# THE FIRST LAMBEOSAURIN (DINOSAURIA, HADROSAURIDAE, LAMBEOSAURINAE) FROM THE UPPER CRETACEOUS OJO ALAMO FORMATION (NAASHOIBITO MEMBER), SAN JUAN BASIN, NEW MEXICO 

ROBERTM. SULLIVAN ${ }^{1}$, STEVEN E. JASINSKI ${ }^{1}$, MERRILEE GUENTHER ${ }^{2}$ and ${ }^{2}$ SPENCER G. LUCAS ${ }^{3}$

${ }^{1}$ Section of Paleontology and Geology, The State Museum of Pennsylvania, 300 North Street Harrisburg, PA 17120-0024;<br>${ }^{2}$ Elmhurst College, 190 Prospect Ave., Elmhurst, IL 60126;<br>${ }^{3}$ New Mexico Museum of Natural History and Science, 1801 Mountain Rd NW, Albuquerque, NM 87104


#### Abstract

A nearly complete robust left humerus (SMP VP-2263) and right jugal (SMP VP-1534) belonging to a lambeosaurin lambeosaurine (= Lambeosaurus + (Corythosaurus + Hypacrosaurus $)$ ) dinosaur have been recovered from two separate localities in the Naashoibito Member (Ojo Alamo Formation), San Juan Basin, New Mexico. Measurements of the humerus are: length $=550 \mathrm{~mm}$; deltopectoral crest length $=260 \mathrm{~mm}$; deltopectoral width $=135 \mathrm{~mm}$. The robust morphology and measurements of the humerus confirm it pertains to a member of the lambeosaurin clade, which we formally establish. The jugal has a maximum rostrocaudal length of 255 mm and a shape that is inconsistent with the jugals of all species of Parasaurolophus. These specimens, which are very similar to the humerus and jugal of Corythosaurus and Hypacrosaurus, constitute definite records of lambeosaurines from the Naashoibito Member, despite previous erroneous reports of the occurrence of Parasaurolophus tubicen from this horizon. The putative hadrosaurine, NMMNH P-19147, is re-interpreted as a lambeosaurin lambeosaurine, based primarily on the morphology of the pubis. Recovery of additional lambeosaurine material in the Naashoibito Member lends further support to a pre-Lancian age for this interval and for the Alamo Wash local fauna.


## INTRODUCTION

Hadrosaurid dinosaurs from the Ojo Alamo Formation (Sandstone) have been known for a century. Many of the early records cite the hadrosaurids, and other dinosaurs, as coming from the Ojo Alamos beds (Brown, 1910; Gilmore, 1916; Lehman, 1981, 1985). Only four hadrosaurid genera have been recognized in the Upper Cretaceous deposits of the San Juan Basin (Anasazisaurus, Kritosaurus, Naashoibitosaurus and Parasaurolophus). Two of these taxa are still regarded by some to be of questionable validity (Anasazisaurus and Naashoibitosaurus), and all four genera are from the Kirtland Formation (Williamson, 2000). To complicate matters, two of the San Juan Basin hadrosaurids (Naashoibitosaurus and Parasaurolophus) were originally reported as coming from the Naashoibito Member, but are now known to be restricted to the De-na-zin Member of the Kirtland Formation (Williamson, 1998; Williamson and Sullivan, 1998; Sullivan and Williamson, 1999; Sullivan et al., 2005a, b). The Naashoibito Member was previously included in the Kirtland Formation, but is now considered to be part of the overlying Ojo Alamo Formation (Lucas and Sullivan, 2000; Sullivan et al., 2005b).

Recently, a number of new lambeosaurines from North America and Asia have been documented, and phylogenetically assessed (Godefroit et al., 2001, 2004, 2008; Gates et al., 2007; Prieto-Márquez, 2010a, b). Other studies, most notably that of Guenther (2009), have developed methods to recognized ontogenetic development of postcranial elements within hadrosaurid taxa that help to discriminate lambeosaurine from hadrosaurine taxa.

In Asia, lambeosaurines are now known from Maastrichtian units of Russia (Amurosaurus riabinini [Udurchukan Formation]) (Godefroit et al., 2004; Van Itterbeeck et al., 2005) and northeastern China (Charonosaurus jiayinensis and Sahaliyania elunchunorum [Yuliangze Formation]) (Godefroit et al., 2001, 2008). Although some of these occurrences are considered late Maastrichtian ( $\sim 69.2$ to 65.5 Ma , as defined by Ogg et al., 2004), based on correlation using palynozones, we consider these correlations to lack precision. Recently, in Europe, a new lambeosaurine Arenysaurus ardevoli, from the lower part of the upper Maastrichtian (normal polarity Chron 30) Tremp Formation of Spain, has been described based on an incomplete skull roof and braincase
(Pereda-Suberbiola et al., 2009). In North America, lambeosaurines are unknown from strata younger than 67 Ma (the base of the Lancian LVA, see below). Although a putative lambeosaurine has been reported from the Hell Creek Formation, lambeosaurines are not known from either the Lance or upper part of the Hell Creek formations (latest Maastrichtian/ Lancian) of the Western Interior. Moreover, lambeosaurine dinosaurs are not considered a faunal component of the Lancian LVA, which spans 65.8-67.61 Ma (latest Maastrichtian). The youngest known North American lambeosaurin, Hypacrosaurus altispinus, is from the Horseshoe Canyon Formation of Alberta, and it comes from the upper part of the formation (unit 4), which is dated at 69-68 Ma. Unit 4 of the Horseshoe Canyon Formation correlates with the Naashoibito Member - both are $\sim 69 \mathrm{Ma}$.

Here, we document a humerus (SMP VP-2263) and jugal (SMP VP-1534) of a lambeosaurin lambeosaurine from separate localities in the Naashoibito Member and discuss their biostratigraphic significance. We also re-assess the taxonomic assignment of NMNNH P-19147, from the Naashoibito Member, originally interpreted as representing a lambeosaurine dinosaur close to either Lambeosaurus or Corythosaurus (Hunt and Lucas, 1991) based on the morphology of the pubis, and, to a lesser extent, the scapula. The identity of NMMNH P-19147 had been dismissed by Williamson (2000), who considered it to be an indeterminate hadrosaurine.

Institutional abbreviations: $\mathrm{NMMNH}=$ New Mexico Museum of Natural History and Science, Albuquerque; SMP = The State Museum of Pennsylvania, Harrisburg.

## TAXONONOMIC NOTE

We note here that the terms "corythosaur clade" and "parasauroloph clade" were introduced by Chapman and Brett-Surman (1990) as informal clades. The "corythosaur clade" included Corythosaurus, Hypacrosaurus, Lambeosaurus, and Nipponosaurus. Juvenile specimens of "Procheneosaurus" were also assumed to be members of this clade. The "parasauroloph clade" included Parasaurolophus, Bactrosaurus and Tsintaosaurus. The taxonomic composition of these two informal clades was changed by Godefroit (2004), who united Parasaurolophus with Charonosaurus in the "parasauroloph clade"
and Lambeosaurus with Corythosaurus, Hypacrosaurus and Olorotitan in the "corythosaur clade." This later clade was elevated to formal usage ("Corythosaurini") by Evans and Reisz (2007, p. 388), and named the other clade "Parasaurolophini."

