M. peeblesorum* (each approximately 1 m in length), still within the nest, imply an altricial dependence and extended parental investment. Consequently, adults would have been required to return to the nest with food, or alternatively, the young would have ventured out with the parents to forage. Gregarious behaviour and consequent herding may have also served a defensive function. This “strength in numbers” strategy is compatible with the absence of any evidence of physical defensive structures (i.e. claws, horns, armor, etc.) among hadrosaurs.

The functional significance of hadrosaurian cranial crests has long been debated. Hadrosaurs are believed to have been capable of vocalization, which may have permitted intraspecific communication (e.g. alarm calling) and reduced predation on the herd. Vocalization among the lambeosaurines may have been facilitated by the passage of air through the complex narial passage of their hollow crest (Heaton, 1972), which possibly functioned as a resonating chamber to amplify sound (Ostrom, 1961; Hopson, 1975). In addition to acting as a vocalization device for intraspecific communication, Hopson (1975) suggested that differences in crest morphology were used as visual cues for species specific recognition. This theory is supported by a diversity of crest development between the two subfamilies of hadrosaurs, ranging from the non- and solid-crested condition in hadrosaurines, to the elaborately developed hollow crests of lambeosaurines. In addition, Dodson (1975) identified what he thought to be sexual dimorphism of crest morphology among lambeosaurine hadrosaurs, further supporting the role of crests as intraspecific visual cues. Although hadrosaurines lacked an elaborate crest, they did appear to have had a narial diverticulum located on the circumnarial depression of the

skull. This feature has been preserved in a mummified specimen of *Edmontosaurus* (Lull and Wright, 1942). It has since been interpreted as a fleshy and inflatable display organ that was functionally analogous to that of the lambeosaurine crest (Hopson, 1975).

Charles M. Sternberg (1885-1981) collected the type specimen of the hadrosaurine dinosaur *Brachylophosaurus canadensis* in 1936 from sandstone sediments of the Oldman Formation (Belly River Group), located in what is now Dinosaur Provincial Park - Alberta, Canada (fig. 1). Although the original description (Sternberg, 1953) included an excellent lateral photograph of the skull, the postcranial skeleton was incompletely described and illustrated.

More recently, specimens of *B. canadensis* have been reported from the lower Judith River Formation of northeastern Montana (Prieto-Márquez, 2001; and 2005). However, since the type specimen (NMC 8893) had been mounted for display at the time, detailed comparison with this new material was not possible. Consequently, a premature revision of the taxon was completed without revisiting the holotype. The type material has since been removed from exhibit and is now available for study.

The purpose of this study is to: 1) Describe in detail the anatomy of the type specimen of *B. canadensis* (NMC 8893), including an evaluation of cranial kinesis and chewing mechanics. 2) Compare the anatomy of NMC 8893 to other recently described Montana specimens of *B. canadensis* and other hadrosaurines. 3) Use 1 & 2 as the basis for a review of the previous cladistic analysis used to establish the taxonomic position of *B. canadensis* within the Hadrosauridae.

Figure 1. Holotype location of *Brachylophosaurus canadensis* (modified from Weishampel *et al.*, 2004)

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
 ORNITHISCHIA Seeley, 1888
 ORNITHOPODA Marsh, 1881
HADROSAURIDAE Cope, 1869
 HADROSAURINAE Lambe, 1918
BRACHYLOPHOSAURUS Sternberg, 1953
BRACHYLOPHOSAURUS CANADENSIS Sternberg, 1953

Modified from Sternberg (1953):

Holotype – No. NMC 8893, Canadian Museum of Nature (previously National Museum of Natural Sciences, National Museums of Canada); consists of skull, partial hyoids, all 14 cervicals, the anterior nine dorsal vertebrae, ribs, complete right scapula, complete right coracoid, humeri, left ulna and radius, and partial left manus.

Horizon – Oldman Formation of Belly River Group (Weishampel *et al.*, 2004), Upper Cretaceous (Late Campanian), 7.5 meters below the Dinosaur Park Formation-Oldman Formation contact (pers. com. David Evans).

Geological Setting – The Belly River Group represents a clastic wedge composed of the Foremost, Oldman, and Dinosaur Park Formations, of which the upper 20 m of the Oldman and the entire Dinosaur Park Formations are exposed within Dinosaur Provincial Park (fig. 2). Light coloured alluvial sandstones and mudstones comprise the southwest thickening Oldman Formation. The sandstones are “very fine grained to fine grained, contain no extraformational pebbles or cobbles, and crop out as yellow, steep-faced, and blocky surfaces” (Eberth, 2005). Strata are commonly horizontal to low angle inclined, indicating shallow, high velocity, ephemeral flow of low-sinuosity fluvial systems (Eberth, 2005). The Cretaceous climate of the alluvial-coastal plains of Dinosaur

Figure 2. Stratigraphy of Belly River Group at Dinosaur Provincial Park. Abbreviations: IHS, inclined heterolithic strata; c.z., coal zone; ss., sandstone (Eberth, 2005).

Provincial Park has been interpreted as warm and temperate, and this is supported by palynomorphs and macroplant fossils from the area (Braman and Koppelhus, 2005; Koppelhus, 2005). Conifers formed much of the denser canopy, and ferns, tree-ferns, and flowering plants formed much of the understory. The groundcover included mosses, lichens, fungi, small ferns, lycopods, and angiosperms (see Braman and Koppelhus [2005] and Koppelhus [2005] for species lists).

Locality – Little Sandhill Creek, NE. ¼, sec. 6, tp. 21, rge. 11, W. of 4th mer., 60 feet above Red Deer River, Alberta.

Emended Diagnosis – Revised from Prieto-Márquez (2005): nasals greatly developed into paddle-like solid crest extending posterodorsally, overhanging dorsal region of skull; prefrontal projecting posteriorly over frontal, and more posteriorly, ventromedially directed to underlie nasal crest and contribute to anterior border of supratemporal fenestra; only anterior sharp tip of lacrimal contacting maxilla; jugal with ventrally projected semicircular flange deeper overall than that of *M. peeblesorum* but more lightly built than all other known hadrosaurines; extremely elongated, rod-like anterior maxillary process projecting medial to narial cavity; and rhomboidal quadratojugal with non-crescentic posterior margin forming paraquadratic foramen with quadrate.

Institutional abbreviations – CMN, Canadian Museum of Nature (formerly National Museum of Natural Sciences, National Museums of Canada); FMNH, Field Museum of Natural History; MOR, Museum of the Rockies; RTMP, Royal Tyrrell Museum of Paleontology; UCMP, University of California, Museum of Paleontology.

CHAPTER II

MATERIALS AND METHOD

During the original preparation, the skull was partially disarticulated, allowing the left maxilla and associated bones to be photographed and studied in medial view (Sternberg, 1953, plate XXXIX). Subsequently, the skull was reassembled using steel armature for the purpose of mounting the skeleton for exhibition. Unfortunately, this armature lines the internal skull, obscuring some details. Also, the centra of the vertebrae were drilled so that they could be strung along a steel rod, and were then backfilled with plaster. The vertebrae have since been separated from the steel rod, but permanent damage has been done to these bones, especially to the dorsal series.

The analysis of the holotype of *Brachylophosaurus canadensis* (NMC 8893) comprised three parts.

1) Slide Film Imaging and Reconstruction

Slide film images were taken and scanned to document the actual preservational quality of the fossil material, including any distortion or damage. Outline tracings of projected slide film images at ½ original size provided a template from which reconstructive drawings were made. Proportional dividers were used to take measurements directly from the specimen in order to correct for photographic parallax or foreshortening, and damage or distortion produced during preservation. The corrected image was then further reduced to ¼ its original size and traced on to strathmore paper. Inking was done using a Rapidograph® pen. The skeletal reconstructions of *B. canadensis* provide a basis upon which comparisons with other hadrosaur taxa can be made.

2) Morphological Description and Comparison

A thorough anatomical description, including a review of cranial joint morphology, was completed for *B. canadensis*. Comparative material from the Royal Tyrrell Museum, Drumheller, and the Royal Ontario Museum, Toronto was examined. Analysis included 1) A detailed comparison with other specimens of *Brachylophosaurus* in order to diagnose the species and to determine the range of intraspecific variation. 2) A comparison with closely related hadrosaurines. The disarticulated skull of *Edmontosaurus regalis* (NMC 2289) was laser scanned in colour by the Arius 3D lab (CMN) using 3D camera technology. The scanned data was then imported into animation software 3DS Max V.8 and the skull was digitally reassembled by the 3D Arius lab and myself. Using a series of animation techniques (inverse kinematics, wiring system, and keyframing), the Arius lab created a biokinematic animation of the streptostyly chewing mechanism, as applied to *Edmontosaurus* (Appendix IV). With the cranial joints described for *B. canadensis*, the chewing mechanics of the streptostyly model were evaluated for the holotype skull. 3) A more general comparison with other hadrosaurs, both hadrosaurine and lambeosaurine.

3) Phylogenetic Analysis

The morphological analysis of *B. canadensis* was then applied to the most recent phylogenetic analysis of hadrosaurs (Horner *et al.*, 2004), and characters in the latter were reevaluated and recoded where necessary. The resulting data matrix was input to MacClade 4.03 and analyzed using PAUP 4.0b10 (Swofford, 1999), and a new hypothesis of relationships of the Hadrosauridae was generated.

CHAPTER III

OSTEOLOGY

The skull of the holotype of *Brachylophosaurus canadensis* is virtually complete. Most of the skull elements remain in articulation, obscuring some aspects of its constituent bones. Nevertheless, it provides the basis for a comprehensive description and comparison to other hadrosaurs. The descriptive osteology for the axial and appendicular skeleton is also completed, providing details not included in the original holotype description (Sternberg, 1953).

Skull

Facial Unit (figs. 3, 4, 5, 6; plate I)

Premaxilla – The coossified premaxillae comprise a single median element (hereafter referred to as the premaxilla) composed of an anterior beak and slender radiating posterodorsal and posterolateral processes. The premaxilla forms the majority of the deep nasal arch that is characteristic of *B. canadensis*, and much of the borders of the external nares. Anteriorly, the oral margin of the premaxilla is ventrally deflected in contrast with the dorsally reflected state observed in other hadrosaurines such as *Edmontosaurus regalis* (NMC 2288) and *Gryposaurus notabilis* (NMC 2278). Lateral expansion of the oral margin produces a spatulate shape when viewed dorsally. The anterior oral margin of the premaxilla is rugose, especially so on its anteroventral surface. Although poorly preserved, ventrally projecting denticles are present along the anterior premaxillary oral margin. Just posterior to these denticles, in a shallow sulcus on the palatal surface of the premaxilla, is a series of circular divots that likely represent the

Figure 3. Left lateral reconstruction of skull

Figure 4. Dorsal reconstruction of skull

Figure 5. Posterior reconstruction of skull

Figure 6. Anterior reconstruction of skull

“small circular foramina” of Prieto-Márquez (2001). This area is poorly preserved however, and the sulcus is most obvious on the left lateral premaxillary oral margin.

The premaxilla is laterally and dorsally excavated just posterior to the oral margin at the base of the posterodorsal premaxillary process, forming the anterior extent of the outer narial depression. The type specimen of *B. canadensis* lacks any evidence of an accessory premaxillary foramen that was reported in other *B. canadensis* specimens (Prieto-Márquez, 2005). Positioned just posterior to the outer narial depression is the forward extent of a poorly developed circumnarial depression. The anterior margin of the circumnarial depression is perforated by a conspicuous premaxillary foramen (Sternberg, 1953), that bifurcates as it descends towards the palatal surface of the premaxilla. The circumnarial depression is continued posteriorly as a concavity running along the lateral surface of the ascending posterolateral premaxillary process (posteroventral process of Prieto-Márquez [2005]), and terminates posteriorly as a gentle bowl-like depression just posterior to the external naris.

The thin posterolaterally directed premaxillary process bears a horizontal trough on its medial surface to accommodate an anterior process of the maxilla. The trough is of near constant width for most of its length, but opens slightly near its anterior end, as it slants ventromedially towards its anterior limit. All surfaces forming the trough are smooth, suggesting that there was no sutural connection with the anterior maxillary process. The dorsal edge of the posterolateral process gently flares laterally, forming almost the entire ventral border of the external naris. The ventral border rests on the dorsolateral surface of the anterior maxilla and curls dorsolaterally. The posterolateral

process flattens to a thin slip of bone as it continues posterodorsally and begins to overlap the lateral surface of the nasal. A narrow gap between the ventral border of this process and the dorsal edge of the lacrimal exposes a small section of the more medially placed nasal. Posteriorly, the posterolateral process contacts the dorsal margin of the lacrimal, causing the gap between the bones to narrow. The posterolateral process then overlaps the anterior prefrontal before terminating at the prefrontal's contact with the nasal above.

The steeply ascending posterodorsal process creates the tall nasal arch characteristic of *B. canadensis*. Its ventral surface forms most of the dorsal margin of the external naris. As it projects dorsally it tapers to a point that inserts itself medial to the anterior nasal. The posterior extent of this process is approximately in line with the anterior limit of the anteroventral maxillary process.

Maxilla – The maxilla, bearing the upper dental battery, is a large triangular bone that articulates with the premaxilla anteriorly, laterally with the jugal, posterodorsally with the ectopterygoid, posteriorly with the pterygoid, and posteromedially with the palatine. The anterolateral surface of the maxilla is longitudinally concave. More posteriorly the lateral surface flattens, and its ventral margin forms the border of the curved maxillary tooth row. Anteriorly, the dorsolateral surface is dominated by an excavation that forms a flattened, anteroventrally sloped shelf (anteroventral process of Prieto-Márquez [2001; 2005]) to receive the ventral surface of the posterolateral premaxillary process.

Immediately posterior to the anteroventral process, the lateral maxillary surface is pierced by a large maxillary foramen, which may have delivered neurovasculature to the nasal vestibule (Horner *et al.*, 2004). Its medial perforation is not visible, but it may have been

obscured by steel mounting armature or the displaced left vomer. Three additional smaller maxillary foramina are present; one located immediately posterior to the main maxillary foramen, and two just ventral to the anterior portion of the jugal facet.

The rugose jugal facet dominates the dorsolateral surface of the maxilla at its approximate midlength. Posterior to this facet, a flattened shelf to accommodate the ectopterygoid forms the dorsolateral maxillary surface and gently slopes ventrally at its posterior extent. A small, gently striated process (posterior maxillary process of Heaton [1972]; posteromedial pterygoid process of Prieto-Márquez [2005]) originates medial to the ectopterygoid shelf for articulation with the pterygoid, and projects posteriorly to reinforce the maxillary/pterygoid articulation. Posteroventral to this process, the maxilla terminates in a rounded facet that is cupped from behind by the ectopterygoid ramus of the pterygoid.

Projecting anteriorly from the anteromedial surface of the maxilla is an elongate, mediolaterally compressed, anterior maxillary process (anterodorsal process of Prieto-Márquez [2001; 2005]; medial rostral process of Horner *et al.* [2004]). This is a primitive hadrosaurine character (Horner *et al.*, 2004). The process is deepest posteriorly and tapers to a point anteriorly. The lateral surface is flat while the medial surface appears slightly concave. The anterior maxillary process projects anteriorly into a well-defined medial premaxillary trough, extending into the external naris.

A thin flange of bone (jugular process of Prieto-Márquez [2005]) projects dorsally from the posterior extent of the anterior maxillary process. Laterally offset from the dorsomedial surface of the maxilla, the flange articulates the medial surfaces of the anterior lacrimal and jugal. It is typically triangular in shape in other hadrosaurs;

however, deformation has obliterated its apex in the left maxilla and the entire flange is missing from the right element. Posterior to this flange, the anteriorly rising dorsomedial edge of the maxilla articulates with both the pterygoid and palatine. This surface is incomplete in the right element, and the left has been crushed and is partially obscured by the pterygoid and palatine, thus obscuring the details of their sutural union.

Some details of the medial aspect of the maxillae are not available from the holotype specimen. The left maxilla is obscured by the displaced left vomer, and both the right and left elements have steel armature attached to their medial surfaces. However, some observations can still be made. The medial surface is relatively flat in comparison to the lateral maxillary surface. Much of this surface is occupied by the dental lamina, which blocks the medial view of the dental battery. As noted by Prieto-Márquez (2001), a dorsally arched row of dental foramina marking the dorsal limit of the dental lamina is visible on the medial surface of the right maxilla. Although poor preservation makes it difficult to clearly delineate individual foramina in some cases, the morphology suggests that there is one dental foramen for each tooth row (Lull and Wright, 1942; Prieto-Márquez, 2001; and Horner *et al.*, 2004). A small groove, most prominent at the approximate midlength of the tooth row, is present just above the ventromedial maxillary surface. Its anterior extent is not preserved and the posterior limit is not clear. However, it appears to meet the ventromedial maxillary edge well anterior the posterior end of the tooth row. This groove, also noted by Lull and Wright (1942) and Prieto-Márquez (2001), may be a vascular channel (Lull and Wright, 1942).

