A Revision of the Hadrosauridae (Reptilia: Ornithischia) And Their Evolution

During the Campanian and Maastrichtian

By

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A Dissertation submitted to

The Faculty of

The Graduate School of Arts and Sciences
of The George Washington University in partial satisfaction
of the requirements for the degree of the Doctor of Philosophy

February 19, 1989

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ACKNOWLEDGMENTS

I wish to thank the following people for their help during the course of this study; Richard Fox, Phil Gingerich, James Jensen, Dan Chure, the late Ted White, the late Russell King, Don Lindsey, Joanne Lindsey, the late Robert Makela, James Madsen, Christopher McGowan, William Morris, John Storer, William Turnbull, the late C.C. Young, Joseph Gregory, Robert Long, Fred Collier, Jann Thompson, Laurel Collins, and Tim Collins.

Special thanks are owed to David Berman, John Bolt, A. Gordon Edmund, Eugene Gaffney, Erle Kauffman, Harold E. Koerner, Guy D. Leahy, Halska Osmolska, Dale Russell, Samuel P. Welles, Robert Purdy, and Raymond Rye.

I am particularly indebted to the following individuals for their generous time and effort in aiding me during this study by providing data, equipment, photographs, helpful discussions and for their active support when I became quite sick of typing the Nth revision. They are Don Baird, Jennifer Clark, John Horner, Nicholas Hotton III, Douglas A. Lawson, George Olshevsky, John Ostrom, Gregory S. Paul, Phil Currie, Peter Galton, John S. McIntosh, Chip Clark, Hans-Dieter Sues, and Ralph Chapman.

A special note of praise is due for my dissertation committee. Nicholas Hotton III is the dissertation director and Anthony Coates, David Atkins and Daryl Domning are the main readers.

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ABSTRACT

A new taxonomy of the hadrosaurian dinosaurs is developed by a review of characters previously used to define genera, and an original analysis of the postcranial elements.

Fifty-six morphological characters are commonly used for defining the hadrosaurids, and these are evaluated in terms of new data from ontogeny, paleopathology, and postcranial studies. Features once used to define taxa are now evaluated as the result of ontogeny.

Forty-eight genera of hadrosaurids are taxonomically evaluated using both a "lumped" and "split" taxonomy. Synapomorphies are given for the family, two subfamilies and five tribes. Both "cladistic" and "evolutionary" principles are applied.

Hadrosaurid macroevolution is discussed in light of paleobiogeography, morphological evolution and preservational biases in the fossil record.

A new hypothesis of hadrosaurid extinction is proposed and named "Niche Assimilation". Its possible effects on other theories of dinosaur extinction are examined.

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List of Abbreviations For Plates and Tables

ACF	acromion fossa
ACR	acromion ridge
ACT	acetabulum
AST	astragalus
CAL	calcaneum
CRF	coracoid fossa
CRL	carpals
CRR	coracoid ridge
DE	dentary
DLF	deltoid Fossa
DLP	deltopectoral crest
DLR	deltoid ridge
FEM	femur
FIB	fibula
FMH	femoral head
GL	glenoid
GTR	greater trochanter
H	height
HH	humeral head
HL/FL	hindlimb/forelimb ratio
HND	sternal handle
HUM	humerus
ILP	iliac peduncle
ISFH	ischial foot - heel
ISFT	ischial foot - toe
ISP	ischial peduncle
JU	jugal
L	length
LA	lacrimal
LTR	lesser trochanter
MC3	metacarpal III
MC3/H	metacarpal III/humerus ratio
MT3	metatarsal III
MT3/F	metatarsal III/femur ratio
NA	nasal
OBF	obturator fossa
OBP	obturator process
OLN	olecranon notch
OLP	olecranon process
PBH	pubic blade height
PBL	pubic blade length
PD	predentary
PDL	sternal paddle
PF	prefrontal
PM1	premaxilla - 1
PM2	premaxilla - 2

PO	postorbital
POEP	post-orbital eye pocket
POP	post-acetabular process
PP	postpubis
PRP	pre-acetabular process
PUB	pubic blade
PUN	pubic neck
PUP	pubic peduncle
QJ	quadratojugal
QU	quadrate
R/H	radius/humerus ratio
RAD	radius
RPL	reflected premaxillary lips
SCAP	scapula
SCBL	scapular blade
SHF	shaft
SQ	sqamosal
STB	sternal body (paddle)
STH	sternal handle
SUIC	supra-iliac crest
T/F	tibia/femur ratio
TIB	tibia
TR3	third trochanter
TR4	fourth trochanter
TRS	tarsals
U/H	ulna/humerus ratio
ULN	ulna
UNG	ungual
W	width

List of Museum Acronyms

American Museum of Natural History - AMNH
New York

British Museum (Natural History) - BM(NH)
London

Brigham Young University Museum - BYU
Provo

Carnegie Museum of Natural History - CM
Pittsburgh

Cleveland Museum of Natural History - CMNH
Cleveland

Museum of Natural History of the City of
Denver - DMNH

Ekalaka Museum - EM
Ekalaka, Montana

Field Museum of Natural History - FMNH
Chicago

Geol. Inst. Mongolian People's Republic - GSP
Ulan Bator

Inst. Vert. Palaeo. Palaeoanthro., Academic
Sinica, Beijing - IVPP

Los Angeles County Museum, Natural History - LACM
Los Angeles

Museum of Northern Arizona - MNA
Flagstaff

Museum National d'Histoire Naturelle - MNHN
Paris

Naatuurhistorisch Mus. Maastricht, Holland - NHMM

National Museum of Natural Sciences - NMC
Ottawa

Palaeontological Institute, Academy of Natural
Sciences - PIN, Moscow

Beijing Museum of Natural History - PMNH
Beijing

Palaeontological Museum - PMU.R
Uppsala

Royal Ontario Museum - ROM
Toronto

San Diego Museum of Natural History - SDMNH
San Diego

Senckenberg Museum, - SM
Frankfurt am Main

Texas Memorial Museum, - TMM
Austin

Tyrrell Museum of Palaeontology - TMP
Drumheller

University of Alberta, Dept. Geol. - UA
Edmonton

Museum of Paleontology, Univ. Calif. - UCMP
Berkeley

University of Michigan Mus. Paleontology - UMMP
Ann Arbor

University of Nebraska State Museum - UNSM
Lincoln

National Museum of Natural History, Smithsonian
Institution - USNM,Washington, D.C.

Peabody Museum of Natural History, Yale Univ. - YPM
New Haven

Peabody Museum of Natural History, Yale Univ.,
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CHAPTER 1

INTRODUCTION

The purpose of this study is to make an original analysis of hadrosaurid postcrania and its effect on hadrosaurid taxonomy at the generic level. A revised diagnosis of all supra-generic clades is based on these new data, and the origin of the family and its palaeobiogeography are discussed. Major evolutionary trends are examined and hadrosaurid extinction is reviewed in light of extinction of all dinosaurs.

The morphological features used to define the hadrosaurids, in both the past and the present, are reviewed and discussed. New finds, especially in studies on the postcrania, establish the taxonomic validity of both cranial and postcranial characters and show how they relate to ontogeny.

Forty-eight genera of the family Hadrosauridae are reviewed. Synapomorphies are provided for each recognized subfamily and for each of the five clades newly recognized in this report. Both "cladistic" and "evolutionary" principles are used to delineate clades. A new definition of each family, subfamily and tribe is given.

An original overview of hadrosaurid paleobiology, paleobiogeography, and macroevolution is presented. A decline in diversity and numbers of individuals, from the Campanian through the Maastrichtian, is newly demonstrated to be consistent and independent of 'lumping' or 'splitting'.

Finally, current theories of hadrosaurid extinction are discussed, with a new look at their philosophical basis. A new hypothesis of hadrosaurid extinction is proposed that is time-independent of the K-T boundary and may also reflect on dinosaur extinction as a whole, as well as on the decline of giant dinosaurs at the J-K boundary. Principles of niche assimilation and specialized feeding habits are added to previous aspects of dinosaur extinction.

A series of tables lists both original syntheses, and compilations of hadrosaurid data generated by other workers. Fundamental information is tabulated in seven appendices as follows:

Appendix 1 - A listing of all previously published taxa to species level and their disposition in this report.

Appendix 2 - All formations worldwide that contain hadrosaurid remains.

Appendix 3 - Stages of the Jurassic and Cretaceous periods discussed in the text.

Appendix 4 - A diagram and explanation of the measurements and landmarks used for the ratios presented in tables 1 through 5.

Appendix 5 - A fully labeled lambeosaurine skull to show which elements are visible in lateral view, the view most often used to choose characteristics when diagnosing genera of hadrosaurids.

Appendix 6 - The specimens used in this work listed by museum and museum number for easy reference.

Appendix 7 - The newer ROM museum numbers for specimens which were published under the older GSC museum numbers.

Tables 1 through 10 provide original measurements and comparisons of postcranial remains for both traditionally recognized subfamilies (Hadrosaurinae and Lambeosaurinae fide Langston 1960), and also of selected camptosaurids and iguanodontids for use in outgroup comparisons. Eighteen full-page original figures of crania and postcrania are assembled along with new full-body skeletal and flesh reconstructions based on studies presented in this report.

HISTORY OF THE STUDY

In the summer of 1973, the Department of Paleontology and the Museum of Paleontology of the University of California at Berkeley launched the Berkeley Archosaur Documentation Expedition. The purpose of this expedition was to photograph as many fossil bones of archosaurs as permitted by time and funding. The expedition was supervised by Dr. Samuel P. Welles. Mr. Robert A. Long combed the archives of the many museums we visited for information about the bones that were photographed. I was the chief photographer and was assisted by Mr. Douglas A. Lawson. For seventeen weeks, Mr. Long, Mr. Lawson and I visited the twenty leading museums of North America for archosaur paleontology. Over 535 rolls of film were taken and are now archived in the Museum of Paleontology at Berkeley under the care of Mr. Long.

While visiting the Field Museum of Natural History in Chicago, I discovered the partial remains of a hadrosaur from the Rio Chico area of Argentina that had been collected in 1923. At the time of the Berkeley expedition only one hadrosaur had been reported from all of Gondwana, and that find was represented by only a partial tail (Casamiquela, 1964). The material at the Field Museum consisted of two ilia and a pubis plus other fragments. I borrowed the specimen in the hope of writing a short paper describing this unexpected find.

During the course of the expedition I visited many libraries and talked with many paleontologists at the institutions we visited. An examination of the literature revealed that all the authors of the major papers on hadrosaurids believed that hadrosaurid postcrania 'all looked alike'. A comparison of some of the photos I had taken showed this belief to be incorrect. While visiting Yale University I had a chance to talk with Dr. John Ostrom and his graduate student Peter Dodson who, at the time, were the two leading authorities on hadrosaurids. Both expressed the opinion that I would probably be disappointed by trying to find consistent postcranial differences that reflected the different lineages within the two known subfamilies of hadrosaurids, but they encouraged me to persevere. In order not to trespass on other people's ongoing research, it was agreed that I concentrate on hadrosaurid postcrania while Peter Dodson concentrate on hadrosaurid crania. In 1975 Peter Dodson published his classic paper on lambeosaurine cranial allometry. His work is now being carried on by John R. Horner and his students. In that same year, I presented the results of my studies on the postcrania at the annual meeting of the Society of Vertebrate Paleontology.

In the following months, I was informed by Drs. Horner, Baird, Ostrom and Dodson that they agreed with my observations and that my Master's thesis was being extensively distributed. In this thesis, I was able to show that the postcrania of hadrosaurian dinosaurs were diagnostic in some cases to one of five lineages that I delineated. I did not formally name these five lineages. In 1979, I published a revised phylogeny and classification of the hadrosaurs which has not been challenged in the literature. That paper was the first phylogeny of the hadrosaurids that used all the known genera and not just the North American forms.

This work summarizes the results of my continuing investigations into hadrosaurid paleobiology with emphasis on the postcrania. One of the goals of this study is to provide a database on hadrosaurid specimens. At present, I have over 500 specimens cataloged. The specimens used in this report are listed in Appendix 6. Many of the measurements on the few complete specimens available for study, and results of this study, have already been distributed to ornithischian workers around the world.

The original contributions in this report are 1) the first complete morphological analysis of hadrosaurid postcrania and its influence on the taxonomy of the family at the generic level; 2) the recognition of features that represent old age in some taxa and valid taxonomic distinctions in others; 3) new diagnoses of the Hadrosauridae based on cranial and postcranial features at the family, subfamily and tribe levels; 4) documentation of the evolution of hadrosaurids from iguanodontids; 5) a contribution to the paleobiogeography of hadrosaurids; 6) an original hypothesis of hadrosaurid extinction based on niche assimilation and specialized feeding habits; and 7) the naming of the new genus Anatotitan.

Future works that are based on my original studies, and that will be started immediately following the dissertation are 1) a cladistic analysis using PAUP and McCLADE; 2) an annotated bibliography of the hadrosaurids, 1856-1987; and 3) a history of hadrosaurian taxonomy.

MATERIALS AND METHODS

Specimens of hadrosaurids were measured and analyzed from data based on photographs, personal observations, and the literature. In most cases photos of specimens taken during the Berkeley Archosaur Expedition were used. Photographs of postcranial bones were assembled into two sets. The first set was sorted by element and then by morphology to see what basic morphological types were represented for each element. [For example, the ilium of _Parasaurolophus_ has a unique appearance. All ilia of that shape were placed in a package without regard to which taxa they came from. Only the roll and photograph number were recorded on each photo in order to avoid _a priori_ bias by knowing which taxon was represented by each picture.] The second set of photographs was sorted taxonomically and then by element. The two sets were compared to see if any morphological shape fell outside of a previously defined clade (e.g. Lull and Wright, 1942 or Ostrom, 1961). The photographs were then reanalyzed to see if any clade had elements whose morphology resembled that of any elements from another clade. In both analyses, the shape of each element and the presence of unique features consistently fell into one clade. The measurements in Tables 6-10 represent a compilation of the most complete associated and articulated hadrosaurid remains.

Concurrent with an analysis of the photographs was a compilation of the hadrosaurid literature dating from 1856. All papers were read to discern geologic occurrences, association of body parts, degree of restoration of body parts, and taxonomic history of the specimen.

All major results of this study were distributed to ornithischian workers for review on a continuing basis. The text figures and plates presented here were drawn directly from photographs. The full body restorations were reconstructed from photographs of the most complete specimens available for each taxon where there was enough material to provide an accurate figure. Individual elements were also drawn from photographs using a camera- lucida. The measurements cited here are my own based on the diagrams given below. Dodson (1975) reported that after taking over fifty skull measurements, only three were useful. The same trend is seen with postcranial measurements. The only postcranial measurements of taxonomic use were those associated with the iliac length versus height, and the neural spine height of the sacral vertebrae. All other characters that proved to be of taxonomic use were based on the presence of non-quantitative derived features. These helped to delineate morphological types in isolated specimens but no single measurement or ratio could be used to identify taxa. As with most dinosaurs, diagnoses are based on the presence or absence of features, not on quantitative measurements.

CHAPTER 2

AN ORIGINAL ANALYSIS OF HADROSAURID POSTCRANIA

In this section, hadrosaurid postcrania are analyzed for morphological consistencies within clades, and to determine which features of each element are most valuable for taxonomic diagnoses. Abbreviations used in the text are listed in the Introduction.

PECTORAL GIRDLE AND FORELIMB

SCAPULA

In hadrosaurids, two regions of the scapula (Plate 1A, Tables 2 and 4) show morphological variations of taxonomic significance. The proximal part includes the suture for the coracoid, as well as the deltoid ridge (DLR in Plate 1A) which arises on the dorsal margin and angles in a posterior-ventral direction to the ventral border. Anterior to this ridge is the deltoid fossa (DLF in Plate 1A), the posterior border of which terminates at the narrowest part of the scapula, called here the 'neck'. The second or posterior part of the scapula consists of the 'blade' (SCBL) which is flattened and rectangular in shape. In natural articulation (Plate 9) the scapula lies parallel to the vertebral column. Two morphs are here recognized, the hadrosaurine scapula (Plates 1A, 9) and the lambeosaurine scapula (Plate 16A).

In the hadrosaurine scapula (Plate 1A), the blade is relatively longer (antero-posteriorly) and not as wide (dorso-ventrally in natural position) compared to the lambeosaurines. An excellent example is that of <u>Brachylophosaurus</u> (NMC 8893). This blade is relatively the longest of any known hadrosaurid, while the width (measured dorso-ventrally) is relatively the smallest. This results in a length/width ratio greater than in any other genus.

In the lambeosaurine scapula (Plate 16A), the blade is relatively shorter (antero-posteriorly in natural position) and wider (dorso-ventrally) than in most hadrosaurines. An excellent example is found in the scapula of <u>Parasaurolophus cyrtocristatus</u> (see especially Ostrom, 1963). The blade is short and robust with a length/width ratio smaller than in any other genus. The only exception to this morphological variety is seen in a specimen of <u>Lambeosaurus</u> (ROM 1218), which more closely resembles the hadrosaurine variety.

The scapula displays considerable variation within clades and even within genera. There is much overlapping of shapes among genera, therefore it is impossible to diagnose scapulae to the generic level or to use length/width ratios to separate taxa. As stated above, Brachylophosaurus stands out from the other genera with its unique length/width ratio of the blade, but a sample size of one does not justify the delineation of its own morphotype. One can only say that a scapula is either long and thin (most likely a hadrosaurine) or it is shorter and wider (most likely a lambeosaurine). There are blades that expand abruptly just distal to the neck and have parallel dorsal and ventral borders, or convex dorsal borders (Prosaurolophus, ROM 787). Tables 3 and 5 demonstrate how much the length/width ratios overlap.

As individuals mature, the deltoid ridge becomes elongate and more robust until it finally reaches the lower scapular border in adults. In juveniles, the area of the glenoid (GL) is larger than the area for the suture with the coracoid (AMNH 6577), while in adults (AMNH 5730) the area of the glenoid and the area of the coracoid suture are about equal in extent. In juveniles, the suture for the coracoid is slightly roughened, but in adults it is extremely rugose and massive (e.g., USNM 2413, a coracoid showing the scapular sutural area). In many juveniles, the dorsal and ventral borders of the blade diverge slightly posteriorly (as in the ancestral iguanodontids), while in adults the dorsal and ventral borders are parallel so that the blade appears rectangular in lateral aspect.

The scapular blade of adults is relatively longer than that of juveniles. It appears that the major area of ossification is at the distal end of the blade, possibly to increase the area for muscle attachment in supporting the larger bulk. I find that hadrosaurids maintain the same scapular proportions throughout life. It would appear that this is accomplished solely by increasing the length and width of the scapular blade relative to the proximal portion of the scapula.

It is impossible at this time to distinguish morphological types that may be referred to specific genera or clades because of inadequate sample size. It is only possible to recognize two basic types which correspond to the two traditionally recognized subfamilies, the Hadrosaurinae and the Lambeosaurinae.

CORACOID

In hadrosaurids, the coracoid (Plate 1A) terminates anteriorly in a large hook-like process. Arising from this hook is the coracoid ridge (CRR) which forms the anterior border of the coracoid and ends at the juncture with the dorsal border of that element. The coracoidal ridge is deflected medially on the dorsal surface just where the acromion ridge originates. This latter ridge proceeds posteriorly and ends at the suture with the scapula. Halfway between the dorsal and ventral borders of the coracoid and just anterior to the suture with the scapula is the coracoid foramen (CRF). This foramen is entirely surrounded by the coracoid in hadrosaurids in contrast with the iguanodontids where it lies partly within the suture with the scapula. The glenoid (GL) lies at the base of the coracoid-scapular suture and has a hyperbolic cone-shaped depression at its center. The scapular suture is rugose with rounded knobs and deep depressions. The main body of this element is three to four times as thick as the coracoid ridge and hook.

The coracoid (Plate 1A) does not display sufficient variation among the lineages to make it an element of diagnostic value. Indeed, most coracoids are crushed flat, which makes it difficult to ascertain their original shape. The only exception is a complete, uncrushed element from a moderately old individual (USNM 2413). It appears that in hadrosaurines the coracoid is longer (antero-posteriorly) and lower (dorso-ventrally) than in lambeosaurines, but the sample size is too small for complete justification of this proposed dichotomy.

The only difference between the early forms, such as <u>Bactrosaurus</u> (AMNH 6577) and <u>Gilmoreosaurus</u> (AMNH 6581), and the more derived late Cretaceous forms, is that the coracoidal hook (CRR) is smaller and pointed more ventrally than antero-ventrally.

The coracoid is frequently lost. Those specimens that have one are usually display specimens in which coracoids are difficult to examine. The association of the coracoid with the rest of the skeleton is questionable unless it is definitely known that the skeleton has been preserved in its entirety.

There are enough specimens to discern several growth characteristics. In juveniles, the coracoidal hook is small (as in iguanodontids) and points ventrally. The coracoid foramen is entirely enclosed within the coracoid, unlike some early iguanodontids. Dorsally, the knob at the end of the acromion

Plate 1A

Left scapula and coracoid of the hadrosaurid **Kritosaurus navajovius** in left lateral view based on AMNH 5465. Scapular length is 792mm.

Plate 1B

An iguanodontoid left scapula and coracoid of **Camptosaurus browni,** in left lateral view based on USNM 4282. Scapular length is 482mm.

Plate 1C

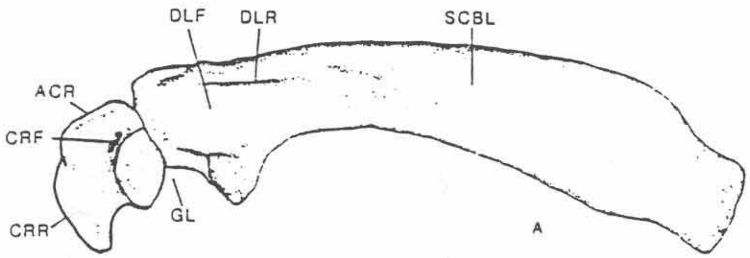
The left sternum of **Tsintaosaurus** (PMNH V125), a lambeosaurine of the **Parasaurolophus** lineage as seen in anterior view. Sternal length is 420mm.

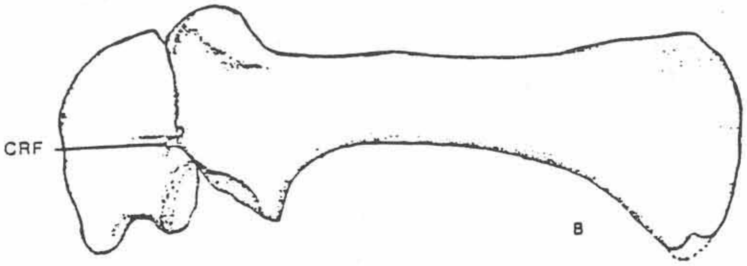
Plate 1D

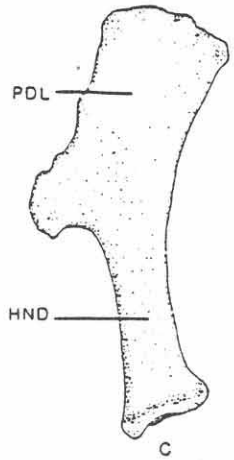
The left sternum of **Shantungosaurus** (a hadrosaurine, PMNH, no number available - redrawn from Hu, 1973) as seen in anterior view. Sternal length is 705mm.

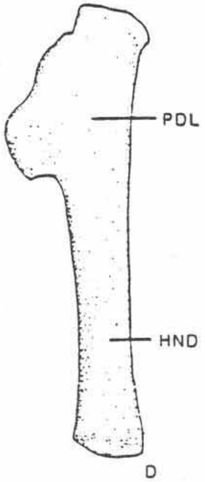
Drawings A and B made from photo tracings by D.A. Lawson. Drawings C and D made from photo tracings by G. Paul. All drawings under my direction.

ABBREVIATIONS FOR ALL PLATES LISTED IN THE INTRODUCTION









ridge (ACR) is small and rounded and generally smooth. The glenoid is deep as in adults but the depression is symmetrically shaped. The scapular suture is slightly rugose. The main body of the coracoid is slightly thicker than that of the coracoidal hook.

One growth feature of great interest is that with increasing size, the coracoid abruptly becomes thicker (latero-medially) and more rugose. This feature has been observed on other postcranial elements, notably the ilium. It is as though there exists a definite old age condition that can be attained by hadrosaurids, possibly with declining ability to regulate calcium deposition. The excessive deposition of bone in hadrosaurines mimics taxonomic features in the lambeosaurines where bones are generally more robust and thicker than in hadrosaurines.

STERNALS

Of the sternal elements examined, there appear to be two morphs that correspond to the two subfamilies (Plates 1C and 1D). Each sternal is composed of two parts. The main part is the more proximally placed and rounder body (or 'paddle', PDL in Plate 1) which is relatively longer (dorso-ventrally) in lambeosaurines (Plate 1C). The ventral part is the 'handle' (HND) which is relatively longer and thinner in hadrosaurines (Plate 1D).

Sternals of iguanodontids are much closer in shape to hadrosaurids than they are to camptosaurids in which the 'handle' is absent. As restored by Dollo (1883) and Norman (1980), there is space between the coracoids and sternals for a cartilaginous xiphisternum. This may also have been true for hadrosaurids.

Sternals are the most difficult elements to study. They are rarely preserved or prepared and are virtually ignored in the literature (see Parks, 1920, for the only complete description of a sternal).

HUMERUS

The humerus (Plates 2B,C, Tables 2,3,4 and 5) is divided into two parts. The dorsal part contains the head (HH) which fits into the glenoid formed by the scapula and coracoid. Immediately below the humeral head, the proximal part of the shaft expands antero-laterally to form the deltopectoral crest (DLP). The lateral border of this crest is parallel to the medial border of the proximal part of the humeral shaft. At the halfway point along the shaft, the deltopectoral crest abruptly ends and the shaft narrows to its minimum width. From the distal part of the deltopectoral crest to the distal end of the element extends the second part of the humerus. At the distal end of the humerus, the element expands into lateral and medial condyles for articulation with the radius and ulna.

As with the scapula, two types of humeri can be distinguished (Plate 2), but there are many intermediate forms. Only the most extreme morphs are useful for the identification of clades.

In hadrosaurines (Plate 2C), the deltopectoral crest is slightly less than three times as long (dorso- ventrally) as it is wide (latero-medially). The asymptote of the ventro-lateral border is at, or just above, the midpoint of the humerus. The overall aspect of the humerus is that of a long and gracile element compared to the thicker and more robust lambeosaurine humerus.

In lambeosaurines (Plate 2B), the deltopectoral crest is about twice as long as wide. The asymptote of the ventro-lateral border is at, or just below, the midpoint of the element. The overall aspect is that of a thicker and more robust element than in hadrosaurines. Because the deltopectoral crest is relatively wider in lambeosaurines, the length/width ratio of the crest is generally smaller than in hadrosaurines.

Several growth characteristics may be observed. In juveniles, the lateral tuberosities at the proximal end are poorly developed, if present at all. The head is relatively smaller compared to adults and the deltopectoral ridge is thinner. The distal condyles are relatively smaller and there is little difference in size between the lateral and medial tuberosities. In adults, more emphasis is placed on the medial distal condyle as the condyles increase in size.

The only observable difference amongst hadrosaurids is that the humerus of Parasaurolophus cyrtocristatus (FMNH P27393) appears to be more robust than that of other genera. Its proximal and distal articulations are relatively more expanded than in other hadrosaurids of the same size. The length/width ratio of the shaft is also relatively larger. Extreme caution must be taken when considering thickness as a taxonomic character. As in the coracoid, thickness is more a product of age than of taxonomy.

RADIUS

The radius (Plate 2G, Tables 2,3,4 and 5) is a long, straight columnar element that has a circular cross-section at midshaft. The proximal end, which articulates with the medial-distal condyle of the humerus, abruptly expands into a circular, cup-shaped process and resembles the top of a Doric column in anterior view. The distal end is flattened and is rectangular in anterior view.

Lull and Wright (1942) stated that the radius/humerus length ratio is diagnostic at the subfamilial level, the humerus being longer in the hadrosaurines and the radius longer in lambeosaurines. This idea must now be abandoned. The radius (Plate 2) is longer than the humerus in the hadrosaurines _Saurolophus osborni_ (AMNH 5220), _Edmontosaurus edmontoni_ (NMC 2288), _Anatotitan copei_ (AMNH 5730) and in the lambeosaurine _Hypacrosaurus altispinus_ (NMC 8501). The radius is shorter than the humerus in the hadrosaurines _Kritosaurus (=Hadrosaurus ?) incurvimanus_ (ROM 764), _Prosaurolophus maximus_ (ROM 787), _Edmontosaurus annectens_ (YPM 2182) and in the lambeosaurine _Parasaurolophus walkeri_ (ROM 768). This feature is not consistent within any clade and is therefore useless for taxonomic purposes. The sample size of articulated individuals is too small within any genus to know if the radius/humerus ratio has any value to delineate species or sexes.

ULNA

The ulna (Plate 2F, Tables 2 and 4) has the overall shape of an inverted, triangular, conical section. The proximal end forms a three-pronged process with each prong radiating at ninety degrees from the other prongs. The medially and anteriorly projecting processes form a cradle-like structure that receives the radius. The proximally projecting olecranon process (OLP in Plate 2F) articulates with the posterior side of the humerus between the two distal condyles, which sit in the olecranon notch (OLN) of the ulna. The distal end of the ulna is flattened like that of the radius.

The transition from juvenile to adult results in a great enlargement of the olecranon notch of the ulna and an increase in robustness of the olecranon process. The lateral process becomes thicker. The distal end does not show any great increase in width compared to its circumference, but the shaft undergoes a tremendous increase in length compared to its circumference. This results in the forelimb becoming relatively thinner with increasing age.

Plate 2

A) Right humerus of **Camptosaurus browni**, an iguanodontoid, as seen in lateral view. Based on USNM 4282. Maximum length is 360mm.

B) Right humerus of **Parasaurolophus walkeri**, a lambeosaurine, in lateral view. Based on AMNH 5893 and ROM 768. Length is 520mm.

C) Right humerus of **Kritosaurus navajovius**, a hadrosaurine, in lateral view. Based on AMNH 5465. Length is 764mm.

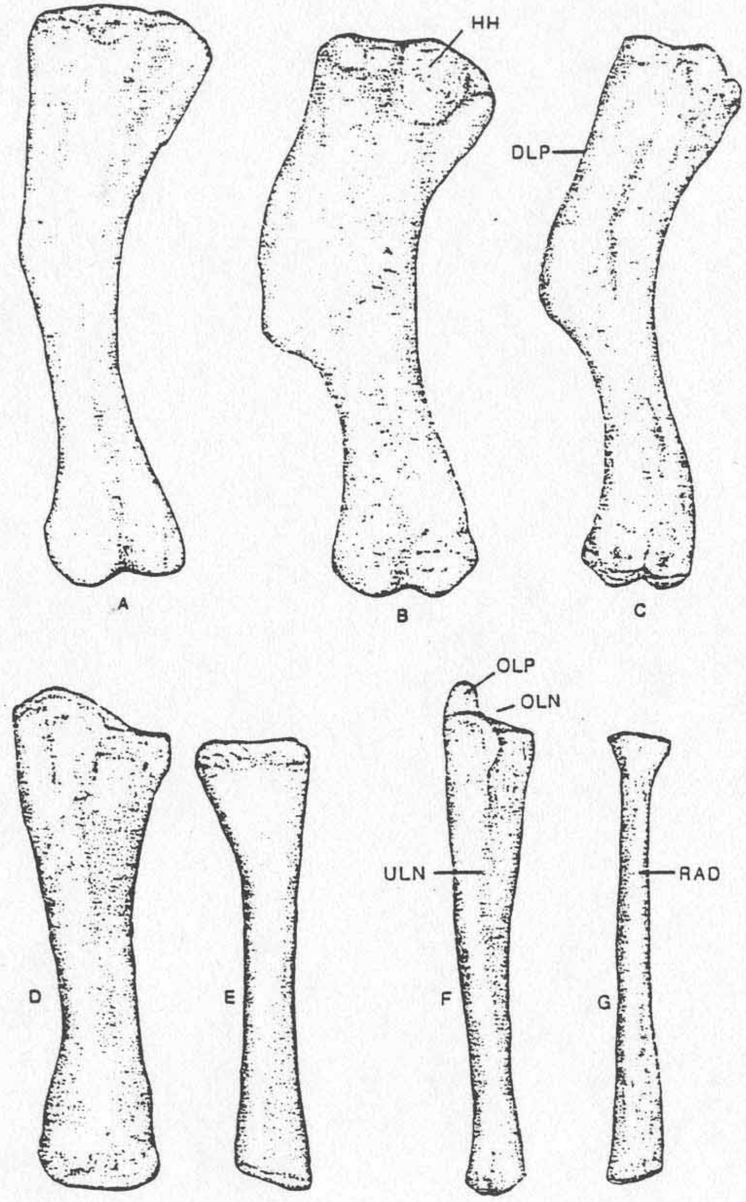
D) Right ulna of **Camptosaurus browni**, an iguanodontoid, based on USNM 4282 in anterior view. Length is 262mm.

E) Right radius of **Camptosaurus browni**, an iguanodontoid, based on USNM 4282 in anterior view. Length is 232mm.

F) Right ulna of **Parasaurolophus cyrtocristatus**, a lambeosaurine, based on FMNH P27393 in anterior view. Length is 665mm.

G) Right radius in anterior view, same as in F. Length is 585mm.

All drawings by D.A. Lawson under my direction.



The only variation observed among the ulnae of hadrosaurids is in that of Parasaurolophus cyrtocristatus (FMNH P27393), which appears to be relatively thicker than in the other genera. Kritosaurus (ROM 764) and Brachylophosaurus (NMC 8893) have ulnae that are long, thin, and generally very gracile. As with most elements, the hadrosaurines appear to have limb elements that are more slender and less thick than those of lambeosaurines of the same size.

CARPALS

The block-like carpals (Plate 3B) resemble a section of a cylinder. They are circular in cross-section and about one-half as tall (dorso-ventrally) as wide (latero-medially).

The sample of carpals is insufficient to determine the range of variation present in hadrosaurids. The intermedium (provisional designation) is slightly larger than the radiale (provisional designation) which, in one specimen (AMNH 5886), had an overhanging lateral process that fit over the second metacarpal. (It is not even known if the usage of the term intermedium is appropriate.) Only two carpals are seen, when preserved, and what is termed the intermedium here could very well be the ulnare. Of all the postcranial elements, the carpals suffer most from lack of preservation and/or preparation. The only specimens that I observed were on mounted specimens which made their study extremely difficult. It is probable that the carpals are not mounted because they are too much trouble to mount for such small elements and they are so poorly known. Most collections do not have carpals. Because of their concretion-like appearance, they are most likely unrecognized and inadvertently destroyed during preparation, if they are preserved at all.

The positions of these elements are also in doubt. In Corythosaurus casuarius (CM 9461), the radiale and the intermedium are mounted next to each other, both under the radius and each over a different metacarpal. In a specimen of Anatotitan copei (Plate 3B, AMNH 5886) they are mounted on top of one another, both over the third metacarpal. The situation is further confused by another mount of Anatotitan copei (AMNH 5730). In this specimen, there are two carpals, one on top of the other, between the radius and the third metacarpal. There is also another carpal between the ulna and fourth metacarpal. This would suggest that the radiale and ulnare are in the normal position but that the intermedium has either changed position or has been replaced by a distal carpal, which appears only in this

Plate 3

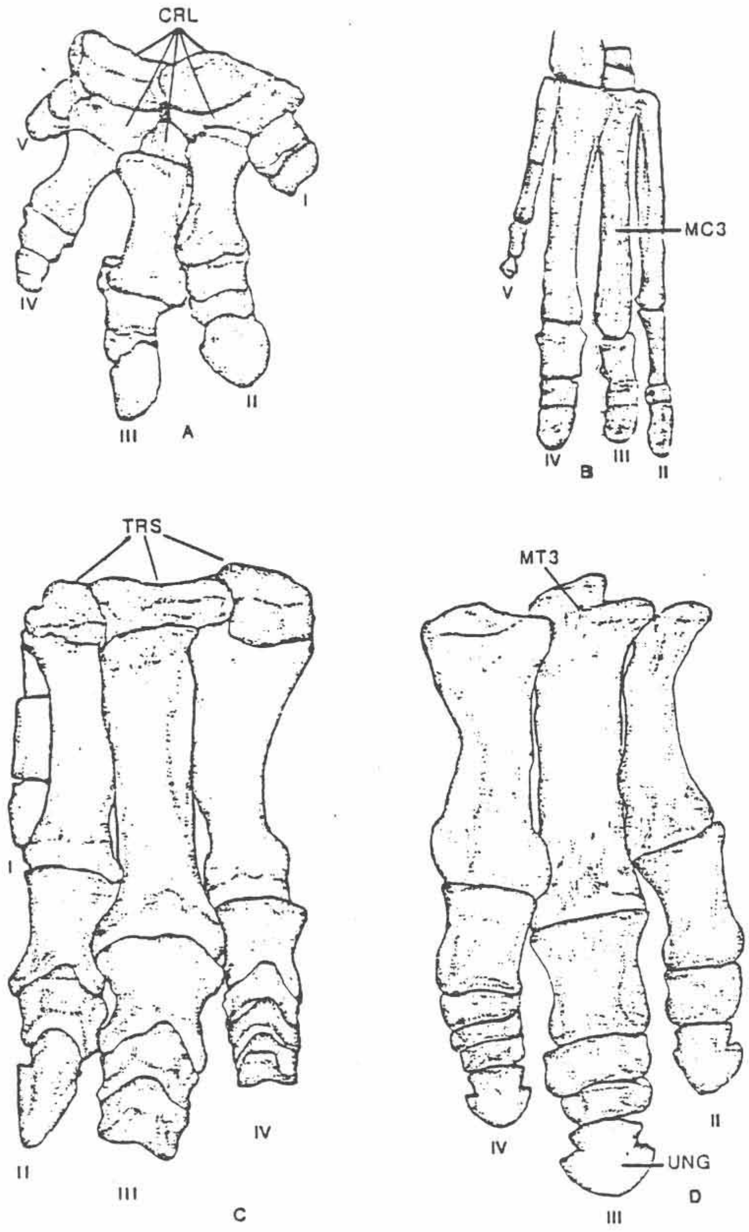
A) Right manus of **Camptosaurus dispar**, an iguanodontoid, based on USNM 4277 in anterior view. Length of metacarpal-3 is 78mm.

B) Right manus of **Anatotitan copei**, a hadrosaurine, based on AMNH 5886 in anterior view. Length of metacarpal-3 is 310mm.

C) Left pes of **Camptosaurus dispar**, an iguanodontoid, based on USNM 4277 in anterior view. Length of metatarsal-3 is 234mm.

D) Right pes of **Saurolophus osborni**, a hadrosaurine, based on AMNH 5270. Length of metatarsal-3 is 340mm.

Drawings by D.A. Lawson under my direction.



specimen. It is likely that the lack of carpals, and the complete uncertainty as to their true position, may be due to the fact that they only ossified very late in life. Only the older, larger adults seem to have them. Even a well-preserved hand of a "mummy" described by Versluys (1923) does not have them. However, John Horner has informed me (pers. comm. 1985) that hatchling hadrosaurids (most likely Maiasaura) from the Two Medicine Formation do possess carpals. This would indicate that in some taxa the carpals are reabsorbed early in life and that their presence in adults is the result of re-ossification.

Little variation in morphology of the carpals was noted among the genera. Parasaurolophus cyrtocristatus (FMNH P27393) appears to have more robust carpals than in other genera. Measurements of these elements did not prove to be of diagnostic value. It is common for the hand not to be preserved in most specimens. There appears to be a taphonomic pattern such that the head, manus and pes are the first parts to become separated from the main portion of the skeleton (Dodson 1971). None of the bones of the manus or pes are fused to one another, or to the limbs, thus making separation quite easy prior to final burial.

METACARPALS

The metacarpals (Plate 3B, Tables 2,3,4 and 5) are pencil-shaped and have smooth, featureless articular ends. Metacarpal 1 is lost and metacarpal 5 is reduced. The manus is functionally tridactyl with metacarpal 3 slightly longer than metacarpal 2 and metacarpal 4, which are equal in length.

I was unable to detect any differences among the genera of hadrosaurids using the morphology of the metacarpals. The sample size of the specimens with a complete manus is too small at this time to detect any trends even at the level of subfamily.

PHALANGES

The phalanges of hadrosaurids are most similar to iguanodontids (fide Norman 1980). They are longer (proximo-distally) than wide (latero-medially) and flattened. The general formula is 0,3,3,3,3. The unguals are hoof-shaped but relatively less developed and laterally flared than the pedal phalanges.

There is one slight difference between the phalanges (Plate 3B) of some of the hadrosaurines and lambeosaurines. In the hadrosaurines, the second row of phalanges (distally from the metacarpals) of digits II, III, and IV generally consists of well developed elements that are proportionally as large as the proximal row of phalanges. In the lambeosaurines, this row generally consists of elements that are considerably reduced and often pebble-like. These phalanges, so far, can only be distinguished in articulated mounts where the process of mounting them renders their exact nature and relationship doubtful.

Plate 4

A) Ilium of **Edmontosaurus annectens**, a hadrosaurine from the **Edmontosaurus** lineage, based on DMNH 1493. Maximum length between perpendiculars is 1160mm.

B) Ilium of **Parasaurolophus cyrtocristatus**, a lambeosaurine from the **Parasaurolophus** lineage based on FMNH P27393. Length is 975mm.