According to Article 37.1 of the International Code of Zoological Nomenclature (1999) "When a family-group taxon is subdivided, the subordinate name that contains the taxon that contains the type genus of the superior taxon is denoted by the same name the nominotypical name." Thus, given that "Corythosaurini" is a subdivision (tribe) of Lambeosaurinae coordinate with Parasaurolophini, the proper name of the tribe should be Lambeosaurini, not "Corythosaurini." The following formal subdivisions of the Lambeosaurinae encompass two clades: Lambeosaurini clade (included taxa are Lambeosaurus, Hypacrosaurus, Olorotitan, Corythosaurus and Velafrons) and the Parasaurolophini clade (included taxa are Parasaurolophus cyrtocristatus, P. walkeri, P. tubicen and Charonosaurus jianyinensis).

## MATERIALS AND METHODS

Hadrosaurid postcranial material (jugals, humeri and scapulae) in the collections of the New Mexico Museum of Natural History and Science in Albuquerque and the State Museum of Pennsylvania were examined and compared. Studies characterizing the morphologies of these elements by Sullivan and Williamson (1999) Sullivan and Bennett (2000), Godefroit et al. (2001, 2004, 2008), Evans and Reisz (2007), Guenther (2009), and Prieto-Márquez (2010a,b) were also used. The characters and data matrix used herein (Appendix 1) are from Evans and Reisz (2007) along with four new additional jugal characters identified by Sullivan et al. (2009).

## SYSTEMATIC PALEONTOLOGY

## DINOSAURIA Owen, 1842 ORNITHSCHIA Seeley, 1888 HADROSAURIDAE Cope, 1869 <br> LAMBEOSAURINAE Parks, 1923 <br> LAMBEOSAURINI, new tribe <br> Lambeosaurini indeterminate

Referred material: SMP VP-2263, nearly complete left humerus (Fig. 1), SMP loc. 403b, De-na-zin Microsite (SE); SMP VP- 1534 (Fig. 3), nearly complete right jugal (badly weathered), SMP loc. 392b, De-nazin Wash (SE).

Horizon and Age: Naashoibito Member (Ojo Alamo Formation), early Maastrichtian.

Description of Humerus: The left humerus (SMP VP-2263) is nearly complete (Fig. 1). In caudal view, the articular (humeral) head and the proximal edges of the medial side are eroded. Though eroded, the humeral head constitutes one third of the width of the proximal articular margin. It bears a complete and prominent deltopectoral crest; its lateral margin has a strong, well-developed edge for the attachment of the $M$. deltoideus clavicularis and M. scapulohumeralis rostral (Dilkes, 2000; Evans and Reisz, 2007). The muscle scar of the latissimus dorsi is weakly developed. The degree of angulation of the ventral margin of the deltopectoral crest is strong (character 221 of Prieto-Márquez, 2010a). In cranial view, the bicipital sulcus is also well-developed and widens proximally, expanding to almost the full width of the element. The caudal surface of the shaft is damaged, and it is highly fractured in a region immediately adjacent to the midpoint of the shaft; however, an accurate reflection of the proportions of the element is not compromised by this damage. The radial and ulnar condyles are complete, with the ulnar condyle slightly larger than the radial condyle. The olecranon fossa is well-developed and deeper than the coronoid fossa. Measurements of the humerus are: length $=550 \mathrm{~mm}$; deltopectoral crest length $=260 \mathrm{~mm}$; deltopectoral width $=135 \mathrm{~mm}$; width of the shaft $=68 \mathrm{~mm}$. Ratio of deltopectoral width to the shaft width $=0.5037$. The ratio of the length of the
deltopectoral crest to the proximodistal length of the humerus $=0.47$ (character 219 of Prieto-Márquez, 2010a). The ratio between the total length and the width of the lateral surface of the proximal end of the humerus is 3.6 (character 222 of Prieto-Márquez, 2010a).

Remarks: The robust morphology and measurements of the humerus confirm it pertains to a member of the "lambeosaurin" clade based on a bivariate plot analysis of hadrosaurid taxa, including average measurements for hadrosaurid humeri of various genera (Fig. 2). The length of the deltopectoral crest of this specimen is more than twice the width of the humeral shaft, characteristic of a lambeosaurine humerus. Note that we calculated a ratio of 1.78 for the lateroventral expansion of the deltopectoral crest of the humerus (character 220 of Prieto-Márquez, 2010a), which is nearly the mean for the expanded deltopectoral crest. Thus, SMP VP-2263 lacks the wide deltopectoral crest seen in Parasaurolophus, but has a narrower shaft, like Corythosaurus and Hypacrosaurus. Shafts of Hypacrosaurus tend to be proportionally longer than those of Corythosaurus, so we believe that SMP VP-2263 is more like Corythosaurus than Hypacrosaurus. This specimen also lacks the rotated orientation of the deltopectoral crest observed in some specimens of Hypacrosaurus.

Description of Jugal: SMP VP-1534 (Fig. 3) is a badly weathered, but nearly complete, right jugal. Despite its poor condition, enough of the element is preserved to allow comparison to other hadrosaurines. The jugal has a maximum rostrocaudal length of 255 mm . The shape of the jugal conforms to that of lambeosaurines, but it has a morphology that is inconsistent with jugals of all species of Parasaurolophus (see Sullivan and Bennett, 2000). Specifically, SMP VP-1534 is characterized by: 1) having an inferior infratemporal border that is wider than the inferior orbital border; 2) lacking a short dorsal caudal process; 3 ) having a fan-shaped caudal process border; and 4) lacking the distinctive "W"-shaped articulation between the rostral process of the jugal and the lacrimal, a feature seen only in species of Parasaurolophus. These are new characters for the jugal (see Appendix 1, below). In addition, in SMP VP-1534 the jugal is also expanded dorsoventrally and forms the lower part of the orbital rim; the borders of the infratemporal fenestra form an acute angle between the jugal and postorbital bars; the jugal is dorsoventrally constricted beneath the infratemporal fenestra; and the ventral flange of the jugal is rounded. The shape of the rostral process is uncertain due to breakage.

Remarks: As noted above, based on the characters of the jugal, SMP VP-1534 clearly pertains to a lambeosaurine. Moreover, the lack of the distinctive " $W$ "-shaped articulation between the superior border of the rostral jugal process, and the inferior border of the lacrimal, indicates that the jugal is not from Parasaurolophus. Prieto-Márquez (2010a) identified 13 jugal characters ( 103 through 115), but only a few can be assessed due to the incomplete nature of SMP VP-1534. These characters include: strong inclination of the bony rim that bounds the medial articulation surface of the jugal rostral process (character 108 of PrietoMárquez, 2010a); auricular shape of the quadratojugal flange (character 111 of Prieto-Márquez, 2010a); relatively wide and pronounced concavity of the ventral margin located between the caudoventral and quadratojugal flanges, despite the fact that the medial section of the ventral margin is broken and missing in SMP VP-1534 (character 112 of Prieto-Márquez, 2010a); and wider orbital margin and relatively constricted ventral margin of the infratemporal fenestra (character 112 of Prieto-Márquez, 2010a).

## PHYLOGENETIC ANALYSIS

We scored both the humerus (SMP VP-2263) and jugal (SMP VP1534) using the data matrix of Evans and Reisz (2007) and added four more (new) characters (32-35) identified by Sullivan et al. (2009) for the jugal (see Appendix 1). We ran two analyses: 1) for the jugal; and 2) for the jugal and humerus combined. The later scenario assumes that the two elements are from a single taxon. The data analyses were run using PAUP 4.0b10 (Swofford, 2002).


FIGURE 1. Indeterminate lambeosaurin, SMP VP-2263, nearly complete left humerus, from the Naashoibito Member (Ojo Alamo Formation), San Juan Basin, NM. A, caudal view; B, cranial view. Abbreviations: hh, humeral head; ms(lb), muscle scar on the lateral border of the humerus; and ms(ld), muscle scar of the latissimus dorsi. Bar scale $=10 \mathrm{~cm}$.