Maxillary Teeth – The longitudinal curvature of the upper tooth row follows the contour of the maxilla. Teeth are tightly aligned adjacent to one another and each tooth crown

projects near vertically from the alveolar groove of the maxilla, giving the upper dental battery a more peg-like appearance than the lower dental battery. A maximum of 46 vertical tooth rows are present. This differs markedly from 49 reported by Sternberg (1953), as well as 40-43 reported in other specimens of *B. canadensis* (Prieto-Márquez, 2005). Individual tooth size is generally greatest towards the midlength of the tooth row. A continuous occlusal surface forms along their ventromedial surfaces. This surface is diagonal to the horizontal plane, faces ventromedially, and is formed by one functional tooth for each vertical tooth row. However, in a few positions, two teeth contribute to this surface. One functional tooth per tooth row is also seen in the paratype of *Edmontosaurus regalis* (NMC 2289). Each functional tooth in the holotype of *B. canadensis* bears a shallow divot on its occlusal surface. The lateral surface of each tooth forms a diamond-shaped enamelled crown bisected by a longitudinal carina, and is squared off at its apex. The enamel appears to be restricted to the lateral wall of the crown, with dentine forming the occlusal surface of the tooth, just as in other hadrosaurs (Lull and Wright, 1942). However, because the majority of the vertical tooth rows contribute only one functional tooth to the occlusal surface, ridges of enamel that normally occur between multiple functional teeth per tooth row are not present. This condition seems atypical, as Horner *et al.* (2004) report that one to two functioning teeth per tooth row is only observed in *Telmatosaurus*, while other hadrosaurids exhibit two to three. One functional tooth per tooth row also differs from other reports of *B. canadensis* (Prieto-Márquez, 2001; and 2005), where two teeth form the occlusal surface at each tooth row. Replacement teeth for each tooth row are covered by the dental lamina.

Consequently, a comparative count with other specimens of *B. canadensis* was not possible.

Nasal – Dorsally, the anterior projections of the nasals begin to diverge laterally from one another at approximately the posterior extent of the posterodorsal premaxillary process. Each nasal arm (anterodorsal process of Prieto-Márquez [2005]) cradles the posterodorsal premaxillary process laterally before tapering to a point anteriorly.

Although the nasal shares the dorsal border of the external naris with the premaxilla anteriorly, the posterior portion of the external naris is formed solely by a triangular, wedge-like extension of nasal bone (anteroventral process of Prieto-Márquez [2005]).

Laterally, the anteroventral nasal process is partially obscured by the posterolateral premaxillary process. However, its ventral border follows the dorsal margin of the lacrimal posteriorly, and eventually contacts the prefrontal along this same border, which lies medial to the posterior limit of the posterolateral premaxillary process. The dorsal suture between the medial prefrontal and lateral nasal tapers medially as it continues posteriorly. Posteriorly, it is obscured by the initiation of the nasal crest.

Dorsally, a swelling is present on the dorsomedial surface of the nasal, just above the posterior extent of the external naris. This feature is most similar to, although not as pronounced as, the condition seen in the holotype of *Gryposaurus notabilis* (NMC 2278). A similar structure occurs in *Aralosaurus*, *Naashoibitosaurus*, and *Lophorhynchon* (the laterally compressed “hump” or crest of Horner *et al.* [2004]). A less prominent second nasal swelling is present in the holotype of *B. canadensis*, just posterior to the first at the position of the anterior orbit. When viewed laterally, these nasal swellings, in combination with the deep nasal arch, give the skull of *B. canadensis* a distinctly dorsally

flat profile. These nasal swellings and flat dorsal profile do not appear to be as conspicuous in MOR 794, as figured by Prieto-Márquez (2005).

The nasal crest arises between the anterior and posterior nasal swellings. It begins as a slightly raised ridge on the dorsolateral nasal, and extends posteriorly as a solid, raised spatulate crest, widening through the interorbital region. The crest is dorsoventrally compressed, raised medially, and gently concave lateral to its midline. The bilateral concavity is most exaggerated posteriorly, where the lateral edge of the crest is slightly dorsally reflected. The crest covers all but the anterolateral corner of the upper temporal fenestra. This condition appears intermediate to robust and slender morphs described by Prieto-Márquez (2005). In the robust morph, the nasal crest totally covers the upper temporal fenestra, and in the slender morph the nasal covers only approximately half the width of the upper temporal fenestra.

Due to the articulated nature of the holotype skull, the ventral contact surface of the nasal crest is not visible, so the relationship between the nasal and the underlying bones cannot be ascertained. However, there is no indication that the relationships of these bones in the holotype differ significantly from that described in other *B. canadensis* specimens (see fig. 8A of Prieto-Márquez [2005]). Posteriorly, the nasal crest overrides the anterior border of the upper temporal fenestra, formed by a posteromedial extension of prefrontal, before suspending itself above the upper temporal fenestra.

Lacrima – The lacrimal is a triangular bone that is bound by the prefrontal above and the jugal below. Its posterior surface, which partially forms the anterior orbital margin, is pierced by a conspicuous lacrimal foramen (lacrimal canal of Horner *et al.* [2004]). The internal surface of the lacrimal is poorly preserved and the path of this foramen is not

clear, nor is the internal relationship of the lacrimal and prefrontal. However, a triangular orbital prefrontal process is seen on the posterior lacrimal surface extending above the lacrimal foramen to help unite the lacrimal to the prefrontal, and reinforce the anterior orbit.

Ventral to the lacrimal foramen, the lacrimal contacts the jugal with a stout jugal process (see Chapter VI for interpretation of this joint). Its medial surface is difficult to interpret due to previous repair work. This contact can be traced laterally where the lacrimal exhibits a distinct concavity that accommodates a small dorsal process of the anterior jugal process. Anterior to this depression, the lacrimal is deflected ventrally and tapers to a slender anterior maxillary process that contacts the lacrimal flange of the maxilla medially. The ventral descent of the anterior maxillary process follows the dorsal margin of the jugal laterally, and the anterior tip extends well past the anterior limit of the jugal, terminating on the lateral maxilla. This area is identified just above the main maxillary foramen by a small ridge that represents the dorsal edge of a well defined articular facet.

The dorsal margin of the anterior maxillary process of the lacrimal approximately parallels the ventral border of the anteroventral nasal process before overlapping its lateral surface, just ventral to the anteroventral corner of the prefrontal. In this region, the dorsolateral lacrimal is overlapped by the prefrontal.

Jugal – The jugal forms the cheek and lower margins of both the orbit and lower temporal fenestra. Anteriorly, the jugal comprises a symmetrical, triangular shaped maxillary process. The process is mediolaterally compressed, thinnest at its anterior limit and thickest posteriorly, and firmly articulates the jugal facet of the lateral maxilla. The

attenuating anterior tip is incomplete in both left and right elements, and the presence of an anteroventral arch described by Prieto-Márquez (2005) cannot be confirmed. The posterior limit of the maxillary process is dorsoventrally flared. A small triangular process projects from the dorsal margin of the maxillary process and fits into a concavity on the ventrolateral surface of the lacrimal. Posterior to this process, the jugal swells laterally to form its articular surface for the jugal process of the lacrimal (see Chapter VI for interpretation of this joint). The medial surface of the posterodorsal maxillary process is not well preserved, making it difficult to interpret its articulation with the anterolateral jugal process of the palatine.

The jugal constricts dorsoventrally posterior to the maxillary process to form the ventral rim of the orbit as it thins mediolaterally. Both the lateral and medial surfaces are smooth. More posteriorly, the jugal projects an ascending, posteromedially directed postorbital process. This process forms the posteroventral corner of the orbit before thinning anteroposteriorly to cradle the jugal process of the postorbital posteriorly. Slight lateral twisting of the anterior face of the postorbital process is observed as it accommodates the jugal process. A distinct groove on the proximal anterior face of the postorbital process accommodates the distal tip of the descending jugal process of the postorbital.

As noted by Prieto-Márquez (2005), an oval boss expands from the ventral margin of the jugal at its approximate midlength. It thickens slightly mediolaterally, and only thins minimally at its distal edges. Distinct striations are visible on both its medial and lateral margins. Posteriorly, the dorsal margin of the jugal forms the ventral rim of the lower temporal fenestra. At its posterior extent, the jugal flares dorsoventrally to

form the quadratojugal process. The medial surface of this process is striated and gently excavated, its dorsal extent clearly identified by a ridge following the dorsomedial margin of the element. This condition is more developed in *Edmontosaurus regalis* (NMC 2289), in which the anteroventral margin of the excavation is deeper and ends abruptly in a distinct slot to accommodate the quadratojugal.

Prefrontal – The prefrontal forms the anterodorsal corner of the orbital rim and contributes minimally to the dorsal skull roof. It exhibits a solid union with the lacrimal. In the anterodorsal corner of the orbit, the prefrontal interlocks with the orbital prefrontal process of the lacrimal, and the anterolateral prefrontal overlaps the medially placed lacrimal. Anteromedially, the prefrontal contacts the nasal. Although this suture is partially concealed by the overlapping posterolateral premaxillary process, their contact becomes visible posterior to the posterolateral premaxillary process as the suture tapers medially before being obscured by the nasal crest above.

The dorsoventrally compressed lateral margin of the prefrontal flares laterally to form the anterodorsal portion of the orbital rim. A small supraorbital foramen pierces its dorsal surface at this point. Posterior to this foramen, the anterodorsal orbital rim becomes increasingly thickened and rugose. At approximately the midlength of the dorsal orbital rim, the prefrontal contacts the frontal. Sternberg (1953, plate XXXVIII) clearly indicated the ventral prefrontal-frontal orbital suture. Although the original ink tracing is still visible on the type specimen, some of the bone surface in this area has been restored, casting doubt on the accuracy of the course of the suture. Dorsally, the contact of the prefrontal and frontal is clearly visible, as the prefrontal tapers medially with its dorsolateral suture overriding the frontal and paralleling the lateral margin of the nasal

crest. Posteriorly, this extension of the prefrontal extends posteriorly over the transverse contact of the parietal and frontal, and turns medially to form the anterior border of the upper temporal fenestra. This portion of the prefrontal is overridden by the nasal crest dorsally, but due to poor preservation its specific relationships remain unclear.

Postorbital – The postorbital forms the posterodorsal rim of the orbit, much of the posterior rim, the anterolateral rim of the upper temporal fenestra, and contributes to the anterior and dorsal boundaries of the lower temporal fenestra. The postorbital is positioned posterior to the lateral orbital extension of the frontal. An interdigitated suture tapers posteromedially and traces the articulation of these bones dorsally. The anterodorsal portion of the postorbital is robust and its lateral surface is deeply pitted. An anteroposteriorly compressed jugal process forms almost the entire posterior orbit. The jugal process projects ventrally and slightly laterally, and attenuates ventrally to a rounded distal tip. The tip is cradled posteriorly by a well defined facet on the anterior surface of the postorbital process of the jugal. The posterior surface of the jugal process helps to form the anterior limit of the lower temporal fenestra, and contributes to its dorsal margin as it transitions posteriorly into the squamosal process.

Posteriorly, the postorbital is represented as a dorsoventrally compressed squamosal process, which forms the anterolateral border of the upper temporal fenestra. Posterior to this region, it is bound by the squamosal on all surfaces, excluding its dorsal and lateral faces. Posteriorly, the squamosal process thins to a slip of bone that rests on the dorsal surface of the squamosal, and extends to the level of the posterior margin of the upper temporal fenestra.

The ventromedial surface of the postorbital is obscured by steel armature, and its relationships with the parietal and laterosphenoid cannot be determined.

Squamosal – The postorbital process of the squamosal projects anteriorly, undercutting the squamosal process of the postorbital, and binding it dorsomedially, medially, ventromedially, and posteroventrally. This morphology permits the squamosal to contribute to the lateral and posterior borders of the upper temporal fenestra, and the dorsal border of the lower temporal fenestra.

A distinct quadrate cotylus is present ventrolaterally. Its roughened surface accommodates the head of the quadrate. Pre- and postquadratic processes mark the anterior and posterior limits of the cotyle. The prominent prequadratic process is oval shaped in cross section and stouter and more robust than those observed in other hadrosaurs, such as *Edmontosaurus saskatchewanensis* (NMC 8509), *Prosaurolophus maximus* (NMC 2870), and *Lambeosaurus lambei* (NMC 2869, NMC 8633, and NMC 8703). In *B. canadensis* it projects ventrolaterally and slightly anteriorly. All of its surfaces bear fluting, although this is best developed on its posterior face. The postquadratic process projects posteroventrally and slightly laterally from the cotyle, as its medial surface follows the contour of the opisthotic-exoccipital of the paroccipital process. A conspicuous suture on the posterolateral surface of the paraoccipital process marks the union of these bones. The mediolaterally compressed postquadratic process hooks anteriorly as it attenuates distally.

Approaching its posterior extent, the squamosal projects medially to enclose the upper temporal fenestra from behind. The left and right posteromedial processes (parietal process of Prieto-Márquez [2005]) converge on one another medially, but are separated

by a posterior extension of the parietal sagittal crest. However, the specific articulation of the posteromedial squamosal processes and the parietal crest cannot be identified as a result of slight distortion to this area. In posterior aspect, the squamosal arches over the dorsal exoccipital before tapering dorsomedially toward the midline where it contributes to the deeply excavated insertion for the ligamentum nuchae (Lull and Wright, 1942).

Quadrate – The dorsoventrally elongate quadrate is composed of a lateral shaft and a broad anteromedially directed pterygoid flange. The anterior portion of the shaft is mediolaterally compressed, thicker posteriorly, and slightly posteriorly curved when viewed laterally. A continuous longitudinal concavity is formed between the medial surface of the shaft and the anterior face of the pterygoid flange. Anteriorly, the quadrate shaft is embayed just below its approximate midheight. Much of the surface area forming the embayment is roughened, including the dorsal and ventral margins that form the articular facets for the quadratojugal. However, the bone surface of the embayment between the facets is smooth and does not appear to have contacted the quadratojugal. Striations are present on almost the entire shaft surrounding the embayment. These striations extend ventrolaterally to the mandibular condyle. On the posterior surface of the shaft, at about midheight of the quadratojugal embayment, the quadrate swells medially to articulate with the posteroventral process of the pterygoid. The presence of this medial swelling causes the quadrate shaft to have a mediolaterally thicker profile when viewed posteriorly. Just ventral to this area on the posterior shaft, the quadrate is gently concave as it approaches the ventral tip.

The dorsal half of the quadrate shaft is turned medially and terminates in a mediolaterally thickened head that articulates the quadrate cotyle of the squamosal. The

roughened head is oval in shape when viewed dorsally. Fluting, present on all surfaces circumscribing it, extends down the anterolateral surface of the shaft. A small depression, located just ventral to the head on the anteromedial surface of the shaft, accommodates the prequadratic process of the squamosal. A small process projects posterolaterally from the posterior margin of the dorsal shaft, also just ventral from the head. Although not seen in the holotype, Horner (1992) and Prieto-Márquez (2005) noted a scar on the adjacent anterolateral face of the postquadratic process of the squamosal in *Prosaurolophus blackfeetensis* and Montana specimens of *B. canadensis*, respectively.

Ventrally, the distal quadrate swells mediolaterally to form a triangular mandibular condyle. The lateral surangular condyle is rugose and rounded, with gentle striations present on all the surfaces just dorsal to the condyle. An anteroposteriorly compressed flange radiates dorsomedially from the ventral tip of the surangular condyle. The anterior surface of the flange is concave and its medial border ascends dorsomedially to the pterygoid flange. Its posterior surface is rugose as it joins the posteromedial surface of the surangular condyle. Prieto-Márquez (2001) indicated this flange contacts the anterodorsal surface of the articular ventrally in *B. canadensis*, however, despite an incompletely preserved articular, this relationship does not appear likely in the holotype.

The dorsal border of the anteromedially directed pterygoid flange descends from the head of the quadrate, and the ventral border ascends from the medial flange of the mandibular condyle. A posteromedially concave, broad sheet of bone forms between these borders. This curvature compliments the anterolateral surface of the posterior alar projection of the pterygoid. The posteromedial portion of the flange that overlaps the

pterygoid is identified by its roughened and striated surface. The right quadrate bears a small ridge that indicates the extent of overlap with the pterygoid. Although partially obscured by mounting armature, this ridge can be traced dorsally to a triangular depression that indicates where the posterodorsal tip of the posterior alar projection articulates. The anterolateral face of the pterygoid flange is smooth.

Quadratojugal – As noted by Prieto-Márquez (2001), the quadratojugal is a rhomboidal shaped bone with parallel posterodorsal and anteroventral margins. Its posterior border lacks the crescentic shape observed in *Edmontosaurus* and other hadrosaurs. Nearly all of the medial and lateral surfaces of the quadratojugal are conspicuously striated. It is thickest posteriorly where it articulates the quadrate. The posteroventral corner appears to be mediolaterally expanded to increase its contact with the quadrate, but this surface is obscured as a result of being glued in place. A small paraquadratic foramen occurs between the posterodorsal and posteroventral contact of the quadratojugal with the quadrate. The occurrence of this foramen is thought to be restricted to iguanodontids and not present in hadrosaurs (Appendix I). A depression on the anterolateral surface marks the articulation with the jugal.

Palatal Unit (figs. 3, 5; plate I)

An excellent description of the hadrosaur palate was provided by Heaton (1972). Both lambeosaurines and hadrosaurines were examined, including a review of the palatal elements belonging to the holotype of *Brachylophosaurus canadensis*. This source is recommended as further reference when interpreting the palatal elements described below.