C) Ilium (medial view) of **Kritosaurus navajovius**, a hadrosaurine from the **Kritosaurus** lineage based on USNM 8058. Length is 900mm.

D) Ilium of **Lambeosaurus lambei**, a lambeosaurine from the **Corythosaurus** lineage based on ROM 1218. Length is 1003mm.

E) Ilium of **Tanius sinensis**, a hadrosaurine, redrawn from Wiman 1929, figure 1. Length is 920mm.

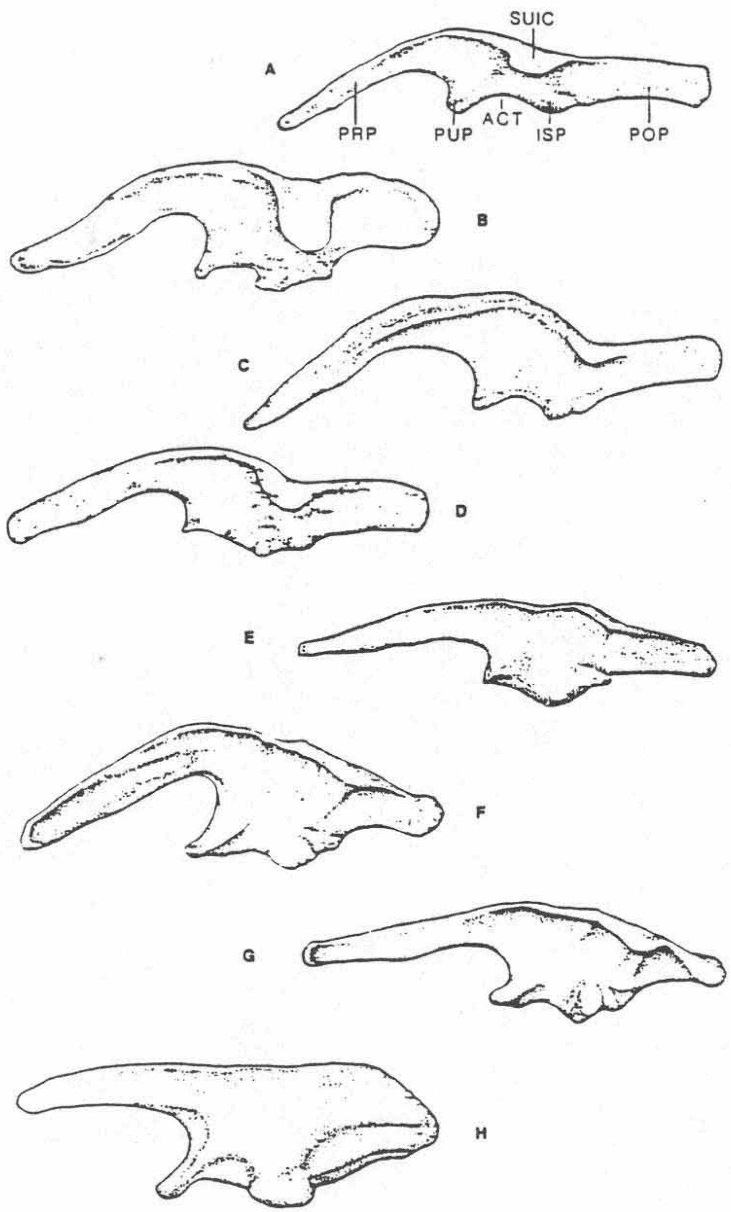
F) Ilium of **Bactrosaurus johnsoni**, a lambeosaurine from the **Parasaurolophus** lineage based on AMNH 6577. Length is 690mm.

G) Ilium of **Gilmoreosaurus mongoliensis**, a hadrosaurine, based on AMNH 6551. Length is 650mm.

H) Ilium of **Camptosaurus dispar**, an iguanodontoid, based on USNM 5473. Length is 642mm.

Drawings by D.A. Lawson under my direction.

All figures are left ilia in lateral view except for figure 6C which is a right ilium in medial view.



PELVIS AND HINDLIMB

ILIUM

The ilium (Plate 4, Tables 2,3,4 and 5) is composed of three distinct portions. The pre-acetabular process (PRP) is blade-like, curves ventrally, and is flattened in most adults. The mid-section of the ilium contains the acetabulum (ACT). The dorsal margin bears the antitrochanter [(or supra-iliac crest,(SIUC)]. The middle area between the dorsal and ventral margins contains the concave depression for the *m. ilio-femoralis*. The medial side of the ilium contains the articulations for the sacral ribs. The post-acetabular process (POP) is blade-like and rectangular in lateral view.

Five types of ilia are recognized among the hadrosaurids (Plate 4). The first type is represented by *Bactrosaurus* and *Gilmoreosaurus*, the stratigraphically earliest known hadrosaurids. In this type (Plate 4F+G), the preacetabular process is ventrally deflected as in later hadrosaurids. Both ischial (ISP) and pubic (PUP) peduncles are structured in typical hadrosaurian fashion as is the *m. ilio-femoralis* depression. The postacetabular process has been greatly modified from the camptosaurid (Gilmore 1909) and iguanodontid condition (Norman 1980) where this process is rudimentary (if present at all), but it is not as well developed as in the more advanced hadrosaurids *Edmontosaurus* and *Parasaurolophus*. The antitrochanter is rudimentary and is more of a laterally projecting lip on the dorsal margin of the ilium as in iguanodontids. In other hadrosaurids, it is a massive process. (Compare *Bactrosaurus* in Plate 4F to *Parasaurolophus* in Plate 4B). The dorsal margin is curved in the typical hadrosaurian fashion.

A second type of ilium is exemplified by *Edmontosaurus* (Plate 4A) and *Anatotitan*. In these genera, the ilium is greatly elongated and not relatively as high as in other genera, which results in a L/H ratio that is greater than in any other iliac type. In lateral view, the ilium is thin and greatly elongated, in contrast to the more robust appearance of a form such as that in *Parasaurolophus*. The postacetabular process also has the greatest L/H ratio of any clade. The body is relatively shallow and the antitrochanter, although well developed, is not as large, nor does it project as far laterally as in the other clades. An excellent example is *Edmontosaurus annectens* (DMNH 1493, Plate 4A).

Kritosaurus defines the third type of ilium (Plate 4C).

This is similar in appearance to the second type of ilium in lateral view but the distinctive features here are the relatively higher body (height) and the markedly ventral deflection of the preacetabular process. This deflection is more pronounced than in any other clade. The postacetabular process also appears to be deflected dorsally, giving the overall aspect of the ilium in this clade an accentuated 'sigmoidal' curve. This feature is unique to this clade.

A fourth type of ilium is exemplified by Corythosaurus and Saurolophus (Plate 4D). In this type the L/H ratio is smaller than that of the previous types (see Tables 3 and 5). The preacetabular process is usually more ventrally deflected as in the Kritosaurus clade. The postacetabular process has a smaller L/H ratio than in any other hadrosaurine clade. The antitrochanter is large and prominent and projects farther laterally than in other hadrosaurines.

The fifth type of ilium is represented by Parasaurolophus (Plate 4B). As in the previous type, the preacetabular process is strongly deflected ventrally, but it is thicker and wider than in all other clades. The body is the deepest (measured dorso-ventrally) of any lineage and the postacetabular process has the smallest L/H ratio of any lineage. The antitrochanter is relatively more massive and extends farther laterally than in any other clade. The range of variation of this process is exceptional due to its size. In the type of Parasaurolophus cyrtocristatus (FMNH P27393), the antitrochanter on one ilium reaches from the dorsal rim of the ilium to the dorsal rim of the ischial peduncle. On the other ilium, it covers the entire side of the element and descends to the ventral part of the ischial peduncle.

In summary, as one compares iliac types two through five, the ilium becomes progressively more massive. The L/H ratio of the element as a whole decreases while the antitrochanter and the postacetabular process increase in robustness. This is a consequence of an increase in the relative and absolute size of the antitrochanter. The result is increased surface area for the attachment and size of the m. ilio-tibialis, m. ilio- femoralis, and m. caudifemoralis externus muscle complexes in the lambeosaurines. This would make the legs more powerful than those of the relatively longer limbed hadrosaurines, but does not imply greater speed.

Plate 5

A) Pubis of **Parasaurolophus cyrtocristatus**, a lambeosaurine, based on FMNH P27393. Length of the pre-pubic blade is 430mm.

B) Pubis of **Corythosaurus casuarius**, a lambeosaurine, based on AMNH 5240. Length is 490mm.

C) Pubis of **Prosaurolophus maximus**, a hadrosaurine, based on ROM 787. Length is 533mm.

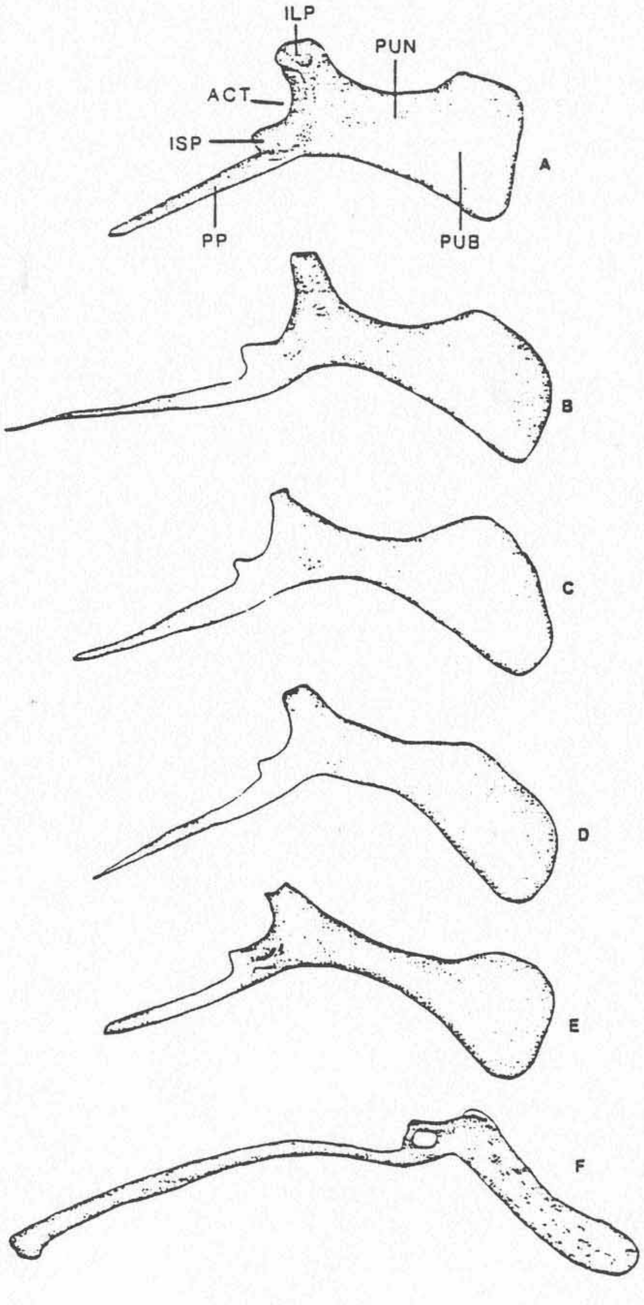
D) Pubis of **Kritosaurus incurvimanus** , a hadrosaurine, based on ROM 764. Length is 534mm.

E) Pubis of **Edmontosaurus annectens**, a hadrosaurine, based on DMNH 1493. Length is 630mm.

F) Pubis of **Camptosaurus medius**, an iguanodontid, based on YPM 1880. Length is 336mm.

All drawings by D.A. Lawson from photos and under my direction.

All figures are right pubes in lateral view.



There are also several differences in the ilium that may be of diagnostic value at the subfamilial level.

TABLE 1

THE HADROSAURID ILIUM

<u>Hadrosaurines</u>	<u>Lambeosaurines</u>
Preacetabular process relatively less deflected ventrally (average=32 degrees)	Relatively more deflected ventrally (average=42)
L/H ratio of ilium averages 5.41 (Standard deviation =0.5)	Ratio averages 4.43 (SD=0.5)
Postacetabular process L/H ratio averages 2.46 (SD=0.14)	Ratio averages 1.88 (SD=0.25)
Iliotibialis process rarely extends to meet the peduncle.	Often extends to meet ischialischial peduncle. peduncle.
Ischial and pubic peduncles less robust.	Relatively more robust.

Characters that could be attributed to growth were surprisingly few in number considering the diversity of forms. The ilium maintains its general shape and dimensions throughout life. Juveniles can be recognized only by their absolute size. In some large, and presumably very old individuals, however, the internal shelf for the articulation with the sacral vertebrae becomes much thicker and progressively moves forward onto the preacetabular process. The dorsal rim also becomes much thicker (USNM 4278). This may be due to the increase in calcium deposition resulting in a more massive element, with features that mimic other taxa.

PUBIS

The pubis (Plate 5, Tables 2,3,4 and 5) is divided into 3 portions. The most posterior section contains the postpubic process (PP) which extends postero- ventrally along the ventral margin of the ischium. It is rod-like and often vestigial. The middle section forms the acetabular margin (ACT) with the posteriorly projecting ischial peduncle (ISP) and the dorsally projecting iliac peduncle (ILP). The most anterior portion is the prepubic process, comprising a 'neck' (PUN) and 'blade' [(PUB), Plate 5A].

There are five different pubic morphologies (Plate 5) corresponding to five clades. The first type is exemplified by Edmontosaurus (Plate 5E) and also by the stratigraphically earliest hadrosaurine, Gilmoreosaurus. The neck is relatively longer and thinner than in other clades. The blade is symmetrically expanded in most cases with a slight emphasis to the dorsal side. The surface area of the blade (in lateral view) is relatively the smallest of any clade.

Kritosaurus characterizes the second type of pubis (Plate 5D). This type is notable for having a blade with parallel dorsal and ventral borders. The prepubic part of this element is strongly deflected ventrally. The neck is relatively shorter and wider than in Edmontosaurus.

The third type is typified by Saurolophus (Plate 5C). The blade contains a dorsally projecting asymmetrical bulge which gives this portion an overall triangular shape in lateral view. The anterior border projects sharply in the ventral direction. The tip is well rounded, grading gradually into the ventral border which is straight. The neck is relatively shorter and wider than in other hadrosaurines.

Corythosaurus represents the fourth type of pubis (Plate 5B). The blade closely resembles that of Saurolophus but the dorsally projecting bulge is more flattened, giving this portion of the element a more trapezoidal aspect in lateral view rather than a triangular one. The dorsal border is deflected ventrally but not as abruptly as in Saurolophus. The dorsal and ventral borders are sub-parallel, almost as in Kritosaurus, but the blade is relatively much shorter. The anterior border is well rounded and longer than in the other clades and the neck is shorter and wider.

Parasaurolophus and Bactrosaurus represent the fifth type of pubis (Plate 5A). In this type, the blade is relatively

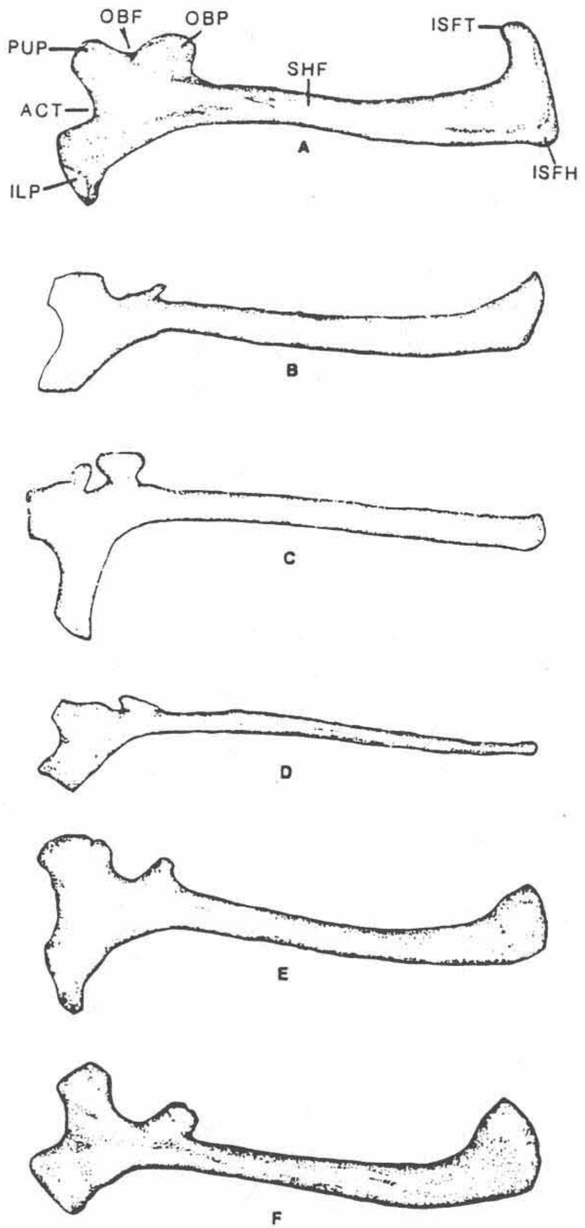


Plate 6

A) Ischium of **Parasaurolophus cyrtocristatus,** a lambeosaurine, based on FMNH P27393. Length is 1078mm.

B) Ischium of **Corythosaurus casuarius,** a lambeosaurine, based on AMNH 5240. Length is 1030mm.

C) Ischium of **Shantungosaurus giganteus,** a hadrosaurine, redrawn from Hu 1973, figure 5. Length is 1602mm.

D) Ischium of **Anatotitan copei,** a hadrosaurine, based on AMNH 5730. Length is 1160mm.

E) Ischium of **Gilmoreosaurus mongoliensis,** a hadrosaurine, based on AMNH 6551. Length is 718mm.

F) Ischium of **Camptosaurus dispar,** an iguanodontoid, based on YPM 1878. Length is 553mm.

Drawings by D.A. Lawson from photographs and under my direction. All figures are right ischia in lateral view (inverted).

shorter and wider than in other clades. In lateral view, the blade resembles a rectangle with the longer axis of the rectangle oriented vertically. The dorsal and ventral borders are sub-parallel in most cases. The anterior border is perpendicular to the dorsal and ventral borders and is relatively longer than in the Corythosaurus-like pubis. The neck is very short and relatively wider than in other clades giving it a robust appearance. One difference that is unique to this clade is the massiveness of the iliac peduncle. The contact is deep, cup-like and well rounded. In other clades, the iliac peduncle is long and thin with a shallow cup. Parasaurolophus cyrtocristatus (FMNH P27393) displays a large ridge which runs from the iliac peduncle to the ischial peduncle. This ridge is not as well developed as in the other genera. The type of Parasaurolophus walkeri is notable in having a pathological fusion of the pubis and ilium at the pubic peduncle.

In summary, as one compares pubic types one through five, the pubis increases in robustness by increasing the surface area of the blade and enlarging the attachment with the prepubic neck by increasing its width and decreasing its length. The most gracile forms (the edmontosaurs) have the most elongate prepubis compared to animals of comparable size in other clades. The most robust forms (the parasaurolophs) have the shortest prepubis. Analysis of a large sample of pubes failed to turn up any forms where the pubis of a given genus more closely resembled the pubis of another clade. In this regard, the pubis proved to be of equal, if not superior, value to the ilium in the diagnosis of clades.

Juveniles have pubes with the same morphology as the adults. It is remarkable that hadrosaurids show such a uniformity of pattern throughout the ontogeny of the individual. The postpubis, due to its lack of distinctive features and rare preservation, proved to be of no value for the diagnosis of genera.

It is proposed here that the pubis acted mainly for abdominal support and as a site for the origin of the m. rectus abdominis complex, which was probaly used in respiration. It is known that crocodiles use their m. rectus abdominis to push the liver into the lungs as a 'pseudodiaphragm' (Pooley and Gans, 1976). I expect that as the size of the narial apparatus grew in complexity, the need for powerful muscles to force air through these convoluted hadrosaurid pathways would increase. This would be reflected in the increased size of the m. rectus abdominis and its origin on the prepubis. This is exactly what is found in hadrosaurids. There is a high correlation between the complexity of the narial structures and the size and robustness of the prepubic blade and neck. The *Parasaurolophus* clade has the most complex nares and it is here that the prepubic blade is the thickest, shortest, and widest. The orientation of the blade is directly in line with the ribcage so the force on the prepubis is transmitted along its longitudinal axis, thereby minimizing lateral components of force. The lateral forces that exist as a result of the actions of the ambiens and the pubo-ischio-femoralis externus muscles are braced by the sacral ribs and cartilage (Maryanska and Osmolska 1981).

Plate 7

A) Left lateral view of the fibula, tibia, and calcaneum of **Camptosaurus nanus,** an iguanodontoid, based on USNM 2210. Distal end width of tibia is 79mm. Distal end width of fibula is 26mm.

B) Lateral and anterior views of the fibula, tibia, and calcaneum of **Anatotitan copei,** a hadrosaurine, based on AMNH 5730. Width of astragalus is 174mm. B1 is a left lateral view - B2 is a left anterior view.

C) Left lateral view of the tibia and fibula of **Lambeosaurus lambei,** a lambeosaurine, based on ROM 1218. Calcaneum not preserved in this mounted specimen on display at the ROM. Depth (antero-posteriorly) of calcaneum is 51mm.

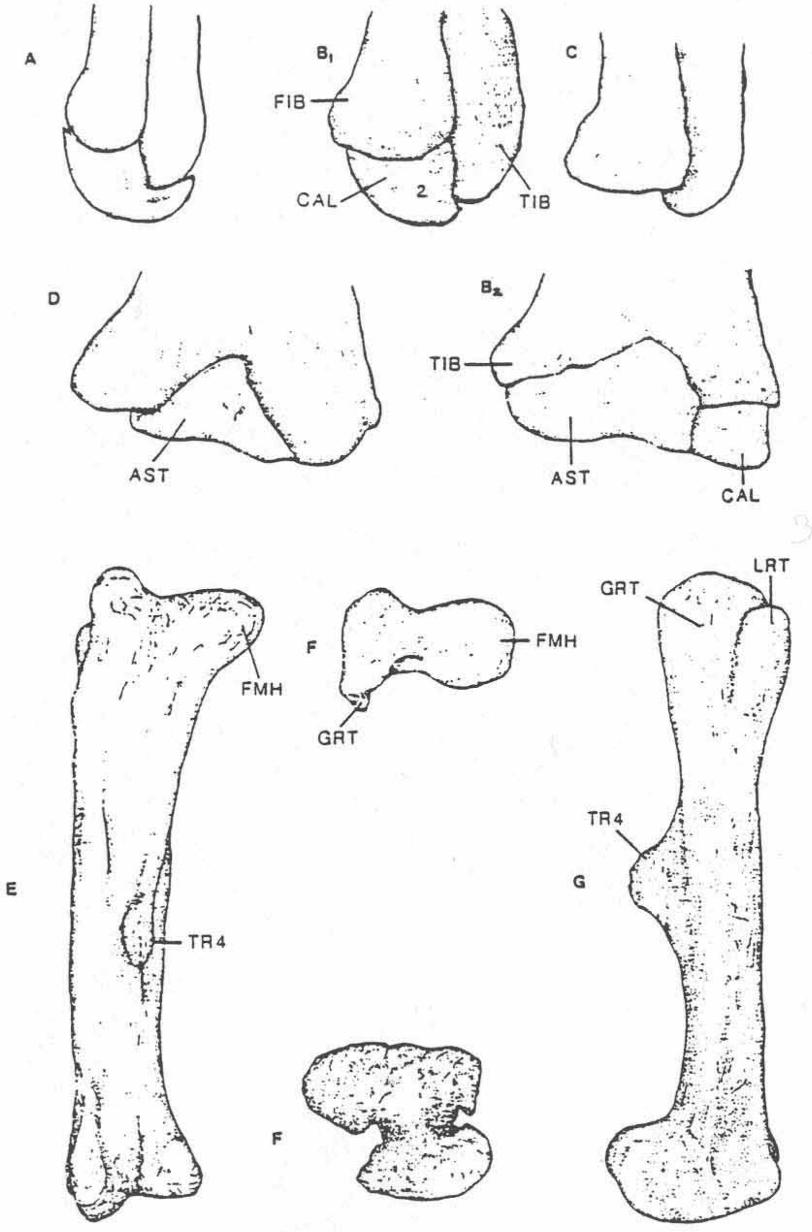
D) Left anterior view of the astragalus and tibia of **Parasaurolophus cyrtocristatus,** a lambeosaurine, based on FMNH P27393. The calcaneum may be lost in the **Parasaurolophus** clade (Brett-Surman, 1975).
Width of the astragalus is 165mm.

E) Posterior view of the femur of **Anatotitan copei,** a hadrosaurine, based on AMNH 5730. Femur length is 1135mm.

F) Proximal (labelled) and distal (unlabelled) view of the femur of **Gilmoreosaurus mongoliensis,** a hadrosaurine, based on AMNH 6551.

G) Lateral view of the femur of **Corythosaurus casuarius,** a lambeosaurine, based on CM 9461. Length is 760mm.

Drawings from my photos by D.A. Lawson under my direction.



ISCHIUM

The ischium projects at a forty-five degree angle postero-ventrally from the acetabulum and is composed of three portions. The most proximal portion contains the acetabulum (ACT), the iliac (ILP) and pubic (PUP) peduncles, and the frequently damaged obturator process (OBP) and fenestra (OBF). The middle portion contains the ischial shaft (SHF) which is columnar and featureless. The most distal portion contains the terminal knob or 'foot' (Plate 6E), composed of the 'heel' (ISFH) and 'toe' [(ISFT), Plate 6A)].

Four types of ischia can be recognized. Three are represented by late Cretaceous forms. The first type is exemplified by Gilmoreosaurus (Plate 6E) and displays an intermediate morphology between iguanodontids (Norman 1980) and hadrosaurines. In this type, the obturator notch is open in adults as it is in the iguanodontids. The shaft is relatively more decurved than in other hadrosaurids, but the degree of curvature is less than that of most iguanodontids. Distally, the shaft terminates in a rounded knob that protrudes asymmetrically to the ventral side.

The second type of ischium is represented by the hadrosaurines, the best example of which is Anatotitan copei (Plate 6D). In this type, the relative size of the peduncles is considerably reduced in most forms. The obturator notch is open except in old adults. The shaft is long, straight, and relatively thinner than in any other type of ischium. The distal end usually tapers to a rounded point. A knob is rarely present. If present, however, it is rudimentary and always considerably smaller than in other types.

Corythosaurus and Lambeosaurus exemplify the third type of ischium (Plate 6B). In this type, the pubic and ischial peduncles are equal in size or the iliac peduncle is slightly larger. The shaft is long, straight, and generally much thicker than in hadrosaurines of the same size. Posteriorly, the diameter of the shaft gradually increases distally where it terminates in an abrupt expansion into a structure resembling a 'foot' in lateral view. This expansion is totally in a ventral direction when the ischium is viewed laterally in natural articulation. There is no 'heel' but there is a slight tapering of the foot at the 'toes' (see Plate 6A). An example is Lambeosaurus lambei (ROM 1218).

The fourth type of ischium is represented by Hypacrosaurus and Parasaurolophus (Plate 6A). This type is most distinctive for its robustness. All landmarks previously cited are relatively larger in size and thicker than in any other type of ischium. The iliac peduncle displays a prominent 'lip' that projects posteriorly on its articular surface. The pubic peduncle is a large roughened process with a broad articulation. The obturator notch is closed in adults, but this area is frequently damaged during fossilization, breaking open the margin of the obturator notch and creating the impression that it is normally open. The shaft is long, straight, and does not increase in diameter for the proximal half of its length. The distal half gradually increases in diameter until the distal end where there is an abrupt expansion into a large foot-like process that is up to 50% larger than in the other forms displaying this structure. This foot has a distinctive 'heel' (ISFH) and 'toes' [(ISFT), Plate 6A)], and relative to other forms is more prominent, massive, and projects farther posteriorly. A ridge runs from the pubic peduncle, across the shaft to the posterior side and continuing onto the foot. This ridge has not been noted in other ischial types, but it may be a growth feature rather than a generic characteristic.

One growth feature is noticeable in the ischium. The distally enlarged knob or 'foot' is ontogenetically variable. Excellent examples demonstrating this fact are present in the Two Medicine faunal collection (Campanian) housed in the U.S. National Museum (lot number USNM 358593). In this fauna, as well as the Iren Dabasu fauna (e.g. specimens of Bactrosaurus and Gilmoreosaurus housed at the AMNH), there are three size or age groups. The first may be termed hatchlings. These are animals of hindlimb length less than one foot. The second age group may be called juveniles and have a hindlimb length of one to three feet. The adult age group consists of the largest animals. There is no indication of an ischial foot in any of the hatchlings. The juveniles have a distal enlargement that is not quite a 'foot' but definitely too large to be from a hadrosaurine. The true "foot" appears suddenly in this group - within the time it takes the ischium to grow another two inches in length (USNM lot number 358593). Perhaps this signals the attainment of sexual maturity. This is the only major growth feature I have seen in an appendicular element that appears after the hatchling stage.

It is noteworthy that only pelvic elements have clearcut characteristics which can be of diagnostic value to the level of subfamily and clade. All other postcranial elements display either a complete intergradation of form with only the extremes exhibiting subfamilial features (such as the humerus as discussed above), or the postcrania are too similar in all the genera to be of taxonomic use.

THE HINDLIMB

FEMUR

The femur (Plate 7, Tables 2,3,4 and 5) is a long, cylindrical element. The head of the femur (FMH) is cylindrical and relatively larger than in other ornithopods. The greater trochanter (GRT) is massive and covers the entire lateral aspect of the proximal part of the femur when seen in lateral view. The lesser trochanter (LRT) is relatively much smaller and often fuses to the greater trochanter in old adults (Plate 7G). The greater and lesser trochanters are usually separated from each other by a small cleft. The shaft of the femur is straight and circular in cross-section, with the fourth trochanter (TR4) lying at the midpoint. The distal condyles are larger and more robust than in any ornithopod clade and project posteriorly. The anterior condyles may fuse to form an anterior condylar canal in old adults (USNM 7582, 7948).

The lesser trochanter (LRT) displays considerable variation in size, orientation, and degree of fusion to the greater trochanter (GRT). This is due to individual variation, for virtually every skeleton examined shows differences between the right and left sides of the animal. Variability of the lesser trochanter thus is of no value in the diagnosis of species.

Individual variation is manifest in the hadrosaurian femora but the general morphology is identical in all clades (Plate 7). The two stratigraphically earliest hadrosaurids, Gilmoreosaurus and Bactrosaurus, are typically hadrosaurian in design and do not display any features intermediate between hadrosaurids and the ancestral iguanodontids. Femora are known for all genera except Brachylophosaurus and Secernosaurus. No ontogenetic features were observed.

TIBIA

The tibia (Plate 7, Tables 2,3,4 and 5) is long and straight with a larger cnemial crest than in other ornithopods. The distal end of the tibia (TIB) conforms ventrally to the shape of the astragalus (AST), which fits cup-like onto the tibia and is concave upwards.

No variation was observed between the genera of hadrosaurids.

ASTRAGALUS

The astragalus (AST) of hadrosaurids (Plate 7D) is similar to the iguanodontids (fide Norman 1980) but has a relatively higher anterior ascending process.

In the hadrosaurids, two types of astragali were observed. The first type (Plate 7B) is represented by all the genera except Parasaurolophus. In this type, the astragalus is triangular in shape when viewed anteriorly, but skewed laterally into a 25-50-105 degree configuration rather than the equilateral shape of Parasaurolophus. The outer malleolus of the tibia is relatively smaller and less rugose in this type.

The second type (Plate 7D) is represented solely by Parasaurolophus. In this type, the astragalus is triangular in shape when viewed anteriorly. It is much reduced in size and thickness compared to other astragali in animals of similar dimensions, and does not extend as far medially under the inner malleolus. To compensate for the reduced astragalus, the inner malleolus of the tibia is relatively more rugose and expanded than in the other genera. This increase is related to the possible loss of the calcaneum in Parasaurolophus as discussed below.

Small, presumably juvenile, specimens of hadrosaurines and lambeosaurines, especially Corythosaurus, with tibiae 60 cm or less in length, tend to have astragali resembling the first type but with a more triangular ascending process. Except in Parasaurolophus, the astragali of larger individuals enlarge and expand medially. This suggests that the form of the astragalus changes with growth. The sample size is too small at this time for any definitive conclusions.

FIBULA

The fibula (Plate 7B) is extremely similar to that of iguanodontids (fide Norman 1980). It is long and straight. The proximal end forms a concave cup that receives the lateral projections of the proximal tibial crest. The distal end of the fibula (FIB) is expanded into a knob which sits in the dorsally projecting cup of the calcaneum.

Two morphs were observed. The first morph (Plate 7B) is typified by all genera except Parasaurolophus. In this type, the distal end of the fibula is moderately expanded into the shape of a ball.

The second morph (Plate 7C) is represented by Parasaurolophus. In this type, the distal end is relatively greatly expanded compared to all other hadrosaurids. The calcaneum is unknown in Parasaurolophus, in which the greatly enlarged fibula may compensate for the lack of this element.

CALCANEUM

The calcaneum [Plate 7B, (CAL)] is shaped like a quarter section of a circle. The arc of the circle forms the articulation for the metatarsals and faces anteriorly in natural position. The two radii marking this quarter section form two cups, one facing proximally to receive the fibula and one facing posteriorly to receive the tibia.

The calcaneum is small and does not extend ventro-posteriorly beneath the tibia all the way to the posterior side. The distal end of the tibia fits in a slight concavity on the posterior side of the calcaneum. In Camptosaurus (USNM 4282), the calcaneum forms the entire surface of articulation for the distal tarsals on the lateral side. In hadrosaurids (of type 1), the calcaneum and the posterior side of the tibia both articulate with the distal tarsals on the lateral side. The astragalus is notched on the lateral side to receive a peg-like process from the calcaneum. This is the opposite of what has been reported elsewhere for ornithopods (Chatterjee, 1982).

The loss of the calcaneum deserves comment. The enlarged knob at the distal end of the fibula may represent the fusion of the calcaneum to the fibula. The calcaneum may also have failed to ossify and the fibula has enlarged to compensate for its loss. Because the sample is based only on the type of Parasaurolophus cyrtocristatus, there is a distinct possibility that the calcaneum simply was not fossilized. This is doubtful due to the lack of space for the calcaneum to occupy and the absense of any articular feature on the astragalus.

METATARSALS

The metatarsals (Plate 3C,D, Tables 2,3,4 and 5) of all hadrosaurids resemble one another closely. No consistent variation was observed among the genera, however, the sample size for complete and articulated metatarsals is insufficient at this time for any definitive statement.

PHALANGES

In hadrosaurids, the pedal phalanges (Plate 3) are of similar shape except in *Gilmoreosaurus* where the unguals are more claw-like and therefore similar to the iguanodontid pattern. This is peculiar in light of the fact that *Bactrosaurus johnsoni*, a species sympatric with *Gilmoreosaurus*, has typical hadrosaurian phalanges with more hoof-like unguals (UNG).

The most proximal row of phalanges are longer (proximo-distally) than wide (latero-medially). The reverse condition is true for all other phalanges of the pes. The proximal row is noticeably larger and more robust than the more distal rows. The general phalangeal formula is 0,3,4,5,0(?). See Gregory (1948) for a discussion of whether the fifth digit is present. For this report, the lack of any material unquestionably articulated and possessing a fifth digit requires that the fifth digit be regarded as absent.

Remarks on the Pes

Although it appears that the pes is not diagnostic to subfamilial level, differences have been noted (Brown, 1913). In a comparison of the types of *"Diclonius mirabilis"* (=*Anatotitan*) and *Hypacrosaurus*, Brown, (1913, figure 7) observed that the hadrosaurine pes has relatively less robust metatarsals but wider, flatter and sometimes longer phalanges. Lambeosaurines, in contrast, have relatively more robust metatarsals but less robust phalanges. This results in a hadrosaurine foot that is shorter and wider than the more elongated lambeosaurine foot. Perhaps they represent an adaptation of the hadrosaurines to their more heavily overgrown lowland environments, in contrast to the more open lambeosaurine environments where cursorial abilities would be at a premium.

CHAPTER 3

A REVIEW OF CRANIAL FEATURES PREVIOUSLY USED IN THE DIAGNOSIS OF HADROSAURIAN DINOSAURS

Before a new diagnosis of the hadrosaurian clades can be made, based on the postcranial studies presented here, the cranial (and postcranial) features previously cited in the literature and used to diagnose genera must be reviewed. The following discussion evaluates each character with regard to growth, sexual differences, and populational variation where it can be determined.

The predominance of cranial characters in delineating genera has a long history (see Lull and Wright 1942, Ostrom 1961 and references therein). The most notable works are by the Canadian paleontologists Lambe (1914, 1917A,B, 1920), Parks (1920, 1922, 1923, 1924), and C.M. Sternberg (1926, 1935).

PREVIOUSLY CITED CRANIAL CHARACTERS

1) Size: Absolute size has been used for many years, especially in the comparison between the "procheneosaurs" and other lambeosaurines such as *Corythosaurus* and *Lambeosaurus*. Many of the characters discussed in the literature relate to absolute size as measured in skull length or height. Absolute skull size cannot be used to separate "procheneosaurs" from "cheneosaurs" because a new skull of *"Procheneosaurus"* (TMP 78.16.1) is almost twice as long as skulls referred to *"Cheneosaurus"* and *Corythosaurus*. In Lull and Wright's revision (1942), the relatively smaller skulls of *"Trachodon"*, *Diclonius*, *Claosaurus*, and *Thespesius*, originally placed in separate species, were all placed in species of *Anatosaurus* (except for *A. copei*) and the largest skulls were placed in species of *Edmontosaurus*. This ontogenetic growth feature must be abandoned as a taxonomic character because of its lack of consistency within any clade.

2) The traditionally and frequently cited lack of a crest as a difference between "procheneosaurs" and "cheneosaurs" has been refuted by Dodson (1975), using morphometric techniques.

These two clades have also been separated according to stratigraphic occurrence with the "procheneosaurs" occurring in geologically older beds (Lull and Wright 1942). This criterion of stratigraphic occurrence must be abandoned in favor of strictly defined morphological features. The presence/absence of hollow crests in other taxa are diagnostic as discussed below.

3) The relative cranial width, length, and height are parameters often used but hard to quantify (see Lull and Wright 1942 for diagnosing _Edmontosaurus_ versus _Anatosaurus_). Length is traditionally measured as the distance between the anterior tip of the premaxilla and the back of the paroccipital process; height is traditionally measured from the ventral tip of the quadrate to the most dorsal extension of the cranium; and width is generally measured at the point of maximum breadth whether it lies at the muzzle or across the jugal area. The length/height ratio has some value in the comparison between _Edmontosaurus_ (L/H = 1.5) and _Anatotitan_ (L/H = 3.0, Plates 8 and 10), but no absolute boundaries can be drawn because these ratios converge in hatchlings (see Horner and Makela 1979 for pictures of a _Maiasaura_ hatchling and adult skull). This causes problems because the converging nature of ratios precludes the use of dichotomous characters such as the presence/absence of unique/derived features. Skulls are always taller in the Lambeosaurinae (fide Langston 1960) because of the crests that project above the frontals and parietals (the traditional skull roof bones). The degree of crushing and deformation can alter the length/height ratio in closely related genera such as _Edmontosaurus_ and _Shantungosaurus_. Consistency in the measurement of this ratio can best be attained by measuring skull height as quadrate height, thereby eliminating the lambeosaurine crest and restricting height measurements to homologous bones in all clades. This ratio, as previously used, is more a measure of individual age, because the muzzle undergoes elongation after hatching. In the crestless genera, the skulls become longer and undergo a relative decrease in height. This not true for crested genera, in which skull height dramatically increases because of the crest, while skull length stays relatively the same. The almost complete overlap of ratios in closely related genera obviates the use of this feature.

4) A hollow vs. a solid crest is the most often cited character to distinguish the two main subfamilies (fide Langston 1960) of hadrosaurids. This feature is dichotomous, with no known intermediate conditions to blur the rigid separation of characters. It has shown its consistency in all hadrosaurid adults of Campanian and Maastrichtian age. It must be stressed,

however, that only adults can be used because juveniles lack a fully formed crest (Dodson 1975).

5) A crest most highly developed over the eye or more forwardly inclined: this feature has been used by Sternberg (1953) and more recently and quantitatively by Dodson (1975). At the time of this writing, only Corythosaurus and Lambeosaurus can be separated using this character, and it has proven to be consistent.

6) The presence of a posterior spur on the crest of certain lambeosaurines is another condition that is consistent and absolute but of limited application. Only Lambeosaurus possesses it, which indicates that it is the more derived genus compared to the most morphologically similar taxon Corythosaurus.

7) Frontal doming was noted by Langston (1960) but was not considered significant. Sternberg (1935) had previously noted its appearance and used it to distinguish the "Procheneosauridae" (fide Lull and wright 1942), but it now appears to be a growth feature in the Lambeosaurinae (Langston 1960).

8) The presence/absence of a sutural contact between the parietals and squamosals has been cited as useful in distinguishing Edmontosaurus from Anatosaurus by Lull and Wright (1942), but no one has used it since. Any large sample of adult skulls shows this feature to be variable within populations, and it occurs at irregular intervals in an ontogenetic series in species of Edmontosaurus (E. annectens versus E. regalis, NMC specimens). It should therefore be abandoned in taxonomic use.