## Width of Deltopectoral Crest of Humerus



FIGURE 2. Bivariate plot of the width of the humeral shafts versus the width of the deltopectoral crest among selected hadrosaurids. Note that SMP VP2263, falls within the lambeosaurines, having closest affinities to Corythosaurus and Hypacrosaurus.

Both analyses produced 470 trees, a tree length of 125 , and a consistency index $=0.8400$; retention index $=0.8330$ and rescaled consistency index $=0.7418$. A strict consensus tree and $50 \%$ majority-rule consensus tree are presented in Figure 4 for both the jugal alone and for the jugal + humerus combined.

## DISCUSSION

Based on our analyses, both SMP VP-1534 and VP-2263 clearly fall within the Lambeosaurinae and cluster with the Corythosaurus-like taxa. The strict consensus tree suggests they are distinct from both Lambeosaurus and Parasaurolophus (Fig. 4C), whereas the $50 \%$ majority rule consensus tree (Fig. 4D) shows both forming a polytomy with Corythosaurus, Velafrons, Olorotitan and Amurosaurus, with Lambeosaurus + Hypacrosaurus as a sister group. Based on these analyses and our personal observation, we conclude that both these elements are from a Corythosaurus-like lambeosaurine that appears to be closer to Corythosaurus than to Hypacrosaurus. We consider both to be indeterminate lambeosaurin ["corythinosaurin"] lambeosaurines.

The presence of a Corythosaurus-like hadrosaur in the Naashoibioto Member, based on these two specimens, reopens the question of the identity of NMMNH P-19147 (Fig 5). This specimen, which was first described by Hunt and Lucas (1991), consists of an incomplete right scapula, parts of both pubes, two dorsal vertebrae, five neural spines and 22 ribs and/or partial ribs. Williamson (2000) later noted that the specimen also included the distal end of the left tibia.

In their taxonomic assessment of this specimen, Hunt and Lucas (1991) noted that the pubes and scapula were the most (potentially) diagnostic elements of this specimen. Unfortunately, the scapula offered little help in actually determining the generic identity of the hadrosaurid.

The right pubis, on the other hand, was complete enough to compare to other hadrosaurids and had features that suggested relationships to known taxa. Hunt and Lucas (1981) noted that the right pubis (Fig. 5A, B) was relatively short and broad, as in most lambeosaurines. They also noted that the shape of the scapula was variable in Corythosaurus, so it is inferred that the parallel dorsal and ventral morphology of the scapular blade described by them was considered to be too ambiguous to allow for any taxonomic identification. They concluded that NMMNH P-19147 represented a lambeosaurine that was related to either Corythosaurus or Lambeosaurus (Hunt and Lucas, 1991).

Williamson (2000, p. 205) reinterpreted NMMNH P-19147, based on the morphology of the pubis, and stated that "the neck of the pubis is narrow rather than broad as in lambeosaurines" and that the scapula blade is long with sub-parallel margins, despite the fact that Hunt and Lucas (1991) stated that variation in blade morphology is dubious among Corythosaurus specimens. Williamson (2000) reinterpreted NMMNH $\mathrm{P}-19147$ as a hadrosaurine rather than a lambeosaurine.

A re-evaluation of the morphology of the right pubis (Fig. 5A-B) clearly shows that NMMNH P-19147 is, in fact, a lambeosaurine that is close to Corythosaurus. Prieto-Márquez (2010a) identified a number of characters of the pubis, most of which we can use to determine the affinities of NMMNH P-19147. We have presented a reconstruction of the prepubic process of the pubis based on the directions of the preserved dorsal, ventral and cranial margins. Our reconstruction suggests that the ventral region is more expanded than the dorsal region (character 252 of Prieto-Márquez, 2010a). Despite its broken condition, it is evident that the geometry of the dorsoventral expansion of the prepubic process of the pubis of NMMNH P-19147 is oval shaped (Fig. 5B), being dorsoventrally taller than craniocaudally long (character 253 of


FIGURE 3. Indeterminate lambeosaurin, SMP VP-1534, badly weather right jugal, from the Naashoibito Member (Ojo Alamo Formation), San Juan Basin, NM. A, lateral view; B, medial view. Bar scale $=10 \mathrm{~cm}$.


FIGURE 4. Cladograms. A, strict consensus tree (jugal only); B, $50 \%$ majority rule consensus tree (jugal only); C, strict consensus tree (jugal + humerus); D, $50 \%$ majority rule consensus tree (jugal + humerus); black dot is the node for the Lambeosaurini The inclusion of Amurosaurus is equivocal based on analyses of Godefroit (2004, 2008), Evans and Reisz (2007) and Evans (2010). Amurosaurus and Sahaliyania form a clade within Lambeosaurini in the analysis presented by Prieto-Márquez (2010a, b). The taxon Sahaliyania elunchunorum is considered to be a lambeosaurine, but was not included in our data set (see Appendix 2).


FIGURE 5. NMMNH P-19147, lambeosaurin indeterminate. Incomplete right pubis, A, medial view; B, lateral view. Incomplete right scapula, C, lateral view; D, medial view. Dotted line is the restored prepubic blade based on dorsal, ventral and distal margins of the pubis. Asterisk and black dot indicate position of maximum concavity for the dorsal and ventral margins (B), after Prieto-Márquez (2010a). Abbreviations: ap, acromion process; p, depth of proximal end of scapula; $\mathbf{s b}$, maximum distal depth of scapula blade; and $\mathbf{s n}$, minimum depth of scapula neck. Bar scales $=10 \mathrm{~cm}$.

Prieto-Márquez, 2010a). We are unable to determine the ratio between the dorsoventral expansion of the prepubic process relative to the width of the acetabular margin (character 254 of Prieto-Márquez, 2010a) because the acetabular region in NMMNH P-19147 is largely missing. The craniocaudal length of the proximal constriction of the prepubic process is longer than the dorsoventral expansion (character 255 of PrietoMárquez, 2010a). The relative position of the maximum concavity of the dorsal margin is located distally relative to the point of maximum convexity along the ventral margin (character 256 of Prieto-Márquez, 2010a). The morphology of the acetabular margin (character 257 of PrietoMárquez, 2010a) is unknown because the region is not preserved in NMMNH P-19147. The obturator foramen as well as the iliac and ischial peduncles (characters 258 through 261 of Prieto-Márquez, 2010a) are also not preserved, so their morphologies and related measurements cannot be assessed. Finally, the total length of the pubis (character 262 of Prieto-Márquez, 2010a) is not known due to the incomplete nature of the pubis.

Our examination of the scapula also confirms that its morphology is consistent with that of Corythosaurus based on the recent analyses of Prieto-Márquez (2010a). The dorsal margin of the scapula is curved (character 211 of Prieto-Márquez, 2010a). The ratio of the craniocaudal length and the dorsoventral depth is 5.0, a little less than C. casuarius and C. intermedius (character 212 of Prieto-Márquez, 2010a). Dorsoventral expansion of the distal region (character 213 of Prieto-Márquez, 2010a) appears slight, but the scapula's dorsal and ventral margins are broken. Nevertheless, we calculated a ratio of $1.0+$ for this character that would support its lambeosaurine affinities. The ratio between the dorsoventral length of the proximal constriction and the dorsoventral depth of the cranial end of the scapula is 0.75 , a value that is nearly the same as those for Corythosaurus ( 0.70 to 0.72 ) (character 214 of Prieto-Márquez, 2010a). The acromion process is directed dorsally and is slightly recurved (characters 215 and 216 of Prieto-Márquez, 2010a). The deltoid ridge is weakly developed and is confined to the proximal region of the
scapula (character 218 of Prieto-Márquez, 2010a), a situation similar to Hypacrasaurus stebingeri. Therefore, we reject Williamson's (2000) interpretation and conclude that the specimen is a Corythosaurus-like hadrosaurid and is not a hadrosaurine.