Pterygoid – The wing-shaped pterygoid comprises a central plate, a posterior quadrate ramus, and anterior palatine and ectopterygoid rami.

The lateral surface of the central plate is approximately saddle-shaped. The central plate of the right pterygoid is slightly disarticulated from the maxilla and ectopterygoid, revealing a distinct groove on its anterolateral surface to accommodate the posteromedial pterygoid process of the maxilla. The left pterygoid remains articulated with the maxilla and ectopterygoid, obscuring its articulation with the posteromedial process of the ectopterygoid. The right pterygoid has been slightly damaged in this area, and is also partially obscured by the ectopterygoid. The dorsolateral surface of the central plate is marked by a gentle ridge that projects dorsally into a mediolaterally compressed spike-like projection. Its medial surface provides the dorsal portion of Heaton's (1972) "saddle-like" groove for reception of the pterygoid process of the basisphenoid. This conspicuous groove, or basal articulation, is deeply excavated on the medial surface of the central plate. The ventral floor of the groove is formed by a dorsoventrally compressed flange of bone that projects medially (main pterygoid flange or buttressing flange of Heaton [1972]) from the central plate.

The quadrate ramus of the pterygoid is composed of two parts, the posteroventral projection and the posterior alar projection. The posteroventral projection (postero-inferior projection of Heaton [1972], caudoventral projection of Horner *et al.* [2004], and ventral quadrate ramus of Prieto-Márquez [2005]) originates medially as a posterior continuation of the main pterygoid flange. The flange tapers posterolaterally before flaring dorsoventrally to form the distal extent of the posteroventral projection. This projection is lost in the right pterygoid of the holotype, and the left posteroventral

projection is somewhat distorted, but essentially remains in its proper position abutting the posteromedial quadrate. The distal face of the posteroventral projection is much taller than it is wide and appears slightly roughened, as in *Edmontosaurus regalis* (NMC 2289). The lateral surface of the posteroventral projection sits medial to the pterygoid flange of the quadrate and is therefore obscured. However, the dorsal margin, visible in medial aspect, can be traced dorsally where it forms the posterior margin of the posterior alar projection. The anterior margin of the triangular, mediolaterally compressed posterior alar projection (caudal alar projection of Horner *et al.* [2004], and dorsal quadrate wing of Prieto-Márquez [2005]) projects posterodorsally from the central plate, just above the dorsolateral margin of the basal articulation. The posterior alar projection forms a broad wing as it tapers distally to a point, and conforms to the contour of the pterygoid flange of the quadrate as it articulates its posteromedial surface. Both the lateral and medial surfaces of the posterior alar projection are roughened with conspicuous fluting.

Two processes project anteriorly from the central plate, the ectopterygoid ramus and the palatine ramus. The ventrally directed ectopterygoid ramus is the stouter of the two. A thin sheet of bone (bifurcating flange of Heaton [1972]) bifurcates from the ventral surface of the main pterygoid flange and descends ventrolaterally to form the posteromedial margin of the ectopterygoid ramus. The margin hooks anteriorly as it descends, giving the posteromedial margin a rounded outline as it transitions into the anteriorly directed maxillary facet. The posterolateral border of the ectopterygoid ramus is formed by an anterior extension of the ventral border of the posteroventral ramus. A small cavity is formed between the posteromedial and posterolateral margins of the ectopterygoid ramus. The main pterygoid flange forms its dorsal border. The

ectopterygoid ramus thickens mediolaterally across the maxillary facet. A gentle depression on the lateral surface of the ectopterygoid ramus identifies the articulation site for the deflected posterior portion of the ectopterygoid.

The palatine ramus projects anterodorsally from the central plate of the pterygoid as an elongate, thin wing of bone. It articulates with the palatine and maxilla along its anteroventral border (see figs. 2-4 of Heaton [1972]). The medial border of the palatine ramus rises anteriorly from the main pterygoid flange, while the anteroventral border ascends steeply from the ectopterygoid ramus. The latter of these borders is incomplete as it leads to the ectopterygoid ramus. The surface joining the medial and anteroventral margins is thin and dorsolaterally arched, making the lateral surface of the palatine ramus convex and the ventromedial surface concave. As noted by Heaton (1972), this ventromedial concavity helps form the posteroventral nasal passage leading to the trachea. The distal anterodorsal tip of the palatine ramus is incomplete in the holotype of *B. canadensis*, but appears to have ended in a dorsoventrally compressed blunt tip. An anteroposteriorly elongate, dorsoventrally compressed, laterally facing palatine articular facet is present on the anterolateral surface of the palatine ramus. This differs from the conspicuous dorsoventrally expanded facet observed in *Edmontosaurus regalis*.

Vomer – The vomer is an elongate, triangular bone forming the medial surface of the internal naris. As originally noted by Sternberg (1953), the left vomer has been displaced and lies against the medial surface of the left maxilla, making its relationships with the other bones unclear. The vomer is mediolaterally compressed, tallest posteriorly, and tapers anteriorly to a point (see fig. 1 of Heaton [1972]). Heaton (1972) noted a slight mediolateral thickening at the anterior tip, indicating where the vomers meet medially

between the premaxillae. Just posterior to the thickened tip, the gently concave medial surface of the anterior half of the vomer is set off from a second more distinctly concave surface that forms the posteriormost portion of the vomer. Small divots surround the posterior concavity dorsally and posteriorly. The ventral surface is obscured by steel mounting armature. The posterodorsal margin of the vomer curves medially before descending gently anteriorly to a process, rounded in outline, on the posteroventral corner of the vomer. This process is partially obscured by steel armature.

Ectopterygoid – The ectopterygoid is formed by an elongate anterior portion and a posteriorly deflected lamina. The dorsoventrally compressed anterior process has a slight anteroposterior dorsal arch to accommodate the ectopterygoid shelf of the maxilla with which it articulates ventrally. The anterior tip of the ectopterygoid comes to a rounded point. The medial and lateral margins of the anterior process are near parallel, diverging only slightly posteriorly. The anterior process thickens slightly towards its posterior deflection, and its posterodorsal surface declines laterally as it transitions into the posterolateral deflection. At this point, the ectopterygoid projects ventrolaterally as a mediolaterally compressed semicircular slip of bone that is only slightly thicker than the anterior process. The posteromedial border of the ectopterygoid is reflected slightly dorsally. Its ventral surface is incomplete and obscured in both the right and left elements, and consequently the presence of a posteromedial process (triangular process of Heaton [1972]) described by Prieto-Márquez (2005) cannot be confirmed. Posteriorly, the posteromedial reflection tapers ventrally to meet the deflected border of the ectopterygoid. This allows the entire posterior ectopterygoid segment to follow the contour of the ectopterygoid ramus of the pterygoid, to which it articulates medially.

Palatine – The palatine is a trapezoidal shaped element articulating with the jugal anterolaterally, the maxilla ventrally, and the pterygoid and vomer dorsomedially. Although the right palatine is missing, the left is nearly complete and close to its natural position. The central portion of the left palatine is mediolaterally compressed, with anterodorsal and anterolateral processes radiating from its forward margin, and an expanded posteroventral border. Its medial surface is smooth, but appears to lack the gently concave state as noted by Heaton (1972) for *Edmontosaurus regalis* (NMC 2289). The absence of this character may very well be due to postmortem distortion.

The mediolaterally compressed anterodorsal process expands from the central palatine and tapers at its neck before flaring anteroposteriorly at its distal margin. The dorsal margin of the distal “fan” is posterolaterally directed, offset from the more parasagittally aligned central portion of the palatine. Fluting is observed on the medially face of the distal fan.

The laterally directed anterolateral jugal process is slightly thicker than the central portion of the palatine. The lateral contact of this process has been positioned to articulate with both the lacrimal and the jugal process of the maxilla. However, this relationship is not clear in the holotype due to poor preservation at the distal tip of the anterolateral jugal process. Prieto-Márquez (2005) reported its lateral contact was limited to the jugal, and that it does not contact the lacrimal as Horner (1992) described in *Prosaurolophus blackfeetensis*. The dorsal border of the anterolateral process is formed by the descending anterior margin of the anterodorsal process. Its anteroventral border is incomplete.

Neurocranial Unit (figs. 3, 4, 5, 6, 7; plate I)

Frontal – The coossified frontal bones in hadrosaurs form much of the dorsal skull roof. However, in *B. canadensis* the frontal is obscured by the nasal crest. The only visible portion of the holotype frontal is the portion contributing to the dorsal orbital rim. As noted by Sternberg (1953) and Prieto-Márquez (2005), this lateral frontal extension contacts the prefrontal anteriorly and the postorbital posteriorly. Its dorsal surface is more gnarled and robust than the orbital contribution of the prefrontal. Anteromedially, the frontal undercuts the prefrontal, and posterodorsally it forms an interdigitating suture with the postorbital. Ventrally, its sutural contacts with the prefrontal and postorbital are not as clearly visible as originally figured by Sternberg (1953), making their true path difficult to trace.

Parietal – The coossified parietals form the dorsal roof of the braincase, and although incomplete, can be clearly seen to extend a conspicuous sagittal crest dorsomedially that separates the upper temporal fenestrae. Although the anterior margin of the parietal of hadrosaurs has been shown to contact the frontal along a broad, transverse interdigitated suture (Ostrom, 1961; Horner *et al.*, 2004; Prieto-Márquez, 2005), the specific relationship of this contact is obscured in the holotype by what is interpreted as a posteromedial extension of the prefrontal. A suture on the anterodorsal surface of the parietal marks the articulation of the parietal and the overhanging prefrontal above. It cannot be confirmed that the parietal wedges between the posteromedial corners of the frontals, as reported by Prieto-Márquez (2005). An anterolateral postorbital process extends laterally from the parietal, but its articulation with the postorbital is unclear due to poor preservation, the presence of steel armature, and previous repair work.

Figure 7. Left lateral reconstruction of braincase

The lateral surface of the parietal is gently concave and forms the medial surface of the upper temporal fenestra. A near-horizontal suture marks the ventral articulation of the parietal with the anterior positioned laterosphenoid (alisphenoid of Lull and Wright [1942]), and the more posterior opisthotic. Due to the lack of visible sutures, it is impossible to ascertain whether the dorsolateral surface of the prootic fails to reach the parietal, as reported by Prieto-Márquez (2005). Steel armature obscures the anterior tracing of the ventral suture of the parietal and damaged bone surface makes its posterior path unclear.

The specific relationship between the posterior portion of the parietal and its contact with the squamosal and supraoccipital is unclear due to unpreserved sutures and damaged bone surface. Although distorted, a mediolaterally thickened posterior extension of the parietal sagittal crest prevents the posteromedial processes of the squamosal (parietal process of Prieto-Márquez [2005]) from contacting one another medially. The posterior extension of the parietal appears to also contact the anterior surface of the posteromedial process of the squamosal, and the supraoccipital below.

Braincase – The endochondral bones of the holotype braincase are preserved with good detail; however, coossification is advanced and the sutures indicating their mutual relationships cannot be traced (fig. 7). The occipital condyle occupies much of the posterior aspect of the braincase. The basioccipital, forming the floor of the foramen magnum, is ventrally convex along its anteroposterior and transverse axes. A conspicuous bulb-like extension of the exoccipital forms the lateral surface of the occipital condyle. Its suture with the basioccipital is not visible in posterior or lateral aspect. More dorsally, the exoccipitals fuse medially and form the roof of the foramen

magnum. A small keel forms medially, just dorsal to the foramen magnum, separating two deep depressions lateral to it. The opisthotic-exoccipital projects laterally and posteroventrally from each depression to contribute to the attenuating paroccipital process. The postquadratic process of the squamosal articulates along the anterolateral surface of the opisthotic-exoccipital. Dorsal to the depressions, the exoccipital articulates the rugose, triangular-shaped supraoccipital along a broad horizontal contact on the posterior aspect of the braincase. Although this arrangement is not conspicuous in the holotype of *B. canadensis*, comparison with the holotype of *Corythosaurus* “*excavatus*” (NMC 8676) confirms its presence. Prieto-Márquez (2005) reported an “anteroposteriorly short exoccipital-supraoccipital roof posterior and dorsal to foramen magnum” as an autapomorphy for *Brachylophosaurus*, but this character is not obvious in the holotype and does not differ significantly from the condition observed in *Edmontosaurus*, or other hadrosaurs. The supraoccipital also contacts the squamosal laterally, and possibly the posterior extension of the parietal sagittal crest dorsolaterally and dorsally. This area is slightly distorted, however, and the suture between the parietal and supraoccipital is not obvious in posterior aspect. The posterior surface of the supraoccipital is concave and forms the insertion point for the ligamentum nuchae (Lull and Wright, 1942).

Many foramina are preserved in the lateral view of the braincase. The arrangement of the foramina generally conforms to that seen in other hadrosaurs, although the constituent bones forming their margins cannot be confirmed due to the advanced state of coossification. A deep transverse groove indicating the articulation of the basal tubera of the basioccipital and the more anterior basisphenoid is one of the few

remnants of sutural contacts on the braincase. A conspicuous basisphenoid flange (alar processes of Prieto-Márquez [2005]) projects posterolaterally from the lateral surface of the basisphenoid. Each flange is approximately triangular in outline, anteroposteriorly thin, and bears fluting on both its anterior and posterior surfaces. Just anterior to each flange, a prominent pterygoid process projects ventrolaterally from the basisphenoid to insert into a groove on the dorsal surface of the main pterygoid flange. Each pterygoid process maintains its mediolateral width along its length, but is slightly expanded distally, is slightly concave along its dorsal surface, and bears a roughened anterior face that contacts the pterygoid. Medial to the pterygoid processes, a smaller near-straight anteroposteriorly compressed process projects posteroventrally from the basisphenoid. This process is also present in *Edmontosaurus regalis* (NMC 2289) and *E. saskatchewanensis* (NMC 8509), although not nearly as pronounced.

Mandibular Unit (fig. 8; plate II)

Dentary – The horizontally elongate dentary, the largest bone of the mandible, contacts the prementary anteriorly (although the prementary is not preserved), the angular posteroventrally, the splenial posteromedially, and the surangular posteriorly. Between the diastema and the coronoid process, the lateral face of the dentary is convex along its dorsoventral axis, and slightly concave along its anteroposterior axis. A minimum of four dental foramina are present on this surface. A diagonally oriented groove runs adjacent to the lateral tooth row, separating the teeth from the lateral face of the element.

The medial surface of the dentary is convex along both its anteroposterior and dorsoventral axes, reflecting the curvature of the dental battery that occupies much of its medial surface. As in the maxilla, a thin dental lamina obscures much of the medial

Figure 8. Left lateral reconstruction of mandible

dental battery. At the base of the dental battery, a flattened, ventromedially directed, narrow ridge separates the dental lamina from the dental foramina (see plate II C). The circular dental foramina occur in a dorsally concave series. All foramina are constant in size except the posterior three or four that are slightly smaller. There are 38 foramina in the sequence, nearly one foramen for each of the 39 vertical tooth row positions. Immediately dorsal to the 17th dental foramen, an additional foramen pierces the dentary. A shallow groove on the ventromedial surface of the dentary originates more or less immediately below the first vertical tooth row, deepening as it progresses posteriorly. A heavy ridge separates this groove from the dental foramina. Posteriorly, the groove widens dorsoventrally and opens medially to the Meckelian canal as described by Prieto-Márquez (2001). A conspicuous, anteriorly attenuating facet for the angular is seen just ventral to this groove. Its anterior extent reaches approximately to the midpoint of the tooth row. The facet widens posteriorly to accommodate the angular.

The mediolaterally thin diastema flares slightly laterally from the dentary. Its dorsal margin is especially thin, and has been partially reconstructed to smooth out the damaged edge. The anterolateral surface of the diastema is convex and the medial surface is deeply concave, with its anteroventral corner ventromedially directed. The portion of the diastema forming the mental symphysis has not been preserved in either dentary, and the facet for the articulation with the missing predentary has been lost. Although Sternberg (1953) indicated only three dental foramina on the anterolateral surface of the dentary, four are preserved in a diagonal row, the largest being the most anteroventrally positioned. Horizontal striations cover the surface area surrounding these foramina.

The massive coronoid process originates from the lateral surface of the dentary, well anterior to the posterior limit of the tooth row, and projects dorsomedially above the tooth row. It is anteroposteriorly constricted at its approximate midheight, and distally it is anteroposteriorly flared and mediolaterally compressed with gentle fluting covering most of these surfaces. The medial surface of the distal expansion is gently concave. A shallow groove is present on the posterior surface of the dorsal expansion that accommodates the dorsal tip of the anterolateral process of the surangular. The posterolateral margin of the coronoid continues ventromedially and cradles the more dorsomedial surangular. The posteromedial margin of the coronoid descends ventrally before projecting posteriorly as a mediolaterally compressed, dorsoventrally attenuating splenial process that inserts itself on the medial surface of the splenial. The Meckelian canal separates the posteromedial surface of the coronoid process and the more medial portion of the dentary.