9) The number of tooth rows is a condition of which the taxonomic utility is still debated. The studies of Russell (pers. comm.) and Dong (1979) indicate that it is useful to delineate species, but my work and that of Sternberg (1936) indicate that it is not valid at any taxonomic level. It can be seen that the number of tooth rows of newly hatched hadrosaurids starts at about 9 and increases constantly throughout life up to 64, as reported in a 1.17 meter long skull of "Anatosaurus" copei (Lull and Wright 1942). The number of tooth rows may one day serve as an excellent indicator of age, if the rate of increase of rows can be shown to be consistent, but it must be abandoned in taxonomy.

10) Tooth length/depth ratio was originally cited by Sternberg (1936) to separate the two subfamilies of hadrosaurids

that he recognized, and has been verified by Horner (in prep.). The root and enamelled face form an obtuse angle in the Hadrosaurinae and are parallel in the Lambeosaurinae. Sternberg's study was based on the dentary teeth, but I have observed that the dentary teeth change in size and shape during ontogeny, and their shape also changes from front to back in the jaw. It is not clear, based on Sternberg's paper (1936), if the angle of the root and enamelled face is accurate for all dentary teeth or whether it only applies to certain dentary teeth from a specific age group. A full comparison must be made between the maxillary and dentary teeth for a full growth series in all clades. This feature should not be used until it has been more thoroughly tested.

11) The primary ridge on the tooth crown is a feature that gradually varies over geologic time. The iguanodontid tooth (representing the ancestral or plesiomorphic condition in <u>Iguanodon</u> or <u>Kangnasaurus</u>) has one or two large ridges with many large papillae along the lateral edges of the teeth. In the transition to hadrosaurids, the laterally placed papillae become smaller and more numerous, and only one large medially placed ridge remains. For Campanian and Maastrichtian genera, this condition is uniform and not useful in delineating taxa, though Horner disagrees (in prep.).

12) Rounded vs. pointed tooth apex is another character that is contentious among hadrosaurid specialists. The teeth of early Campanian hadrosaurids have more rounded apices, a primitive condition that is also present in the Iguanodontidae (see Norman 1980). The point of contention is whether or not this feature is present and/or diagnostic at the supra-generic level. Horner (pers. comm., 1987) believes that hadrosaurid teeth may be diagnostic at the generic level, but I remain skeptical. Rounded apices are found in all clades and are also more common in pre-Maastrichtian deposits. This feature should not be used until the publication of Horner's work, and until it can be shown to be useful in both worn and unworn teeth.

13) The number of papillae per 10 mm on the tooth margin has been used in the past to diagnose hadrosaurids. With increasing age, the number of papillae increases along the lateral edge of the crown as the absolute size of the tooth increases. Until Horner's systematic studies on hadrosaurid teeth are published, this feature should not be used in taxonomy.

14) The folding of the premaxillary area of the external nares into 'pockets' (Plate 8) must be considered separately

from the expansion of the premaxilla, which so easily separates the crested genera from the non-crested genera. As can be seen in Edmontosaurus (USNM 12711), the anterior region of the premaxilla (which is not expanded into a crest), is divided into 3 major and several minor pockets which Osmolska (1979) believes housed salt glands and/or expanded Jacobson's organs. These pockets are seen only in the genera Edmontosaurus (USNM 12711), Anatotitan (AMNH 5730), and Shantungosaurus (Hu 1973). This is a complex, derived character that is taxonomically consistent within a clade.

15) The relative length of the edentulous portion of the mandible seems to vary greatly between the two subfamilies (fide Langston 1960). In the hadrosaurines, the edentulous portion of the mandible generally equals or exceeds the length of the tooth row (Anatotitan). In the lambeosaurines, the tooth row exceeds the edentulous portion in length regardless of whether or not the anterior portion of the mandible is deflected (as in Parasaurolophus). This, of course, applies only to adults. In hatchling hadrosaurids, the edentulous portion is minimal because the muzzle has not yet become elongate. Anatotitan shows the relatively greatest elongation of the edentulous portion, more so than in any other genus (Plate 10). In Kritosaurus (Plate 14), the elongation is less developed and in Saurolophus (Plate 17A) the condition is more like that of the crested genera. This elongation of the muzzle area is evidently for increased efficiency of food gathering. The different muzzle lengths in each clade may be indicative of resource partitioning, but this is speculative. Presence or absence of this feature appears to be of diagnostic value at the level of subfamily (fide Langston 1960).

16) The degree of ventral deflection of the anterior part of the mandible is quite evident in crested forms such as Lambeosaurus lambei (NMC 2869) and absent or slightly developed in the non-crested forms such as Kritosaurus navajovius (AMNH 5799). This is another feature that appears to be useful to delineate subfamilies (fide Langston 1960), but a more complete study is needed of the rare genera Saurolophus and Prosaurolophus, which are the two most lambeosaurine-like hadrosaurines.

17) The presence of an internarial septum, as seen in lateral view, is an important feature that seems to have gone unnoticed, even by Lull and Wright (1942) where their figures of the skull outlines show this most clearly. In the Hadrosaurinae (Plate 10), the external nares lack an internarial septum, so that one can see through the skull in lateral view.

Edmontosaurus and Kritosaurus show this equally well but in Saurolophus the internarial septum is more similar to that of the Lambeosaurinae. In the Lambeosaurinae (Corythosaurus, Appendix 5), the left and right external nares are separated by an internarial septum, therefore one cannot see through the skull in lateral view. The presence/absence of this feature is most consistent at the subfamilial level. The degree of separation by the internarial septum, however, is too variable to be used below the level of subfamily.

18) The presence/absence of a sutural contact between the maxillaries and the lacrimals shows remarkable variability from a complete contact (Corythosaurus casuarius adult, AMNH 5249) to no contact (C. casuarius juvenile, ROM 870). This feature appears to be consistent in some genera, but a contact can be present internally and not be visible externally. Most skulls are not prepared internally and it is probable that many useful characters remain undiscovered.

Hadrosaurid skulls show tremendous allometry during ontogeny, especially in the muzzle region. Contacts between bones in this area may be as variable as the number of tooth rows during ontogeny.

19) Maxillary symmetry has been cited by Gilmore (1933) and verified by Weishampel and Horner (1986). In the Hadrosaurinae, the maxilla forms an equilateral triangle in lateral view, while in the Lambeosaurinae the apex of the triangle is skewed posteriorly. To date, no exceptions have appeared, so this feature is a valid character to use at the level of subfamiliy.

20) The presence/absence of a maxillary groove on the dorsal surface of the maxilla [for a sliding, kinetic contact with the premaxilla (Weishampel and Horner, 1986)], is present in the Lambeosaurinae but absent in the Hadrosaurinae.

21) The presence of reflected premaxillary borders [(RPL), Plate 8] is consistent and invariable in the Lambeosaurinae, but varies in the Hadrosaurinae. The primitive or iguanodontid condition (Norman 1980) is the absence of a folded anterior premaxillary border, and this is also seen in the more derived Lambeosaurinae. Apparently the strong reflection of the premaxillary border into a lip-like structure is a derived feature in the Hadrosaurinae (Plate 8). It may have been secondarily lost in the Lambeosaurinae (Appendix 5, Plate 16A) or, as Horner proposes (Horner, 1985), it may indicate that the Lambeosaurinae have an independent origin from

the Iguanodontidae, implying a diphyletic origin for the hadrosaurids. This topic is treated in more detail below. In the Hadrosaurinae, the 'lips' are largest in Edmontosaurus (Plate 8), smaller in Kritosaurus (Plate 14), and smallest in Saurolophus (Plate 17A) where the condition is identical to that of lambeosaurines. The presence of a reflected border can be used to delineate only Kritosaurus-like and Edmontosaurus-like hadrosaurids.

22) The presence of a postorbital pocket [(POEP), Plate 8] is a condition seen only in Edmontosaurus (Plate 8), Anatotitan (Plate 10), and in Shantungosaurus (Hu, 1973). This pocket may have housed an enlarged salt gland (Osmolska, 1979), reflecting restriction of edmontosaurs to mostly lowland areas where brackish conditions prevailed. The postorbital pocket is a synapomrphy for all three genera. Its presence is a taxonomically useful feature to separate these edmontosaurs from the other hadrosaurids.

23) The shape of the quadrate is one of the features commonly cited as being 'more curved' in the Lambeosaurinae and 'less curved' in the Hadrosaurinae. Curvature is usually restricted to the proximal one-fifth of the quadrate, but forms with short quadrates such as Anatotitan (Plate 10, Hadrosaurinae) and Parasaurolophus (Plate 16A, Lambeosaurinae) show a consistent anterior- convex curvature throughout. It is impossible to quantify this curvature in any consistent or meaningful manner. With time, and a larger sample, this character may have taxonomic value but I do not find it to be of any taxonomic utility at present.

A) In summary, the following cranial features traditionally used to diagnose hadrosaurid genera are found to be of little or no taxonomic utility:

1) absolute size

2) presence/absence of crests in "procheneosaurs"

3) cranial length/heigth ratio

4) presence/absence of frontal doming

5) presence/absence of a parietal-squamosal suture

6) number of tooth rows

7) presence/absence of medial ridge on tooth

8) rounded vs. pointed tooth apex

9) number of papillae per tooth

10) degree of anterior ventral mandibular deflection

11) presence/absence of lacrimal-maxillary suture

12) the shape of the quadrate

B1) The following cranial features traditionally used are confirmed to be of taxonomic utility at the level of subfamily (fide Langston 1960):

15) presence/absence of a hollow crest

16) tooth length/depth ratio

17) maxillary symmetry

18) presence/absence of a maxillary groove

B2) The following features in the crania are newly shown to have taxonomic utility at the level of subfamily:

1) ratio of edentulous portion to tooth row length

2) presence/absence of an inter-narial septum

C1) The following traditionally used cranial features are of taxonomic utility at the level of genus or groups of genera.

1) apex of crest above the orbit or anterior to the orbit

2) presence/absence of a posterior spur on the crest

3) presence/absence of premaxillary pockets

4) presence/absence of postorbital pockets

C2) The following new cranial feature is of taxonomic utility at the level of genus or groups of genera:

1) presence/absence and degree of folding of reflected premaxillary margins.

CHAPTER 4

A REVIEW OF **POSTCRANIAL** FEATURES PREVIOUSLY USED IN HADROSAURIAN TAXONOMY

The following postcranial features are reported in the literature as diagnostic of genera and subfamilies, and are here reviewed on the basis of the present work.

1) The ratio between the lengths of the radius and humerus was cited by Lull and Wright (1942) to differentiate between the two subfamilies, the Hadrosaurinae having a humerus longer than the radius and the Lambeosaurinae having a radius longer than the humerus. These authors cited several exceptions to this rule but retained it as a valid character at the subfamily level. A larger sample, including genera from both subfamilies, shows this feature to be too variable to be valid at any taxonomic level (Tables 3 and 5).

2) The ratio between the length and height of the scapular blade (Plate 1) was originally cited (Brett- Surman, 1975) as a subfamilial indicator. In the Hadrosaurinae, the scapular blade is relatively longer and the height at the distal end smaller (Plate 1A) than in the Lambeosaurinae. Larger samples indicate that this feature cannot be used to diagnose subfamilies because the overlap between the two subfamilies is too great. No isolated scapula can be assigned to any taxonomic group with certainty, with the exception of _Brachylophosaurus_ (NMC 8893), in which the scapula has the greatest length and the least height of any hadrosaur. This feature must now be abandoned as a taxonomic indicator.

3) The foot of the ischium (Plate 6) is often cited in the diagnoses of subfamilies (Lull and Wright, 1942). It is a thoroughly consistent and dichotomous feature for Campanian and Maastrichtian genera. In the Hadrosaurinae, the ischium lacks a foot. This is a derived condition because all the iguanodontids and camptosaurids have a clubbed distal end, and the Lambeosaurinae have a fully expanded foot. _Bactrosaurus_ and _Gilmoreosaurus_ have a clubbed ischium but these two genera are pre-Campanian in age.

4) The loss of the fifth metatarsal has been noted for all hadrosaurids (except _Claosaurus_, see Gregory 1948). This loss is noted in all hadrosaurids of Campanian and Maastrichtian age. This feature is not of taxonomic utility because it is based on a single Santonian (?) occurrence rather than on

morphological comparisons between genera of the same geologic age. Loss of the fifth metatarsal may become more useful for taxonomic purposes for all hadrosaurids of all geologic ages with larger samples from pre-Campanian strata, but for the present it is mentioned only for the sake of completeness.

5) The number of sacrals is a growth feature of hadrosaurids because the sacrals fuse to form a 'synsacrum', as they do in most Upper Cretaceous ornithischians. Juvenile hadrosaurids begin with 5 or 6 sacrals, and all adults have from 8 to 10. Most are incorporated from the caudal series. The sacral count has no taxonomic utility unless it can be shown that specific taxa either begin with less than 5 sacrals or consistently have more than 10 as adults. The one diagnostic feature of the sacrals published to date was reported by Gilmore (1933), who observed that in the Hadrosaurinae there is a sacral groove along the ventral surface of the fused sacrals. The Lambeosaurinae have a ridge. This feature is consistent and therefore useful to distinguish subfamilies.

6) The height/width ratio of the neural spines has been used for certain taxa such as _Hypacrosaurus_ (Brown 1913) and _Barsboldia_ (Maryanska and Osmolska, 1981). The neural spines increase in height and thickness from juveniles to adult in all genera and they also increase in relative height when comparing hadrosaurines (such as _Edmontosaurus_, Plate 9) to lambeosaurines (such as _Parasaurolophus_, Plate 16A) of the same body weight. The neural spine height/spine width ratio is about 2:1 in _Edmontosaurus_ (DMNH 1493) and ranges to about 7:1 in _Hypacrosaurus_ (NMC 8501). _Kritosaurus_ and _Saurolophus_ have neural spine h/w ratios intermediate between those of _Edmontosaurus_ and _Corythosaurus_. The overlap in ratios between all the clades is too great for precise separation of taxa, although the ratio can be used to distinguish subfamilies in extreme cases where it approaches that of _Edmontosaurus_ or _Hypacrosaurus_.

Another indication of juvenile status, viz. neural arches unfused to their centra, does not apply to most hadrosaurids, in which neural arches fuse completely very soon after hatching. I have not seen an unfused neural arch in any animal with a snout-vent length greater than 3 feet.

POSTCRANIAL FEATURES NOT PREVIOUSLY CITED

1) The presence of coracoidal rugosities and ridges is thought by some (Morris, pers. comm. 1975; Dobie, pers. comm., 1983) to be a valid generic indicator. The scapular articular

facet becomes more rugose from genera of Campanian age to genera of Maastrichtian age, and also increases in the course of individual growth. The degree of rugosity is most strongly marked in individuals of old age from the Maastrichtian (Edmontosaurus annectens, USNM 2413). The enlargement of the dorsal acromial ridge (Plate 1A) follows the same pattern. These are growth features and have no taxonomic utility.

The placement of the coracoidal foramen (Plate 1A, 1B) also falls into this category. Its placement relative to the scapular articulation changes over geologic time. In camptosaurids and iguanodontids (fide Norman 1980), the foramen is near or at the articulation between the scapula and coracoid. In hadrosaurids, from the Santonian to the Maastrichtian, the foramen migrates away from the articulation more towards the middle of the coracoid.

The increasing robustness of the rugosities on the articular surface of the scapula with increasing ontogentic age, and the migration of the foramen over geologic time, are interesting functional features but cannot be used taxonomically.

In some cases, the extreme rugosities in the Hadrosaurinae mimic taxa in the Lambeosaurinae. The lambeosaurines have more robust and rugose landmarks, and have more robust and shortened elements than the hadrosaurines; consequently very old hadrosaurines may be mistaken for lambeosaurines. Although hadrosaurine coracoids are more elongated than in the lambeosaurines, the overlap in shape between the two subfamilies is too great to use this feature as a synapomorphy.

2) The sternals (Plate 1C and 1D) are largely unknown because they are rarely preserved and usually not mounted. It is probable that these elements become separated from the body as a result of various taphonomic processes. Analysis of sternals as taxonomic criteria in hadrosaurids is limited to this work.

Iguanodontids and hadrosaurines are similar in having a smaller 'paddle' and 'handle' (Plate 1D) as compared to the lambeosaurines (Plate 1C), where the paddle is relatively larger and the handle forms the smallest part of the element. These characters are apparent at the level of subfamily, but the sample size includes only three hadrosaurines (Shantungosaurus, Anatotitan, Edmontosaurus) and two lambeosaurines (Corythosaurus and Tsintaosaurus).

3) The deltopectoral l/w ratio (Plate 2, Tables 2 and 4) was a feature previously used to separate the Hadrosaurinae from the Lambeosaurinae (Brett-Surman 1975). In general, the hadrosaurines have a longer and narrower deltopectoral crest than the lambeosaurines, but the sample size is now large enough to show that this ratio is insufficient to delineate subfamilies. This feature must therefore be abandoned as a taxonomic criterion.

4) The ridges on the radius and ulna (Plate 2) are believed by Baird (pers. comm.) to be useful in distinguishing genera. These ridges, with growth, become more prominent and they should be taxonomically ignored until an adequate sample of a complete growth series from both subfamilies can be quantitatively analyzed.

5) The metacarpals (Plate 3) have proven to be of no value taxonomically after an analysis of more than thirty specimens covering both subfamilies. These elements show a consistent reduction in size and complexity during the history of the family.

6) The carpals are the rarest and most poorly understood elements of the hadrosaurid body. Their appearance is neither consistent among taxa nor in age groups. The few available specimens are circular with no apparent landmarks. They are missing in many complete specimens (including the famous "mummy", _Edmontosaurus annectens_, AMNH 5060; see Osborn, 1912) but are present in one specimen of _Anatotitan_ (AMNH 5730).

7) The ratios between the length and height of the ilium as a whole, and between the length and height of the postacetabular process (Tables 3 and 5, Plate 4), can be valuable in distinguishing subfamilies, and in some cases, groups of genera. Within groups of genera, the shape of the ilium (Plate 4) is consistent (Brett-Surman, 1975). _Edmontosaurus_ and _Anatotitan_ have relatively the longest ilia with relatively the shortest height. _Kritosaurus_ is noted for the sigmoidal shape of the dorsal margin of the ilium. _Parasaurolophus_ has the largest and most robust antitrochanter of any hadrosaurid. In the Hadrosaurinae, the ilium is relatively longer and lower, with smaller sacral ridges and a smaller antitrochanter than in the Lambeosaurinae.

8) The l/w ratio for the postacetabular portion of the ilium (Plate 4, Tables 2 and 4) is an example of the problem of quantifying the slight shape differences. In the most derived lambeosaurines, such as _Parasaurolophus_ (_P. cyrtocristatus_, FMNH

P27393), this process is shorter (measured antero-posteriorly) and higher (measured dorso- ventrally) than in the more derived hadrosaurines such as Edmontosaurus (E. annectens, DMNH 1493). In clades that are less derived, such as Saurolophus (a hadrosaurine) and Corythosaurus (a lambeosaurine), the postacetabular processes are similar in shape, and at no time can a single specific ratio be used to quantify this shape.

9) The size of the antitrochanter (Plate 4) is a feature that can be used to distinguish the more derived genera such as Parasaurolophus from the less derived genera (compare Plate 4A to 4B), but cannot be used to distinguish more closely related genera (compare Plate 4A to 4C).

10) The shape of the prepubic process (Plate 5) is consistent within the five new tribes to be named in this report (see below) but cannot be quantitatively defined. For example, in Anatotitan and Edmontosaurus (Plate 5E), the prepubic process is axe-shaped. In Kritosaurus (Plate 5D), the prepubic process is shaped like a hockey stick with parallel dorsal and ventral borders. In Prosaurolophus and Saurolophus (Plate 5C), the prepubic process resembles half of a double-bladed axe with diverging dorsal and ventral borders, and in Corythosaurus, Hypacrosaurus, and Lambeosaurus (Plate 5B), the prepubic process is also similar to Saurolophus but the dorsal border is more parallel to the ventral border than in the saurolophs. In Parasaurolophus, Bactrosaurus, and Tsintaosaurus, the prepubic process is relatively taller (dorso-ventrally) and less wide (antero- posteriorly) than in any other clade.

11) The presence of an obturator foramen (Plate 6) that is entirely enclosed by bone is a feature unique to the hadrosaurids within the ornithopods. The foramen can only be seen in ischia with an undamaged margin, a condition that is extremely rare. The proximal end of the ischium frequently suffers damage, and this results in the appearance that the ischial foramen is not enclosed by bone (as seen in Plate 6). The specimens with a complete border are very old individuals, which may indicate that the foramen is completely enclosed only in later ontogenetic stages.

12) The lesser trochanter of the femur (Plate 7) is separated from the greater trochanter by a cleft and varies in position and size. Some believe (Davies, unpublished thesis, University of Texas, 1985) that the size of the cleft between the lesser and greater trochanter is diagnostic for distinguishing genera. However, the size of the cleft is variable even between the sides of the same individual and is

age-related. The angle of the lesser trochanter with the femoral shaft is a taphonomic feature due to compression.

13) The fusion of the anterior extensions of the distal condyles of the femur into an intercondylar canal has been cited by Galton (1976) as being of taxonomic value among genera in ornithopods. Galton has since reversed his position (pers. comm., 1987) and believes the fusion of the condyles is an age-related feature and can occur in all old individuals (USNM 4278).

14) The ratio between the length of the femur and the length of the tibia was cited by Lull and Wright (1942) as being of taxonomic utility. They stated that the femur to tibia ratio was 1:0.8 in hadrosaurines and 1:0.9 in lambeosaurines. Tables 2 and 4 show that this ratio is quite variable and not dichotomous as originally thought. The range of overlap is too great between all clades to make this ratio useful in taxonomic studies.

15) There are two basic types of astragali and calcanea, designated 'Types 1 and 2' by Brett-Surman (1975). An astragalus of Type 1 (discussed above, Plate 7B) is of the typical ornithopod form with a large and shallow concave proximal surface for reception of the tibia. There is a small ascending process on the anterior side. In anterior view, the element is triangular with an apex that is offset laterally. The astragalus has a peg in a notch articulation with the calcaneum but the two elements are never fused. The Type 1 tarsus is found in all hadrosaurids except <u>Parasaurolophus cyrtocristatus</u> (FMNH P27393), which has a Type 2 tarsus.

An astragalus of Type 2 (Plate 7D) has the shape of an isosceles triangle with no lateral projection. It is relatively smaller and less robust than Type 1 and does not appear to have a calcaneum associated with it. The distal end of the fibula is noticeably expanded to compensate for lack of a calcaneum. This may represent a derived condition in <u>Parasaurolophus</u>. Nothing further can be said about the taxonomic utility of the differences between the types of tarsi because the tarsus of <u>Parasaurolophus</u> is only known from the type of <u>P. cyrtocristatus</u> (FMNH P27393).

17) Ossified tendons are known in all well preserved hadrosaurids. The latticework of two diagonally overlapping sets has not been extensively studied because only a handful of specimens have complete sets preserved. The only specimen with a complete series of ossified tendons is <u>Corythosaurus casuarius</u>

(AMNH 5338), which has two sets of nine tendons per spine on each side. It is not known whether the number of tendons is taxon-specific or dependent on the height of the neural spine. Until a larger sample is found, this feature, though intriguing, is not taxonomically useful.

NON-MORPHOLOGICAL FEATURES USED TO DIAGNOSE GENERA OF HADROSAURS

1) Stratigraphic position, at the level of formation, has traditionally been used to delineate genera, especially at the Campanian-Maastrichtian boundary (see papers by Cope, Marsh, Parks). This practice has been justified by past writers on the assumption that deposition of a single formation takes 'several' million years. Because the lifespan of a mammal species is traditionally thought to be about one million years (Simpson, 1944), the time encompassed by a formation is supposedly more than sufficient to account for the appearance of another species. Such is the case with _Anatosaurus_ (fide Lull and Wright, 1942), where _A. edmontoni_ is separated from _A. annectens_ even though they are both of Maastrichtian age, but from different stratigraphic levels. This practice is unjustifiable because taxa must be based on shared derived morphological features.

2) Geographic position on the same continental plate has also been used to distinguish taxa, most notably between the faunas of western North America versus those of Asia (Riabinin 1930, Rozhdestvenskii 1967). In comparing Asia with western North America, two species of _Saurolophus_ have been recognized. _S. angustirostris_ (Rozhdestvensky 1957) in Asia is viewed as distinct from _S. osborni_ (Brown 1912) in North America, but the morphological differences are of body size and crest size (heavily restored in _S. angustirostris_), and apparently nothing else (Maryanska and Osmolska 1981). This practice is also unacceptable for reasons stated above.

SUMMARY OF POSTCRANIAL FEATURES

Fifteen features are found to be of no taxonomic utility, as follows:

1) radius/humerus length ratio

2) scapular blade l/h ratio

3) presence of coracoidal rugosities

4) deltopectoral l/w ratio

5) ridges on the radius and ulna

6) metacarpal shape and metacarpal/humerus ratio

7) presence and placement of an ischial foramen

8) size and degree of fusion of the lesser trochanter

9) degree of fusion of the anterior femoral canal

10) femur/tibia length ratio

11) shape of the astragalus and calcaneum

12) presence or size of the fifth metatarsal

13) number of sacrals

14) size and number of ossified tendons

Seven features are found to be of taxonomic utility above the level of genus, as follows:

1) sternal 'blade/paddle' ratio

2) iliac l/h ratio

3) postacetabular l/h ratio

4) antitrochanter shape and size

5) shape of the prepubic process

6) presence/absence of a footed or clubbed ischium

7) neural spine height

"OLD AGE" FEATURES

During the course of this study, several features were noted in large and presumably old individuals. These features are important and are unreported in the literature. The conclusions listed below are based mainly on a study of Edmontosaurus (USNM 3814), a hadrosaurine.

An individual of large size displays features more commonly seen in the Lambeosaurinae, such as relatively thicker elements. Old individuals can be recognized by the greater deposition of bone on articular surfaces, ridges, and processes well beyond anything seen in younger animals. In each case, the increased deposition of bone is manifest as increased robustness and thickness of elements typical of lambeosaurines such as <u>Corythosaurus</u> and <u>Parasaurolophus</u>. Because hadrosaurines of very old age therefore tend to mimic lambeosaurines morphologically, very large or old hadrosaurines represented by postcranial remains without skulls may be misidentified and assigned to the lambeosaurines. This can lead to taxa assigned to the lambeosaurines at the expense of hadrosaurines.

Lull and Wright (1942) cited five features in hadrosaurids which are the result of growth:

1) increased number of tooth rows with age,

2) incorporation of caudals into a synsacrum,

3) increased size of the pre-orbital muzzle area,

4) increase in the relative length of the edentulous portion of the mandible,

5) increase in the relative size of the antitrochanter.

In addition, the following eight features have been observed by me in hadrosaurids:

1) The lesser trochanter of the femur (Plate 7G) is variable in size and shape but normally is separated from the greater trochanter by a deep cleft. Only in the largest, oldest individuals can one see complete (or almost complete) fusion of the lesser trochanter with the greater trochanter, with obliteration of the cleft.

2) The fourth trochanter is always large and is shaped like an isosceles triangle (Plate 7G) with its apex directed posteriorly. Normally it is smooth and is more than twice as long (measured parallel to the femoral shaft) as wide (measured perpendicularly from the femoral shaft). In the largest animals, it is over three times longer than wide. The outer surface becomes roughened, and in some individuals it is fluted, presumably because muscle insertions become exaggerated with age.

3) The distal articulations of the femur are greatly expanded posteriorly into large 'rockers' (Plate 7F). The articulations are parallel and between them form a very deep cleft, through which pass tendons. In very large animals, the rockers fuse distally to form a functional canal instead of a trench. Galton (1976) used this fusion to delineate species of ornithopods but has since abandoned this position (pers. comm.).

4) The articular ends of the femur are generally smooth, and only the lateral surfaces are pitted or roughened, possibly for an attachment for the cartilaginous coverings and joint capsules. In large animals, all the articular surfaces become deeply pitted and very roughened, as in sauropods.

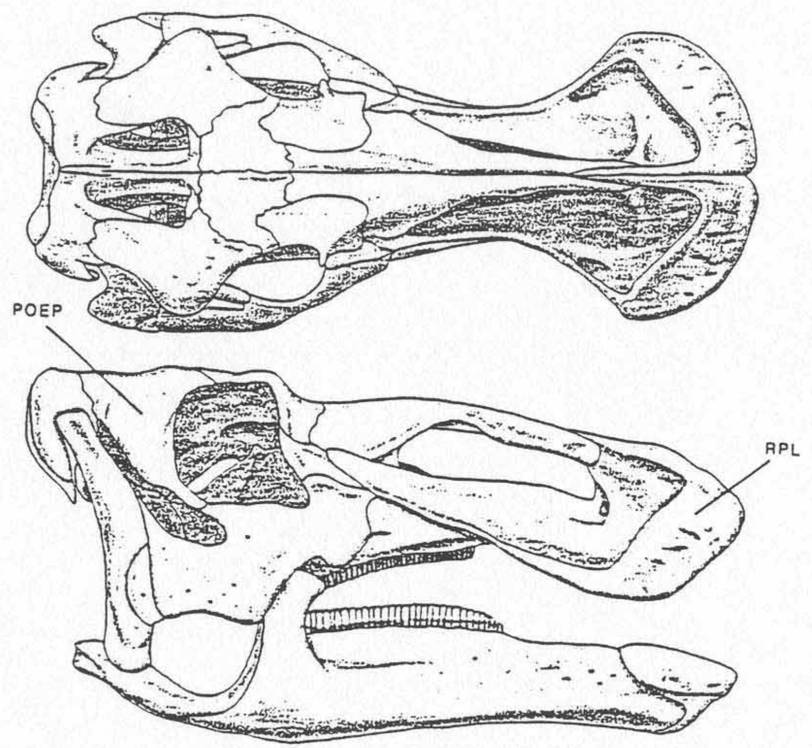
5) The distal ends of the neural spines are usually smooth, only slightly expanded, and are parallel- sided when viewed anteriorly. In the largest animals, the spines are roughened, much expanded, thickened, and seem to flare outward when viewed in anterior aspect. <u>Barsboldia</u> (Maryanska and Osmolska 1981, a lambeosaurine) was established on the basis of expanded neural spines, which throws into doubt the taxonomic validity of this genus.

6) Muscular insertions are generally smooth. Most of the ridges and bumps on the long bones are smooth, generally short in extent, and do not project far from the shafts. In the largest animals, the ridges may become exaggerated, and the bumps become large, pitted, and rugose, with a tendency to look pathological. On the medial side of the ilium, for example, there is a ridge that extends onto the preacetabular bar (Plate 4C, shown in medial view) for reception of the sacral ribs. In one large specimen (USNM 3814), the preacetabular bar has thickened and grown a medial process from the dorsal rim to such an extent that it has changed from a vertically oriented blade-like process (in cross-section) into a T- shaped thickened bar.

7) Most hadrosaurids lack carpals. These elements are preserved neither in complete and fully articulated adults nor in 'mummified' specimens (AMNH 5060). Horner (pers. comm. 1985) states that the carpals are preserved in a few of the hatchling <u>Maiasaura</u> specimens. The presence of carpals in hatchlings, but not in adults, is unexpected, but if true, indicates that the carpals are resorbed later in life or are cartilaginous in adults. In very large adults in other taxa, where the carpals are ossified, they may have re-ossified from cartilage.

Plate 8

The skull of **Edmontosaurus regalis** based on NMC 2288 and USNM 12711 in dorsal view (top) and right lateral view (bottom). Quadrate length is 420mm. Original reconstruction by Gregory S. Paul under my direction.



8) The unguals (Plate 3) are generally smooth along the anterior edges in both the manus and pes. In some very large animals, the unguals are pitted with roughened edges and have deep gouges at the leading anterior edge (Bactrosaurus, AMNH 6553).

SUMMARY

On the basis of these features, four size classes, based on gross morphology, are inferred to reflect individual age. The first class (hatchling) represents hadrosaurs with little or no expansion of the muzzle, small and smooth articulations, five or six sacrals, and less than 20 tooth rows. The second class (juvenile) has a noticeable muzzle, 20 to 40 tooth rows, articulations with some rugosities on the long bones, six or seven sacrals, and in the Lambeosaurinae, the appearance of incipient cranial crests and an ischial foot. The third size class (adult) is the size range for which most of the defining features of the hadrosaurids are known. For the purpose of diagnosing new taxa, this should be the only age group used. Features that separate the two subfamilies in this age group are a fully formed ischial foot, cranial crests, more than six sacrals, more than 40 tooth rows, and a muzzle length equal to or greater than the height of the skull. The fourth class (old age) is characterized by ten or more sacrals, all bony projections greatly increased in size and rugosity, fusion of the distal femoral condyles anteriorly, pitting of the articular ends of the long bones, frilling of the ends of the unguals and clubbing of the apices of the neural spines. Care must be taken not to confuse old age features with damage, or with pathological developements that are not associated with increasing age.

CHAPTER 5

REDEFINING HIGHER CLADES OF HADROSAURIDS

Ostrom (1961), in the latest major work on the hadrosaurids, recognized the following seven 'lineages' within the hadrosaurids on the basis of overall skull shape and the presence/absence of hollow crests.

1) kritosaurs

2) edmontosaurs

3) saurolophs

4) procheneosaurs

5) corythosaurs

6) lambeosaurs

7) parasaurolophs

Ostrom's phylogeny included only North American genera. Brett-Surman (1979) published the first phylogeny that included all the known genera throughout the world, and recognized five 'lineages' (unnamed) as follows:

1) hadrosaurs (=kritosaurs)

2) edmontosaurs

3) saurolophs

4) corythosaurs

5) parasaurolophs

This present report, and a refinement of previously used cranial characters, show that the lambeosaurs are part of the corythosaur lineage. I concur with Dodson (1975) that the procheneosaurs are juvenile corythosaurs. All the remaining hadrosaurids fit into the five lineages established by Brett-Surman (1979) and their defining features are summarized below. The family and two subfamilies of hadrosaurids (fide Langston, 1960) are redefined on the basis of new postcranial data, and reanalysis of older cranial data. The five lineages cited above are assigned the rank of TRIBE.

REVISED DIAGNOSIS OF THE HADROSAURIDAE

FAMILY HADROSAURIDAE:

Bipedal ornithopods with up to 60 interlocking rows of teeth; teeth diamond-shaped with a single medial ridge; teeth enamelled on one side; tooth battery bowed dorsally when seen in lateral view; dentary occlusal surface tilted to lateral side; maxillary occlusal surface tilted to medial side; edentulous portion of mandible longer than in any other ornithopod; beak decurved and laterally expanded in a duck-like manner; nasal region expanded, sometimes into a hollow crest; external nares elongate and enlarged; entire skull heightened dorsally; quadrate elongate and straight; coronoid process of mandible the highest of any ornithopod; retroarticular process elongate; cervicals opisthocoelous; presacrals 30-34; 'synsacrum' with 6 (juvenile) to 10 (adult) sacrals; caudals 60+; vertebral neural spines taller than in other ornithopods; lattice- work of ossified tendons in two series on each side with 8-9 tendons per neural spine per series; scapula elongate and broad; humerus with parallel-sided deltopectoral process; radius and ulna elongate; metacarpals reduced and rod-like with poorly ossified ends; manus covered with a fleshy 'mitten' and not webbed; digits not divergent; unguals hoof-like; forearms relatively longer than in other ornithopods; pelvic elements unfused; ilium with decurved preacetabular process; iliac postacetabular process elongate, rectangular with parallel dorsal and ventral borders; antitrochanter present and the most robust of all ornithopods; prepubis elongate and ventrally deflected, blade greatly expanded, with prepubic neck elongate; postpubis much reduced and rod-like; ischium straight; fourth trochanter of femur shaped like an isosceles triangle and at midpoint of shaft; hindlimb/forelimb ratio averages 1.66; pedal unguals hoof- like; pedal phalangeal formula 0,3,4,5,1.

SUBFAMILY HADROSAURINAE:

Nasal elements folded except in the <u>Saurolophus</u> clade; fossa, presumably for salt glands, in the <u>Edmontosaurus</u> clade; nasal passages direct; skull long and low with no hollow crests; preorbital portion of skull elongate; edentulous portion of skull longer than in the Lambeosaurinae; scapula relatively longer than in the Lambeosaurinae but not as wide; deltopectoral process of humerus with larger L/W ratio than in the lambeosaurines; ilium longer but not as tall (dorso-ventrally); ilium with largest length/width ratio, and longest postacetabular process of all ornithopods; pubis with longest pre-pubic 'blade' and pre-pubic 'neck'of all ornithopods; ischium unfooted but clubbed in Gilmoreosaurus; tarsus relatively wider than lambeosaurines; appendicular elements generally more gracile than in the Lambeosaurinae; neural spines not as tall as in the Lambeosaurinae; sacral centra with a ventral groove running longitudinally; neural spines of sacrals with a L/W ratio generally less than 4.5.

TRIBE Edmontosaurini (new taxon)

Premaxillary borders more highly reflected than in other hadrosaurine clades; premaxillae within the external nares highly folded with fossae present; edentulous portion of the mandible proportionally longer than in other hadrosaurines; postorbital fossa larger than in other hadrosaurines; medial premaxillary rami unexpanded; ilium with larger length/width ratio than in other hadrosaurines; pubis with proportionally longer pubic neck than in other hadrosaurines; neural spine height less than in other hadrosaurines.

TRIBE Hadrosaurini (new taxon)

Medial rami of the premaxillae expanded into a 'roman nose' configuration; external nares relatively larger than in other hadrosaurines; nasals expanded dorso- posteriorly; anterior margin of the mandible noticeably deflected ventrally; scapula relatively longer with a lower scapular blade length/width ratio than in other hadrosaurines; ilium with a pronounced sigmoidal curve of the dorsal margin; dorsal and ventral borders of the pubic blade parallel; ischium longer, thinner, and more gracile than in other hadrosaurines.

TRIBE Saurolophini (new taxon)

Anterior margin of the premaxillae not reflected; nasals expanded into a solid crest-like structure resembling a spike; ilium and pubis more similar in shape to the Corythosaurini than to other hadrosaurines; limbs proportionally longer and more robust than in other hadrosaurines.

SUBFAMILY LAMBEOSAURINAE:

Skull shorter and narrower than in the Hadrosaurinae; muzzle not as long nor as wide as in the Hadrosaurinae (except in the Saurolophini); preorbital region shorter; external nares simpler, not as expanded and not folded; nasal apparatus greatly expanded into hollow crests with multiple chambers and looped narial passages; mandible more strongly deflected ventrally; edentulous portion of mandible proportionally shorter than in the Hadrosaurinae; scapula shorter but wider than in the Hadrosaurinae; deltopectoral process of humerus more robust than in the Hadrosaurinae; forearms shorter than in the Hadrosaurinae but thicker; ilium more robust, postacetabular process with a smaller L/H ratio, ilium with lowest length/width ratio and shortest postacetabular process; pubis with shorter prepubic 'blade' and 'neck'; 'blade' expanded dorso-ventrally, 'neck' shorter than in the Hadrosaurinae; ischium footed except in Bactrosaurus where it is clubbed; ischial shaft thicker; tarsus relatively less wide than in the Hadrosaurinae and taller; appendicular elements generally more robust; sacral centra with a ventral ridge running longitudinally; sacral neural spines with a L/W ratio generally greater than 4.5.

TRIBE Corythosaurini (new taxon)

Premaxillae expanded into a hollow Corinthian- shaped, helmet-like crest; neural spines higher than in other hadrosaurids.

TRIBE Parasaurolophini (new taxon)

Premaxillae expanded into a tubular, hollow crest; external nares smaller than in other hadrosaurids; appendicular elements more robust and thicker than in other hadrosaurids; limbs proportionally shorter than in other hadrosaurids; ilium and pubic 'blade' with a lower length/width ratio than in other hadrosaurids; ischium with a 'heel' and 'toe'.

Plate 18

Restoration of **Tsintaosaurus spinorhinus**, a lambeosaurine, based on PMNH V728. Original art by Gregory S. Paul done under my direction. Femur length is 1000mm. Skeleton in left lateral view.