## BIOSTRATIGRAPHIC SIGNIFICANCE

Hunt and Lucas (1991) considered NMMNH P-19147 to represent a possible range extension for lambeosaurines (Corythosaurus or Lambeosaurus) because the Naashoibito Member was considered to be late Maastrichtian age (equivalent to the Lancian) and because there were no lambeosaurine hadrosaurs known from Lancian age deposits in North America. The Naashoibito Member is regarded by us to be pre-Lancian (early Maastrichtian) and has been dated at 69 Ma based on the occurrence of Alamosaurus sanjuanensis, which is restricted to the Naashoibito Member in the San Juan Basin (Sullivan and Lucas, 2003, 2006). Nonetheless, NMMNH P-19147, and the jugal and humerus described above, each from separate localities, are among the youngest known lambeosaurines (Hypacrosaurus altispinus being the other) in North America. More importantly, these specimens may represent the youngest known Corythosaurus-like genus.

## ACKNOWLEDGMENTS

We thank Michael Brett-Surman (United States National Museum) for discussions regarding hadrosaurid postcrania. We also thank David Evans (Royal Ontario Museum, Toronto) for earlier discussions regarding lambeosaurines and issues regarding the PAUP analyses. Special thanks are extended to Peter Dodson (University of Pennsylvania) and Pascal Godefroit (Royal Institute of Natural Sciences of Belgium, Brussels) for their respective critiques and suggestions that improved the manuscript. Thanks are extended to the Bureau of Land Management for issuing the Paleontological Resource Use permits SMP-8270-RS-01C and SMP-827 RS-04-D and their continuing support in the field.

## REFERENCES

Boyd, C. and Ott, C.J., 2002, Probable lambeosaurine (Ornithischia, Hadrosauridae) specimen from the Late Cretaceous Hell Creek Formation of Montana: Journal of Vertebrate Paleontology, v. 22, Supplement to no. 3, 38A.
Brink, K.S., Zelenitsky, D.A., Evans, D.C., Therrien, F. and Horner, J.R., 2010, A sub-adult skull of Hypacrosaurus stebingeri (Ornithischia: Lambeosaurinae): anatomy and comparison: Historical Biology, 2010, DOI:0.1080/08912963.2010.49916910.
Brown, B., 1910, The Cretaceous Ojo Alamo beds of New Mexico with a description of the new dinosaur genus Kritosaurus: Bulletin of the American Museum of Natural History, v. 28, p. 267-274.
Chapman, R.E. and Brett-Surman, M.K., 1990, Morphometric observations on hadrosaurid ornithopods; in Carpenter, K. and Currie, P. J., eds., Dinosaur systematics: perspectives and approaches: Cambridge, Cambridge UniversityPress, p. 163-177.
Dilkes, D.W., 2000, Appendicular mycology of the hadrosaurian dinosaur Maiasaura peeblesorum from the Late Cretaceous (Campanian) of Montana: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 90, 87-125.
Eberth D.A., Currie, P.J., Brinkman, D., Ryan, M.J. and Braman, D.R., 2001, Alberta's dinosaurs and other fossil vertebrates: Judith River and Edmonton groups (Campanian-Maastrichtian); in Hill, C.L., ed., Mesozoic and Cenozoic paleontology in the Western Plains and Rocky Mountains: Museum of the Rockies Occasional Paper, no. 3, p. 49-74.
Evans, D.C. and Reisz, R., 2007, Anatomy and relationships of Lambeosaurus magnicristatus, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation: Journal of Vertebrate Paleontology, v. 27, 373-393.
Evans, D.C., Reisz, R. and Depuis, K., 2007, A juvenile Parasaurolophus (Ornithischia: Hadrosauridae) braincase from Dinosaur Provincial Park,

Alberta, with comments on crest ontogeny in the genus: Journal of Vertebrate Paleontology, v. 27, p. 642-650.
Evans, D.C., 2010, Cranial anatomy and systematics of Hypacrosaurus altispinus, and comparative skull growth in lambeosaurine hadrosaurids (Dinosauria: Ornithischia): Zoological Journal of the Linnean Society, v. 159, p. 398-434.

Gates, T.A., Sampson, S.D., Delagado de Jesús, C.R., Zanno, L.E., Eberth, D., Hernandez-Rivera, R., Aguillón Martinez, M.C. and Kirkland, J.I., 2007, Velafrons coahuilensis, a new lambeosaurine hadrosaurid (Dinosauria: Ornithopoda) from the late Campanian Cerro del Pueblo Formation, Coahuila, Mexico: Journal of Vertebrate Paleontology, v. 27, p. 917-930.
Gilmore, C.W., 1916, Contributions to the geology and paleontology of San Juan County, New Mexico. 2. Vertebrate faunas of the Ojo Alamo, Kirtland, and Fruitland formations: U.S. Geological Survey, Professional Paper 98, p. 279-302.
Gilmore, C.W., 1919, Reptilian faunas of the Torrejon, Puerco, and underlying Upper Cretaceous formations of the San Juan Basin, New Mexico: U.S. Geological Survey, Professional Paper 19, p. 1-68.

Gilmore, C.W., 1924, On the skull and skeleton of Hypacrosaurus, helmetcrested dinosaur from the Edmonton Cretaceous of Alberta: Canada Geological Survey, Bulletin 38, p. 49-64.
Godefroit, P., Zan, S. and Jin, L., 2001, The Maastrichtian (Late Cretaceous) lambeosaurine dinosaur Charonosaurus jiayinensis from northeastern China: Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, v. 71, p. 119-168.
Godefroit, P., Bolotsky, Y.L. and Van Itterbeeck, J., 2004, The lambeosaurine dinosaur Amurosaurus riabinini, from the Maastrichtian of Far Eastern Russia: Acta Palaeontologica Polonica, v. 49, p. 585-618.
Godefroit, P., Shulin, H., Tingxiang, Y. and Lauters, P., 2008, New hadrosaurid
dinosaur from the uppermost Cretaceous of northeastern China: Acta Palaeontologica Polonica, v. 53, p. 47-74.
Hunt, A.P. and Lucas, S.G., 1991, An associated Maastrichtian hadrosaur and a Turonian ammonite from the Naashoibito Member, Kirtland Formation (Late Cretaceous: Maastrichtian), northwestern New Mexico: New Mexico Journal of Science, v. 31, p. 27-35.
Lehman, T.M., 1981, The Alamo Wash local fauna: a new look at the old Ojo Alamo Fauna; in Lucas, S., Rigby, Jr., J.K., and Kues, B., eds., Advances in San Juan Basin Paleontology: Albuquerque, University of New Mexico Press, p. 189-221.
Lehman, T.M., 1985, Depositional environments of the Naashoibito Member of the Kirtland Shale, Upper Cretaceous, San Juan Basin, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Circular 195, p. 55-79.
Lucas, S.G. and Sullivan, R.M., 2000, Stratigraphy and vertebrate biostratigraphy across the Cretaceous-Tertiary boundary, Betonnie Tsosie Wash, San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 95-104.
Ogg, J.G., Agterberg, F.P. and Gradstein, F.M., 2004, The Cretaceous Period; in Gradstein, F., Ogg, J., and Smith, A., eds., A Geologic Time Scale: Cambridge, Cambridge University Press, p. 344-383.
Guenther, M.F., 2009, Influence of sequence heterochrony on hadrosaurid postcranial development: The Anatomical Record, v. 292, p. 14271441.

