



HOKKAIDO UNIVERSITY

Title	HERBIVOROUS ADAPTATIONS OF DINOSAURIA : HADROSAURID FORAGING STRATEGY AND ARCHOSAUR GASTROLITHS
Author(s)	高崎, 竜司
Degree Grantor	北海道大学
Degree Name	博士(理学)
Dissertation Number	甲第13911号
Issue Date	2020-03-25
DOI	https://doi.org/10.14943/doctoral.k13911
Doc URL	https://hdl.handle.net/2115/94520
Type	doctoral thesis
File Information	Ryuji_TAKASAKI.pdf



Doctoral Dissertation

HERBIVOROUS ADAPTATIONS OF DINOSAURIA :
HADROSAURID FORAGING STRATEGY AND ARCHOSAUR GASTROLITHS

(恐竜類における植物食性適応：
ハドロサウルス科の採餌適応および主竜類の胃石)

Ryuji Takasaki

Graduate School of Science, Hokkaido University

Department of Natural History of Sciences

March 2020

ABSTRACT

Feeding is essential for any animal in order to acquire energy and nutrition for survival and reproduction. In order to obtain energy efficiently, various feeding adaptations were established in animals including Dinosauria, one of the most successful terrestrial vertebrates during the Mesozoic. The major dinosaur clades, Ornithischia and Saurischia, each have unique dietary ecomorphologies: presence of keratinous beak and consumption of gastroliths (geo-gastroliths). This study investigates how beak shape variations and use of gastroliths affect dinosaur feeding strategy and evolutionary history. Beak shape variation was investigated focusing of “duck-billed” dinosaur Hadrosauridae, one of the most successful herbivorous dinosaurs during the late Cretaceous which inhabited even in the Arctic. Re-examinations of the Arctic hadrosaurids imply that latitudinal environmental differences do not affect hadrosaurid morphological disparity. At the same time, however, the new discovery of a lambeosaurine material suggests that the Arctic hadrosaurids might have had different environment preferences as mid-latitude hadrosaurids do, emphasizing possible importance of adaptations to local environments. In fact, present study revealed that hadrosaurid beak shapes, as well as their limb proportions, differ by their habitat environments. The ecomorphological differences suggest that terrestrial taxa were

adapted for mass food consumption in limited foraging range whereas marginal taxa were more adapted for selective food consumption in larger foraging ranges. The present result suggests that hadrosaurid beak shape had important role in regional environmental adaptations.

In order to investigate the physiologies regarding gastroliths uses, experiments using 76 male layer chicks were conducted. The experiments suggest that chicks selectively consume sharper stones, which are abraded and become rounded inside stomach upon aiding gastric mechanical digestions. The degrees of gastroliths abrasions are larger in the groups provided herbivorous diet, especially in the group with large initial gizzard muscularity. The comprehensive comparisons of neornithine stomach and gastroliths suggest that although neornithines demonstrate much wider stomach morphological variations than previously considered, the relationships among gastroliths shapes, diet, and gizzard muscularities generally follow the trend observed under the experiments. Discriminant analyses based on gastroliths shapes demonstrate high discriminant accuracies in living archosaur dietary habits (up to 78%), suggesting gastroliths shapes could be a proxy predicting dinosaur dietary habits. Dinosaur dietary habit predictions are generally concordant with the previous assumptions based on osteological features in theropods, but are conflicting in non-theropod dinosaurs. The conflicts may indicate

that gastroliths shapes reflect how intensely the gastroliths are used for aiding gastric mechanical digestion. The correlations between archosaur stomach muscularity and gastroliths shapes further supports the interpretation. The ancestral state reconstructions suggest that highly muscular stomach that may represent “gastric mill” was acquired by the ancestral node of Coelurosauria, which correspond appearances of edentulous theropods. Together with the associations of highly rounded gastroliths and teeth loss in Mesozoic birds, the acquisition of the basis for “gastric mill” is likely to be an innovative feature that allows theropod edentulism. The present work therefore represents an example of internal organ delimiting the restrictions of osteological modifications in archosaurs.

ACKNOWLEDGEMENTS

I would like to thank so many people, whom I would not have been able to complete this thesis without any of them. To start with, I would like to thank my supervisor Dr. Yoshitsugu Kobayashi not only for teaching me tastes of scotch but for knocking me into shape. I learned importance of the very basic stuffs: be patient and sincere to data, spend time and efforts, and inspect a phenomenon in all possible aspects. I would never forget the words he gave me when I was about to give up – “no pain, no gain”. I truly appreciate my advisor Dr. Anthony Fiorillo, for offering me the great chance to work on the Alaskan hadrosaur. The cold summers we spent together were great opportunity for me learn the importance of field paleontology and exploring something new. I am also grateful to my advisor Dr. Yasuhiro Iba for his critical comments which always brew my mind and provided me new insights.

I would like to express my gratitudes to Dr. Khishigjav Tsogtbaatar and the staffs of Institute of Paleontology, Mongolian Academy of Science, Mongolia. Field works in Mongolia are always great fun and productive thanks to their kind help. I can never forget my excitement when I found a dinosaur skeleton for the first time in my life. I deeply appreciate Hobetsu district of Mukawa Town, Hokkaido Prefecture, Japan, and the staffs at the Hobetsu Museum namely Dr. Tomohiro Nishimura and Mr. Kazuhiko

Sakurai for letting me get involved in excavation and study of *Kamuysaurus japonicus*, the most complete dinosaur from Japan. It was a great opportunity for me not only to for scientific purposes, but also to think about how paleontology can and should corroborate with local museums in Japan.

All of the volunteer staffs at the Hokkaido University Museum always supported me, and I would like to express my special thanks and respects to the late Mr. Kei Nakano.

His passion and enthusiasm to learn something new is an ideal style of life for me.

Many thanks to my labmates, past and present, especially Junki Yoshida, Tsogtbaatar Chinzorig, Masaya Iijima, and Tomonori Tanaka. It was great to grow up with you, bros.

And my dear friends Takashi Saito and Atsushi Hori, having conversations and beers with you always supported me.

In the end, I would like to thank my parents for all of their, love, supports and patience.

TABLE OF CONTENTS

ABSTRACT	i
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS	vi
LIST OF TABLES	xii
LIST OF FIGURES	xiv
LIST OF SUPPLEMENTARY INFORMATION	xxvi
BACKGROUND AND CONTEXT.....	xxix
CHAPTER 1: RE-EXAMINATION OF ALASKAN HADROSAURIDS	1
Chapter 1.1: The first definite lambeosaurine bone from the Liscomb Bonebed of the Upper Cretaceous Prince Creek Formation, Alaska, United States	1
Abstract.....	1
1.1.1 Introduction.....	3
1.1.2 Material and method	7
1.1.3 Results.....	9
1.1.3.1 Systematic paleontology.	9
1.1.3.2 Description.	9
1.1.4 Discussion.....	16

1.1.5 Acknowledgments	25

Chapter 1.2: Re-examination of the cranial osteology of the Arctic Alaskan

hadrosaurine with implications for its taxonomic status	26

Abstract.....	26

1.2.1 Introduction.....	28

1.2.2 Institutional abbreviations.....	30

1.2.3 Materials and methods	31

1.2.3.1 Phylogenetic analyses	31

1.2.3.2 Disparity analysis	32

1.2.4 Results.....	33

1.2.4.1 Description	33

1.2.4.2 Phylogenetic analysis	73

1.2.5 Discussion.....	78

1.2.5.1 Taxonomic status of “Ugrunaaluk kuukpikensis”	78

1.2.5.2 Influence of latitudinal habitat difference on hadrosaurine evolution ...	83

1.2.6 Acknowledgements.....	87

CHAPTER 2: ENVIRONMENTAL ADAPTATIONS OF HADROSAURID

FORAGING FEATURES	89

Abstract.....	89
2.1 Introduction.....	91
2.2 Material and method	93
2.3 Results.....	97
2.3.1 Beak shape.....	97
2.3.2 Limb lengths.....	100
2.3.3 Evolutionary rate	102
2.4 Discussion.....	107
2.5 Acknowledgements.....	115

CHAPTER 3: REGULATORY FACTORS OF AVIAN GRIT USE INVESTIGATED

BY LAYER CHICKENS	116
Abstract.....	116
3.1 Introduction.....	118
3.2 Materials and methods	120
3.2.1 Birds, experimental design, and management.....	120
3.2.2 Evaluation of stone characteristics	122
3.2.3 Stone consumption	123
3.2.4 Grit modification	124

3.2.5 Stone excretion.....	124
3.2.6 Statistical analyses.....	125
3.3 Results.....	125
3.3.1 Bird growth and adjustment of gizzard muscularity	125
3.3.2 Initial stone selection.....	128
3.3.3 Grit retention and abrasion.....	129
3.3.4 Stone excretion.....	130
3.4 Discussion.....	131
3.4.1 Initial stone consumption	131
3.4.2 Grits inside gizzards	132
3.4.3 Grit excretion.....	134
3.4.4 Regulatory system of grit use and implication on behavioral flexibility	135
3.5 Acknowledgements.....	137

CHAPTER 4: EVOLUTIONARY HISTORY OF AVIAN STOMACH AND THEIR

GASTROLITHS USES	139
Abstract.....	139
4.1 Introduction.....	141
4.2 Material and method	143

4.3 Results.....	146
4.3.1 Stomach description	146
4.3.2 Diet, stomach type, gizzard muscularity, and gastroliths.....	155
4.4 Discussion.....	165
4.4.1 Evolutionary history of avian stomachs	165
4.4.2 Gastroliths as a proxy for archosaur diet.....	169
4.5 Acknowledgements.....	172

CHAPTER 5: A NOVEL NEW METHOD OF ARCHOSAUR DIET PREDICTION

WITH IMPLICATIONS ON EVOLUTIONARY HISTORY OF ARCHOSAUR

STOMACH	173
Abstract.....	173
5.1 Introduction.....	175
5.2 Material and method	177
5.3 Results.....	179
5.3.1 Review and description of dinosaur gastroliths	179
5.3.2 Statistical analyses.....	197
5.4 Discussion.....	204
5.5 Acknowledgements.....	209

SUPPLEMENTARY INFORMATION	211
BIBLIOGRAPHY	248

LIST OF TABLES

Table 1.1-1. Selected measurements and ratios of hadrosaurid supraoccipitals	11
Table 1.1-2. List of hadrosauroid supraoccipital features.	19
Table 1.2-1. Comparisons among <i>Edmontosaurus</i>	83
Table 1.2-2. Partial disparities of hadrosaurines.	86
Table 2 - 1. Summary of hadrosaurid foraging ecomorphology differences by environments	108
Table 3 - 1. Summarized results of the experiments.	136
Table 4 - 1. Phylogenetic signals of neornithine dietary habits, stomach types, and stomach muscularities.	158
Table 4 - 2. P-values obtained from multiple comparisons on gizzard muscularity by stomach type and dietary habits.	158
Table 4 - 3. Results of PGLS of stomach type and diet type against gizzard muscularity in mean (top) and median (bottom) values of the 100 iterations performed.	159
Table 4 - 4. Gastroliths occurrence frequencies by stomach type and diet.	160
Table 4 - 5. Results of PGLS of stomach type, diet type, and gizzard muscularity on gastroliths occurrence frequencies.....	161

Table 4 - 6. Summarized discriminant accuracies on stomach type and diet type by gastroliths shapes in the six analyses performed by different minimum number of gastroliths. Detail is provided in the Supplementary Table 4-4.	164
Table 4 - 7. Results of regression analyses of PC1 value of gastroliths shapes against gizzard muscularity in the six analyses performed by different minimum number of gastroliths.	165
Table 5 - 1. Results of the regression analyses between PC1 scores of gastroliths shapes evaluated based on qualitative and quantitative methods.....	200
Table 5 - 2. Summary of the diet type discriminance accuracies by gastroliths shapes in the six analyses performed by different minimum number of gastroliths. Detail is provided in the Table S5-2.	202
Table 5 - 3. Predicted diets of extant archosaurs based on gastroliths shapes under six analyses performed under different minimum gastroliths numbers. Refer Table S5-3 for posterior probabilities.....	204
Table 5 - 4. Results of the regression analyses on PC1 values of gastroliths shapes against archosaur stomach muscularities.....	206

LIST OF FIGURES

Figure 1.1-1. Lambeosaurine supraoccipital (DMNH 2014-12-266) from the Liscomb

Bonebed. a) Dorsal view. b) Ventral view. c) Left lateral view. d) Posterior view.

e) Anterior view. f) Right lateral view. Abbreviations: asp, ascending process; eo,

articulation surface for the exoccipital-opisthotic complex; eog, exoccipital groove;

ptg, post-temporal groove; sqb, squamosal boss. Scale = 2 cm. 10

Figure 1.1-2 Hadrosaurid supraoccipitals. DMNH 2014-12-266 (a, f). *Edmontosaurus*

sp.: cast of UAMES 21544 (b, g); cast of UAMES 4291 (c, h); DMNH 22807 (d,

i); cast of UAMES 12727 (e, j). Indeterminate lambeosaurines: UALVP 48 (k, q);

UALVP 53092 (l, r); UALVP 53106 (m, s); CMN 0170 (n, t); UALVP 55300 (o,

u); UALVP 54569 (p, v). Dorsal (a-e, k-p) and ventral (f-j, q-v) views.

Abbreviations: asp, ascending process; ap, anterior process; eo, articulation surface

for the exoccipital-opisthotic complex; eog, exoccipital groove; nc, nuchal crestp,

articulation surface for the parietal, ptg, post-temporal groove; sqb, squamosal boss.

Scale = 2 cm. 14

Figure 1.1-3. Supraoccipitals of Liscomb hadrosaurid DMNH 2014-12-266 (a, d), an

indeterminate lambeosaurine CMN 0170 (b, e), and *Edmontosaurus annectens*

DMNH EPV 127701 (c, f) in dorsal (a-c) and posterior (e-f) views. Posterior views

of articulated skulls of *Hypacrosaurus stebingeri* (g) and *Edmontosaurus annectens* (h). Abbreviations: asp, ascending process; eo, articulation surface for the exoccipital-opisthotic complex; ptg, post-temporal groove; sqb, squamosal boss; Ex, Exoccipital-opisthotic complex, Sq, Squamosal. Scale = 2 cm (a-f), 5cm (g, h). Dashed line represents the boundary of supraoccipital in (g) and (h). 17

Figure 1.1-4. Paleogeographical records records of lambeosaurines during the Late Cretaceous. The red star represents the Liscomb lambeosaurine reported herein. Map is redrawn from Deep Time Maps(Blakey, 2018). The paleocoordinates are obtained from the Paleobiology Database (www.paleobiodb.org)..... 23

Figure 1.1- 5. Schematic drawing of differential habitat preference between hadrosaurines and lambeosaurines. 25

Figure 1.2-1. Premaxillae of the PCF hadrosaurine (A-F). Cast of DMNH 22716, partial right and left premaxillae in left lateral (A), dorsal (B), and anterior (C) views. UAMES 12995, partial right premaxilla in right lateral (D), anterior (E), and dorsal (F) views. Premaxillae of Immature *Edmontosaurus annectens* ROM 53525(G), mature *Edmontosaurus annectens* ROM 64076 (H), *Edmontosaurus regalis* FMNH P15004 (I), *Prosaurolophus maximus* CMN 2870 (J), *Brachylophosaurus*

<i>canadensis</i> CMN 8893 (K), and <i>Gryposaurus notabilis</i> CMN 2278 (L) in dorsal views.....	35

Figure 1.2-2. Cast of left maxilla (UAMES 4250) in lateral (A) and medial (B) views.

(C) Height-length relationships of hadrosaurines, demonstrating negative allometry among Edmontosaurini.....	38

Figure 1.2- 3. Cast of left nasal (UAMES 4940) in lateral (A) and medial (B) views.

Right prefrontal (DMNH 22972) in lateral (C), medial (D), and posterior (E) views.	
Casts of left (F-H) and right (I-K) lacrimals the PCF hadrosaurine in lateral (F, I), posterior (G, J), and medial (H, K) views. Isolated right lacrimals of a large (ROM 64076; L, M) and a small (ROM 53512; N, O) <i>Edmontosaurus annectens</i> in lateral (L, N) and medial (M, O) views.	40

Figure 1.2-4. Cast of right jugal of the PCF hadrosaurine (UAMES 4187) in lateral (A)

and medial (B) views. Anterior process of left jugal of <i>Edmontosaurus annectens</i> (C: ROM 53518; D: DMNH EPV. 95220; E: DMNH EPV. 130653) in medial view, demonstrating intraspecific variation of the angle between the palatine process and the posterior margin of the maxilla contact surface. Left quadratojugal (DMNH 2014-12-661) in lateral (F), medial (G), and posterior (H) views. Right quadrate (DMNH 21044) in lateral (I), anterior (J), medial (K), and posterior (L) views....	45

Figure 1.2-5. Cast of left squamosal (UAMES 12266) in lateral (A), dorsal (B), and posterior (C) views. Right postorbital (DMNH 2014-12-486) in lateral (D), anterior (E), and medial (F) views. Parietal (DMNH 2014-12-265) in dorsal (G) and ventral (H) views. Left frontal (DMNH 2014-12-635) in dorsal (I), ventral (J), lateral (K), and medial (L) views. 50

Figure 1.2-6. Cast of left pterygoid (UAMES 4215) in lateral (A) and medial (B) views. Right ectopterygoid (DMNH 2014-12-492) in lateral (C) and medial (D) views. Cast of left palatine (UAMES 4257) in lateral (E) and medial (F) views. Cast of right laterosphenoid of the PCF hadrosaurine (UAMES 4352) in lateral (G) and medial (H) views. Laterosphenoids of *Edmontosaurus annectens* (I; ROM 53507), *Hypacrosaurus stebingeri* (J; USNM 11893), and *Eolambia caroljonesa* (K; CEUM 34366). 55

Figure 1.2-7. Cast of left prootic (UAMES 4357) in lateral (A) and medial (B) views. Cast of left exoccipital (UAMES 4263) in lateral (C) and anterior (D) views. Supraoccipital (DMNH 22807) in dorsal (E), right lateral (F), anterior (G), and posterior (H) views. Cast of basisphenoid (UAMES 4301) in left lateral (J), dorsal (K), anterior (L), and ventral (M) views. Cast of basioccipital (UAMES 34723) in left lateral (N), dorsal (O), anterior (P), and ventral (Q) views. 60

Figure 1.2-8. Cast of a partial predentary (UAMES 4437) in dorsal (A), ventral (B), and anterior (C) views. Right dentary (DMNH 2014-12-531) in lateral (D), dorsal (E), and medial (F) views. Left surangular (DMNH 2014-12-456) in lateral (G), medial (H), and dorsal (I) views..... 67

Figure 1.2-9. Maxillary teeth (DMNH 22718) in labial (A) and lingual (B) views. Dentary teeth (DMNH 22851) in lingual view (C). Isolated dentary tooth (DMNH 22338) in lingual (D) and mesial (E) views. Close-up of the marginal denticles of the dentary tooth (F). 72

Figure 1.2- 10. (A) Strict consensus tree of the MPTs obtained from the first phylogenetic analysis. Numbers above each branch represent bootstrap values and those below the branch represent Bremer decay values. Bootstrap values below 20 and Bremer decay values below 1 are not shown. The polytomy clade of the PCF hadrosaurine + *Edmontosaurus annectens* + *Edmontosaurus regalis* is formed by the two conflicting topologies shown in the small box. (B) Strict consensus tree of MPTs obtained from the second phylogenetic analysis which incorporated two juvenile *Edmontosaurus annectens* OTUs, showing relationship within Hadrosaurinae. 76

Figure 1.2-11. Morphospace of hadrosaurines recovered from the principal coordinate analysis using the phylogenetic cranial characters. Abbreviations: *Ag*: *Acristavus gagslarsoni*, *Bc*: *Brachylophosaurus canadensis*, *Ea*: *Edmontosaurus annectens*, *Er*: *Edmontosaurus regalis*, *Gl*: *Gryposaurus latidens*, *Gm*: *Gryposaurus monumentensis*, *Gn*: *Gryposaurus notabilis*, *Hf*: *Hadrosaurus foulkii*, *Kj*: *Kamuysaurus japonicus*, *Km*: *Kerberosaurus manakini*, *Kn*: *Kritosaurus navajovius*, *La*: *Lophorhothon atopus*, *Ly*: *Laiyangosaurus youngi*, *Mp*: *Maiasaura peeblesorum*, *Pb*: *Probrachylophosaurus bergei*, *Pm*: *Prosaurolophus maximus*, *Rc*: *Rhinorex condrupus*, *Sa*: *Saurolophus angustirostris*, *Sg*: *Shantungosaurus giganteus*, *Sk*: *Secernosaurus koeneri*, *So*: *Saurolophus osborni*, *Wd*: *Wulagasaurus dongi*..... 85

Figure 2 - 1. (A) Landmarks (grey points) and semi-landmarks (blank points) used for the beak geometric morphometric analysis. (B) The hadrosaurid appendicular elements measured herein..... 94

Figure 2 - 2. Boxplots comparing PC scores within Hadrosauridae (A), Hadrosaurinae (B), and Lambeosaurinae (C). Colored boxes represent statistically significant differences (red, $p < 0.001$; pink, $p < 0.05$). Beak shape variations along (D) PC1 of Hadrosauridae, (E) PC4 of Hadrosaurinae, and (F) PC1 of Lambeosaurinae in

dorsal, left lateral, and anterior views from left to right. Red and blue points represent high and low PC scores, respectively. Abbreviations: H, Hadrosaurinae; L, Lambeosaurinae; M, marginal; T, terrestrial.....	98
Figure 2 - 3. Boxplots comparing fore- hind-limb ratio and PC scores of the normalized hadrosaurid limb elements without estimated measurements (A) and with estimated measurements (B).	101
Figure 2 - 4. Evolutionary rates of hadrosauroid beak (A), forelimb (B), and hind-limb (C) phylogenetic characters. The branch colors represent the median evolutionary rate value of the 100 iterations performed. Pie-charts represent the ratio of significantly fast (red), insignificant (white), and significantly slow (blue) branch evolutionary rates in the 100 iterations performed.....	104
Figure 2 - 5. Evolutionary rates of hadrosauroid beak (A), forelimb (B), and hind-limb (C) phylogenetic characters. The branch colors represent the median evolutionary rate value of the 100 iterations performed. Pie-charts represent the ratio of significantly fast (red), insignificant (white), and significantly slow (blue) branch evolutionary rates in the 100 iterations performed.....	106
Figure 2 - 6. Visualized summary of foraging ecomorphology and inferred behaviors	113

Figure 3 - 1. Graphical image of the experimental design. G1, G2, G3, and G4 each contain 17 chicks and G5 and G6 each contain 4 chicks. The chicks are given no access to grits until after day 22. 122

Figure 3 - 2. Results of the statistical analyses. (A) Boxplots showing gizzard muscularities by experimental groups. (B) Boxplots showing amount of stone consumed by experimental groups, shown per stone size categories. (C) Boxplots comparing shapes of the stones provided and the stones left uneaten by each experimental group, shown per stone size categories. (D) Boxplots comparing shapes of the stones by the experimental groups, shown per stone size categories. The brackets represent p-values < 0.05. 127

Figure 3 - 3. Schematic summary of the results obtained from the present experiments. 136

Figure 4 - 1. Representatives of type A stomachs. Stomach of *Anas acuta* in (A) left and (B) right lateral views. (C) Internal cavity of the *Anas acuta* stomach. (D) Transverse section of the ventriculus at the level of the pyloric region. Note that the pyloric region does not form a distinct chamber but is a groove in between two large gastric folds. (E) Transverse section of the ventriculus at its maximum width. F-G, Stomach of *Dromaius novaehollandiae* in (F) left and (G) right lateral views.

Stomach of *Struthio camelus* in (H) left and (I) right lateral views. Abbreviations:
 ct, centrum tendineum; d, duodenum; e, esophagus; gi, gastric isthmus; k, koilin
 layer; l, lumen; *M. c cd*, *M. crassus caudodorsalis*; *M. c cv*, *M. crassus*
cranioventralis; *M. t cd*, *M. tenuis craniodorsalis*; *M. t. cv*, *M. tenuis*
cranioventralis; pr, proventriculus; pv, proventriculus; *sca*, *sulcus caudalis*; *scr*,
sulcus cranialis; v, ventriculus. 148

Figure 4 - 2. Type C stomachs (A-E). Stomach of *Phalacrocorax carbo* in (A) left and
 (B) right lateral views. (C) Internal cavity of the *Phalacrocorax carbo* stomach.
 Stomach of *Ardea cinerea* in (D) left and (E) right lateral views. (F) Internal cavity
 of the *Ardea cinerea* stomach. Type B stomachs (G-J). Stomach of *Strix uralensis*
 in left (G) and right (H) lateral views. Transverse sections of *Picus awokera* (I) and
Milvus migrans (J) ventriculus. Type D stomach *Puffinus tenuirostris* (K-N). Left
 lateral view of the whole stomach (K). *Puffinus tenuirostris* ventriculus in left
 lateral, (L) right lateral, (M) and transverse views. 152

Figure 4 - 3. Evolutionary history of stomach type (left) and diet type (right) along the
 majority-rule consensus tree of the 100 trees analyzed. The branch color represents
 transition of gizzard muscularity. 157

Figure 4 - 4. (A) Mosaic plot of diet against stomach type. Box plots of gizzard	
muscularity against stomach type (B) and diet (C).	158
Figure 4 - 5. Mosaic plots of gastroliths occurrence frequencies against stomach type	
(A) and diet (B).	160
Figure 4 - 6. (A) Bivariate plots of LD1 and LD2 values obtained from the discriminant	
analyses grouped by stomach types. The inner ellipse and the outer ellipses	
represent 50% and 95% confidences, respectively. (B) Discriminance accuracies in	
each stomach type in the analyses with different minimum gastroliths numbers. (C)	
Bivariate plots of LD1 and LD2 values obtained from the discriminant analyses	
grouped by dietary habits. The inner ellipse and the outer ellipses represent 50%	
and 95% confidences, respectively. (D) Discriminance accuracies in each dietary	
habit in the analyses with different minimum gastroliths numbers. (E). results of	
the regression analyses of PC1 values of gastroliths shapes against stomach	
muscularities in the analyses with different minimum gastroliths numbers.	163
Figure 5 - 1. Ornithischian gastroliths. A, <i>Psittacosaurus mongoliensis</i> (AMNH FARB	
6253); <i>Haya griva</i> (B, IGM 100/2015; C, IGM 100/3182); and D, <i>Edmontosaurus</i>	
(AMNH FARB 5863).	181

Figure 5 - 2. Theropod gastroliths. A, large *Sinornithomimus dongi* (uncatalogued) in right lateral view; B, heat map representing sizes of the gastroliths, warm color representing small and cold color representing large sizes; C, sagittal CT-image of the gastroliths mass of the small *Sinornithomimus dongi* (uncatalogued); D, small *Sinornithomimus dongi* (uncatalogued) in right lateral view; E, *Deinocheirus mirificus* (MPC-D 100/127); F, *Limusaurus inextricabilis* (IVPP V15297) in left lateral view; G, *Limusaurus inextricabilis* (IVPP V15293) in right lateral view; H, *Tarbosaurus bataar* (MPC-D 552-1) in ventrolateral view; I, schematic drawing of the *Tarbosaurus* gastralia and positions of the gastroliths; J, *Caudipteryx dongi* (IVPP V12344) in left lateral view; K, *Caudipteryx* sp. (IVPP V12430) in left lateral view. 185

Figure 5 - 3. Mesozoic bird gastroliths. *Archaeorhynchus spathula* (A, IVPP V14287; B, IVPP V17075; C, IVPP V17091; D, IVPP V20312); E, *Bellulornis rectusunguis* (IVPP V17970); F, *Changzuornis ahgm* (AGB 5840); *Gansus yumenensis* (G, CGCS 05-CM-014; H, CGCS 06-CM-011; I, CGCS 07-CM-001); *Iteravis huchzermeyeri* (J, IVPP V18958; K, V20133; L, IVPP V20134)..... 195

Figure 5 - 4. Results of the regression analyses between the PC1 of the quantitative gastroliths shape proxies and the PC1 of the qualitative gastroliths shape proxies.