Dentary Teeth – Although the lateral edge of the lower dental battery is near straight along its anteroposterior axis, the medial surface is convex along both its anteroposterior and dorsoventral axes. Thirty-nine vertical tooth rows are tightly arranged next to one another, with individual tooth size increasing towards the midlength of the tooth row. The number of vertical tooth row positions in the holotype disagrees with a previously reported maximum count of 33 in other specimens of *B. canadensis* (Prieto-Márquez, 2005). The continuous dorsolaterally facing occlusal surface forms across the vertical tooth rows. Unlike the upper dental battery that exhibits one functional tooth per vertical tooth row, in all but the reduced first two vertical tooth rows of the lower dental battery two or three teeth per row contribute to the occlusal facet. Each functional tooth bears a

small divot on its occlusal surface, which is predominantly formed by dentine, and a dark transverse line that represents a remnant of the enamel carina. Small anteroposteriorly oriented ridges form between function teeth of the same vertical tooth row position where the dentine has been worn faster than the harder enamel. As is common for all hadrosaurs (see figs. 9-10 of Lull and Wright [1942]; 20.8 of Horner *et al.* [2004]), the medially exposed teeth reveal the diamond-shaped enamel crown of each tooth that is bisected by a conspicuous carina. The presence of the dental lamina prevents a replacement tooth count.

Surangular – The concave anterior portion of the surangular inserts into the Meckelian canal, medial to the coronoid process. A mediolaterally compressed anterolateral process rises approximately vertically from the surangular to contact the posterior margin of the coronoid process. A conspicuous ridge on the lateral face of the anterolateral process indicates where the ventrolateral portion of the coronoid process overlaps it laterally. The posterior edge of the anterolateral process descends posteriorly, and swells medially to form the anterior and medial extent of the rugose, oval mandibular glenoid. The lateral margin of the concave glenoid is formed by a dorsally reflected rim of the surangular that bears gentle fluting on its ventrolateral surface. A small foramen is present at the base of the anterolateral process of the surangular, just anterior to the mandibular glenoid. Posteriorly, the surangular ascends dorsally as it tapers mediolaterally from the posterior portion of the glenoid to form part of the retroarticular process. The fluted and concave ventrolateral surface of this process forms an approximately vertical mediolaterally compressed flange that articulates with the angular, splenial, and articular medially. The angular continues to contact the surangular anteriorly along its ventromedial border.

Articular – The right articular is not preserved in the holotype and the left appears incomplete along its anterior border. It is wedged between the posterior ends of the splenial and surangular where it contributes to the retroarticular process, and all but its roughened dorsal surface are obscured, making it difficult to confirm its shape. The mandibular contribution to the jaw joint appears to be provided entirely by the surangular in the holotype. This differs from Prieto-Márquez (2005), who indicated the dorsolateral border of the articular contacted the quadrate.

Splenial – The splenial is a mediolaterally compressed bone that is medially concave and laterally convex along its anteroposterior axis. Anteriorly, it bears a triangular-shaped head that tapers dorsoventrally to a point that articulates with the posteromedial surface of the dentary, just ventral to the posterior dental foramina. At the base of the head, where the splenial is tallest, the dorsal edge flares laterally and is ventrally concave to cradle the dentary posterior to the tooth row. The ventral concavity continues posteriorly on the lateral surface of the splenial. A small, anteroposteriorly directed ridge is present on the ventromedial surface of the splenial, and the posteriorly directed splenial process of the dentary inserts between this ridge and the ventral concavity above. In medial aspect, the splenial constricts dorsoventrally from the base of the head to the region just posterior to its midlength. It then projects posteriorly as a dorsoventrally expanded, mediolaterally thin articular process that bears fluting on its posteromedial margin. This process contacts the articular laterally, and forms the medial surface of the retroarticular process. Excluding the anterior and posterior ends, the ventral surface of the splenial is mediolaterally expanded and horizontally flat for its articulation with the angular below.

Angular – The anteroposteriorly elongate angular attenuates anteriorly, and is mediolaterally compressed and dorsoventrally expanded posteriorly. Ventrolaterally, it articulates along a well defined facet on the dentary, and the surangular more posteriorly. The posterodorsal edge of the angular articulates with the splenial above. Posteriorly, a conspicuous splenial facet on the dorsomedial portion of the angular indicates the dorsal edge of the angular that wedges between the ventrolateral corner of the splenial and the medial surface of the surangular. When viewed in lateral aspect, the ventral rim of the posterolateral surface of the angular is exposed below the surangular. However, the angular appears to have been displaced slightly, as its entire lateral surface is normally covered by the surangular in other hadrosaurs.

Hyoid – Although not mentioned by Sternberg (1953), the anterior portions of the left and right hyoids are preserved in the holotype of *B. canadensis*. Each element bears a dorsoventrally expanded head that is mediolaterally compressed, roughened on its anterior surface, and exhibits fluting on its lateral and medial surfaces. The shaft tapers dorsoventrally from the head and is oval in cross-section.

Axial Skeleton

Cervical Vertebrae (figs. 9, 10, 11, 12; plate III A-K) – Based on the number of vertebrae that exhibit parapophyses on the lateral surface of their centrum, a completely preserved cervical series of 14 vertebrae is present in the holotype of *B. canadensis*. Although, this count falls within the 12-15 range for hadrosaurs (Horner *et al.*, 2004), it disagrees with a previous count of 13 cervicals for *B. canadensis* (Prieto-Márquez, 2001).

Figure 9. Left lateral reconstruction of axis (second cervical) and third cervical vertebra (dashed lines represent missing or badly damaged bone)

Figure 10. Anterior (A) and right lateral (B) reconstructions of fourth cervical vertebra

Figure 11. Anterior (A) and right lateral (B) reconstructions of sixth cervical vertebra

Figure 12. Anterior (A) and right lateral (B) reconstructions of eleventh cervical vertebra

When the cervical vertebrae are articulated, the neck exhibits a subtle dorsiflexed curvature, as in other hadrosaurs (Maryńska and Osmólska, 1983; Horner *et al.*, 2004). However, distortion of many of the vertebrae makes it difficult to reconstruct the curvature precisely.

Atlas – The atlas is composed of an intercentrum, paired neural arch pedicels, and an odontoid that has fused with the axis (described under axis). The intercentrum has undergone reconstructive work using plaster to smooth out damaged edges, but this repairwork does not appear to obscure the overall morphology of the element. Viewed anteriorly, the dorsal midline of the intercentrum is ventrally depressed, giving it a bowl-shaped outline. A slight groove on its dorsal surface extends between the rugose lateral projections. A lateral tubercle is present on the anterior surface of the intercentrum, just above its ventral rim. A less developed medial tubercle is also present along the midline of the intercentrum. Together, these structures may contribute to the articular facet for the occipital condyle. The anteroventral surface of the intercentrum curves posteriorly, and is excavated on its posterior surface, resulting in a posteriorly projecting lip that passes ventral to the axis intercentrum. This posterior lip may represent an incipient cotyle that is more fully developed in the other vertebrae. A thickened shelf separates this lip from a deep concavity on the posterodorsal surface. This concavity supports the base of the anterior projecting odontoid.

The paired atlas neural arch pedicels are morphologically distinct from those of the other cervical vertebrae. Viewed laterally, an arrowhead-shaped projection points ventrally. The anterior face of this projection is slightly concave and contributed to the articulation with the occipital condyle. The medial face of the anteroposteriorly

constricted neck of the ventral projection bears an incised concavity. This concavity extends ventrally to invade the interior medial surface of the ventral projection. The dorsal portion of the neural arch is composed of a conspicuous transverse process, although no atlantal rib is preserved, and a medially projected, dorsoventrally compressed sheet of bone. The transverse process projects posterodorsally from the posterolateral corner of each arch. The distal extent of this short process is bulb-like and roughened. Enclosing the neural canal dorsally, the dorsal sheet of bone shows a slight depression on its dorsolateral surface and a distinct ovoid postzygapophysis on its ventral midline for articulation with the prezygapophysis of the axis. Dorsomedially, arch halves remain unfused.

Axis – The axis is characterized by a prominent neural spine, well developed pre- and post zygapophyses and an odontoid fused to the anterior surface of the centrum. In ventral view, the centrum of the axis is hourglass-shaped, much as described in other specimens of *B. canadensis* (Prieto-Márquez, 2001). This is due to an expanded posterior cotyle and a laterally constricted midline, which is most evident in the ventral half of the vertebra. In contrast with specimens of *Brachylophosaurus* from Montana (Prieto-Márquez, 2001), a median ridge is lacking on the ventral surface of this element. In contrast to Horner *et al.* (2004), the axis bears ribs, as indicated by the presence of a well-defined parapophysis on the anterolateral surface of the centrum. A relatively small and wedge-like intercentrum, clearly fused to the centrum, protrudes from the anteroventral face of the centrum to form an anteriorly projecting lip.

A broad, anteriorly directed odontoid originates just above the ventral lip of the intercentrum. Although part of the atlas segment, the odontoid has become fused with

the anterior face of the axis centrum. It is deepest across its base and thins anteriorly to form a curved lip at its anterior margin. Although the odontoid is distorted in the type specimen, its dorsal surface would normally appear concave, forming part of the ventral rim of the cotyle that receives the occipital condyle of the skull.

Paired neural arch pedicels rise dorsally from the centrum and encircle the neural canal. A prominent prezygapophyseal process, bearing an oval dorsolaterally facing articular facet, projects anteriorly from each pedicel. Posterolaterally, the prezygapophysis smoothly transitions into a delicate, posterolaterally directed diapophysis. The posterior surface of the diapophysis grades seamlessly into the anterior support of the postzygapophysis. The prominent neural spine is thinnest at its base, and thickens distally to eventually form a rugose diamond shaped dorsal surface.

Conspicuous fluting radiates from the dorsal surface onto the circumscribing surface of the neural spine. Anteriorly, the neural spine abruptly ends as a sharp point, its forward extent clearly ending posterior to the anterior limit of the prezygapophyses. This condition is contrary to MOR 794 (Prieto-Márquez, 2001), where the anterior tip of the neural spine is conspicuously hook-like, and extends well past the anterior margin of the prezygapophyses. Posteriorly, laterally diverging postzygapophyseal flanges project from the median neural spine. The dorsal surface of each flange is roughened.

Conspicuous fluting extends from this dorsal surface down onto the anterolateral surface. Each flange projects a robust postzygapophyseal process that bears a large ventrolaterally directed ovoid facet. Postzygapophyseal flange morphology differs between the holotype of *B. canadensis* and at least some specimens of *B. canadensis* from Montana (Prieto-Márquez, 2001). The transition between the neural spine and the postzygapophyseal

flange region is comparatively truncated and abrupt in the holotype, whereas Prieto-Márquez (2001) figures a gently sloping and gradual dorsal transition. In addition, the holotype does not exhibit the medial incision between the individual postzygapophyseal flanges described in the Montana specimens.

C3 – C14 – The third through fourteenth cervicals are generally similar in shape, except for the last, which is distinctly intermediate in shape between the more anterior cervicals and the dorsal vertebrae. The cervical vertebrae are deeply opisthocoelous. The centra of more anterior cervicals are oval in anterior view and flat along their anterodorsal surface. However, the centra of the more posterior cervicals are vaguely heart-shaped in anterior view, although distortion often obscures the specific shape. The lateral surfaces of centra C3-C11 bear stout parapophyses. By C12 the parapophyses are reduced to only roughened facets. Between C12-C14 the parapophyses progressively move to a more dorsolateral position on the centrum. As in the axis, the centra of C3 to C11 are deeply excavated ventrolaterally, but this is less pronounced in C12–C14. The large neural canal remains fairly consistent in size throughout the cervical vertebrae. Based on the size of the incompletely preserved neural spines and their broken bases, the neural spines appear to be taller and more robust toward the posterior end of the series. All prezygapophyseal facets face dorsomedially, and, as in the axis, the facets of the third, fourth, and fifth cervicals extend anterior past the anterior edge of their respective transverse process. Beginning with the sixth cervical and continuing throughout the series, the prezygapophyseal facets are positioned laterally to the base of the pedicels and do not extend anterior to the transverse process. The ventrolateral surface of each prezygapophysis bears a dorsoventrally compressed diapophysis that is roughened and

swelled at its distal end. The diapophyses of C13 and C14 are more robust than the preceding cervicals, and both are concave along the posterior surface. The conspicuous postzygapophyseal processes project dorsolaterally to overhang the posterior margin of the cotyles, and their facets face ventromedially. The postzygapophyseal processes of C14 have fused medially, posterodorsal to the neural spine, and the postzygapophyseal facets are positioned closer to the midline of the element (plate III J-K).

Dorsal Vertebrae (plate III L) – The dorsal vertebrae can be differentiated from the cervicals by the presence of a parapophysis on the lateral surface of their neural arch. Nine dorsal vertebrae are preserved in the holotype. This represents an incomplete dorsal series, as Horner *et al.* (2004) reported sixteen to twenty occurring in hadrosaurs and Prieto-Márquez (2001) reported 18 in other specimens of *B. canadensis*. The dorsal vertebrae differ distinctly in their morphology from the last cervical. Although the centra have been badly damaged from being drilled and strung on steel mounting armature, they are clearly weakly opisthocoelous. They are anteroposteriorly longer than transversely wide, laterally compressed, and dorsally arched along their keeled ventral surface. The neural canal remains circular, but is approximately half the size of that observed in the cervical series by D3. The prezygapophyses are located more medially on the neural arch above the neural canal, and are more steeply inclined relative to the horizontal when compared with the cervicals. The transverse processes, no longer bearing the prezygapophyses, project posterodorsally from the neural arch. They are most steeply inclined to the horizontal in D4-D7, and less so in the relatively shorter transverse processes of D8 and D9. Fluting is present on both the flat dorsal and gently concave anteroventral surfaces of the transverse process. Its posterior surface is also concave,

with a deep pit forming at its proximal base just dorsal to the neural canal. Distally, the transverse process is roughened and triangular in outline. The mediolaterally compressed, posteriorly tilted neural spine is extremely well-developed throughout the preserved dorsal series. The neural spine of the first dorsal vertebra is not as anteroposteriorly broad as the remaining vertebrae in the series; however, fluting is present on the lateral surfaces of every spine. The postzygapophyses have been reduced to steep ventrolaterally facing facets that project from the posteroventral margin of the neural spine.

Cervical Ribs (figs. 9, 10, 11, 12; plate III I) – Except for the atlas, each cervical vertebra bears double-headed ribs, of which ribs C2-C11 fuse to their respective vertebrae. The axial rib, although poorly preserved, appears to have a medially shortened capitulum compared to the other cervical ribs. The capitulum of ribs C3-C11 is elongate, dorsoventrally compressed, and bears a swelling on its medial termination articulate with the parapophysis on the lateral surface of the centrum. The axial rib tuberculum has been damaged and its articulation with the diapophysis is not preserved. The stouter tuberculum of the remaining cervical ribs projects dorsally at approximately 90° to the capitulum, is mediolaterally compressed, and swells at its dorsal margin to contact the diapophysis above. The gradual dorsal migration of the parapophysis and capitulum on C12-C14 suggest the tuberculum may have become reduced, as in the dorsal vertebrae. In C3-C11 a small attenuating process extends from the anterior surface of where the capitulum and tuberculum converge. This process appears absent in the axial rib, but poor preservation makes it unclear. Posteriorly, the ribs of C2-C11 project as a short,

dorsoventrally compressed shaft. The ribs C12-14 do not fuse to their centra and do not appear to have been preserved.

Dorsal Ribs (plate IV) – Many of the dorsal ribs are incomplete, and missing sections have been restored. Nevertheless, it is possible to establish the approximate position of most of the better preserved ribs in the rib cage. The dorsal ribs increase in size towards the middle of the rib cage. The capitulum remains the larger of the two rib heads, bears conspicuous fluting on most of its proximal surfaces, and is oval in cross section to contact the parapophysis by a roughened articular facet. The tuberculum becomes reduced but maintains a roughened surface that commonly bears gentle fluting on its anterior and posterior surfaces. The shafts of the dorsal ribs are anterolaterally-posteromedially compressed, and project ventrolaterally. Just ventral to the tuberculum, the larger dorsal ribs exhibit an anteroposteriorly expanded flange on the lateral surface of their shaft that is roughened and fluted on much of its surface. The anteromedial and posterior surface between the flange and the more medial portion of the shaft are concave; however, these concavities subside as the flange tapers to meet the main shaft of the rib. Distally, the dorsal ribs are mediolaterally compressed and terminate in a blunt edge.

Appendicular Skeleton

Scapula (plate V) – The thickened proximal margin of the scapula articulates with the coracoid. Together, these elements form the posteroventrally directed glenoid fossa. A prominent deltoid ridge originates on the dorsal surface of the proximal scapular margin, and projects laterally as the element curves posterodorsally. The deltoid ridge gently

recedes as it extends distally, subsiding before reaching the ventral edge of the scapula. The deeply concave deltoid fossa is located on the lateral surface between the deltoid ridge and the glenoid fossa. The deltoid fossa continues posteroventrally beneath the deltoid crest, and eventually terminates at the neck of the scapula, which is the thinnest point along this element. The scapular blade thins transversely towards its distal end, but becomes broader dorsoventrally. As suggested for other hadrosaurs (Lull and Wright, 1942; Brett-Surman, 1989), the scapular blade was probably positioned parallel to the axis of the anterior thoracic vertebral column in life.