Pereda Suberbiola, X., Canudo, J.I., Company, J., Cruzado-Caballero, P., Barco, J.L. López-Martínez, N., Oms, O. and Ruiz-Omenaca, N., 2009, The last hadrosaurid dinosaurs of Europe: a new lambeosaurine from the uppermost Cretaceous of Aren (Huesca, Spain): Comptes Rendus Palevol, v. 8, p. 559-572.

Prieto-Márquez, A., 2010a, Global phylogeny of Hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian inference: Zoological Journal of the Linnean Society, v. 159, p. 435-502.
Prieto-Márquez, A., 2010b, Global historical biogeography of hadrosaurid dinosaurs: Zoological Journal of the Linnean Society, v. 159, p. 503525.

Sullivan, R.M. and Bennett, G.E., III, 2000, A juvenile Parasaurolophus (Ornithischia: Hadrosauridae) from the Upper Cretaceous Fruitland Formation of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 215-220.
Sullivan, R.M., Boere, A.C. and Lucas, S.G., 2005a, Redescription of the ceratopsid dinosaur Torosaurus utahensis (Gilmore, 1946) and a revi-
sion of the genus: Journal of Paleontology, v. 79, p. 564-582.
Sullivan, R.M. and Lucas, S.G., 2003, The Kirtlandian, a new land-vertebrate "age" for the Late Cretaceous of western North America: New Mexico Geological Society, Guidebook 54, p. 369-377.
Sullivan, R.M. and Lucas, S.G., 2006, The Kirtlandian land-vertebrate "age" - faunal composition, temporal position and biostratigraphic correlation in the nonmarine Upper Cretaceous of western North America: New Mexico Museum of Natural History and Science, Bulletin 35, p. 729.

Sullivan, R.M., Lucas, S.G. and Braman, D.R., 2005b, Dinosaurs, pollen, and the Cretaceous-Tertiary boundary in the San Juan Basin, New Mexico: New Mexico Geological Society, Guidebook 56, p. 395-407.
Sullivan, R.M. and Williamson, T.E., 1999, A new skull of Parasaurolophus (Dinosauria: Hadrosauridae) from the Kirtland Formation of New Mexico and a revision of the genus: New Mexico Museum of Natural History and Science, Bulletin 15, 52 p.
Sullivan, R.M., Jasinski, S.E., Lucas, S.G. and Spielmann, J.A., 2009. The first "lambeosaurin" (Dinosauria, Hadrosauridae, Lambeosaurinae) from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member) San Juan Basin, New Mexico: further implications for the age of the Alamo Wash local fauna: Journal of Vertebrate Paleontology, v. 29, p. 188A.
Swofford, D.L., 2002, PAUP*: Phylogenetic Analysis Using Parsimony (and other methods), version 4.0b10: Sunderland, Massachusetts, Sinauer Associates.
Van Itterbeeck, J., Bolotsky, Y.L., Bultynck, P. and Godefroit, P., 2005, Stratigraphy, sedimentology and palaeoecology of the dinosaur-bearing Kundur section (Zeya-Bureya basin, Amur Region, far eastern Russia): Geological Magazine, v. 142, p. 735-750.
Williamson, T.E., 1998, Review of dinosaurs of the Alamo Wash local fauna, Naashoibito Member, Kirtland Formation, San Juan Basin, New Mexico: New Mexico Geology, v. 20, p. 54.
Williamson, T.E., 2000, Review of Hadrosauridae (Dinosauria, Ornithischia) from the San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 191-213.
Williamson, T.E. and Sullivan, R.M., 1998, A new local fauna, the Willow Wash local fauna, from the Upper Cretaceous (Campanian), Kirtland Formation, New Mexico: Journal of Vertebrate Paleontology, v. 18, p. 86A.
Wiman, C., 1931, Parasaurolophus tubicen n. sp. aus der Kreide in New Mexico: Nova Acta Regiae Societatis Scientiarum Upsaliensis, v. 7, p. 111.

## APPENDIX 1

Characters and data matrix used in cladistic analysis (modified from Evans and Reisz, 2007).

## Skull

1. Premaxilla, 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) (Horner et al., 2004, character 25).
2. 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) (Horner et al., 2004, character 22).
3. 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, external nares exposed in lateral view (0); caudoventral and caudodorsal processes elongate and join behind external opening of narial passages to exclude nasals, nasal vestibule completely enclosed by tubular premaxillae, left nasal passage divided from right passage, homologue of hadrosaurine external naris not exposed in lateral view (1) (Horner et al., 2004, character 27, modified).
4. Premaxilla, external naris shape: bony external naris formed by premaxilla and nasal (0); naris defined entirely by premaxilla, naris elongate (1); lacriform in shape, naris constricted caudally, primarily by lateroventral expansion of caudodorsal premaxillary process (2); lacriform in shape, naris constricted caudally primarily by dorsal expansion of caudolateral premaxillary process (3) (Morris, 1978).
5. Premaxilla, vertical groove on the caudolateral process rostral to the maxillary dorsal process that extends ventrally from a small lateral opening between the premaxillary caudal processes: absent (0); present (1).
6. Premaxilla, elongation of the caudolateral process above the prefrontal: absent (0); present (1) (Suzuki et al., 2004, character 4, modified).
7. Position of nasal cavity: nasals flat caudodorsally and restricted to area rostral to braincase, nasal cavity rostromedial to orbits $(0)$; premaxilla extended caudally and nasals retracted to lie over braincase in adults, resulting in a convoluted, complex narial passage and hollow crest that extend supraorbitally (1) (Horner et al., 2004, character 33, modified).
8. Nasal vestibule morphology, s-loop in the enclosed premaxillary passages rostral to dorsal process of maxilla: absent (0); s-loop present (1) (Weishampel, 1981).