Solid lines are the regression lines and the dotted lines represent the 95% prediction intervals. 199

Figure 5 - 5. (A) Bivariate plots of LD1 and LD2 scores obtained from the discriminant analyses under six different minimum gastroliths numbers. Inner and outer ellipses represent 50% and 95% confidences for each diet categories, respectively. (B) Discriminance accuracies of diet types in the six analyses under different minimum gastroliths numbers. (C) Hypothetical evolutionary history of archosaur stomach muscularity, represented by gastroliths shape (LD1 value)..... 201

LIST OF SUPPLEMENTARY INFORMATION

Data S1.2 - 1. ROM specimens used for phylogenetic analysis.....	211
Data S1.2 - 2. Character-taxon matrix used for the phylogenetic analyses.....	212
Text S1.2 - 1. Additional phylogenetic characters	217
Table S1.2 - 1. Hadrosaurine maxilla measurements.	218
Data S2 - 1. List of the hadrosaurid skulls analyzed	219
Data S2 - 2. Measurements of the hadrosaurid limbs analyzed. Bolds represent estimated measurements.	220
Table S2 - 1. Results of the regression analyses between beak shape and skull size proxies.	221
Table S2 - 2. P-values of student's t-test on beak shapes categorized by environment and subfamily.	222
Table S2 - 3. P-values of student's t-test on relative fore- hind-limb lengths categorized by environment and subfamily.	223
Table S2 - 4. Factor loadings of the PCA on the normalized limb segments with and without estimated measurements.....	224
Table S3 - 1. Differences in body mass among experimental groups. Bolds represent p-values less than 0.05.....	225

Table S3 - 2. Differences in gizzard muscularity among experimental groups. Bolds represent p-values less than 0.05.	226
Table S3 - 3. Differences in average amount of stones consumed among the different sizes of the stone provided. Bolds represent p-values less than 0.05.	227
Table S3 - 4. Differences in average amount of stones consumed among the experimental groups. Bolds represent p-values less than 0.05.	228
Table S3 - 5. Differences in average shapes of the stones initially provided and stones left uneaten. Bolds represent p-values less than 0.05.	229
Table S3 - 6. Differences in average amount of grits recovered from gizzards. Bolds represent p-values less than 0.05.	230
Table S3 - 7. Differences in average size of grits recovered from gizzards. Bolds represent p-values less than 0.05.	231
Table S3 - 8. Differences in average shapes of the stones initially provided and the grits recovered from gizzards. Bolds represent p-values less than 0.05.	232
Table S3 - 9. Differences in average shapes of the grits recovered from gizzards among the experimental groups. Bolds represent p-values less than 0.05.	233
Table S3 - 10. Differences in average size and shapes of the stones excreted among the experimental groups. Bolds represent p-values less than 0.05.	234

Table S3 - 11. Differences in average size and shapes of the stones excreted and the grits recovered from gizzards. Bolds represent p-values less than 0.05.....	235
Data S4 - 1. List of the stomachs observed.	236
Data S4 - 2. Summary of gastroliths features observed.	239
Table S4 - 1. Proportion of variance and factor loadings obtained from the six PCA with different minimum gastroliths numbers.	241
Table S4 - 2. Results of the discriminant analyses grouped by stomach type and dietary habits.....	242
Data S5 - 1. List of extant archosaurs examined	243
Data S5 - 2. List of the extant archosaur gastroliths examined	244
Table S5 - 1. Results of the PCA under six different minimum gastroliths numbers. .	245
Table S5 - 2. Results of the discriminant analyses under six different minimum gastroliths numbers.....	246
Table S5 - 3. Posterior probabilities of the archosaur diet predictions based on gastroliths shapes under six different minimum gastroliths numbers. Bolds represent the highest posterior probability for the individual in the analysis.....	247

BACKGROUND AND CONTEXT

Feeding is essential for any animal in order to acquire energy and nutrition for survival and reproduction. Adaptations toward feeding ecologies therefore served as a strong driving force for diversification (e.g., Gill et al., 2014). Dinosauria, one of the most successful terrestrial vertebrates during the Mesozoic, demonstrates a wide variety of features that are related to their feeding ecology (Fowler et al., 2011; Zanno and Makovicky, 2011; Mallon and Anderson, 2013). Unfortunately, however, the vast majority of dinosaur ecomorphological features known today are limited to osteological features due to the inevitable loss of soft tissues during fossilization processes.

The present thesis focuses on two factors related to feeding ecology. The first is foraging strategy of Hadrosauridae, one of the most successful herbivorous dinosaur groups which inhabited throughout the world including the Arctic and the Atlantic during the late Cretaceous (Weishampel et al., 2004). While multiple studies infer great oral digestion efficiency of hadrosaurids (e.g., Erickson and Zelenitsky, 2015), few study examined their foraging strategy. Therefore, an investigation on evolutionary history of hadrosaur foraging strategy is performed based on their limb proportions and beak morphology. Limb proportions of terrestrial tetrapods are strongly tied with locomotor efficiency therefore limb proportions are expected to be related with the

approaching phase of the foraging strategy. Multiple studies suggest that beak morphology is related with food types and feeding ecology, which represent the consumption stage of the foraging strategy, in modern mammals and birds (Carrano et al., 1999). This thesis tests if the hadrosaurid foraging strategy is associated with surrounding environments and investigate how these features contributed to hadrosaurid prosperity.

The other feature this thesis focuses on is archosaur gastroliths (geo-gastroliths; Wings and Sander, 2007). Gastroliths are known as “teeth” of herbivorous birds and aid mechanical digestion inside their stomachs (Moore, 1998c). Therefore, gastroliths of non-avian dinosaurs have been considered as one of the definitive evidences of herbivory (Zanno and Makovicky, 2011). However, gastroliths have been known from multiple non-herbivorous modern archosaurs (Lambrecht, 1933; McKeown, 1934; Taylor, 1993), thus presence of gastroliths alone cannot explain diet of archosaurs. This study evaluates multiple features of gastroliths (e.g., size, shape, amount) and investigate their relationships with feeding ecologies. Central to this study is the comprehensive comparisons of gastroliths features among modern birds. Relationships between gastroliths features and feeding ecologies are primarily investigated under animal experiments and then tested if the same trend can be observed on wild

archosaurs, prior to application on non-avian dinosaurs. Understandings of relationships between gastroliths features and feeding ecologies of archosaurs is expected to shed light on evolutionary history of gastric mechanical digestive system of archosaurs.

This project aims to investigate how adaptations on feeding ecologies contributed to evolutionary history of archosaurs. This will be accomplished by a combination of osteological comparisons, animal experiments, anatomical dissections, and statistical analyses.

CHAPTER 1: RE-EXAMINATION OF ALASKAN HADROSAURIDS

Chapter 1.1: The first definite lambeosaurine bone from the Liscomb Bonebed of the Upper

Cretaceous Prince Creek Formation, Alaska, United States

Abstract

The Prince Creek Formation of Alaska, a rock unit that represents lower coastal plain and delta deposits, is one of the most important formations in the world for understanding vertebrate ecology in the Arctic during the Cretaceous. Here we report on an isolated cranial material, supraoccipital, of a lambeosaurine hadrosaurid from the Liscomb Bonebed of the Prince Creek Formation. The lambeosaurine supraoccipital has well-developed squamosal bosses and a short sutural surface with the exoccipital-opisthotic complex, and is similar to lambeosaurine supraoccipitals from the Dinosaur Park Formation in having anteriorly positioned squamosal bosses. Affinities with Canadian lambeosaurines elucidate more extensive faunal exchange between the Arctic and lower paleolatitudes which was previously suggested by the presence of *Edmontosaurus*, *Pachyrhinosaurus*, tyrannosaurids, and troodontids in both regions. The presence of one lambeosaurine and nine hadrosaurine supraoccipitals in the

Liscomb Bonebed suggests hadrosaurine dominated faunal structure as in the Careless Creek Quarry of the USA that was also deposited under a near-shore environment. It differs from the lambeosaurine dominant structures of localities in Russia and China interpreted as inland environments. This may suggest that lambeosaurines had less preference for near-shore environments than hadrosaurines in both Arctic and lower paleolatitudes.

1.1.1 Introduction

Vertebrate animals in the Arctic have experienced physiological, behavioral, and morphological adaptations to survive in an extreme environment (Scholander et al., 1950; Prestrud, 1991; Blix, 2005). Rocks from the North Slope of Alaska are important for the understanding of the ecology of fossil vertebrates in the Arctic during the Cretaceous Period (Fiorillo, 2008a; Fiorillo, 2018). There are abundant fossiliferous exposures of the lower part of the Prince Creek Formation on the North Slope, which range from Campanian to early Maastrichtian in age (Mull et al., 2003). The Prince Creek Formation is a non-marine succession deposited on a high-latitude, low-gradient alluvial/coastal plain. An integrated reconstruction of pedogenic processes and biota (Fiorillo et al., 2016) suggests that this ancient Arctic coastal plain was influenced by seasonally fluctuating water table levels and floods, and in distal areas, marine waters. The formation has yielded a diverse dinosaur assemblage that includes ceratopsids, dromaeosaurids, hadrosaurids, basal ornithopods, pachycephalosaurids, troodontids, and tyrannosaurids (Davies, 1987; Clemens and Nelms, 1993; Fiorillo, 2008b, a; Fiorillo et al., 2009; Brown et al., 2011; Fiorillo and Tykoski, 2012; Fiorillo and Tykoski, 2013, 2014; Mori et al., 2016; Fiorillo, 2018).

The Liscomb Bonebed is one of the most prolific dinosaur bearing localities within this rock unit. Radiometric dating based on tephra near the bonebed indicates that the Liscomb Bonebed is early Maastrichtian with estimated ages of 71-68 Ma (McKee et al., 1989), 69.1 ± 0.3 Ma (Conrad et al., 1992), and younger than 69.2 ± 0.5 Ma (Flaig et al., 2014). These dates are concordant with palynomorph analyses which suggest early Maastrichtian age (Brouwers et al., 1987; Flores et al., 2007). The rocks were deposited at an estimated paleolatitude of $74.5^\circ \pm 7.5^\circ$ (Witte et al., 1987). The Liscomb Bonebed is from the distal area of coastal plain and is represented by lower delta plain facies (Fiorillo et al., 2016). Further, the stratigraphic interval containing the Liscomb Bonebed represents a series of episodic floods (Gangloff and Fiorillo, 2010; Flaig et al., 2014) and specifically these episodic flood events created deposition by fine-grained viscous hyperconcentrated flows that transported the remains of scores of juvenile dinosaurs onto floodplains adjacent to distributary channels. The Liscomb Bonebed is characterized by high specimen density (up to 160-220 elements/m²) and has yielded over six thousand bones (Fiorillo et al., 2010; Mori et al., 2016). It is a monodominant multitaxic bonebed consisting of three theropod taxa (dromaeosaurid, troodontid, and tyrannosaurid) (Fiorillo and Gangloff, 2000; Fiorillo, 2008b; Fiorillo et al., 2016) and

hadrosaurid skeletal elements which comprises 98.5% of dinosaur skeletal elements (Gangloff and Fiorillo, 2010).

The Hadrosauridae is a derived clade of Hadrosauroidea and comprise two stem-sister lineages, Lambeosaurinae and Hadrosaurinae (Horner et al., 2004). The Liscomb hadrosaurid materials were initially identified as Lambeosaurinae (Brouwers et al., 1987), although osteological features to support the identification were not provided. Comparisons based on isolated cranial elements later demonstrated that the Liscomb hadrosaurs showed close similarity to the hadrosaurine *Edmontosaurus saskatchewanensis* (Nelms, 1989), which is now considered a junior synonym of *Edmontosaurus annectens* (Campione and Evans, 2011). Since then, a general consensus formed that the Liscomb hadrosaur bones represent specimens of *Edmontosaurus* (Gangloff, 1998; Fiorillo and Gangloff, 2001; Bell and Snively, 2008; Fiorillo, 2008a; Gangloff and Fiorillo, 2010; Chinsamy et al., 2012; Watanabe et al., 2013; Xing et al., 2014). Recently, it was proposed that the Liscomb hadrosaur bones represent a new distinct hadrosaurine taxon, *Ugrunaaluk kuukpikensis* (Mori et al., 2016). However, subsequent workers argued that the proposed new taxon was invalid in part because it was diagnosed on immature growth stage features preserved in the known specimens (Xing et al., 2017). Despite of the taxonomic controversy, these

studies have agreed upon the presence of a hadrosaurine hadrosaurid in the Liscomb Bonebed.

Here we report the first definitive lambeosaurine hadrosaurid fossil from the Liscomb Bonebed (DMNH 2014-12-266), represented by an isolated cranial material, a supraoccipital. The supraoccipital demonstrates that the Liscomb Bonebed contains both lambeosaurine and hadrosaurine materials. While co-occurrences of hadrosaurine and lambeosaurine are widely known in the northern hemisphere such as Careless Creek Quarry (Fiorillo, 1989; Fiorillo, 1991; Prieto-Márquez and Gutarra, 2016) and Jack's Birthday Site (Varricchio, 1995) of Montana, United States; Blagoveschensk locality (Bolotsky and Godefroit, 2004; Godefroit et al., 2004b) and Kundur (Godefroit et al., 2012a; Godefroit et al., 2012b) localities of southern Amur region, Russia; and Wulaga locality (Godefroit et al., 2008) of northern Heilongjiang Province, China, the Liscomb Bonebed is the first to demonstrate the co-occurrence in the Arctic. Therefore, the new discovery offers an important opportunity to infer possible determinant factors of hadrosaurid taxonomic structure in the Arctic, in comparison with lower latitude regions.

1.1.2 Material and method

DMNH 2014-12-266, collected from the Liscomb Bonebed and stored in the collection of the Perot Museum of Nature and Science, Dallas, USA, was examined and described herein. Its symmetrical shape and the endocranial wall suggest that the bone is a sagittal endocranial element such as basioccipital, basisphenoid, and supraoccipital. Absences of structures present in basioccipital and basisphenoid (occipital condyle, sphenoccipital tubera, foramina for cranial nerves, basipterygoid process) leaves supraoccipital the only possible candidate. Although multiple large tetrapods are known from the Prince Creek Formation, complete exclusion of supraoccipital from the foramen magnum, suggested by the rugose sutural surface for the exoccipital-opisthotic complex, indicate that the supraoccipital does not belong to basal ornithomimid (Norman et al., 2004), dromaeosaurids (Barsbold and Osmólska, 1999), pachycephalosaurines (Maryńska et al., 2004), troodontids (Currie and Zhao, 1993), or tyrannosaurids (Currie, 2003). Additionally, the absence of the rostradorsal process suggest that it does not belong to ceratopsids (Dodson et al., 2004). On the other hand, DMNH 2014-12-266 resembles to supraoccipitals of hadrosaurids in complete exclusion from foramen magnum (Horner et al., 2004) and lambeosaurines and non-hadrosaurid hadrosauroids in presence of well-developed squamosal bosses (Gilmore, 1937; Langston, 1960;

Horner, 1992; Godefroit et al., 1998; Godefroit et al., 2012c; Prieto-Márquez et al., 2016). Therefore, DMNH 2014-12-266 is identified as a supraoccipital of hadrosauroid.

Comparisons with isolated supraoccipitals of hadrosaurines from the Liscomb Bonebed (DMNH 22807 and casts of UAMES 4291, UAMES 12727, UAMES 21544, housed at the Canadian Museum of Nature), *Prosaurolophus maximus* (, MOR 447-8-8-7-14 Horner, 1992), *Hypacrosaurus stebingeri* (USNM 11893, Gilmore, 1937; Horner and Currie, 1994), an indeterminate lambeosaurine (CMN 0170, Langston, 1960; Horner, 1992), and non-hadrosaurid hadrosauroids *Bactrosaurus johnsoni* (Godefroit et al., 1998), *Batyrosaurus rozhdestvenskyi* (Godefroit et al., 2012c), *Eolambia caroljonesa* (McDonald et al., 2012), and *Eotrachodon orientalis* (Prieto-Márquez et al., 2016) were made for taxonomic identification. To further investigate similarities and differences with the late Cretaceous lambeosaurines in Canada, DMNH 2014-12-266 is compared with isolated lambeosaurine supraoccipitals from the Campanian Oldman Formation (UALVP 48, UALVP 53092, UALVP 53106) and the Campanian Dinosaur Park Formation (CMN 0170, UALVP 55300, UALVP 54569). Because Xing et al. (2017) argued that *Ugrunaaluk kuukpikensis* is a *nomen dubium*, we conservatively regard the hadrosaurine specimens from the Liscomb Bonebed as *Edmontosaurus* sp. as they were in prior works (Gangloff, 1998; Fiorillo

and Gangloff, 2001; Bell and Snively, 2008; Fiorillo, 2008a; Gangloff and Fiorillo, 2010; Chinsamy et al., 2012; Flaig et al., 2013; Watanabe et al., 2013; Fiorillo et al., 2016).

1.1.3 Results

1.1.3.1 Systematic paleontology.

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Cerapoda Sereno, 1986

Ornithopoda Marsh, 1881

Iguanodontia Dollo, 1888

Hadrosauridae Cope, 1870

Lambeosaurinae Parks, 1923

1.1.3.2 Description.

The new supraoccipital (DMNH 2014-12-266; Figure 1.1-1) is nearly complete but missing both anterior processes and anterodorsal end of the ascending process. Its maximum width along the posteroventral margin is 44.8 mm, which is slightly larger

than those of *Edmontosaurus* sp. specimens from the Liscomb Bonebed, nearly equivalent with that of the indeterminate lambeosaurine CMN 0170 (Langston, 1960; Horner, 1992), and smaller than that of *Prosaurolophus maximus* (MOR 447-8-8-7-14; Horner, 1992) (Table 1.1-1). The width is also much less than the posteriorly exposed supraoccipital surfaces of adult articulated skulls of *Edmontosaurus regalis* (100.3 mm, CMN 2278), *Gryposaurus notabilis* (102.4 mm, CMN 2288), *Hypacrosaurus stebingeri* (87.1 mm, MOR 553s; 98.0 mm, MOR 455), and *Lambeosaurus lambei* (79.5 mm, ROM 1218). Its small size may indicate that the supraoccipital (DMNH 2014-12-266) belonged to an immature individual.

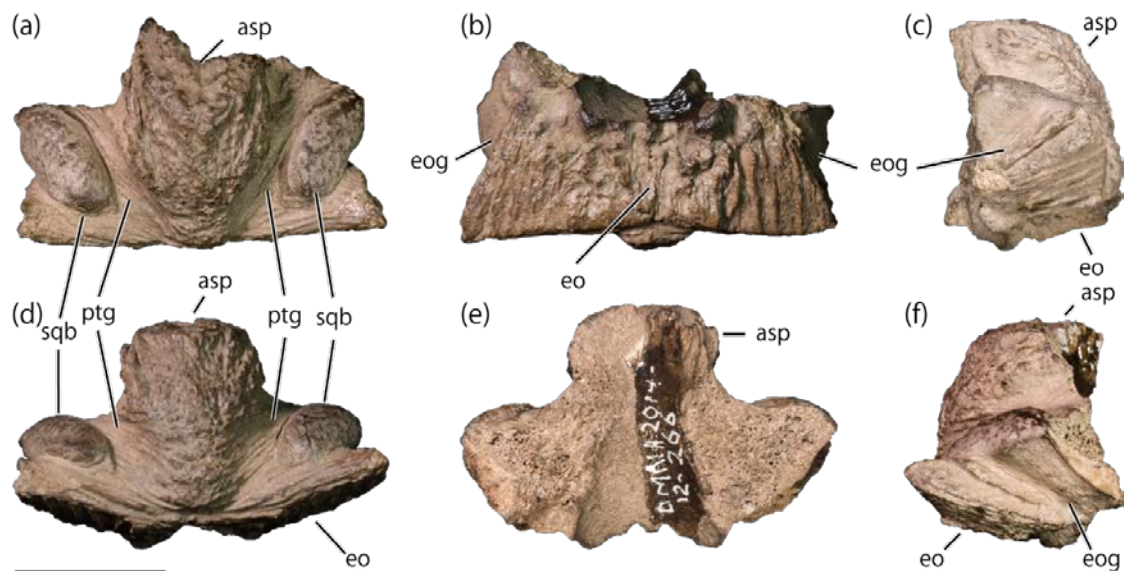


Figure 1.1-1. Lambeosaurine supraoccipital (DMNH 2014-12-266) from the Liscomb Bonebed. a) Dorsal view. b) Ventral view. c) Left lateral view. d) Posterior

view. e) Anterior view. f) Right lateral view. Abbreviations: asp, ascending process; eo, articulation surface for the exoccipital-opisthotic complex; eog, exoccipital groove; ptg, post-temporal groove; sqb, squamosal boss. Scale = 2 cm.

Table 1.1-1. Selected measurements and ratios of hadrosaurid supraoccipitals

ID	Formation	Subfamily	Taxa	Length, ventral surface (mm)	Width, posteroventral margin (mm)	Maximum height (mm)	L/W ratio (%)	H/W ratio (%)
DMNH 2014-12-266	Prince Creek Formation	Lambeosaurina	unknown	12.0	44.8	24.9	26.8%	55.6%
USNM 11893	Two Medicine Formation	Lambeosaurina	<i>Hypacrosaurus stebingeri</i>	17.9	52.8	35.3	33.9%	67.0%
UALVP 48	Oldman Formation	Lambeosaurina	unknown	13.4	38.1	22.2	35.2%	58.3%
UALVP 53092	Oldman Formation	Lambeosaurina	unknown	25.8	66.3	37.9	38.9%	57.1%
UALVP 53106	Oldman Formation	Lambeosaurina	unknown	17.5	48.4	-	36.0%	-
CMN 0170	Dinosaur Park Formation	Lambeosaurina	unknown	19.4	46.8	24.1	41.4%	51.5%
UALVP 54569	Dinosaur Park Formation	Lambeosaurina	unknown	28.4	-	29.1	-	-
UALVP 55300	Dinosaur Park Formation	Lambeosaurina	unknown	17.1	43.2	26.2	39.7%	60.7%
DMNH EPV 127701	Lance Formation	Hadrosaurinae	<i>Edmontosaurus annecte</i>	66.0	48.5	33.6	135.9%	69.2%
MOR 447-8-8-7-14	Two Medicine Formation	Hadrosaurinae	<i>Prosaurolophus maxim</i>	43.0	85.7	34.7	50.1%	40.5%
DMNH 22807	Prince Creek Formation	Hadrosaurinae	<i>Edmontosaurus</i> sp.	24.4	30.2	15.3	80.9%	50.5%
UAMES 4291	Prince Creek Formation	Hadrosaurinae	<i>Edmontosaurus</i> sp.	24.4	31.5	15.8	77.4%	50.1%
UAMES 12727	Prince Creek Formation	Hadrosaurinae	<i>Edmontosaurus</i> sp.	36.6	37.8	12.7	97.0%	33.6%
UAMES 21544	Prince Creek Formation	Hadrosaurinae	<i>Edmontosaurus</i> sp.	20.5	29.2	15.4	70.3%	52.7%

The ascending process is well-developed, taller and wider anteriorly than posteriorly, and divides the bone along the midline (Figure 1.1-1a, d). It extends posterior to the posterior margin of the articulation surface with the exoccipital-opisthotic complex (Figure 1.1-1a, b), unlike the anteriorly positioned ascending process of *Edmontosaurus* sp. (DMNH 22807, UAMES 4291, UAMES 12727, UAMES 21544; Figure 1.1-2). The ascending process is convergent posteroventrally (Figure 1.1-1a, d) as in *Hypacrosaurus stebingeri* (USNM 11893, Gilmore, 1937; Horner and Currie, 1994), while those of *Edmontosaurus* sp. (DMNH 22807, UAMES 21544, UAMES 4291,

UAMES 12727; Figure 1.1-2b-e) and *Prosaurolophus maximus* (Horner, 1992) are nearly parallel or divergent, and those of non-hadrosaurid hadrosauroids *Bactrosaurus johnsoni* (Godefroit et al., 1998), *Batyrosaurus rozhdestvenskyi* (Godefroit et al., 2012c), *Eolambia caroljonesa* (McDonald et al., 2012), and *Eotrachodon orientalis* (Prieto-Márquez et al., 2016) are strongly divergent posteroventrally. The dorsal surface of the ascending process is rounded (Figure 1.1-1d) unlike the bi-lobed ascending process of *Hypacrosaurus stebingeri* (USNM 11893, Gilmore, 1937; Horner and Currie, 1994). The dorsal surface is rugose and lacks the nuchal crest. On either side of the ascending process, a deep post-temporal groove (Langston, 1960) runs anteroposteriorly (Figure 1.1-1a, d) unlike in supraoccipitals of non-hadrosaurid hadrosauroids which have no distinct post-temporal groove (Godefroit et al., 1998; Godefroit et al., 2012c; McDonald et al., 2012; Prieto-Márquez et al., 2016). The grooves are strongly divergent anteriorly as in the indeterminate lambeosaurine (Figure 1.1-2n) (CMN 0170, Langston, 1960; Horner, 1992), differing from those of *Prosaurolophus maximus* (MOR 447-8-8-7-14, Horner, 1992) and *Edmontosaurus* sp. (DMNH 22807, UAMES 4291, UAMES 12727, UAMES 21544; Figure 1.1-2b-e) which run nearly parallel to or only slightly divergent from each other. Lateral to the groove, an anterolaterally oriented squamosal boss is present (Figure 1.1-1a, d). The squamosal bosses are well-developed

unlike in *Prosaurolophus maximus* (MOR 447-8-8-7-14, Horner, 1992) and *Edmontosaurus* sp. (DMNH 22807, UAMES 4291, UAMES 12727, UAMES 21544; Figure 1.1-2b-e). The squamosal bosses of DMNH 2014-12-266 are formed solely by the supraoccipital without participation of the exoccipital-opisthotic complex. This morphology of the squamosal boss differs from those of *Hypacrosaurus altispinus* (AMNH FARB 5248, Evans, 2010), *Hypacrosaurus stebingeri* (USNM 11893, Gilmore, 1937; Horner and Currie, 1994), the indeterminate lambeosaurine (CMN 0170, Langston, 1960; Horner, 1992) (Figure 1.1-2n), and non-hadrosaurid hadrosauroids *Bactrosaurus johnsoni* (Godefroit et al., 1998), *Batyrosaurus rozhdestvenskyi* (Godefroit et al., 2012c), and *Eolambia caroljonesa* (McDonald et al., 2012), in which the boss is also formed in part of the exoccipital-opisthotic complex.

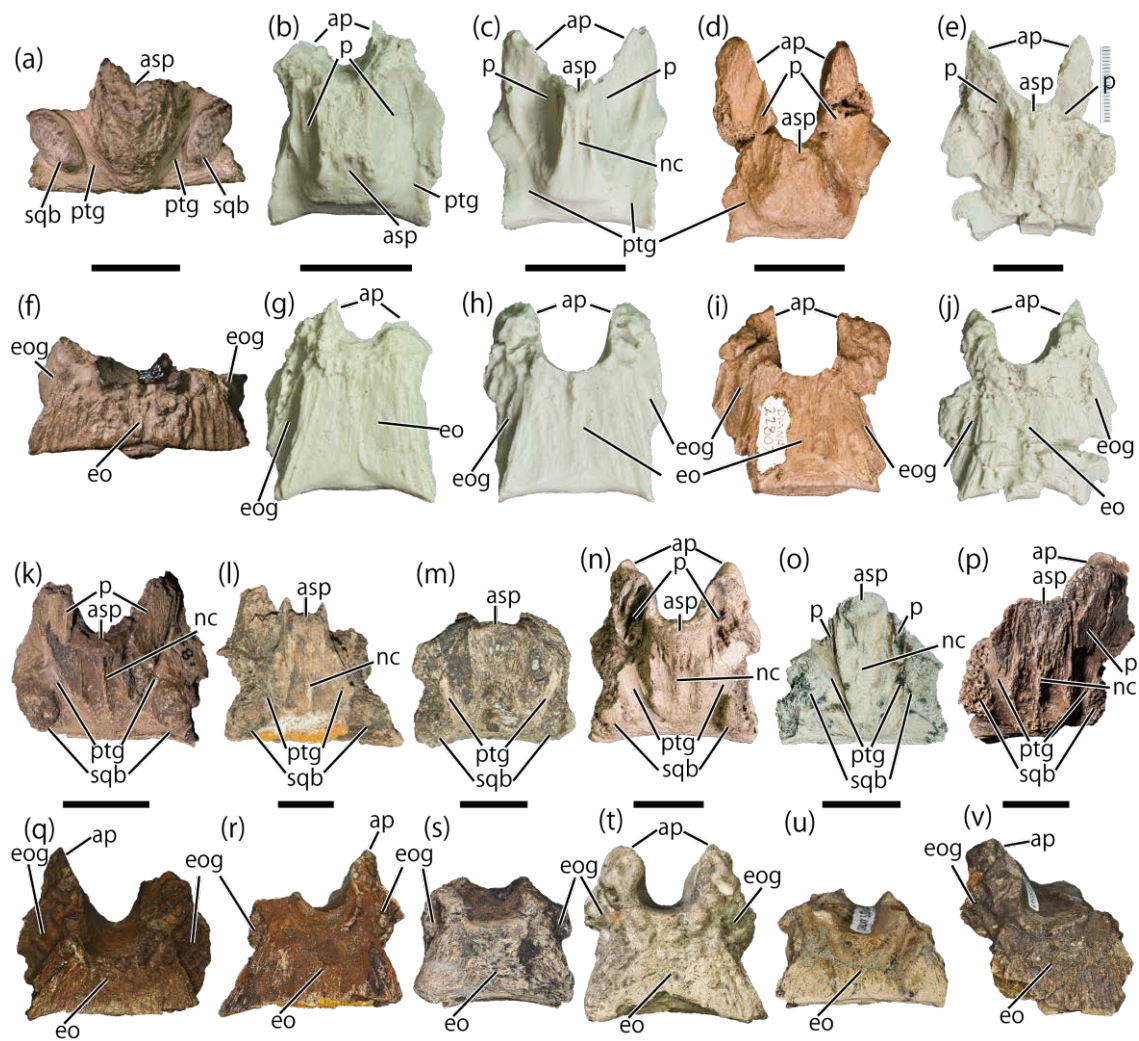


Figure 1.1-2 Hadrosaurid supraoccipitals. DMNH 2014-12-266 (a, f).