Coracoid (plate V) – The bone surfaces of the anterior and medial portion of the coracoid are poorly preserved. The central portion of the coracoid is mediolaterally compressed, and pierced by a conspicuous coracoid foramen on its lateral surface. The medial opening of the foramen has not been preserved. Posterodorsally, the coracoid firmly articulates with the scapula along a suture that is deeply incised laterally, but due to poor preservation, barely distinguishable anteriorly and medially. The lateral suture extends posteriorly and divides the glenoid fossa into unequal scapular and coracoid contributions. The coracoid swells mediolaterally to form its portion of the glenoid fossa. The articular surface and outer margins of the fossa are roughened and rugose. At the ventral margin of the glenoid fossa, the coracoid curves sharply anteriorly before projecting posteroventrally to form the posterior surface of the well-developed, mediolaterally compressed sternal process. The anterior surface of the poorly preserved sternal process rises anterodorsally before making a sharp posterior turn to form the dorsal surface of the coracoid.

Humerus (plate VI) - The long axis of the proximal half of the robust humerus is offset approximately 40° from the more distal humeral shaft. The rugose and mediolaterally flared proximal head of the humerus represents the maximum width of the element. A prominent ball-like articular condyle projects posterodorsally from its position adjacent to the proximal edge. The enlarged deltopectoral crest is deflected anterolaterally forming a concavity on the anterior face of the humerus. The rugose anterolateral edge of the deltopectoral crest shows evidence of the insertion of the pectoralis. The posterolateral face of the crest also shows muscle scarring and a prominent ridge running proximally to the lateral tuberosity. This area would have provided the insertion for the deltoideus. Rising approximately one third the distance from the proximal margin of the humerus and extending proximally along its posteromedial margin, a protuberance (7 cm long) represents the area for the insertion of the latissimus dorsi. Extending distally, the deltopectoral crest reaches half the length of the humerus before tapering to eventually meet the thickened distal shaft.

The distal humeral shaft is anteroposteriorly compressed and transversely expanded. Both ulnar and radial condyles are well developed, although the medial ulnar condyle is the larger of the two. Both condyles project anteriorly and are rugose with rounded articulating surfaces. Longitudinal striations, evident on all circumscribing surfaces just proximal to both condyles, are probably associated with attachment of the joint capsule.

Radius (plate VII A-B) – The radius is a long and slender bone. Its rugose, enlarged proximal head is irregular in shape, and bears a slightly concave articular surface. Viewed proximally, it is quasi-triangular in shape. A conspicuous thickening on the

anteromedial surface and a thin flange on the posterolateral corner project from the proximal head. Both recede slowly to meet the narrow radial shaft. Longitudinal striations are visible on all surfaces of the proximal head.

The radial shaft shows no appreciable curvature along its length, although the anterior face flattens as the distal portion is approached. Distally, the radius bears a slightly swelled head and conspicuous fluting. Viewed distally, the head is circular in outline with an indentation on the posterolateral edge.

Ulna (plate VII A-B) – The ulna is the longest bone of the forelimb. It is slightly S-shaped along its length. A rugose and well-developed olecranon process protrudes well above the proximal articular surface of the ulna. A prominent long and narrow anterior process projects anteromedially from the base of the olecranon process. This process is widest proximally and tapers distally to join the shaft of the ulna. A smaller lateral process projects laterally at approximately 90° to the anterior process. It subsides quickly as it extends onto the ulnar shaft. A concavity formed between these processes accommodates the proximal expansion of the radius. Muscle scarring is evident on every surface of the proximal ulnar head.

The posterolateral face of the ulnar shaft is gently convex throughout the length of the element. The remaining surfaces become flattened, most conspicuously on the anterodistal surface of the shaft, where the radius is closely aligned to the ulna. The slightly expanded distal end of the ulna is highly rugose. The terminal articular surface is slightly convex and triangular in distal view.

Manus (plate VI C-D) – Only the left metacarpal III and an isolated phalanx are preserved. Metacarpal III is a long, slender anteroposteriorly compressed bone that

tapers mediolaterally towards the distal end of its shaft. Its swollen proximal and distal ends bear roughened articular surfaces, the proximal larger than the distal, with fluting radiating from each end onto the shaft. Except for a shallow depression proximally, the entire anterior surface of the shaft is convex. The posterior surface is essentially flat.

The phalanx is a stout hourglass-shaped element in outline. Both the proximal and distal articular surfaces are roughened, but the heart-shaped proximal end is larger than the distal. The entire shaft bears fluting, and tapers anteroposteriorly distally.

Reconstruction of the Skull Elements

Upon initial examination, the holotype of *Brachylophosaurus canadensis* appears quite well preserved. However, closer inspection reveals substantial postmortem distortion. This is especially evident throughout the skull, where many adjustments were necessary to produce an accurate reconstruction (figs. 3-6). In cases where bones are missing or poorly preserved, bilateral symmetry was assumed, and the better preserved elements of the opposite side were used for the reconstruction. Comparisons with other hadrosaurines were also used to guide the reconstruction.

The entire rostrum has been depressed from its natural position, exposing nasal articular facets on the lateral surfaces of the posterodorsal premaxillary processes. In order to rearticulate these processes to the nasals, it was necessary to elevate the rostrum by approximately 1.5 cm.

In addition to the overall ventral depression of the rostrum, the anterior end of the right premaxilla has been pulled dorsally and has incurred distortion on its dorsal surface. This dorsal torsion accounts for the unnatural curvature of the posterodorsal premaxillary

process when viewed anteriorly. The left posterolateral process is badly buckled, and consequently, the relatively undistorted right posterolateral process was used to restore its shape. An articular facet on the external surface of the left prefrontal immediately below its contact with the nasal indicates the posterior limit of the posterolateral premaxillary process.

Although the anterior end of the right nasal sits closer to its natural position, its left counterpart has been displaced medially to diminish the divergence that should occur between the anterior ends of these elements. Once the rostrum was elevated to its proper position, the nasals were realigned with their nasal articular facets on the posterodorsal premaxillary processes.

The ventral border of the right lacrimal has been crushed and the anterior portion of the bone has been displaced dorsomedially to lay internal to the right posterolateral premaxillary process. Plaster reconstruction is visible on the lateral surface of the left lacrimal, and also on its orbital contribution. As a result, the left lacrimal duct has been obscured. This damage must have occurred after Sternberg (1953, plate XXXVIII) took his original photographs, as they show no apparent damage or reconstruction. Despite this damage, the left lacrimal does not appear to have been displaced from its natural position. This conclusion is supported by the position of an exposed lacrimal facet on the maxilla, just above the main maxillary foramen, on the opposite (*right*) side of the skull. The left lacrimal was used in the final reconstruction based on its preservation of overall shape and proper natural positioning.

Both prefrontals have been somewhat distorted, the right more so than the left. This is especially noticeable in the right posterior prefrontal contributing to the orbit,

where the suture of this bone is not nearly as obvious as in its left counterpart.

Consequently, the left prefrontal was used in the final reconstruction along with Sternberg's (1953) original photograph for guidance.

The majority of the frontal is obscured by the nasal, except for a lateral orbital process. Its ventral suture with the postorbital is partially visible, and was illustrated in the reconstruction. The ventral placement of the frontal-prefrontal suture remains unclear in the holotype, and has been drawn using a dashed line.

The right orbit has been pushed medially, giving the right side of the skull an unnaturally narrow perspective. The left orbit lies closer to its natural position, although the posteriorly directed squamosal process of the postorbital has been depressed ventrally. Consequently, the position of the left orbit was used for reconstruction with slight medial compensation for lateral flaring, while the non-distorted posterior right postorbital was used for reconstructing the squamosal process.

The left squamosal has dropped ventrally from its proper positioning, and the distal end of the prequadratic process has been lost. The complete and correctly positioned right squamosal was consequently chosen for illustration.

Both quadrates remain well preserved with only the anterior margin of the pterygoid flange of both elements incomplete. However, the left quadrate has clearly dropped ventrally from its articulation with the squamosal, and its ventral end has rotated laterally. This has been corrected for in the final reconstruction.

Both quadratojugals have sustained damage along their dorsal and anterior margins, losing much of these areas. Although both appear in proper position relative to the quadrate, the left quadratojugal was used for illustration. Reconstruction of the lost

borders of this element was based on comparison with RTMP 90.104.01 and a description of other specimens of *B. canadensis* (Prieto-Márquez, 2001).

The right jugal has been displaced medially and is missing the posterior extent of its quadratojugal process. The left jugal lies in a more natural position, having undergone only slight lateral flaring. Consequently, the relatively complete left jugal was used for the final reconstruction with slight medially compensation.

Posteriorly, the left paraoccipital process and occipital condyle have been unnaturally shifted to the left. The right, non-distorted paraoccipital process was used to establish its proper position, while the occipital condyle was centred along the midline of the skull.

The braincase itself is reasonably well preserved. It was possible to remove the right quadrate from the steel armature without damage. This proved very useful in exposing the braincase for detailed study. Both alar processes of the basisphenoid (basisphenoid flange of Lull and Wright [1942]) have lost their lateral margins. Reconstruction was based on conservative estimates of the full extent of these margins. In addition, the left pterygoid process has become detached from its origin on the basisphenoid and is unnaturally fused in its corresponding groove on the pterygoid. The right, undamaged basiptyergoid process was used in the final reconstruction to establish its proper orientation.

The anterior edge of the parasphenoid is broken, and comparison with other hadrosaurs indicates the anterior extension of the cultriform process is missing. The tip would have projected anteriorly following the ventral surface of the preserved parasphenoid.

Although the left maxilla sits in its proper position, its anterolateral surface has experienced slight distortion. This has resulted in the loss of the detail in this area, obscuring the precise location of the maxillary foramina. The undistorted right maxilla was used to restore this detail, although the position of the left maxilla was used in the final reconstruction.

The left and right pterygoids sit in their approximate proper positions, but the bone surface of the left is poorly preserved. The right pterygoid is missing the posterior portion of its posterior alar projection. However, its extent on the quadrate is clearly indicated by a depressed area on the posteromedial surface of the pterygoid flange of the right quadrate. The right pterygoid is also missing its posteroventral projection of the quadrate ramus, and the incompletely preserved left posteroventral projection was used in the final reconstruction. The anterior portion of the right palatine ramus is missing, but the essentially complete left counterpart gives an indication of its anterior limit.

The right palatine has not been preserved. The left palatine remains essentially complete and undistorted, but the distal articulation of its anterolateral jugal process remains unclear due to poor preservation.

CHAPTER IV

MORPHOLOGICAL VARIATION IN *BRACHYLOPHOSAURUS CANADENSIS*

In a recent revision of *Brachylophosaurus canadensis* (Prieto-Márquez, 2005), several specimens collected from the lower Judith River Formation of Montana (MOR 794, MOR 1071, and UCMP 130139) and a single specimen from the Two Medicine Formation of Alberta (FMNH 862) were described. However, the holotype specimen was not considered in the rediagnosis. Although the specimens of *B. canadensis* do not differ greatly in their stratigraphic positions and the redescription of the holotype accords with many of the conclusions made by Prieto-Márquez (2005), there are a number of points of disagreement (Table 1).

True or perceived morphological differences between individuals of the same species can be a consequence of ontogenetic change, intraspecific variation, dimorphism, postmortem damage, or misinterpretation. Each of the discrepancies listed in Table 1 is briefly reviewed to help identify their source of conflict.

Minor repair work and slightly roughened bone surface makes the absence of an accessory premaxillary foramen difficult to confirm in the holotype, but there is no obvious evidence of its presence. Also, Sternberg (1953) had access to the holotype prior to the repair work and at no time was the presence of an accessory premaxillary foramen indicated. As such, the absence of an accessory foramen is maintained in the holotype specimen.

Thirty-five maxillary tooth positions were reported in subadult specimens of *Brachylophosaurus* (Prieto-Márquez, 2001) and 40-43 in adult specimens. The holotype, although about the same size as Prieto-Márquez's adults, has 46 maxillary tooth

Table 1. Morphological discrepancies between the holotype of *Brachylophosaurus canadensis* and other described specimens assigned to this species

Character	Holotype	Specimens described by Prieto-Márquez (2001 and 2005)
1. Accessory premaxillary foramen	Doubtful	Present
2. Number of vertical maxillary tooth row positions	46	40-43
3. Number of teeth contributing to the maxillary occlusal surface per vertical tooth position	All but four positions contribute one	Two
4. Number of vertical dentary tooth row positions	39	33
5. Constituent bones of mandibular glenoid	Surangular	Surangular and articular
6. Nasal foramina	Absent	Present
7. Nasal crest morphology (as described by Prieto-Márquez [2005])	Intermediate	Robust or slender
8. Number of cervical vertebrae	14	13
9. Axis: anterior neural spine morphology	Truncated	Elongate and hooked
10. Axis: dorsal transition between neural spine and postzygapophyseal flanges	Truncated	Elongate and gently sloping
11. Axis: medial incision between postzygapophyseal flanges	Absent	Present

positions, suggesting that tooth positions continued to be added even after full adult size was reached. This observation indicates the importance of using only adult specimens to avoid improperly scoring characters when assessing the phylogenetic position of a species.

Prieto-Márquez (2005) reported that two teeth contributed to the occlusal surface for each maxillary tooth row. This is consistent with Horner *et al.*'s (2004) statement that only *Telmatosaurus* has “one or two functioning teeth per family, while other hadrosaurids have at least two or three”, and that in both the maxilla and dentary “the occlusal surface cuts across two or more functional teeth...”. However, the majority of the tooth rows in the holotype of *B. canadensis* contribute only one tooth to the occlusal surface (also the condition observed by the author in *Edmontosaurus regalis* [NMC 2289]). Since the holotype is the only specimen accessible to the author, it is difficult to ascertain the source of conflict. Although unlikely, the discrepancy may be attributed to ontogenetic change or potential misinterpretation of the specimens described by Prieto-Márquez (2005).

Prieto-Márquez (2001) indicated that 33 vertical dentary tooth positions occur in most specimens, both adult and subadult, but that one subadult (MOR 1071-8-1-99-313) exhibited only 26 vertical positions. However, 39 vertical tooth row positions are observed in the dentary of the holotype. This trend suggests a strong ontogenetic influence, and that the specimens displaying 33 tooth positions, despite reaching an overall adult size, had not yet obtained their adult maximum of 39 vertical tooth row positions.

Prieto-Márquez (2005) reported that both the surangular and articular contacted the mandibular condyle of the quadrate in *Brachylophosaurus*, effectively supporting the reported relationship for hadrosaurs in general (Lull and Wright, 1942; Horner *et al.*, 2004). However, in the holotype of *B. canadensis*, when the quadrate is repositioned in its approximate natural position with the squamosal and the lower jaw is repositioned to articulate the mandibular condyle of the quadrate, both the surangular condyle and its medial flange make contact with only the surangular, precluding an articulation with the articular. This was also noted by Sternberg (1953), who stated that the articular “is so far back that it could have had little contact, if any, with the quadrate”. The specific relationships of these bones require further investigation.

Prieto-Márquez (2005) described the nasals of *B. canadensis* as possessing an “anteroposteriorly oriented groove terminating in elongated foramen, located medial to prefrontal”. However, their presence is figured for only MOR 1071-7-7-98-86 (see figs. 6b-c and 9a of Prieto-Márquez [2005]), making it unclear if these structures are present in other specimens. No anteroposteriorly oriented groove or nasal foramina are present in the holotype specimen, and cannot be considered an autapomorphy of the species, as proposed by Prieto-Márquez (2005).

Largely based on conspicuous differences in crest morphology, Prieto-Márquez (2005) identified two morphotypes of *Brachylophosaurus*. A robust form exhibits a well developed nasal crest that extends to the posterodorsal margin of the squamosal, completely obscures the supratemporal fenestra in dorsal view, and widens slightly posteriorly. The prefrontal extends posteromedially under the nasal crest and ends posterior to the orbit to form the anterior border of the supratemporal fenestra. A slender

morphotype exhibits a lesser developed nasal crest that compared to the robust morphotype, does not extend as far posteriorly, is not as wide, and narrows posteriorly rendering approximately half of the supratemporal fenestra visible from dorsal view. The prefrontal does not extend as far posterior as the orbit. The holotype of *B. canadensis* appears intermediate in its crest morphology. It shares with the robust form a well developed nasal crest that reaches just posterior to the supratemporal fenestra (but does surpass the posterior margin of the skull), and the prefrontal extends posterior to the orbit and turns medially at its posterior limit to form the anterior border of the supratemporal fenestra. As in the slender form, the nasal crest of the holotype does not obscure the entire supratemporal fenestra (the anterolateral corners are visible in dorsal aspect), is not as mediolaterally wide as the robust form, and narrows posteriorly.

If two morphs are actually present, an intermediate crest morphology can only be explained by the robust form exhibiting a delayed development in its crest that did not begin until the onset of adulthood. If so, the crest would appear intermediate in its morphology from the onset of crest development until it reached its full development. Therefore, to support the proposed dimorphs, the holotype specimen must be shown to have been in this period of crest development. Based on skull size the holotype is considered an adult. However, based on the additional number of maxillary and dentary tooth rows, it is also considered older than MOR 794 that exhibits a “robust” nasal crest morphology. Consequently, it is more parsimonious to assume that the crest in *Brachylophosaurus* indicates considerable intraspecific variability.