414
9. Hollow nasal crest tubular, elongate, and extends caudally well beyond the occiput: absent (0); present (1) (Horner et al., 2004, character 36, in part).
10. Hollow nasal crest shape, solid plate-like extension of premaxilla, or "cockscomb," above the nasal passages in the rostral region of the crest (i.e., crest raised into a large vertical fan): absent (0); present (1) (Hopson, 1975; Horner et al., 2004, character 36, in part; Suzuki et al., 2004, character 11).
11. Hollow nasal crest shape, helmet-shaped crest with apex above orbit and nasal forms a large, plate-like portion of the caudal external crest surface: absent (0); present (1) (Norman, 2002, character 9, modified; Godefroit et al., 2004, character 14 , modified).
12. Hollow nasal crest, length: crest absent or extends beyond occiput less than basal skull length (0); extends posterior to occiput more than basal skull length (1) (Sullivan and Williamson, 1999).
13. Hollow nasal crest, crest-snout angle along dorsal margin of premaxilla in lateral view: absent (0); less than 110 degrees, crest procumbent (1); present, angle between 110 and 155 degrees (2); facial profile shallowly concave in lateral view, angle between 155 and 180 degrees (Suzuki et al., 2004, character 12, modified).
14. Hollow nasal crest, relative shape of the two lobes of caudoventral process of premaxilla (PM2): absent (0); present, rostral lobe approximately level with or higher than caudal lobe (1); present, caudal lobe higher than rostral lobe (2) (Horner et al., 2004, character 35).
15. Hollow nasal crest, enclosure of the nasal passages on lateral crest surface between the caudolateral process of the premaxilla and nasal: absent (0); premaxilla nasal-fontanellae persist into late ontogenetic stages (1), crest fontanellae completely closed in subadult individuals (2). (Norman, 2002, character 5, modified).
16. Hollow nasal crest, composition of caudal margin of fan-shaped crest: absent (0); present, composed of largely of the premaxilla caudodorsal process (PM1), nasal contributes to the lateroventral portion of a solid caudal process only (1); present, composed of nasal, nasals have long external internasal joint along caudal and caudoventral margin of crest (2) (Horner et al., 2004, character 37, modified).
17. Hollow nasal crest, rostral 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 in which a long, finger-like process of the nasal has an extensive overlapping joint with caudodorsal process of the premaxilla in the rostral region of the crest (2) (Horner et al., 2004, character 34 , modified).
18. Hollow nasal crest, premaxilla caudodorsal process with accessory rostroventral flange that overlaps the lateral surface of the nasal in the rostral region of the crest: absent (0); present (1) (Evans and Reisz, 2007, character 18).
19. Maxilla, rostrodorsal 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, rostrodorsal margin of maxilla forms a sloping shelf that underlies the premaxilla (1) (Horner et al., 2004, character 42).
20. Maxilla, dorsal process shape in lateral view: low and gently rounded (0); tall and sharply peaked (1) (Horner et al., 2004, character 48, modified).
21. Maxilla, position of apex in lateral view: well caudal to center (0); at or rostral to center (1) (Horner et al., 2004, character 47).
22. Maxilla, location of large rostral maxillary foramen: opens on rostrolateral body of maxilla, exposed in lateral view (0); opens on dorsal surface of maxilla along maxilla-premaxilla suture (1) (Horner et al., 2004, character 44, modified).
23. Maxilla-lacrimal contact: present externally (0); largely covered externally by a jugal-premaxilla contact (1) (Horner et al., 2004, charac-
ter 45 , modified).
24. Maxilla, ectopterygoid ridge: poorly developed (0); strongly developed, thickened horizontal ridge on lateral surface of maxilla (1) (Godefroit et al., 2004, character 24).
25. Ectopterygoid-jugal contact: present (0); absent, palatine-jugal contact enhanced (1) (Horner et al., 2004, character 51).
26. Lacrimal-nasal contact: present (0); absent (1) (Norman, 2002, character 12).
27. Jugal, expansion of rostral end below lacrimal: dorsoventrally narrow, forms little of the rostral orbital rim (0); expanded dorsoventrally in front of orbit, lacrimal pushed dorsally to lie completely above the level of the maxilla, jugal forms lower portion of orbital rim (1) (Horner et al., 2004, character 52).
28. Jugal, rostral process shape: asymmetrical with a pointed process between the maxilla and lacrimal (0); truncated and symmetrical (1) (Horner et al., 2004, characters 53 and 54, modified).
29. Jugal contribution to infratemporal fenestra, acute angle between postorbital bar and jugular bar: absent (0); present (1) (Horner et al., 2004, character 71).
30. Jugal, development of free ventral flange: absent, jugal expands gradually below intrafenestra to meet the quadratojugal-quadrate (0); present, jugal dorsoventrally constricted beneath infratemporal fenestra to set off flange rostral to constriction (1) (Horner et al., 2004, character 55).
31. Jugal, ventral flange shape: rounded or lobate (0); angular (1) (Suzuki et al., 2004, character 21).
32. Jugal, inferior infratemporal border wider then inferior orbit border: present (0); not present (1) (NEW, Sullivan et al., 2009).
33. Jugal, dorsal portion of caudal process shorter then ventral portion of caudal process: present (0); not present (1) (NEW, Sullivan et al., 2009).
34. Jugal, border of caudal jugal process fan-shaped rather then subrectangular: present (0); not present (1) (NEW, Sullivan et al., 2009).
35. Jugal-lacrimal contact of dorsal border of anterior jugal process "W"shaped: present (0); not present (1) (NEW, Sullivan et al., 2009).
36. Prefrontal, medial margin forms a thin vertical flange that laps onto the base of the crest: absent (0); present (1) (Godefroit et al., 2004, character 16).
37. Prefrontal, medial flange extends caudally over the dorsal surface of the frontal and above the prefrontal-postorbital joint in lateral view (in adults): absent (0); present (1).
38. Supraorbital articulation: freely articulate on orbit rim (0); fused to orbit rim or absent (1) (Horner et al., 2004, character 59).
39. Postorbital, bifurcation of the caudal process: absent (0); present (1).
40. Postorbital, caudal process: elongate above of infratemporal fenestra (0); short and deep, resulting in a constricted dorsal region of the infratemporal fenestra (1).
41. Postorbital, dorsal 'promontorium': absent (0); present in adults (1) (Godefroit et al., 2004, character 17).
42. Frontal, upward doming over braincase in adults: absent ( 0 ); present (1) (Horner et al., 2004, character 58).
43. Frontal, exposed along dorsal margin of orbit: present (0); excluded from orbital rim by an extensive prefrontal-postorbital joint (1) (Horner et al., 2004, character 57).
44. Frontal, platform for nasal articulation: absent (0); present, comprised of two thin, rostroventrally curved tongues that form a median cleft (1); or thickened and steeply angled, with median cleft absent (2) (Evans and Reisz, 2007, character 40).
45. Frontal, nasal articulation surface extends posterodorsally to overhang the parietal in adults: absent (0); present (1) (Godefroit et al., 2004, character 4, in part).
46. Frontal, shape of ectocranial surface: elongate with an ectocranial length/width $>0.8(0)$; relatively short, with a length/width $<0.8$ (1);
greatly shortened length/width ratio $<0.4$ ) (2) (Godefroit, 2004, character 6, modified).
47. Frontal, shape of the ventral annular ridge that defines the rostral extent of the cerebral fossa: long, low and gently rounded in medial view (0); annular ridge sharp (1) (Evans and Reisz, 2007).
48. Parietal midline crest: straight and level with skull roof or slightly down-warped along length ( 0 ); sagittal crest deepens caudally (strongly down-warped) (1) (Horner et al., 2004, character 69, modified).
49. Parietal midline crest, length: long, parietal narrows 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) (Horner et al., 2004, character 70).
50. Parietal, shape: long, length/width ratio greater than $2(0)$; less than 2 (1) (Godefroit et al., 2004, character 2).
51. Squamosal, separation of squamosals in caudal view: completely separated by the parietal (0); extensive intersquamosal joint present at the midline (1) (Suzuki et al., 2004, character 33, modified).
52. Squamosal, shape of caudoventral surface: shallowly exposed in caudal view ( 0 ); form a deep, near vertical, well-exposed face in caudal view (1) (Horner et al., 2004, character 64).
53. Squamosal, height above quadrate cotylus: lateral side relatively low (0); markedly expanded dorsally above the cotylus (1) (Godefroit et al., 2004, character 18).
54. Quadrate, 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) (Horner et al., 2004, character 60).
55. Laterosphenoid, complete enclosure of ophthalmic sulcus by bone laterally: absent (0); present (1) (Ostrom, 1961).
56. Supraoccipital, ventral margin: bowed or expanded ventrally along midline (0); horizontal, strong ridge developed along supraoccipitalexoccipital suture (1) (Horner et al., 2004, character 30).
57. 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) (Horner et al., 2004, character 67).