Edmontosaurus sp.: cast of UAMES 21544 (b, g); cast of UAMES 4291 (c, h);

DMNH 22807 (d, i); cast of UAMES 12727 (e, j). Indeterminate lambeosaurines:

UALVP 48 (k, q); UALVP 53092 (l, r); UALVP 53106 (m, s); CMN 0170 (n, t);

UALVP 55300 (o, u); UALVP 54569 (p, v). Dorsal (a-e, k-p) and ventral (f-j, q-v)

views. Abbreviations: asp, ascending process; ap, anterior process; eo, articulation

surface for the exoccipital-opisthotic complex; eog, exoccipital groove; nc, nuchal

crestp, articulation surface for the parietal, ptg, post-temporal groove; sqb, squamosal boss. Scale = 2 cm.

The anteroposterior length of the ventral sutural surface is short (Figure 1.1-1b), being 26.8% of the mediolateral width along the posteroventral margin. The ratio is much smaller than those of the Liscomb *Edmontosaurus* sp. (DMNH 22807, UAMES 4292, UAMES 21544, UAMES 12727), *Edmontosaurus annectens* (DMNH EPV 127701), and *Prosaurolophus maximus* (MOR 447-8-8-7-14), but resembles to lambeosaurines (Table 1.1-1). The sutural surface with the exoccipital-opisthotic complex is bowed ventrally toward the midline (Figure 1.1-1d) as in largest supraoccipital of *Edmontosaurus* sp. from the Liscomb Bonebed (UAMES 12727), but unlike in the smaller three. The exoccipital groove, located laterodorsal to the ventral sutural surface with the exoccipital-opisthotic complex, faces lateroventrally (Figure 1.1-1b, c, f). The exoccipital groove is mediolaterally narrower than those of *Prosaurolophus maximus* (MOR 447-8-8-7-14; Horner, 1992) and *Edmontosaurus* sp. (DMNH 22807, UAMES 4291, UAMES 12727, UAMES 21544; Figure 1.1-2g-j), but resembles the indeterminate lambeosaurine (CMN 0170, Langston, 1960; Horner, 1992) (Figure 1.1-2t). The anterior surface of the supraoccipital is smooth and slightly

concave to form a part of the endocranial wall (Figure 1.1-1e). However, detailed morphology of the endocranial wall is uncertain because of the missing anterior processes. The height of the supraoccipital is 55.6% of its posteroventral width (Figure 1.1-1d, e; Table 1.1-1).

1.1.4 Discussion

The new hadrosaurid supraoccipital DMNH 2014-12-266 largely differs from those of the Liscomb *Edmontosaurus* sp. in presence of the well-developed squamosal bosses (Figure 1.1-2a-e) and the short exoccipital articulation surface (Figure 1.1-2f-j; Table 1.1-2). The length of the exoccipital articulation surface is equivalent with a phylogenetic character that differentiates hadrosaurines from lambeosaurines and non-hadrosaurid hadrosauroids: degree of the caudal extension of the supraoccipital-exoccipital shelf (Godefroit et al., 2004a; Xing et al., 2017; Prieto-Márquez et al., 2019). The well-developed squamosal bosses are widely seen in lambeosaurines as well as in a few non-hadrosaurid hadrosauroids, but has never been reported in hadrosaurines (Figure 1.1-3; Table 1.1-2). Although the appearance of squamosal bosses is a ontogenetic change in the non-hadrosaurid hadrosauroid *Bactrosaurus johnsoni* (Godefroit et al., 1998); however, the presence of well-developed

squamosal bosses in both juvenile (AMNH FARB 5461, skull length approximately 30% of the holotype MOR 549; Figure 1.1-3g) and adult (MOR 455) individuals of *Hypacrosaurus stebingeri* suggests that the well-developed squamosal boss of DMNH 2014-12-266 is unlikely to be a result of ontogenetic variation but more likely is a taxonomic difference.

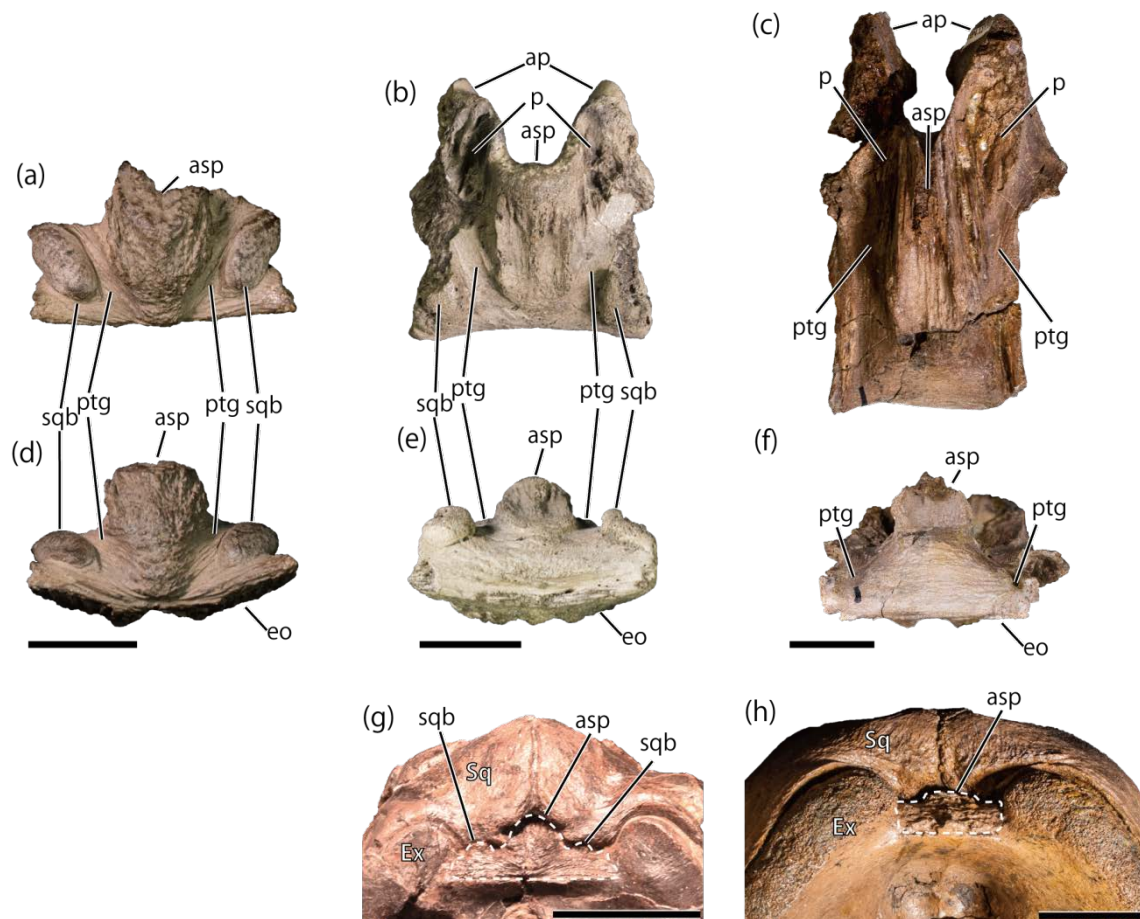


Figure 1.1-3. Supraoccipitals of Liscomb hadrosaurid DMNH 2014-12-266 (a, d), an indeterminate lambeosaurine CMN 0170 (b, e), and *Edmontosaurus annectens* DMNH EPV 127701 (c, f) in dorsal (a-c) and posterior (e-f) views. Posterior views

of articulated skulls of *Hypacrosaurus stebingeri* (g) and *Edmontosaurus annectens*

(h). Abbreviations: asp, ascending process; eo, articulation surface for the

exoccipital-opisthotic complex; ptg, post-temporal groove; sqb, squamosal boss; Ex,

Exoccipital-opisthotic complex, Sq, Squamosal. Scale = 2 cm (a-f), 5cm (g, h).

Dashed line represents the boundary of supraoccipital in (g) and (h).

Table 1.1-2. List of hadrosauroid supraoccipital features.

Taxon	ID	Group	Squamosal boss	Length of the exoccipital articulation surface	Ascending process	Post-temporal groove	Posterior exposure of the ascending process	Reference
-	DMNH 2014-12-266	Lambeosaurinae	Present	Less than half of the width of the posteroventral margin of the supraoccipital	Converge posteroventrally	Present, converge posteroventrally	?	-
<i>Amurosaurus riabinini</i>	AEHM 1/232	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	Godefroit et al. (2004)
<i>Aralosaurus tuberiferus</i>	PIN 2229	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	Godefroit et al. (2004)
<i>Charonosaurus jiangxiensis</i>	CUST JV 1251-57	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	Godefroit et al. (2001)
<i>Corythosaurus casuarius</i>	ROM 776	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	-
<i>Hypacrosaurus altispinus</i>	AMNH 5248 CMN 2247 CMN 8675 ROM 702	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	Evans (2010)
<i>Hypacrosaurus stebingeri</i>	AMNH 5461 USNMH 11893	Lambeosaurinae	Present	Less than half of the width of the posteroventral margin of the supraoccipital	Converge posteroventrally	Present, nearly parallel to each other	Much less than half of the width of the posteroventral margin of the supraoccipital	-
<i>Jaxartosaurus ardensis</i>	PIN 5009/1	Lambeosaurinae	Present	?	?	?	?	Rozhdestvensky (1968)
<i>Lambeosaurus lambei</i>	CMN 1218 CMN 2739	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	-
<i>Olorotitan arharensis</i>	AEHM 2/845	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	Godefroit et al. (2012)
<i>Velociraptor coahuilensis</i>	CPC-59	Lambeosaurinae	Present	?	?	?	Much less than half of the width of the posteroventral margin of the supraoccipital	Gates et al. (2007)
<i>Acristans gaglianoni</i>	UMNHVP 16607	Hadrosaurinae	Absent	?	?	?	More than half as wide as the posteroventral margin of the supraoccipital	Gates et al. (2011)
<i>Edmontosaurus annectens</i>	DMNH EPV. 127701 ROM 53494 ROM 59786 ROM 64623	Hadrosaurinae	Absent	Half or more than the width of the posteroventral margin of the supraoccipital	Diverge posteroventrally	Present, nearly parallel to each other	More than half as wide as the posteroventral margin of the supraoccipital	-
<i>Edmontosaurus regalis</i>	CMN 2289	Hadrosaurinae	?	?	?	?	More than half as wide as the posteroventral margin of the supraoccipital	Xing et al. (2017)
<i>Gryposaurus notabilis</i>	AMNH FARB 5350	Hadrosaurinae	?	?	?	?	More than half as wide as the posteroventral margin of the supraoccipital	Prieto-Marquez (2010)
<i>Maiasaura peeblesorum</i>	ROM 44770 ROM 66182	Hadrosaurinae	?	?	?	?	More than half as wide as the posteroventral margin of the supraoccipital	-
<i>Prosaurolophus maximus</i>	MOR 447-3-8-7-14	Hadrosaurinae	Absent	Half or more than the width of the posteroventral margin of the supraoccipital	Nearly parallel	Present, nearly parallel to each other	?	Hornier (1992)
<i>Bactrosaurus johnsoni</i>	SBDE 95E5/29	Non-hadrosauroid hadrosauroid	Present	?	Diverge posteroventrally	Absent	?	Godefroit et al. (1998)
<i>Batyrosaurus rozhdestvenskyi</i>	AEHM 4/1	Non-hadrosauroid hadrosauroid	Absent	?	Diverge posteroventrally	Absent	?	Godefroit et al. (2012)
<i>Edmontia carolinensis</i>	CEUM 14525 CEUM 355626	Non-hadrosauroid hadrosauroid	Absent	Less than half of the width of the posteroventral margin of the supraoccipital	Diverge posteroventrally	Absent	?	-
<i>Eotrachodon orientalis</i>	MSC 7949	Non-hadrosauroid hadrosauroid	Absent	?	Diverge posteroventrally	Absent	?	Prieto-Marquez et al. (2016)
<i>Lamsonia transmontana</i>	USNM 538191	Non-hadrosauroid hadrosauroid	Present	?	?	?	?	Sues and Averianov (2009)

DMNH 2014-12-266 shows a posteroventrally convergent ascending process (Figure 1.1-2a), which is seen only in lambeosaurines (*Hypacrosaurus stebingeri* USNMH 11893; indeterminate lambeosaurines UALVP 48, UALVP 55300, UALVP 54569; Figure 1.1-2k, o, p), but different from a posteroventrally divergent ascending process

in non-hadrosaurid hadrosauroids (Godefroit et al., 2012c; McDonald et al., 2012; Lee et al., 2014; Prieto-Márquez et al., 2016) and a parallel or posteroventrally divergent ascending process in hadrosaurines (e.g., *Edmontosaurus annectens*, DMNH EPV 127701; *Prosaurolophus maximus* (Horner, 1992)) (Table 1.1-2). Additionally, the gently curved posterodorsal border of the ascending process (Figure 1.1-1c, f) suggests anterior inclination of the posterior surface of the supraoccipital in articulation, which is a synapomorphic character of hadrosaurids (Horner et al., 2004; Xing et al., 2017).

Therefore, the combination of the four characters mentioned above (the short exoccipital articular surface, well-developed squamosal bosses, posteroventrally convergent ascending process, and anteriorly inclined posterodorsal surface of the ascending process) is unique to Lambeosaurinae (Table 1.1-2), suggesting DMNH 2014-12-266 is a supraoccipital of a lambeosaurine hadrosaur.

Isolated lambeosaurine supraoccipitals from the Oldman and Dinosaur Park formations can be divided into two morphotypes by the position of the squamosal bosses. While the squamosal bosses of the first morphotype (UALVP 48, UALVP 53092, and UALVP 53106 from the Oldman Formation and CMN 170 from the Dinosaur Park Formation; Figure 1.1-2k, l, m, n) are posteriorly positioned, those of the other morphotype (UALVP 55300 and UALVP 54569 from the Dinosaur Park

Formation; Figure 1.1-2o, p) are anteriorly positioned, which are also seen in the Liscomb lambeosaurine (Figure 1.1-2a). Although the Liscomb lambeosaurine shares this character with UALVP 55300 and UALVP 54569, it differs from UALVP 55300 in having posteriorly extended ascending process (Figure 1.1-2a, f, o, u, p, v). Additionally, the Liscomb lambeosaurine differs from all other lambeosaurine supraoccipitals from the Oldman and the Dinosaur Park formations in having a rugose surface of the ascending process, the laterally completed squamosal bosses, and the ventrally bowed posteroventral margin (Figure 1.1-1, Figure 1.1-2). Furthermore, the Liscomb lambeosaurine also differs from penecontemporaneous lambeosaurine *Hypacrosaurus altispinus* (AMNH FARB 5248) from the Horseshoe Canyon Formation, which has weakly developed ascending process and squamosal bosses that are partly formed by the exoccipital-opisthotic complex (Evans, 2010). Comparisons of supraoccipital characters with the Canadian specimens indicate that the Liscomb lambeosaurine is distinct from the Canadian specimens but shows affinities with the supraoccipitals from the Dinosaur Park Formation.

Previous studies suggested presence of lambeosaurine in the Arctic (Russell, 1988, 1990; Gangloff, 1998) with no definitive descriptions of fossil materials. Russell (1988), cited by Rich et al. (1997), noted occurrence of lambeosaurine from the Bylot Island of

Canada, but details of the record are unknown. Russell (1990) and Gangloff (1998) mentioned possible lambeosaurine records from the North Slope of the Alaska, but the identification in the former was based on a personal communication (by John R. Horner) and the latter did not provide a specimen number or the basis for the identification. The Liscomb lambeosaurine is the first definitive occurrence of this group from the Arctic and confirms that lambeosaurines inhabited the ancient Arctic terrestrial environment. This greatly expands the paleogeographic distribution of lambeosaurines much further north than previously known from taxa such as *Hypacrosaurus altispinus* from southern Alberta, Canada (Figure 1.1-4). At the same time, the morphological affinities with the Canadian lambeosaurines elucidate more extensive faunal exchange between the Arctic and lower paleolatitudes within North America than previously suggested, which is also supported by the presence of *Edmontosaurus*, *Pachyrhinosaurus*, tyrannosaurids, and troodontids in both regions (Fiorillo and Gangloff, 2000; Fiorillo and Tykoski, 2012; Fiorillo and Tykoski, 2013; Mori et al., 2016; Xing et al., 2017; Fiorillo, 2018).

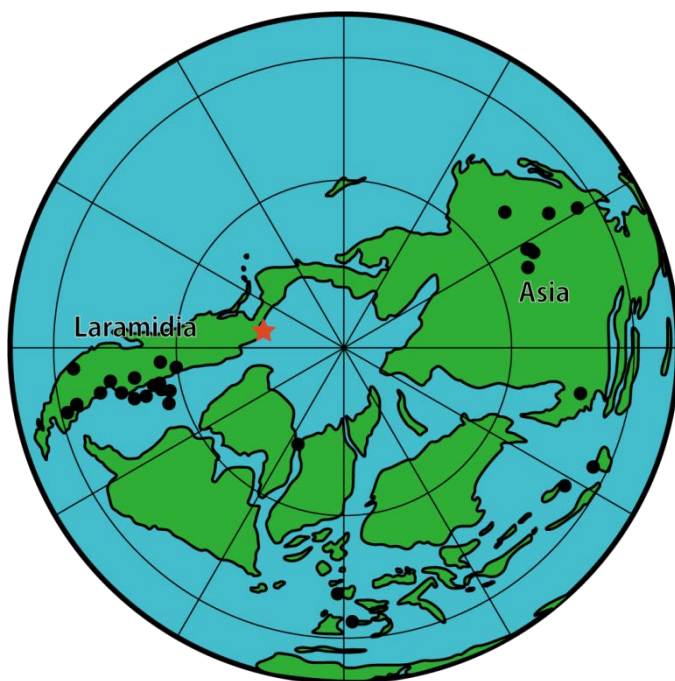


Figure 1.1-4. Paleogeographical records of lambeosaurines during the Late Cretaceous. The red star represents the Liscomb lambeosaurine reported herein. Map is redrawn from Deep Time Maps(Blakey, 2018). The paleocoordinates are obtained from the Paleobiology Database (www.paleobiodb.org).

The co-occurrence of hadrosaurine and lambeosaurine supraoccipitals from the Liscomb Bonebed suggests that the validity of *Ugrunaaluk kuukpikensis* should be treated with caution because hadrosaur bones from the bonebed may consist of these hadrosaurid sub-families as well as different ontogenetic stages (Xing et al., 2017) and, more importantly, indicates that hadrosaurine and lambeosaurine dinosaurs co-existed in the Cretaceous Arctic region. The presence of one lambeosaurine supraoccipital and

eight previously reported hadrosaurine supraoccipitals (Mori et al., 2016), as well as additional unpublished hadrosaurine specimens in the Perot Museum of Nature and Science collections, suggests numerical dominance of hadrosaurines over lambeosaurines in the ancient Liscomb region. While the hadrosaurine dominance may indicate their better adaptation to Arctic environment than lambeosaurines, hadrosaurine dominance is known from lower latitudes marine deposits (Horner, 1979) and regions closer to paleoshorelines of North America (Béland and Russell, 1978) and eastern Asia (Godefroit et al., 2001; Bolotsky and Godefroit, 2004; Godefroit et al., 2004b; Godefroit et al., 2008; Godefroit et al., 2012a; Godefroit et al., 2012b; Xing et al., 2014), indicative of near-shore environment preferences by hadrosaurines. Consequently, the hadrosaurine dominant faunal structure of the Liscomb Bonebed, deposited in lower coastal environment, may indicate that Arctic hadrosaurids performed environment preferences similar to those in the lower latitudes (Figure 1.1-5).

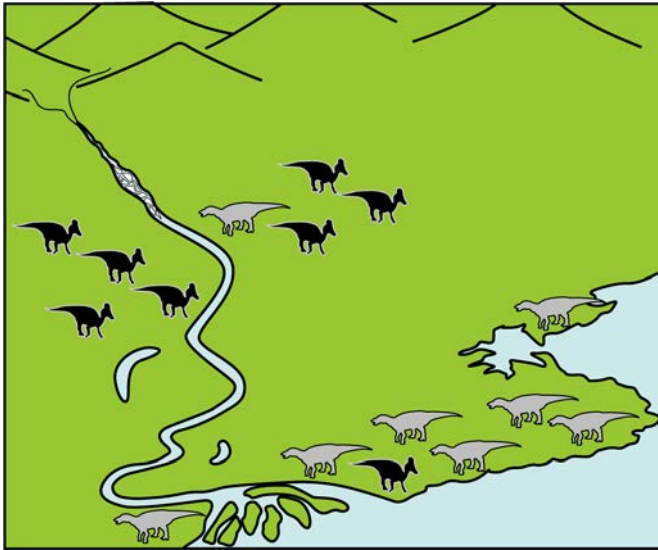


Figure 1.1- 5. Schematic drawing of differential habitat preference between hadrosaurines and lambeosaurines.

1.1.5 Acknowledgments

We thank Kevin Seymour, Margaret Currie, and Clive Coy for their kind help during collection visits for comparisons. We are also grateful to Greg Funston and Kristen MacKenzie for their kind help on photography. The first author is thankful to Masaya Iijima, Junki Yoshida, and Yoshihiro Tanaka for their comments on earlier versions of the manuscript. The fieldworks were financially supported by the National Office of Polar Programs (OPP 0424594 and OPP 0425636) and National Geographic Society (W221-12). The collection visits are supported by Grant-in-Aid for JSPS Research Fellow Grant Number 17J06410.

Chapter 1.2: Re-examination of the cranial osteology of the Arctic

Alaskan hadrosaurine with implications for its taxonomic status

Abstract

Hadrosaurid fossils from the Liscomb Bonebed, Prince Creek Formation of the North Slope of Alaska, were the first dinosaur fossils discovered from the Arctic. While the Prince Creek Formation hadrosaurids were long identified as *Edmontosaurus*, a member of the sub-clade Hadrosaurinae, they were recently assigned to a newly erected taxon, *Ugrunaaluk kuukpikensis*. However, taxonomic status of the new taxon is ambiguous largely due to the immature nature of the specimens upon which it was based. Here we reexamine cranial elements of the Prince Creek Formation hadrosaurine in order to solve its taxonomic uncertainties. The Prince Creek Formation hadrosaurine possesses a short dorsolateral process of the laterosphenoid, one of the diagnostic characters of *Edmontosaurus*. The Prince Creek Formation hadrosaurine also shows affinity to *Edmontosaurus regalis* in the presence of a horizontal shelf of the jugal and the presence of a posteroventral projection of the quadratojugal. These features and our phylogenetic analysis demonstrate that the Prince Creek Formation hadrosaurine should be re-assigned to *Edmontosaurus*. Because the Prince Creek Formation *Edmontosaurus*

shows differences with lower latitude *Edmontosaurus* in dorsoventrally short maxilla, presence of a secondary ridge on the dentary teeth, and the absence of the transverse ridge between basiptyergoid processes of the basisphenoid, we consider that the Prince Creek Formation *Edmontosaurus* should be regarded as *Edmontosaurus* sp. until further discoveries of mature hadrosaurines from the Prince Creek Formation Bonebed and/or equivalently juvenile *Edmontosaurus* specimens from the lower latitudes allow direct comparisons. The retention of the Prince Creek Formation hadrosaurine as *Edmontosaurus* re-establishes a significant latitudinal distribution for this taxon. Despite of the large latitudinal distribution, the morphological partial disparity of *Edmontosaurus* is extremely small within Hadrosaurinae. Additionally, the evolutionary rates analyses demonstrate moderate or significantly low evolutionary rates for *Edmontosaurus*, indicating the latitudinal habitat differences among *Edmontosaurus* did not drive their morphological modifications. The present results may indicate that *Edmontosaurus* were highly adapted to various environments and they required minimal morphological change associated with habitat differences.

1.2.1 Introduction

Increasing work in the late Cretaceous deposits of the ancient Arctic is revealing a new appreciation for higher dinosaur diversity in the region than had been previously recognized (Godefroit et al., 2009; Gangloff, 2012; Fiorillo, 2018). The most abundant Arctic dinosaur fossil record is known from Alaska where multiple dinosaur groups including ankylosaurid (Gangloff, 1995), ceratopsids (Fiorillo and Tykoski, 2012; Fiorillo and Tykoski, 2013; Tykoski et al., 2019), dromaeosaurids (Fiorillo and Gangloff, 2000), hadrosaurids (Davies, 1987; Takasaki et al., 2019), ornithomimosaur (Watanabe et al., 2013), basal ornithopods (Clemens and Nelms, 1993; Brown et al., 2011), pachycephalosaurid (Gangloff et al., 2005; Sullivan, 2006), troodontids (Fiorillo and Gangloff, 2000; Fiorillo, 2008b; Fiorillo et al., 2009), and tyrannosaurids (Gangloff, 1994; Gangloff, 1998; Fiorillo and Gangloff, 2000; Fiorillo and Tykoski, 2014) are known from skeletal material. Numerous dinosaur footprints (Fiorillo and Adams, 2012; Fiorillo et al., 2014a; Fiorillo et al., 2014b; Fiorillo and Tykoski, 2016; Flaig et al., 2017; Fiorillo, 2018; Fiorillo et al., 2018) have now been reported as well.

One of the most abundant dinosaurs collected in Alaska are the large herbivorous Hadrosauridae. All of the hadrosaurid fossils in Alaska are known from the Upper Cretaceous Prince Creek Formation (PCF) which crops out along the Colville River,

North Slope, Alaska. The Liscomb Bonebed in the PCF is especially rich in hadrosaurid fossils, known for bone concentrations of up to 220 elements/m² (Fiorillo et al., 2010).

The Liscomb hadrosaurid was initially considered to belong to the clade

Lambeosaurinae (Brouwers et al., 1987), but Nelms (1989) later identified the Liscomb hadrosaurid as a member of Hadrosaurinae, *Edmontosaurus saskatchewanensis*, which is now a junior synonym of *Edmontosaurus annectens* (Campione and Evans, 2011).

Although subsequent work has reached a general consensus that the PCF hadrosaurine belong to *Edmontosaurus* (Gangloff, 1998; Bell and Snively, 2008; Fiorillo, 2008a;

Gangloff and Fiorillo, 2010; Campione and Evans, 2011; Chinsamy et al., 2012; Xing et al., 2014), Mori et al. (2016) recently proposed that the Liscomb hadrosaurines, together with additional hadrosaurid materials from the Prince Creek Formation, represent a new and distinct taxon *Ugrunaaluk kuukpikensis*. However, the taxonomic status of the PCF

hadrosaurine remains ambiguous. Xing et al. (2017) and Wosik et al. (2019) both proposed that *Ugrunaaluk kuukpikensis* is not a valid taxon, because it is based upon

disarticulated and disassociated parts from multiple, immature individuals that are not ontogenetically comparable to known specimens of *Edmontosaurus annectens* and

Edmontosaurus regalis. Furthermore, the recent discovery of lambeosaurine material from the Liscomb Bonebed demonstrated that the PCF bears at least two different

hadrosaurids (Takasaki et al., 2019), raising the possibility that *Ugrunaaluk kuukpikensis* could be a chimera taxon. Therefore, reexamination of the PCF hadrosaurine material is mandatory in order to either uphold or refute the taxonomic validity of *Ugrunaaluk kuukpikensis*.

Here we present the first full description of the cranial elements of the PCF hadrosaurine. We focus on cranial material due to the difficulties in distinguishing immature hadrosaurine postcranial elements from those of lambeosaurines (Brett-Surman and Wagner, 2007; Guenther, 2009; Guenther, 2014; Takasaki et al., 2017). Comparisons of the PCF hadrosaurine cranial materials with other hadrosaurines, especially with *Edmontosaurus*, are in the hope that such detailed examination can resolve the taxonomic uncertainty of the PCF hadrosaurine. Reexamination of the PCF hadrosaurine from the Arctic also offers great opportunity to understand how latitudinal environmental differences might have influenced hadrosaurid evolution.

1.2.2 Institutional abbreviations

AMNH FARB, American Museum of Natural History, New York, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; DMNH, Perot Museum of Nature and Science, Dallas, USA; DMNH EPV, Denver Museum of Nature and Science, Denver,

USA; NMMNH P, New Mexico Museum of Natural History and Science, Albuquerque, USA; ROM, Royal Ontario Museum, Toronto, Canada; TMP, Royal Tyrrell Museum of Paleontology, Drumheller, Canada; UAMES, University of Alaska Museum, Fairbanks, USA; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA.

1.2.3 Materials and methods

1.2.3.1 Phylogenetic analyses

Phylogenetic analyses were conducted based on the most recent published data matrix by Kobayashi et al. (Kobayashi et al., 2019). In addition to the PCF hadrosaurine, two OTUs (Operational Taxonomic Unit) of immature *Edmontosaurus annectens* (AMNH FARB 5046, an articulated partial skull; and disarticulated juvenile specimens stored in Royal Ontario Museum: list of specimens in Data S1.2-1) were added to the data matrix. Four new characters were added to the analyses' character list (Text S1.2-1). The data matrix was then comprised of 73 OTUs with 354 equally weighed, unordered characters (DataS1.2-2). Two phylogenetic analyses, one excluding the two immature *Edmontosaurus annectens* OTUs and one including the two OTUs, were conducted in order to test how maturity of the representative specimens could

potentially affect the phylogenetic position of *Edmontosaurus* taxa and the PCF hadrosaurine.