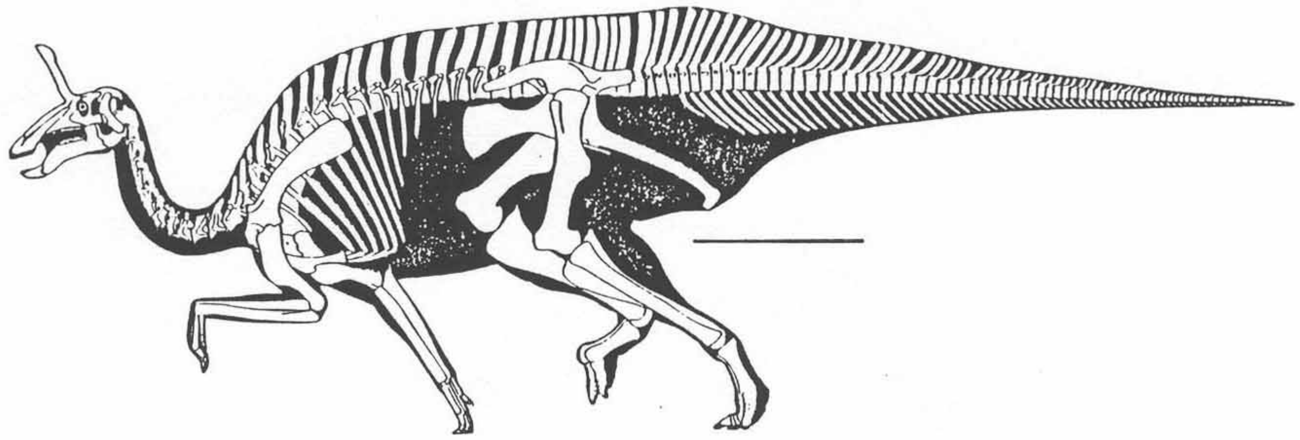
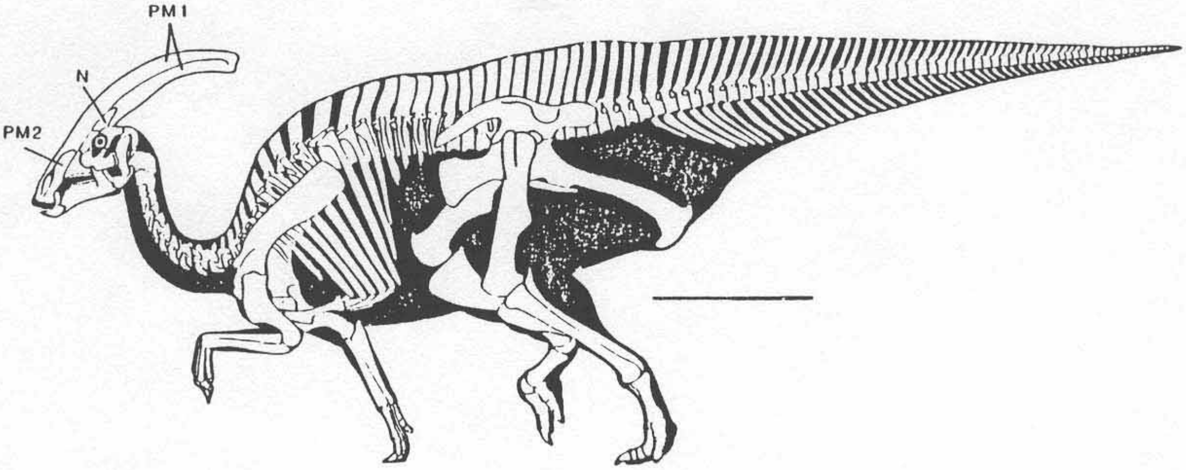


Plate 17A

Restoration of **Prosaurolophus maximus**, a hadrosaurine, based on ROM 787 as seen in left lateral view. Femur length is 997mm.

Plate 17B

Life restoration of **Prosaurolophus maximus.** Original art for both figures by Gregory S. Paul under my direction.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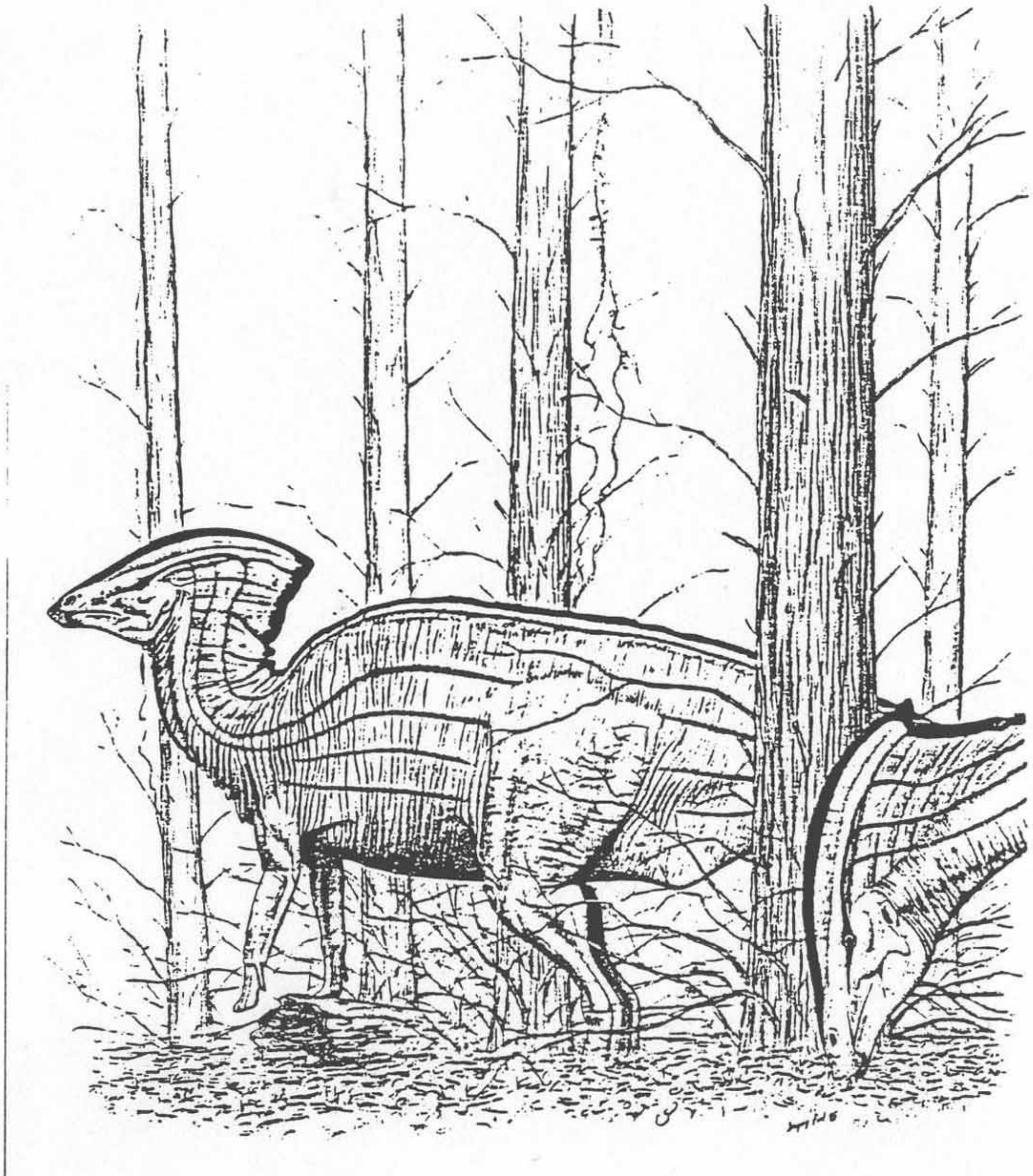


Plate 16A

Restoration of **Parasaurolophus crytocristatus**, a lambeosaurine, as seen in left lateral view based on FMNH P27393. Femur length is 1171mm.

Plate 16B

Life restoration of **Parasaurolophus cyrtocristatus.**

Original art of both figures by Gregory S. Paul under my direction.

Plate 15

Life restoration of **Maiasaura peeblesorum**, a hadrosaurine, in right lateral view by Gregory S. Paul under my direction.

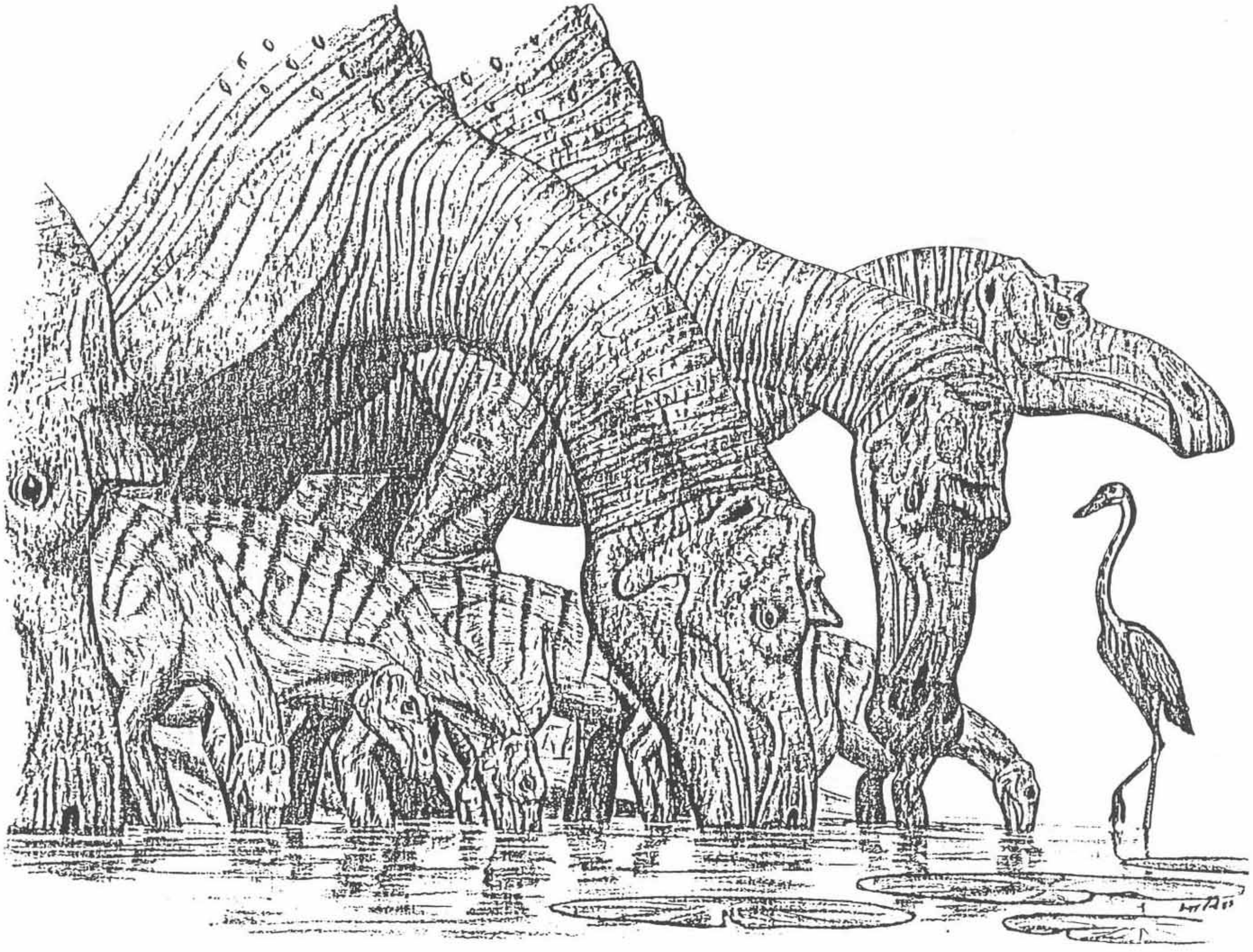
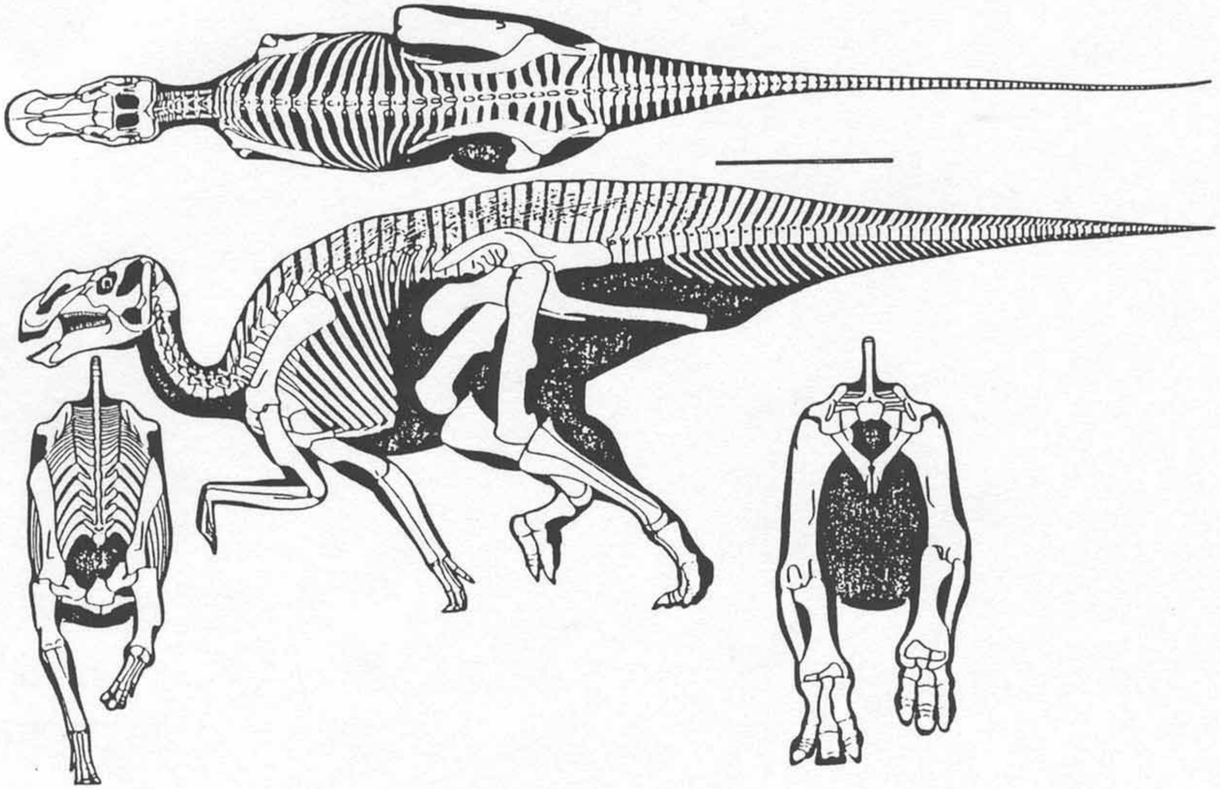
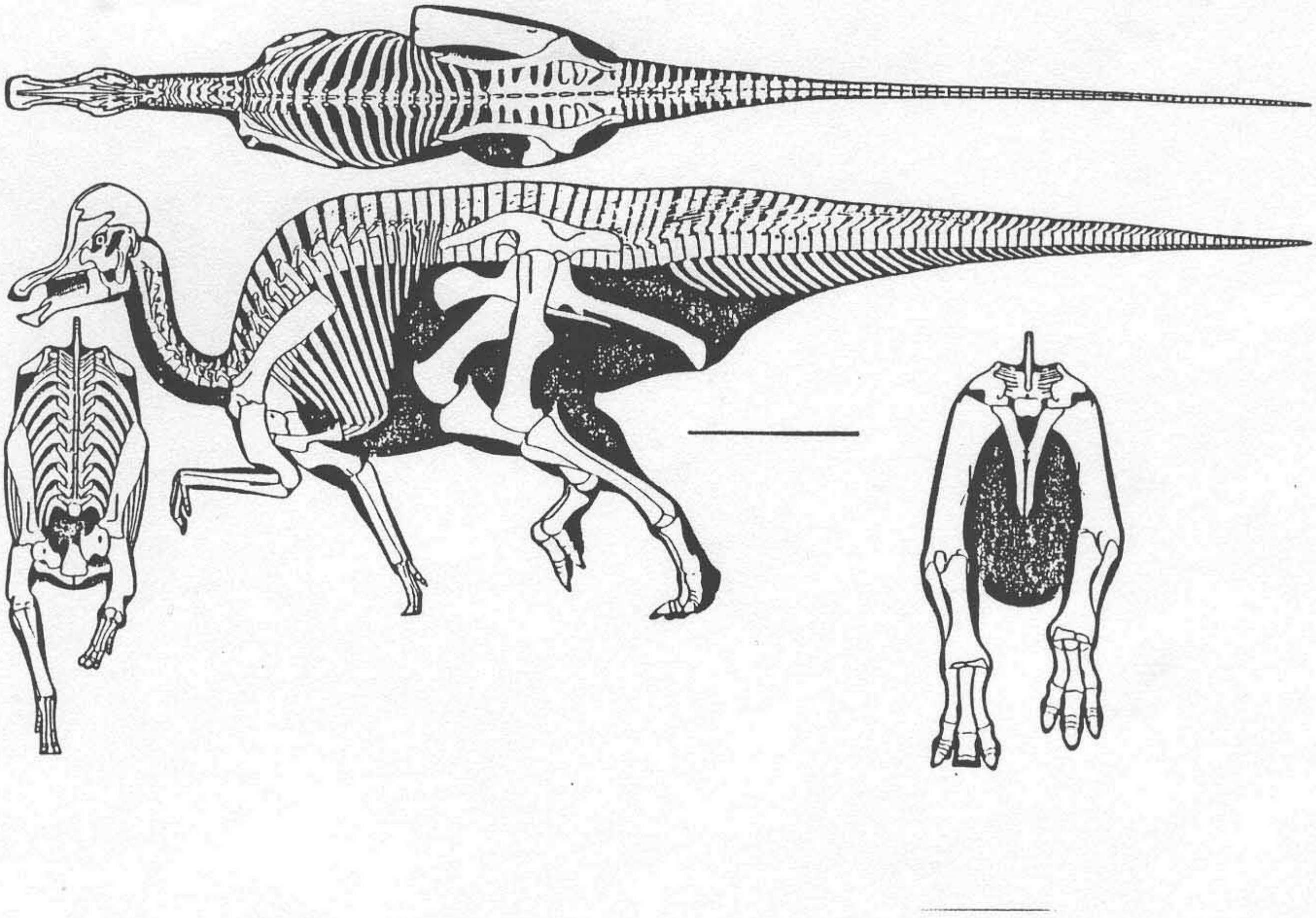


Plate 14

Restoration of **Kritosaurus navajovius**, a hadrosaurine, based on ROM 764. Original art by Gregory S. Paul under my direction. Femur length is 1041mm. Top figure is a dorsal view. Far left figure is the pectoral girdle and the forelimbs in anterior view with the skull and cervicals removed. Middle figure is a left lateral view. Far right figure is the pelvic girdle and hindlimbs in posterior view with the tail removed.





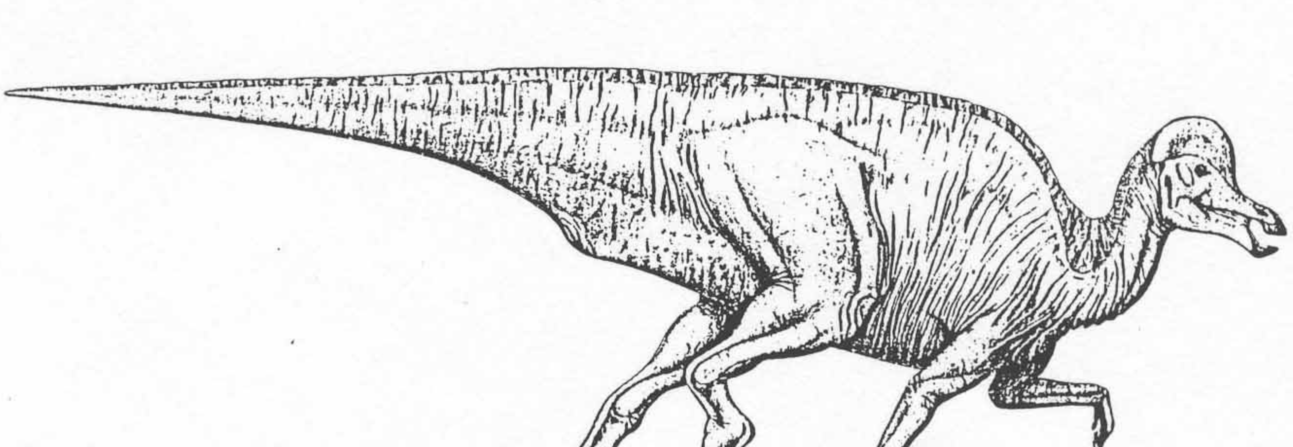


Plate 13A

Restoration of **Corythosaurus casuarius,** a lambeosaurine based on AMNH 5240 and 5338. Original art by Gregory S. Paul done under my direction. Femur length of AMNH 5240 is 1080mm. Top figure is a dorsal view. Far left figure is the pectoral girdle and the forelimbs in anterior view with the skull and cervicals removed. Middle figure is a left lateral view. Far right figure is the pelvic girdle and hindlimbs in posterior view with the tail removed.

Plate 13B

Life restoration of **Corythosaurus casuarius.** Original art by Gregory S. Paul under my direction.

Plate 12

Restoration of **Bactrosaurus johnsoni**, a lambeosaurine, based on AMNH 6553 and 6577 as seen in left lateral view. Original art by Gregory S. Paul done under my direction. Femur length is 800mm.

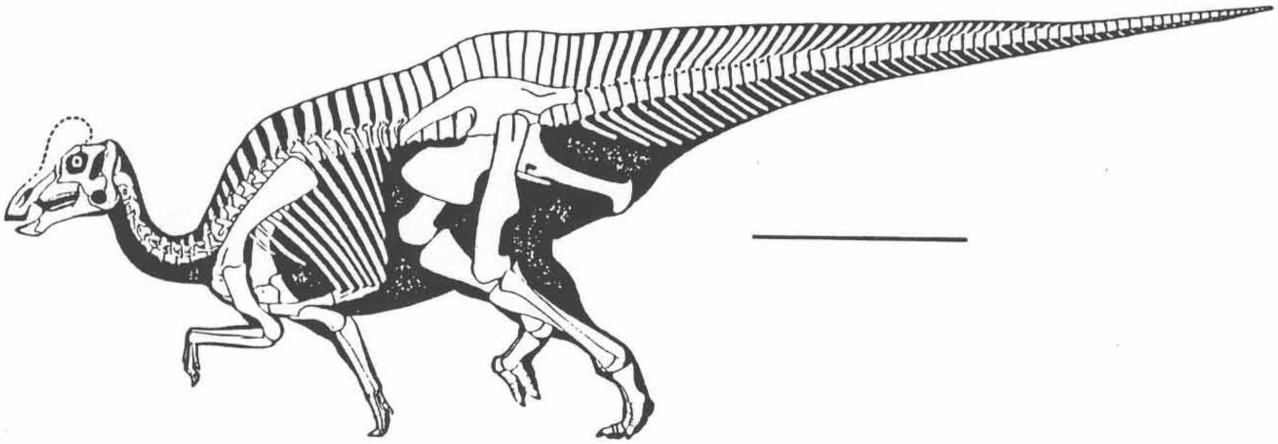


Plate 11

Flock (herd) of **Anatotitan copei**, a hadrosaurine.

Original art by Gregory S. Paul under my direction.

Height at hips is about 8 feet in adults.

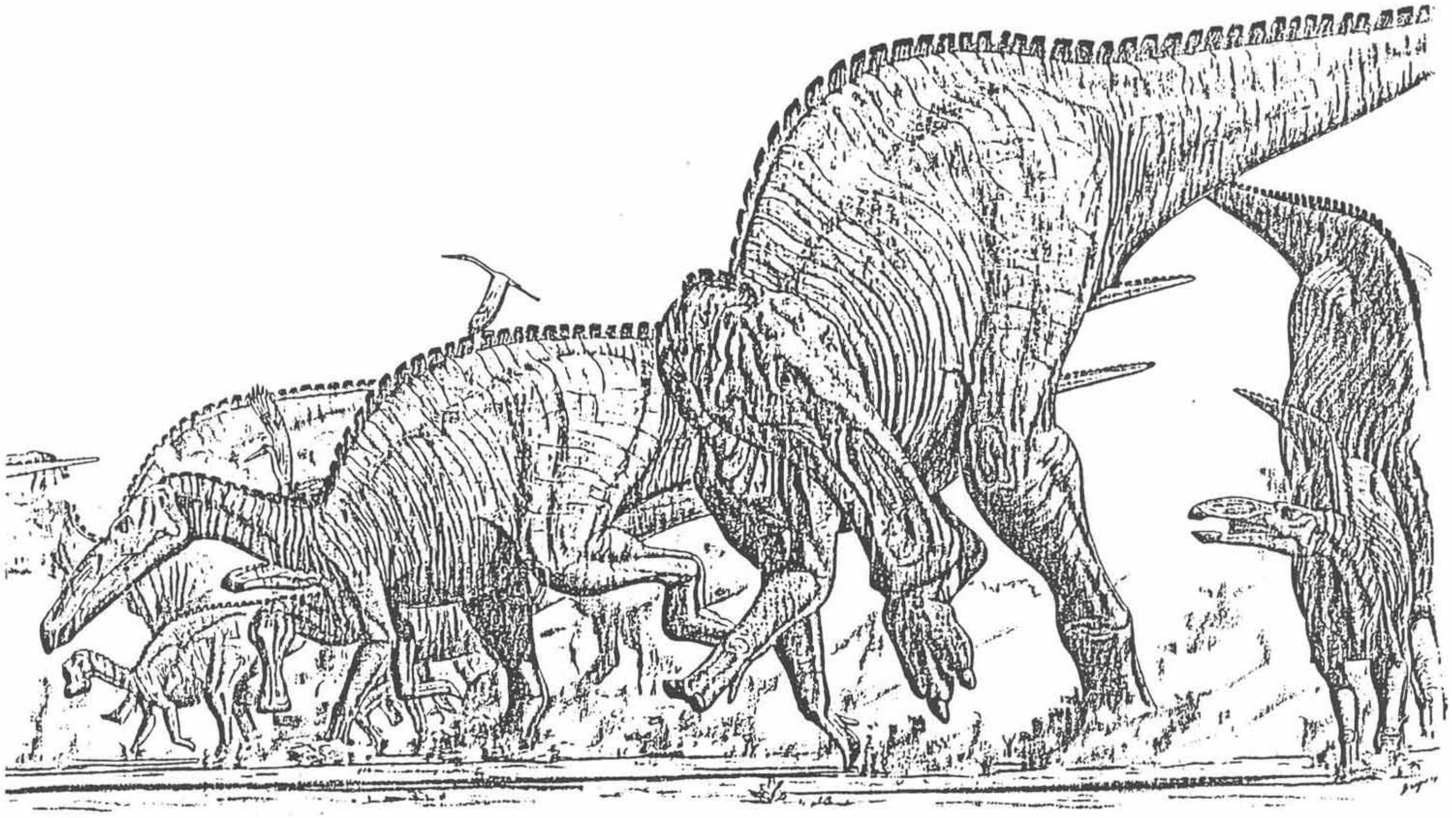


Plate 10

The skull of **Anatotitan copei** based on AMNH 5730 and AMNH 5886 in dorsal view (top) and right lateral view (bottom). Quadrate length is 320mm. Original reconstruction by Gregory S. Paul under my direction.

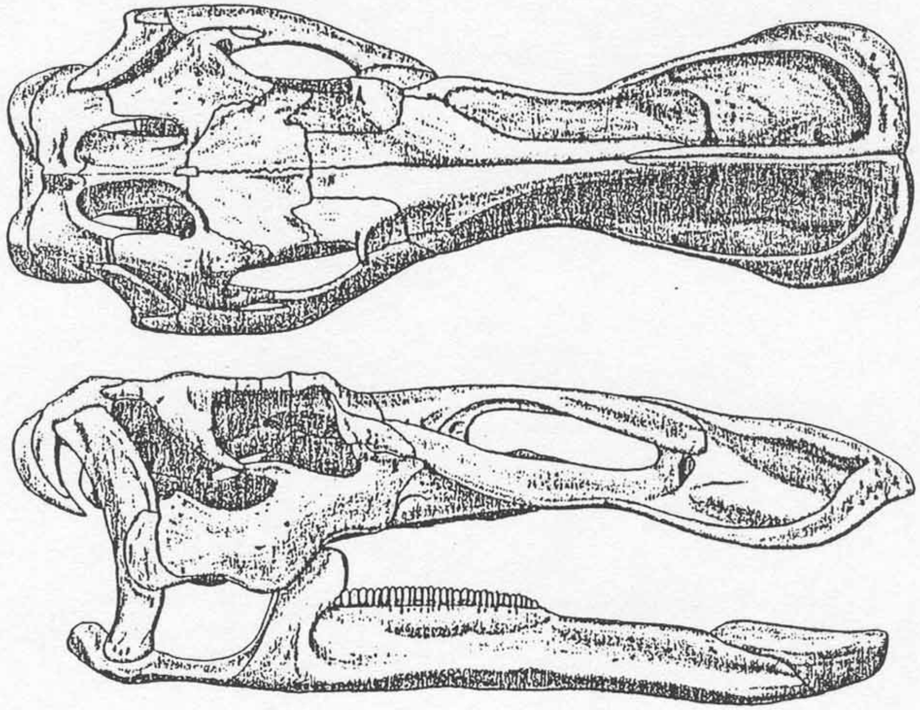


Plate 10

The skull of **Anatotitan copei** based on AMNH 5730 and AMNH 5886 in dorsal view (top) and right lateral view (bottom). Quadrate length is 320mm. Original reconstruction by Gregory S. Paul under my direction.

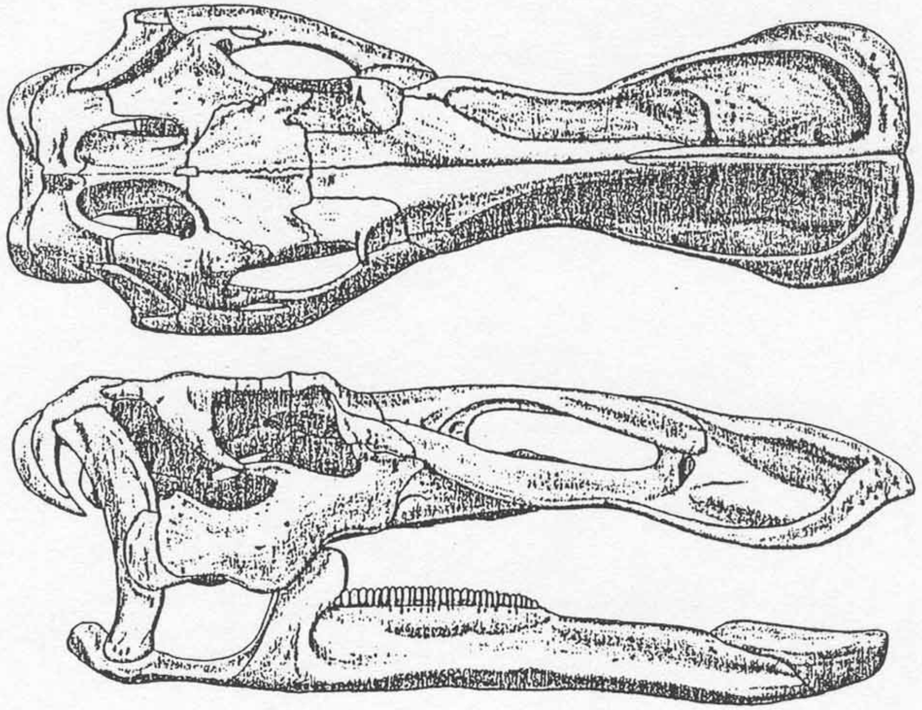


Plate 9

Restoration of **Edmontosaurus annectens**, a hadrosaurine, based on YPM 2182. Original art by Gregory S. Paul under my direction. Femur length is 1053mm. Left lateral view.

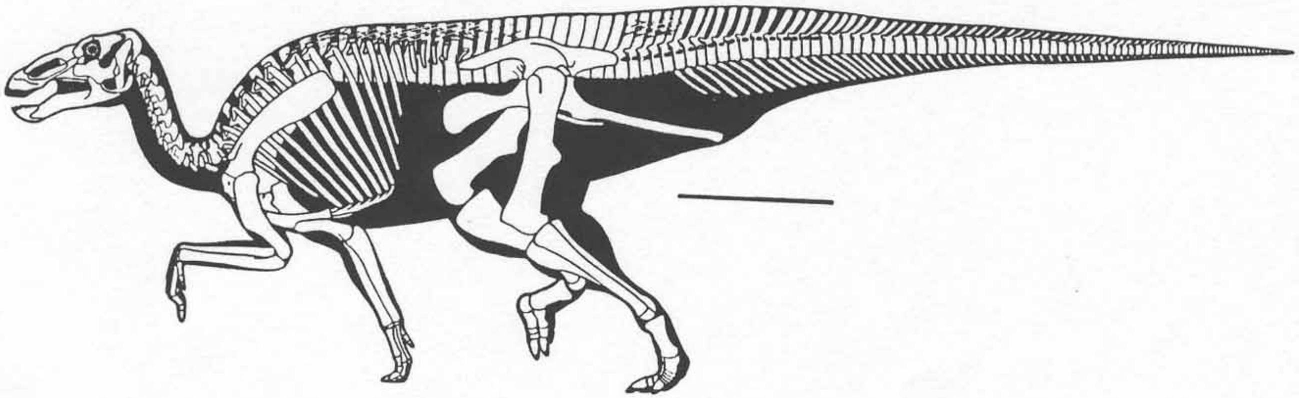


TABLE 2

SELECTED POSTCRANIAL MEASUREMENTS OF THE HADROSAURINAE

	SCAP-L	SCAP-W	HUM-L	DPL-L	DPL-W
Anatotitan copei (AMNH 5730)	950	215	670	350	155
Brachylophosaurus canadensis (NMC 8893)	890	90	590	290	110
Edmontosaurus annectens (YPM 2182)	895	195	590	294	131
Edmontosaurus edmontoni (NMC 2288)	1015	215	587	340	124
Edmontosaurus regalis (ROM 867)	800	178	*	*	*
Gilmoreosaurus mongoliensis (AMNH 6551)	430e	106e	315	145	120
Hadrosaurus foulkii (ANSP 10005)	*	*	556	236	120
Kritosaurus incurvimanus (ROM 764)	800	178	597	330	114
Prosaurolophus maximus (ROM 787)	870	213	533	268	140
Saurolophus osborni (AMNH 5220)	900	220	590	290	180
Secernosaurus koerneri (FMNH P13423)	400e	95	*	*	*
Shantungosaurus giganteus (Hu 1973)	1365	270	1020	585	218
Tanius sinensis (Wiman,1929,Pl.1-9)	820	110	510	240	150

Abbreviations:L=length,W=width,H=heigth,SCAP=scapula,HUM=humerus, DLP=deltopectoral process,RAD=radius,ULN=ulna,MC3=metacarpal III, FEM=femur,TIB=tibia,MT3=metatarsal III, R/H=radius/humerus ratio, U/H=ulna/humerus ratio,MC3/H=metacarpal III/humerus ratio, HL/FL= hindlimb/forelimb ratio, PAL=pubic length, PAH=pubic heigth, T/F= tibia/femur ratio,MT3/F=metatarsal III/femur ratio : see table 11 for the system of measurements used.

TABLE 2 CONTINUED

	RAD-L	ULN-L	MC3-L	FEM-L	TIB-L	MT3-L
Anatotitan copei (AMNH 5730)	615	690	310	1135	940	430
Brachylophosaurus canadensis (NMC 8893)	650	725	*	*	*	*
Edmontosaurus annectens (YPM 2182)	555	600	273	1053	947	276
Edmontosaurus edmontoni (NMC 2288)	610	655	272	1118	930	345
Edmontosaurus regalis (ROM 867)	*	*	*	965	902	330
Gilmoreosaurus mongoliensis (AMNH 6551)	307	358	*	720	660	*
Hadrosaurus foulkii (ANSP 10005)	504	540	*	984	892	288
Kritosaurus incurvimanus (ROM 764)	559	616	229	1041	889	324
Prosaurolophus maximus (ROM 787)	473	546	238	997	860	321
Saurolophus osborni (AMNH 5220)	555	640	330	1190	1000e	340
Secernosaurus koerneri (FMNH P13423)	*	*	*	*	*	*
Shantungosaurus giganteus (Hu 1973)	852	1042	398	1650	1448	550e
Tanius sinensis (Wiman 1929)	561	*	*	1050	930	402

TABLE 2 CONTINUED

	ILIUM-L	ILIUM-H	PUBIS-L	PUBIS-H
Anatotitan copei (AMNH 5730) (a=AMNH 5887)	1170a	190a	800	240
Brachylophosaurus canadensis (NMC 8893)	*	*	*	*
Edmontosaurus annectens (YPM 2182)	1195	175	615	280
Edmontosaurus edmontoni (NMC 2288)	1020	196	610	210
Edmontosaurus regalis (ROM 867)	1153	207	533	229
Gilmoreosaurus mongoliensis (AMNH 6551)	666e	150e	*	*
Hadrosaurus foulkii (ANSP 10005)	724e	176	*	*
Kritosaurus incurvimanus (ROM 764)	1012	210	533	171
Prosaurolophus maximus (ROM 787)	991	179	533	210
Saurolophus osborni (AMNH 5220)	1195	265	465	215
Secernosaurus koerneri (FMNH P13423)	533e	102	230	75
Shantungosaurus giganteus (Hu 1973)	1628	315	870	379
Tanius sinensis (Wiman 1929)	920	200	*	*

TABLE 3

SELECTED POSTCRANIAL RATIOS OF THE HADROSAURINAE

	SCAP-L/W	DLP-L/W	R/H	U/H	MC3/H
Anatotitan copei (AMNH 5730)	4.42	2.26	.918	1.03	.463
Brachylophosaurus canadensis (NMC 8893)	5.29	2.64	1.10	1.23	.430
Edmontosaurus annectens (YPM 2182)	4.59	2.33	.942	1.02	.463
Edmontosaurus edmontoni (NMC 2288)	4.72	2.74	1.04	1.12	.463
Edmontosaurus regalis (ROM 867)	4.50	*	*	*	*
Gilmoreosaurus mongoliensis (AMNH 6551)	4.06	1.21e	.970	1.14	*
Hadrosaurus foulkii (ANSP 10005)	*	1.96	.906	.971	*
Kritosaurus incurvimanus (ROM 764)	4.50	2.89	.936	1.03	.383
Prosaurolophus maximus (ROM 787)	4.09	1.91	.886	1.02	.446
Saurolophus osborni (AMNH 5220)	4.09	1.61	.940	1.08	.541e
Secernosaurus koerneri (FMNH P13423)	4.21e	*	*	*	*
Shantungosaurus giganteus (Hu 1973)	5.05	2.69	.835	1.02	.390
Tanius sinensis (Wiman 1929)	7.45e	1.60	1.10	*	*

TABLE 3 CONTINUED

	HL/FL	ILIUM-L/H	PAL/PAH	T/F	MT3/F
Anatotitan copei (AMNH 5730)	1.54	6.16	1.87	.828	.379
Brachylophosaurus canadensis (NMC 8893)	*	*	*	*	*
Edmontosaurus annectens (YPM 2182)	1.61	6.83	2.22	.899	.262
Edmontosaurus edmontoni (NMC 2288)	1.63	5.20	2.66	.832	.308
Edmontosaurus regalis (ROM 867)	*	5.60	2.50	.934	.342
Gilmoreosaurus mongoliensis (AMNH 6551)	*	4.44	3.13e	.920	*
Hadrosaurus foulkii (ANSP 10005)	*	*	*	.906	.293
Kritosaurus incurvimanus (ROM 764)	1.63	4.82	2.55	.853	.311
Prosaurolophus maximus (ROM 787)	1.75	5.57	2.17	.863	.321
Saurolophus osborni (AMNH 5220)	1.66e	4.51	2.00e	.840	.286
Secernosaurus koerneri (FMNH P13423)	*	5.25	4.81	*	*
Shantungosaurus giganteus (Hu 1973)	1.60	5.17	2.54	.877	.333
Tanius sinensis (Wiman 1929)	*	4.60	2.50	.886	.383

TABLE 4

SELECTED POSTCRANIAL MEASUREMENTS OF THE THE LAMBEOSAURINAE

	SCAP-L	SCAP-W	HUM-L	DLP-L	DLP-W
Bactrosaurus johnsoni (AMNH 6577)	520e	120e	*	*	*
Corythosaurus casuarius (AMNH 5240)	890	200	*	310	*
Hypacrosaurus altispinus (NMC 8501)	766	201	510	292	145
Nipponosaurus sachaliensis (HIUM 6590)	*	*	*	*	*
Lambeosaurus lambei (ROM 1218)	914	203	521	298	159
Lambeosaurus magnicristatus (TMP 66.4.1)	780	195	505	270e	150e
Parasaurolophus cyrtocristatus (FMNH P27393)	858	245	565	305	160
Parasaurolophus walkeri (ROM 768)	940	248	520	310	156
Tsintaosaurus spinorhinus (PMNH V728)	968	216	612	280	112

TABLE 4 CONTINUED

	RAD-L	ULN-L	MC3-L	FEM-L	TIB-L	MT3-L
Bactrosaurus johnsoni (AMNH 6553)	*	*	*	800	*	240
Corythosaurus casuarius (AMNH 5240)	635	660	410	1080	1000	380
Hypacrosaurus altispinus (NMC 8501)	620	665	239	1074	995	384
Nipponosaurus sachaliensis (HIUM 6590)	251	263	*	527	477	190
Lambeosaurus lambei (ROM 1218)	610	679	254	1067	953	343
Lambeosaurus magnicristatus (TMP 66.4.1)	675e	*	277	1055	1010	*
Parasaurolophus crytocristatus (FMNH P27393)	585	665	220	1172	1034	350
Parasaurolphus walkeri (ROM 768)	496	560	208	1032	*	*
Tsintaosaurus spinorhiunus (PMNH V728)	752	832	224	1000	1050	336

TABLE 4 CONTINUED

	ILIUM-L	ILIUM-W	PUBIC-L	PUBIC-W
Bactrosaurus johnsoni (AMNH 6577)	690	200	402	348
Corythosaurus casuarius (AMNH 5240)	1035	205	490	270
Hypacrosaurus altispinus (NMC 8501)	917	190	393	216
Nipponosaurus sachaliensis (HIUM 6590)	*	*	*	*
Lambeosaurus lambei (ROM 1218)	1003	203	470	235
Lambeosaurus magnicristatus (TMP 66.4.1)	*	*	*	*
Parasaurolophus cyrtocristatus (FMNH P27393)	975	253	430	285
Parasaurolophus walkeri (ROM 768)	1015	275	516	260
Tsintaosaurus spinorhinus (PMNH V728)	1040	224	528	296

TABLE 5

SELECTED POSTCRANIAL RATIOS OF THE LAMBEOSAURINAE

	SCAP-L/W	DLP-L/W	R/H	U/H	MC3/H
Bactrosaurus johnsoni (AMNH 6553)	2.89	*	*	*	*
Corythosaurus casuarius (AMNH 5240)	4.45	*	*	*	*
Hypacrosaurus altispinus (NMC 8501)	3.81	2.01	1.22	1.30	.496
Nipponosaurus sachaliensis (HIUM 6590)	*	*	*	*	*
Lambeosaurus lambei (ROM 1218)	4.50	1.88	1.17	1.30	.489
Lambeosaurus magnicristatus (TMP 66.4.1)	4.00	1.80	1.34	*	.450
Parasaurolophus cyrtocristatus (FMNH P27393)	3.50	1.91	1.03	1.18	.392
Parasaurolophus walkeri (ROM 768)	3.79	1.99	.953	1.08	.400
Tsintaosaurus spinorhinus (PMNH V728)	4.48	2.50	1.23	1.36	.366

TABLE 5 CONTINUED

	HL/FL	ILIUM-L/W	PAL/PAH	T/F	MT3/F
Bactrosaurus johnsoni (AMNH 6553)	*	3.45	2.14	*	.300
Corythosaurus casuarius (AMNH 5240)	*	5.05	1.80	.926	.352
Hypacrosaurus altispinus (NMC 8501)	1.72	4.83	1.90	.926	.358
Nipponosaurus sachaliensis (HIUM 6590)	*	*	*	.907	.361
Lambeosaurus lambei (ROM 1218)	1.71	4.94	2.40	.893	.321
Lambeosaurus magnicristatus (TMP 66.4.1)	*	*	*	.957	*
Parasaurolophus cyrtocristatus (FMNH P27393)	1.86	3.85	1.50	.883	.298
Parasaurolophus walkeri (ROM 768)	*	3.69	1.66	*	*
Tsintaosaurus spinorhinus (PMNH V728)	1.49	4.64	1.91	1.15	.336

TABLE 6

SELECTED POSTCRANIAL MEASUREMENTS OF THE CAMPTOSAURIDAE AND IGUANODONTIDAE

	SCAP-L	SCAP-W	HUM-L	DLP-L	DLP-W
Camptosaurus dispar (USNM 4282)	482	175	360	152	80
Camptosaurus dispar (CM 11337)	290	117	227	*	*
Iguanodon bernissartensis (IRSNM 1534)	962	187	820	289	159

	RAD-L	ULN-L	MC3-L	FEM-L	TIB-L	MT3-L
Camptosaurus dispar (USNM 4282)	232	262	*	*	*	*
Camptosaurus dispar (CM 11337)	143	160	45	395	360	158
Iquanodon bernissartensis (IRSNB 1534)	530	650	190e	1020	890	340

	ILIUM-L	ILIUM-W	PUBIC-L	PUBIC-W
Camptosaurus dispar (USNM 4282)	618e	115	*	*
Camptosaurus dispar (CM 11337)	400e	70	221	55
Iguanodon bernissartensis (IRSNB 1534)	1030e	200	553	94

TABLE 6 CONTINUED

SELECTED POSTCRANIAL RATIOS OF THE CAMPTOSAURIDAE AND IGUANODONTIDAE

	SCAP-L/W	DLP-L/W	R/H	U/H	MC3/H
Camptosaurus dispar (USNM 4282)	2.75	1.90	.640	.730	*
Camptosaurus dispar (CM 11337)	2.48	2.25	.629	.705	.198
Iguanodon bernissartensis (IRSNB 1534)	6.76	1.82	.633	.827	.242

	HL/FL	ILIUM-L/W	PAL/PAH	T/F	MT3/F
Camptosaurus dispar (USNM 4282)	*	4.60e	1.00	*	*
Camptosaurus dispar (CM 11337)	2.20	3.89	.980	.911	.400
Iguanodon bernissartensis (IRSNB 1534)	1.48	5.13	2.86	.849	.336

CHAPTER 6

THE GENERA OF HADROSAURIDS

A REVIEW OF EACH GENUS IN ALPHABETICAL SEQUENCE

Each genus of hadrosaurid must now be reviewed in the light of the characters, and revised diagnoses of the supra-generic clades, set forth above. The following review covers all forty-seven genera of hadrosaurids named as of 1986. The genera are listed alphabetically for the sake of utility.