## Lower Jaw and Dentition

58. Predentary shape: deep and robust, arcuate rostral margin, neurovascular foramina large and located near midline of predentary body, dorsally directed spike-like 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, rounded, triangular denticles project rostrally and fit into a continuous transverse slot on underside of premaxilla (1) (Horner et al., 2004, character 13, modified).
59. Dentary, orientation of ramus rostral to tooth row in lateral view: approximately straight or moderately down-turned (0); or strongly deflected (1) (Horner et al., 2004, character 11, modified).
60. Dentary, coronoid process inclination: oriented roughly perpendicular to the dentary ramus (0); inclined rostrally (1) (Suzuki et al., 2004, character 39).
61. 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) (Horner et al., 2004, character 17).
62. Dentary, length of diastema between first dentary tooth and predentary: short, less than one-fifth the length of the tooth row (0); long, greater than one-fifth of the length of the tooth row (1) (Horner
et al., 2004, character 9 , modified).
63. Dentary, number of replacement teeth per position: two or less (0); three or more (1) (Horner et al., 2004, character 2).
64. Dentition, number of tooth rows: 32 or less (0); greater than 32 (1) (Horner et al. 2004, character 1; Suzuki et al., 2004, character 46, modified).
65. Dentary crown shape (middle of tooth row): diamond-shaped with a height/width ratio less than 3.0 (0); elongate lanceolate-shaped with a height/width ratio greater than 3.1 (1) (Horner et al., 2004, character 5 , modified).
66. Dentary teeth, number of accessory ridges: two or more prominent ridges ( 0 ); tooth crown dominated by one primary ridge, secondary ridges are faint when present (1) (Godefroit et al., 2004, character 30).
67. Dentary teeth, position of apex: offset to either mesial or distal side, or some teeth curved distally (0); apex central, tooth straight and nearly symmetrical (1) (Horner et al., 2004, character 8, modified).
68. Surangular foramen: present (0); absent (1) (Horner et al., 2004, character 19).
69. Angular, position on lower jaw: large and deep, exposed laterally (0); dorsoventrally narrow and not visible in lateral view (1) (Weishampel et al., 1993, character 26).

## Postcranial Skeleton

70. Cervical vertebrae, number: 13 or fewer (0); greater than 13 (1) (Horner et al., 2004, character 72, modified).
71. Mid-dorsal vertebrae ( $\sim$ D10), neural spine height greater than 4 times centrum height: absent (0); present (1) (Suzuki et al., 2004, character 51, modified).
72. Dorsal (caudal) and sacral neural spines: short, less than three times centrum height (0); elongate, approximately three times centrum height or greater (1) (Horner et al., 2004, character 76, modified).
73. Sacrum, number of sacral vertebrae: seven or fewer (0), eight or more (1) (Horner et al., 2005, character 75).
74. 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) (Horner et al., 2004, character 80).
75. Scapula, dorsal border: straight (0); curved rostroventrally (1) (Norman, 2002, character 43).
76. Scapula, orientation of borders of distal blade: divergent (0); subparallel to one another (1) (Horner et al., 2005, character 81).
77. Coracoid, biceps tubercle size: tubercle small (0); large, laterally projecting biceps tubercle (1) (Horner et al., 2004, character 78, modified).
78. Coracoid, cranioventral process (cranioventral hook): short and weakly developed (0); long, extends well below the glenoid (1) (Horner et al., 2004, character 79).
79. 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 equal to or longer than articulation (1) (Horner et al., 2004, character 77, modified).
80. Humerus, deltopectoral crest length: short, much less than half the length of the humerus (0); extends at least to midshaft or longer (1) (Horner et al., 2004, character 83).
81. Humerus, deltopectoral crest shape: relatively low (0); angular and enlarged (1) (Suzuki et al., 2004, character 59, modified).
82. Humeral distal condyles: compressed mediolaterally, flares little from shaft of humerus (0); mediolaterally broad, flare moderately from shaft of humerus (1) (Horner et al., 2004, character 84, modified).
83. Antebrachium length: humerus subequal to or longer than radius (0); radius significantly longer than humerus (1) (Horner et al., 2004, character 85).

416
84. Carpus: robust, with more than two small bones present and proximal ends of the metacarpals aligned (0); reduced to no more than two small carpals with MCIII offset distally with respect to MCII and IV (1) (Horner et al., 2004, characters 86 and 88, modified; Suzuki et al., 2004, character 57 , modified).
85. Manus, digit 1: metacarpal and one phalanx present (0); entire digit absent (1) (Horner et al., 2004, character 87).
86. Manus, Digit III-1: longer than wide (0); as wide or wider than long (1) (Suzuki et al., 2004, character 66, modified).
87. 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) (Horner et al., 2004, character 91).
88. Ilium, shape of dorsal margin: nearly straight (0); distinctly depressed over supracetabular process and dorsally bowed over base of preacetabular process (1) (Horner et al., 2004, character 100).
89. Ilium, postacetabular process: short and triangular in lateral view with a large brevis shelf ( 0 ); rectangular in outline, brevis shelf absent (1) (Horner et al., 2004, character 93).
90. Pubis, iliac peduncle: relatively small ( 0 ); has the form of a large and dorsally directed process (1) (Horner et al., 2004, character 92, modified).
91. Pubis, height of prepubic process: maximum depth of prepubic blade less than twice the height the minimum constriction (0); expanded,
greater than twice height of minimum constriction (1) (Horner et al., 2004, character 95 , modified).
92. Pubis, length of prepubic process constriction: long, dorsoventral expansion restricted to distal process (0); shaft short, dorsoventral expansion begins at base of process, repubic neck relatively tall (1) (Horner et al., 2004, character 96, modified).
93. Ischium, shape of distal end: small knoblike foot (0); large and pendent foot (1) (Horner et al., 2004, character 99).
94. Ischium, expansion of terminal foot: less than 25 percent the length of the ischium (0); greater than 25 percent the ischium length (1) (Suzuki et al., 2004, character 73, modified).
95. 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) (Horner et al., 2004, character 101).
96. Tarsus, modified with cranial ascending process of astragalus equilateral in shape and expanded distal fibular head: absent (0); present (1) (Godefroit et al., 2004, characters 39 and 40).
97. 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) (Horner et al., 2004, character 104).
98. Pes, shape of unguals: taper evenly distally, clawlike (0); dorsoventrally flattened and broadened, hoof-like (1) (Horner et al., 2004, character 105).