Following previous works (Campione et al., 2013; Prieto-Márquez, 2014; Currie et al., 2016; Mori et al., 2016; Takasaki et al., 2017; Wosik et al., 2019), hadrosauroid ontogenetic variations of character status were evaluated prior to conducting the phylogenetic analyses. Ontogenetically variable characters were scored as multi-states in the PCF hadrosaurine and the two juvenile *Edmontosaurus* OTUs following Takasaki et al. (Takasaki et al., 2017). Phylogenetic analyses were conducted using TNT ver. 1.5 (Goloboff and Catalano, 2016), setting *Ouranosaurus nigeriensis* as the outgroup. The maximum number of trees was set to 99,999 in memory. A traditional search with 1000 replicates of Wagner trees using random additional sequences followed by the TBR branch swapping that held 1000 trees per replicate was performed. Bootstrap resampling using standard absolute frequencies with 5000 replicates and calculation of Bremer decay indices were performed to indicate the support for clades recovered in the resultant trees.

1.2.3.2 Disparity analysis

In order to assess the phylogenetic morphological disparity of hadrosaurines, principal coordinate analyses were conducted using the MorphMatrix2PCoA function of the R package Claddis 0.3.0 (Lloyd, 2016) on R version 3.5.2 (R Core Team, 2019). Only the cranial characters were used in the analysis since postcranial elements of the PCF hadrosaurine were not considered in the present phylogenetic analyses. The Maximum Observable Rescaled Distance was utilized for the distance metric. Partial disparity (Foote, 1993) of the phylogenetic morphological disparity were calculated and compared among hadrosaurine subgroups to explore the relative morphological disparity of *Edmontosaurus*. Partial disparity of each subgroup was obtained by dividing the summed square distances of PC 1 through PC 10 of each individual by $n-1$.

1.2.4 Results

1.2.4.1 Description

1.2.4.1.1 Premaxilla

The posterodorsal process and the anteromedial margin of the oral rim are preserved in DMNH 22716 (Figure 1.2-1A-C) and the prenasal oral platform is preserved in UAMES 12995 (Figure 1.2-1D-F). The premaxilla bears the bony external naris, a gracile posterodorsal process, and distinct circumnasal ridge as in typical hadrosaurines

(Figure 1.2-1). The oral margin of the premaxilla is deflected posterodorsally and forms a prominent lip-like structure that resembles *Edmontosaurus annectens* (e.g., CMN 8509, ROM 57100), *Edmontosaurus regalis* (e.g., CMN 2288, ROM 00801), *Laiyangosaurus youngi* (Zhang et al., 2017), and *Shantungosaurus* (Hu, 1973; Xing et al., 2014). The anterodorsal surface of the lip-like structure is perforated by several small foramina. The prenasal region anterior to the circumnasal ridge is short as in *Brachylophosaurus canadensis* (e.g., CMN 8893) *Edmontosaurus regalis* (e.g., CMN 2288), *Gryposaurus notabilis* (e.g., CMN 2278), and immature *Edmontosaurus annectens* (e.g., ROM 53525). The short prenasal region may either represent the immature state in Edmontosaurini (Campione and Evans, 2011; Prieto-Márquez, 2014; Mori et al., 2016) or be an indication of an affinity to *Edmontosaurus regalis* (Xing et al., 2017). As Mori et al. (2016) highlighted, the vestibular promontory is undeveloped in these small premaxillae, thus the circumnasal depression is not divided into an anteromedial concavity and anterolateral concavity (Figure 1.2-1F), which is similar to the condition in a larger but still relatively immature *Edmontosaurus annectens* (ROM 53525; Figure 1.2-1G). A premaxillary foramen is present at the medioventral margin of the circumnasal ridge. The palatal plane is widely angled from the articulation surface

for its counterpart (135 degrees). The ventral surface of the anterior oral margin of the premaxilla is ornamented by a double-layered denticulate structure.

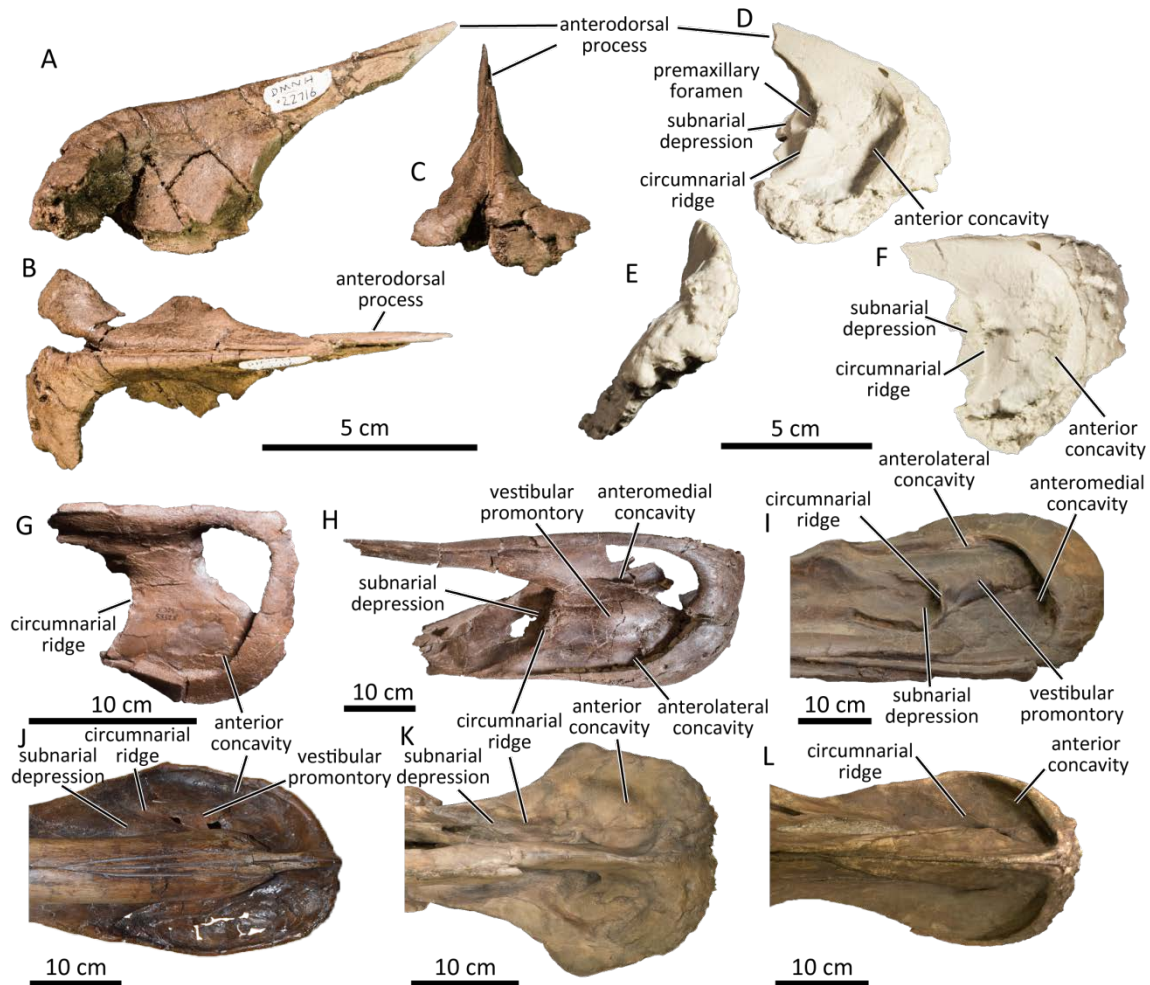


Figure 1.2-1. Premaxillae of the PCF hadrosaurine (A-F). Cast of DMNH 22716, partial right and left premaxillae in left lateral (A), dorsal (B), and anterior (C) views. UAMES 12995, partial right premaxilla in right lateral (D), anterior (E), and dorsal (F) views. Premaxillae of Immature *Edmontosaurus annectens* ROM

53525(G), mature *Edmontosaurus annectens* ROM 64076 (H), *Edmontosaurus regalis* FMNH P15004 (I), *Prosaurolophus maximus* CMN 2870 (J), *Brachylophosaurus canadensis* CMN 8893 (K), and *Gryposaurus notabilis* CMN 2278 (L) in dorsal views.

1.2.4.1.2 Maxilla

The maxilla bears an anterodorsal process and lacks a wide premaxillary shelf as in typical hadrosaurines (Figure 1.2-2A, B). This is significantly different from lambeosaurine maxillae which lack anterodorsal process and have a slender dorsal process. The anterodorsal process extends further anteriorly than the anteroventral process. The anteroventral process forms roughly an angle of 32 degrees with respect to the ventral margin of the maxilla, with some degree of variation (DMNH 22718, DMNH 2014-12-798, UAMES 4250, UAMES 4327). The anteroventral process is straight unlike those of *Brachylophosaurus canadensis* (Prieto-Márquez, 2005) and *Acristavus gagslarsoni* (Gates et al., 2011) which are ventrally deflected. Multiple small foramina penetrate the lateral surface of the maxilla ventral to the jugal sutural surface. The lateral exposure of the dorsal process is subarcuate and its apex is positioned over the anterior one-third of the maxilla. The dorsal process is wider than tall and its apex is

slightly pointed, unlike the rounded apex of larger *Edmontosaurus annectens* (e.g., ROM 64083) and *Edmontosaurus regalis* (e.g., CMN 2289) specimens, but resembles those of *Acristavus gagslarsoni* (Gates et al., 2011), *Brachylophosaurus canadensis* (Prieto-Márquez, 2005), and *Naashoibitosaurus ostromi* (NMMNH P-16106). The apex of the dorsal process is located slightly anterior to the midline of the maxilla as in typical immature hadrosauroids (Horner and Currie, 1994; Prieto-Márquez, 2011, 2014). The dorsal process articulates with the dorsal half of the anterior process of the jugal. Posterior to the sutural surface with the jugal, the ectopterygoid ridge is slightly less than half as long as the maxilla length. The palatine process of the maxilla is dorsally oriented at the posteromedial base of the dorsal flange. The medial surface of the maxilla is perforated by a gently arched row of neural foramina at the mid-height of the maxilla. The available specimens suggest that approximately two maxillary tooth rows are positioned per centimeter, which is expected to be reduced with increased ontogenetic development (Horner and Currie, 1994; Takasaki et al., 2017). As Mori et al. (2016) pointed, the PCF hadrosaurine have low maxillae in which its height is 34% of the anteroposterior length. The ratio, which show negative allometry among Edmontosaurini (Figure 1.2-2C, Table S1.2-1), resembles to *Laiyangosaurus youngi* (Zhang et al., 2017).

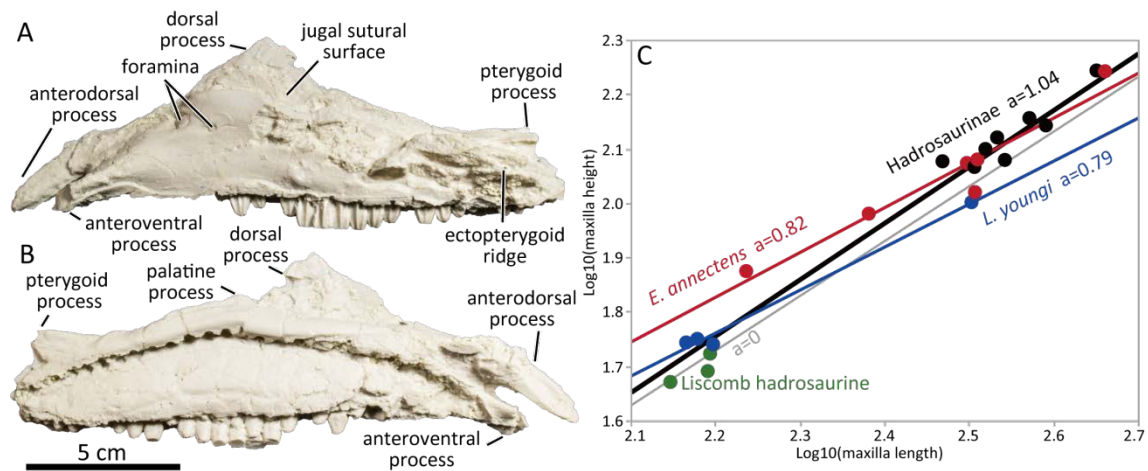


Figure 1.2-2. Cast of left maxilla (UAMES 4250) in lateral (A) and medial (B) views. (C) Height-length relationships of hadrosaurines, demonstrating negative allometry among Edmontosaurini.

1.2.4.1.3 Nasal

The nasal is composed of the elongated anterodorsal process, the main body, and the triangular anteroventral process as in typical non-crested hadrosaurines (Figure 1.2-3A, B). The anterodorsal process is nearly straight for its entire length. Its cross-section is subtriangular proximally and mediolaterally compressed distally. The dorsoventral height of the anterodorsal process is nearly constant throughout its length and has a blunt distal end (UAMES 4271) unlike the pointed distal end seen in *Gryposaurus notabilis* (CMN 2278, ROM 00873, and TMP 1990.022.0001). The medial surface of

the anterodorsal process is flat or slightly concave for articulation with its counterpart proximally and with the premaxilla distally. The lateral surface of the anterodorsal process bears a distinct posterodorsal ridge that defines posterodorsal margin of the circumnarial fossa. The posterodorsal ridge is well-developed as in *Edmontosaurus annectens* (ROM 53523, ROM 53524, ROM 64623), *Edmontosaurus regalis* (CMN 2288, CMN 2289), *Kerberosaurus manakini* (Bolotsky and Godefroit, 2004; Godefroit et al., 2012b) and *Shantungosaurus giganteus* (Xing et al., 2014). The posterodorsal ridge in the small PCF specimens forms a shallow arch, unlike in large *Edmontosaurus annectens* (e.g., USNM 3814) and *Edmontosaurus regalis* (Xing et al., 2017). This could be an ontogenetically variable feature as demonstrated among relatively immature specimens *Edmontosaurus annectens* (DMNH EPV. 95227, DMNH EPV. 95234, ROM 53523, ROM 53524, ROM 64076, ROM 64623, USNM 3814). The triangular anteroventral process projects anteroventrally from the main body of the nasal and is partly covered by the premaxilla laterally. The contact surface with the premaxilla is defined dorsally by the ventral ridge of the main body. The main body of the nasal is trapezoidal and its flat dorsal surface bears a shallow depression posterolaterally for contact with the prefrontal.

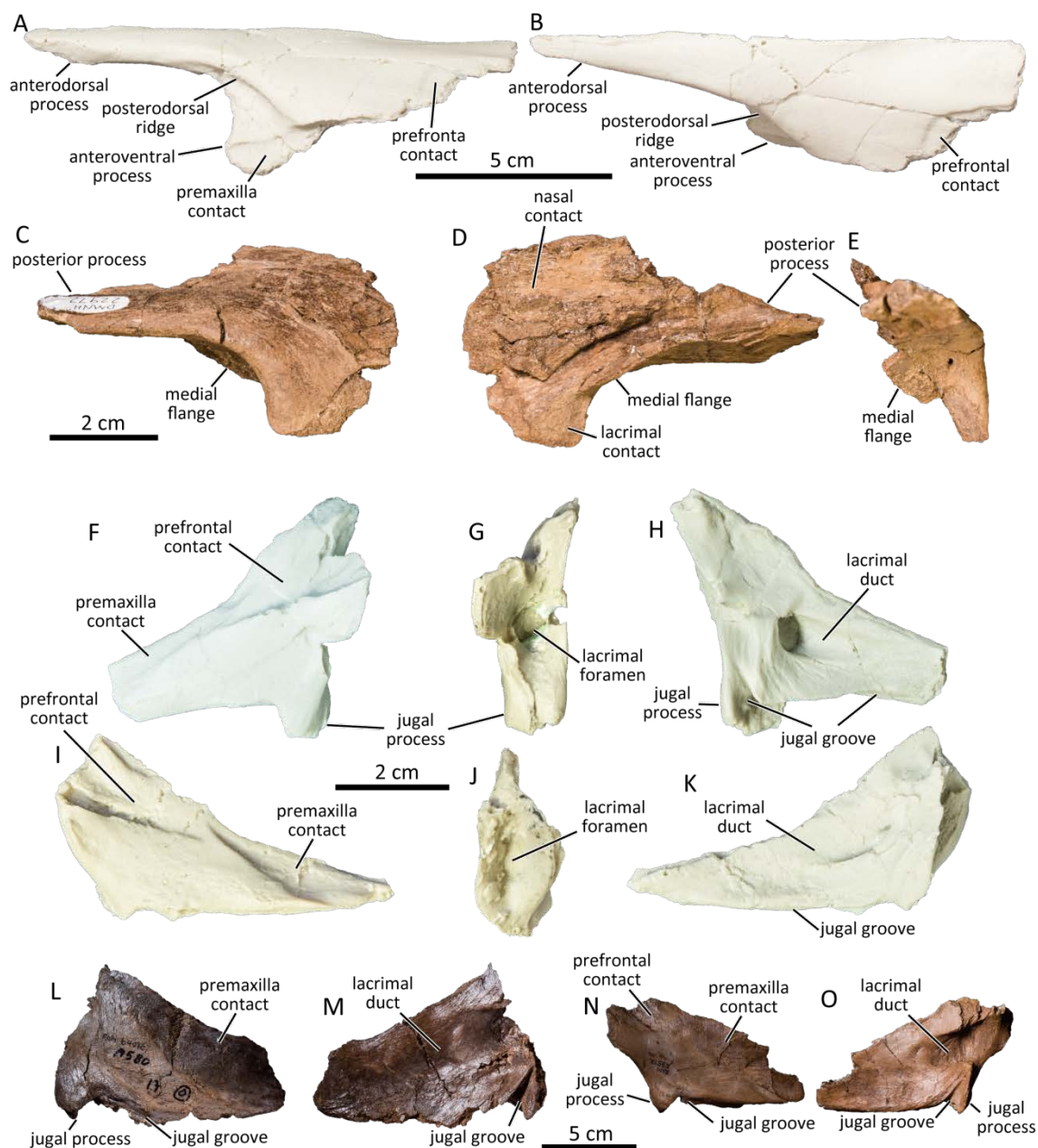


Figure 1.2- 3. Cast of left nasal (UAMES 4940) in lateral (A) and medial (B) views.

Right prefrontal (DMNH 22972) in lateral (C), medial (D), and posterior (E) views.

Casts of left (F-H) and right (I-K) lacrimals the PCF hadrosaurine in lateral (F, I),

posterior (G, J), and medial (H, K) views. Isolated right lacrimals of a large (ROM

64076; L, M) and a small (ROM 53512; N, O) *Edmontosaurus annectens* in lateral (L, N) and medial (M, O) views.

1.2.4.1.4 Prefrontal

The prefrontal lacks a posterodorsal process, as in typical non-crested hadrosaurines (Figure 1.2-3C-E). The anterior preorbital region is mediolaterally thin and anteroposteriorly elongated as in *Edmontosaurus annectens* and *Edmontosaurus regalis* (Xing et al., 2017). The anterior margin of the prefrontal is fan-shaped unlike the nearly square anterior margins of large *Edmontosaurus annectens* (e.g., ROM 64076) and *Edmontosaurus regalis* (e.g., CMN 2289), and is not bifurcated unlike in anterior margins of larger but still relatively immature *Edmontosaurus annectens* (ROM 53499, ROM 53500). The lateral surface of the preorbital region is penetrated by several foramina in some specimens (e.g., UAMES 4305). The orbital margin is nearly right angled anterodorsally unlike the gently arcuate anterodorsal orbital margins of *Brachylophosaurus canadensis* (CMN 8893), *Maiasaura peeblesorum* (Horner, 1983), and *Saurolophus osborni* (AMNH FARB 5221, CMN 8796), but resembles *Edmontosaurus annectens* and *Edmontosaurus regalis* (Xing et al., 2014; Xing et al., 2017), including more immature specimens (e.g., ROM 53499, ROM 53500). The

anteroventral surface of the orbital margin is flat and the medial flange is undeveloped as in the more immature *Edmontosaurus annectens* specimens (e.g., ROM 53499, ROM 53500), resulting in the absence of a deep circular fossa along the lateral half of the posteroventral surface of the prefrontal, which is a diagnostic feature of *Edmontosaurus* (Xing et al., 2014). The prefrontal tapers posteriorly and forms a wedge-shaped posterior process.

1.2.4.1.5 Lacrimal

The lacrimal is much longer anteroposteriorly than its height dorsoventrally unlike lambeosaurine lacrimals (Figure 1.2-3F-K). It is anteroposteriorly elongated, subtriangular, and tapers anteriorly to a point unlike those of large specimens of *Edmontosaurus annectens* (ROM 53511, ROM 53512, ROM 64076) and *Edmontosaurus regalis* (Xing et al., 2017), due to the dorsoventrally short contact surfaces with the premaxilla and prefrontal. These features resemble the condition in the lacrimal of *Maiasaura peeblesorum* (Horner, 1983) and *Brachylophosaurus canadensis* (Cuthbertson and Holmes, 2010; Freedman Fowler and Horner, 2015). The lacrimal duct is medially covered by a thin plate and forms the lacrimal foramen along the orbital rim as in *Edmontosaurus regalis* (Xing et al., 2017) and *Probrachylophosaurus*

(Freedman Fowler and Horner, 2015), but unlike in *Edmontosaurus annectens* (Figure 1.2-3L-O). The ventral margin of the lacrimal is deeply grooved for articulation with the anterior process of the jugal. The jugal process protrudes ventrally from the posterolateral margin of the lacrimal and is nearly right angled with the jugal groove.

1.2.4.1.6 Jugal

The anterior process of the jugal is dorsoventrally expanded with markedly recurved posterodorsal margin (Figure 1.2-4A, B), as in other hadrosaurids. The long, wedge-shaped anterior apex of the anterior process is positioned slightly dorsal to the mid-height of the anterior process. The palatine articular facet is anteriorly inclined at an angle between 125° – 136° from the line connecting the ventral apices of the infratemporal fenestra and the orbit. Mori et al. (2016) proposed that the angle between the palatine articular facet and the posterior margin of the maxilla contact surface of the jugal of the PCF hadrosaurine is greater than that of *Edmontosaurus annectens* of comparable size, and they proposed that a hypothetical ontogenetic trajectory of this feature would be distinct from that of *Edmontosaurus*. However, additional observations of *Edmontosaurus annectens* jugals demonstrate a high degree of intraspecific variation in this angle regardless of size (Figure 1.2-4C-E). Therefore this

feature is not unique to the PCF hadrosaurine. The dorsal contact surface with the lacrimal bears a narrow groove. The contact surface widens mediolaterally along the posterodorsal margin, but does not form the posterolateral projection along the orbital margin that is present in *Edmontosaurus regalis* (Xing et al., 2017). The convex ventral edge of the anterior process is pointed as in several immature *Edmontosaurus annectens* specimens (e.g., DMNH EPV. 95220).

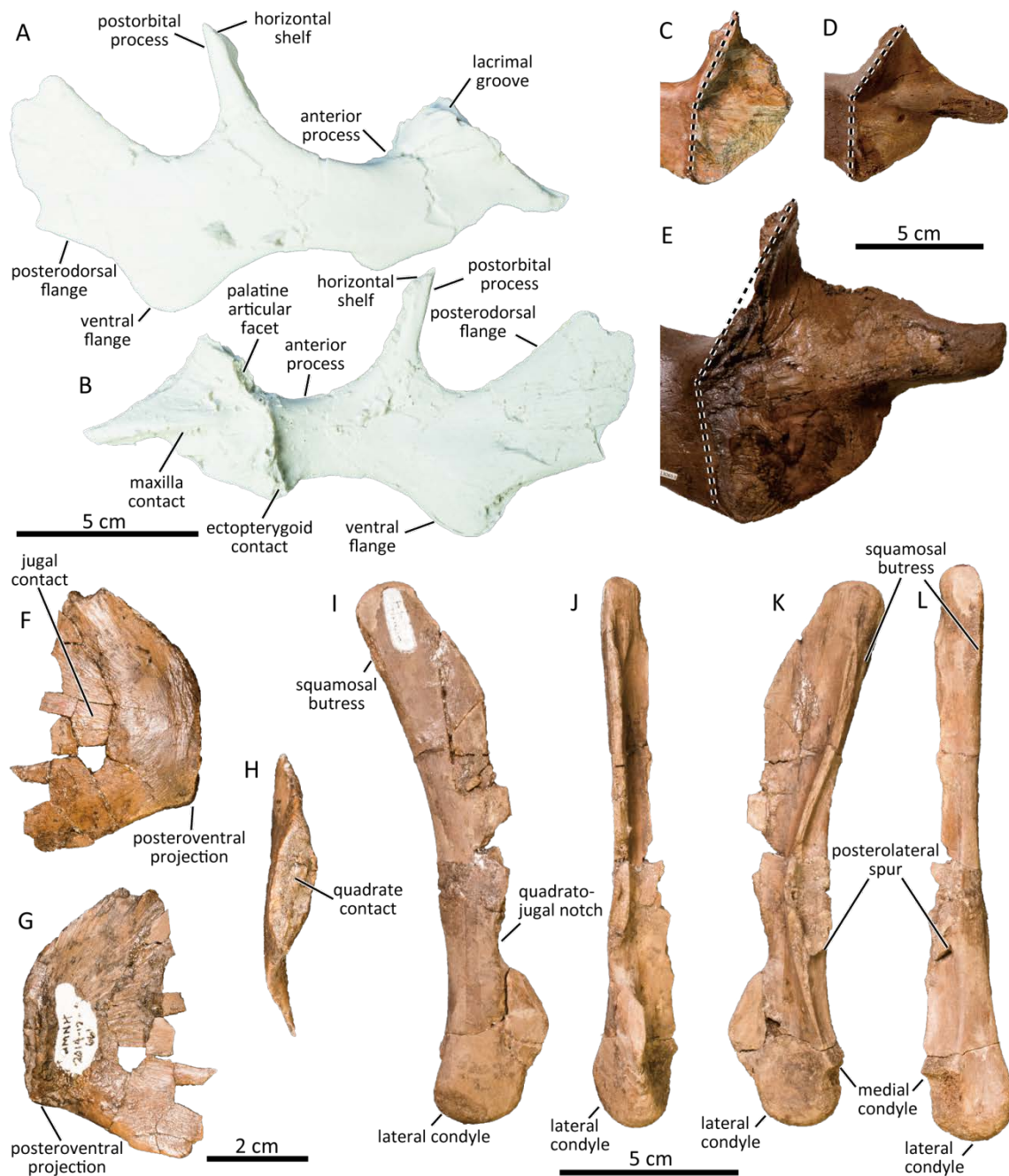


Figure 1.2-4. Cast of right jugal of the PCF hadrosaurine (UAMES 4187) in lateral (A) and medial (B) views. Anterior process of left jugal of *Edmontosaurus annectens* (C: ROM 53518; D: DMNH EPV. 95220; E: DMNH EPV. 130653) in medial view, demonstrating intraspecific variation of the angle between the

palatine process and the posterior margin of the maxilla contact surface. Left quadratojugal (DMNH 2014-12-661) in lateral (F), medial (G), and posterior (H) views. Right quadrate (DMNH 21044) in lateral (I), anterior (J), medial (K), and posterior (L) views.

The postorbital process is inclined at around 73 degrees posteriorly relative to the line connecting the ventral apices of the infratemporal fenestra and the orbit. The postorbital process bears an anterodorsally oriented shelf, which could be equivalent to the horizontal shelf on the postorbital process of the jugal in *Edmontosaurus regalis* (Xing et al., 2017). The posteroventral flange of the jugal is well-developed and rounded as in *Edmontosaurus annectens* (e.g., ROM 57100) and *Edmontosaurus regalis* (e.g., AMNH FARB 5254). The ventral flange of the jugal is approximately 1.24 times as wide as the posterior constriction ventral to the infratemporal fenestra , and the posterior constriction is approximately 0.64 times as wide as the length between the ventral apices of the orbit and the infratemporal fenestra (UAMES 4187, UAMES 7336). The posteroventral margin of the posterodorsal flange of the jugal is slightly concave and divergent from the anterodorsal margin of the posterodorsal flange.

Quadratojugal

The quadratojugal is flat and slightly bowed laterally (Figure 1.2-4F-H). Its posteroventral corner is acutely angled and forming a small projection as in *Edmontosaurus regalis* (e.g., AMNH FARB 5254) and lambeosaurines, but is different from the strongly hooked posteroventral corners of *Brachylophosaurus canadensis* (e.g., CMN 8893) and *Maiasaura peeblesorum* (e.g., ROM 44770), and the gently curved posteroventral corners of the quadratojugal in *Edmontosaurus annectens* (e.g., ROM 57100) and *Kamuysaurus japonicus* (Kobayashi et al., 2019). The anterior half of the lateral surface is slightly depressed for the jugal contact. The lateral exposure of the quadratojugal is large (Mori et al., 2016). The quadrate contact faces posteriorly in some (e.g., DMNH 2014-12-661) and posteromedially in other specimens (e.g., DMNH 2014-12-813), demonstrating a large degree of intraspecific morphological variation or possible presence of lambeosaurine quadratojugals in the sample.