1) *Aachenosaurus* Smets, 1888:

[Type species *A. multidens*]

The type specimen of *Aachenosaurus* consists of fossil wood (Dollo 1888) and is therefore not valid and must no longer be cited as a hadrosaurid.

2) *Anatosaurus* Lull and Wright, 1942

[Type species *A. annectens*]

Anatosaurus was erected by Lull and Wright (1942) to end the confusion generated by a wealth of species of such obsolete taxa as *Trachodon*, *Thespesius*, and *Diclonius*. Lull and Wright concluded that most of the older terms for the flat-headed forms (Hadrosaurinae) were no more than *nomina dubia* for isolated postcranial remains, worn teeth, and headless specimens. By erecting *Anatosaurus*, they hoped to separate the latest Maastrichtian forms from the more robust and earlier *Edmontosaurus* (Plates 8 and 9). Ironically, they chose the most *Edmontosaurus*-like form, *Anatosaurus saskatchewanensis*, as the basis for their comparison. The characters used by Lull and Wright (1942) for the distinction were as follows:

1) The muzzle of *Edmontosaurus* is more "tumid" in appearance.

2) The outline of the orbit is more nearly subtriangular in *Anatosaurus*.

3) The infratemporal fossa of *Edmontosaurus* is more

restricted dorsally.

4) In Edmontosaurus, the squamosals meet in the midline.

5) Edmontosaurus lacks a frontal dome.

Character number one is invalid because both Edmontosaurus and Anatosaurus have equally "tumid" muzzles. A tumid premaxilla is a synapomorphy of the Edmontosaurini as defined above. The process of fossilization also causes frequent and severe damage to this area, which also applies to character number two. These characters are present in all members of the Edmontosaurini and cannot be used to separate genera.

Character number three is invalid because it applies to most hadrosaurids. Virtually all skulls are preserved lying on their sides. Lateral compression after burial tends to squeeze the two halves of the skull together, resulting in the impression of 'closure' of open spaces.

Characters four and five are invalid because they vary with age within populations (Langston, 1960). Frontal doming is also a characteristic of juveniles (see especially Langston, 1960 and Ostrom, 1961).

At the generic level, Anatosaurus and Edmontosaurus (with the exception of "A." copei) are inseparable cranially and postcranially. I therefore follow Rozhdestvenski (1968) in regarding Anatosaurus (fide Lull and Wright, 1942) as the junior synonym of Edmontosaurus (fide Lambe, 1920). Only "A." copei stands out morphologically on both cranial and postcranial evidence. It is distinct from all Edmontosaurus and Anatosaurus species at the generic level and therefore deserves its own generic name. I am establishing the following new generic name for the reception of "A." copei (Brett-Surman, MS and Plates 10 and 11).

3) Anatotitan new genus

[type species A. copei (Lull and Wright)]

Diagnosis: Skull longer, lower and wider than in any other hadrosaurid; quadrate length/mandibular length the smallest of any hadrosaurid of the same size; edentulous portion of the mandible the longest of any hadrosaurid; appendicular elements relatively longer and more gracile than in any hadrosaurines of the same size; limb elements up to 10% longer than in an Edmontosaurus of the same age; neck of the prepubic blade longer and shallower than in any other hadrosaurid. Borders of postacetabular process tend not to be parallel.

Discussion: Anatotitan is the epitome of hadrosaurine evolution. The type skull (AMNH 5730), which is relatively longer and lower than in any other hadrosaurid, would tend to give the impression, from pictures, that it was crushed (Molnar 1978) but an analysis of the type shows this is certainly not the case. The quadrates are slightly bowed out laterally at their ventral extremity, which is to be expected in a skull that was fossilized in 'natural' position. The type skull of Edmontosaurus (NMC 2288) is also skewed, but in a more oblique-dorsal direction. The rest of the skull of Anatotitan is undamaged and all the sutures are intact. The slight deformation has been taken into account in the restorations presented here (Plate 10). Even total compaction would not obliterate the most diagnostic feature of the skull, the extreme elongation of the preorbital area. In essence, Anatotitan has increased the muzzle area (laterally and anteriorly) into a snow-shovel-shaped structure that seems adapted to gather in more plants per mouthful.

Anatotitan had the weakest anterior bite of any hadrosaurid. [For the most complete discussion of hadrosaurid jaw mechanics, see Weishampel (1983) and references therein]. To compensate for the weakness of the bite, the mandible was slightly deeper for increased muscle attachment, and the dental battery was concentrated in the rear of the jaw for a more forceful bite. The ratio of tooth row length to mandible is quite small, but the mandible is so long that the absolute length of the tooth row is equal to that of any other hadrosaurid. Up to 60 rows of teeth have been counted. The edentulous portion, however, is larger than in other hadrosaurids. The hindlimbs are also relatively longer than in most other hadrosaurids, a condition shared with Saurolophus.

Removal of Anatotitan from Edmontosaurus leaves two, rather than three, distinct morphs for Edmontosaurus. These two morphotypes are represented by E. regalis on the one hand and E. annectens and E. edmontoni on the other. E. regalis could be a male and both E. annectens and E. edmontoni could be females. It is also possible that they are 'stratigraphic species' because E. regalis is known only from the Campanian whereas E. annectens and E. edmontoni are restricted to the Maastrichtian. This cannot be confirmed without more specimens of E. regalis.

4) Aralosaurus Rozhdestvenskii, 1968

[Type species A. tuberiferus]

The diagnosis was based on a partial skull from the Santonian(?) of eastern Europe. The nasal apparatus closely resembles that of Kritosaurus. Several postcranial elements were referred to the type but not figured or identified by museum number. Their association with the type skull is therefore not documented.

Kritosaurus seems to be a cosmopolitan genus as it is found in both Euramerica and Asiamerica as well as Gondwanaland (Bonaparte 1986). Aralosaurus may be a species of Kritosaurus, but material currently available is insufficient for resolving this question. I am adopting the position, for this report, that the two taxa can be synonymized only if complete specimens (skull and both pectoral and pelvic girdles) can be found, for Aralosaurus. This taxon is, in any case, referrable to the Kritosaurini.

5) Arstanosaurus Shilin and Suslov, 1982

[Type species A. akkurganensis]

Arstanosaurus is based on a partial maxilla with worn teeth. The diagnosis of Shilin and Suslov (1982) lists three characters which are as follows:

1) Maxilla massive and low.

2) Dorsal edge of maxilla practically straight.

3) Horizontal edge above shelf.

The first two features are not useful because of the incomplete and worn condition of the type specimen, and because both features are plesiomorphic for hadrosaurids. Feature number two is unusually worded and too vague to be useful. The dorsal edge of the maxilla forms an obtuse angle, and both sides are relatively straight in all known hadrosaurids. The third feature may reflect ontogenetic or populational variation and is not diagnostic at the generic level. The type material is insufficient for a new genus and therefore this form should be considered a nomen dubium.

Both Kurzanov (letter) and Sereno (pers. comm.) have informed me of several adult and complete specimens of Arstanosaurus. These forms may indeed be new to science and deserve a complete description, although the name Arstanosaurus should not be used for them. Weishampel (pers. comm.) states that one of the holotype teeth is double-rooted, which would make it a ceratopsian tooth and not a hadrosaurid.

6) *Bactrosaurus* Gilmore 1933

[Type species *B. johnsoni*]

Bactrosaurus (Plate 12) is founded on a partial skeleton and an unassociated partial skull, with several juveniles from the same quarry. It has been proposed as the first true member of the Lambeosaurinae (Brett- Surman, 1979). Postcranially, *Bactrosaurus* is most similar to *Parasaurolophus* (Plate 16) and *Tsintaosaurus* (Plate 18). Both have a greatly expanded, 'footed' ischium, a very thick ischial shaft, prepubes with the largest l/h ratio of the pubic blade, and the smallest l/h ratio of the pubic neck. *Bactrosaurus* shows some evidence of a cranial crest in isolated, referred cranial elements (Weishampel and Horner, 1986). Although the vast majority of the specimens originally collected are juveniles, the type is certainly an adult, as demonstrated by its size and the robustness of its ischium. Because of the difference in geologic age, and the similarity of the pelvic girdle with *Parasaurolophus*, *Bactrosaurus* may be ancestral to *Parasaurolophus*.

Young (1958) questioned whether *Bactrosaurus* and *Tanius* might be congeneric or whether both genera are too poorly founded for a proper determination of their synonymy. Comparison of the postcranial material referred to *Tanius* by Young (1958) shows it to fall well within the boundaries of the Hadrosaurinae as rediagnosed here. The postcranial bones of *Bactrosaurus* are clearly lambeosaurine-like. After an analysis of the type material, I am fully confident that *Bactrosaurus* is well founded and it is here assigned to the Parasaurolophini. The type is based on an adult and there is only one large adult present, the other specimens in the quarry being of younger ontogenetic age.

7) *Barsboldia* Maryanska and Osmolska, 1981

[Type species *B. sicinskii*]

The type material consists of a very robust series of dorsal and sacral vertebrae with an associated ilium. The material is very close to *Hypacrosaurus* and unlike any other Asian hadrosaurid. The sigmoidal curve of the dorsal border of the ilium is like *Kritosaurus* but the robustness and height of the ilium, relative to its length, falls within the

Lambeosaurinae. The distal ends of the neural spines are club-like and may be the result of 'old age', but the sample size of very old hadrosaurids is insufficient at this time for a definitive statement concerning vertebrae. I regard this genus as an Asian lambeosaurine but a *nomen dubium*.

8) *Brachylophosaurus* Sternberg, 1953

[Type species *B. canadensis*]

This genus has been placed by Sternberg (1953) and Ostrom (1961) into the Saurolophinae because the nasals extend posteriorly over the frontals in a flat 'crest'. This 'crest' is reminiscent of *Saurolophus* but only in its posterodorsal position and not in its shape. In *Brachylophosaurus*, the nasals are flat and straight as compared to *Kritosaurus*, where they are elevated above the profile of the face in lateral aspect. *Kritosaurus*- like nasals are also present in *Brachylophosaurus*, hence I transfer *Brachylophosaurus* from the Saurolophini to the Kritosaurini. The postcranial evidence also supports this view. The scapula and humerus are more similar to those of *Kritosaurus* than to those of either *Saurolophus* or *Prosaurolophus*.

9) *Cheneosaurus* Lambe, 1917A

[Type species *C. tolmanensis*]

Dodson (1975), in a study of cranial morphology in *Corythosaurus* and *Lambeosaurus*, concluded that the "procheneosaurs" (*Cheneosaurus* and *Procheneosaurus* fide Lull and Wright, 1942) were actually juveniles of *Corythosaurus* and *Lambeosaurus*. I find that the 'foot' on the ischium (Plate 6) in 'procheneosaurs' is acquired during growth (on the basis of USNM lot number 358593), which supports Dodson's hypothesis founded on cranial data.

Cheneosaurus is a genus from the Maastrichtian part of the Scollard Formation (= Edmonton-B of previous authors) and a contemporary of *Hypacrosaurus*. Lull and Wright (1942) have already discussed the relationships between *Procheneosaurus* and *Cheneosaurus* and between *Corythosaurus* and *Hypacrosaurus*. As stated below, the differences between *Corythosaurus* and *Hypacrosaurus* may be specific differences rather than generic. On the basis of postcranial data (Brett-Surman 1975,1979; Abel, 1924; and Nopsca and Heidsieck, 1933) and cranial data (Dodson 1975), *Cheneosaurus* is considered a juvenile of *Hypacrosaurus* and hence its name becomes a junior synonym of *Hypacrosaurus*.

Possible evidence against 'procheneosaurs' being juveniles of Corythosaurus is a skull of "Procheneosaurus" that exceeds in size an adult Corythosaurus skull. This skull (TPM 78.16.1) from the Judith River Formation (= Oldman Formation of other authors) of Alberta, was collected in 1978. It appears to be an excellent example of neoteny in which the juvenile morphology of an incipient crest has been carried over late into life. Even though "cheneosaurs" fit well into Corythosaurus and Lambeosaurus, some authors may retain the 'procheneosaurs' as valid taxa until a more complete growth series in the same horizon can be found. (see also Procheneosaurus).

10) Cionodon Cope, 1874

[Type species C. arctatus]

This genus was based on a partial maxilla, two dorsal vertebrae, the distal end of the third metatarsal, and a partial ulna. None of these elements permit a diagnosis at any taxonomic level, therefore Cionodon should be considered a nomen dubium.

11) Claorhynchus Cope, 1892

[Type species C. trihedrus]

Lull and Wright (1942) restudied this material, removed it from the Ceratopsia, and placed it in the Hadrosauridae. They stated that the material consists of a hadrosaur premaxilla and dentary. The writer and Douglas A. Lawson rediscovered the type material in the basement of the American Museum in New York and after having examined the specimen (AMNH 3978) concluded that it is part of a ceratopsian frill, most likely the lateral edge of the squamosal of Triceratops. Although the type is undiagnostic at the familial level because of its incompleteness, it is certainly not a hadrosaurid.

12) Claosaurus Marsh, 1872

[Type species C. agilis]

This genus was founded on Claosaurus agilis (YPM 1190) from the Niobrara Formation of Kansas. The material consists of a partial skull and a badly crushed skeleton that has been heavily restored in plaster. The ilium is the only complete postcranial element that displays diagnostic features and is hadrosaurine in morphology. Several iguanodontid-like (i.e., primitive) features are present. The l/h ratio of the ilium is smaller than in other hadrosaurines and the postacetabular process is relatively shorter and less developed than in other hadrosaurines. Only Secernosaurus has an ilium of more primitive appearance. The preacetabular process is slightly deflected and resembles that of the iguanodontids, but this may be due to crushing. The problematic presence of the first (possibly the fifth?) metatarsal has been discussed elsewhere (Gregory 1948).

Claosaurus, as currently defined, should be maintained as a valid taxon of hadrosaurines until more specimens are found in the Niobrara Formation or other early Campanian deposits. I regard this genus as a hadrosaurine, incertae sedis.

13) Corythosaurus Brown, 1914

[Type species C. casuarius]

This genus is based on a series of skulls and articulated skeletons (see Lull and Wright, 1942; Plates 13A and 13B, and Appendix 5). The postcranial elements, however, are inseparable from those of Lambeosaurus. It is possible that Lambeosaurus and Corythosaurus are different species of the same genus. Lambeosaurus magnicristatus and L. lambei could be respectively a male and female of one species and Corythosaurus casuarius and C. intermedius respectively a male and female of the other species.

Corythosaurus and Lambeosaurus should be retained as redefined by Dodson (1975) and Weishampel (1981) until more specimens of the rarer Lambeosaurus can be found and studied by multivariate techniques. (See also the discussion under Hypacrosaurus and Pteropelyx).

14) Diclonius Cope, 1876

[Type species D. pentagonus]

This is one of Cope's famous 'tooth genera' based on a combination of dentary and maxillary teeth. The teeth are heavily worn and isolated from their dental battery, which makes them absolutely useless for diagnostic purposes. Lull and Wright (1942) cited two of the three cotypes as lost, but in 1973 I found some worn teeth in the basement of the American Museum of Natural History in New York that were labelled Diclonius in faded ink in a handwriting that closely resembled Cope's. These teeth are heavily worn and have no taxonomic value below the level of family. They were turned in for cataloging and I have not seen them since. This genus is regarded as Hadrosauridae nomen dubium.

15) Didanodon Osborn in Osborn and Lambe, 1902

[Type species D. altus]

Didanodon was mentioned in passing by Osborn (1902) in reference to Lambe's species Procheneosaurus altus. The exact citation is "P. (Didanodon) altus", which implies that Osborn intended the name to signify either a subgenus or a taxon to be erected at full generic rank. It does not appear in the Bibliography of Fossil Vertebrates, and the only recent citation is in Steel (1969). In any event, the name was never republished and never diagnosed or discussed, and is therefore a nomen nudum.

16) Dysganus Cope, 1876

[Type species D. encaustus]

This is another of Cope's 'tooth genera'. The four species named by Cope are based on isolated, worn teeth of both hadrosaurids and ceratopsians. Lull and Wright (1942) reported that Matthew had chosen certain ceratopsian teeth as lectotypes for each species, but these lectotype designations were never published. None of the teeth is diagnostic below the family level and all the species are therefore nomina dubia. The ceratopsian genus is listed here because it appears in Lull and Wright (1942).

17) Edmontosaurus Lambe, 1917B

[Type species E. regalis]

Edmontosaurus is based on a complete skeleton (unprepared) and skull, with many complete specimens referred (Plates 8 and 9). As discussed under Anatotitan, this genus characterizes the Edmontosaurini. Enough complete specimens exist to assure that Edmontosaurus is the senior synonym of Anatosaurus (Brett-Surman, 1979).

Although there are several species assigned to Edmontosaurus (E. edmontoni, E. annectens, E. regalis, E. saskatchewanensis), I recognize only two morphotypes. The first, which is the rarest, is illustrated by the type species E. regalis (NMC 2288), with robust skull and low skull length/height ratio. The more common second morphotype is illustrated by E. annectens (such as YPM 2182), with a longer, lower, and less robust skull. E. edmontoni (NMC 8399) is morphologically indistinguishable from E. annectens and is therefore a junior synonym of it. E. saskatchewanensis was made a junior synonym of E. regalis by Russell and Chamney (1967). This creates the possibility that E. annectens and E. regalis are actually two sexes, the more robust E. regalis representing the male, and the more gracile E. annectens the female. The most parsimonious interpretation is that this suite represents one species with two sexual morphs.

18) Gilmoreosaurus Brett-Surman, 1979

[Type species G. mongoliensis]

Gilmore (1933) described a new species of Mandschurosaurus (M. mongoliensis), from the Iren Dabasu beds of Mongolia. Examination of the plates of Riabinin's original description of Mandschurosaurus (1930) shows that every diagnostic feature of the holotype of the type species (M. amurensis) is missing and that the major landmarks of each element are restored in plaster, which Young (1958) also reported. Gilmore's species, "M." mongoliensis, is well described and diagnostic, but cannot be placed in Mandschurosaurus because the type species must be considered a nomen dubium (Brett-Surman 1979). The species "M". mongoliensis has been placed in a new combination, Gilmoreosaurus mongoliensis (Brett-Surman 1979), and represents the most primitive member of the Hadrosaurinae.

Many of the features of Gilmoreosaurus are transitional between the iguanodontids (fide Norman 1980) and the hadrosaurids. They are most striking in the pelvis of Gilmoreosaurus, where the ischium is curved and has a clubbed (but not fully footed) distal end, a plesiomorphic condition also found in the iguanodontids. The ilium has a definite postacetabular process which is smaller than in other hadrosaurids except Claosaurus agilis, and is twisted dorsomedially as in Secernosaurus. The antitrochanter is rudimentary and the pubic peduncle is large and thick, as in Bactrosaurus. The pubic blade curves ventrally as in true hadrosaurids. In the proximal row of pedal phalanges, the proximal margins of the phalanges are wider than the distal margins. The unguals are more clawlike (an iguanodontid feature) than hooflike (a hadrosaurid feature). Gilmoreosaurus is a contemporary of the first true lambeosaurine, Bactrosaurus.

19) Gryposaurus Lambe, 1914

[Type species G. notabilis]

The taxonomic history of this name has been adequately covered by Lull and Wright (1942) and need not be repeated here. It is agreed by most ornithischian workers that Gryposaurus is the junior synonym of Kritosaurus, which in turn is thought by Baird and Horner (1977) to be the junior synonym of Hadrosaurus. I also regard Gryposaurus as synonymous with Kritosaurus and well within the variation of that genus.

Horner (pers. comm. 1986) is resurrecting Gryposaurus as distinct from Hadrosaurus (=Kritosaurus fide Baird and Horner, 1977). Gryposaurus will be restricted to G. notabilis, a species from Alberta. The other species of Hadrosaurus (fide Baird and Horner 1977) is H. navajovius and is restricted to the San Juan Basin of New Mexico. This geographic partitioning will result in a northern genus (Gryposaurus) and a southern genus (Hadrosaurus), presumably the result of allopatric speciation. The morphological criterion for the separation of these two genera is based primarily on tooth structure, which I regard as suspect for taxonomic purposes. As I have not seen Horner's justification for his separation, I regard Gryposaurus as a junior synonym of Hadrosaurus, on the basis of my studies.

20) Hadrosaurus Leidy, 1858

[Type species H. foulkii]

Hadrosaurus has several species referred to it but only the type species, H. foulkii (holotype ANSP 10005), is based on diagnostic postcranial material. Several isolated fragments found with the type, especially a humerus, are strikingly similar to Kritosaurus (fide Brown 1910, Parks 1920). Kritosaurus is based on many excellent skulls and skeletons. Hadrosaurus does not have adequate cranial material referred to any of its species, hence comparisons with the types of these genera can only be made with postcranial elements. Baird and Horner (1977) made an extensive study of the cranial and postcranial material referred to both genera and concluded that they are congeneric, with Hadrosaurus retaining priority. I prefer to retain Kritosaurus (Plate 14) for current use, because it is better defined, has associated complete skulls with skeletons, and because it is the most widely known and best represented genus in its clade. Genera cannot be separated taxonomically in the Kritosaurini on the basis of only postcrania because the morphological overlap between the genera is extensive.

In conclusion, *Hadrosaurus* is here restricted to the type species, *H. foulkii*, and is not considered the senior synonym of *Kritosaurus* (fide Baird and Horner 1977) and *Gryposaurus* (fide Lull and Wright 1942). Studies of the postcrania show that *Kritosaurus*, *Hadrosaurus*, and *Gryposaurus* are too similar to each other to be separated taxonomically, therefore the final determination of their taxonomic status must be made on complete cranial material.

21) *Hypacrosaurus* Brown, 1912

[Type species *H. altispinus*]

This genus is based on several skulls and partial skeletons (most notably NMC 8501, and AMNH 5204) from early Maastrichtian deposits. The cranium and pelvis suggest a very close relationship to *Corythosaurus*, except that the foot on the ischium is more like that of *Parasaurolophus*. The only differences between *Hypacrosaurus* and *Corythosaurus* are in the more robust 'toes' and 'heel' in the 'foot' of the ischium (Plate 6), and the taller neural spines. These are features that can be produced by bone deposition in very large individuals. In the skull, the crest is more pointed in *Hypacrosaurus*, the S-shaped narial loop is missing, and the fenestra on the medial wall of the lateral diverticulum is missing (Weishampel 1981). I regard these features as specific and not generic differences, in which case it would be easy to derive *Hypacrosaurus* from *Corythosaurus* and synonymize the latter with the former. Both taxa should be retained until a more adequate sample of *Hypacrosaurus* can be obtained to test the possibility of synonymy with *Corythosaurus*. Should a sufficient series of *Hypacrosaurus* specimens be found, all of which fall within the range of *Corythosaurus*, (as I suspect they will), then *Hypacrosaurus* has priority over *Corythosaurus* by one year.

22) *Hypsibema* Cope, 1869B

[Type species *H. crassicauda*]

Hypsibema is based on postcranial elements (USNM 6136, 7189) which consist of a caudal centrum, partial tibia, and second metatarsal. None of the elements expresses diagnostic features, so this genus is a *nomen dubium*. Baird and Horner (1979) transferred *Hypsibema* to the Sauropoda and synonymized it with Parrosaurus on the basis of the morphology of the caudal centrum. This has not met with universal acceptance (McIntosh, pers. comm.), so the question of its subordinal assignment remains open. It is to be hoped that the report of Baird and Horner (1979) will inspire someone to return to the site and excavate the remainder of this enigmatic animal. Until the question is resolved, Hypsibema should not be used in statistical summaries or in paleobiogeographic studies.

23) Jaxartosaurus Riabinin, 1939

[Type species J. aralensis]

The type species is based on a partial skull from the Santonian(?) of eastern Europe in the area of the Jaxartes River. Because there is no evidence of a lambeosaurine crest, Jaxartosaurus was assigned to the Hadrosaurinae. Rozhdestvenskii (1968) described new cranial material of a hadrosaurid which he referred to this genus. Because the new material showed features similar to Corythosaurus, a lambeosaurine, he redefined the genus and transferred it to the Lambeosaurinae. The postcranial material referred to this genus does not contain any pelvic elements so the postcranials cannot be used to aid in a taxonomic diagnosis. It is possible that postcranial elements were recovered but there is no indication of this in the literature. It must be emphasized that although this genus is now treated as "the Asian lambeosaurine", new species must not be referred to Jaxartosaurus because the type species is indeterminate and a nomen dubium.

Nipponosaurus (see below), a juvenile lambeosaurine, is considered a synonym of Jaxartosaurus by some workers because Nipponosaurus is a juvenile and Jaxartosaurus is an adult and both are from Asia. This is a non sequitur; therefore the two genera must be kept separate because they cannot be either distinguished or synonymized from one another on the basis of morphology.

24) Kritosaurus Brown, 1910

[Type species K. navajovius]

The history of this name has been adequately summarized in Lull and Wright (1942) and in Baird and Horner (1979). Although Kritosaurus has been synonymized with Hadrosaurus (Baird and Horner 1979), papers subsequently published have not accepted this synonymy. In contrast to Hadrosaurus, which has no complete skull referred to it, and is restricted to the eastern part of the United States, Kritosaurus is well founded on complete skulls and skeletons (most notably NMC 2278, ROM 764; Plate 14) and is cosmopolitan in occurence. New discoveries since the turn of the century have turned up many specimens of Kritosaurus but no new skeletons of Hadrosaurus. These two genera should be kept separate, as discussed above under Hadrosaurus, until such time as a complete specimen or skull of Hadrosaurus from the eastern United States can be compared to Kritosaurus from the same geologic time and from the same ontogenetic age.

25) Lambeosaurus Parks, 1923

[Type species L. lambei]

The history of this genus has been extensively covered by Lull and Wright (1942). Dodson (1975) verified the status of Lambeosaurus in his morphometric study. The only autapomorphies separating Lambeosaurus from its closest contemporary Corythosaurus are the forward orientation of the crest and the vertically stacked chambers in the anterior part of the crest, in contrast to the vertically oriented crest and laterally placed chambers in the crest in Corythosaurus (Ostrom 1961, Dodson 1975). In all other features, these two genera are identical, especially in the postcranial elements. Both genera occur in the same beds, but Corythosaurus is by far the more numerous. It is possible that these small morphological differences are due to the differences between sibling-species, or between two sexes of the same species. These speculations may be resolved with larger sample sizes.

26) Lophorhothon Langston, 1960

[Type species L. atopus]

This genus is based on a partial skull and fragments of postcranial elements (FMNH P27383). The nasal crest is most similar to Prosaurolophus and especially to Maiasaura. The postcranial elements are too fragmentary and incomplete to be useful for diagnostic purposes. I agree with Langston (1960) in favoring retention of Lophorhothon on the basis of cranial features, despite the fragmentary nature of the material on which it is founded. The presence of an incipient crest is a condition present in all pre- Maastrichtian members of the Saurolophini, and Horner also (pers. comm.) maintains the separation of Lophorhothon from Maiasaura, which is based on a complete skull that has a relatively wider crest.

27) _Maiasaura_ Horner and Makela, 1979

[Type species _M. peeblesorum_]

This genus has gained great fame from its association with thousands of eggs found in Montana, but the type is a complete skull of an adult [YPM(PU)22405] found near a nest of hatchlings. It is easily distinguishable from all other genera, with its incipient solid crest widened laterally into a scoop-shaped structure (Plate 15), and relatively primitive teeth, on which the papillae are larger than in other hadrosaurines. _Maiasaura_ may be synonymous with _Lophorhothon_, but the latter is too fragmentary to support such a decision. A complete description of the _Maiasaura_ postcranials is in preparation by Horner's students (Horner, pers. comm.).

28) _Mandschurosaurus_ Riabinin, 1930

[Type species _M. amurensis_]

The history of this genus has been covered elsewhere (Brett-Surman 1979). _Mandschurosaurus_ is considered the principal "Asian hadrosaurine" (much as _Jaxartosaurus_ is viewed as the principal "Asian lambeosaurine") but the type of _Mandschurosaurus_ is mostly restored in plaster and original photos of the actual remains show that every diagnostic landmark of the postcrania and crania has been restored. This genus is a _nomen dubium_ and should not be used.

29) _Microhadrosaurus_ Dong, 1979

[Type species _M. nanshiungensis_]

This genus is based on a partial left mandible of a juvenile. The type specimen (IVVP 4732) is edentulous and only eighteen rows of tooth files are present. There is a complete absence of any diagnostic materials or autapomorphic features.

During ontogeny, the number of tooth rows increases to an average of about fifty-five in adults, and up to sixty rows have been counted in _Anatotitan_ (_Anatosaurus copei_ in Lull and Wright, 1942). The number of tooth rows is age-dependent and cannot be used for diagnostic purposes (Sternberg 1936). The teeth also change in proportion during ontogeny. The skull changes to an extraordinary degree in lambeosaurines (Dodson, 1975), the postcrania undergo a few 'pre-adult' changes (see above), and hadrosaurines have fewer diagnostic postcranial characteristics to rely on. The uncertainty of Asian stratigraphic correlation with faunas of other provinces and with marine beds renders the naming of 'biostratigraphic taxa' unacceptable. The use of juveniles as holotypes should be avoided. In the absence of any morphologic features of taxonomic utility, I regard _Microhadrosaurus_ as a _nomen dubium_.

30) _Nipponosaurus_ Nagao, 1936

[Type species _N. sachaliensis_]

A partial skull and skeleton of a single individual from Sakhalin Island (Union of Soviet Socialist Republics) is the basis of the type species, which was well described in two papers by Nagao (1936, 1938). The skull has an incipient cranial dome closest in appearance to the "procheneosaurs" (fide Lull and Wright, 1942). Cranial doming is a known juvenile characteristic (Langston 1960). The length of the hindlimb (femur length 533 mm) also indicates that the type is a juvenile (average femur length in adult hadrosaurids is about 1000 mm, see Tables 2 and 4). The postcranial elements, especially the ischium, are definitely lambeosaurine in appearance. The metacarpals are not uniformly straight and featureless as in most hadrosaurids. The third metacarpal is especially well developed and expanded at both articular ends, and its shaft is slightly curved. This could indicate the retention of a primitive character from an iguanodontid condition. Nor can the possibility of pathology be dismissed. _Nipponosaurus_ may prove to be a juvenile of an already established Asian lambeosaurine (Nagao, 1938) such as _Jaxartosaurus_. The name should be retained until adult specimens are found but as a lambeosaurine _incertae sedis_.

The horizon of the specimen is uncertain. The last available stratigraphic determination published was "Belly River equivalent" which would make it approximately Campanian (Nagao, 1938). The type specimen is currently being restudied by Professor T. Kamei (M. Kato, pers. comm.).

31) _Notoceratops_ Tapia, 1918

[Type species _N. bonarellii_]

The original specimen (an edentulous jaw) is lost but is now being actively sought (Bonaparte, pers. comm., 1983). Molnar (1980) stated that _Notoceratops_ (originally assigned to the Ceratopsia by Tapia) was a hadrosaurid because ceratopsians are not known from South America. This is circular reasoning. Taxonomic determinations should be based on morphology, not biogeography. Notoceratops must remain a ceratopsian until it can be shown to be otherwise on morphological grounds. Notoceratops should not be used in syntheses based on taxonomy because the type is lost and the available morphological descriptions are inadequate. The only available figure is an outline drawing that does not provide adequate information for an accurate taxonomic determination.

32) Ornithotarsus Cope, 1869

[Type species O. immanis]

This genus is based on a partial hindlimb consisting of the astragalus, calcaneum, and the distal ends of the fibula and tibia. The astragalus is typical of most genera (Type 1 as discussed above, Plate 7B) and a calcaneum is present. On this basis, it can be stated that Ornithotarsus is not synonymous with Parasaurolophus but any speculation beyond that point is unjustified. Ornithotarsus, due to the lack of diagnostic features, should be considered a nomen dubium.

Baird and Horner (1977) believe that Ornithotarsus and Hadrosaurus foulkii are synonymous, but this determination is based on biogeography, and the present material does not allow any more substantive statement than Hadrosauridae nomen dubium.

33) Orthomerus Seeley, 1883

[Type species O. dolloi]

The type is based on juvenile limb bones from the Maastrichtian of Holland, which were originally assigned to the Iguanodontidae. Seeley (1883) stated that there are no pelvic, tarsal, or cranial elements. Nopsca (1928) figures a referred partial sacrum with a ridged ventral surface, a lambeosaurine character. The precise status of Orthomerus must remain undetermined at this time and its traditional inclusion in the Iguanodontidae should be retained until it can be redefined on the basis of more complete specimens. This genus should be restricted to O. dolloi [BM(NH) 42955], the type species, and I regard the name as a nomen dubium. The one hadrosaurid referred to this genus, O. transylvanicus, is discussed below under Telmatosaurus.

34) Parasaurolophus Parks, 1922

[Type species P. walkeri]

This genus represents the most highly derived crested lambeosaurine (Plates 16A and 16B). The type species, P. walkeri, is based on a complete skull and complete postcranial skeleton (ROM 768) lacking only the hind limbs and the posterior two-thirds of the tail. A second species, P. cyrtocristatus (FMNH P27393), referred to this genus by Ostrom (1961B), is represented by an even more complete specimen. As this genus is well diagnosed, and unlike any other hadrosaurid (Parks 1922), it is clearly valid.

35) Pneumatoarthrus Cope, 1870

[Type species P. peloreus]

This genus has been thoroughly restudied by Baird and Horner (1977), who transfered it to the Testudinata. The caudal vertebrae are nothing like those of hadrosaurids, and I agree completely with their judgment. This genus should no longer be cited in hadrosaurid studies.

36) Procheneosaurus Matthew, 1920

[Type species not named]

Dodson (1975), in a landmark study, showed that the "procheneosaurs" were actually juveniles of Lambeosaurus and Corythosaurus. The lack of a footed ischium, as seen in procheneosaurs, is a growth feature in lambeosaurines (see above and the section on Cheneosaurus). The foot on the ischium appears when the ischium reaches a length of about 30 cm. The same reasoning applies to Cheneosaurus, which is regarded as a juvenile Hypacrosaurus based on cranial data (Dodson 1975) and on a comparison of postcranial elements of Hypacrosaurus with those of Cheneosaurus (Brett-Surman 1979). The idea that procheneosaurs and cheneosaurs are juvenile corythosaurs is not new, having been alluded to by Abel (1924) and Nopsca and Heidseick (1933). The name Procheneosaurus should be relegated to synonymy with Corythosaurus and Lambeosaurus.

37) Prosaurolophus Brown, 1916

[Type species P. maximus]

Prosaurolophus is well founded and based on several excellent skulls and skeletons (AMNH 5386, ROM 787; Plates 17A and 17B). Prosaurolophus is one of the few genera that has never been challenged taxonomically. The incipient spike on the skull shows a similarity to Maiasaura and Lophorhothon and is a shorter version of what is seen in *Saurolophus*. The shortened crest in *Prosaurolophus*, in the absence of any other major differences between it and *Saurolophus*, could be regarded as a specific difference. *Prosaurolophus* should be maintained until it can be shown, on the basis of a larger sample, that *Prosaurolophus maximus* and *Saurolophus osborni* are not chronospecies.

38) *Pteropelyx* Cope, 1889

[Type species *P. grallipes*]

The type species is based on pelvic and limb bones (AMNH 3791) indistinguishable from *Corythosaurus*. *Corythosaurus* and *Pteropelyx* are sympatric and are here regarded as synonymous on the basis of the postcranial similarities. *Pteropelyx* was described before *Corythosaurus*, and can be considered the senior synonym of *Corythosaurus*. However, as the type of *Pteropelyx* lacks a skull, and because the name has had only one specimen referred to it, it is not advisable to propose a synonymy that would cause unnecessary confusion. The name *Pteropelyx* should be abandoned in favor of *Corythosaurus*. This can only be done by appeal to the I.C.Z.N..

39) *Saurolophus* Brown, 1912

[Type species *S. osborni*]

Both species of *Saurolophus* are well founded on both skull and postcranial material (*S. osborni*, AMNH 5220; *S. angustirostris*, PIN 551-8). Although *Saurolophus* has an unfooted ischium, the postcranial elements are more like those of lambeosaurines than hadrosaurines in their robustness and iliac l/h ratio. The elongated, solid spike on top of the skull is unlike any other genus and there is no reason to question the validity of this taxon.

40) *Secernosaurus* Brett-Surman, 1979

[Type species *S. koerneri*]

This genus is based on a partial pelvis with ilium and pubis, several partial vertebrae, and a fragment of the basicranium (FMNH P13423). The morphology of the highly diagnostic ilium is most similar to that of the earliest hadrosaurine *Gilmoreosaurus*, (Plate 4G). Both *Secernosaurus* and *Gilmoreosaurus* share a postacetabular process that is dorso-medially twisted and proportionally shorter than in other hadrosaurids. These are features similar to what is seen in iguanodontids.

At present, *Secernosaurus* is one of two hadrosaurids named from South America - the other is *Kritosaurus australis* (Bonaparte 1983). Although it is not generally advisable to name taxa of hadrosaurids solely on the basis of postcrania, *Secernosaurus* was named because of the unique morphology of the ilium and the fact that it does not resemble other hadrosaurids except *Gilmoreosaurus*. I regard *Secernosaurus* as Hadrosaurinae *incertae sedis*.