Prieto-Márquez (2001) reports thirteen cervical vertebrae in *Brachylophosaurus*, but it is unclear what criteria were used to define them and distinguish them from dorsal

vertebrae. In this thesis, the cervical vertebrae were defined as those bearing parapophyses on their centra (rather than on the base of their neural arches). According to this definition, the holotype has fourteen cervical vertebrae. Although this discrepancy may represent a difference in how cervical vertebrae are defined, it should be noted that Prieto-Márquez (2001) reports his last cervical vertebra differs in shape from both the other cervicals and the dorsal vertebrae. This description also applies to the last cervical in the holotype, suggesting the holotype cervical series truly does bear an extra vertebra.

At this time, interindividual variation seems the likely cause for the differences in morphology of the postzygapophyseal flanges observed among the axes of *B. canadensis*. However, only further discoveries will clarify this.

CHAPTER V

PHYLOGENETIC ANALYSIS

Horner *et al.* (2004) hypothesized an updated hadrosaurian phylogeny based on 105 characters (reproduced in Appendix I and fig. 13). Using a subset of forty-three characters from Horner *et al.* (2004) and four new characters, Prieto-Márquez (2005) reanalyzed the phylogeny of Hadrosaurinae. However, his work was largely ignored because justification of character choice was not provided, and Horner *et al.* (2004) incorporated more taxa and characters.

Using the original data matrix provided by Horner *et al.* (2004) (see Appendix I), their strict consensus tree was reproduced using PAUP 4.0b10 and MacClade 4.03 with no observable differences (189 steps, consistency index [C.I.] = 0.640, retention index [R.I.] = 0.741) (Note: Although Horner *et al.* [2004] stated there was a “Strict consensus of 19 most parsimonious trees”, this is likely a typographical error and should read “Strict consensus of 9 most parsimonious trees”). Although I agree with much of the interpretation provided by Horner *et al.* (2004), some inconsistencies were noticed and are reviewed below.

Based on limited information, *Nipponosaurus* was included in Horner *et al.*’s (2004) analysis and was placed as the sister group to Euhadrosauria (Lambeosaurinae + Hadrosaurinae), directly above *Telmatosaurus*. However, this position was considered tentative, and, although included in the analysis, *Nipponosaurus* was not placed in the cladogram. This explains why 19 ingroup taxa are cited by Horner *et al.* (2004), yet their tree included only 18 taxa. The significance of including *Nipponosaurus* as one of the analyzed 19 ingroup taxa is discussed below.

Figure 13. Cladogram depicting a phylogenetic analysis of Hadrosauridae based on data matrix in Appendix I. Strict consensus of 19 most parsimonious trees. L = 189 steps, C.I. = 0.640, R.I. = 0.741 (Horner *et al.*, 2004)

Although Horner *et al.* (2004) cited 11 unambiguous synapomorphies supporting Hadrosauridae, only 10 were listed (character numbers provided in bold and underlined, followed by state): 1) **2(1)** – three or more replacement teeth per tooth family, 2) **10(1)** – distal extension of the dentary tooth row to terminate caudal to apex of the coronoid process, 3) **18(1)** – caudalmost termination of the dentary well behind the coronoid process, 4) **19(1)** – absence of the surangular foramen, 5) **51(1)** – absence of contact between the ectopterygoid and jugal, 6) **59(1)** – absence or fusion of the supraorbital to the orbit rim, 7) **74(1)** – elevation of the cervical zygapophyseal peduncles on neural arches to extend well above the level of the neural canal, long and dorsally arched postzygapophyses, 8) **79(1)** – a coracoid with a long cranioventral process that extends well below the glenoid, 9) **80(1)** – a dorsoventrally narrow proximal scapula with an acromion process that projects horizontally, a notched cranioventral corner and a reduced area for its articulation with the coracoid, and 10) **101(1)** – a deep intercondylar extensor groove on the femur, whose edges meet or nearly meet cranially to enclose the extensor tunnel. By tracing each of the 105 characters in MacClade, character **60(1)** (lateral condyle of mandibular condyle of quadrates expanded rostrocaudally so that condyles appear subtriangular in distal view, lateral condyle longer than medial one) is identified as the missing eleventh unambiguous synapomorphy.

For the hadrosaurine trichotomy of *Naashoibitosaurus*, *Saurolophus*, and “*Kritosaurus*” *australis*, Horner *et al.* (2004) reported that this clade is united by exhibiting “a jugal whose pointed rostral process is symmetrically triangular in shape”, and that this feature (**54[2]**) is also observed in the lambeosaurine clade of *Parasaurolophus* + *Hypacrosaurus* + *Corythosaurus* + *Lambeosaurus*. However, based

on personal observation and their data matrix, this statement is erroneous. Character state 2 is observed in only *Brachylophosaurus*, *Maiasaura*, and *Telmatosaurus*; *Corythosaurus*, *Hypacrosaurus*, and Lambeosaurs display character state (0). The remaining ten Hadrosauridae genera, including *Naashoibitosaurus*, *Saurolophus*, and “*Kritosaurus*” *australis*, display character state (1).

Horner *et al.* (2004) indicated the hadrosaurine clade of *Edmontosaurus*, *Brachylophosaurus*, and *Maiasaura* shared one unambiguous synapomorphy: **20(2)** – a premaxillary bill that is greatly expanded transversely to a width subequal to the distance across the jugal arches. It should be noted that they share an additional unambiguous synapomorphy: **9(2)** – an extremely long diastema that is equal to approximately one third of the tooth row.

Modifications to the Data Matrix of Horner *et al.* (2004)

In describing the osteology of the holotype of *Brachylophosaurus canadensis*, numerous problems emerged concerning the characters listed by Horner *et al.* (2004). Although the entire suite of characters is not preserved in the holotype specimen, those that are present and demonstrate problems are now briefly described. Each character number corresponds to those in Horner *et al.* (2004) (see Appendix I).

1. Number of tooth positions: The holotype of *B. canadensis* exhibits 46 maxillary tooth positions and 39 dentary tooth positions. This creates two problems with the current character state description: a) 46 tooth positions is not listed in the possible ranges of teeth, and b) maxillary and dentary tooth counts are clumped into one character, and there is no range that represents 39-46 tooth positions. Although beyond the scope of this

project, such a difference in maxillary and dentary tooth positions suggests either two characters should be used to represent the upper and lower tooth row, or the currently described character should be restricted to either the upper or lower teeth. For the purposes of this research, the maxillary count of 46 is used and the range of teeth in character state (2) is expanded from 42-45 to 42-46. As such, the scoring of this character remains unchanged.

3. Number of functional teeth per tooth position: A maximum of four tooth positions on the better preserved left maxilla exhibit two teeth forming the occlusal surface. The remaining positions contribute only one tooth to the occlusal surface, indicating the scoring of this character should be changed from (1) to (0). Additionally, when interpreting Weishampel's (1984) lingual worn zone (see pages 89-90 of this thesis for a discussion on the lingual worn zone) as the functional portion of the tooth row, *B. canadensis* exhibits at least 11 dentary tooth positions that contribute only one tooth to the functional occlusal surface, with 6 of these occurring in the 11 posterior tooth positions. However, due to potential confusion on the position of the lingual worn zone and buccal worn zone, the dentary was not included in the amendment to the current character state.

41 (27 and 29). Shape of posterior margin of external naris: Character 41 was removed from the final analysis based on its questionable significance. The shape of the posterior margin of the external naris of hadrosaurs is dependant on the constituent bones that form it. The latter relationship is the significant character and was indicated in both character 27 and 29 of Horner *et al.*'s (2004) data matrix. However, because the constituent bones

vary among hadrosaurs, the posterior margin of the external naris is an analogous feature and not useful in assessing relatedness.

Character 27 is a valid character. It identifies the development of the posterodorsal and posterolateral premaxillary processes, and their relationship relative to the external naris and the nasal bone. However, character 29 repeats the relationship of the constituent bones forming the posterior apex of the external naris, essentially doubling the weight of this character. Also, because the lambeosaurines exhibit a modified tubular external naris, Horner *et al.* (2004) were not able to identify the bones forming the posterior margin of the external naris and recorded it as unknown for the entire group. Lastly, *Saurolophus* is the only genus that exhibits the derived state (1) of character 29, therefore this is an autapomorphy of the genus and not useful in establishing phylogenetic relationships. As such, character 27 was kept and character 29 was removed from the analysis.

52. Anterior expansion of jugal: Although the jugal is dorsoventrally expanded anterior to the orbit, the lacrimal has not been “pushed dorsally to lie completely above the level of the maxilla”, as outlined by character state (1). This statement should be removed from the character description because the morphology of the jugal is the focus of this character, and the maxilla-lacrimal contact has already been identified in character 45. This amendment allows this character to remain unchanged in the final analysis.

61. Paraquadratic notch: *Iguanodon atherfieldensis* (see fig. 19.2A of Norman [2004]) bears a paraquadratic foramen that forms between the posterior margin of the quadratojugal and a conspicuous paraquadratic notch in the posteroventral corner of the embayment of the quadrate. The quadrate of *B. canadensis* does not bear a paraquadratic

notch, but a narrow elliptical paraquadratic foramen still occurs between the embayment of the quadrate and the straight posterior margin of the quadratojugal that occupies it. In other hadrosaurs, the posterior margin of the quadratojugal becomes crescent-shaped and no paraquadratic foramen is present. The occurrence of a paraquadratic foramen in *B. canadensis* indicates the definition of character 61 should be changed to reflect the presence/absence of the paraquadratic foramen and not the detail of the paraquadratic notch. Under this definition, the scoring for *Brachylophosaurus* is changed from a (1) to a (0), and the other taxa remain unchanged.

99. Shape of distal ischium: Horner *et al.* (2004) indicated the distal ischia of *B. canadensis* and *Maiasaura peeblesorum* was large and footed like that of lambeosaurs. However, in agreement with Prieto-Márquez (2001: figs. 62 and 63; 2005) the scoring of this character is amended to reflect the hadrosaurine condition (0) for both genera.

Discussion of Phylogenetic Position

With the above mentioned changes made to Horner *et al.*'s (2004) matrix, the cladistic analysis was rerun. No changes in the topology of the tree were observed, and the distribution of shared characters outlined by Horner *et al.* (2004) was maintained. Also, the C.I. and R.I. values remained the same. The length of the consensus tree was reduced to 184 steps, a consequence of deleting two problematic characters from the data matrix.

The significance of including *Nipponosaurus* in the analysis emerged as a point of interest. When this genus was removed from the analysis, the topology of the cladogram changed (fig. 14). The monophyly of Hadrosauridae remained supported by the same 11

Figure 14. Cladogram depicting a phylogenetic analysis of Hadrosauridae based on modifications made to data matrix in Appendix I (*Nipponosaurus* excluded from analysis). Strict consensus of 117 most parsimonious trees. L = 181 steps, C.I. = 0.68, R.I. = 0.78

unambiguous synapomorphies. “*Kritosaurus*” *australis*, a hadrosaurine in Horner *et al.*’s (2004) cladogram, becomes the sister group to Euhadrosauria (Hadrosaurinae + Lambeosaurinae). Euhadrosauria is supported by 17 unambiguous synapomorphies, 10 of which agree with Horner *et al.* (2004): 15(1), 16(1), 17(1), 64(1), 68(1), 71(1), 75(1), 86(1), 90(1), and 102(1); and 7 which are new: 72(1), 87(1), 88(1), 89(1), 103(1), 104(1), and, 105(1). Hadrosaurinae remains united by character 31(1), although a polytomy is formed between half of its members and a clade formed by *Brachylophosaurus*, *Maiasaura*, *Edmontosaurus*, and *Gryposaurus*. As outlined by Horner *et al.* (2004), *Edmontosaurus*, *Brachylophosaurus*, and *Maiasaura* remain united by character states 9(2) and 20(2). Lambeosaurinae remain united by the same four synapomorphies listed by Horner *et al.* (2004), 42(1), 44(1), 48(1), and 70(1), but all relationships within this clade are unresolved. Although Hadrosauridae and Euhadrosauria appear well supported, the removal of *Nipponosaurus* indicates the weak relationships among the members of each subfamily. This observation indicates the need to redefine the characters listed in Appendix I. Also, additional fossil material will help to better establish the relationships of the less complete specimens.

CHAPTER VI

THE CHEWING MECHANICS OF *BRACHYLOPHOSAURUS CANADENSIS*

The chewing mechanics of hadrosaurids has long been debated (see pages 3-5 of Weishampel [1984] for an excellent review of this history). Much of the controversy has centred on potential cranial kinesis, with the question of quadrate and mandibular mobility often being discussed. Weishampel (1983; 1984) and Norman and Weishampel (1985) interpreted previously proposed models as kinematic linkage systems using three dimensional computer simulations. An analysis of ornithomimid cranial joints established kinetic limitations of each link (or component part), which were subsequently used to define the constraints within the simulations. The simulations were then run to provide tooth wear predictions for each of the proposed models. These predictions were then compared to the observed tooth wear in each associated test specimen. Agreement between the predicted and actual tooth wear patterns would support the proposed chewing model, and differences would reject the proposed model. Ultimately, all of the theories were rejected (Appendix II), and a new streptostyly mechanism (pleurokinetic hinge model) that includes vertical adduction of the mandible with lateral flaring of the maxillae, and posterolateral movement of the quadrates was proposed (Weishampel, 1983; Weishampel, 1984; Norman and Weishampel, 1985).

Due to the relative completeness and overall good preservation of the skull, the holotype of *Brachylophosaurus canadensis* is an ideal candidate for testing the streptostyly mechanism. An examination of the cranial joint morphology of *B. canadensis* was completed, and used to identify kinetic limitations of each element. The streptostyly mechanism was then applied to the skull of *B. canadensis* to test whether the

kinetic restrictions were accommodated. The disarticulated skull of *Edmontosaurus regalis* (CMN 2289), another hadrosaurine, was used to aid in interpretation of less well preserved portions of the skull. Only relevant osteology is considered in this chapter. The reader should refer to Chapter III – Osteology for further details on structure.

Based on joint structure and kinetic limitations, an upper and lower unit was identified within the skull.

The Upper Unit

The upper unit is formed by the maxilla, jugal, palatine, pterygoid, quadratojugal, and quadrate. The head of the jugal forms a broad scarf joint with the robust jugal articular facet of the maxilla, suggesting the jugal and maxilla functioned as a single unit. The structure of the palatine is very similar in *Brachylophosaurus* and *Edmontosaurus*. The ventral surface of the palatine, accessible in *E. regalis*, bears a dorsally concave groove and flat ridge that articulates the maxilla below. The morphology of this joint, in addition to the nature of the articulation of the anterolateral jugal process of the palatine with the jugal, suggests no movement occurred between these elements. As noted by Heaton (1972), the pterygoid is “suturally fused” to the dorsomedial surface of the palatine. This butt joint is visible in *E. regalis* as a small ridge on the dorsomedial surface of the palatine. Dorsal to this ridge, the thin palatine forms a lap joint with the lateral surface of the pterygoid. These joints would have restricted any movement between the palatine and pterygoid. Independent movement of the pterygoid is further restricted by its articulation with the maxilla and ectopterygoid. It forms an interlocking joint with the posteromedial pterygoid process of the maxilla, and more ventrally the

ectopterygoid ramus of the pterygoid wedges between the maxilla and ectopterygoid. Posteriorly, a broad scarf joint is formed between the posterior alar projection of the pterygoid and the posterior surface of the pterygoid flange of the quadrate. The last link of the upper unit joins the quadratojugal with the quadrate and jugal. In *B. canadensis* the posterodorsal edge of the quadratojugal articulates with the quadrate in a scarf joint, and posteroventrally the quadratojugal forms a butt joint with an articular facet on the quadrate. A similar arrangement occurs in *E. regalis*, but the quadratojugal contacts the quadrate along its entire posterior margin. Although not nearly as pronounced in the holotype of *B. canadensis*, the left jugal of *E. regalis* displays a distinct slot on its medial surface for reception of the anterior edge of the quadratojugal. This broad lap joint suggests sliding between the jugal and quadratojugal did not occur. The structure of the above mentioned joints precludes independent movement of any of the bones that form the upper unit. This limits the capacity for transverse and propalinal movement of the upper unit, as discussed below.

Transverse movement – In *B. canadensis* the anterior process of the maxilla is oval to teardrop-shaped in cross-section, and inserts into a medial trough of the premaxilla that conforms to its shape. Coossification between these elements did not occur, suggesting the possibility of kinetic movement, but specific movements are limited by the morphology of the joint. Any form of lateral or medial rotation or flaring of the maxilla is restricted by the interlocking relationship of the process and trough. The premaxillary trough does not afford the space required for the anterior maxillary process to rotate, rendering transverse movement of the maxilla impossible.

Further limiting lateral movement of the maxilla within the upper unit is the articulation between the maxilla and lacrimal. The lacrimal articulates with the dorsolateral surface of the maxilla, but there is no indication that this articulation coossified, suggesting the potential for movement. However, the articulation between the lacrimal and prefrontal effectively prevents this. In posterior aspect, the lacrimal forms a peg and socket synarthrosis with the prefrontal above, ensuring its immobility. Consequently, the fixed anterior maxillary process of the lacrimal cannot accommodate lateral movement of the maxilla. Furthermore, the gracile postorbital bar bears a scarf joint formed between the postorbital process of the jugal and the jugular process of the postorbital. This inflexible joint is poorly suited to accommodate transverse movement of the jugal.