1.2.4.1.7 Quadrate

The quadrate is strongly curved posteriorly (140°) as in immature *Edmontosaurus annectens* (Figure 1.2-4I-L). The squamosal buttress is weakly developed, unlike the well-developed squamosal buttress of *Gryposaurus notabilis* (TMP 80.22.1) and

Brachylophosaurus canadensis (CMN 8893). A symmetrical, arcuate quadratojugal notch is located much lower than half the height of the quadrate, unlike in lambeosaurines. The quadratojugal notch is shallow and barely reaches half of the anteroposterior depth of the lateral flange. The dorsal margin of the quadratojugal notch is gently curved whereas the ventral margin is strongly recurved and oriented anteriorly. The dorsal margin of the quadratojugal notch is shallowly grooved. The lateral surface of the quadrate dorsal to the quadratojugal notch lacks a large depression for the lateral scarf joint connection with the quadratojugal, as seen in nestling *Edmontosaurus annectens* (Wosik et al., 2019) but unlike larger specimens of *E. annectens* (e.g., ROM 53522, ROM 64076). The posterolateral spur is located slightly dorsal to the apex of the quadratojugal notch. A groove for contact with the posteroventral projection of the quadrate ramus of the pterygoid is present anterior to the posterolateral spur. Ventrally, the medial condyle is positioned much more dorsally than the lateral condyle as in other hadrosaurids. The lateral condyle is slightly longer anteroposteriorly than mediolateral width of the ventral end of the quadrate as in nestling (Wosik et al., 2019) *Edmontosaurus annectens* in some specimens (e.g. DMNH 2014-12-567) and significantly shorter in some specimens (e.g., UAMES 4235).

1.2.4.1.8 Squamosal

The squamosal is dorsoventrally narrow as in typical hadrosaurines (Figure 1.2-5A-C). The two deep grooves for articulation with the squamosal process of the postorbital reach dorsal to the precotyloid process. The deep precotyloid fossa tapers posteriorly and does not reach dorsal to the quadrate cotylus. The precotyloid process is triangular in cross section and is as long as the anteroposterior length of the quadrate cotylus, as also seen in immature specimens of *Edmontosaurus annectens* (e.g., ROM 53510). However, the precotyloid process is relatively much shorter than in mature hadrosaurines other than in Brachylophosaurini. The postcotyloid process is massive and its posteroventral surface is striated for contact with the exoccipital paroccipital process. The medial ramus is straight and defines the posterior margin of the supratemporal fenestra. Its medial surface is extremely rugose for contact with the parietal.

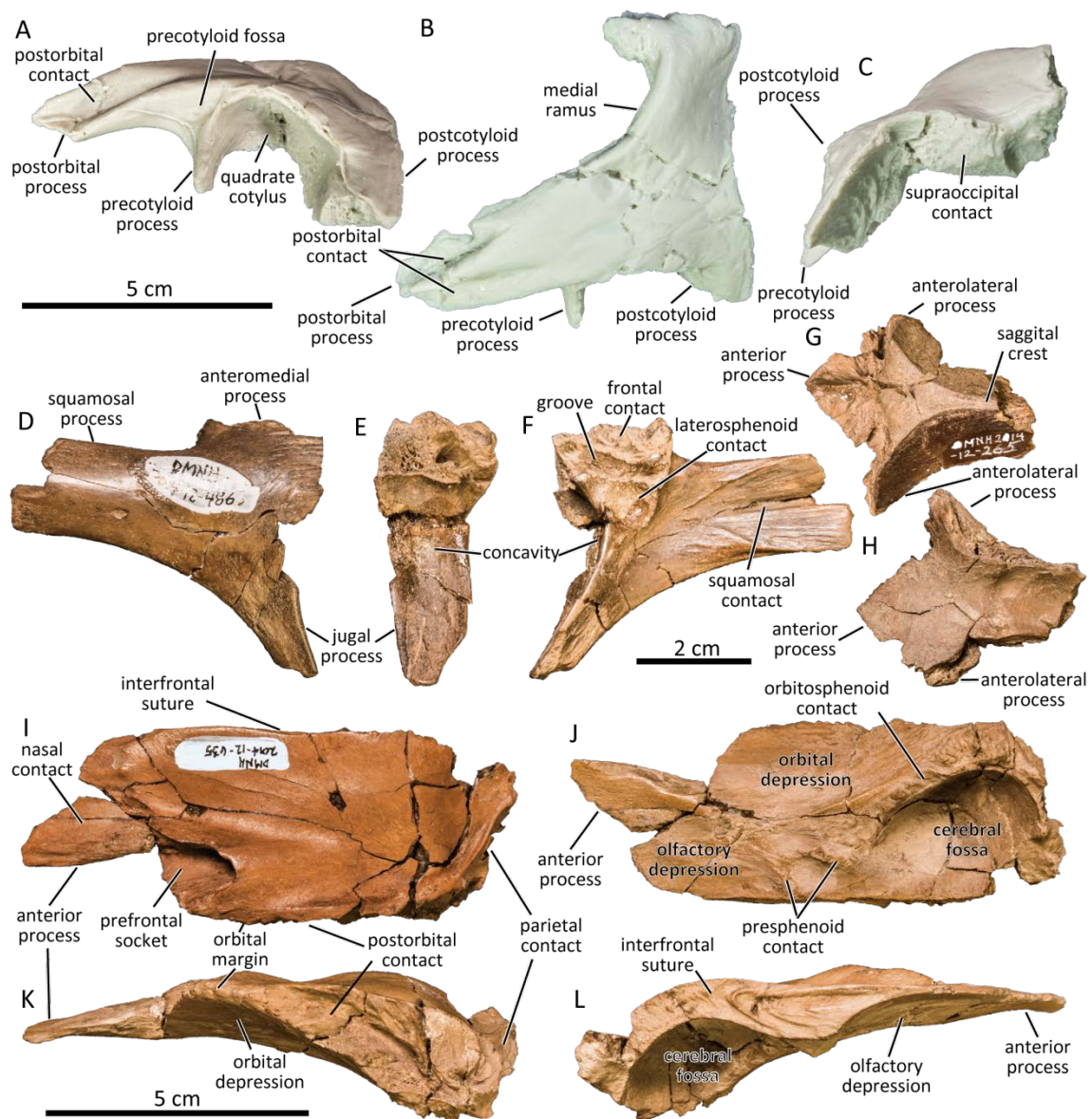


Figure 1.2-5. Cast of left squamosal (UAMES 12266) in lateral (A), dorsal (B), and posterior (C) views. Right postorbital (DMNH 2014-12-486) in lateral (D), anterior (E), and medial (F) views. Parietal (DMNH 2014-12-265) in dorsal (G) and ventral (H) views. Left frontal (DMNH 2014-12-635) in dorsal (I), ventral (J), lateral (K), and medial (L) views.

1.2.4.1.9 Postorbital

The postorbital is a triradiate bone composed of anteromedial, posterior, and jugal processes (Figure 1.2-5D-F). The dorsal surface of the postorbital is flat and lacks the dorsal promontrium and the deep depression above the jugal process present in derived lambeosaurines (e.g., *Corythosaurus casuarius*, *Lambeosaurus lambei*). The orbital margin of the postorbital is deeply arcuate. The anteromedial process of the postorbital is short, with a medial surface for articulation with the frontal that is rugose and bears an anteroposteriorly traversing groove. The triangular laterosphenoid facet is positioned ventral to the contact with the frontal. The squamosal process is long and bifurcates posteriorly. The articular surface for the squamosal reaches the proximal base of the squamosal process. The jugal process is slender and shallowly concave anteriorly. The anterior surface of the jugal process does not form a deep pocket unlike in large specimens of *Edmontosaurus regalis* and *Edmontosaurus annectens*. Although Mori et al. (2016) urged that the absence of the deep pocket differentiates the PCF hadrosaurine from *Edmontosaurus*, this feature changes drastically through ontogeny in *Edmontosaurus* (Campione and Evans, 2011; Xing et al., 2017). The anterior concavity of the Arctic hadrosaurine (UAMES 33308) is certainly much shallower compared to

the deep pocket in an equivalent sized postorbital of *Edmontosaurus annectens* (ROM 53513). However, the anterior concavity of UAMES 33308 is also relatively much wider than the pocket of the immature *Edmontosaurus annectens*. The wide anterior concavity of the PCF hadrosaurine may resemble an immature *Edmontosaurus regalis* in which the postorbital pocket is much wider than in *Edmontosaurus annectens* in their adult forms (Xing et al., 2017). However, the absence of an equivalently immature *Edmontosaurus regalis* postorbital in the record hinders further comparisons. As a result, it is impossible to confirm either the presence or absence of this character in *E. regalis*, and hence renders its utility as a diagnostic character of the PCF taxon highly suspect.

1.2.4.1.10 Parietal

The anterior half of the parietal is known (Figure 1.2-5G, H). The interfrontal process of the parietal is mediolaterally narrow and finger-shaped as in *Edmontosaurus* and *Shantungosaurus giganteus* (Xing et al., 2014; Xing et al., 2017). The interfrontal process is much wider in the ventral surface. The dorsal surface of the parietal posterior to the interfrontal process is flat and is bounded by arched ridges that run from the anterolateral processes. The ridges merge posteromedially and are continuous with the

straight sagittal crest. Ventrally, the parietal is concave and forms the posterior part of the cerebral fossa.

1.2.4.1.11 Frontal

The frontal of the PCF hadrosaurine is nearly twice as longer as it is mediolaterally wide, unlike the short frontals of lambeosaurines (Figure 1.2-5I-L). The dorsal surface of the frontal is flat medially and slightly elevated laterally as in *Edmontosaurus annectens*, *Edmontosaurus regalis*, and *Shantungosaurus giganteus* (Xing et al., 2014; Xing et al., 2017). The contact surface for the nasal is limited to being anterior to the socket for posterior process of the prefrontal, as in members of Edmontosaurini other than *Kamuysaurus japonicus* (Kobayashi et al., 2019). The entire posterior margin of the frontal is rugose for articulation with the parietals, suggesting that the frontal is excluded from the supratemporal fenestra. The postorbital suture is aligned nearly parallel to the interfrontal suture. Anterior to the postorbital suture, the frontal largely participates in the dorsal margin of the orbit as other members of Edmontosaurini (Xing et al., 2014). Medially, dorsal plate of the frontal is thin anteriorly and thick posteriorly. Ventrally, the frontal bears three depressions: the olfactory depression, the orbital depression, and the cerebral fossa. The olfactory depression is shallow and

anteroposteriorly elongated. It is separated from the orbital depression by a faint ridge.

The cerebral fossa is the deepest among the three depressions and is wider and deeper posteriorly than anteriorly.

1.2.4.1.12 Pterygoid

The palatine process and the distal half of the dorsal quadrate process are missing (Figure 1.2-6A, B). The lateral surface of the main body of the pterygoid is flat posteriorly and shallowly depressed anteriorly for the ectopterygoid contact as in typical hadrosaurines (Heaton, 1972). The pterygoid bears a deep incision that interlocks the pterygoid process of the maxilla anterior to the ectopterygoid contact surface. Ventrally, the ectopterygoid ramus is anteroposteriorly compressed and bears a spike-like lateral process. The ridge connecting the ectopterygoid ramus and the ventral quadrate process is straight and well-developed ventrally. Medially, the anterior and the posterior buttressing flanges form an angle of 40 - 45 degrees as in *Edmontosaurus regalis* (Heaton, 1972) and meet dorsally at the medial process.

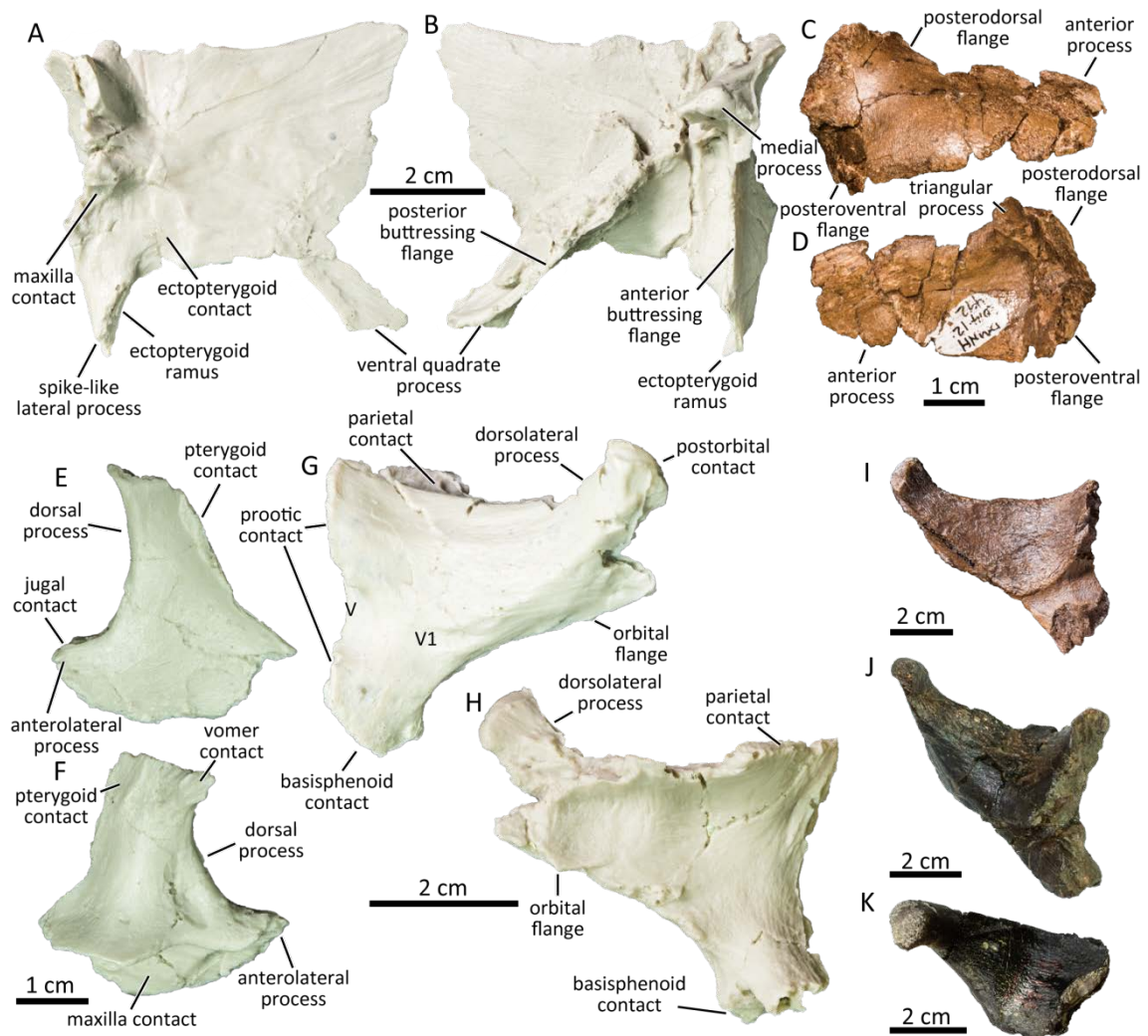


Figure 1.2-6. Cast of left pterygoid (UAMES 4215) in lateral (A) and medial (B) views. Right ectopterygoid (DMNH 2014-12-492) in lateral (C) and medial (D) views. Cast of left palatine (UAMES 4257) in lateral (E) and medial (F) views. Cast of right laterosphenoid of the PCF hadrosaurine (UAMES 4352) in lateral (G) and medial (H) views. Laterosphenoids of *Edmontosaurus annectens* (I; ROM 53507), *Hypacrosaurus stebingeri* (J; USNM 11893), and *Eolambia caroljonesa* (K; CEUM 34366).

1.2.4.1.13 Ectopterygoid

The anterior process of the ectopterygoid is thin and slightly sinuous in lateral view (Figure 1.2-6C, D). The posterodorsal flange and the posteroventral flange flare laterally, forming a crescent shaped posteromedial surface that articulates with the pterygoid. The posterodorsal and the posteroventral flanges of the ectopterygoid are small, resembling the condition in relatively immature *Edmontosaurus annectens* (e.g., ROM 53505). The posteroventral process is recurved ventrally to overlap the posterodorsal surface of the maxilla. Medially, the triangular process, a character present in members of Hadrosaurinae (Heaton, 1972), is located at the junction between the anterior process and the posterodorsal flange. The triangular process articulates with the main body of the pterygoid and the pterygoid process of the maxilla.

1.2.4.1.14 Palatine

The dorsal process of the palatine is robust (Figure 1.2-6E, F), unlike those of lambeosaurines (e.g., CMN 8633). The dorsal process is hook-shaped and is pointed anteriorly. The dorsal process is slightly concave laterally and convex medially. The medial surface of the dorsal hook has a rugose contact for the vomer anteriorly and the

pterygoid contact posteriorly. Ventrally, the contact surface with the maxilla is characterized by a deep anteroposterior groove. The anterolateral process and the jugal contact surface are less developed compared to those of *Edmontosaurus regalis* (Xing et al., 2017).

1.2.4.1.15 Laterosphenoid

The laterosphenoid is a subtriangular bone composed of the dorsolateral process, the orbital flange, and the temporal plate (Figure 1.2-6G, H). The dorsolateral process is short and stout, being less than 70% the length of the temporal plate (68.9% in UAMES 4352 and 57.1% in UAMES 15284) as in *Edmontosaurus* (e.g., ROM 53507; Figure 1.2-6I). All other hadrosauroids besides *Edmontosaurus* have this ratio larger than 90% (Xing et al., 2017) (Figure 1.2-6J, K). The extremely short dorsolateral process of the laterosphenoids of the PCF hadrosaurines demonstrates the strong affinity of these specimens to *Edmontosaurus*. The distal end of the dorsolateral process is oval-shaped with a smooth surface for articulation with the laterosphenoid fossa of the postorbital. The orbital flange is directed medially to contact with the orbitosphenoid. A weak anteroventral ridge separates the orbital flange from the dorsolateral process and the temporal plate. The temporal plate is strongly concave medially and forms the lateral

braincase wall. The posterior margin of the laterosphenoid bears the anterior half of the foramen for the trigeminal nerve (CN V). The wide horizontal groove for the ophthalmic branch (CN V1) extends anteriorly from the foramen for the trigeminal nerve. The region between the anterior margin of the trigeminal nerve and the anteroventral ridge is narrow compared to the region in other hadrosaurines

Brachylophosaurus canadensis (CMN 8893), *Gryposaurus notabilis* (AMNH FARB 5350), *Saurolophus osborni* (AMNH FARB 5221), and *Maiasaura peeblesorum* (ROM 66181), but resembles to the region in *Edmontosaurus annectens* (CMN 8509, ROM 53507, ROM 53508, AMNH FARB 427, AMNH FARB 59786, AMNH FARB 64623) and *Edmontosaurus regalis* (CMN 2288). The passage for the mandibular branch (CN V3) is absent in the available laterosphenoids of the PCF hadrosaurines

1.2.4.1.16 Prootic

The main body of the prootic defines the dorsal, posterior, and ventral margins of the trigeminal foramen (Figure 1.2-7A, B). Posteriorly, the anterodorsal margin of the large fenestra ovalis is unclear in the available specimens. The foramen for the facial nerve (CN VII) pierces the prootic posterior to the trigeminal foramen. The foramen for the facial nerve is contiguous with two narrow grooves that run along the posterior margin

of the prootic. The shorter, less defined groove that runs posterodorsally conducted the hyomandibular branch of the facial nerve and the longer groove that runs anteroventrally accommodates with the palatine branch (Evans, 2010). On the dorsolateral surface of the prootic, the crista otosphenoidalis is more developed than in *Brachylophosaurus canadensis* (CMN 8893) and resembles those of *Edmontosaurus annectens* (CMN 8509) and *Edmontosaurus regalis* (CMN 2289). The lateral surface ventral to the trigeminal foramen is largely excavated for articulation with the alar process of the basisphenoid. The thin posterodorsal process of the prootic contacts the exoccipital medially and the parietal dorsally.

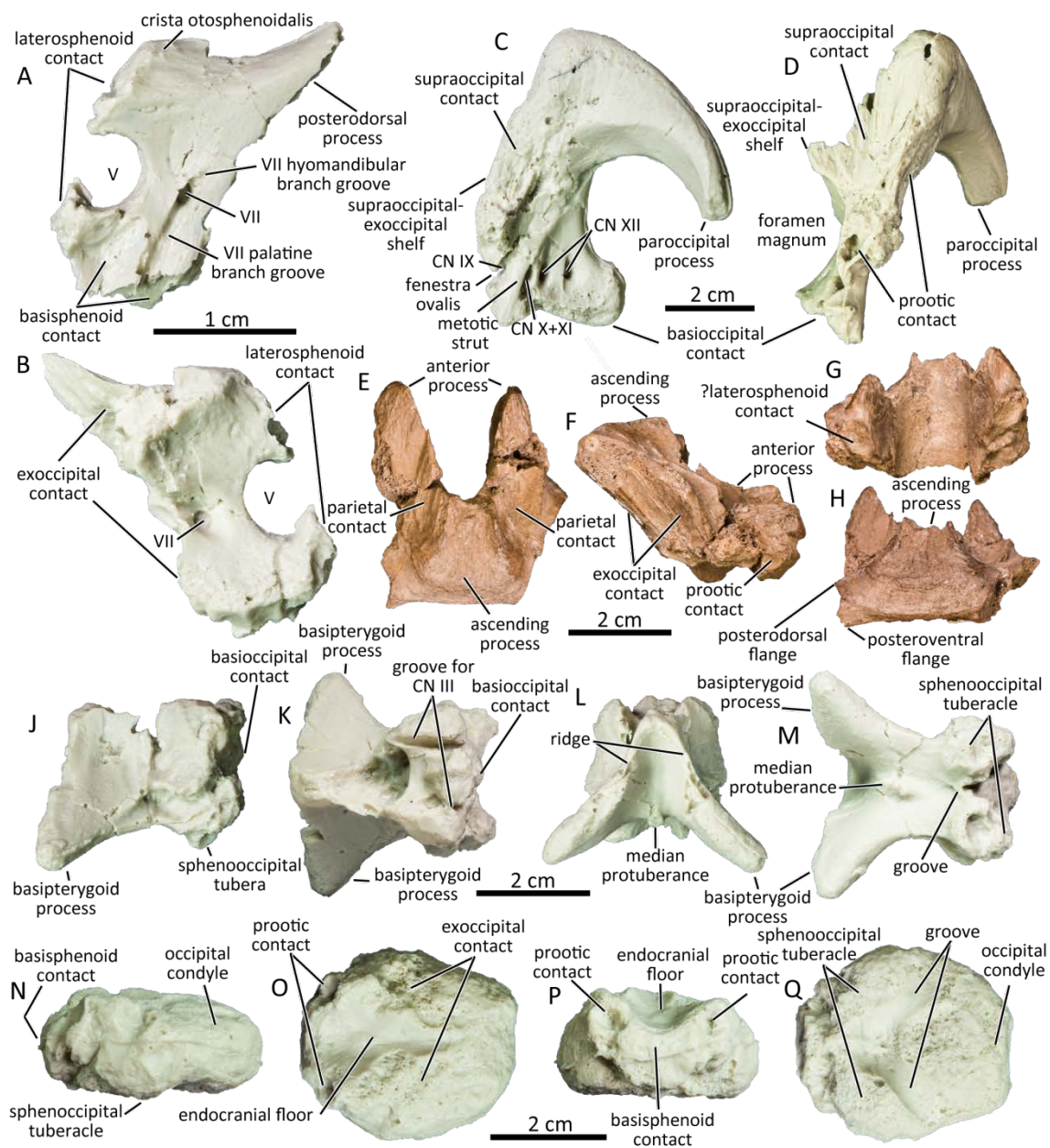


Figure 1.2-7. Cast of left prootic (UAMES 4357) in lateral (A) and medial (B) views.

Cast of left exoccipital (UAMES 4263) in lateral (C) and anterior (D) views.

Supraoccipital (DMNH 22807) in dorsal (E), right lateral (F), anterior (G), and

posterior (H) views. Cast of basisphenoid (UAMES 4301) in left lateral (J), dorsal

(K), anterior (L), and ventral (M) views. Cast of basioccipital (UAMES 34723) in left lateral (N), dorsal (O), anterior (P), and ventral (Q) views.

1.2.4.1.17 Exoccipital–opisthotic complex

No distinguishable suture between the exoccipital and opisthotic is present in the PCF hadrosaurines (Figure 7C, D) in concordance with other immature hadrosaurids (Horner, 1992). Therefore, we refer to exoccipital-opisthotic complex simply as the exoccipital. The right and left exoccipitals contact each other above the foramen magnum and forms the supraoccipital-exoccipital shelf. The supraoccipital-exoccipital shelf is moderately elongated posteriorly unlike in lambeosaurines. The anterior margin of the occipital plate defines the posterior half of the fenestra ovalis and the metotic foramen for the glossopharyngeal nerve (CN IX) adjacent to it (Langston, 1960; Evans et al., 2009). Posterodorsal to the fenestra ovalis, the lateral surface of the exoccipital is rugose where it contacts the prootic. The metotic strut is located posterior to the fenestra ovalis. Posterior to the metotic strut, three foramina pierce the occipital plate. The anterior foramen represents foramen for the vagus nerve (CN X) and the accessory nerve (CN XI) (Langston, 1960; Ostrom, 1961; Evans et al., 2009; Xing et al., 2017). The posterior two large foramina represent the foramen for hypoglossal nerve (CN XII).

The ventral margin of the exoccipital for contact with the basioccipital is slightly sinuous. The condyloid is subtriangular in occipital view as in immature *Edmontosaurus* (Xing et al., 2017). The paroccipital process is directed lateroventrally and gradually tapers to a blunt tip. Unlike in larger specimens of *Edmontosaurus*, the paroccipital process does not curve anteriorly.

1.2.4.1.18 Supraoccipital

Hadrosaurine supraoccipitals lack squamosal bosses and are anteroposteriorly elongated (Figure 1.2-7E-H), unlike in lambeosaurines, including a recently described lambeosaurine supraoccipital from the Liscomb bonebed locality (Takasaki et al., 2019). The dorsolateral surfaces of the supraoccipital are excavated for articulation with the posterolateral processes of the parietals. The excavations are deep in large specimen (UAMES 12727) as in juvenile *Edmontosaurus annectens* (ROM 53494), but shallower in smaller specimens (UAMES 4291, UAMES 21544). The ascending process is wide and low in small specimens and becomes narrower and taller in large specimens. The posterior surface of the ascending process is markedly inclined anteriorly. The anterior surface of the supraoccipital is smooth and defines the posterior surface of the endocranial cavity. The lateroventral surface of the anterior process is triangular and

contacts with the posterodorsal process of the prootic (Horner, 1992). Whether there is contact with laterosphenoid at the anterior end of the supraoccipital as in

Prosaurolophus maximus (Horner, 1992) is unclear in the PCF hadrosaurines.

Posteriorly, the lateroventral surface of the supraoccipital is shallowly grooved for receipt of the exoccipital. The ventral exoccipital contact surface is flat and ornamented with several longitudinal striations. The posterior surface of the supraoccipital is smooth and has a straight ventral margin. The lateral projections for squamosal contact present in *Prosaurolophus maximus* (Horner, 1992) and *Gryposaurus notabilis* (Prieto-Márquez, 2010a) are undeveloped, unlike the ones in lambeosaurine supraoccipitals (Gilmore, 1937; Langston, 1960; Takasaki et al., 2019).

1.2.4.1.19 Basisphenoid–parasphenoid complex

The basisphenoid and the parasphenoid are indistinguishably fused to each other (Figure 1.2-7J-M) as in embryonic lambeosaurines (Horner and Currie, 1994). The basiptyergoid processes of the basisphenoid are lateroventrally directed, diverging from each other in slightly greater than 100 degrees. The angle resembles other hadrosaurines including *Brachylophosaurus canadensis* (CMN 8893), *Edmontosaurus annectens* (AMNH FARB 5046, CMN 8509), *Edmontosaurus regalis* (Xing et al., 2017), and

Prosaurolophus maximus (Horner, 1992), but is unlike lambeosaurines which are acutely angled. Each basipterygoid process is triangular-shaped and terminates in a blunt point. The anterior margin of the basipterygoid process gradually narrows anterodorsally to form a narrow ridge ventral to the proximal base of the cultriform process, which is not preserved in the available specimens. The median protuberance is present in between the basipterygoid processes. The transverse ridge is absent in the PCF basisphenoid UAMES 34723 as in derived lambeosaurines (e.g., *Hypacrosaurus altispinus*), suggesting UAMES 34723 could possibly belong to a member of Lambeosaurinae. This feature could also be individually variable, as in some *Edmontosaurus annectens* (present in ROM 59786, absent in AMNH FARB 00427). The posterior surface for articulation with the basioccipital is extremely rugose. The bulbous posterior region of the basisphenoid forms anterior region of the paired sphenoccipital tubera, which is less developed than those of other hadrosaurines such as *Brachylophosaurus canadensis* (CMN 8893) and *Edmontosaurus annectens* (CMN 8509). The sphenoccipital tubera are likely to develop ontogenetically as they fuse with the basioccipital. The sphenoccipital tubera are separated ventrally by a shallow groove at the midline. Two parallel grooves run anteroposteriorly along the dorsal surface of the sphenoccipital tubera for the oculomotor nerve (CN III) (Horner, 1992).

1.2.4.1.20 Basioccipital

The basioccipital is a semi-circular bone that is slightly longer anteroposteriorly than mediolaterally wide (Figure 1.2-7N-Q). It is of almost constant dorsoventral thickness. Its dorsal surface bears a wide groove, the ventral surface of the endocranial cavity. The dorsal surface lateral to the endocranial cavity are rugose for contact with the exoccipital. The deep depressions located at the anterolateral corners of the basioccipitals are likely the prootic contacts as in *Prosaurolophus maximus* (Horner, 1992). On the ventral surface of the anterior half of the basioccipital, two prominent protuberances represent the posterior region of the sphenoccipital tubera. Two posterolaterally directed grooves are located between the tubera and the occipital condyle. Posteriorly, the occipital condyle is positioned on the same level with the rest of the basioccipital, as in the isolated basioccipital of an immature *Edmontosaurus annectens* (ROM 53538) but is less angled than in larger *Edmontosaurus annectens* (e.g., ROM 64623).