41) *Shantungosaurus* Hu, 1973

[Type species *S. giganteus*]

Shantungosaurus is the largest known hadrosaurid and approaches sauropods in size. According to Hu (1973), the type specimen (IVPP, no number given) is a composite of "middle-sized" individuals. The femur from the figured specimen measures 1850 mm in length. (The largest referred femur is 2000 mm long.) With the exception of features related to size, such as robustness and elongated neural spines, *Shantungosaurus* is indistinguishable from *Edmontosaurus* and may be congeneric with it. This cannot be demonstrated because only one composite specimen has been published to date. *Shantungosaurus* should be maintained as a valid member of the Edmontosaurini until other material is found.

42) *Tanius* Wiman, 1929

[Type species *T. sinensis*]

This poorly known genus is based on disarticulated and unassociated cranial and postcranial material (ilium, Plate 4E) from the Campanian (?) of China. Referred pelvic material, as figured by Young (1958), shows that the ilium is more like that of a hadrosaurine than that of a lambeosaurine. A referred species, *T. chingkankouensis* (Young 1958), is close to *Gilmoreosaurus*, but the postacetabular process is proportionally longer. A referred skull (Young 1958) clearly shows *Tanius* to be a hadrosaurine, yet the proportionally taller sacral neural spines are more similar to those of the lambeosaurines. *Tanius* is therefore regarded as a hadrosaurine *incertae sedis*.

43) *Telmatosaurus* Nopsca, 1903

[Type species *T. transsylvanicus*]

Telmatosaurus transsylvanicus is based on a single specimen [BM(NH) R3386], and the genus is referred to as a junior synonym of *Orthomerus* by Steel (1969). This genus cannot, and should not, be referred to *Orthomerus* because the type species of *Orthomerus* is a *nomen dubium* based on inadequate material without cranial remains (see above), and the type femur of *Orthomerus dolloi* belongs to a juvenile. *T. transsylvanicus*, with an almost complete skull [BM(NH) R3386], was originally referred to *Limnosaurus* Marsh (preoccupied), and then to *Hecatasaurus* Brown (improperly defined), therefore the final designation by Nopsca (1903) as *Telmatosaurus* is the correct one. The skull of *Telmatosaurus* is most similar to that of *Edmontosaurus*. The postcrania of *Telmatosaurus* are still undescribed. This genus is here regarded as a member of the Edmontosaurini.

44) *Tetragonosaurus* Parks, 1931

[Type species *T. praeceps*]

[See discussion under *Corythosaurus* and *"Procheneosaurus"*]. This genus was proposed as a replacement name for *Procheneosaurus* because the latter was named without a species, making *Procheneosaurus* a *nomen nudum*. *Tetragonosaurus* has since been abandoned, and a complete history of this name is given in Lull and Wright (1942).

45) *Thespesius* Leidy, 1856

[Type species *T. occidentalis*]

This genus was based on several posterior caudal centra and a few phalanges of uncertain association (USNM 219, 220, 221). These elements are not diagnostic, even at the level of subfamily. A multitude of species with skulls and skeletons have been referred to this genus, but Lull and Wright (1942) placed them all in *"Anatosaurus"*. The name must be considered a *nomen dubium*.

46) *Trachodon* Leidy, 1856

[Type species *T. mirabilis*]

A single dentary tooth (ANSP 9260) is the lectotype for this genus. Hadrosaurid teeth are extremely variable and differ in morphology all along the dental battery. One can only discern that the more papillae a tooth has, the more 'primitive' it is. Teeth are here considered useless for diagnosis at the generic level but Horner is preparing evidence that teeth can be used to diagnose certain hadrosaurine genera. Sternberg (1936) stated that teeth could be used for diagnostic purposes only at the subfamilial level, but a useful diagnosis requires unworn teeth from the middle of the jaw. There are no postcranial elements with the type of Trachodon or with any referred species. Lull and Wright (1942) correctly considered the name Trachodon unusable; hence it is a nomen dubium.

47) Tsintaosaurus Young, 1958

[Type species T. spinorhynus]

Traditionally, this genus (Plate 18) was assigned to the Saurolophinae (Young 1958; Steel 1969). The cranial and postcranial elements (IVVP V725) indicate that Tsintaosaurus is more closely related to Parasaurolophus (Plate 16A) than to any other genus. The pelvic elements in particular are very similar to those of Parasaurolophus.

The skull of Tsintaosaurus also shows many similarities to Parasaurolophus (Plate 16A), including the possession of a hollow crest (Young 1958). The nasals are hollow tubes that are expanded distally and project dorso-posteriorly, unlike Saurolophus, in which the nasals are not hollow and do not expand distally. Tsintaosaurus differs from Parasaurolophus in one respect, that the premaxillae are neither expanded nor do they overide the nasals dorso-posteriorly. This is a primitive characteristic and could mean that Tsintaosaurus represents a relict genus, more closely related to the earliest members of the Parasaurolophini than to the geologically latest member of the clade, Parasaurolophus. In both Tsintaosaurus and Parasaurolophus, the mandible is shorter and wider than in any other clade. The anterior part of the type skull in Tsintaosaurus is badly damaged, making a detailed comparison to other lambeosaurs very difficult.

Postcranially, only the tarsals differ in Tsintaosaurus and Parasaurolophus. The tarsal bones of Tsintaosaurus are typical of most hadrosaurids (Plate 7B) while the tarsus of Parasaurolophus cyrtocristatus (FMNH P27393, Plate 7D) is unique, as indicated in the discussion on the tarsus given above.

The cranial and postcranial evidence indicates that Tsintaosaurus is a lambeosaurine most closely allied to Parasaurolophus. The resemblances to Saurolophus in the shape of the crest are superficial, while the weight of cranial and postcranial evidence favors a lambeosaurine relationship (Brett-Surman, 1979).

PROBLEMATIC TAXA

"Gadolosaurus" (no type designated) appeared in a popular book (Saito 1979) about a Russian exhibit of dinosaurs that toured through Japan. This taxon is published as coming from the same horizon as Protoceratops, according to the specimen label in the picture. Gadolosaurus does not occur in the same beds as Protoceratops but is instead from the Bayn Shireh Formation (Kurzanov, letter, 1985) and is considered by Kurzanov to be a juvenile Arstanosaurus. Gadolosaurus is said to be represented by a juvenile hadrosaurid about 71 cm high, but the figures in Saito (1979) show more similarities with iguanodontids than with hadrosaurids. Despite the many iguanodontid features seen in the published photo, D. Norman, H. Osmolska, and P. Sereno (pers. comm., 1985) all have informed me that they also consider "Gadolosaurus" to be a juvenile Arstanosaurus. Original photos, and a letter provided by Kurzanov (letter, 1986), show that the iguanodontid features illustrated by Saito (1979) are plaster reconstructions.

The name Gadolosaurus appears only on a specimen label in a photograph, and in a generic list on another page. "Gadolosaurus" is Japanese for "baby dinosaur" or simply a Japanese phoneticization of the Cyrillic spelling gadrosavr ("hadrosaur") (Olshevsky 1983, pers. comm.). "Gadolosaurus", or Arstanosaurus, should not be cited until more specimens are described - but under a new generic name, as Arstanosaurus is a nomen dubium (see above).

SUMMARY

The following list summarizes the taxonomic disposition of each genus examined for the present work. A separate determination at the species level is presented in Appendix 1.

NAME	DISPOSITION
Aachenosaurus	not an animal
Anatosaurus	*Edmontosaurus* and *Anatotitan*
Anatotitan	Edmontosaurini
Aralosaurus	Kritosaurini, but possibly synonymous with *Kritosaurus*
Arstanosaurus	*nomen dubium*
Bactrosaurus	Parasaurolophini
Barsboldia	Lambeosaurinae *incertae sedis*
Brachylophosaurus	Kritosaurini
Cheneosaurus	*Hypacrosaurus*
Cionodon	*nomen dubium*
Claorhynchus	a ceratopsian
Claosaurus	Hadrosaurinae *incertae sedis*
Corythosaurus	Corythosaurini
Diclonius	*nomen dubium*
Didanodon	*nomen nudum*
Dysganus	a ceratopsian
Gadolosaurus	*nomen nudum*
Edmontosaurus	Edmontosaurini
Gilmoreosaurus	Hadrosaurinae *incertae sedis*

Gryposaurus	*Kritosaurus*
Hadrosaurus	Hadrosaurini
Hypacrosaurus	Corythosaurini
Hypsibema	*nomen dubium*
Jaxartosaurus	Lambeosaurinae *incertae sedis*
Kritosaurus	Kritosaurini
Lambeosaurus	Corythosaurini
Lophorhothon	Saurolophini
Maiasaura	Saurolophini
Mandschurosaurus	*nomen dubium*
Microhadrosaurus	*nomen dubium*
Nipponosaurus	Lambeosaurinae *incertae sedis*
Notoceratops	ceratopsian ?
Ornithotarsus	*nomen dubium*
Orthomerus	*nomen dubium*
Parasaurolophus	Parasaurolophini
Pneumatoarthrus	chelonian
Procheneosaurus	*Corythosaurus* and *Lambeosaurus*
Prosaurolophus	Saurolophini
Pteropelyx	*Corythosaurus*
Saurolophus	Saurolophini
Secernosaurus	Hadrosaurinae *incertae sedis*
Shantungosaurus	Edmontosaurini
Tanius	Hadrosaurinae *incertae sedis*

Telmatosaurus	Edmontosaurini
Tetragonosaurus	see *Procheneosaurus*
Thespesius	*nomen dubium*
Trachodon	*nomen dubium*
Tsintaosaurus	Parasaurolophini

The following taxonomy results from applying the new diagnosis of the hadrosaurids as presented above.

- Family Hadrosauridae Cope 1869
    - Subfamily Hadrosaurinae Lambe 1918
        - Tribe Edmontosaurini Brett-Surman
            - *Anatotitan* Brett-Surman
            - *Edmontosaurus* Lambe
            - *Shantungosaurus* Hu
            - *Telmatosaurus* Nopsca
        - Tribe Kritosaurini Brett-Surman
            - *Aralosaurus* Rozhdestvenski
            - *Brachylophosaurus* Sternberg
            - *Hadrosaurus* Leidy
            - *Kritosaurus* Brown
        - Tribe Saurolophini Brett-Surman
            - *Lophorhothon* Langston
            - *Maiasaura* Horner and Makela
            - *Prosaurolophus* Brown
            - *Saurolophus* Brown
    - Subfamily Hadrosaurinae *incertae sedis*

        - <u>Claosaurus</u> Marsh
        - <u>Gilmoreosaurus</u> Brett-Surman
        - <u>Secernosaurus</u> Brett-Surman
        - <u>Tanius</u> Wiman
- Subfamily Lambeosaurinae Parks 1923
    - Tribe Corythosaurini Brett-Surman
        - <u>Corythosaurus</u> Brown
        - <u>Hypacrosaurus</u> Brown
        - <u>Lambeosaurus</u> Parks
    - Tribe Parasaurolophini Brett-Surman
        - <u>Bactrosaurus</u> Gilmore
        - <u>Parasaurolophus</u> Parks
        - <u>Tsintaosaurus</u> Young
- Subfamily Lambeosaurinae <u>incertae sedis</u>
        - <u>Barsboldia</u> Maryanska and Osmolska
        - <u>Jaxartosaurus</u> Riabinin
        - <u>Nipponosaurus</u> Nagao

Family Hadrosauridae <u>incertae sedis</u>

- <u>Arstanosaurus</u> Shilin and Suslov
- <u>Cionodon</u> Cope
- <u>Diclonius</u> Cope
- <u>Hypsibema</u> Cope
- <u>Mandschurosaurus</u> Riabinin
- <u>Microhadrosaurus</u> Dong

Ornithotarsus Cope

Orthomerus Seeley

Thespesius Leidy

Trachodon ? Leidy

CHAPTER 7

AN OVERVIEW OF HADROSAURID EVOLUTION

Hadrosaurids As Ornithopods

The camptosaurids, iguanodontids, and hadrosaurids are traditionally recognized as a phyletic series (Romer, 1966; Galton, 1972). They are linked by many shared features such as the relatively largest body size of all ornithopods; increased tooth count as compared to dryosaurids, fabrosaurids and hypsilophodontids; longer and lower skulls than in other ornithopods; expanded premaxilla, loss of premaxillary teeth, larger size and robustness of the premaxillary 'beak' as compared to dryosaurids and hypsilophodontids; the most extensive latticework of ossified tendons in the ornithopods; expanded prepubis; greater iliac length as compared to dryosaurids; and formation of the prepubic 'blade'.

The camptosaurids, iguanodontids, and hadrosaurids are here recognized as a natural, monophyletic clade. *Camptosaurus* was placed in the Iguanodontidae by Romer (1966) but is now separated from the Iguanodontidae by Sereno (1986). Excluding the camptosaurids from the iguanodontids results in the restriction of the iguanodontids to the Cretaceous. As the two most derived ornithopod clades, the Iguanodontidae and Hadrosauridae are regarded as sister groups (Norman 1980) and share the following characteristics not found in other ornithopods or in the Camptosauridae:

1) muzzle broader, expanded antero-laterally

2) skull deeper and broader in the post-orbital area

3) coronoid process taller

4) teeth more numerous

5) sacral vertebrae more than 5

6) ossified tendons more numerous per vertebra

7) sternals elongate with distinct 'handle' and 'paddle'

8) humeral head flanked by prominent tuberosities

9) olecranon process larger

10) ilium elongate

11) postpubis shortened

12) femur straight

13) calcaneum reduced

Hadrosaurids are known only from the Upper Cretaceous, while iguanodontids are known from the Lower and Upper Cretaceous. I follow Galton (1972) in having the hadrosaurids arise from the iguanodontids in the Upper Cretaceous. These families show less variation between them than can be found within most living families of artiodactyls. If the fossil record of the early Upper Cretaceous were more complete, the transition of iguanodontids into hadrosaurids would be so gradual as to require the combination of the two clades into one family.

Iguanodontids vs. Hadrosaurids

The following cranial characters (modified from Weishampel, 1981 and Sereno, 1986), differentiate the Hadrosauridae from the Iguanodontidae. The following list gives the hadrosaurid condition. The opposite condition (e.g. its absence) represents the iguanodontid condition:

1) Tooth batteries fully interlocking.

2) Enamel surface of tooth diamond-shaped with a prominent median keel.

3) Mandible with antero-ventral deflection.

4) Premaxillary 'beak' laterally expanded.

5) Premaxilla-nasal complex expanded into folds or crests (compare the premaxillae of Plates 8 and 16A).

The following tables compare the postcranial elements of the iguanodontids with those of their more derived sister-taxon, the hadrosaurids, on the basis of this report, casts of *Iguanodon* at the American Museum of Natural History, and Norman (1980) on *Iguanodon*.

IGUANODONTIDS VERSUS HADROSAURIDS
POSTCRANIAL COMPARISON TABLES

TABLE 7
PECTORAL GIRDLE
SCAPULA

Iguanodontids	Hadrosaurids
Glenoid shallow, smaller in area compared to area for suture with the coracoid.	Glenoid deep and equal in area to coracoidal suture.
Deltoid ridge rudimentary;does not reach ventral scapular border but does reach anterior border and meets coracoid.	Deltoid ridge large,robust, reaches ventral border of scapula but does not reach anterior border.
Glenoid lateral border a smooth low ridge, not robust or extensive.	Glenoid lateral border a robust and massive ridge.
Suture with coracoid tall (dorsoventrally in natural articulation) and narrow (mediolaterally).	Suture with coracoid short and rounded.
Deltoid fossa shallow,small in area, does not reach lower scapular border in most cases.	Deltoid fossa large, deep, and reaches lower border of scapula.
Scapular blade proportionally much shorter than in the hadrosaurids, terminates posteriorly in a strong posteroventrally-directed hook.	Scapular blade much longer than in iguanodontids, terminates abruptly with dorsal and ventral borders parallel to each other and perpendicular to posterior end.

CORACOID

Iguanodontids	Hadrosaurids
Rectangular in shape,dorsoventrally elongated.	Not rectangular, elongated anteroposteriorly.
Glenoid facet is shallow, oriented posteroventrally.	Facet is deep, oriented ventrally.
Scapulocoracoid suture twice as large as glenoid facet viewed laterally.	Scapulocoracoid suture and glenoid facet equal in area.
Coracoid hook small, rudimentary, blunt, points ventrally, does not protrude anteriorly.	Large, massive, sharp point, pointed anteroventrally, protrudes far anteriorly.
Superior border a thin sharp edge, continues unbroken as the coracoid ridge.	Superior ridge ending in a blunt knob dorsally, and not connected to the coracoidal ridge.
Coracoid ridge vertical, edge rounded, small and not robust	Oriented anteroventrally, forms superior border of the hook, edge massive and rugose.
Coracoid foramen opens into scapulocoracoid suture.	Foramen lies within coracoid.

STERNALS

Iguanodontids	Hadrosaurids
'Body' relatively larger.	Relatively shorter.
Borders of body convergent proximally.	Borders subparallel.
Medial ridge present on proximal half.	Ridge rudimentary or absent.
'Handle' relatively shorter.	Relatively longer.

TABLE 8
FORELIMB

HUMERUS

Iguanodontids	Hadrosaurids
Head relatively smaller and extends slightly posteriorly.	Head greatly enlarged,massive, well rounded,extends dorsally as well as posteriorly.
Proximal end smooth with no major landmarks at lateral and medial extremities.	Lateral and medial ends expanded into large rugose tuberosities.
Proximal end has a triangular shape; deltopectoral ridge not parallel to shaft,does not extend below midpoint of shaft.	Proximal end greatly expanded at midpoint of shaft resulting in rectangular shape; deltopectoral ridge parallel to shaft, usually extends at or below midpoint in adults.
Medial distal condyle slightly larger than lateral condyle.	Medial condyle much larger than lateral condyle.

RADIUS

Iguanodontids	Hadrosaurids
Proximal end slightly expanded in the proximal one-fourth, asymmetrically shaped with emphasis to the ulnar side.	Proximal end greatly expanded only at the extreme proximal end.
Cross-section of shaft is a flattened ellipsoid.	Croos-section more rounded than flattened.
No ridge for proximal ulnar articulation.	Ridge prominent and sharp.
Shaft relatively thicker and wider.	Shaft more slender and elongate.

TABLE 8 (con't)

ULNA

Iguanodontids	Hadrosaurids
Articulation for the humerus wide and shallow; olecranon process rudimentary.	Articular area relatively deeper and narrower; olecranon process larger and more robust,hook-like.
Proximal end gently subtriangular in cross-section; lateral ridges relatively not as developed.	Proximal end strongly triradiate, olecranon process the larger part; lateral ridges massive and well developed.
Radial articulation shallow.	Radial articulation proportionally deeper.
Distal end wider and more flattened.	Relatively not as expanded, rounder.
Shaft relatively much shorter and thicker.	Shaft much longer and thinner.

CARPALS

Iguanodontids	Hadrosaurids
Radiale, intermedium and ulnare well developed.	Radiale and intermedium(?) reduced to flat, round disks; ulnare(?) absent.
Five distal carpals present in most forms.	Distal carpals absent.

METACARPALS

Iguanodontids	Hadrosaurids
Five present, digits I and IV reduced.	Four present,digit I absent,digit-V considerably reduced.
Elements relatively shorter, MC-V half as long as MC-III.	Elements much longer and thinner, MC-V one-third to one-fourth as long as MC-III.
Metacarpals well developed with prominent articulations, typical of other ornithopods.	Highly elongate and rod-like with articulations poorly developed, if present.
MC-III 30%-50% of manus length.	MC-III 67% of manus length.

TABLE 8 (con't)

PHALANGES OF THE MANUS

Iguanodontids	Hadrosaurids
Proximal phalanx of digit II slightly longer than the other phalanges,width and heigth about equidimensional.	Proximal phalanx of digit II twice as long; phalanges relatively flatter.
Intermediate phalanges well developed;length and width equidimensional;two intermediate phalanges on digits I-IV,one on digit V in early forms.	Well developed,wider than long; only one intermediate phalanx present in each digit.
Unguals I-III claw-like in early forms;IV+V pebble-like and reduced.	Unguals II-IV hoof-like; ungual of digit V pebble-like.
All five digits present in early forms.	Digit I absent,digit IV extremely reduced.
Total length of phalanges of digit III up to 115% of metacarpal III length.	Phalanges of digit III about 45% of metacarpal III length.

TABLE 9

PELVIC GIRDLE

ILIUM

Iguanodontids	Hadrosaurids
Dorsal rim usually flat in early forms,convex in later forms.	Sinusoidally curved.
Preacetabular process deflected ventrally up to 20 degrees in most forms.	Deflection strong, averaging 40 degrees.
Pubic peduncle a long massive process extending anteroventrally.	Peduncle reduced in size, more pointed, less massive - does not extend anteroventrally relatively as far.
Ischial peduncle a single large rugose knob.	Peduncle consists of two small protrusions separated by a shallow depression.
Postacetabular process small with a shallow ventral trough, deflected dorso-medially; process is taller than long, l/h ratio averages .98.	Process greatly elongated, no ventral trough, vertically oriented in Campanian and Maastrichtian forms; longer than tall, l/h ratio averages 2.17.
Iliotibialis process absent in early forms, rudimentary in later forms.	Present and relatively larger than in other ornithopods.
M. iliotrochanterus depression rudimentary with no well defined posterior border.	Deep and well developed; bordered posteriorly by the supra-iliac process.
Ilium L/H ratio averages 4.0	L/H ratio averages 5.0

PUBIS

Iguanodontids	Hadrosaurids
Prepubis scimitar-shaped and equal in height in most forms.	Five different shapes corresponding to the five clades; height varies throughout its length.
Obturator foramen present.	Obturator foramen absent.
Iliac peduncle a roughened knob in early forms.	Peduncle a large projecting process.
Prepubic blade and neck indistinct in most forms; when distinct,neck is larger than blade in surface area.	Blade and neck distinct with blade always larger in surface area than neck.
Acetabulum shallow.	Acetabulum deep.
Postpubis a rod equal to or longer than prepubis, sometimes distally expanded.	Postpubis a thin process shorter than prepubis, tapers distally.

ISCHIUM

Iguanodontids	Hadrosaurids
Iliac peduncle relatively wider with a broad base; no 'lip' projecting dorsally in most forms.	Peduncle longer (anteroposteriorly) than wide;broad base usually absent in hadrosaurines;dorsally projecting 'lip' in lambeosaurines.
Pubic peduncle a large robust process with a distinct neck.	Pubic peduncle much less robust, neck absent.
Obturator foramen open.	Closed in very large adults.
Shaft curved.	Shaft straight.
Distally, shaft expanded into knob.	Knob absent in hadrosaurines except Gilmoreosaurus,present as a 'foot' in lambeosaurines.

TABLE 10

HINDLIMB

FEMUR

Iguanodontids	Hadrosaurids
Shaft curved in early forms.	Shaft straight.
Head sub-rounded in shape.	Head oval when viewed anteriorly.
Large deep cleft always present between lesser and greater trochanters.	Cleft small when present, trochanters sometimes fused together.
Fourth trochanter a ventrally projecting hook,resembles a 30-60-90 triangle,usually situated at or above midshaft.	Fourth trochanter shaped like an isosceles triangle, usually situated at or below midshaft.
Distal condyles protrude posteriorly,no noticeable anterior protrusion in lateral aspect.	Condyles protrude noticeably anteriorly in lateral aspect.
Intercondylar groove open and wide.	Groove narrower and closed in old adults.

TIBIA

Iguanodontids	Hadrosaurids
Tibial shaft curved distally (twisted) in early forms.	Shaft straight.
Tibial malleoli relatively less robust.	Malleoli relatively more robust.

ASTRAGALUS

Iguanodontids	Hadrosaurids
Astragalus more rectangular in anterior aspect.	Astragalus more triangular in anterior aspect.
Ascending process proportionally smaller and shallower.	Process larger and deeper and extends more laterally.

TABLE 10 (con't)

FIBULA

Iguanodontids	Hadrosaurids
Fibula relatively shorter.	Fibula relatively longer.
Distal end a slightly expanded knob.	Distal end relatively more expanded into a large knob.

CALCANEUM

Iguanodontids	Hadrosaurids
Calcaneum extends ventrally under tibia to posterior side.	Calcaneum does not extend under tibia to posterior side.
On lateral side,only calcaneum articulates with distal tarsals.	Calcaneum and tibia articulate with distal tarsals.
Calcaneum always present.	Absent(?) in *Parasaurolophus*.

METATARSALS

Iguanodontids	Hadrosaurids
Metatarsal I considerably reduced; metatarsal V absent.	Metatarsal I absent except in (possibly) *Claosaurus*;metatarsal V absent.
Proximal half of metatarsal II applied to metatarsal III in most forms.	Proximal two-thirds of metatarsal II applied to metatarsal III.

PHALANGES OF THE PES

Iguanodontids	Hadrosaurids
Phalanges, except unguals, as wide as long and less flattened.	Intermediate phalanges two to three times as wide as long and relatively more flattened.
Unguals clawlike in early forms, but more hooflike in later forms.	Unguals relatively wider and more hooflike.

The difference between hadrosaurids and iguanodontids tends to be exaggerated because of the presence of cranial crests in hadrosaurids. Several of the iguanodontids show hadrosaurid features, such as premaxilla/nasal complex expanded into the 'Roman nose' condition, as seen in *"Iguanodon orientalis"* (PIN 3386/50). The most hadrosaurid-like iguanodontid is *Ouranosaurus*, with its laterally expanded beak, longer diastema, more hoof-like unguals, and the greatly expanded neural spines, which approach the condition of *Hypacrosaurus*.

Evolution of the Hadrosaurids

Phylogeny

Horner (1985) postulates that hadrosaurids are diphyletic. His reasons are that iguanodontids such as _Iguanodon_ share with the Hadrosaurinae an unfooted ischium, a anterior peg-like maxillary process that contacts the premaxilla, and small neural spines. In contrast, the iguanodontid _Ouranosaurus_ shares with the Lambeosaurinae a footed ischium, no anterior maxillary process, and extremely tall neural spines. These postulated synapomorphies are of doubtful validity because the anterior maxillary peg is also found in the Hypsilophodontidae and Dryosauridae (Sues and Norman, in prep.), and defines a broader clade. There are not two types of ischia in the iguanodontids and hadrosaurids (Horner, in prep.) but three. The first type of ischium has a clubbed distal end and is found in the iguanodontids and in the two earliest hadrosaurids, _Gilmoreosaurus_ and _Bactrosaurus_. The second type of ischium is the fully footed lambeosaurine condition. The third or unfooted (hadrosaurine) type is simply the undeveloped or neotenic condition. The anterior maxillary process and the footed ischium cannot be used as synapomorphies at the familial level; therefore, the hadrosaurids remain a monophyletic clade as defined above and as shown in Plate 20.

The first phylogeny of the hadrosaurids to include all taxa on all continents was by Brett-Surman (1979). Previous phylogenies (Ostrom 1961) have concentrated only on North American forms because ninety-five percent of all taxa are found in North America, and because foreign taxa are relatively difficult for American paleontologists to study. Foreign taxa are mostly undated radiometrically, leaving their ages to be estimated according to their morphological similarity with North American forms.

Paleobiogeography

The record of Asia contains the largest known hadrosaurid, _Shantungosaurus_, which is based on several skeletons from the Wangshih Series, now known from magnetostratigraphy to be of Campanian age (Weishampel, pers. comm.). Also present in Asia are _Gilmoreosaurus_ and _Bactrosaurus_ which are mostly complete and include some unassociated cranial material referred to both taxa.

They are from one quarry sample in the Iren Dabasu area of Mongolia. Nipponosaurus is based on one partial juvenile (Nagao 1936) from Sakhalin Island just north of the main islands of Japan. Tanius, from China, is incomplete, and numerous fragments have been used to name "Mandschurosaurus" and a species of "Procheneosaurus" (Rozhdestvenski 1968). Several isolated specimens in Mongolia and in Kazakhstan (Russia) have been referred to two species of the North American genus Saurolophus (Maryanska and Osmolska 1981).

South America has produced three specimens - a tail (Casamiquela, 1964); a partial skeleton (possibly of a juvenile), which formed the type of Secernosaurus koerneri (Brett-Surman, 1979); and a postcranial skeleton referred to the North American genus Kritosaurus and named Kritosaurus australis (Bonaparte, 1983). There are no hadrosaurids in Antarctica, Africa, India or Australia to date, but this is negative evidence.

Europe only has one hadrosaurid, which is represented by a partial skull referred to Telmatosaurus. At one time or another, Telmatosaurus has had four different generic names applied to it: Hecatasaurus, Limnosaurus, Orthomerus, and Telmatosaurus. Unless a worker is familiar with hadrosaurid systematics, a glance at listings of generic names in encyclopedias (Steel 1969) or dictionaries (Glut 1983) may result in all four names being used for tabulations.

The record outside of North America comprises about five percent of the total record and is statistically inadequate. The predominance of data on North American hadrosaurids is the result of the greater numbers of North American workers, the lack of hadrosaurid specialists outside of North America, the accessibility of abundant upper Cretaceous sediments here, and the lack of continuous explorations of foreign deposits over the last century.

During the Upper Cretaceous, continents were distributed in different patterns than they are today (Smith and Briden, 1977). Western North America and eastern Asia were connected to form one biogeographic province called Asiamerica (Cox 1974). Eastern North America and Europe were connected to form another province called Euramerica (Cox 1974). The great epeiric sea that stretched from the Gulf of Mexico to the Arctic intermittently separated Asiamerica and Euramerica during most of the Cretaceous (Dott and Batten, 1976). This separation finally ended at the very end of the Maastrichtian when the Sheridan Delta cut across the Pierre sea and the inland waters retreated to the north and south (Gill and Cobban, 1973). Such intermittent isolation had limited effects on the dispersal of the hadrosaurines, which are found almost exclusively in lowland deposits. In contrast, the epeiric seas had a larger impact on the lambeosaurines which preferred more savannah-like habitats away from the ancient shorelines (see below).

Origin of Hadrosaurids

Although evidence is limited, Asiamerica is currently the most likely site for hadrosaurid origins (Rozhdestvenskii, 1967). Both the earliest hadrosaurids and the iguanodontids closest to them (*"Iguanodon orientalis"*, *Probactrosaurus*) are found in Asia (Gilmore 1933; Rozhdestvenskii 1968). *Bactrosaurus* (Plate 12) and *Gilmoreosaurus* represent the first diagnostic hadrosaurids (respectively a lambeosaurine and a hadrosaurine), recording the appearance of both subfamilies at the beginning of the hadrosaurian radiation (Brett-Surman 1979). Hadrosaurids appeared slightly later on other continents. The dating of these events is not based radiometrically but rather by the old method of 'morphological advancement'. Different dating techniques can result in highly disparate boundaries (Kent and Gradstein, 1985). The earliest known hadrosaurid in North America was reported by Russell and Chamney (1967) as being Santonian in age. Because of uncertainties of absolute ages and boundaries, one can only say that *Bactrosaurus* and *Gilmoreosaurus* are "pre-Campanian".

If hadrosaurids originated in the Asian part of Asiamerica (Rozhdestvenskii 1968), then the most parsimonious dispersal to other paleoprovinces must have been westward across the Turgai Straits into Euramerica and eastward across the Bering Straits into North America. The advance into South America was probably down the coasts of eastern North America and/or by island hopping across the Caribbean arc (Brett-Surman 1979) or along a proto-Panamanian Isthmus (Bonaparte 1986) during the Campanian.

A single pattern stands out in the global placement of the taxa. Of the tribes defined above (Edmontosaurini, Kritosaurini, and Saurolophini representing the hadrosaurines; Corythosaurini and Parasaurolophini representing the lambeosaurines), only hadrosaurines are currently known outside of Asiamerica. South America, still part of Gondwanaland at this time, has Secernosaurus and Kritosaurus australis, both hadrosaurines. Europe is represented by Telmatosaurus. The Corythosaurini and Parasaurolophini are restricted to Asiamerica. The "procheneosaurs" of Asia are juveniles and therefore cannot be properly determined taxanomically. Adult lambeosaurines are unknown in Asia except for Tsintaosaurus and Jaxartosaurus, but the assignment of the latter to a specific clade is uncertain.

Lambeosaurines and hadrosaurines arose at the same time, and most likely dispersed at the same time. The conspicuous absence of lambeosaurines in Euramerica may possibly be explained by habitat preferences. The Campanian and Maastrichtian deposits of eastern North America represent mostly lowland deposits. This is the favored habitat of hadrosaurines, as almost all hadrosaurines are found in deltas and deposits of meandering streams of low gradient, associated with nearby coal deposits (e.g., Lance Formation and Hell Creek Formation). Lambeosaurines are found almost exclusively in coastal plain, riparian, and 'upland' deposits, represented by the Judith River (Dodson, 1971) and Two Medicine Formations (Horner 1984). Lambeosaurines may have preferred non-coastal areas where their favored plants occurred. This would effectively prevent lambeosaurines from crossing from one landmass to another and would explain the restriction of lambeosaurines to Asiamerica (the site of the origin of the family).

The Hadrosaurinae

The relationships of the tribes presented here (Plate 20) reflect a paleobiogeographic distribution based on an origin in Asiamerica. The least derived clade, the Kritosaurini, contains such forms as Kritosaurus, Hadrosaurus, Aralosaurus, and Brachylophosaurus. The 'Roman nose' of the Kritosaurini is identical to the condition seen in the iguanodontid "Iguanodon orientalis". Aralosaurus is the only representative from Asia and is of uncertain geologic age. Brachylophosaurus is the most derived member of this clade and comes from Canada. In this genus, the premaxilla has expanded posteriorly into a flat and wide paddle-like structure similar in shape to a 'beaver-tail'. It is regrettable that this unusual genus is only known from the anterior half of one individual (NMC 8893, Sternberg 1953).

The most cosmopolitan genus in this clade is Kritosaurus, which has the distinction of being the only member of its clade to occur in both the Campanian and Maastrichtian, and is the only genus in this clade to have more than one species referred to it. The species of Kritosaurus are mostly based on geographic location rather than morphologic variability. K. australis is the Gondwanaland member (Argentina), K. notabilis is the Canadian member and K. navajovius is the New Mexican member. It is interesting to note that the Kritosaurini are represented by the second fewest number of taxa, but the largest distribution, and it is the only clade to occur in both Laurasia and Gondwanaland.

The Saurolophini (Plate 17A) resemble lambeosaurines in the unreflected dorsal margins of the premaxillae (thin 'lips'), and in having the medial rami of the premaxillae overriding the frontals. The Saurolophini include several early forms from America, such as Maiasaura (Plate 15) and Lophorhothon. The only upper Campanian genus is Prosaurolophus, and the only Maastrichtian genus is Saurolophus, which also occurs in Asia. Tsintaosaurus (Plate 18) has been referred to this lineage in the past (Rozhdestvenski, 1967), but the postcranial elements and aspects of the crania are most similar to Parasaurolophus (Plate 16A), and this genus has been transferred to the Parasaurolophini (Brett-Surman 1979). On the basis of a more lumped taxonomy, Maiasaura and Lophorhothon would be different only at the species level. They share an incipient crest formed by the premaxilla and the frontal, which project just above the top margin of the skull (Plate 15).

Prosaurolophus and Saurolophus would also be distinguished at the level of species, in this case chronospecies, as the former appears to be ancestral to the latter. Prosaurolophus and Saurolophus share a solid projection of the premaxilla posteriorly over the frontal. The members of this clade cannot be distinguished from one another on the basis of postcranial data. The Saurolophini were placed in their own subfamily, the Saurolophinae, by Lull and Wright (1942) and Ostrom (1961), but are considered members of the Hadrosaurinae because they share hadrosaurine characters such as an unfooted ischium, a longitudinal furrow on the ventral side of the sacrals, and a solid crest (Sternberg 1954, Langston 1960). Even though this clade has more genera than the Kritosaurini, it is numerically the rarest of all the hadrosaurid clades. All genera are monospecific except Saurolophus, which has three species referred to it (S. osborni, S. angustirostris, and S. kryschtofovici), but the the latter two are geographically defined. The only difference between the species of Saurolophus is the length of the crest, which is a function of growth, and in most specimens is restored in plaster.

The Edmontosaurini (Plates 10 and 20) make up the most derived clade of Hadrosaurinae. They share the following synapomorphies: a highly reflected premaxillary anterior lip (Plate 8), a deep postorbital pocket (Plate 8, POEP), a highly folded anterior depression in the external nares, a posteriorly unexpanded premaxilla, and the relatively longest edentulous portion of the mandible (Plate 10). The most common member of this clade is Edmontosaurus (Plate 9), which now includes Anatosaurus, Trachodon, and Diclonius as junior synonyms. Edmontosaurus is the only member of this clade known from both the Campanian and the Maastrichtian. Shantungosaurus and Tanius are the only Asian members of this clade and Telmatosaurus is the only European member. All other forms are from North America. Claosaurus may be the earliest member (pre-Campanian), but it is more properly regarded as a hadrosaurine incertae sedis.
Brett-Surman (1979) placed Secernosaurus in this clade but it is more properly regarded as a hadrosaurine incertae sedis being represented only by a partial skeleton without skull.

Shantungosaurus, Edmontosaurus and Telmatosaurus all share a postorbital pocket and a fully developed and elongated postacetabular process (Plate 4). Tanius has referred skull material, but it lacks the diagnostic muzzle area. Secernosaurus is incertae sedis because it lacks skull material. This leaves Edmontosaurus as the most durable genus with a possible eighteen-million-year lifespan (all of the Campanian and Maastrichtian). The most derived form, Anatotitan, is the last to appear, in the upper Maastrichtian. Anatotitan appears to have a more peromorphic muzzle than its sister-taxon, Edmontosaurus. In summary, the subfamily Hadrosaurinae has a wider distribution and a larger number of genera than the Lambeosaurinae, even with a more 'lumped' taxonomy. Hadrosaurines are also the most abundantly represented in lowland deposits and are less derived than the lambeosaurines.

The Lambeosaurinae

The subfamily Lambeosaurinae is inferior to the Hadrosaurinaein number of taxa, number of specimens, and geographic distribution. The Corythosaurini hold the distinction of having the largest number of species per genus in the same time unit (see Corythosaurus in Appendix 1), and of specimens per formation (over 100; Currie, pers. comm.). Other members of this clade include Asian forms such Jaxartosaurus (poorly known), Nipponosaurus (juvenile), and "Procheneosaurus convincens". This latter taxon has many complete specimens referred to it in popular books, but the only technical publication to date (Rozhdestvenskii 1967) is a short description of a partial skull which may belong to a juvenile. The North American genera include Lambeosaurus and Hypacrosaurus. Hypacrosaurus appears to be a chronospecies of Corythosaurus (Brett-Surman, 1979). The only differences between Corythosaurus and Hypacrosaurus are the more pointed crests in the latter, the more developed footed ischium, and the taller neural spines. Weishampel (1981) also reports that Hypacrosaurus lacks an S-shaped narial loop and a fenestra in the wall of the cranial lateral diverticulum. These features are what one may postulate to occur in Hypacrosaurus if it is a sister-taxon (or chronospecies) of Corythosaurus, and do not represent new or more derived features, but are differences that may occur with increased ontogenetic age and/or sexual variation. I regard these differences as too slight to warrant generic separation (admittedly a subjective judgement). Because Hypacrosaurus is essentially based on two specimens (AMNH 5240, NMC 8501), I have chosen not to synonymize it with the taxonomically junior, but more abundant and better known Corythosaurus.

Corythosaurus and Lambeosaurus are indistinguishable from one another on the basis of postcranial features alone. The only two major differences between them are that in Corythosaurus, the crest is vertically oriented and symmetrical in outline (Plate 13A, Appendix 5). In Lambeosaurus, the crest is deflected anteriorly and has a prominent "handle-bar" projecting dorso-posteriorly from the base of the crest. It is possible that Corythosaurus represents one sex (female?) and Lambeosaurus the other sex (male?) of one species. Although Dodson (1975) considered and dismissed this idea, based on morphometric analysis, I consider the question still open. I view *Corythosaurus* as an ancestor of *Hypacrosaurus*, which lasts into the Maastrichtian but not, apparently, to the K-T boundary (Russell, pers. comm.).

The Parasaurolophini are typified by the most derived hadrosaurid, *Parasaurolophus* (Plate 16A). This clade is defined by a tubular, hollow crest, composed chiefly of the premaxilla, posteriorly overriding the frontal bone. Members of the Parasaurolophini are postcranially the most robust of all the hadrosaurids. The Asian genus *Tsintaosaurus* was formerly included in the Saurolophinae (Steel 1969) because the crest seemed to be solid, not hollow, and was shaped very much like that of *Saurolophus*. It was transferred to the *Parasaurolophus* clade (Brett-Surman, 1979) because Young (1958) reported the crest as hollow, and because postcranial elements are almost identical to those of *Parasaurolophus*, especially the pelvis, in which the ischium has both the 'heel' and 'toe', and the antitrochanter is extremely well developed. The postcrania of the other Asian genus in this clade, *Bactrosaurus*, are identical to *Parasaurolophus* in the great expansion of the pubis and ischium, which is unexpected, considering that *Bactrosaurus* is from the early Santonian (?), while *Parasaurolophus* is late Campanian. *Bactrosaurus* (Plate 12) is restored here as having a crest, but the evidence is sparse (Weishampel and Horner 1986). Both *Gilmoreosaurus* and *Bactrosaurus* are known from only one quarry in the Iren Dabasu Formation, although Rozhdestvenskii (1968) has referred some partial, non-diagnostic remains to *Bactrosaurus prynadai*, more likely because of location and age than because of morphology. The most derived member of this clade is *Parasaurolophus*, which has been the subject of intensive study from Parks (1922) to Weishampel (1981). Its elongated and tubular crest is most distinctive.