Propalinal (anteroposterior) movement – Although the quadrate-squamosal joint appears to be synovial in structure, the jugal-postorbital and jugal-lacrimal joints show little capacity for movement. The rigidity of the scarf joint formed between the postorbital process of the jugal and the jugular process of the postorbital would not permit translation between these processes. The jugal-lacrimal orbital joint, although partially damaged in *B. canadensis*, does not appear to differ significantly between *B. canadensis* and *E. regalis*. The lacrimal in *E. regalis* clearly interlocks with the jugal by a tongue and groove joint. As a result, propalinal movement of the maxilla is effectively blocked.

The articulation of the lacrimal with the maxilla also appears to limit propalinal movement in the upper unit. Although these bones are not fused, the delicate anterior portion of the lacrimal overlaps the dorsolateral surface of the maxilla. A mobile maxilla

would be required to slide past the stationary lacrimal, a movement that the delicate lacrimal seems ill-designed to accommodate.

The Lower Unit

The lower unit is formed by the mandible, which comprises the prementary, dentary, surangular, splenial, angular, and articular. As noted by Weishampel (1984), the postdentary bones articulate with each other through firm butt or scarf joints, and likely did not provide any degree of mandibular kinesis. The prementary is missing in the examined specimens of *B. canadensis* and *E. regalis*, suggesting that it did not coossify with the dentary. However, in other described material the lateral processes of the prementary overlap the lateral surfaces of each dentary, the anterior surface of the dentary butts the prementary, and the posteriorly projecting symphyseal process and bifurcated posteroventral process bind the mandibular symphysis dorsally and ventrally, respectively (Weishampel, 1984; Prieto-Márquez, 2005). This configuration does not suggest significant movement occurred between these elements. However, accommodation of slight compression, tension, or twisting experienced at the unfused mandibular symphysis may have been possible.

Potential movement – Having fewer bones with simpler sutural relationships, the lower unit appears less restricted in its movement than the upper unit. Although significant movement of the mandible is not possible anteriorly, more freedom appears likely posteriorly at the surangular-quadrato joint. Although movement would be limited by the relatively immobile prementary-dentary joint, slight propalinal and/or transverse motion

in addition to simple hinge-like rotation during jaw abduction/adduction cannot be rejected.

Consideration of the Streptostyly Mechanism (Pleurokinetic Hinge Model)

Weishampel (1983; 1984), and Norman and Weishampel's (1985) proposed streptostyly mechanism includes vertical adduction of the mandible with lateral flaring of the maxillae, in combination with posterolateral movement of the quadrates. These primary actions drive a series of linked secondary motions (Table 2, Appendix III for schematic drawings, and Appendix IV for streptostyly animation). However, based on bone morphology and the kinematic limitations imposed by joint structure described above, this collective series of motions cannot be recreated in the holotype of *Brachylophosaurus canadensis*.

Lateral rotation of the maxilla during mandibular adduction is prevented by the structure of the joint between the anterior maxillary process and the premaxilla, as well as by the articulation of the stationary lacrimal to the dorsolateral surface of the maxilla. Posterolateral rotation of the quadrate also appears impossible in *B. canadensis*, since this movement would require the quadrate or quadrate-pterygoid to function independently from the upper unit. However the quadrate forms a broad contact with the pterygoid, and the pterygoid forms a rigid complex with the palatine-ectopterygoid-maxilla, precluding a mobile hinge joint between the pterygoid and the palatine-ectopterygoid-maxilla complex. Other kinematic limitations observed in *B. canadensis* render many of the other secondary movements unlikely. The scarf joint between the postorbital and jugal effectively prevents translocation, and there is no evidence that the quadratojugal was

Table 2. Movements associated with the hadrosaurian streptostyly mechanism (Weishampel, 1984).

Primary Movements	Secondary Movements
1. Vertical adduction of the mandible.	1. Translation between the postorbital and the jugal.
2. Lateral rotation of the maxilla at the maxilla-premaxilla joint.	2. Rotation and/or translation between the quadratojugal and the quadrate.
3. Lateral rotation of the jugal-maxilla complex at its contact with the lacrimal.	3. Cylindrical movement (rotation plus translation) between the pterygoid process of the basisphenoid and the pterygoid.
4. Posterolateral rotation of the quadrate at its contact with the squamosal.	4. Symphyseal rotation of the mandibles.
	5. Rotation between the pterygoid and the palatine-ectopterygoid-maxilla complex.
	6. Rotation of the ventral head of the quadrate against the mandibular glenoid.

capable of dislocating from its articulation with the quadrate. The proposed cylindrical movement between the pterygoid process of the basisphenoid and the pterygoid seems possible if this joint is considered in isolation, but the movement of the pterygoid is limited by its association with the upper unit, effectively blocking significant rotation.

The movements that seem most possible are the motions associated with the mandible. Mandibular symphyseal rotation in association with jaw adduction, as suggested by Weishampel (1984), would be limited by the restricted flexibility at the symphysis and the dentary-predentary joint. However, the limits of this relationship remain unclear. The structure of the mandibular glenoid, in particular the relatively open dish-shaped articular surface of the surangular, probably could have accommodated some translation as well as rotation of the mandible about the fixed quadrate.

Tooth Wear Patterns

Weishampel (1984) examined the teeth of several species of hadrosaurs and found that the wear patterns conformed to those predicted by his model. However, some of these patterns are not present in *B. canadensis*.

Facet angulation – Weishampel (1984) predicted that the facet angulation of the tooth row would be variable along the occlusal surfaces of hadrosaurs, and that this condition was confirmed in hadrosaurs. However, in *E. regalis* and *B. canadensis*, both the occlusal surfaces of the maxillary and dentary teeth show a consistent facet angulation along the length of their respective tooth rows.

Difference in lengths between opposing occlusal surfaces – In order to render tooth rows of unequal length functional, propalinal movement in either the upper or lower jaws

is expected. Although Weishampel (1984) reported that his hypothesis could not predict a difference in the lengths of the maxillary and dentary tooth row (Appendix II), our computer simulation that is based on his streptostyly model (Appendix IV) clearly shows posterolateral retraction of the quadrates and mandible, which is compatible with dentary and maxillary tooth rows of unequal lengths. The worn portion of the maxillary tooth row is approximately 10 mm longer than the dentary tooth row in *B. canadensis*, suggesting that at least 10 mm of relative anteroposterior movement occurred between the upper and lower tooth rows. However, as previously argued, the articulations with the pterygoid and quadratojugal render the quadrate immobile in *B. canadensis*, and preclude posterolateral movement of the quadrates and jaws. The mandibular glenoid, which appears capable of accommodating some translation as well as rotation, is the only point in the skull where limited propalinal movement was likely to have occurred.

Disposition of enamel and enamel-dentine interface – As in all hadrosaurs, the enamel of *B. canadensis* is largely restricted to the lateral surfaces of the maxillary teeth and the medial surface of the dentary teeth. The occlusal surfaces of the functional maxillary and dentary teeth are gently concave. In each functional dentary tooth the enamel-dentine interface is flush along its leading edge where the enamel has shielded the adjacent dentine from wear. On its more lateral trailing edge, the unprotected dentine has worn faster than the harder enamel resulting in a step-like interface. This pattern indicates the direction of the power stroke (Appendix V); a vertical component is necessary with the upper tooth row first grinding over the more medial leading enamel-dentine interface, followed by contact with the more lateral trailing enamel-dentine interface. However,

this pattern could be reproduced by any chewing model that includes orthal motion of the lower jaws, and as such its diagnostic potential is limited.

Microstriae orientation – Transverse to slightly oblique microstriae were predicted by the streptostyly model. This model cannot be rejected on this tooth wear pattern, as the presence of transverse microstriae on the occlusal surface of both maxillary and dentary teeth were confirmed (Weishampel, 1984). However, this pattern indicates a lack of significant propalinal movement during the power stroke of the chewing cycle, and rejects models such as that described by Ostrom (1961).

Macrofeatures and mediolateral curvature of tooth rows – The occlusal surface of the dentary tooth row in hadrosaurs is generally described as “concave” (Ostrom, 1961; Weishampel, 1984; Horner *et al.*, 2004). However, in both *B. canadensis* and *E. regalis*, the occlusal surface of preserved dentary teeth is divided into a continuous, vertically inclined, dorsolaterally facing surface that is set off from a more horizontal facet by an angle of approximately 140° near the midlength of the tooth row. The transition between the two surfaces is curved (longitudinal groove of Weishampel [1984]). Both the vertical and horizontal facets are best developed on teeth in the middle of the tooth row, and become reduced in size both posteriorly and anteriorly. Weishampel (Appendix VI) named the vertically inclined facets the “lingual worn zone”, and the more lateral horizontal facets the “buccal worn zone”. I agree with Weishampel (1984) that the “lingual worn zone” represents the portion of the tooth row bearing the functional occlusal surface. The functional significance of the “buccal worn zone” is uncertain however, as at one point it is also referred to as an “unworn portion” (see page 62 of Weishampel [1984]).

Due to the curved transition between the functional and non-functional teeth (observed in *B. canadensis*, *E. regalis* and *E. saskatchewanensis* [NMC 8509]), a false impression is given that the mediolateral width of the tooth row is concave. Although slight medial rotation of the dorsal portion of the dentary, accommodated by a flexible mandibular glenoid, probably produced this curvature, the purported concave shape of the occlusal surface of the tooth row is largely an illusion in *Brachylophosaurus*. Only the more vertical facets (lingual worn zone) actually occluded the maxillary tooth row. The eroded stumps that collectively comprise the horizontal facets (buccal worn zone) of the concave surface are all that remain of the teeth that have migrated laterally out of reach of the maxillary teeth. Thus, the “concave occlusal surface” that drove much of the speculations regarding cranial kinesis in hadrosaurs appears to be an illusion in at least *Brachylophosaurus*.

Dorsoventral curvature of tooth rows – A dorsoventral curvature to the tooth rows is listed as expected for the streptostyly mechanism and possible for the remaining hadrosaurian chewing models (Appendix II). However, no justification or interpretation is provided for either of these predictions, and as such this tooth wear pattern cannot be analyzed further.

Conclusions

The cranial morphology of *B. canadensis* supports the conclusion of Weishampel (1983; 1984) and Norman and Weishampel (1985) that the widths of the upper and lower jaws of hadrosaurs are equivalent, and the primitive reptilian isognathic condition is maintained. However, based on cranial joint morphology, the generalized streptostyly

mechanism proposed for hadrosaurs is rejected for *B. canadensis*. A simplified model based on a rigid upper unit that does not contribute movement related to the chewing cycle, and a lower unit that exhibits limited freedom at its mandibular glenoid and appears to have been capable of slight propalinal movement and minimal medial rotation about its long axis cannot be rejected. Also, the generalized tooth wear predictions proposed by Weishampel (1984) deviate from those observed in *Brachylophosaurus*, but can be explained by the simplified model. Further comparison of tooth wear patterns and cranial joint morphology is required to establish whether the chewing mechanism was variable among the Hadrosauridae.

CHAPTER VII

SUMMARY

This thesis provides the first thorough description for the holotype of *Brachylophosaurus canadensis*. Its systematic position within the Hadrosaurinae is confirmed, with the holotype exhibiting the following autapomorphies: the nasals greatly developed into a paddle-like solid crest extending posterodorsally, overhanging the dorsal region of skull; the prefrontal posteriorly projected over the frontal, and, more posteriorly, ventromedially directed to underlay the nasal crest and contribute to the anterior border of the supratemporal fenestra; only the anterior sharp tip of the lacrimal contacting the maxilla; a jugal with a ventrally projected semicircular flange that is deeper overall than that of *M. peeblesorum*, but more lightly built than in the remaining hadrosaurines; an extremely elongated, rod-like anterior maxillary process projecting medial to the narial cavity; and a rhomboidal shaped quadratojugal with a non-crescentic posterior margin that forms a paraquadratic foramen with the quadrate. Morphological discrepancies with other specimens of *Brachylophosaurus* are identified and provide new areas of research. The holotype specimen also demonstrates that the chewing mechanics of hadrosaurs are far from clear. The dynamic streptostyly mechanism cannot be reproduced in *Brachylophosaurus*, and a simplified model with a mobilized mandible cannot be rejected at this time. The dental morphology of *Brachylophosaurus* does not conform to the previously proposed generalized tooth wear patterns for hadrosaurs, suggesting variation in the hadrosaur chewing mechanism may have existed. Further research is required to confirm or disprove this possibility.

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PLATES

Plate I: A, lateral view of left skull; B, lateral view of right skull; C, dorsal view of skull; D, posterior view of skull; E, anterior view of skull

Plate I: continued

Plate II: A, lateral view of left lower jaw; B, lateral view of right lower jaw; C, medial view of left lower jaw; D, medial view of right lower jaw; E, lateral view of right hyoid (bottom) and left hyoid (top); F, medial view of right hyoid (bottom) and left hyoid (top)

Plate II: continued

Plate III: A, lateral view of left atlas neural arch; B, lateral view of right atlas neural arch; C, medial view of left atlas neural arch; D, medial view of right atlas neural arch; E, posterior view of atlas intercentrum; F, anterior view of atlas intercentrum; G, lateral view of left-side of axis and third cervical vertebra; H, lateral view of right-side of axis and third cervical vertebra; I, anterior view of cervical vertebrae four – thirteen; J, anterior view of fourteenth cervical vertebra; K, lateral view of left-side of fourteenth cervical vertebra; L, anterior view of dorsal vertebrae one – nine (D2 not shown due to poor preservation)

Plate III: continued

E.

5 cm

F.

G.

10 cm

H.

10 cm

Plate III: continued

Plate III: continued

Plate III: continued

Plate IV: Dorsal ribs

Plate V: A, medial view of scapula and coracoid; B, lateral view of scapula and coracoid

Plate VI: A, posterior view of humeri; B, anterior view of humeri

Plate VII: A, lateral view of ulna (left) and radius (right); B, anterior view of ulna (left) and radius (right); C, anterior view of manus elements; D, posterior view of manus elements

Plate VII: continued

APPENDICES

Appendix I: Character description and data matrix for Hadrosauridae (Horner *et al.*, 2004)

1. Number of tooth positions in maxillary and dentary tooth rows: 30 or fewer (0); 34–40 (1); 42–45 (2); 47 or more (3).
2. Number of replacement teeth per tooth position: one or two (0); three or more (1).
3. Number of functional teeth per tooth position: one (0); at least two, and often three, teeth in the vertical series contribute to the occlusal surface (1).
4. Maxillary tooth crown length:width ratio at center of tooth row: broad relative to length, ratio less than 2.4:1 (0); elongate and lanceolate, ratio at least 2.5:1 (1).
5. Dentary tooth crown length:width proportions at center of tooth row: broad, ratio of 2.9:1 or less (0); elongate, ratio of 3.2–3.8:1 (1).
6. Dentary teeth, ornamentation on lingual surface: numerous subsidiary ridges present (0); only one or two subsidiary ridges present, located mesial and distal to primary carina (1); loss of all but primary carina (2).
7. Maxillary teeth, ornamentation on labial surface: subsidiary ridges present (0); loss of all but primary carina (1).
8. Teeth, position of apex: offset to either mesial or distal side, tooth curved distally (0); central, tooth straight and nearly symmetrical (1).
9. Dentary, length of diastema between first dentary tooth and prementary: short, no more than width of four or five teeth (0); long, equal to approximately one-fifth to one-fourth length of tooth row (1); extremely long, equal to approximately one third of tooth row (2).
10. Dentary tooth row, caudal extent of tooth row relative to apex of coronoid process: tooth row terminates even with or rostral to apex (0); tooth row terminates caudal to apex (1).
11. Dentary, orientation of dentary rostral to tooth row: moderately downturned, dorsal margin of prementary rests above ventral margin of dentary body (0); strikingly downturned, dorsal margin of rostral dentary extends below the ventral margin of dentary body, premaxillary bill margin extends well below level of maxillary tooth row (1).

Appendix I: continued

12. Dentary tooth row, shape in occlusal view: bowed lingually, curves in toward coronoid process (0); straight (1).
13. Prementary shape: deep and robust, arcuate rostral margin, neurovascular foramina large and located near midline of prementary body, dorsally directed spikelike denticles on rostral margin that fit into slots on underside of premaxilla (0); gracile and shovel-shaped, straight to gently rounded rostral margin, numerous nutrient foramina across entire rostral margin, loss of spikelike denticles and gain of rounded, triangular denticles that project rostrally and fit into a continuous transverse slot on underside of premaxilla (1).
14. Prementary triturating surface, orientation: horizontal, oral margin of premaxilla rests on dorsal prementary (0); canted dorsolaterally to form a nearly vertical surface, oral margin of premaxilla broadly overlaps lateral surface of prementary (1).
15. Angular size: large, deep, exposed in lateral view below the surangular (0); small, dorsoventrally narrow, exposed only in medial view (1).
16. Coronoid bone: present (0); absent (1).
17. Coronoid process configuration: apex only slightly expanded rostrally, surangular large and forms much of caudal margin of coronoid process (0); dentary forms nearly all of greatly rostrocaudally expanded apex, surangular reduced to thin sliver along caudal margin and does not reach to the distal end of the coronoid process (1).
18. Caudal extent of the caudoventral dentary: ends even with or rostral to apex of coronoid process (0); caudally expanded to terminate well behind the coronoid process (1).
19. Surangular foramen: present (0); absent (1).
20. Premaxilla, width at oral margin: narrow, expanded laterally less than twice width at narrowest point (postoral constriction), margin oriented nearly vertically (0); expanded transversely to more than twice postoral width but not more than interorbital width, margin flared laterally into a more horizontal orientation (1); further expanded transversely to width subequal to that across jugal arches (2).
21. Premaxilla, undercut ("reflected") rim around oral margin: absent (0); present (1).