1.2.4.1.21 Predentary

The right half of the anterior ramus of the prementary is preserved (Figure 1.2-8A-C). The anterior edge of the prementary is denticulated with four trapezoidal projections and one subtriangular midline projection. The denticles are slightly separated from each other. Unlike the spoon shaped prementary of *Kritosaurus* sp.(Nabavizadeh, 2015), the prementary of the PCF hadrosaurine is flat and shovel shaped with nearly right angled anterolateral corner as in *Edmontosaurus regalis* (CMN 2289). The dorsal process is not preserved. The bi-lobed ventral process at the anteroventral margin of the prementary is split at its base and is much less developed compared to the prementary of larger *Edmontosaurus annectens* (e.g., USNM 3814).

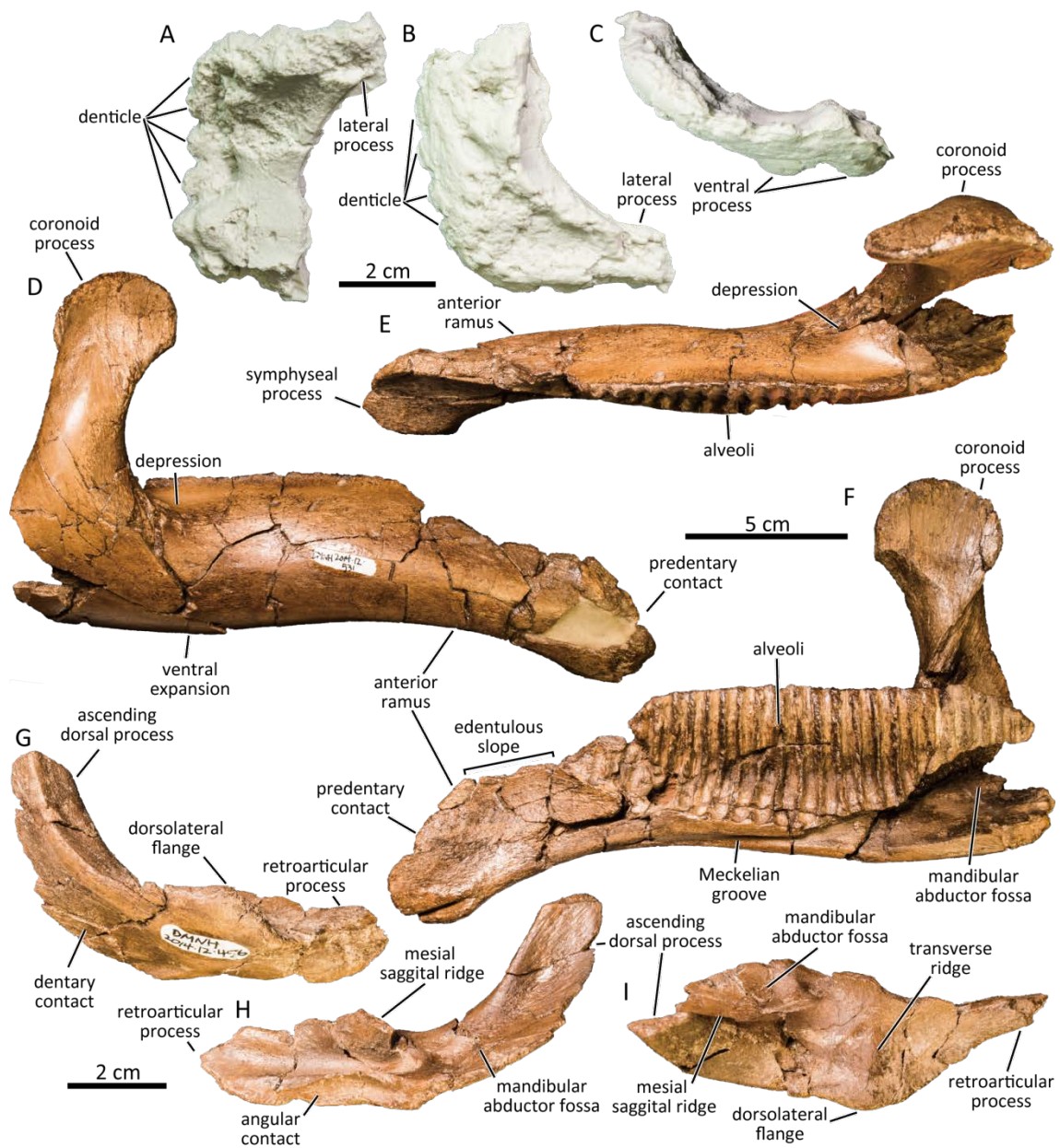


Figure 1.2-8. Cast of a partial prementary (UAMES 4437) in dorsal (A), ventral (B), and anterior (C) views. Right dentary (DMNH 2014-12-531) in lateral (D), dorsal (E), and medial (F) views. Left surangular (DMNH 2014-12-456) in lateral (G), medial (H), and dorsal (I) views.

1.2.4.1.22 Dentary

Multiple nearly complete dentaries are preserved (Figure 1.2-8D-F). The main body of the dentary is approximately four times as long as its dorsoventral height. The bowed expansion ventral to the coronoid process and the ventral deflection of the anterior ramus gives the dentary a slightly sinuous outline in lateral view. The ventral deflection of the anterior ramus forms an angle of about 23 degrees relative to the horizontal level. The degree of deflection is much stronger than in large *Edmontosaurus annectens* and *Edmontosaurus regalis*, but resembles immature specimens of *Edmontosaurus annectens* (e.g., ROM 53529, ROM 53530). The symphyseal process of the dentary is gently curved lingually and is generally 1.5 times as wide as the minimum width of the dentary immediately posterior to it, unlike in lambeosaurines which have wider symphyseal process (Prieto-Márquez and Wagner, 2009). The anterodorsal margin of the predentary contact is convex and descends gradually unlike in *Brachylophosaurus canadensis* (CMN 8893) which is strongly concave. The lengths of the proximal edentulous margins vary from 12% to 17% of the length from the anterior end of the alveoli to the posterior margin of the coronoid process in the available specimens. The ratios are lower than those of larger but still immature individuals of *Edmontosaurus annectens* (e.g., ROM 53529, AMNH FARB 5730) as Mori et al. (2016) demonstrated,

but are expected to increase during ontogeny (Wosik et al., 2019). The dentary tooth row bears no less than 1.5 alveoli per cm, which are separated by thin and sheet-like septa. The alveoli are narrow and aligned perpendicular to the dorsal alveolar margin of the dentary in the posterior half, whereas they are slightly inclined posteriorly in the anterior half of the dental battery. The posterior most alveolus is positioned posterior to the caudal margin of the coronoid process. The coronoid process is slightly inclined anteriorly in various angles between 75-85 degrees. Its apex is subcircular, lacking the sharp projection present in *Brachylophosaurus canadensis* (CMN 8893) and some specimens of *Edmontosaurus annectens* (AMNH FARB 5730, ROM 53530). The dorsal apex of the coronoid process is more developed anteriorly than posteriorly as in immature *Edmontosaurus annectens* (e.g., ROM 53529, ROM 53530). The base of the coronoid process is widely separated from the dentary dental battery by a deep depression unlike in nestling *Edmontosaurus annectens* (Wosik et al., 2019). The Meckelian groove runs anteroposteriorly along the ventral margin of the dentary, fading out at the ventral deflection of the anterior ramus.

1.2.4.1.23 Surangular

The surangular is composed of the mediolaterally thin ascending dorsal process, dorsoventrally compressed dorsolateral flange, and mediolaterally compressed retroarticular process (Figure 1.2-8G-I). The lateroventral surface of the ascending process is shallowly excavated for articulation with the dentary. The articulation surface continues to the anterior half of the ventral surface. The ascending dorsal process is excavated dorsomedially to form the mandibular abductor fossa. The dorsolateral flange is ventrally twisted as is typical in hadrosaurines. The dorsolateral flange is asymmetrical with sharp lateral apex in some specimens (e.g., DMNH 2014-12-490,) as in juvenile *Edmontosaurus annectens* (Wosik et al., 2019), although the flange in several specimens exhibit more “adult form” (e.g., DMNH 2014-12-456). A faint transverse ridge is present at the level of the lateral apex of the dorsolateral flange. The transverse ridge defines the anterior margin of the quadrate glenoid, while the mesial sagittal ridge defines the medial margin of the quadrate glenoid. Posteriorly, the retroarticular process is widely angled from the anterior half of the surangular. The retroarticular process is slightly recurved dorsally and has a gently arcuate posteroventral margin as in other hadrosaurines.

1.2.4.1.24 Maxillary teeth

DMNH 22718, an associated maxilla and dentaries which show hadrosaurine features, demonstrate that a maximum of two maxillary teeth are functional per alveolus (Figure 1.2-9A, B). One prominent primary ridge and a maximum of one faint secondary ridge exist on the labial enameled surface of the maxillary teeth. The primary ridge is positioned at the midline of the tooth crown and is nearly straight in all of the teeth. The maxillary tooth crowns bear small marginal denticles apically. The anterior dental battery consist maximum of two replacement teeth per alveoli in addition to a functional tooth in DMNH 22718. The newer replacement teeth overlap the prior one mediodorsally.

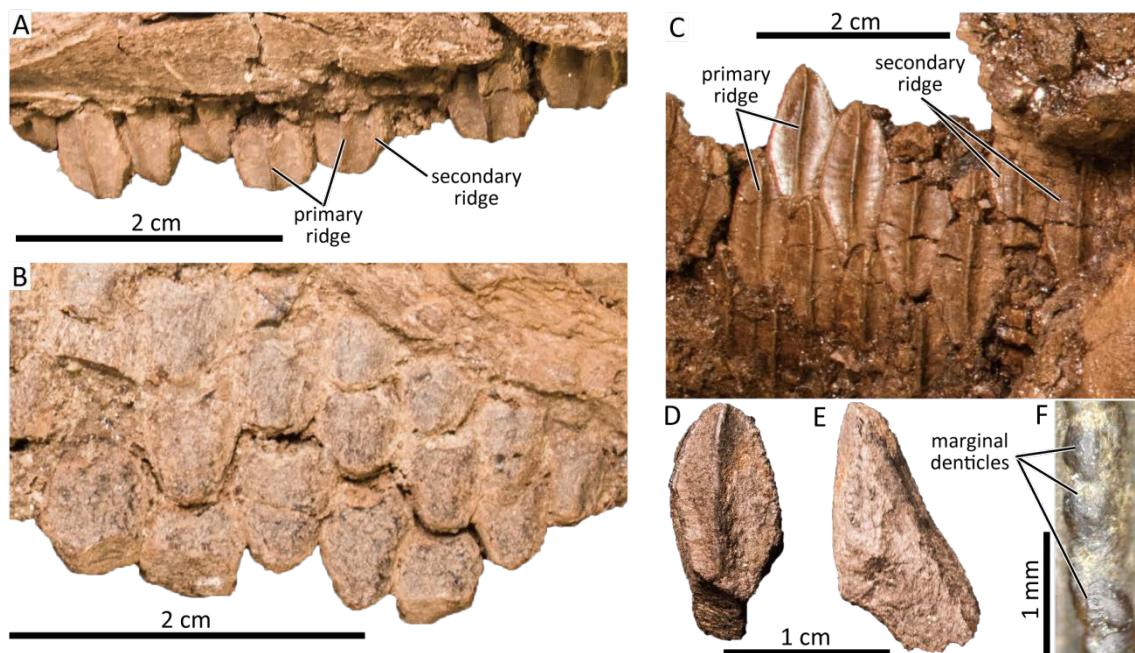


Figure 1.2-9. Maxillary teeth (DMNH 22718) in labial (A) and lingual (B) views.

Dentary teeth (DMNH 22851) in lingual view (C). Isolated dentary tooth (DMNH 22338) in lingual (D) and mesial (E) views. Close-up of the marginal denticles of the dentary tooth (F).

1.2.4.1.25 Dentary teeth

DMNH 22851 demonstrates at least two functional teeth are present in each of the dentary's anterior tooth rows (Figure 1.2-9C-F). A maximum of three teeth are present in an alveolus of the anterior region of a right dentary. The tooth crowns are diamond-shaped and the available specimens show variant height/width ratios ranging from 2.04-2.33. The tooth crowns bear one primary ridge and a secondary ridge in some

teeth on its lingual enameled surface as in some *Edmontosaurus regalis* (present in a few teeth of CMN 2289) and lambeosaurines. The primary ridge of the dentary teeth is positioned at the midline of the tooth crown and is slightly sinuous. Small marginal denticles are present on both margins of the apical half of the dentary teeth. Each denticle consist one small knob-like protrusion (Figure 1.2-9F) as in *Edmontosaurus* (Prieto-Márquez and Wagner, 2009; Prieto-Márquez, 2010c) and *Kamuysaurus japonicus* (Kobayashi et al., 2019). The root of the isolated dentary teeth are angled more than 140 ° from the tooth crown.

1.2.4.2 Phylogenetic analysis

As explained earlier, two cladistic, phylogenetic analyses were conducted in this study. The first phylogenetic analysis resulted in 384 equally most parsimonious trees (MPTs) of 1181 steps, each with a consistency index of 0.440 and a retention index of 0.848. The topology of the strict consensus tree is similar to that of Kobayashi et al. (Kobayashi et al., 2019) other than the inclusion of the PCF hadrosaurine (Figure 1.2-10A). The present phylogenetic analysis recovers the PCF hadrosaurine as a member of Edmontosaurini and demonstrates that the PCF hadrosaurine is in an unresolved polytomy with *Edmontosaurus annectens* and *Edmontosaurus regalis*.

Among the four synapomorphies recovered for Edmontosaurini, the PCF hadrosaurine shares marginal denticle of dentary teeth composed of one rounded knob, the thick lip-like structure of the premaxillary oral rim, and the absence of the specialized development of the nasal. The PCF hadrosaurine exhibits two features among the six synapomorphies of the clade of *Shantungosaurus giganteus* and *Edmontosaurus*: a finger-shaped anterior process of the parietal, and a weakly deflected occipital condyle. Although the PCF hadrosaurine does not share three synapomorphies of the clade (number of dental alveoli more than 45, jugal process of the postorbital wide anteroposteriorly, and short squamosal process of the postorbital) which are ontogenetically variable (Takasaki et al., 2017), the present analysis infers that these features may appear in mature individuals of the PCF hadrosaurine. The PCF hadrosaurine and *Edmontosaurus* share the feature of a great reduction of the laterosphenoid postorbital process. Among the other six synapomorphies of the unresolved PCF taxon and *Edmontosaurus* clade, the present analysis indicates that the short edentulous slope of the dentary, the moderate anterior inclination of the coronoid process, the absence of the deep pocket of the postorbital of the PCF hadrosaurines are all characters that are ontogenetically variable in their expression. Their presence or

absence cannot be objectively assessed or considered phylogenetically informative in the absence of equivalent ontogenetic exemplars of each of the pertinent taxa.

The present analysis recovered a combination of three characters potentially unique to the PCF hadrosaurine: dentary teeth with a secondary ridge, basisphenoid without a ventral transverse ridge, and an anteroposteriorly elongated maxilla. The presence of a secondary ridge on the dentary teeth is shared with lambeosaurines and several hadrosaurines (*Kritosaurus navajovius*, *Lophorhothon atopus*, and some *Edmontosaurus regalis* specimens such as CMN 2289). The absence of the ventral transverse ridge could be intraspecific variation since expression of this structure is also present in *Edmontosaurus annectens* (ROM 59786). Additionally, since a definite lambeosaurine is now recognized in the Prince Creek Formation (Takasaki et al., 2019), the feature shared with derived lambeosaurines *Corythosaurus* and *Hypacrosaurus* may simply indicate that this element belongs to a member of Lambeosaurinae, although it also has a hadrosaurine feature (see description section). The anteroposteriorly long maxilla is unique to the PCF hadrosaurine and *Laiyangosaurus youngi* (Zhang et al., 2017).

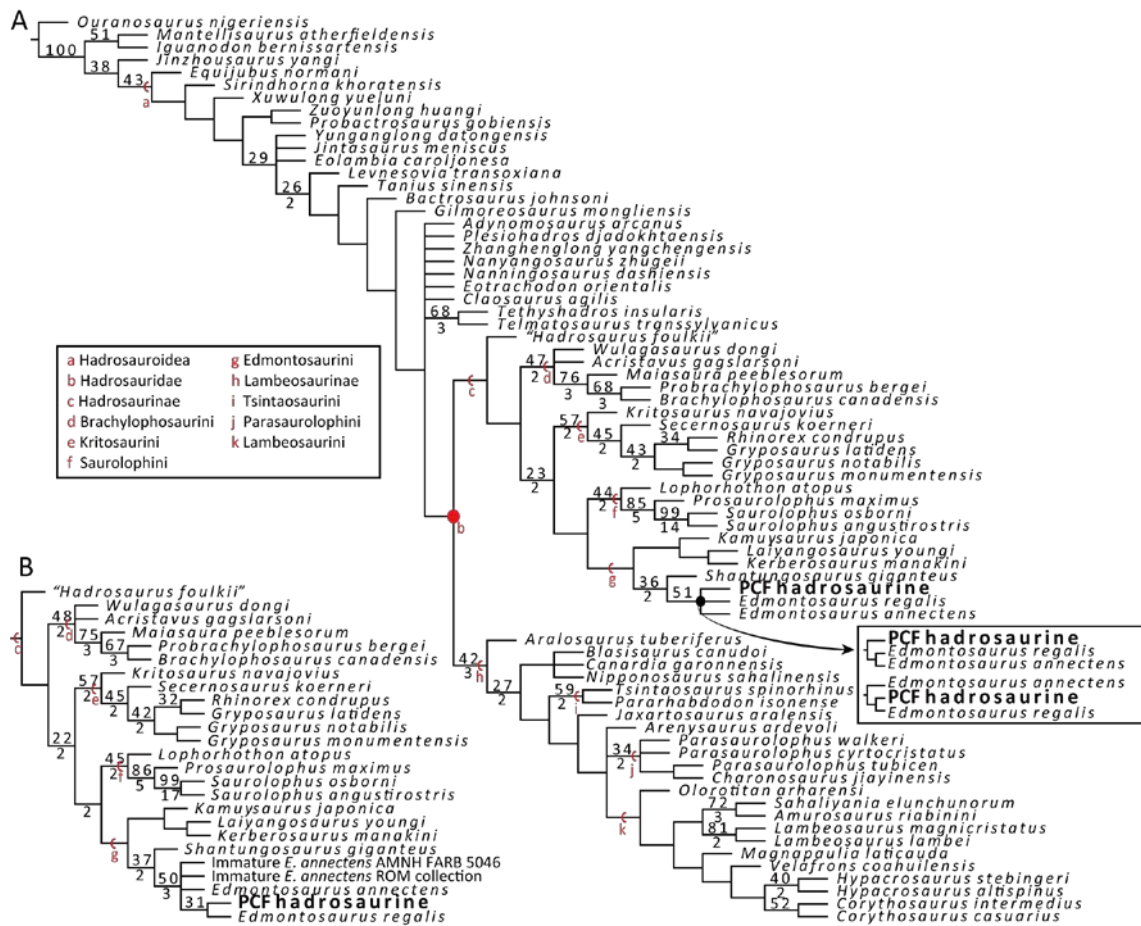


Figure 1.2- 10. (A) Strict consensus tree of the MPTs obtained from the first phylogenetic analysis. Numbers above each branch represent bootstrap values and those below the branch represent Bremer decay values. Bootstrap values below 20 and Bremer decay values below 1 are not shown. The polytomy clade of the PCF hadrosaurine + *Edmontosaurus annectens* + *Edmontosaurus regalis* is formed by the two conflicting topologies shown in the small box. (B) Strict consensus tree of MPTs obtained from the second phylogenetic analysis which incorporated two

**juvenile *Edmontosaurus annectens* OTUs, showing relationship within
Hadrosaurinae.**

The polytomy of the PCF hadrosaurine + *Edmontosaurus* is a result of two conflicting topologies recovered in the 384 MPTs. In one topology, the PCF hadrosaurine is positioned as the sister taxon the *Edmontosaurus* clade (*Edmontosaurus annectens* + *Edmontosaurus regalis*) because the two species of *Edmontosaurus* are united by a single character to the exclusion of the PCF taxon: a straight primary ridge on the dentary tooth crown (slightly curved or sinuous in the PCF specimens). In the second recovered topology, the PCF hadrosaurine is the sister-taxon to *Edmontosaurus regalis* to the exclusion of *Edmontosaurus annectens*. The two are united in this scenario by the shared presence of a horizontal shelf on the postorbital process of the jugal.

The second cladistic analysis incorporated two immature *Edmontosaurus annectens* as separate OTUs. This analysis recovered 384 MPTs of 1157 steps (CI = 0.438, RI = 0.846). The strict consensus tree of the analysis recovered the PCF hadrosaurine as the sister-taxon to *Edmontosaurus regalis* (Figure 1.2-10B), a relationship supported by two characters: the acutely angled and slightly projected posteroventral margin of the

quadratojugal and the anteroposteriorly short prenasal region of the premaxilla. The PCF hadrosaurine + *Edmontosaurus regalis* clade was part of a larger clade that included *Edmontosaurus annectens* and the two immature *Edmontosaurus annectens* OTUs. However, there was a polytomy between the three *Edmontosaurus annectens* OTUs and the *Edmontosaurus regalis* + PCF hadrosaurine clade. It is important to note that the immature *Edmontosaurus annectens* OTUs and mature *Edmontosaurus annectens* OTU did not form a monophyletic clade with each other to the exclusion of *Edmontosaurus regalis* and the PCF hadrosaurine.

1.2.5 Discussion

1.2.5.1 Taxonomic status of “*Ugrunaaluk kuukpikensis*”

Mori et al. (2016) proposed eight diagnostic characters for *Ugrunaaluk kuukpikensis*. Among the eight characters, three were proposed to differentiate *Ugrunaaluk kuukpikensis* from *Edmontosaurus*, four from *Edmontosaurus annectens*, and one from *Edmontosaurus regalis*. However, the three characters proposed to differentiate *Ugrunaaluk* from *Edmontosaurus* are problematic. The first character, a posterolaterally projected circumnasal ridge without a premaxillary vestibular promontory, is present in at least one immature *Edmontosaurus annectens* specimen (ROM 53525). The second,

an anteriorly inclined posterior margin of the anterior process of the jugal, is also present in immature specimens of *Edmontosaurus annectens* (e.g., DMNH EPV.95220) and the degree of inclination is highly variable intraspecifically in large, assumedly mature specimens as well (Figure 1.2-4C-D). While the third character, absence of the deep postorbital fossa, is markedly different from immature specimens of *Edmontosaurus annectens*, the character cannot be legitimately assessed in *Edmontosaurus regalis* because no specimens of equivalent size and ontogenetic stage as the PCF specimens have been reported for *Edmontosaurus regalis*. Therefore, the wide and shallow postorbital fossa in the Arctic PCF hadrosaurine that Mori et al. (2016) considered diagnostic could potentially be present in immature individuals of *Edmontosaurus regalis*. This is pertinent because the postorbital fossa in large *Edmontosaurus regalis* specimens is markedly wider than that of comparably mature *Edmontosaurus annectens*. Based on these shortcomings, the characters Mori et al. (2016) proposed are insufficient to diagnose and differentiate *Ugrunaaluk* from *Edmontosaurus*. Additionally, all of the eight characters are widely seen among members of Hadrosaurinae, and are thus inappropriate to diagnose *Ugrunaaluk* as a distinct taxon.

The unresolved clade of *Edmontosaurus* + the PCF hadrosaurine recovered in the present phylogenetic analysis (Figure 1.2-10A) indicates that the PCF hadrosaurine should be considered a member of the *Edmontosaurus* clade. The subsequent analysis that included two immature *Edmontosaurus annectens* OTUs provided additional support for deeply nesting the PCF hadrosaurine within the *Edmontosaurus* clade, potentially more closely related to *Edmontosaurus regalis* than *Edmontosaurus annectens* (Figure 1.2-10B). In fact, one of the synapomorphies of the PCF hadrosaurine + *Edmontosaurus* clade (presence of a short postorbital process of the laterosphenoid) was already one of the diagnostic characters of *Edmontosaurus* in prior analyses (Xing et al., 2014; Xing et al., 2017). Given the relationships recovered here that show the PCF taxon is a member of the *Edmontosaurus* clade, the absence of any unequivocally diagnostic characters differentiating the PCF taxon from *Edmontosaurus*, and the presence of at least one diagnostic character of *Edmontosaurus* present in the Alaskan material, the name “*Ugrunaaluk*” is invalid, and the PCF hadrosaurine is assigned to *Edmontosaurus*.

At the same time, the PCF *Edmontosaurus* exhibits some differences from *Edmontosaurus annectens* and *Edmontosaurus regalis* as previously documented (Mori et al., 2016; Xing et al., 2017; Wosik et al., 2019). The most significant difference is the

relatively anteroposteriorly elongated maxilla in the PCF *Edmontosaurus*. The maxilla is expected to elongate through ontogeny along with overall cranial elongation (Horner and Currie, 1994; Campione and Evans, 2011; Prieto-Márquez, 2011), and the height-length ratio of the maxilla in Edmontosaurini shows negative allometry (Figure 1.2-2C), evidence that the elongated maxilla of the PCF *Edmontosaurus* is not a result of the relative immaturity of the specimens feature. Taxonomic significance of other features that may be different from *Edmontosaurus annectens* and *Edmontosaurus regalis* is ambiguous. The anteroposteriorly elongated lacrimal in the small Alaskan specimens differs from that of adult *Edmontosaurus regalis*, but this could be a size and ontogeny dependent feature and the lack of ontogenetically equivalent specimens of *Edmontosaurus regalis* means we are currently unable to test the possibility. The large lateral exposure of the quadratojugal suggested by Mori et al. (2016) may also differ from the condition in *E. regalis*, but it is important to note that quadratojugal morphology is known to be variable intraspecifically (see description), thus it seems unlikely to be a taxonomically valid character. The absence of the transverse ridge between basiptyergoid processes of the basisphenoid and the presence of the secondary ridge of the dentary teeth are recovered as unique to the PCF *Edmontosaurus* in the present phylogenetic analysis, but taxonomic importance of these characters are

questionable due to their intraspecific variations and the multitaxic nature of PCF hadrosaurids (see description).

Therefore, the elongated maxilla of the PCF *Edmontosaurus* is the only feature that may be reasonably different from the other members of *Edmontosaurus* (Table 1.2-1). However, this feature might prove inadequate to diagnose the taxon since an anteroposteriorly elongated maxilla is also present in another member of the Edmontosaurini, *Laiyangosaurus youngi* (Zhang et al., 2017). For the reasons listed above, the validity of the species “*kuukpikensis*” is left as questionable and unresolved. Therefore, we agree with Mori et al. (2016) as well as the subsequent works by Xing et al. (2017) and Wosik et al. (2019) that adult material is critical for determining the finer-scale taxonomy of this hadrosaur. We advocate for the more conservative approach and recommend the PCF hadrosaur be referred to *Edmontosaurus* sp. until further discoveries of more mature individuals from the Prince Creek Formation and/or comparably immature *Edmontosaurus annectens* and *Edmontosaurus regalis* allow comparison of anatomy of individuals of all three taxa from the same ontogenetic stages.

Table 1.2-1. Comparisons among *Edmontosaurus*.

	PCF <i>Edmontosaurus</i>	<i>E. annectens</i>	<i>E. regalis</i>	Ontogenetic variation	Intraspecific variation	Lambeosaurine possibility	Taxonomic validity
Possibly different from <i>E. annectens</i> and <i>E. regalis</i>							
Height/length ratio of maxilla	<0.34	>0.37	0.39	Ratio get smaller	Present	Absent	Possible
Possibly different from <i>E. annectens</i> and <i>E. regalis</i>, but cannot be tested							
Lacrimal shape	Anteroposteriorly elongated, wedge-shaped	Robust, blunt anterior end	Robust, blunt anterior end	?	?	Unlikely	Dubious
Bi-lobed ventral process of the prementary	Short	Long	Long	?	?	?	Dubious
Ventral transverse ridge between the basipterygoid processes of the basisphenoid	Absent	Present	Present	?	Present	Possible	Dubious
Secondary ridge of dentary teeth	Present	Absent	Absent	?	Present	Absent	Dubious

1.2.5.2 Influence of latitudinal habitat difference on hadrosaurine evolution

The reattribution of the PCF hadrosaurine to *Edmontosaurus* highlights a seemingly great latitudinal distribution for this taxon from northern Colorado (approximately 41° N) (Carpenter and Young, 2002; Weishampel et al., 2004) to northernmost Alaska (approximately 70° N). However, in the modern world there are at least two genera of mammalian vertebrates that have ranges of comparable latitudinal magnitude, the wolf (*Canis lupus*) and the wild sheep of North America (*Ovis* sp.). Thus the latitudinal range seen in the fossil record for *Edmontosaurus* is within reason, though deserved of elaboration.