Diphyletic Origin of the Hadrosaurids

At one time, I entertained the idea that the hadrosaurines might be paedomorphic lambeosaurines with the slightly expanded hadrosaurine nasals and premaxillae representing lambeosaurine crests frozen in an early stage of development. This would have been supportable if advanced hadrosaurines were morphologically closer to the earliest members of both subfamilies, such as *Gilmoreosaurus* and *Bactrosaurus*, and less derived than the Lambeosaurinae proper. This is not the case, however. The distal end of the hadrosaurine ischium would have to be clubbed, as it is in most of the early hadrosaurines and lambeosaurines, and in the ancestral iguanodontids. The hadrosaurine ischium is actually completely unfooted, a condition which is more derived than that of the peromorphic-footed ischium in lambeosaurines. If the hadrosaurines were paedomorphic, their skulls would be more derived than the more closely linked lambeosaurines and iguanodontids. This is not supported by the evidence. The hadrosaurines are intermediate in development between the iguanodontids and lambeosaurines in the extent of the premaxillae and nasals, the relative width of the enamel face on the teeth, the number of papillae on each tooth, and the relative length of the neural spines. The overall shapes of the skulls of hadrosaurines and iguanodontids are more similar to each other than to the lambeosaurines. This confirms the traditional view (Ostrom 1961) that lambeosaurines are more derived than the hadrosaurines.

Evolutionary Trends

Hadrosaurids can be arranged into a series composed of the five tribes (defined above) from most hadrosaurine-like to most lambeosaurine-like as pictured below and in Plate 20.

Edmontosaurini ---->

Kritosaurini ---->

Saurolophini ---->

Corythosaurini ---->

Parasaurolophini

Several new patterns emerge that are proposed here for the first time. [In the following discussion, the term 'relative' refers specifically to structures compared in two animals of the same body size.]

Cranially, the trend is from extremely long skulls with a distinctly reflected premaxilla, to shorter and higher skulls with less reflected premaxillary borders. The jaws in the Edmontosaurini have a relatively long edentulous region and shorter coronoid process as compared to the Parasaurolophini, in which the jaw is shorter and less of an edentulous portion, and the coronoid process is higher, yielding a stronger bite. The muzzle becomes narrower distally in the Parasaurolophini, and there is less folding of the external nares into pockets or excavated areas. Overall, the external nares become smaller, while the internal nares are greatly enlarged. The hadrosaurine folded external nares, and lack of a hollow crest, seem analogous to a reed instrument, while the hollow lambeosaurine crests without large external nares are analogous to a woodwind instrument (see also Weishampel, 1981).

Most of the trends are apparent in the pelvic region. From the Edmontosaurini to the Parasaurolophini, the ilium becomes thicker, heavier, and relatively narrower and taller. The postacetabular process shows the same trend. The antitrochanter is relatively more robust and extends ventrally to the ischial peduncle. The pubis has a shorter neck and relatively much deeper blade. The ischium is also relatively thicker and has a 'foot'.

The dorsal and sacral vertebral neural spines increase in height from the Edmontosaurini to the Parasaurolophini. Distal clubbing of the neural spines is viewed as a growth feature associated with old age and not taxonomically consistent. The increased number of ossified tendons per vertebra cannot be determined to be of taxonomic value as it may simply be a result of the absolute increase in the area to be occupied by ossified tendons.

A correlation is also seen between the size of the narial crest and the size and robustness of the prepubis. A functional connection may be that the larger the crests, the stronger the exhalation needed for sound production, hence the stronger the abdominal musculature. This is analogous to crocodilian respiration in which the muscles originating from the pubis help power the breathing cycle (Pooley and Gans, 1976).

Problems With Diversity Studies

Taxonomic procedure is a continuum of which the extremes are commonly characterized as 'lumping' and 'splitting'. It is known that mutually exclusive taxonomies can be generated by the extremes of lumping and splitting of a single set of data, which in turn leads to a series of conclusions regarding faunal composition and/or macroevolution that are likewise mutually exclusive. As a test for this report, an extremely split taxonomy was generated by recognizing all named taxa (from 1856-1986) as valid. Conversely an extremely lumped taxonomy was generated by recognizing most generic differences as only species differences and differences at the tribe level as generic differences on the basis of the diagnoses for the tribes named above. When extreme 'splitting' is applied to the Hadrosauridae, the resulting taxonomy yields 2 families, 5 subfamilies, 44 genera, and 91 species, in contrast to this report which recognizes 1 family, 2 subfamilies, and 21 genera. An extremely lumped taxonomy yields 1 family, 2 subfamilies, and 8 genera. A bar diagram depicting highly different results of a diversity study of species per genus resulting from 'lumping' and 'splitting' is presented in Plate 19.

The eighteen previously named species

of the Corythosaurini (Appendix 1) cover an interval of approximately 12 million years (Campanian to middle Maastrichtian according to Sloan et al., 1986; see time chart in Appendix 3). Each species lasts for about 0.67 million years and the 'lifetime' of a genus is about 1.5 million years. The split taxonomy implies a rapid production of species, one that equals or exceeds that of modern mammals.

In contrast, an extremely lumped taxonomy of the Corythosaurini would place everything into Hypacrosaurus, with the differences in the crest of Hypacrosaurus, Corythosaurus, and Lambeosaurus dismissed as specific, sexual or ontogenetic variation. This results in only one genus and two species per 12 million years. A tribe is thereby reduced to two species.

When one puts these taxonomies into the context of the end of the age of dinosaurs, one has the choice between the extinction of one species versus the disappearance of an entire lineage with eighteen species. With the split taxonomy, the lineage is rapidly evolving, diversified into many genera, and comes to a sudden end, which fits a gradualistic model, albeit a tachytelic one. The lumped taxonomy shows a static lineage coming to a gradual end which fits the punctuated model.

Hadrosaurids have been recorded from about seventy-eight formations worldwide (Appendix 2), but almost all of the adequate samples of populations, and complete specimens, come from only four formations, the Two Medicine (lower Campanian), the Judith River (upper Campanian), the Lance (upper Maastrichtian), and the Hell Creek Formations (upper Maastrichtian). Each of the four is heavily biased towards one taxon. Each of the large samples was preserved, probably, as a consequence of a catastrophe (Two Medicine Formation, Horner, 1984), or of the concentration of carcasses along a stream system (Judith River Formation, Dodson, 1971) or in a deltaic sequence (Hell Creek Formation, Archibald, 1982). The following list gives the genus that represents over ninety percent of the genera in each of these bonebeds:

Kritosaurus - Two Medicine Fm., Campanian

Corythosaurus - Judith River Fm., Campanian

Edmontosaurus - Lance Fm., Maastrichtian

Edmontosaurus - Hell Creek Fm., Maastrichtian

In temporal sequence, from oldest (Two Medicine Fm.) to youngest (Hell Creek Fm.), the absolute numbers of specimens preserved in the formations decrease. Although *Edmontosaurus* is dominant in the Lance and Hell Creek Formations, it is represented by fewer specimens than the dominant genera in the other formations.

The collections of the National Museum of Natural History, Smithsonian Institution (USNM), can serve as an example of how few specimens are available for identification to species level, even with a large sample. The USNM collections are a relatively unbiased sample because the USNM receives specimens from other federal agencies and private donors where the collection of vertebrates is not aimed at any particular group, but at overall samples of the formation being studied. The following list covers all the hadrosaurids curated and/or reviewed by me as of 1987:

Total number of hadrosaurs: 209

Hadrosaurs identified to species level: 25

Hadrosaurs with associated skulls: 6

This gives a museum sample of only 2.8% diagnostic material.

In another example, the following list represents the total number of specimens which have been referred in publications to the Parasaurolophini:

Bactrosaurus: AMNH 6553 (body only), 6365 (skull only)

Tsintaosaurus: PMNH V125

Parasaurolophus; FMNH P27393, ROM 768

All that we know about these three taxa (from publications) is based on five individuals. There are other partial specimens referred to these taxa in various museums but in the absence of cranial remains their assignments are more of convenience, or best guesses.

Decline of the Hadrosaurids

From the standpoint of numbers of taxa of hadrosaurids, another pattern emerges, and is summarized here. No matter what taxonomic philosophy is followed (lumped or split taxonomies), there is a consistent decline in the number of taxa from the Campanian to the Maastrichtian. There is also a consistent decline in the number of specimens as shown in the list on the following page:

	CAMPANIAN	MAASTRICHTIAN
Number of species from a split taxonomy	48	18
Number of genera from a split taxonomy	20	11
Number of genera, this paper	12	6
Number of genera from a lumped taxonomy	7	5
Hadrosaurine genera (split taxonomy)	11	4
Lambeosaurine genera (split taxonomy)	5	2
Hadrosaurine genera (this paper)	8	4
Lambeosaurine genera (this paper)	4	2
Hadrosaurine genera (lumped taxonomy)	4	3
Lambeosaurine genera (lumped taxonomy)	3	2

Summary

Hadrosaurids became extinct at the end of the Maastrichtian. Their abundance and diversity in the Santonian is unknown, therefore there is only 'one rate' of evolution that can be studied, that of Campanian to Maastrichtian. One cannot assume that a taxon present in one stage lived for the entire stage. One can only summarize the taxa in each clade as follows:

In the Edmontosaurini, only *Edmontosaurus* appears in both theupper Campanian and Maastrichtian, and therefore Edmontosaurus has a taxonomic lifespan of about 12 million years. All other members of this clade are one-bed/one-taxon occurrences and do not have any geologic range. In the Kritosaurini, only Kritosaurus occurs in both the Campanian to middle Maastrichtian and has a lifespan of about 14 million years. All others are, again, one-shot occurrences. In the Saurolophini, no taxa occur in more than one stage. In the Corythosaurini, Corythosaurus occurs in the upper Campanian and Hypacrosaurus occurs in the lower Maastrichtian. If they are considered separate taxa, there is no range for either because each occurs in only one time stratum. If Corythosaurus casuarius and Hypacrosaurus altispinus are considered chronospecies of a single genus, the range of the genus is 8 million years. Among the Parasaurolophini, only Parasaurolophus occurs in the upper Campanian and the Maastrichtian for a range of about 12 million years. This yields an average duration per genus of about 10 million years.

On the basis of present evidence, the hadrosaurids reached their peak in the Campanian and declined to the end of the Maastrichtian. The adaptive radiation and diversification up to their Campanian peak is as yet entirely unknown.

If one also looks at hadrosaurids per biogeographic province, and then compares provinces, the following patterns stand out. At no time in hadrosaur history is there evidence of parallel evolution, iterative evolution, or convergent evolution. It must be emphasized that almost all of the preserved record of hadrosaurids is restricted to the last half of the hadrosaurid radiation. Hadrosaurid genera appear to be long-lived taxa that display stasis once they appear, initially supporting the punctuated model; but the exceedingly small sample and the particular facies preference of each genus make the punctuated model suspect. It cannot be ruled out that new genera appear by punctuation and then evolve by gradualism once in place.

The evolutionary patterns of hadrosaurids contrast sharply with that of elephants, animals of comparable size and perhaps, to some degree, of comparable ecological requirements. At the maximum diversity of hadrosaurids in the upper Campanian, there are about nine species in nine genera. In Pleistocene elephantids, there are ten species in three genera (Maglio 1973). For the last eight million years of the history of each, there are six species of hadrosaurids and twenty-two species of elephants. Thus hadrosaurids appear as monospecific genera, with low diversity, at their best times, in contrast to elephants with high species diversity during their acme. If there is a valid conclusion to be drawn from this comparison, it is twofold. First, hadrosaur diversity must be combined with ceratopsian diversity to get a picture of Campanian diversity. Ecologically, it may be that one elephantid equals one hadrosaurid plus one ceratopsian. Second, hadrosaurids, and possibly dinosaurs as a group, occupied more niches in their lifetime than any mammal. For example, a hadrosaurid adult would be expected to forage at heights up to seven meters (<u>Shantungosaurus</u>) with juveniles of the same species restricted to less than one-third that height. This can be called Niche Assimilation, a factor that may have played a role in hadrosaurid extinction as discussed in the final section.

Plate 20

An evolutionary diagram of the five tribes named in this report displaying the skulls and pelvic girdles in lateral view.

A) Edmontosaurini

B) Kritosaurini

C) Saurolophini

D) Corythosaurini

E) Parasaurolophini

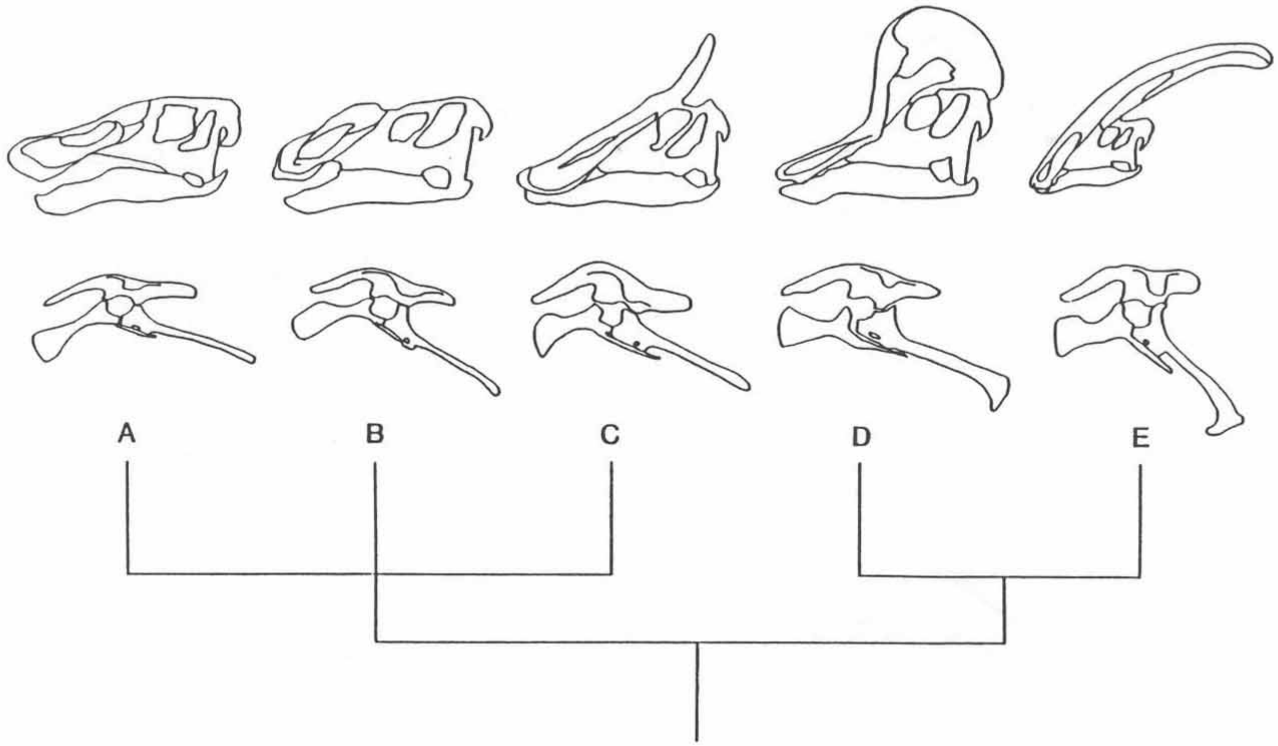
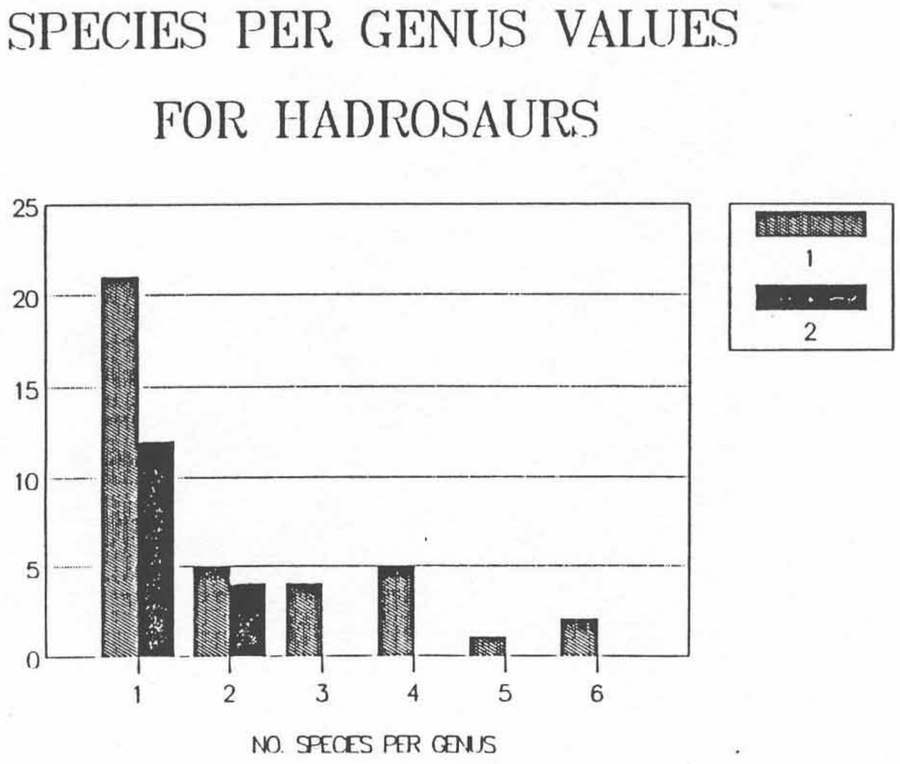


Plate 19

The number of species per genus using a lumped taxonomy (solid bar) versus a split taxonomy (shaded bar). The Y-axis represents the number of genera. The X-axis represents the number of species per genus. It can be seen that in the lumped taxonomy, many genera have only one species. In the split taxonomy, most genera have multiple species. A split taxonomy implies a much higher diversity. In both cases, the same database was used.



CHAPTER 8

SPECULATIONS ON HADROSAURID EXTINCTION

Hypotheses of hadrosaurid extinction are largely untestable because of the patchiness of Latest Cretaceous beds and the poor resolution of the terrestrial stratigraphic record (Dingus 1984). In this section, I propose a hypothesis about hadrosaurid extinction on the basis of loss of niche space, withdrawal of epeiric seas, increased patchiness of preferred environments and isolated hadrosaurid population distributions, accelerated floral turnover, decreased hadrosaurid population sizes, and niche assimilation. In the concept of niche assimilation (also called competitive niche exclusion), a species of very large size, which inhabits many different niches and/or habitats during its ontogeny, may be expected to exclude other species from these niches due to competition. For example, K-selected hadrosaurids, with their large size and parental care (Horner 1984), would feed at many levels (up to heights of seven meters) occupying many niches that would today be filled by many species of mammals. In other words, resource partitioning would take place within a single taxon rather than among several taxa. This would lead to a depauperate community less able to respond to ecological shifts.

The Current Model of Extinction

A current hypothesis of dinosaur extinction is the asteroid model of Alvarez et al. (1980, 1984). This hypothesis postulates a collision between the Earth and an asteroid, which injected finely-divided crustal material into the atmosphere, blocked solar radiation to the surface long enough to disrupt photosynthesis, and destroyed the terrestrial food chain. The resulting mass die-off from lack of food and lowered ambient temperatures reduced population sizes to levels too low for recovery for many species. K-selected animals with long lifespans would be especially affected by this event. The frequent assumption is that no animals over 50 kg in mass would survive more than a few months of this 'nuclear winter' climatic deterioration (Pollack et al. 1983). It is implicit in these assumptions that all flesheaters over 50 kg would only feed on herbivores of the same size because they would be unable to catch smaller prey, especially if those smaller animals which weathered the event by burrowing and/or hibernating.

Demonstration that an asteroid struck the Earth before the dinosaurs became extinct is necessary, but not sufficient, to confirm that impact as the primary cause, and the beginning of, dinosaur extinction. Most pro-asteroid papers deal primarily with the evidence to prove an impact, with the implicit assumption that the extinctions were a direct consequence of the impact. These authors try to show that the drop in diversity at the K-T boundary was sharp and sudden (e.g. Retallack and Leahy 1986).

At present, a large amount of evidence supports an impact (Nichols et al. 1986, Kerr 1983, 1987, Brooks et al. 1984, Kastmer et al. 1984, Wilde et al. 1986, Hartnady 1986, Bohor et al. 1984, 1987). These arguments have been opposed by Hallam (1987). The major argument against an impact centers on the assumption that stratigraphic concentrations of iridium, or iridium spikes, result solely from extraterrestrial causes (Fenner and Presley 1984, Carter et al. 1986, Orth et al. 1982, Van Valen 1984, Officer et al. 1987, Surlyk 1980). A major line of evidence supporting an impact is the discovery of shocked quartz, which appears to be due only to impacts, and has largely been ruled out as originating from volcanism (Bohor et al. 1984, Wolbach et al. 1985, despite objections from Naslund et al. 1986).

The evidence from paleobotany also suggests an impact because pollen samples at the K-T boundary change abruptly in the same layer as the iridium spike (Pillmore et al. 1984, Nichols et al. 1986, Saito et al. 1986, Tschudy et al. 1984, 1986).

For the purposes of the present discussion, it is conceded that an asteroid may have struck the Earth at the end of the Cretaceous and that the effect of the impact is reflected in the sudden change in the pollen record. Clemens (1982) proposed that the K-T boundary be redefined as the Iridium Layer, if it can be shown that there is only a single iridium-producing event. Acceptance of the Clemens suggestion does not imply acceptance of the impact as the primary cause of dinosaur extinction, but it does provide a worldwide event, geologically instantaneous, to serve as an absolute boundary. This frees paleontologists from relying on events of low resolution such as the 'last occurrence' of a species.

The K-T Fauna

One of the most important areas of research deals with the question of synchronicity between the impact layer, the last dinosaur occurrence, the change in pollen, and other extinctions. There are two major questions that remain unanswered. The first is whether there was one impact, or several, and if there was more than one, over what span of time did they occur? The second question is whether the impact(s) occurred before or after dinosaur extinction (Officer and Drake 1983, Dingus 1984, Haq et al. 1987, Tipper 1983, Fastovsky and Dott 1987, Kent and Gradstein 1985, Jablonsky 1986, Clemens 1986, Morner 1982).

A corollary question concerns the number of dinosaur families that were still extant at the time of the impact (Clemens 1982, Fastovsky and Dott 1987). Some workers assume that dinosaurs were fully diverse and possibly increasing in diversity up to the terminal events (Retallack and Leahy 1986, Sheehan and Morse 1986, Russell 1981, 1984). I see a demonstrable decline in the numbers of individuals and taxa during the Maastrichtian, with a diachronous extinction of ankylosaurians, hadrosaurids, theropods, and ceratopsians on the basis of work by Clemens (1986), Archibald and Clemens (1984), Carpenter (1983), and Sloan et al. (1986), and this work. The best evidence to date from field studies of the Hell Creek and Lance formations indicates that the ankylosaurians disappeared first (Carpenter 1983), followed by hadrosaurids, theropods, and finally the ceratopsians, with Triceratops as the last identifiable dinosaur taxon present (Carpenter and Breithaup 1986, Clemens 1986). At Hell Creek, the last six feet of sediments before the impact event are devoid of dinosaur bones (Clemens 1986), but Retallack and Leahy (1986) point out that these beds are carbonate-poor and may not preserve bones. An erosional hiatus may also be present in the K-T boundary layers (Fastovsky and Dott, 1987). Even if this is demonstrated to be a correct interpretation, the three meters of sediments before these soil conditions prevail (postulated to represent about 500,000 years in papers by Clemens et al.) have a highly reduced dinosaur fauna with only ceratopsians present.

It follows that the most parsimonious explanation for hadrosaurid extinction must take into account the following factors:

1) extinction of hadrosaurids worldwide in all environments;

2) extinction in the absence of a global catastrophe;

3) extinction even if hadrosaurids survived well into the Tertiary;

4) extinction of small dinosaurs which because of their size would have had a better chance of survival in refugia;

5) the lack of extinctions in eutherian mammals, turtles, lizards, snakes, crocodiles, champsosaurs and birds;

6) the decline of all dinosaurs during the Maastrichtian;

7) the possible diachronous extinction of all the major groups of dinosaurs except ceratopsians prior to the impact event;

8) the lack of synchronicity of dinosaur extinction in the western interior of the United States;

The best stratigraphic evidence (Clemens, 1982; Carpenter, 1983) indicates that hadrosaurids preceded most other dinosaur groups into extinction. This evidence supports the following assertions:

1) That marine extinctions are separate from the terrestrial extinctions (Kauffman 1984).

2) That dinosaurs were either extinct or down to one major clade (Ceratopsia) by the time of the impact event (Clemens, 1982, 1983, 1986; Archibald, 1982, 1983, 1985; Carpenter, 1983).

3) That dinosaurs show a consistent decline in numbers of individuals and taxa during the Maastrichtian (Carpenter and Breithaupt, 1986).

These assertions, and the data which support them, are here augmented by the works of Van Valen and Sloan (1977), Schopf (1982), and Van Valen (1984A,B) to generate a new three-fold hypothesis on hadrosaurid extinction.

A NEW HYPOTHESIS ON HADROSAURID EXTINCTION

The first part of the proposal assumes that large species of dinosaurs assimilated niches throughout life, as individuals increased in age and size. Species such as the Nile Crocodile (Cott 1961) that pass through several orders of size may move from niche to niche. Most mammals tend to inhabit one major niche in life because adult size is attained quickly, with parents providing for the young. Although parental care is also known in dinosaurs (Horner 1984), the tremendous size increase of dinosaurs would mandate the occupation of more than one niche, especially for the theropods. A yearling *Tyrannosaurus rex* would feed on small forms that a fully grown adult would ignore, and probably could not catch, and a yearling *T. rex* could not possibly feed on the prey of a full-grown adult. The estimated 200-year longevity of large dinosaurs (Colbert 1983) could have resulted in individuals from an overlapping series of age groups occupying a series of separate niches throughout life.

Niche assimilation, so conceived, results in a depauperate community dominated by a few species whose extremely long lifespans produce a slow turnover of generations. This may account for the slow rate of evolution over the eight-million-year duration of the Maastrichtian, when the only new taxa of hadrosaurids to appear are *Anatotitan*, *Saurolophus*, and *Hypacrosaurus*. As shown above, hadrosaurids underwent a fifty percent decline in diversity from the Campanian to the Maastrichtian irrespective of taxonomic procedure.

Dinosaurs laying clutches of eggs on a yearly basis would produce a series of age groups occupying niches that would otherwise have been filled by many more species of mammals. At the end of the Cretaceous, most of the herbivores were large as adults, except for the hypsilophodontids.

The second part of this proposal assumes that if dinosaur species were dependent on specific species of plants, especially during breeding or migratory seasons, and the biological extinction rate of these plants exceeded the speciation rate of dinosaurs, then the dinosaurs would be gradually eliminated over geologic time. The probability of dinosaur extinction would become certainty if population levels in the dinosaurs were reduced below a viable reproductive capacity because of a severe reduction or seasonal absence of the primary food source. This would result in an extremely patchy distribution of herbivorous dinosaurs as the herds migrated to alternate food sources. A secondary effect would be a decrease in the population size of theropods as their herbivorous dinosaur food supply dwindled. Any factor that greatly increases the probability of extinction due to stereotypic behavior must be considered along with ecological causes. The loss of a plant species for any reason would put a dinosaur species under severe ecological stress, depending upon the seasonal needs and behavioral patterns of the dinosaur. This is seen today in the Giant Panda, _Ailuropoda_, where the limitation of plant species and niche space has all but eliminated this genus, even with positive human intervention.

The third part of this proposal assumes that hadrosaurids and ceratopsians had diversified as a result of the angiosperm radiation in the Middle Cretaceous. Angiosperms are known to have begun their radiation in the Aptian-Albian (Hickey and Doyle 1977). Hadrosaurids and ceratopsians do not have an extensive fossil record until the Campanian, about twenty million years later. It is assumed that the turnover rate of both angiosperms and gymnosperms was high at the species level during the Maastrichtian (Wing and Tiffney 1987). Hadrosaurids and ceratopsians may not have initially fed exclusively on angiosperms, but were able to switch to them as they became the most important component of the flora.

It is postulated that dinosaur extinction was accelerated by a process of niche assimilation, in communities dominated by dinosaurs where the taxonomic turnover rates of plants were higher than those of dinosaurs. The extreme longevity and large size of dinosaur adults resulted in a species-poor community inhabited by few individuals in highly dispersed and patchy populations. Predation and juvenile mortality would increase over time as the theropods had fewer species of herbivores to choose from. Over a span of eight million years, and with the withdrawal of the epeiric seas, the remaining dinosaurs occupied more niches per dinosaur species as they also assimilated the niches occupied by newly extinct herbivorous dinosaurs, while the distribution of plants increased in patchiness. It is postulated that dinosaurs would have decreased in numbers per population and populations would have become more isolated. The result is an increasingly patchy distribution of both plants and dinosaurs, with an increase in dinosaur inbreeding, and reduced ability to migrate to other areas with the proper flora.

The same process can be seen today with African elephants. Although each breeding group is perfectly viable, and adapted to local conditions, the requirements of each local population exceed the productivity of the habitat. Humans act to remove niche space and habitats from the elephants just as the loss of the epeiric seas 'removed' niche space from the dinosaurs. Overconsumption by dinosaurs may have led to local extinction just as overgrazing leads to the starvation and death of modern elephants (Moss 1988). For modern elephants, overpopulation and starvation are avoided by controlled herd-thinning. This option was not available in the Cretaceous. Continuous predation by theropods and the increased patchiness of plant species would have eventually brought all population sizes down below a critical level. The increasing patchiness of the environments would have increased the isolation of breeding groups. Although none of the foregoing factors, by itself, would have increased the extinction rate, taken all together at the same time and place, and applied over an eight-million-year period, they weakened the dinosaur communities sufficiently to force minimal breeding groups into increasingly restricted and isolated areas. The situation became an ecological 'vicious circle' with each factor reinforcing the others.

Like the African Elephant, the dinosaurs dominated wherever they occurred, but their niche space continued to be reduced until their world consisted only of the area inhabited by each isolated population. The dinosaurs were not outcompeted, they did not freeze to death, nor were they killed by asteroids. They were perfectly viable in their particular niche. In the end, however, they had no niche in which to be viable. There have been other asteroids (Wilde et al. 1986) without major extinctions. It is not necessary for hadrosaurids and the other dinosaurs to be treated differently. In the end, only one genus out of seven orders remained (Clemens 1982). The processes of stereotypic behavior, niche assimilation, and decreasing niche space are processes that can explain the decrease of any macro-herbivore at any time, and in any place. Hadrosaurids occurred in both Laurasia and Gondwanaland, yet it was the ceratopsians, that were restricted to Laurasia, that lasted until the end. This may indicate that niche width was more important than geographic distribution for dinosaurs. The fact that theropods did not outlast the herbivores suggests that dinosaurs made up a closed ecological community.

SUMMARY

Hadrosaurid extinction is presented as gradual, rather than catastrophic, and as preceding the extinction of the ceratopsians, and as taking place before the K-T boundary impact event. The new hypothesis of niche assimilation, in combination with stereotypic behavior (specialized feeding habits), and loss of habitat space, is proposed as factors that caused a continual decrease in hadrosaurid population size and numbers, making hadrosaurid distribution more patchy over a span of eight million years. Despite varying taxonomic procedures, which can produce mutually exclusive diversity databases, hadrosaurids decline in numbers of both individuals and taxa during the entire Maastrichtian. If any dinosaurs survived until the impact event, current studies suggest that these dinosaurs comprised a single species of ceratopsian.

APPENDIX 1
Taxonomy Used In This Report

ORIGINAL NAME	THIS REPORT
Aachenosaurus multidens	Not a dinosaur
Anatosaurus annectens	Edmontosaurus annectens
Anatosaurus copei	Anatotitan copei
Anatosaurus edmontoni	Edmontosaurus annectens
Anatosaurus longiceps	Edmontosaurus regalis
Anatosaurus saskatchewanensis	Edmontosaurus regalis
Anatotitan copei	Anatotitan copei
Aralosaurus tuberiferus	Aralosaurus tuberiferus
Arstanosaurus akkurganensis	Genus indet.
Bactrosaurus johnsoni	Bactrosaurus johnsoni
Bactrosaurus prynadai	Genus indet.
Barsboldia sicinskii	Genus indet.
Brachylophosaurus canadensis	Brachylophosaurus canadensis
Cheneosaurus tolmanensis	Hypacrosaurus altispinus
Cionodon arctatus	Genus indet.
Cionodon stenopsis	Genus indet.
Claorhynchus trihedrus	Ceratopsian
Claosaurus affinis	Claosaurus agilis
Claosaurus agilis	Claosaurus agilis
Claosaurus annectens	Edmontosaurus regalis
Corythosaurus bicristatus	Corythosaurus casuarius
Corythosaurus brevicristatus	Corythosaurus casuarius
Corythosaurus casuarius	Corythosaurus casuarius
Corythosaurus excavatus	Corythosaurus casuarius
Corythosaurus frontalis	Lambeosaurus lambei
Corythosaurus intermedius	Corythosaurus casuarius
Diclonius calamarius	Genus indet.
Diclonius mirabilis	Anatotitan copei
Diclonius pentagonus	Genus indet.
Diclonius perangulatus	Genus indet.
Didanodon ?	Hypacrosaurus sp.
Dysganus bicarinatus	Ceratopsian
Dysganus encaustus	Ceratopsian
Dysganus haydenianus	Ceratopsian
Dysganus peiganus	Ceratopsian
Edmontosaurus regalis	Edmontosaurus regalis
Gilmoreosaurus mongoliensis	Gilmoreosaurus mongoliensis
Gryposaurus notabilis	Kritosaurus notabilis
Hadrosaurus agilis	Claosaurus agilis
Hadrosaurus breviceps	Genus indet.
Hadrosaurus foulki	Hadrosaurus foulki
Hadrosaurus minor	Genus indet.
Hadrosaurus tripos	Genus indet.

Hypacrosaurus altispinus	Hypacrosaurus altispinus
Hypsibema crassicauda	Genus indet.
Jaxartosaurus aralensis	Genus indet.
Jaxartosaurus fuyanensis	Genus indet.
Kritosaurus australis	Kritosaurus australis
Kritosaurus incurvimanus	Kritosaurus notabilis
Kritosaurus navajovius	Kritosaurus navajovius
Kritosaurus notabilis	Kritosaurus notabilis
Lambeosaurus clavinitialis	Lambeosaurus lambei
Lambeosaurus lambei	Lambeosaurus lambei
Lambeosaurus magnicristatus	Lambeosaurus magnicristatus
Lophorhothon atopus	Lophorhothon atopus
Maiasaura peeblesorum	Maiasaura peeblesorum
Mandschurosaurus amurensis	Genus indet.
Mandschurosaurus jiainensis	Genus indet.
Mandschurosaurus laoensis	Genus indet.
Microhadrosaurus nanshiungensis	Genus indet.
Nipponosaurus sachalinensis	Lambeosaurine indet.
Ornithotarsus immanis	Genus indet.
Orthomerus dolloi	Iguanodontidae
Orthomerus transylvanicus	Telmatosaurus transylvanicus
Parasaurolophus cyrtocristatus	Parasaurolophus walkeri
Parasaurolophus tubicen	Parasaurolophus walkeri
Parasaurolophus walkeri	Parasaurolophus walkeri
Pneumatoarthrus peloreus	Chelonian
Procheneosaurus convincens	Genus indet.
Procheneosaurus cranibrevis	Genus indet.
Procheneosaurus erectofrons	Hypacrosaurus altispinus
Procheneosaurus n. nud.	Hypacrosaurus sp.
Procheneosaurus praeceps	Lambeosaurus lambei
Prosaurolophus maximus	Prosaurolophus maximus
Pteropelyx grallipes	Corythosaurus casuarius
Saurolophus angustirostris	Saurolophus osborni
Saurolophus kryschtofovici	Saurolophus osborni
Saurolophus osborni	Saurolophus osborni
Secernosaurus koerneri	Hadrosaurine indet.
Shantungosaurus giganteus	Shantungosaurus giganteus
Tanius chingkankouensis	Tanius sinensis
Tanius sinensis	Tanius sinensis
Tetragonosaurus cranibrevis	Corythosaurus casuarius
Tetragonosaurus erectofrons	Corythosaurus casuarius
Tetragonosaurus praeceps	Lambeosaurus lambei
Thespesius edmontoni	Edmontosaurus annectens
Thespesius occidentalis	Genus indet.
Thespesius saskatchewanensis	Edmontosaurus regalis
Trachodon altidens	Genus indet.
Trachodon cantabridgiensis	Genus indet.
Trachodon longiceps	Genus indet.

Trachodon marginatus	Genus indet.
Trachodon mirabilis	Anatotitan copei
Trachodon selwyni	Genus indet.
Tsintaosaurus spinorhinus	Tsintaosaurus spinorhinus

APPENDIX 2

World List of Formations With Hadrosaurian Remains based on my studies, Weishampel and Weishampel (1983), and Guy D. Leahy (pers. comm. 1988).

Aguja Fm, Campanian
Almond Fm, Campanian
Bayn Shireh Beds, Santonian-Campanian
Bearpaw Fm, Maastrichtian
Beleutinskaya Beds, Turonian-Santonian ?
Black Creek Fm, Campanian-Maastrichtian
Blufftown Fm, Campanian
Bonnet Plume Fm, Maastrichtian
Bostobinskaya Beds, Santonian-Campanian ?
Brown Sandstone, ?
Castlegate Fm, Campanian
Chubut Fm, Maastrichtian ?
Cokedale Fm, Campanian
Coli Torro Fm, Maastrichtian ?
Darbazinskaya Beds, Santonian ?
Dawson Arkose, ?
Depunta Fm, Campanian ?
Djadokhta Fm, Campanian ?
El Gallo Fm, Campanian
Eutaw Fm, Campanian
Foremost Fm, Campanian
Fox Hills Fm, Maastrichtian
Frenchman Fm, Campanian
Fruitland Fm, Campanian
Gething Beds, Aptian ?
Gosau Formation, Maastrichtian
Hell Creek Fm, Maastrichtian
Horseshoe Canyon Fm, Maastrichtian
Iren Dabasu Beds, Cenomanian ?
Iren-Noskaya Beds, Santonian ?
Judith River Fm, Campanian
Kaiparowitz Fm, Maastrichtian
Kirtland Shale, Maastrichtian
La Bocana Fm, Campanian
Ladd Fm, Campanian
Lance Fm, Maastrichtian
Laramie Fm, Maastrichtian

Los Alamitos Fm, Campanian
"Maastricht Beds", Maastrichtian
Marshalltown Fm, Campanian
Matawan Fm, Campanian
Menefee Fm, Campanian
Merchantville Fm, Campanian
Milk River Fm, Campanian
Mooreville Chalk, Campanian
Moreno Fm, Maastrichtian
Mount Laurel Fm, Maastrichtian
Nan Huiung Beds, Maastrichtian
Navesink Fm, Maastrichtian
Nemegt Beds, Campanian
New Egypt Fm, Maastrichtian
Niobrara Fm, Campanian
North Horn Fm, Maastrichtian
Pierre Shale, Campanian
Price River Fm, Campanian
Prince Creek Fm, Coniacian ?
Punta Baja Fm, Campanian
Raritan Fm, Campanian
Ravenscrag Fm, Maastrichtian
Ripley Fm, Campanian
Rosario Fm, Maastrichtian
Salamanca Fm, Campanian ?
San Jorge Fm, Maastrichtian ?
Scollard Fm, Maastrichtian
Selma Chalk, Campanian
Severn Fm, Maastrichtian
Snake Ridge Fm, Maastrichtian ?
Sonoita Fm, Campanian
St. Mary River Fm, Maastrichtian
Tornillo Fm, Maastrichtian
Tsagayan Beds, Maastrichtian ?
Two Medicine Fm, Campanian
Valle De Angeles Fm, Cenomanian ?
Wangshih Beds, Campanian ?
Williams Fork Fm, Campanian ?
Woodbine Fm, Campanian ?
Woodbury Fm, Campanian
Wulungo Svita, Campanian ?
Yacoraite Fm, Campanian

Maastrichtian = 30 Formations
Campanian = 42 Formations
Pre-Campanian = 9 Formations
Unnamed formations/units not listed.

APPENDIX 3

A time chart showing the stages of the Upper Jurassic and the Cretaceous with dates based on Haq et al (1987). The begining of the Oxfordian is about 140 million years ago. Camptosaurus lived during the Kimmeridgian and Portlandian.

The hadrosaurs reached their peak in the Campanian which lasted about 12 million years. The final stage for hadrosaurs, and all dinosaurs, was the Maastrichtian which had a span of 8 million years. The Cretaceous ended about 66 million years ago.

APPENDIX 4

THE SYSTEM OF STANDARDIZED MEASUREMENTS

HUMERUS

Length	from a to b
Length of deltopectoral process	from e to f
Width of deltopectoral process	from c to d

PUBIS

Length	from a to b
Length of blade	from a to f
Width of blade	from c to d
Width of neck	from h to i

ILIUM

Length	from a to b
Length of postacetabular process	from a to h
Width of postacetabular process	from e to f
Width of iliac body	from c to d

The placement of points for measurements are as follows: On the humerus (1), line 'ab' are the maximum distances where 'a' falls on the midpoint of the head and 'b' is on the asymptote of the distal trochlea. Line 'ef' define the deltopectoral crest and each point falls on the asymptote. Line 'cd' are perpendicular to 'ef'. Other measurements proved to be taxonomically useless.