Appendix I: continued

22. Premaxillary rostral bill margin shape: horseshoe-shaped, forms a continuous semicircle that curves smoothly to postoral constriction (0); broadly arcuate across rostral margin, constricts abruptly behind the oral margin (1).
23. Premaxillary foramen ventral to rostral margin of external nares that opens onto the palate: absent (0); present (1).
24. Premaxilla, accessory foramen entering premaxilla in outer narial fossa, located rostral to premaxillary foramen: absent (0); present, empties into common chamber with premaxillary foramen, then onto the palate (1).
25. Premaxillae, oral margin with a “double layer” morphology consisting of an external denticle-bearing layer seen externally and an internal palatal layer of thickened bone set back slightly from the oral margin and separated from the denticulate layer by a deep sulcus bearing vascular foramina: absent (0); present (1).
26. Premaxilla, outer (accessory) narial fossa rostral to circumnarial fossa: absent (0); present, separated from circumnarial fossa by a strong ridge (1).
27. Premaxillary caudal processes (PM1, PM2) and construction of nasal passages: caudodorsal premaxillary process short, caudodorsal and caudoventral processes do not meet caudal to external nares, nasal passages not enclosed ventrally, rostral nasal passage roofed by the nasal, external nares exposed in lateral view (0); caudoventral and caudodorsal processes elongate and join behind external opening of narial passages to exclude nasals, nasal passages completely enclosed by tubular premaxillae, left nasal passage divided from right passage, external nares not exposed in lateral view (1).
28. External nares length:basal skull length ratio: 20% or less (0); 30% or more (1).
29. External nares, composition of caudalmost apex: formed entirely by nasal (0); formed equally by nasal (dorsally) and premaxilla (ventrally) (1).
30. Supraoccipital, ventral margin: bowed or expanded ventrally along midline (0); horizontal, strong ridge developed along supraoccipital-exoccipital suture (1).
31. Circumnarial fossa, caudal margin: absent (0); present (1).
32. Circumnarial fossa, caudal margin morphology: absent (0); present, lightly incised into nasals and premaxilla, often poorly demarcated (1); present, well demarcated, deeply incised, and usually invaginated (2).

Appendix I: continued

33. Nasals and rostradorsal premaxilla in adults: flat, restricted to area rostral to braincase, cavum nasi small (0); premaxilla extended caudally and nasals retracted caudally to lie over braincase in adults resulting in a convoluted, complex narial passage and hollow crest, cavum nasi enlarged (1).
34. Hollow nasal crest, nasal-caudodorsal process of premaxilla (PM1) contact: absent (0); present, rostral end of nasal fits along ventral edge of premaxilla (1); present, premaxilla and nasal meet in a complex, W-shaped interfingering suture (2).
35. Hollow nasal crest, relative shape of the two lobes of caudoventral process of premaxilla (PM2): absent (0); present, rostral lobe higher than caudal lobe (1); present, caudal lobe higher than rostral lobe (2).
36. Hollow nasal crest, shape: absent (0); present, tubular and elongate (1); present, raised into a large, vertical fan (2).
37. Hollow nasal crest, composition of caudal margin of crest: absent (0); present, composed of premaxilla caudodorsal process (PM1) (1); present, composed of nasal (2).
38. Solid nasal crest over snout or braincase (does not house a portion of the nasal passage): absent (0); present (1).
39. Solid nasal crest, association with caudal margin of circumnarial fossa: absent (0); solid crest present but circumnarial fossa does not excavate side of crest, fossa terminates rostral to solid crest (1); solid crest present, excavated laterally by circumnarial fossa (2).
40. Solid nasal crest, composition: absent (0); solid crest present, composed of nasals (1); solid crest present, composed of frontals and nasals (2).
41. External nares, shape of caudal margin: lunate (0); V-shaped (1).
42. Maxilla, rostradorsal process: has a separate rostral process that extends medial to the caudoventral process of premaxilla to form part of medial floor of external naris (0); rostral process absent, rostradorsal margin of maxilla forms a sloping shelf that underlies the premaxilla (1).
43. Antorbital fenestra, external opening: present (0); absent (1).
44. Maxillary foramen, location: opens on rostralateral body of maxilla, exposed in lateral view (0); opens on dorsal maxilla along maxilla-premaxilla suture (1).

Appendix I: continued

45. Maxilla-lacrima contact: present (0); lost or covered due to jugal-premaxilla contact (1).
46. Maxilla-jugal contact: restricted to fingerlike jugal process on caudal margin of maxilla (0); jugal process of maxilla reduced to a short projection but retaining a distinct facet (1); jugal process of maxilla lost, rostral jugal has an extensive vertical contact with maxilla rostral to orbit (2).
47. Maxilla, location of apex in lateral exposure: well caudal to center (0); at or rostral to center (1).
48. Maxilla, shape of apex in lateral exposure: tall and sharply peaked (0); low and gently rounded (1).
49. Prefrontal shape at rostradorsal orbit rim: prefrontal lies flush with surrounding elements (0); prefrontal flares dorsolaterally to form a thin, everted, winglike rim around rostradorsal orbit margin (1).
50. Prefrontal, shape: smoothly curved laterally (0); rostrally broad with square rostromedial corner (1).
51. Ectopterygoid-jugal contact: present (0); absent, palatine-jugal contact enhanced (1).
52. Jugal, expansion of rostral end below lacrima: dorsoventrally narrow, forms little of the rostral orbital rim (0); expanded dorsoventrally in front of orbit, lacrima pushed dorsally to lie completely above the level of the maxilla, jugal forms lower portion of orbital rim (1).
53. Jugal, shape of rostral end: with distinct rostrally pointed process fitting between the maxilla and lacrima (0); point truncated, smoothly rounded rostral margin (1).
54. Jugal, rostrally pointed process: absent (0); present, process restricted to dorsal portion of jugal, rostral jugal appears asymmetrical (1); present, process centered on rostral jugal, rostral jugal appears symmetrically triangular in shape (2).
55. Jugal, development of free ventral flange: absent, jugal expands gradually below infrafenestra to meet the quadratojugal-quadrata (0); present, jugal dorsoventrally constricted beneath intratemporal fenestra to set off flange rostral to constriction (1).

Appendix I: continued

56. Jugal flange size, ratio of depth of jugal at constriction below intratemporal fenestra to length of free ventral flange on jugal: small, 0.70–0.90 (0); prominent, well set off from body of jugal, 0.55–0.66 (1).
57. Frontal at orbit margin: forms part of margin (0); excluded by prefrontal-postorbital contact (1).
58. Frontals, upward doming over braincase in adults: absent (0); present (1).
59. Supraorbital articulation: freely articulate on orbit rim (0); fused to orbit rim or absent (1).
60. Quadrates, shape of mandibular condyle: mediolaterally broad, lateral and medial condyles subequal in size (0); lateral condyle expanded rostrocaudally so that condyles appear subtriangular in distal view, lateral condyle longer than medial one (1).
61. Paraquadrate notch: ventral margin of notch extends dorsally to form an acute and well-defined opening (0); well-defined notch absent, reduced to a poorly defined embayment of quadrate (1).
62. Paroccipital process and accompanying squamosal, orientation: straight and ventrally directed (0); curved rostrally (1).
63. Squamosals on skull roof, separation: widely separated (0); squamosals approach midline, separated by narrow band of parietal (1); squamosals have broad contact with each other (2).
64. Squamosal, shape of caudoventral surface: shallowly exposed in caudal view (0); form a deep, near vertical, well-exposed face in caudal view (1).
65. Supraoccipital, inclination: caudal surface nearly vertical (0); caudal surface inclined steeply forward at approximately 45° (1).
66. Supraoccipital-exoccipital contact: straight suture that meets squamosal (0); ventrolateral corner of supraoccipital inset into exoccipital so that supraoccipital is “locked” between exoccipitals (1).
67. Transverse width of the cranium in the postorbital region in dorsal view: broad, width maintained from orbit to quadrate head (0); distinctly narrowed at quadrate heads (1).
68. Occiput shape in caudal view: square (0); triangular, narrow dorsally, distal quadrates splay distinctly laterally (1).

Appendix I: continued

69. Parietal, midline ridge: straight to slightly downwarped along length (0); strongly downwarped, dorsal margin bends below the level of the postorbital-squamosal bar (1).
70. Parietal crest, length: long, caudal parietal narrow quickly to form the crest, crest more than half the length of supratemporal fenestrae (0); short, parietal crest narrows gradually caudally, crest less than half the length of the supratemporal fenestrae (1).
71. Infratemporal fenestra, acute angle between postorbital bar and jugular bar: absent (0); present (1).
72. Cervical vertebrae, number: 11 or fewer (0); 12 to 15 (1).
73. Cervical centra axial length: long (0); shortened so that axial length of centrum is less than height of neural arch (1).
74. Cervicals, shape of zygapophyseal peduncles on arches: low (0); elevated, extend well above the level of the neural canal, zygapophyses long and dorsally arched (1).
75. Sacral vertebrae, number: seven or less (0); eight or more (1).
76. Dorsal (caudal) and sacral neural spines: short, less than three times centrum height (0); elongate, more than three times centrum height (1).
77. Coracoid size: large, coracoid:scapula lengths more than 0.2, length of articular surface greater than length of glenoid (0); coracoid reduced in length relative to scapula, glenoid longer than articulation (1).
78. Coracoid, shape of cranial margin: straight or convex, biceps tubercle small (0); concave, large, laterally projecting biceps tubercle (1).
79. Coracoid, cranioventral process: short (0); long, extends well below the glenoid (1).
80. Scapula, shape of proximal end: dorsoventrally deep, acromion process directed dorsally, articulation extensive (0); dorsoventrally narrow (no wider than distal scapula), acromion process projects horizontally, cranioventral corner notched, articulation restricted (1).
81. Scapula, orientation of borders of distal blade: divergent (0); subparallel to one another (1).
82. Scapula, shape of distal end: asymmetrical, either dorsal or ventral border longer than the other (0); symmetrical, dorsal and ventral border terminate at same point (1).

Appendix I: continued

83. Deltopectoral crest: short, much less than half the length of the humerus, narrows noticeably distally (0); extends at least to midshaft or longer, distally broad (1).
84. Humeral distal condyles: mediolaterally broad, flare moderately from shaft of humerus (0); compressed mediolaterally, flares little from shaft of humerus (1).
85. Antebrachium length: humerus subequal to or longer than radius (0); radius longer than humerus (1).
86. Carpus: all elements present (ulnare, radiale, intermedium, distal carpals) and fused, metacarpal I fused onto carpus and divergent from rest of manus (0); reduced to two small, unfused carpals (1).
87. Manus, digit 1: metacarpal and one phalanx present (0); entire digit absent (1).
88. 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).
89. Metacarpal, shape: short and robust, width at midshaft:length ratio 0.2 or greater (0); slender and elongate, width at midshaft:length 0.15 or less (1).
90. Penultimate phalanges of digits II and III, shape: rectangular, lateral sides subequal in length (0); wedge-shaped, medial side significantly shorter than lateral side (1).
91. Ilium, size of supracetabular process: small, projects only as a lateral swelling (0); large, broadly overhangs the lateral side of the ilium and usually extends at least half way down the side of ilium (1).
92. Ilium-pubis articulation: large iliac contribution, pubic peduncle of ilium long, iliac peduncle of pubis small (0); pubic process of ilium short with restricted articular surface, prominent dorsally directed iliac peduncle of pubis (1).
93. Ilium, postacetabular process shape: tapers caudally to nearly a point, wide brevis shelf (0); rectangular, no brevis shelf (1).
94. Ilium, postacetabular process size relative to total length of ilium: less than 40 % (0); more than 40% (1).
95. Pubis, distal width of prepubic process: dorsoventrally expanded to no more than twice the depth of the proximal shaft (0); expanded to more than twice the depth of proximal shaft (1).

Appendix I: continued

96. Pubis, length of prepubic process constriction: long, dorsoventral expansion restricted to distal process (0); shaft short, dorsoventral expansion begins at base of process (1).
97. Pubis, obturator foramen: closed or partially closed ventrally by tubercle arising from pubic shaft (0); fully open, tubercle absent (1).
98. Ischium, shape of shaft in lateral view: strongly curved downward (0); nearly straight (1).
99. Ischium, shape of distal end: small knoblike foot (0); large and pendent foot (1).
100. Ilium, shape of dorsal margin: nearly straight (0); distinctly depressed over supracetabular process and dorsally bowed over base of preacetabular process (1).
101. Femur, development of intercondylar extensor groove: moderately deep, groove fully open (0); deep, edges of groove meet or nearly meet cranially to enclose an extensor tunnel (1).
102. Tarsus, distal tarsals 2 and 3: present (0); absent (1).
103. Metatarsal I, length: short, thin splint (0); absent (1).
104. Pes, distal phalanges of pedal digits II through IV: axially shortened to disclike elements with width at least three times length (0); greatly shortened, width at least four times length (1).
105. Pes, shape of unguals: taper evenly distally, clawlike (0); dorsoventrally flattened and broadened, hooflike (1).

Appendix II: Predictions of hadrosaurid jaw mechanisms (modified from Weishampel, 1984)

Nopcsa's (1900) hypothesis: Fore-aft motion of the quadrate (streptostyly)	Versluys' (1923) hypothesis: Fore-aft motion of the quadrate (streptostyly) with lateral rotation of the mandible	Von Kripp's (1933) hypothesis: Lateromedial motion of the quadrate (streptostyly) with medial rotation of the mandible	Lambe's (1920) hypothesis: Simple mandibular adduction	Ostrom's (1961) hypothesis: Fore-aft translation at the jaw joint	Weishampel's (1984) hypothesis: Vertical adduction with laterally mobile maxillae and posterolateral motion of the quadrate (streptostyly)
Facet angulation					
High or low	Equivocal	Variable	High	High or low	Variable
Difference in length between opposing occlusal surfaces					
Equivocal	Equivocal	None	None	Equivocal	Equivocal
Disposition of enamel					
Transverse	Equivocal	Buccal or lingual	Buccal or lingual	Mesial or distal	Buccal or lingual
Enamel-dentine interface [for lingual (L) or mesial (M) dentary edge]					
Flush (M)	Flush (L) or (M)	Flush (L)	Flush (L)	Flush (M)	Flush (L)
Microstriae orientation					
Mesodistal	Oblique	Transverse	Transverse	Mesodistal	Transverse to slightly oblique
Macrofeatures					
Grooves possible, all teeth flat	Grooves possible, max. teeth concave, dent. teeth convex	Grooves possible, max. teeth concave, dent. teeth convex	Grooves possible, all teeth flat	Grooves possible, all teeth flat	Grooves possible, max. teeth convex, dent. teeth concave
Longitudinal and dorsoventral curvature of tooth rows					
Possible	Possible	Possible	Possible	Possible	Expected
Status					
Rejected	Rejected	Rejected	Rejected	Rejected	Confirmed

Appendix III: Schematic drawings of streptostyly mechanism. A. The skull of *Corythosaurus casuarius* (NMC 8676). B. Kinematic diagram of A. The neurocranial segment (1 in A) is represented by the lines connecting points BCD (D, basipterygoid joint, not shown), the mandibular segment (6 in A) by the line KL. Of the maxillary segment, the parietal unit (7 in A) consists of the line AB, the quadrate unit (3 in A) of the line CL, the muzzle unit (4 in A) of the triangle AEF, and the maxillopalatal unit (5 in A) by the several lines connecting points GHJ (H, palatine-pterygoid joint, not shown). The occlusal surfaces are represented by the opposing planes M and N. C. Kinematic diagram (lateral and anterior aspects) of the streptostylic jaw mechanism, at the beginning of the power stroke. Arrows indicate areas of movement. D. Partial kinematic diagram of *Corythosaurus casuarius* (based on NMC 8676) illustrating movement of the maxilla, mandible, and quadrate. a) frontal view; b) left lateral view; c) view along the maxilla-premaxilla joint; d) dorsal view; e) view of the left quadrate along its plane of motion; f) occlusal view of the left dentary dentition. Arrows indicate direction of relative movement of the maxillary teeth against the dentary teeth (modified from Weishampel, 1984)

Appendix III: continued

Appendix IV: Animation of streptostyly model

See enclosed CD

Appendix V: A and B: relation between the enamel-dentine interface and the direction of the power stroke. D, dentine; E, enamel (Weishampel, 1984)

Appendix VI: Longitudinal groove along the right tooth row in *Brachylophosaurus canadensis* (FMNH PR862) produced by a lingual worn zone (W) and a buccal worn zone (U) (Weishampel, 1984)