The significant morphological similarities within the genus *Edmontosaurus* are also demonstrated with the small phylogenetic morphospace (Figure 1.2-11) and the morphological partial disparity (Table 1.2-2). The partial disparity/OTU of *Edmontosaurus* (3.40%) is well within the range in Hadrosaurinae (2.28% – 6.72%). In

fact, the value is even lower than the hadrosaurine average (4.41%), further suggesting that the latitudinal habitat differences did not increase morphological disparity of *Edmontosaurus*. It is also interesting to note that *Gryposaurus*, a genus with moderate latitudinal distribution from southern Utah (approximately 38° N) (Gates and Sampson, 2007) to southern Alberta (approximately 51° N) (Lambe, 1914), also have a partial disparity/OTU only slightly larger than the average (4.50%). Furthermore, while *Saurolophus* is known from the lower latitudes of both North America and Asia (Brown, 1912; Rozhdestvensky, 1952) and is expected to have a “ghost distribution” in the Arctic (Xing et al., 2017; Kobayashi et al., 2019), its partial disparity/OTU occupies only 4.79% of the total. The low or insignificant partial disparity values of these three groups show that not only in *Edmontosaurus* but overall hadrosaurine morphological disparity is not strongly affected by their latitudinal geographic distribution. Small morphological disparities despite of large latitudinal distribution may be related with the relatively low latitudinal temperature gradient during the latest Cretaceous compared to present day (Amiot et al., 2004), which might not require much morphological adaptations for latitudinal distributions.

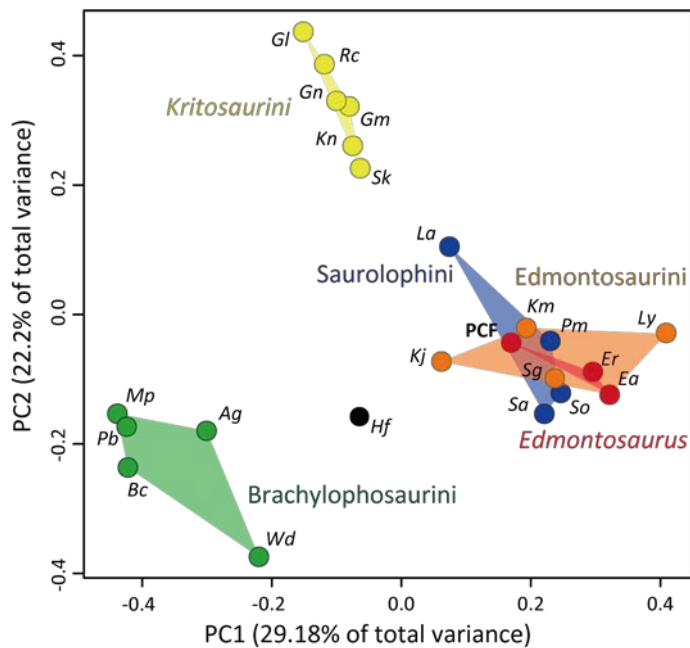


Figure 1.2-11. Morphospace of hadrosaurines recovered from the principal coordinate analysis using the phylogenetic cranial characters. Abbreviations: Ag: *Acristavus gagslarsoni*, Bc: *Brachylophosaurus canadensis*, Ea: *Edmontosaurus annectens*, Er: *Edmontosaurus regalis*, Gl: *Gryposaurus latidens*, Gm: *Gryposaurus monumentensis*, Gn: *Gryposaurus notabilis*, Hf: *Hadrosaurus fouldii*, Kj: *Kamuysaurus japonicus*, Km: *Kerberosaurus manakini*, Kn: *Kritosaurus navajovius*, La: *Lophorhothon atopus*, Ly: *Laiyangosaurus youngi*, Mp: *Maiasaura peeblesorum*, Pb: *Probrachylophosaurus bergei*, Pm: *Prosaurolophus maximus*, Rc: *Rhinorex condrupus*, Sa: *Saurolophus angustirostris*, Sg: *Shantungosaurus giganteus*, Sk: *Secernosaurus koernerii*, So: *Saurolophus osborni*, Wd: *Wulagasaurus dongi*.

Table 1.2-2. Partial disparities of hadrosaurines.

	Genus	PD/Genus	PD/Genus (%)	PD/OTU (%)
Edmontosaurini	<i>Edmontosaurus</i>	0.0224	10.21	3.40
	<i>Kamuysaurus</i>	0.0102	4.64	4.64
	<i>Kerberosaurus</i>	0.0050	2.28	2.28
	<i>Laiyangosaurus</i>	0.0126	5.76	5.76
	<i>Shantungosaurus</i>	0.0086	3.93	3.93
Kritosaurini	<i>Kritosaurus</i>	0.0077	3.50	3.50
	<i>Gryposaurus</i>	0.0296	13.50	4.50
	<i>Rhinorex</i>	0.0095	4.35	4.35
	<i>Secernosaurus</i>	0.0059	2.71	2.71
Saurolophini	<i>Saurolophus</i>	0.0210	9.56	4.78
	<i>Lophorhothon</i>	0.0062	2.84	2.84
	<i>Prosaurolophus</i>	0.0063	2.85	2.85
Brachylophosaurini	<i>Acristavus</i>	0.0097	4.43	4.43
	<i>Brachylophosaurus</i>	0.0129	5.88	5.88
	<i>Maiasaura</i>	0.0131	5.97	5.97
	<i>Probrachylophosaurus</i>	0.0138	6.28	6.28
	<i>Wulagasaurus</i>	0.0147	6.72	6.72
	<i>Hadrosaurus</i>	0.0101	4.60	4.60

In the present-day Arctic, five genera (six species) of large-bodied herbivorous mammals are present (Barrio et al., 2016). Among the arctic large-bodied herbivores, only *Ovis dalli* and *Ovis canadensis*, genus highly adapted for high mountain range inhabitances, have large latitudinal distribution. They together range from north of the Brooks Range to the Baja California Peninsula (Festa-Bianchet, 2008a, b), which is slightly larger than the range of *Edmontosaurus*. Although *Edmontosaurus* are unlikely to inhabit in high mountain ranges, the large latitudinal distribution of *Ovis* may suggest

adaptation toward a certain environment that connects the mid- and high- latitudes have importance in wide distribution of large herbivores. If this was the case, the large latitudinal distribution of *Edmontosaurus* and *Saurolophus*, and the smaller distribution of *Gryposaurus* may originate from differences in the environments these genera preferred. However, further understandings in hadrosaurine behaviors and on the environments of the Late Cretaceous Arctic, as well as more complete fossil records are mandatory to test the role of adaptations toward a certain environment on differences in latitudinal distributions among hadrosaurines genera.

1.2.6 Acknowledgements

Various field crews helped collect the specimens housed at the Perot Museum of Nature and Science, particularly Paul McCarthy (University of Alaska), Kent Newman (formerly Southern Methodist University), Thomas Adams (Witte Museum), Chris Strganac (Perot Museum of Nature and Science) and David Norton (University of Alaska). In addition I thank Karen Morton (Perot Museum of Nature and Science) for the collections care of the PCF *Edmontosaurus* materials, and the various staff and volunteers at the Perot Museum of Nature and Science who helped prepare these specimens. Collection visits were established with kind help of Amanda Millhouse

(Smithsonian National Museum of Natural History), Brandon Stanley (Royal Tyrrell Museum of Palaeontology), Carl Mehling (American Museum of Natural History), Kevin Seymour (Royal Ontario Museum), Kristen MacKenzie (Denver Museum of Nature and Science), Margaret Currie (Canadian Museum of Nature), and Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, China). Discussions and comments of Mateusz Wosik, Jordan Mallon, and Junki Yoshida greatly helped improve this manuscript.

CHAPTER 2: ENVIRONMENTAL ADAPTATIONS OF HADROSAURID FORAGING

FEATURES

Abstract

Hadrosaurids are one of the most widespread as well as one of the most abundant herbivorous dinosaurs during the Late Cretaceous. Their global success is often attributed to the highly efficient oral processing system of hadrosaurids. At the same time, recent findings suggest that environmental factors such as Laramide orogeny and coastal habitat might have enhanced hadrosaurid diversifications. The present study tests if hadrosaurids experienced any morphological adaptations for different living environments, focusing on two foraging ecomorphologies: beak shape and limb proportions. Geometric morphometric analyses on hadrosaurid beak shapes and the limb lengths comparisons suggest that beak shapes and limb proportions show both taxonomic signal and environmental differences. Hadrosaurids recovered from terrestrial habitats tend to have anteriorly wider, posteriorly narrower, and dorsoventrally deeper beak as well as larger forelimb/hind-limb ratio and longer proximal limbs than those from marginal habitats. The wide beak and relatively short hind-limb with long proximal element of the terrestrial habitat hadrosaurids are likely to

be beneficial in mass food consumption and small foraging ranges whereas the pointed beak and relatively long hind-limb with short proximal elements of the marginal habitat hadrosaurids are likely to be beneficial in selective food consumption and long foraging ranges. The morphological and functional differences may be a result of environmental adaptations, therefore supporting the previous hypothesis that environmental adaptations enhanced hadrosaurid diversifications. The high evolutionary rates of the phylogenetic characters related to beak shape and locomotor ecology during Santonian – early Campanian further present the possibility that the rise in sea level triggered modifications on beak and limb morphologies. The present work therefore suggest that in addition to the highly efficient oral processing ability, adaptations on foraging strategies in different environments might had been an important factor for the great success of hadrosaurids during the late Cretaceous.

2.1 Introduction

Hadrosaurids are one of the most successful herbivorous dinosaurs during the Late Cretaceous that established a cosmopolitan distribution (Bonaparte et al., 1984; Weishampel et al., 2004; Lund and Gates, 2006; Prieto-Márquez, 2010b). They are also one of the most abundant dinosaurs in multiple localities (Ram et al., 2015; Cullen et al., 2016; Mori et al., 2016; Nakajima et al., 2018), occupying a large part of local biomass (Farlow, 1976; Brett-Surman, 1979). The hadrosaurid success is often attributed to their highly efficient oral processing system formed of the specialized dentitions with complex grinding surface (Edmund, 1957; Erickson et al., 2012; LeBlanc et al., 2016; Bramble et al., 2017b) and cranial kinetics (Weishampel, 1984; Cuthbertson et al., 2012). In addition, social behaviors of hadrosaurids, enhanced by their unique supracranial crests (Weishampel, 1981; Evans, 2006; Evans et al., 2009; Bell et al., 2014), are also likely to have contributed to their cosmopolitan success. In fact, both the complex feeding apparatus and the unique supracranial crest are considered as the innovative features that are linked to the hadrosaurid diversification (Strickson et al., 2016; Stubbs et al., 2019)

In addition to these well-known features, Gates et al. (2012) proposed that hadrosaurid diversity increased in association with Laramide orogeny. Kobayashi et al.

(2019) also suggested that seaside inhabitation of ancestral hadrosaurids contributed to their early diversification. Both of these works suggest the possibility that changes or differences in living environment contributed to hadrosaurid diversification. In fact, multiple hadrosaurid bonebeds show abundances of either of the two hadrosaurid subfamilies, Hadrosaurinae or Lambeosaurinae (Fiorillo, 1989; Fiorillo, 1991; Bolotsky and Godefroit, 2004; Godefroit et al., 2004b; Godefroit et al., 2008; Godefroit et al., 2012a; Godefroit et al., 2012b; Takasaki et al., 2019). The dominations suggest that more than two hadrosaurid taxa rarely lived in the same time and the space, and infer the possibility that hadrosaurids living in different environments had different morphological and functional adaptations.

Here we test if hadrosaurids experienced any morphological adaptations for different living environments. Since the highly effective oral processing system of hadrosaurids is likely to allow them to digest most things they consume, this study focuses on morphological features related to foraging (approaching phase and capturing phase), which precedes the digestion (processing phase) (Montuelle and Kane, 2019).

Approaching largely depends on locomotor ecology (Ford et al., 2005), whereas the types of plants they eat (capturing) are known to correspond to shapes of the oral rim in present day herbivorous mammals (Gordon and Illius, 1988; Janis and Ehrhardt, 1988;

Spencer, 1995). Therefore, this study tests if locomotor performances and beak shapes of hadrosaurids differ between the environments they lived. The present work not only provides the first comprehensive comparisons of hadrosaurid foraging strategy but also expected to shed light on impacts of surrounding environments in the success of Hadrosauridae.

2.2 Material and method

Hadrosaurid beaks are three-dimensionally reconstructed using software Metashape version 1.5.4.8835. In order to maximize the sample size and minimize the effect of post-mortem deformation, better preserved side of the beak was utilized for the analyses. The final dataset includes 28 models (Data S2-1). The models are scaled prior to the analyses. Three-dimensional geometric morphometrics were performed with 2 fixed landmarks, one at the premaxilla-maxilla contact and the other at the anterior end of the beak, and 18 sliding semi-landmarks (Figure 2-1A). The coordinate data are superimposed using generalized Procrustes analysis and then subject to principal component analysis to reduce the dimensionality. The digitization and the analyses are performed using R package geomorph version 3.1.2 (Adams et al., 2019). Allometry of the beak shape was evaluated by standardized major axis (SMA) regression analysis

using R package smatr version 3.4.8 (Warton et al., 2012). Skull length, quadrate length, and centroid size of the model were used as the predictor variables (Data S2-1).

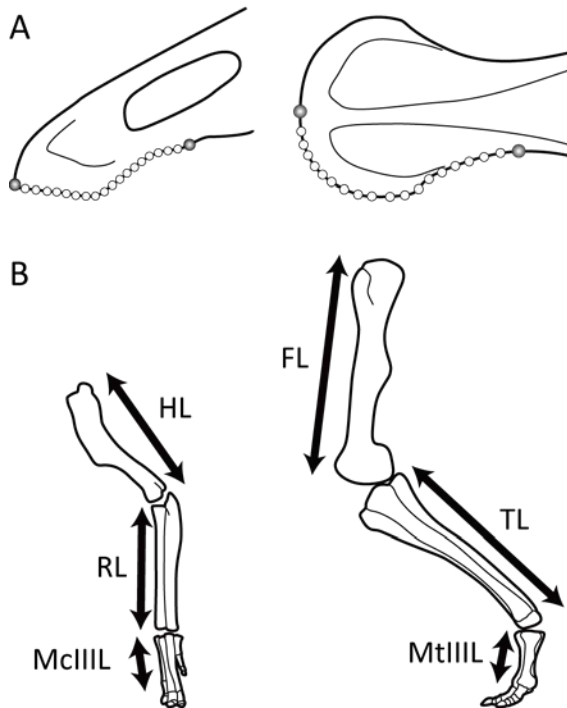


Figure 2 - 1. (A) Landmarks (grey points) and semi-landmarks (blank points) used for the beak geometric morphometric analysis. (B) The hadrosaurid appendicular elements measured herein.

Lengths of the forelimb segments (humerus, radius, and metacarpal III) and hind-limb segments (femur, tibia, and metatarsal III) are obtained from literatures (Brown, 1913; Brown, 1916; Parks, 1920; Gilmore, 1924; Sternberg, 1935; Lull and Wright, 1942; Rozhdestvensky, 1957; Rozhdestvensky, 1968; Maryńska and Osmólska,

1984; Brett-Surman, 1989; Prieto-Márquez, 2001; Prieto-Márquez et al., 2006; Mallon et al., 2013; Prieto-Márquez, 2014; Campione, 2015; Bertozzo et al., 2017; Bramble et al., 2017a; Kobayashi et al., 2019) and direct observations (Figure 2-1B, Data S2-2). To maximize the sample size, missing segment lengths are estimated following (Mallon et al., 2013). The final dataset includes 27 individuals with estimated measurements and 18 without estimates. All analyses on limb segments are conducted on datasets with and without estimated values. Principal component analysis is conducted on the specimens with measurements of all 6 segments to reduce the dimensionality. Segment lengths are normalized by geometric mean (GM) of each individual prior to the principal component analysis.

Each sample is assigned to either “terrestrial” or “marginal” environmental categories compiled in Kobayashi et al. (2019). Species known from both terrestrial and marginal environments are categorized as “marginal” group in this study, owing to small sample size of species known only from marginal environment. While this categorization does not allow complete distinction of the two environments, it is expected to reduce the risk of false detection of morphological differences.

Environmental and taxonomic effect on beak shape and relative limb lengths are tested

by Student's t-test with environmental categories and subfamily as the groups compared.

To further investigate how the foraging features evolved within Hadrosauridae, evolutionary rates of the characters related to beak morphology, pectoral girdle + forelimb, and pelvic girdle + hind-limb are examined using maximum-likelihood methods using R package Claddis version 0.3.4 (Lloyd, 2016), based on the morphological data matrix and the phylogenetic hypothesis of Takasaki et al. (under prep). Both the branch partition test and time bins partition test are conducted. Ten time bins are used to examine hadrosaurid macroevolutionary patterns: Early Cretaceous, Cenomanian, Turonian, Coniacian, Santonian, Early Campanian, Middle Campanian, Late Campanian, Early Maastrichtian, and Late Maastrichtian. Subdivisions of Campanian and Maastrichtian are utilized here since taxonomic diversity of hadrosaurids is highest during this duration. Taxa with character completeness less than 50% are pruned prior to the analyses since missing data leads to extreme results (Lloyd, 2016). Removal of the taxa with low character completeness also provides much better resolution to the phylogenetic tree. The remaining polytomies are randomly resolved prior to the branch partition analyses. For the branch partition analysis, 100 time-calibrated phylogenetic trees which incorporate the ranges of the time of first and

last appearances are constructed based on the equal method (Brusatte et al., 2008) using the R package paleotree (Bapst, 2012). Therefore, the 100 trees for the branch partition analysis have the same topology of different branch lengths. For the time bin partition analyses, 100 time-calibrated trees with randomly resolved polytomies are prepared in order to incorporate the topology uncertainties in evolutionary rates. Therefore, the 100 trees for the time bin partition analysis all have different branch lengths and could have different topologies. Following previous studies (Lloyd et al., 2012; Wang and Lloyd, 2016), this study mainly focuses on whether the evolutionary rates are significantly high or low, although the absolute values are also provided. All analyses are performed on R version 3.6.2 (R Core Team, 2019).

2.3 Results

2.3.1 Beak shape

The principal component analysis showed that more than 90% of the hadrosaurid beak shape variance is explained by the first five PC axes. The first axis (57.5%) is size-related, with small specimens having higher PC scores (Table S2-1). Student's t-test demonstrates that PC1 is reflecting taxonomic differences, as well as environmental differences, although the latter is less supported (Figure 2-2A, Table

S2-2). The high PC1 score represented by Lambeosaurinae and the terrestrial group is characterized by anterior elongation, strong posterior constriction, and the anteroventrally positioned lateral apex of the beak (Figure 2-2D). The lateral apex of the beak is acutely angled in the specimens with high PC1 values whereas it is gently curved in the specimens with lower PC1 values. None of the other PC axes showed signs of size, taxonomic, or environmental effects (Table S2-1, S2-2).

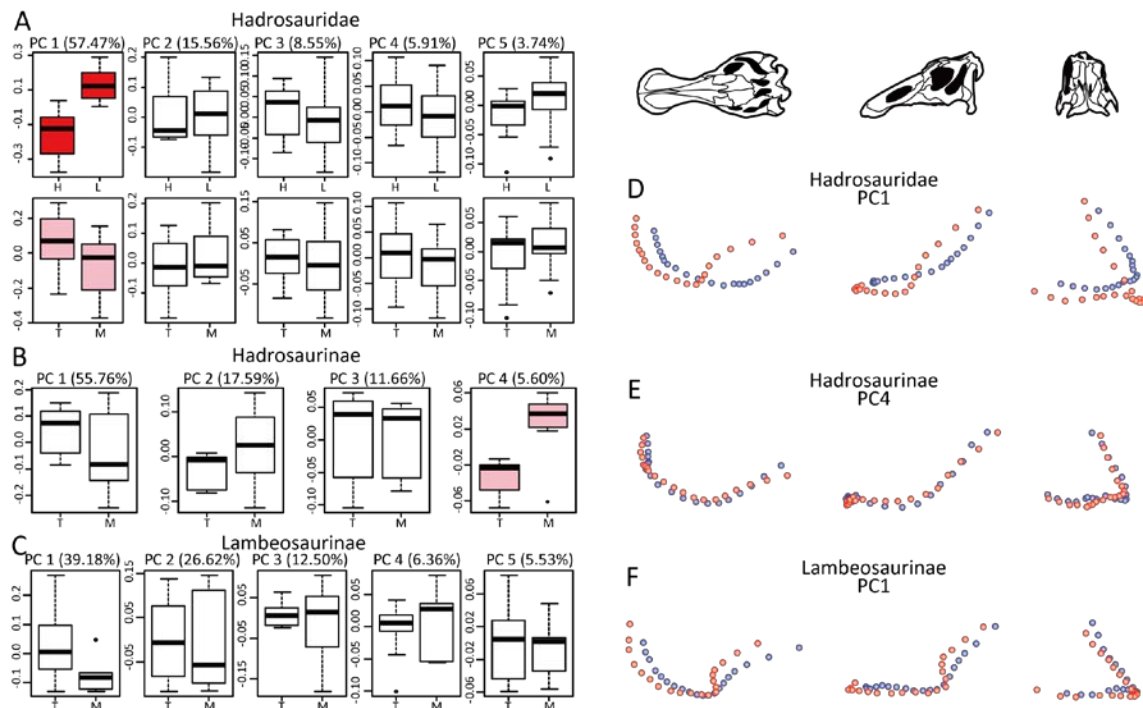


Figure 2 - 2. Boxplots comparing PC scores within Hadrosauridae (A), Hadrosaurinae (B), and Lambeosaurinae (C). Colored boxes represent statistically significant differences (red, $p < 0.001$; pink, $p < 0.05$). Beak shape variations along

(D) PC1 of Hadrosauridae, (E) PC4 of Hadrosaurinae, and (F) PC1 of Lambeosaurinae in dorsal, left lateral, and anterior views from left to right. Red and blue points represent high and low PC scores, respectively. Abbreviations: H, Hadrosaurinae; L, Lambeosaurinae; M, marginal; T, terrestrial.

More than 90% of hadrosaurine beak variance is explained by the first four PC axes. None of the first four PC axes are size-dependent (Table S2-1). Student's t-test demonstrates that PC4 is differentiated by environment category (Table S2-2), being higher in the marginal group than in the terrestrial group (Figure 2-2B). The high PC4 values within hadrosaurines represent anteriorly rounded narrow beak that gently narrows posteriorly, whereas the low PC4 values represent anteriorly truncated wide beak with undulated oral rim that strongly converges posteriorly (Figure 2-2E).

The first five PC axes explain more than 90% of the lambeosaurine beak shape variations. PC1 is correlated with quadrate length (Table S2-1). PC1 values of lambeosaurines are generally high in the terrestrial group than in the marginal group, although not statistically supported (Figure 2-2C, Table S2-2). High PC1 values represent anteriorly wide beak with abrupt posterior constriction, while the beak is

anteriorly pointed and the posterior constriction is gentle in the low PC1 values (Figure 2-2F).

2.3.2 Limb lengths

Results of the analysis with and without estimated values are generally concordant with each other. The present results show absence of taxonomic differences in relative lengths of hadrosaurid forelimb and hind-limb. On the other hand, the measurements clearly demonstrate long forelimbs and short hind-limbs in the terrestrial group than in the marginal group (Figure 2-3, Table S2-3). Although the difference is statistically significant only under analysis without estimated measurements, the analysis with estimates also shows the same trend. The environmental difference is emphasized more strongly in lambeosaurines than in hadrosaurines.

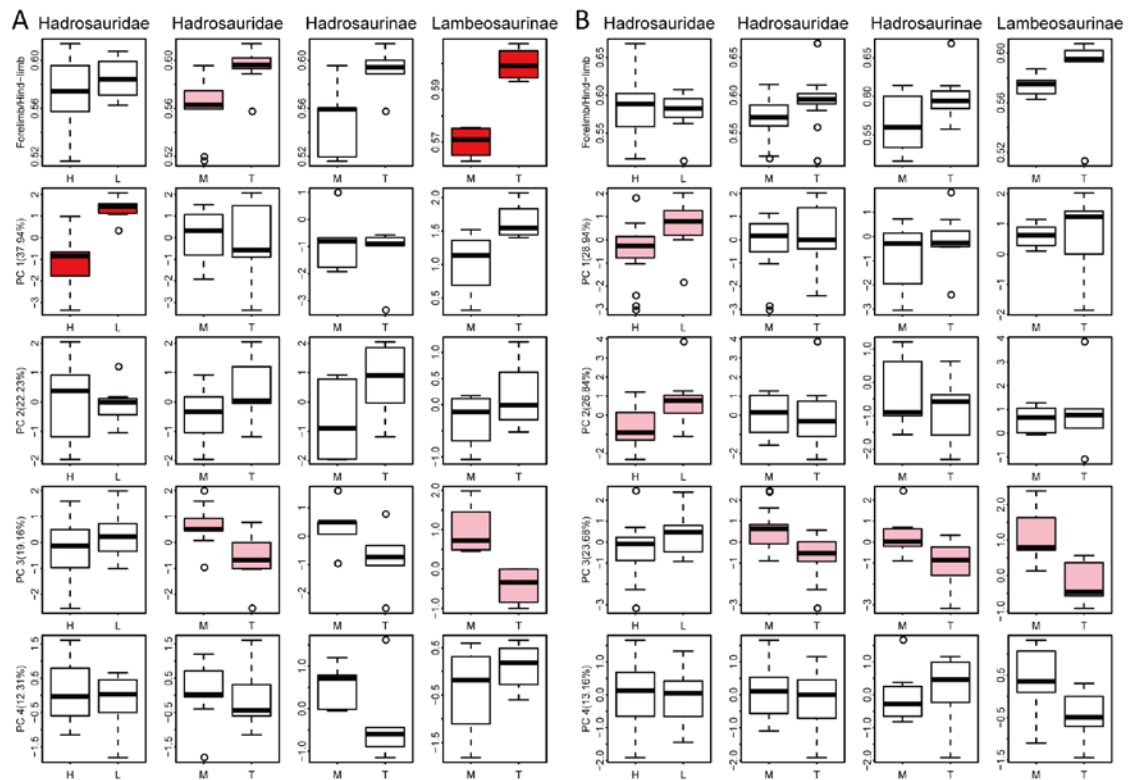


Figure 2 - 3. Boxplots comparing fore- hind-limb ratio and PC scores of the normalized hadrosaurid limb elements without estimated measurements (A) and with estimated measurements (B).

The principal component analysis demonstrates more than 90% of the limb length variations are explained in the first four axes. Factor loadings under the analyses with and without estimates are generally concordant to each other, although the axes may be reversed (Table S2-4). High PC1 represents short humerus + femur relative to radius + metatarsal. It strongly reflects taxonomic difference, being much higher in

hadrosaurines than in lambeosaurines (Figure 2-3). PC2 represents long/short metacarpal relative to tibia and metatarsal. Lambeosaurines are suggested to have short metacarpal relative to metatarsal in the analysis with estimates, although the result is not recovered under the other analysis. PC3, which represents short humerus relative to metacarpal and tibia, is significantly higher in the marginal group than in the terrestrial group, while no taxonomic difference was detected. PC4 represents long/short tibia relative to metatarsal. No significant difference on PC4 was detected taxonomically or environmentally.

2.3.3 Evolutionary rate

The branch partition test on beak shape phylogenetic characters suggest high evolutionary rates on the branches leading to ancestral nodes of Hadrosaurinae and Lambeosaurinae, although they are unlikely to be statistically significant (Figure 2-4A). On the other hand, branch evolutionary rates of the pectoral girdle and forelimb characters are suggested to be significantly high in the branches leading to Hadrosauridae, Hadrosaurinae, and Lambeosaurinae (Figure 2-4B). The branch evolutionary rates of the pelvic girdle and the hind-limbs are high in the branch leading to the clade of *Tethyshadros insularis* + Hadrosauridae and several basal branches of

Hadrosauridae, although only the ones leading to Brachylophosaurini and Kritosaurini are likely to be statistically significant (Figure 2-4C). The evolutionary rate of the terminal branch leading to *Charonosaurus jiyinensis* is suggested to be significantly low.