| Taxon | Character Number |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 98 |
| Probactrosaurus gobiensis | $? 000000000$ | 00000000?0 | 0?000?0000 | 0???? 00000 | 000000?00? | ??000?0000 | 000000000? | $? ? 00000000$ | 00????0000 | ? 0000000 |
| Telmatosaurus transsylvanicus | 0000?00000 | 0000000000 | 10?1110000 | $01000001 ? 0$ | 000000?000 | 00000?0??1 | 000011010? | ?0?110?1?0 | 00???????? | ????1??? |
| Gryposaurus incurvimanus | 100000000 | 0000000000 | 1001101011 | 0000000110 | 0000000000 | 0101011101 | 1111011110 | 0011101111 | 0001101111 | 00001011 |
| Aralosaurus tuberiferus | ?????00??? | 0???????10 | 1001??10?1 | 00??0001?0 | 0000000??1 | 010???0??? | ???0?????? | ?????????? | ?????????? | ???????? |
| Tsintaosaurus spinorhinus | 1????00000 | 0000000011 | 11?1??1??? | 0???? ${ }^{\text {a }}$ ? $101 ? 1$ | 011000?011 | 0101?00111 | 11111??11? | ?????????? | ?????????? | ???????? |
| Jaxartosaurus aralensis | ??????1??? | ?????????? | ?????????? | ?????10111 | 011100?011 | 0?0?0?0??? | ????????1? | ?????????? | ?????????? | ???????? |
| Amurosaurus riabinini | ??????1??? | ????????11 | 11?11?1111 | 01110111?0 | 0111001111 | 0?1101??11 | 1111111? ${ }^{\text {? }}$ | ?????????? | ?????????? | ???????? |
| Charonosaurus jiayinensis | ??????1??? | ?????????1 | 11?11?1111 | 000001?1?0 | 1111021111 | 111101??11 | 111111111? | ??111?1111 | 1????? $11 ? 1$ | ??1011?1 |
| Parasaurolophus cyrtocristatus | ??1?0?1010 | 0000?000?? | ?????1???? | ?11011111? | ?112?2?111 | 111?01???? | ??11111??? | 0111111111 | 1101?11111 | 011111?? |
| Parasaurolophus walkerl | 11130?1010 | 0100?00011 | 1101111011 | 0110111111 | ?112?2?111 | 1111?11101 | 1011111110 | 0111111111 | 1101111111 | 01??1??? |
| Parasaurolophus tubicen | ??1???1010 | 0100?00011 | 11?1111011 | 0110111111 | 1112121111 | 1111011?01 | 101111111? | ?????????? | ?????????? | ???????? |
| Nipponosaurus sachalinensis | ????0??1?? | ????????1? | ???11????1 | 10100????? | ?????????? | ?????1???1 | 1?1??11111 | 01?111111? | ?0?111111? | ??101?11 |
| Olorotitan arharensis | ??1??11?01 | 103??2??11 | 11?1??1111 | 011101?1?? | 0?1??1???? | ???1???111 | 1111?1?1?1 | 01111??1?1 | 1?111?111? | ??10?0?? |
| Lambeosaurus lambei | 1111111101 | 0011111111 | 1111111111 | 0110011110 | 0111011111 | 1111111111 | 1111111111 | 0111111111 | 1011111111 | 10101011 |
| Lambeosaurus magnicristatus | 1111?11?01 | 0011111111 | 1111111111 | 01100111?0 | 011101?111 | 111111?111 | 11?1??1111 | ???1111?11 | 1011111111 | 001010?? |
| Corythosaurus casuarius | 1111111101 | 1022122011 | 1111111111 | 0111011110 | 0111011111 | 1111011111 | 1111111111 | 0111111111 | 1011111111 | 10101011 |
| Hypacrosaurus altispinus | 1112111101 | 1031222111 | 1111111111 | 1110011100 | 0111011111 | 1111011111 | 1111111111 | 1111111111 | 011111111 | 0111011 |
| Hypacrosaurus stebingeri* | 1111111101 | 1031222011 | 1111111111 | 0000011110 | 0111011111 | 1111011111 | 1111111111 | 11111?1111 | 1011111111 | 10101011 |
| Velafrons coahuilensis | 111??11?01 | ???11???11 | 1111111111 | 011101?110 | 0?1????1?? | 1111?11?11 | 11?1????1? | ?????????? | ?????????? | ???????? |
| SMP VP-1534 | ?????????? | ?????????? | ?????? 1 ?11 | 01110????? | ?????????? | ?????????? | ?????????? | ?????????? | ?????????? | ???????? |

*only on MOR 548 (juvenile)

## APPENDIX 2

## SYSTEMATIC PALEONTOLOGY

## FAMILY Hadrosauridae SUBFAMILY Lambeosaurinae TRIBE Lambeosaurini, new tribe

Type species: Lambeosaurus lambei Parks, 1923.
Included species (following Evans and Reisz [2007] and with the additional characters included herein): Corythosaurus casuarius, Hypacrosaurus altispinus, Hypacrosaurus stebingeri, Lambeosaurus lambei, Lambeosaurus magnicristatus, Olorotitan arharensis, and Velafrons coahuilensis.

Equivocal taxa: Amurosaurus riabinini and Sahaliyania elunchunorum (see Prieto-Márquez, 2010a, b).

Diagnosis: Lambeosaurines distinguished from parasaurolophines by the following features: premaxilla has a vertical groove on the caudolateral process rostral to the maxillary dorsal process that extends vertically from a small lateral opening between the premaxillary caudal processes; nasal vestibule morphology consists of an S-loop in the enclosed premaxillary passages rostral to the dorsal process of the maxilla; and 13 or fewer cervical vertebrae present (characters 5, 8 , and 66, respectively, of Evans and Reisz, 2007).

Comments: Previously the Lambeosaurini consisted of four genera: Lambeosaurus, Corythosaurus, Hypacrosaurus, and Nipponosaurus; but later the clade was revised to include Olorotitan (Evans et al., 2007). Recent work by Prieto-Márquez (2010a, b) included the following taxa in this clade: (1) Corythosaurus intermedius, which we consider to be a subjective junior synonym of C. casuarius, and (2) ?Lambeosaurus
laticaudus, a taxon that has been recognized as having a suite of characters similar to those of Hypacrosaurus stebingeri (see Evans and Reisz, 2007), but as currently recognized, is paraphyletic to both Lambeosaurus and Hypacrosaurus, based on the recent phylogenetic analyses presented by Prieto-Márquez (2010a, b). His analysis suggests that " $H$." stebingeri belongs to a genus other than Hypacrosaurus or Lambeosaurus as "H." stebingeri is nested within the "corythosaurs" (which includes Lambeosaurus) whereas ?L. laticaudus is nested within the "hypacrosaurs," but it is excluded from the "corythosaur" clade, which includes Lambeosaurus (see Prieto-Márquez, 2010a, b). A recent study of Hypacrosaurus stebingeri (Brink et al., 2010) concluded that it was more closely related to Corythosaurus than to Lambeosaurus, while another study (Evans, 2010) concluded that $H$. stebingeri is a metaspecies and that it may be the ancestor of H. altispinus. Godefroit $(2004,2008)$, Evans and Reisz (2007) and Evans (2010) considered Amurosaurus rabinini to be a basal lambeosaurine. However, our analysis Amurosaurus forms a polytomy with Olorotitan, Corythosaurus, Velafrons and the jugal and humerus specimens (SMP VP-1534 and VP-2263, resectively). The newly named taxon Sahaliyania elunchunorum formed a polytomy with the Lambeosaurini and Parasaurolophini based on the phylogenetic analysis presented by Godefroit et al. (2008, fig. 18), yet it is
nested within the "hypacrosaur" clade ((Sahaliyania + Amurosaurus) (Hypacrosaurus (Lambeosaurus + Velafrons))) according to PrietoMárquez (2010a, b). Velafrons coahuilensis was part of the polytomic lambeosaurin clade recognized by Gates et al. (2007). Both Sahaliyania and Velafrons are herein included in our modified data set of Evans and Reisz (2007) and are considered to be lambeosaurins. We note that Charonosaurus jiayinensis fell well outside the Lambeosaurini in the modified analysis of Evans and Reisz (2007), which is contrary to its position in the analyses of Prieto-Márquez (2010a, b). Nipponosaurus sachalinensis was omitted by Prieto-Márquez (2010a, b) but it was included in the definition of the clade and analysis of Evans and Reisz (2007) despite the fact that the taxon is based on a juvenile and incomplete individual. Evans and Reisz (2007) noted that the topology of their cladogram did not change with the omission of Nipponosaurus. Therefore, following Prieto-Márquez (2010a, b) we do not recognize Nipponosaurus as belonging to the Lambeosaurini. Our definition of the Lambeosaurini would be equivalent to node 38 of Prieto-Márquez (2010a: fig. 9), with the exception that we include Olorotitan, which may be equivocal. The taxa Amurosaurus riabinini and Sahaliyania elunchunorum are members of the Lambeosaurini based on the recent analysis of PrietoMárquez (2010a, b), but their phylogenetic position is equivocal based on the analysis of Evans and Reisz (2007) and Evans (2010).