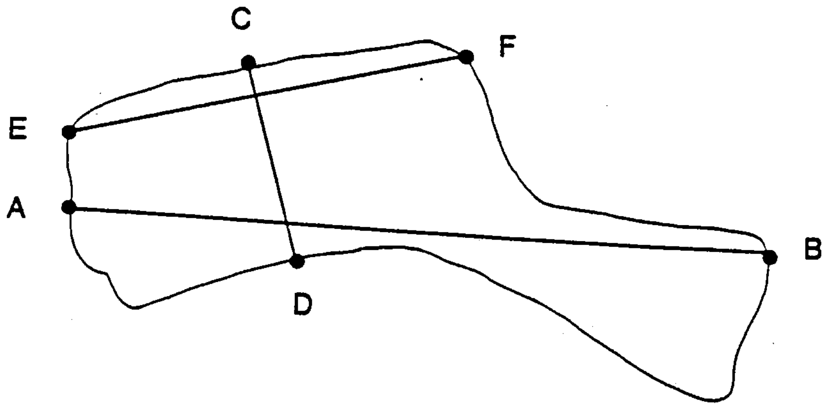
On the pubis (2): Line 'ab' is the length where line 'af' bisects the blade into dorsal and ventral segments. Point 'b' is on the asymptote of the acetabulum. Line 'cd' is perpendicular to 'af' and bisects it. Line 'eg' is perpendicular to 'af' where point 'e' is on the asymptote. Line 'ih' is the minimum width of the neck. Line 'af' is the blade length and line 'cd' is the height.

On the ilium (3): Line 'ab' is the maximum length between perpendiculars. Line 'cd' is perpendicular to 'ab' where 'd' is on the asymptote of the acetabulum. Point 'c' may or may not fall on the anterior border of the antitrochanter. Point 'g' lies on the posterior border of the ischial peduncle. Line 'hg' is drawn perpendicular to line 'ab' at this point. Line 'ah' now defines the postacetabular process length. Line 'ef' bisects this line and is perpendicular to it, thus defining the height. Line 'cb' usually bisects the preacetabular process thus forming angle <DCB which is a good measure of the preacetabular process deflection. These are the most diagnostic elements.

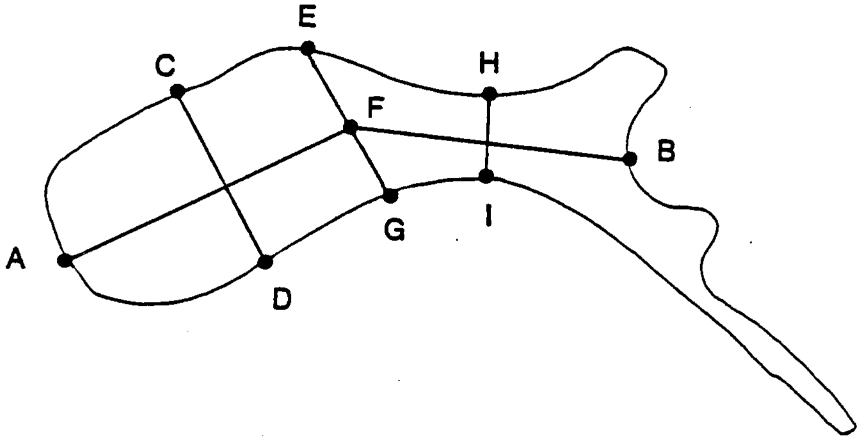
Measurements for other elements are simply the maximum length between perpendiculars and the minimum diameter of the shaft at its midpoint except in the case of the femur where it is taken half-way between the fourth trochanter and the extreme distal end of the femur. The length of the scapula is taken ALONG the dorsal border from the coracoidal ridge to the asymptote of the dorsal border at the end of the scapular blade (see Plate 1A). A line half way along this line perpendicular to the trend of the scapular blade defines the height. This is not possible in camptosaurs because of the exaggerated development of the acromial ridge. The length is therefore measured between perpendiculars (see Plate 1B). The height is now the diameter of the blade midway between these two points.

CAUTIONARY NOTE: I have found during these studies that many of the measurements in Lull and Wright (1942) are taken directly from previous publications. In several cases, their analyses appear to be the result of a 'literature study' rather than a study of the actual specimens. Many measurements that I made from my own photographs varied from actual measurements that I made from the same bone. They seem to vary in direct proportion to the increasing size of the bone. The reader is cautioned against relying totally on the camera.

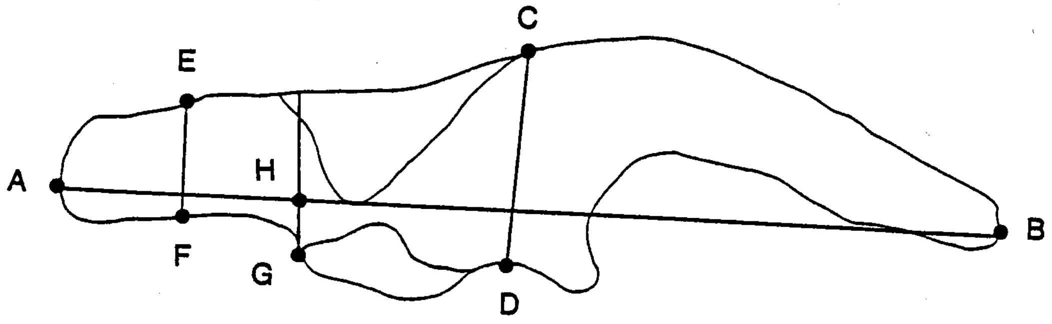
1



2



3



APPENDIX 5

A labelled drawing of the skull of Corythosaurus casuarius (AMNH 5338) showing the bones visible in lateral view. Note the sclerotic rings which are rarely preserved. Abbreviations are the same as listed in the Introduction.

APPENDIX 6

HADROSAURID SPECIMENS USED IN THIS WORK

MUSEUM SPECIMENS AND THEIR ACRONYMS

American Museum of Natural History - AMNH
New York

British Museum (Natural History) - BM(NH)
London

Brigham Young University Museum - BYU
Provo

Carnegie Museum of Natural History - CM
Pittsburg

Cleveland Museum of Natural History - CMNH
Cleveland

Museum of Natural History of the City of
Denver - DMNH

Ekalaka Museum - EM
Ekalaka

Field Museum of Natural History - FMNH
Chicago

Geol. Inst. Mongolian People's Republic - GSP
Ulan Bator

Inst. Vert. Palaeo. Palaeoanthro., Academica Sinica, Beijing
- IVPP

Los Angeles County Museum, Natural History - LACM
Los Angeles

Museum of Northern Arizona - MNA
Flagstaff

Museum National d'Histoire Naturelle - MNHN
Paris

Naatuurhistorich Mus. Maastricht, Holland - NHMM

National Museum of Natural Sciences - NMC

Ottawa

Palaeontological Institute, Academy of Natural
Sciences - PIN, Moscow

Beijing Museum of Natural History - PMNH
Beijing

Palaeontological Museum - PMU.R
Uppsala

Royal Ontario Museum - ROM
Toronto

San Diego Museum of Natural History - SDMNH
San Diego

Senckenberg Museum - SM
Frankfurt am Main, German Federal Republic

Texas Memorial Museum - TMM, Austin

Tyrrell Museum of Palaeontology - TMP
Drumheller

University of Alberta, Dept. Geol. - UA
Edmonton

Museum of Paleontology, Univ. Calif. - UCMP
Berkeley

University of Michigan Mus. Paleontology - UMMP
Ann Arbor

University of Nebraska State Museum - UNSM
Lincoln

National Museum of Natural History, Smithsonian Institution
- USNM, Washington, D.C.

Peabody Museum of Natural History, Yale Univ. - YPM
New Haven

Peabody Museum of Natural History, Yale Univ.,
(Princeton Collection) - YPM(PU,)New Haven

Inst. Paleobiol., Polish Acad. Sci. - ZPAL
Warsaw

AMNH	107	Genus indet.
AMNH	427	Edmontosaurus sp
AMNH	1390	Genus indet.
AMNH	1460	Hadrosaurus foulki
AMNH	1770	Genus indet.
AMNH	1811	Genus indet.
AMNH	2081	Genus indet.
AMNH	2132	Genus indet.
AMNH	2212	Genus indet.
AMNH	2342	Genus indet.
AMNH	2343	Genus indet.
AMNH	2344	Genus indet.
AMNH	2998	Edmontosaurus ?
AMNH	3047	Genus indet.
AMNH	3049	Genus indet.
AMNH	3069	Genus indet.
AMNH	3651	Genus indet.
AMNH	3653	Genus indet.
AMNH	3660	Genus indet.
AMNH	3792	Genus indet.
AMNH	3839	Genus indet.
AMNH	3951	Genus indet. (Cionodon arctatus)
AMNH	3971	Pteropelyx grallipes
AMNH	3973	Genus indet.
AMNH	3974	Genus indet.
AMNH	3975	Genus indet.
AMNH	3978	Claorhynchus (Ceratopsian)
AMNH	3991	Genus indet.
AMNH	4982	Genus indet.
AMNH	4983	Genus indet.
AMNH	5022	Genus indet.
AMNH	5023	Genus indet.
AMNH	5041	Genus indet.
AMNH	5046	Edmontosaurus sp
AMNH	5053	Genus indet.
AMNH	5060	Edmontosaurus annectens
AMNH	5145	Telmatosaurus transsylvanicus
AMNH	5146	Genus indet.
AMNH	5200	Genus indet.
AMNH	5202	Saurolophus sp
AMNH	5203	Saurolophus sp
AMNH	5204	Hypacrosaurus altispinus
AMNH	5206	Hypacrosaurus altispinus
AMNH	5207	'Podischion', Genus indet.
AMNH	5209	Saurolophus sp
AMNH	5210	Saurolophus sp
AMNH	5212	Saurolophus sp
AMNH	5217	Hypacrosaurus altispinus

AMNH	5219	Saurolophus sp
AMNH	5220	Saurolophus osborni
AMNH	5221	Saurolophus osborni
AMNH	5225	Hypacrosaurus altispinus ?
AMNH	5236	Edmontosaurus
AMNH	5240	Corythosaurus casuarius
AMNH	5242	Saurolophus sp
AMNH	5243	Saurolophus sp
AMNH	5247	Saurolophus sp
AMNH	5248	Corythosaurus
AMNH	5250	Saurolophus sp
AMNH	5252	Saurolophus sp
AMNH	5254	Saurolophus osborni
AMNH	5256	Saurolophus osborni ?
AMNH	5258	Saurolophus sp
AMNH	5268	Saurolophus sp
AMNH	5269	Saurolophus sp
AMNH	5270	Saurolophus sp
AMNH	5271	Saurolophus osborni ?
AMNH	5272	Hypacrosaurus altispinus
AMNH	5275	Genus indet.
AMNH	5276	Saurolophus osborni ?
AMNH	5277	Saurolophus osborni ?
AMNH	5278	Hypacrosaurus altispinus
AMNH	5338	Corythosaurus casuarius
AMNH	5340	Lambeosaurus lambei
AMNH	5345	Prosaurolophus maximus ?
AMNH	5348	Corythosaurus casuarius
AMNH	5350	Kritosaurus notabilis ?
AMNH	5353	Lambeosaurus lambei ?
AMNH	5357	Corythosaurus ?
AMNH	5358	Genus indet.
AMNH	5359	Corythosaurus sp
AMNH	5360	Corythosaurus
AMNH	5373	Lambeosaurus lambei ?
AMNH	5378	Prosaurolophus maximus
AMNH	5379	Prosaurolophus maximus ?
AMNH	5382	Lambeosaurus magnicristatus ?
AMNH	5383	Genus indet.
AMNH	5384	Prosaurolophus maximus ?
AMNH	5386	Prosaurolophus maximus
AMNH	5411	Prosaurolophus maximus ?
AMNH	5412	Genus indet.
AMNH	5413	Genus indet.
AMNH	5417	Genus indet.
AMNH	5418	Genus indet.
AMNH	5420	Genus indet.
AMNH	5426	Genus indet.

AMNH	5431	Genus indet.
AMNH	5433	Corythosaurus
AMNH	5436	Genus indet.
AMNH	5441	Genus indet.
AMNH	5447	Genus indet.
AMNH	5451	Hypacrosaurus sp
AMNH	5459	Genus indet.
AMNH	5460	Genus indet.
AMNH	5461	Corythosaurus casuarius
AMNH	5463	Genus indet.
AMNH	5465	Kritosaurus
AMNH	5467	Kritosaurus sp
AMNH	5469	Corythosaurus casuarius
AMNH	5666	Lambeosaurus ?
AMNH	5730	Anatotitan copei
AMNH	5733	Genus indet.
AMNH	5737	Genus indet.
AMNH	5738	Genus indet.
AMNH	5739	Genus indet.
AMNH	5796	Kritosaurus ?
AMNH	5797	Kritosaurus navajovius
AMNH	5799	Kritosaurus navajovius
AMNH	5854	Genus indet.
AMNH	5863	Edmontosaurus sp
AMNH	5879	Edmontosaurus sp
AMNH	5885	Genus indet.
AMNH	5886	Anatotitan copei
AMNH	5887	Genus indet.
AMNH	5888	Genus indet.
AMNH	5890	Genus indet.
AMNH	5892	Genus indet.
AMNH	5893	Genus indet.
AMNH	5894	Edmontosaurus sp
AMNH	5896	Genus indet.
AMNH	5897	Genus indet.
AMNH	5899	Genus indet.
AMNH	6269	Gilmoreosaurus sp
AMNH	6270	Gilmoreosaurus sp
AMNH	6271	Gilmoreosaurus sp
AMNH	6272	Gilmoreosaurus sp
AMNH	6353	Bactrosaurus johnsoni
AMNH	6365	Gilmoreosaurus mongoliensis
AMNH	6366	Gilmoreosaurus mongoliensis
AMNH	6369	Gilmoreosaurus mongoliensis
AMNH	6370	Bactrosaurus johnsoni
AMNH	6371	Gilmoreosaurus mongoliensis
AMNH	6372	Bactrosaurus johnsoni
AMNH	6373	Bactrosaurus johnsoni

AMNH	6374	Gilmoreosaurus mongoliensis
AMNH	6375	Genus indet.
AMNH	6379	Bactrosaurus johnsoni
AMNH	6380	Bactrosaurus johnsoni
AMNH	6384	Bactrosaurus johnsoni
AMNH	6385	Gilmoreosaurus mongoliensis
AMNH	6386	Bactrosaurus johnsoni
AMNH	6388	Genus indet.
AMNH	6389	Bactrosaurus johnsoni
AMNH	6390	Genus indet.
AMNH	6391	Bactrosaurus johnsoni
AMNH	6392	Genus indet.
AMNH	6393	Genus indet.
AMNH	6394	Genus indet.
AMNH	6395	Gilmoreosaurus mongoliensis
AMNH	6396	Bactrosaurus johnsoni
AMNH	6397	Bactrosaurus johnsoni
AMNH	6398	Genus indet.
AMNH	6501	Bactrosaurus johnsoni
AMNH	6545	Genus indet.
AMNH	6551	Gilmoreosaurus mongoliensis
AMNH	6553	Bactrosaurus johnsoni
AMNH	6573	Genus indet.
AMNH	6574	Gilmoreosaurus mongoliensis
AMNH	6575	Bactrosaurus johnsoni
AMNH	6577	Gilmoreosaurus mongoliensis
AMNH	6578	Gilmoreosaurus mongoliensis
AMNH	6580	Genus indet.
AMNH	6581	Bactrosaurus johnsoni
AMNH	6582	Genus indet.
AMNH	6583	Genus indet.
AMNH	6584	Bactrosaurus johnsoni
AMNH	6585	Bactrosaurus johnsoni
AMNH	6586	Bactrosaurus johnsoni
AMNH	6587	Bactrosaurus johnsoni
AMNH	6594	Genus indet.
AMNH	6595	Genus indet.
AMNH	6783	Parasaurolophus walkeri
AMNH	7607	Corythosaurus
AMNH	7622	Genus indet.
AMNH	7626	Genus indet.
AMNH	7647	Corythosaurus
AMNH	7724	Genus indet.
AMNH	8145	Edmontosaurus sp
AMNH	8435	Genus indet.
AMNH	8440	Corythosaurus casuarius
AMNH	8525	Kritosaurus sp
AMNH	8526	Kritosaurus sp

AMNH	8527	Corythosaurus casuarius
AMNH	8528	Corythosaurus casuarius
AMNH	8529	Genus indet.
ANSP	9201	Hadrosaurus foulki
ANSP	9202	Hadrosaurus foulki
ANSP	9203	Hadrosaurus foulki
ANSP	9225	Genus indet., Chelonian
ANSP	9260	Genus indet.
ANSP	10005	Hadrosaurus foulki
ANSP	16969	Corythosaurus sp
Auburn	982	Genus indet.
Auburn	2295	Kritosaurus sp
Auburn	2982	Genus indet.
Auburn	3026	Genus indet.
BM(NH)	R3386	Telmatosaurus transsylvanicus
BM(NH)	42955	Orthomerus dolloi
BYU	2467	Parasaurolophus sp
CM	05	Genus indet.
CM	243	Genus indet.
CM	245	Genus indet.
CM	252	Genus indet.
CM	254	Genus indet.
CM	281	Genus indet.
CM	282	Genus indet.
CM	305	Genus indet.
CM	306	Genus indet.
CM	324	Genus indet.
CM	325	Genus indet.
CM	326	Genus indet.
CM	327	Genus indet.
CM	328	Genus indet.
CM	329	Genus indet.
CM	344	Genus indet.
CM	345	Genus indet.
CM	594	Genus indet.
CM	1064	Genus indet.
CM	1065	Genus indet.
CM	1066	Genus indet.
CM	1067	Genus indet.
CM	1068	Genus indet.
CM	1069	Genus indet.
CM	1071	Genus indet.
CM	1072	Genus indet.

CM	1073	Genus indet.
CM	1074	Genus indet.
CM	1076	Genus indet.
CM	1077	Kritosaurus sp
CM	1202	Genus indet.
CM	1652	Anatotitan copei
CM	3319	Genus indet.
CM	3363	Genus indet.
CM	9461	Corythosaurus casuarius
CM	9970	Genus indet.
CM	11375	Corythosaurus casuarius
CM	11376	Genus indet.
CM	11745	Genus indet.
CM	12100	Genus indet.
CM	12101	Genus indet.
CM	26258	Edmontosaurus regalis
CM	30745	Genus indet.
CM	38321	Genus indet.
CM	38324	Genus indet.
CM	38325	Genus indet.
CM	38328	Genus indet.
CM	38329	Genus indet.
CM	38333	Genus indet.
CM	38343	Genus indet.
CM	38344	Genus indet.
CM	38353	Genus indet.
CM	38355	Genus indet.
CM	38356	Genus indet.
CMNH	10178	Edmontosaurus annectens
CMNH	10406	Lambeosaurus sp
DMNH	1493	Edmontosaurus annectens
FMNH	P1479	Lambeosaurus lambei
FMNH	P27343	Parasaurolophus sp
FMNH	P27383	Lophorhothon atopus
FMNH	P13423	Secernosaurus koerneri
FMNH	P15003	Edmontosaurus regalis
FMNH	P27393	Parasaurolophus crytocristatus
GSP	100/104	Saurolophus angustirostris
IVPP	725	Tsintaosaurus spinorhinus
IVPP	4732	Microhadrosaurus nanshiungensis
LACM	592	Genus indet.

LACM	2760	Genus indet.
LACM	2852	Saurolophus sp. ?
LACM	3743	Corythosaurus casuarius (=CM 9461)
LACM	17703	Lambeosaurus sp.
LACM	17715	Lambeosaurus laticaudus
LACM	20872	Hypacrosaurus sp. ?
LACM	20873	Lambeosaurus sp.
LACM	20874	Lambeosaurus sp.
LACM	20875	Lambeosaurus sp.
LACM	23502	Edmontosaurus annectens
LACM	23504	Edmontosaurus annectens
LACM	28234	Lambeosaurus sp.
MNA	230	Parasaurolophus sp.
MNHN	AMN 17	Edmontosaurus sp.
NHMM	198027	Genus indet.
NMC	290	Genus indet.
NMC	351	Lambeosaurus lambei
NMC	362	Kritosaurus notabilis
NMC	419	Genus indet. (T. marginatus)
NMC	1092	Genus indet. (Didanodon type)
NMC	2246	Hypacrosaurus altispinus
NMC	2247	Hypacrosaurus altispinus
NMC	2277	Prosaurolophus maximus
NMC	2278	Kritosaurus notabilis
NMC	2288	Edmontosaurus regalis
NMC	2289	Edmontosaurus regalis
NMC	2803	Prosaurolophus maximus
NMC	2869	Lambeosaurus lambei (Lecto)
NMC	2870	Prosaurolophus maximus
NMC	8330	Lambeosaurus sp
NMC	8399	Edmontosaurus edmontoni
NMC	8500	see AMNH 5278
NMC	8501	Hypacrosaurus altispinus
NMC	8502	Lambeosaurus sp
NMC	8503	Lambeosaurus lambei
NMC	8509	Edmontosaurus regalis
NMC	8532	Lambeosaurus lambei ?
NMC	8633	Corythosaurus casuarius
NMC	8676	Corythosaurus casuarius
NMC	8703	Lambeosaurus lambei
NMC	8704	Corythosaurus casuarius
NMC	8705	Lambeosaurus magnicristatus
NMC	8893	Brachylophosaurus canadensis
NMC	8917	Corythosaurus sp

PIN	551-8	Saurolophus angustirostris
PIN	551-357	Saurolophus angustirostris
PIN	551-358	Saurolophus angustirostris
PIN	551-359	Saurolophus angustirostris
PIN	559/1	"Iguanodon" orientalis
PIN	2229/1	Aralosaurus tubiferus (type)
PIN	2230/1	"Procheneosaurus" convincens
PIN	2232/1	Probactrosaurus gobiensis
PIN	2232/46	Probactrosaurus alashanicus
PIN	2549/1	Gilmoreosaurus mongoliensis ?
PIN	3386/50	"Iguanodon" orientalis
PIN	5009/1	Jaxartosaurus aralensis
PIN	5009/31	Bactrosaurus prynadai
PIN	5009/32	Bactrosaurus prynadai
PIN	5009/33	Bactrosaurus prynadai
PMU.R	222	Parasaurolophus tubicens
PMU.R	223	Kritosaurus sp.
PMU.R	224	Kritosaurus sp.
PMU.R	231	Kritosaurus sp.
PMU.R	236	Kritosaurus sp.
PMU.R	245	Kritosaurus sp.
ROM	???	Hypacrosaurus altispinus
ROM	430	Genus indet.
ROM	431	Genus indet.
ROM	433	Genus indet.
ROM	435	Genus indet.
ROM	658	Edmontosaurus regalis
ROM	667	Prosaurolophus maximus
ROM	669	Genus indet.
ROM	671	Edmontosaurus regalis
ROM	686	Genus indet.
ROM	687	Genus indet.
ROM	691	Genus indet.
ROM	693	Genus indet.
ROM	694	Genus indet.
ROM	696	Genus indet.
ROM	698	Genus indet.
ROM	702	Hypacrosaurus altispinus
ROM	703	Hypacrosaurus sp.
ROM	706	Genus indet.
ROM	709	Saurolophus sp.
ROM	710	Genus indet.
ROM	711	Genus indet.
ROM	712	Genus indet.
ROM	713	Genus indet.
ROM	714	Genus indet.

ROM	758	Lambeosaurus lambei
ROM	759	Lambeosaurus lambei
ROM	764	Kritosaurus notabilis
ROM	765	Kritosaurus notabilis
ROM	768	Parasaurolophus walkeri
ROM	769	Kritosaurus notabilis
ROM	770	Kritosaurus notabilis
ROM	771	Kritosaurus notabilis
ROM	772	Kritosaurus notabilis
ROM	773	Kritosaurus notabilis
ROM	774	Kritosaurus notabilis
ROM	776	Corythosaurus casuarius
ROM	777	Corythosaurus casuarius
ROM	786	Prosaurolophus maximus
ROM	787	Prosaurolophus maximus
ROM	792	Edmontosaurus sp.
ROM	794	Lambeosaurus lambei
ROM	801	Edmontosaurus regalis
ROM	816	Parasaurolophus walkeri
ROM	817	Parasaurolophus walkeri
ROM	824	Genus indet.
ROM	834	Genus indet.
ROM	845	Corythosaurus casuarius
ROM	855	Genus indet.
ROM	867	Edmontosaurus edmontoni
ROM	868	Corythosaurus casuarius
ROM	869	Lambeosaurus lambei
ROM	870	Corythosaurus casuarius
ROM	871	Corythosaurus casuarius
ROM	873	Kritosaurus notabilis
ROM	874	Lambeosaurus lambei
ROM	875	Corythosaurus casuarius
ROM	1218	Lambeosaurus lambei
ROM	1423	Prosaurolophus maximus
ROM	1424	Genus indet.
ROM	1438	Hypacrosaurus sp.
ROM	1928	Prosaurolophus maximus
ROM	1929	Prosaurolophus maximus (=TMM 41262)
ROM	1933	Corythosaurus casuarius
ROM	1939	Kritosaurus sp
ROM	1940	Corythosaurus sp. ?
ROM	1947	Corythosaurus casuarius
ROM	3083	Genus indet.
ROM	3084	Genus indet.
ROM	3140	Genus indet.
ROM	3141	Genus indet.
ROM	3175	Genus indet.
ROM	3179	Genus indet.

ROM	3195	Genus indet.
ROM	3196	Genus indet.
ROM	3197	Genus indet.
ROM	3201	Genus indet.
ROM	3294	Genus indet.
ROM	3305	Genus indet.
ROM	3382	Genus indet.
ROM	3399	Genus indet.
ROM	3400	Genus indet.
ROM	3498	Genus indet.
ROM	3500	Genus indet.
ROM	3502	Genus indet.
ROM	3503	Genus indet.
ROM	3504	Genus indet.
ROM	3505	Genus indet.
ROM	3506	Genus indet.
ROM	3507	Genus indet.
ROM	3508	Genus indet.
ROM	3514	Genus indet.
ROM	3586	Genus indet.
ROM	3594	Genus indet.
ROM	3595	Genus indet.
ROM	3596	Genus indet.
ROM	3597	Genus indet.
ROM	3598	Genus indet.
ROM	3599	Genus indet.
ROM	3600	Genus indet.
ROM	3601	Genus indet.
ROM	3602	Genus indet.
ROM	3603	Genus indet.
ROM	3604	Genus indet.
ROM	3605	Genus indet.
ROM	3606	Genus indet.
ROM	3607	Genus indet.
ROM	3608	Genus indet.
ROM	3609	Genus indet.
ROM	3610	Genus indet.
ROM	3611	Genus indet.
ROM	3612	Genus indet.
ROM	3613	Genus indet.
ROM	3614	Genus indet.
ROM	3615	Genus indet.
ROM	3616	Genus indet.
ROM	3617	Genus indet.
ROM	3618	Genus indet.
ROM	3619	Genus indet.
ROM	3620	Genus indet.
ROM	3622	Genus indet.

ROM	3623	Genus indet.
ROM	3624	Genus indet.
ROM	3625	Genus indet.
ROM	3626	Genus indet.
ROM	3627	Genus indet.
ROM	3629	Genus indet.
ROM	3630	Genus indet.
ROM	3631	Genus indet.
ROM	3635	Genus indet.
ROM	3636	Genus indet.
ROM	3637	Genus indet.
ROM	3638	Genus indet.
ROM	3639	Genus indet.
ROM	3643	Genus indet.
ROM	3644	Genus indet.
ROM	3645	Genus indet.
ROM	3646	Genus indet.
ROM	3647	Genus indet.
ROM	3649	Genus indet.
ROM	3650	Genus indet.
ROM	3651	Genus indet.
ROM	3652	Genus indet.
ROM	3653	Genus indet.
ROM	3654	Genus indet.
ROM	3655	Genus indet.
ROM	3656	Genus indet.
ROM	3657	Genus indet.
ROM	3658	Genus indet.
ROM	3659	Genus indet.
ROM	3660	Genus indet.
ROM	3661	Genus indet.
ROM	3662	Genus indet.
ROM	3663	Genus indet.
ROM	3664	Genus indet.
ROM	3665	Genus indet.
ROM	3666	Genus indet.
ROM	3667	Genus indet.
ROM	3671	Genus indet.
ROM	3672	Genus indet.
ROM	3707	Genus indet.
ROM	3708	Genus indet.
ROM	3718	Genus indet.
ROM	3719	Genus indet.
ROM	4671	Corythosaurus intermedius
ROM	5685	Genus indet.
SDSNH	2989	Genus indet.

SM	R4036	Edmontosaurus annectens
TMM	41262	Prosaurolophus maximus (=ROM 1929)
TMP	78.16.1	Lambeosaurus sp
TMP	79.2.1	Saurolophus sp
TMP	79.27.3	Prosaurolophus sp
TMP	81.37.1	Lambeosaurus sp
TMP	82.38.1	Lambeosaurus sp
UA	13	Corythosaurus casuarius
UA	300	Parasaurolophus sp
UA	19363	Genus indet.
UCMP	32944	Genus indet.
UCMP	43251	Genus indet.
UMMP	9054	Genus indet.
UMMP	9060	Genus indet.
UMMP	20000	Edmontosaurus annectens
UNM	B-517	Genus indet.
UNM	B-706	Genus indet.
UNSM	1200	Genus indet.
USNM	219	Genus indet.
USNM	220	Genus indet.
USNM	221	Genus indet.
USNM	2109	Edmontosaurus sp
USNM	2357	Edmontosaurus sp
USNM	2413	Edmontosaurus sp
USNM	2414	Edmontosaurus annectens
USNM	3813	Genus indet.
USNM	3814	Edmontosaurus annectens
USNM	4278	Edmontosaurus sp
USNM	4698	Edmontosaurus sp
USNM	4737	Edmontosaurus regalis
USNM	4801	Edmontosaurus annectens
USNM	4804	Genus indet.
USNM	4807	Edmontosaurus sp
USNM	4808	Edmontosaurus sp
USNM	4809	Edmontosaurus sp
USNM	4810	Genus indet.
USNM	4811	Genus indet.
USNM	4869	Genus indet.
USNM	5370	Edmontosaurus annectens

USNM	5457	Lambeosaurus sp
USNM	5459	Genus indet.
USNM	5487	Genus indet.
USNM	5489	Genus indet.
USNM	5492	Genus indet.
USNM	5742	Edmontosaurus sp
USNM	5787	Edmontosaurus sp
USNM	5803	Genus indet.
USNM	5839	Edmontosaurus sp
USNM	5850	Genus indet.
USNM	5851	Genus indet.
USNM	5854	Genus indet.
USNM	5855	Genus indet.
USNM	5856	Genus indet.
USNM	5857	Genus indet.
USNM	5858	Genus indet.
USNM	5947	Genus indet.
USNM	5948	Genus indet.
USNM	5963	Genus indet.
USNM	6070	Edmontosaurus regalis
USNM	6523	Genus indet.
USNM	6524	Genus indet.
USNM	6673	Edmontosaurus regalis
USNM	7093	Genus indet.
USNM	7094	Genus indet.
USNM	7095	Genus indet.
USNM	7096	Genus indet.
USNM	7189	Genus indet.
USNM	7190	Genus indet.
USNM	7582	Genus indet.
USNM	7626	Genus indet.
USNM	7703	Genus indet.
USNM	7723	Genus indet.
USNM	7737	Edmontosaurus sp
USNM	7804	Genus indet.
USNM	7805	Genus indet.
USNM	7948	Hypacrosaurus altispinus
USNM	7955	Genus indet.
USNM	8019	Edmontosaurus regalis
USNM	8025	Genus indet.
USNM	8026	Genus indet.
USNM	8039	Edmontosaurus sp
USNM	8049	Genus indet.
USNM	8052	Genus indet.
USNM	8053	Genus indet.
USNM	8056	Genus indet.
USNM	8057	Genus indet.
USNM	8058	Kritosaurus notabilis

USNM	8354	Kritosaurus sp
USNM	8401	Corythosaurus sp
USNM	8592	Genus indet.
USNM	8628	Kritosaurus sp
USNM	8629	Kritosaurus navajovius
USNM	8630	Kritosaurus sp
USNM	10289	Genus indet.
USNM	10309	Lambeosaurus lambei
USNM	10312	Genus indet.
USNM	10609	Genus indet.
USNM	11893	Corythosaurus casuarius
USNM	11950	Hypacrosaurus altispinus
USNM	12711	Edmontosaurus regalis
USNM	12712	Prosaurolophus maximus
USNM	13492	Parasaurolophus walkeri
USNM	13808	Genus indet.
USNM	13862	Kritosaurus sp
USNM	14724	Kritosaurus sp
USNM	15493	Corythosaurus casuarius
USNM	15578	Corythosaurus casuarius
USNM	15581	Corythosaurus sp
USNM	15586	Corythosaurus casuarius
USNM	16150	Lambeosaurus sp
USNM	16318	Genus indet.
USNM	16600	Corythosaurus casuarius
USNM	16978	Corythosaurus sp
USNM	18596	Genus indet.
USNM	22100	Genus indet.
USNM	22102	Edmontosaurus sp
USNM	25841	Genus indet.
USNM	175583	Genus indet.
USNM	181339	Genus indet.
USNM	187237	Kritosaurus sp
USNM	203385	Genus indet.
USNM	214577	Kritosaurus sp
USNM	214578	Genus indet.
USNM	214579	Kritosaurus sp
USNM	214581	Corythosaurus sp
USNM	214583	Genus indet.
USNM	214585	Corythosaurus sp
USNM	214586	Kritosaurus sp
USNM	214587	Kritosaurus sp
USNM	214588	Kritosaurus sp
USNM	214589	Kritosaurus sp
USNM	214590	Genus indet.
USNM	214591	Corythosaurus sp
USNM	244537	Genus indet.
USNM	256616	Genus indet.

USNM	256679	Genus indet.
USNM	299543	Genus indet.
USNM	299716	Corythosaurus casuarius
USNM	299717	Corythosaurus casuarius
USNM	299718	Hypacrosaurus altispinus
USNM	299719	Prosaurolophus maximus
USNM	299720	Genus indet.
USNM	306531	Genus indet.
USNM	336469	Genus indet.
USNM	337977	Genus indet.
USNM	337978	Genus indet.
USNM	337983	Genus indet.
USNM	337984	Genus indet.
USNM	337988	Genus indet.
USNM	337989	Kritosaurus sp
USNM	357118	Edmontosaurus sp
USNM	357121	Genus indet.
USNM	357122	Edmontosaurus sp
USNM	358551	Edmontosaurus sp
USNM	358552	Kritosaurus sp
USNM	358553	Kritosaurus sp
USNM	358554	Kritosaurus sp
USNM	358555	Kritosaurus sp
USNM	358556	Maiasaura peeblesorum
USNM	358558	Corythosaurus sp
USNM	358559	Corythosaurus sp
USNM	358560	Corythosaurus sp
USNM	358565	Genus indet.
USNM	358566	Genus indet.
USNM	358567	Genus indet.
USNM	358568	Genus indet.
USNM	358569	Genus indet.
USNM	358570	Genus indet.
USNM	358571	Genus indet.
USNM	358572	Brachylophosaurus sp
USNM	358573	Genus indet.
USNM	358574	Genus indet.
USNM	358575	Genus indet.
USNM	358576	Genus indet.
USNM	358577	Genus indet.
USNM	358578	Genus indet.
USNM	358579	Genus indet.
USNM	358580	Corythosaurus sp
USNM	358581	Corythosaurus sp
USNM	358582	Corythosaurus sp
USNM	358583	Corythosaurus sp
USNM	358584	Corythosaurus sp
USNM	358585	Corythosaurus sp

USNM	358586	Corythosaurus sp
USNM	358587	Corythosaurus sp
USNM	358588	Corythosaurus sp
USNM	358589	Corythosaurus sp
USNM	358590	Corythosaurus sp
USNM	358591	Corythosaurus sp
USNM	358592	Corythosaurus sp
USNM	358593	Corythosaurus sp
USNM	358594	Corythosaurus sp
USNM	358601	Genus indet.
USNM	358602	Genus indet.
USNM	358603	Genus indet.
USNM	358604	Genus indet.
USNM	358605	Genus indet.
USNM	358606	Genus indet.
USNM	358607	Genus indet.
USNM	358608	Genus indet.
USNM	358609	Genus indet.
USNM	358610	Genus indet.
USNM	358611	Genus indet.
USNM	358612	Genus indet.
USNM	358613	Genus indet.
USNM	358614	Genus indet.
USNM	358615	Genus indet.
USNM	358616	Genus indet.
USNM	358617	Genus indet.
USNM	358618	Genus indet.
USNM	358619	Genus indet.
USNM	358620	Genus indet.
USNM	358621	Genus indet.
USNM	358623	Genus indet.
USNM	358626	Genus indet.
USNM	365557	Genus indet.
USNM	365559	Genus indet.
USNM	365561	Genus indet.
USNM	365562	Genus indet.
USNM	365567	Genus indet.
USNM	365568	Genus indet.
USNM	365569	Genus indet.
USNM	398262	Genus indet.
USNM	398272	Genus indet.
USNM	406287	Genus indet.
USNM	410284	Genus indet.
USNM	412492	Genus indet.
USNM	412532	Genus indet.
WM	1479	Lambeosaurus lambei

YPM	616	Edmontosaurus sp
YPM	618	Edmontosaurus sp
YPM	1190	Claosaurus agilis
YPM	1587	Genus indet.
YPM	1593	Genus indet.
YPM	1600	Genus indet.
YPM	1779	Hadrosaurus sp
YPM	2182	Edmontosaurus annectens
YPM	3219	Claosaurus sp
YPM	3221	Genus indet.
YPM	3222	Lambeosaurus lambei
YPM	5767	Gilmoreosaurus mongoliensis
YPM(PU)	22400	Maiasaura peeblesorum (15 babies)
YPM(PU)	22405	Maiasaura peeblesorum
ZPAL	I/110	Barsboldia sicinskii
ZPAL	I/159	Saurolophus angustirostris
ZPAL	I/162	Saurolophus angustirostris

APPENDIX 7

Old GSC versus newer ROM numbers

In papers published before 1950 many hadrosaur specimens were cited with their Geological Survey of Canada acronyms. These specimens are now housed at the Royal Ontario Museum and are published with their new acronyms. Workers unfamiliar with this change may regard these specimens as new and different from the Geological Survey of Canada specimens and this may cause an error in estimating the numbers of hadrosaurs which would lead to errors in studies of diversity. This table displays the old and new museum numbers to end this confusion.

AMNH 5278 Hypacrosaurus altispinus, GSC 8500

ROM 694 Genus indet. sp indet., GSC 5413

ROM 696 Genus indet. sp indet., GSC 5423

ROM 758 Lambeosaurus lambei, ("Procheneosaurus praeceps")type, GSC 3577

ROM 759 Lambeosaurus lambei, (Procheneosaurus erectofrons)type, GSC 3578

ROM 764 Kritosaurus incurvimanus, type, GSC 4514

ROM 765 Kritosaurus incurvimanus, part of type, GSC 4515

ROM 768 Parasaurolophus walkeri, type, GSC 4578

ROM 769 Kritosaurus incurvimanus, GSC 4629

ROM 770 Kritosaurus incurvimanus, from the type, GSC 4634

ROM 771 Kritosaurus incurvimanus, GSC 4643

ROM 772 Kritosaurus incurvimanus, GSC 4644

ROM 773 Kritosaurus incurvimanus, from the type, GSC 4644

ROM 774 Kritosaurus incurvimanus, from the type, GSC 4646

ROM 776 Corythosaurus casuarius, C. intermedius type, GSC 4670

ROM 777 Corythosaurus casuarius, C. intermedius type, GSC 4671

ROM 786 Prosaurolophus maximus, GSC 4963

ROM 787 Prosaurolophus maximus, GSC 4971, part at Museo La Plata, Argentina as 79-XI-23-1

ROM 794 Lambeosaurus lambei, GSC 5131

ROM 801 Edmontosaurus regalis, GSC 5167

ROM 816 Parasaurolophus walkeri, GSC 5344

ROM 817 Parasaurolophus walkeri, GSC 5345

ROM 824 Genus indet. sp indet., GSC 5355

ROM 834 Genus indet. sp indet., GSC 5417

ROM 845 Corythosaurus casuarius, GSC 5505

ROM 855 Genus indet. sp indet., GSC 5725

ROM 867 Edmontosaurus edmontoni, GSC 5851

ROM 868 Corythosaurus casuarius, C. bicristatus type, GSC 5852

ROM 869 Lambeosaurus lambei, Corythosaurus frontalis type, GSC 5853, ROM 874 from this skull

ROM 870 Corythosaurus casuarius, C. brevicristatus type,GSC 5856

ROM 871 Corythosaurus casuarius, GSC 5857

ROM 873 Kritosaurus notabilis, GSC 5859

ROM 874 Lambeosaurus lambei, Corythosaurus frontalis type, from the type of C. frontalis ROM 869 (GSC 5853)

ROM 875 Genus indet., GSC 5857+5861

YPM 3222 - Lambeosaurus lambei, old GSC 8631

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