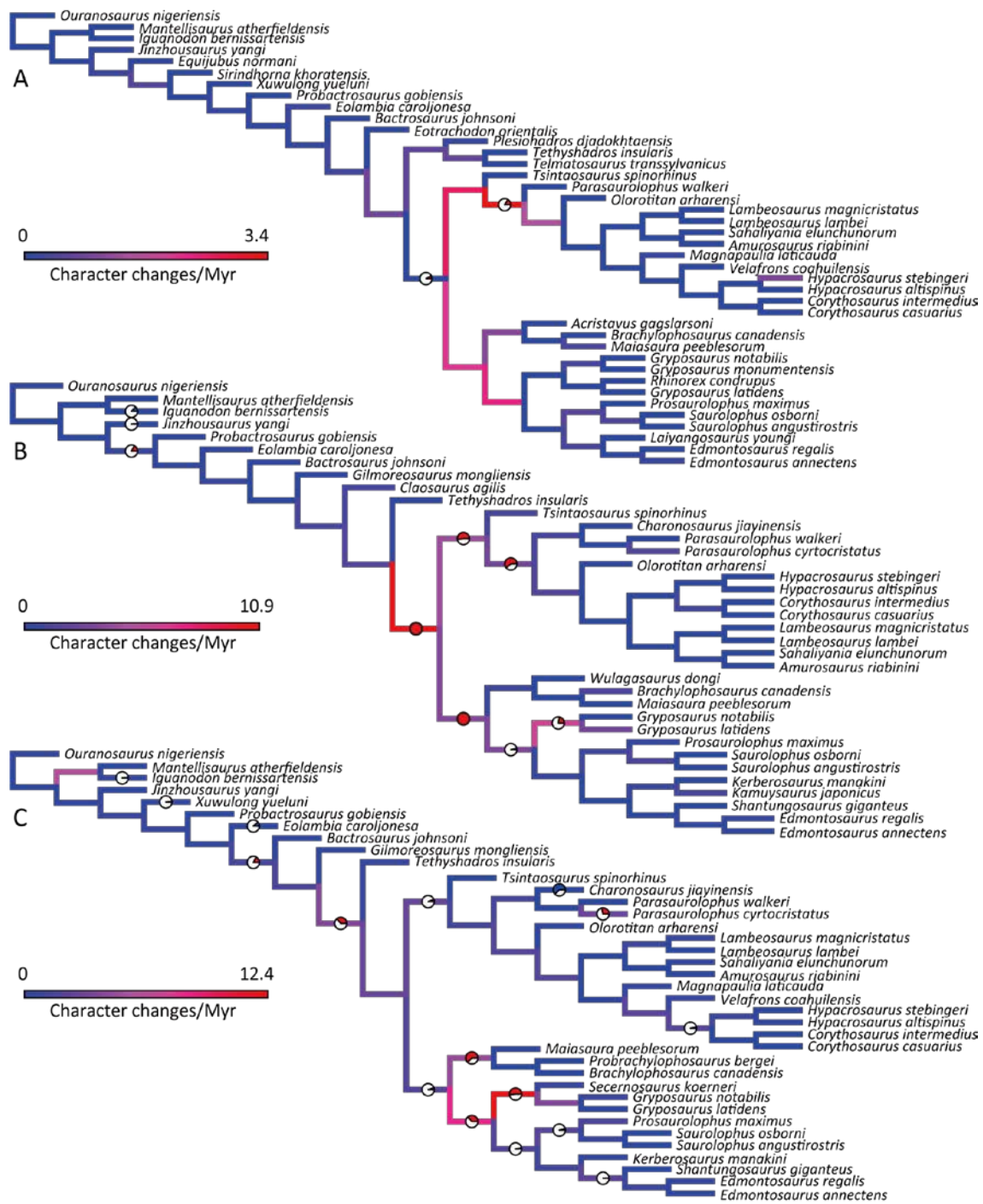


Figure 2 - 4. Evolutionary rates of hadrosauroid beak (A), forelimb (B), and hind-limb (C) phylogenetic characters. The branch colors represent the median evolutionary rate value of the 100 iterations performed. Pie-charts represent the

ratio of significantly fast (red), insignificant (white), and significantly slow (blue) branch evolutionary rates in the 100 iterations performed.

The time bins partition test shows that the characters related to beak shapes had significantly higher evolutionary rates during the early Campanian than in the other time bins (Figure 2-5A). The median evolutionary rates are slightly high during Coniacian and Santonian, but not significant. The evolutionary rates of the pectoral girdle + forelimb characters are significantly high during Santonian and early Campanian (Figure 2-5B). Its peak at the Santonian is preceding the peaks in beak and pelvic girdle + hind-limbs at the early Campanian. The median evolutionary rate is also high during the Coniacian, although it may not be statistically significant. The pectoral girdle + forelimb evolutionary rates are significantly low in the Early Cretaceous time bin and possibly in the early Maastrichtian. Evolutionary rate of the pelvic girdle + hind-limb is significantly high in the early Campanian time bin (Figure 2-5C). The median evolutionary rates are also moderately high from Turonian to Santonian, although they are unlikely to be statistically significant. The evolutionary rates are likely to be significantly low during the early Maastrichtian and possibly low in the Early Cretaceous, late Campanian, and late Maastrichtian time bins.

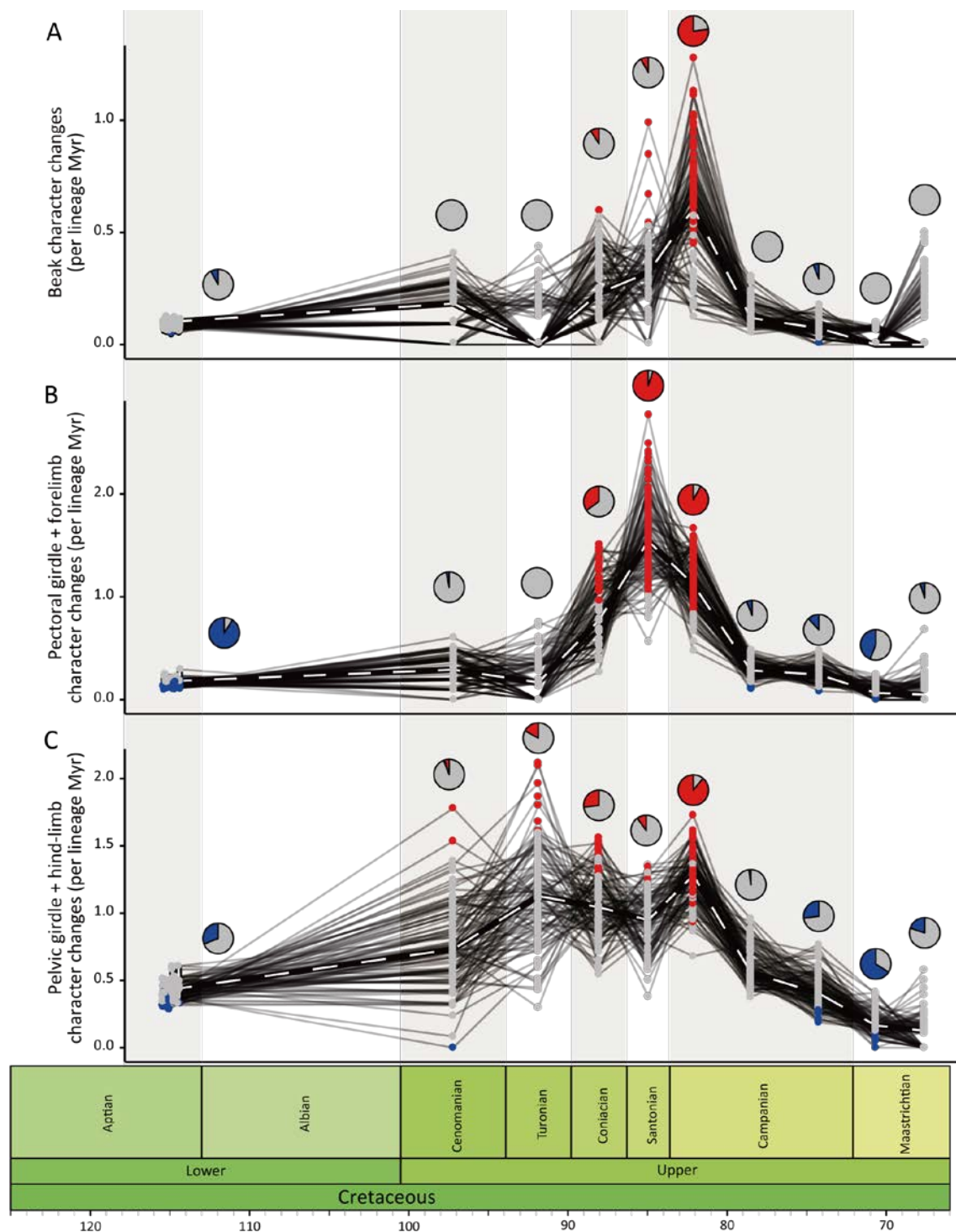


Figure 2 - 5. Evolutionary rates of hadrosauroid beak (A), forelimb (B), and hind-limb (C) phylogenetic characters. The branch colors represent the median

evolutionary rate value of the 100 iterations performed. Pie-charts represent the ratio of significantly fast (red), insignificant (white), and significantly slow (blue) branch evolutionary rates in the 100 iterations performed.

2.4 Discussion

The beak shape analyses show that hadrosaurid beak shape is primarily differentiated by their subfamilies. The result differs from the previous work on two-dimensional geometric morphometrics performed on the Dinosaur Park Formation (DPF) ornithischian dinosaurs (Mallon and Anderson, 2014). While the conflict may occur from differences in the datasets between the present and the prior works, it may also emphasize importance of three-dimensional geometry to capture morphological features. The present beak shape analyses show that Hadrosaurinae have anteriorly narrower, posteriorly wider, and dorsoventrally shallower beak than Lambeosaurinae have. The results are consistent with the trend in skull ecomorphology of DPF hadrosaurids (Mallon and Anderson, 2013). In addition to the differences between the subfamilies, the present analyses recovered considerable degree of differences among the environment groups (Table 2-1). Interestingly, the terrestrial group share beaks that are anteriorly wide or truncated, posteriorly convergent, and dorsoventrally deep with

anteroventrally positioned lateral apex. On the other hand, the beaks of the marginal group are anteriorly narrow or pointed, posteriorly wide and gently convergent, and dorsoventrally shallow with rounded lateral apex. It should also be noted that the hadrosaurid beak shape variation is suggested to be ontogenetically and/or allometrically variable.

Table 2 - 1. Summary of hadrosaurid foraging ecomorphology differences by environments

	Terrestrial	Marginal
Beak anterior oral margin		
Hadrosauridae	Wide and/or truncated	Narrow and/or pointed
Hadrosaurinae	Wide and/or truncated	Narrow and/or pointed
Lambeosaurinae	Wide and/or truncated	Narrow and/or pointed
Beak posterior constriction		
Hadrosauridae	Strongly convergent posteriorly	Weak, subconstantly wide
Hadrosaurinae	Strongly convergent posteriorly	Weak, subconstantly wide
Lambeosaurinae	Strongly convergent posteriorly	Weak, subconstantly wide
Beak lateroventral margin		
Hadrosauridae	Deep, positioned anteroventrally	Shallow, positioned posterodorsally
Hadrosaurinae	Deep, positioned anteroventrally	Shallow, positioned posterodorsally
Lambeosaurinae	Insignificant	Insignificant
Forelimb/hind-limb ratio		
Hadrosauridae	Large	Small
Hadrosaurinae	Large	Small
Lambeosaurinae	Large	Small
Humerus and tibia		
Hadrosauridae	Long humerus, short tibia	Short humerus, long tibia
Hadrosaurinae	Insignificant	Insignificant
Lambeosaurinae	Insignificant	Insignificant

The taxonomic, environmental, and ontogenetic/allometric differences in beak morphology are expected to reflect functional differences. The anteriorly wide beak and the strong posterior constriction (equivalent with narrow palatal width) common in Lambeosaurinae and the terrestrial group is likely to favor less selection on the food they consume, as suggested in modern and extinct mammals (Gordon and Illius, 1988; Janis and Ehrhardt, 1988; Solounias and Moelleken, 1993; Spencer, 1995).

Lambeosaurinae and the terrestrial group is also inferred to have low feeding heights from their wide (Janis, 1995; Arsenault and Owen-Smith, 2008) and ventrally deep beak below the occlusal plane (Janis, 1995; Spencer, 1995; Mendoza et al., 2002).

Conversely, the relatively narrow, anteriorly pointed beak of Hadrosaurinae and the marginal group is likely to allow them selective consumption. The allometric shift from anteriorly wide beak to anteriorly pointed beak may represent a shift from mass feeding to relatively selective feeding.

The analyses on the limb lengths show that the relative lengths of the proximal and the distal limb segments are primarily differentiated by subfamilies (PC1, longer proximal segments in hadrosaurines than in lambeosaurines) as suggested in phylogenetic characters (Norman, 2002). On the other hand, relative lengths of the fore- and the hind-limbs are found to be differentiated primarily by environments instead of

subfamilies (longer hind-limbs in marginal group than in terrestrial group). The result is consistent with the long humerus and short tibia in the terrestrial group than in the marginal group (PC3).

Although hadrosaurid postcranial features have rarely been described in detail with a few exceptions (Maryńska and Osmólska, 1984; Prieto-Marquez, 2007; Cuthbertson and Holmes, 2010; Campione, 2015), the present analyses demonstrate considerable degree of taxonomic and environmental variations in limb proportions. The limb proportion differences are likely to contribute to differences in locomotor ecology.

Since dinosaurs have fully erect gait (Barker, 1971), LiMb model (Pontzer, 2005, 2007) developed to predict locomotor costs of terrestrial mammals should be applicable, although exact metabolic costs cannot be calculated due to the limitations of extinct animals. The long proximal and short distal limb segments of Hadrosaurinae are likely to provide them larger stability during locomotion (Kilbourne and Hoffman, 2013), while the increase in the radius of gyration cause higher cost of locomotion. Conversely, the relatively short proximal and long distal segments of the Lambeosaurinae provide them lower cost of locomotion in exchange of stability during locomotion.

The long forelimb and short hind-limb of the terrestrial group would lower the center of mass, therefore increase their body balance upon locomotion. The distally

positioned limb center of mass, due to the relatively short distal segments, is also expected to provide the terrestrial group greater stability during locomotion (Kilbourne and Hoffman, 2013). Additionally, the short distal limbs of the terrestrial group might had been advantageous in sloped terrains (Higgins and Ruff, 2011). At the same time, their short hind-limb results in shorter stride lengths thus slower speed at a given frequency. Also, cost of locomotion is expected to be high in the terrestrial group due to their long and heavy forelimb, short hind-limb, and short proximal limbs (long radius of gyration) (Pontzer, 2005, 2007).

On the other hand, the long hind-limb of the marginal group provides them long stride lengths thus faster speed at a given frequency. Their relatively long distal segments further benefit them for fast locomotion, although these features are likely to provide less stability (Kilbourne and Hoffman, 2013). While the long hind-limb induces heavy hind-limb relative to the body mass, the merits of elongated tibia and resultant relative shortening of the radius of gyration is likely to surpass the disadvantage (Pontzer, 2005, 2007). The demerits of larger angle of excursion caused by short forelimb are also likely to be overcome by the decreased forelimb mass and the shorter radius of gyration (Pontzer, 2005, 2007). The differences in the fore- and hind-limb configurations therefore suggest that metabolic costs of locomotion within

Hadrosauridae differ among subfamilies and living environments, even though hadrosaurs are generally slow moving (Lockley et al., 1983; Thulborn, 1990).

The differences in feeding and locomotion ecology between the terrestrial and the marginal groups imply that they had different feeding behaviors. The less energy efficient limb lengths configuration of the terrestrial group may represent an adaptation for saving energy by traveling less for foraging. Their wide and deep beak allows the terrestrial group a mass consumption of unselected food, therefore they had less needs on foraging around for long distance. On the other hand, the marginal group was likely to be more adapted for traveling longer distances to search for food, then to consume it selectively using their anteriorly narrow beak. The relatively small forelimb of the marginal group is also expected to be beneficial for food selections in low on ground and high in trees up to 5 meters (Mallon et al., 2013), by reducing the distance of the center of mass movements upon posture change. The differences in behaviors associated with their foraging strategies might have allowed hadrosaurid to live in different environments and perform spatial niche partitioning among closely related relatives (Figure 2-6).

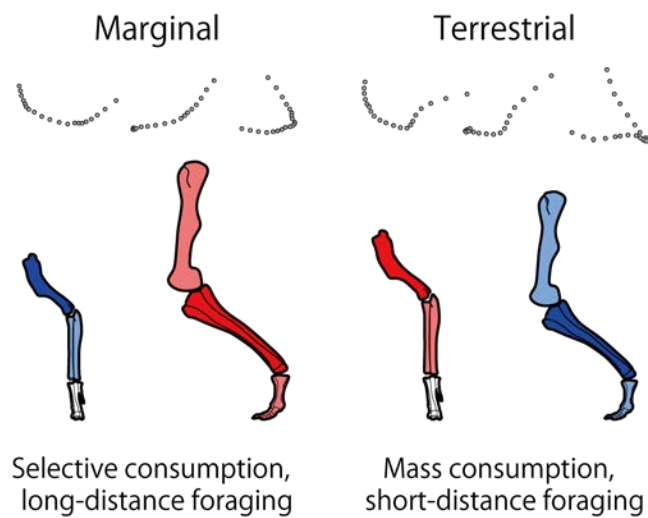


Figure 2 - 6. Visualized summary of foraging ecomorphology and inferred behaviors

The high evolutionary rates of the phylogenetic characters on the basal hadrosaurid branches suggest that the foraging features related to beak and limb morphologies experienced rapid modifications on early stage of hadrosaurid evolution, although not all are statistically significant. The branches of relatively high evolutionary rates of beak shapes do not match with that of mandible and teeth analyzed in Stubbs et al. (2019), indicating that evolution of beak occurred independently from the oral processing characters. The branch partition analyses also suggest different evolutionary histories of pectoral girdle + forelimb and pelvic girdle + hind-limb, suggesting that the features related to locomotor ecology experienced much more complex evolutionary history than

previously considered. The rise of pectoral girdle + forelimb evolutionary rates preceding that of pelvic girdle + hind-limb may be reflecting forelimb adaptation toward quadrupedalism.

The branches with high evolutionary rates of beak and limb phylogenetic characters, especially those of the pectoral girdle + forelimbs, match with the ancestral nodes representing marginal inhabitances (Kobayashi et al., 2019). In addition, the high evolutionary rates of the phylogenetic characters during Santonian – early Campanian match with the timing of long term global sea level rise (Haq, 2014). These two correspondences may indicate that the rise in sea level forced marginal residency to the ancestral hadrosaurids and that triggered modifications on beak and limb morphologies. The present work therefore suggest that together with the adaptations for highly efficient oral processing (Weishampel, 1983; Cuthbertson et al., 2012; Erickson et al., 2012; LeBlanc et al., 2016) and their social behaviors (Weishampel, 1981; Horner, 1984; Evans, 2006; Evans et al., 2009), adaptations on foraging strategies in different environments might also played an important role on the cosmopolitan distribution of Hadrosauridae during the late Cretaceous.

2.5 Acknowledgements

I deeply appreciate kind help of Amanda Millhouse (Smithsonian National Museum of Natural History), Brandon Stanley (Royal Tyrrell Museum of Palaeontology), Carl Mehling (American Museum of Natural History), Tsogtbaatar Chinzorig (IP-MAS), Kevin Seymour (Royal Ontario Museum), Kristen MacKenzie (Denver Museum of Nature and Science), Margaret Currie (Canadian Museum of Nature), and Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, China) upon collection visits.

CHAPTER 3: REGULATORY FACTORS OF AVIAN GRIT USE INVESTIGATED BY LAYER CHICKENS

Abstract

Gizzard is known as the only place for mechanical digestion in Neornithes. To improve the mechanical digestion efficiency inside gizzard, many neornithines are known to consume grits and utilize them as “teeth”. Despite of the importance of grits, the regulatory factors of neornithine grit use remain unknown. In order to investigate regulation system of grit use, this study conducted experiments using 76 male layer chicks. Diet and gizzard muscularity are hypothesized to regulate chicken grit use behaviors in the present experiments. The experiments demonstrated that grits inside gizzards are much more rounded than the stones consumed, indicating that grits are severely abraded inside gizzard therefore grit characteristic do not reflect original stone features upon consumption unlike previously considered. Instead, grits being significantly more rounded under herbivorous diet and muscular gizzard suggest that chicken grit shape reflect dietary habits and gizzard muscularity. Our experiments further demonstrated that chicks have selection on size, amount, and shape of stones upon consumption and excretion. While size and shape of stones consumed and shape

of stones excreted are not regulated by diet or gizzard muscularity, the amount of stones consumed, size and shape of the grits retained in gizzard, and size of the stones excreted differ by different diet and gizzard muscularity. Amount of stones retained in gizzard and excreted also differ by diet but not by gizzard muscularity. The present results suggest that both diet and gizzard muscularity flexibly regulate chicken grit uses upon needs of digesting hard, coarse materials. The behavioral flexibility on grit use is likely to benefit chickens by allowing consuming larger amount of food when high digestion ability is not needed. The flexibility might have contributed to high ability of neornithines to adapt to environmental changes along with seasonal cycles and migrations, though further investigations widely among neornithines are mandatory.

3.1 Introduction

Digestion, or food processing, is a key phase of animal feeding (Montuelle and Kane, 2019). In order to perform efficient digestion, animals have experienced morphological and physiological adaptations during their evolutionary history. Neornithes, the least inclusive clade of living birds, also acquired specialized digestive organs during their evolutionary history. Such organs include crop for temporal storage of food (Proctor and Lynch, 1993), caeca for fermentation of plant fiber (Potter et al., 2006), and gizzard as the only place for mechanical digestion for neornithines, as a substitute of teeth (Moore, 1999). Inside gizzard, ingesta experience strong compressing and translational stress to be mechanically processed (Moore, 1998a). Larger food particles are selectively retained inside the gizzard until they are grinded to a certain small size (Moore, 1999; Hetland et al., 2003), although the particle size control is not perfect when larger amount of large particles occupy the gizzard (Amerah et al., 2007).

For further digestion efficiency, multiple neornithines consume stones and retain those inside gizzards. Some neornithines even travel long distances to obtain stones in cases where there is insufficient sand or gravel in their surrounding environment (McIlhenny, 1932). Stone consumption is especially common in herbivorous and granivorous birds for mechanical breakdown of tough, coarse food (Gionfriddo and

Best, 1999). Previous works generally agree that grits benefits neornithine digestion efficiency, especially of the ones that feed on coarse, less-nutritional food (Fritz, 1937; Smith and MacIntyre, 1959; Hetland et al., 2003; Jin et al., 2014). Together with aid of grits, gizzard is considered to break down food particles as efficiently as non-ruminant mammals do with their teeth (Fritz et al., 2011). Despite of the importance of grits for neornithine mechanical digestions, regulation system of their grit use is not well-understood. One of the problems originates from the situation that multiple studies evaluating neornithine grit uses are based primarily on grits collected from gizzards (e.g., Norris et al., 1975; Best and Gionfriddo, 1991; Gionfriddo and Best, 1996), despite of the fact that neornithine grit characteristics can be strongly modified inside gizzards (Buckner et al., 1926; Wings and Sander, 2007).

Here we report the experiments that attempt to clarify the regulatory system grit use in layer chickens. The present experiments test grit selection, modification, and screening upon consumption, retention, and excretions in order to understand the thorough process of chicken grit uses. To further test chicken grit use flexibility in upon demands, the experiments were conducted on different dietary and gizzard muscularity groups. In addition to the common assumption that diet affect neornithine grit use (e.g., Fritz, 1937; Hoskin et al., 1970; Norris et al., 1975; Soler et al., 1993; Gionfriddo and

Best, 1999), effect of gizzard muscularity difference is also tested because gizzard with higher muscularity is likely to have higher digestion efficiency by itself. Through investigating regulatory system of domestic chickens, the present work is expected to provide insights into how grit use behaviors might have benefited the extremely high diversity of Neornithes today.

3.2 Materials and methods

Ethics statement: The experiments in this study were approved by Hokkaido University (Permission number: 16-0023) and follows the rules specified on Hokkaido University manual for implementing animal experimentation.

3.2.1 Birds, experimental design, and management

A total of 76 one-day-old male layer chicks (*Gallus gallus domesticus*) were purchased from a local feed manufacturer. The sample size was set based on the Hokkaido University regulation, space availability, and several prior experiments conducted on chickens (Hetland et al., 2003; Van der Meulen et al., 2008). Experiments were conducted for four weeks and repeated twice, from May 23, 2016 to June 20, 2016, and from June 23, 2016 to July 21, 2016. Because all of the conditions other than the

dates are equivalent, all individuals are dealt together in the statistical analyses. All chicks were raised in individual cages with wire mesh floor, the room temperature was kept between 28 °C to 30 °C, the lighting was controlled as 12 hrs light and 12 hrs dark, and feces were removed every day. Body weights of each chick were recorded every seven days.

The birds had *ad libitum* access to feed and water throughout the experiments. All of the chicks were fed with commercial starter pellet until 21d old. For half of the chicks, 30wt% of rice hull was mixed to feed in order to enhance development of gizzard by feeding larger amount of insoluble fiber (Sacranie et al., 2012). Muscularity of gizzard is evaluated as relative weight of gizzard and body mass. From 22d to the end of the experiments, the experimental groups were further subdivided into non-herbivorous group, herbivorous group, and control group, resulting in a total of 6 experimental groups. The 6 groups are: Non-herbivorous diet, muscular gizzard (G1), herbivorous diet, muscular gizzard (G2), non-herbivorous diet, less-muscular gizzard (G3), herbivorous diet, less-muscular gizzard (G4), control, muscular gizzard (G5), control, less-muscular gizzard (G6) (Fig. 1). A mixture of Poaceae grass (*Medicag sativa*) and Fabaceae grass (*Phleum pratense*) was fed for herbivorous groups, whereas dried fish (*Engraulis japonicas*) was fed for non-herbivorous groups. Feed were not changed for

the control groups. From the 22d, all of the chicks except the control groups were given ad libitum access to total of 24 grams of stones per chicks, which were provided separate from the feed. Feces were collected for determination of excreted grit characteristics on the last day of the experiment. At the 28d, all of the chicks were weighed and then euthanized by cervical dislocation. Gizzards were removed from all of the carcasses and weighed after removing stomach contents.

day 1	day 21	day 28
Muscular group (fed starter + 30 wt% rice hull)	Non-herbivorous, muscular gizzard (G1) (fed dried fish + grits)	
	Herbivorous, muscular gizzard (G2) (fed grass + grits)	
	Control with muscular gizzard (G5) (fed starter + 30 wt% rice hull)	
Less-muscular group (fed starter only)	Non-herbivorous, less-muscular gizzard (G3) (fed dried fish + grits)	
	Herbivorous, less-muscular gizzard (G4) (fed grass + grits)	
	Control with less-muscular gizzard (G6) (fed starter)	

Figure 3 - 1. Graphical image of the experimental design. G1, G2, G3, and G4 each contain 17 chicks and G5 and G6 each contain 4 chicks. The chicks are given no access to grits until after day 22.

3.2.2 Evaluation of stone characteristics

Grit characteristics were evaluated quantitatively using image processing program ImageJ (Schneider et al., 2012). Circularity, Roundness, and Solidity were employed as the indicators of grit shape. Circularity is calculated as 4 times the product of π and area, divided by square of perimeter. Roundness is an inverse of aspect ratio. Solidity is area of grit divided by area of convex hull. Minor axis was employed as the indicator of grit size. To take the images used for image analyses, stones were positioned segregated from each other and were lighted from beneath to obtain clear outlines.

3.2.3 Stone consumption

Size, shape, and amount of the stones consumed are evaluated to test if there are different preferences on these factors among different diets and gizzard muscularity. To test size preference, the stone size distribution was controlled in advance. Stones were classified into 6 different size classes by sieving (0.5 – 1.0 mm, 1.0 – 1.4 mm, 1.4 – 1.7 mm, 1.7 – 2.0 mm, 2.0 – 2.8 mm, 2.8 – 3.35 mm) and four grams of stones from each size classes are supplied in mixture. To test shape preference, the average values of Circularity, Roundness, and Solidity, of 500 stones from each size classes were evaluated in advance. At the end of the experiments, the leftovers of the stones were

collected and sieved into the 6 size classes. The weights and the shapes of the leftover stones were then compared with those of the originally offered stones.

3.2.4 Grit modification

In order to separate the grits from the other stomach contents, the stomach contents were soaked with water in a beaker over one night. Then, stones were separated from other stomach contents using floatation method (decantation). Stomach contents were put in a beaker and stirred with water, and then low density food particles were gently disposed. This procedure was repeated until only stones are left in the beaker. Characteristics of the grits collected were evaluated and compared among different diet and different gizzard muscularity.

3.2.5 Stone excretion

The stones inside feces were separated from the other fecal particles using the same method used to separate grits from stomach contents. Characteristics of the excreted grits were evaluated and compared with the characteristics of the grits in gizzard to test selective grit excretion. Characteristics of the collected grits were evaluated and compared among different diet and different gizzard muscularity.

3.2.6 Statistical analyses

All statistical analyses were conducted using basic functions of software R (R Core Team, 2019). Tukey-Kramer HSD tests were performed for mean comparisons.

P-values smaller than 0.05 are regarded as statistically significant differences. The birds euthanized following the Hokkaido University rules prior to the end of the experiments were excluded from the analyses.

3.3 Results

3.3.1 Bird growth and adjustment of gizzard muscularity

During the experiments, 2 chicks from the non-herbivorous, muscular group, 1 chick from the non-herbivorous, less muscular group, 5 chicks from the herbivorous, muscular group, and 2 chicks from the herbivorous, less muscular group were euthanized following the Hokkaido University regulations before the end of the experiments. Therefore, all of the analyses are performed on total of 66 chicks.

The average body mass of the chicks at the end of the experiments was higher in the non-herbivorous and in the control groups than in the herbivorous groups (Table S3-1).

The average body mass do not differ significantly between different initial gizzard

muscularity groups. Average gizzard muscularity values of the control groups (G5 and G6) are significantly different from each other (Fig. 3-2A, Table S3-2), suggesting that oat hull feeding successfully differentiated initial gizzard muscularities. The significantly low average gizzard muscularity value of G1 than G5, as well as significantly high average gizzard muscularity value of G4 than G6, together suggests that gizzard experienced reduction and enlargement within a week after diet change. Average gizzard muscularity values of herbivorous groups (G2, G4) are significantly higher than those of carnivorous groups (G1, G3) in both high and low initial gizzard muscularities. While differences in initial gizzard muscularity made significant difference in gizzard muscularity of herbivorous groups at the end of the experiments, the difference was insignificant in the non-herbivorous groups.

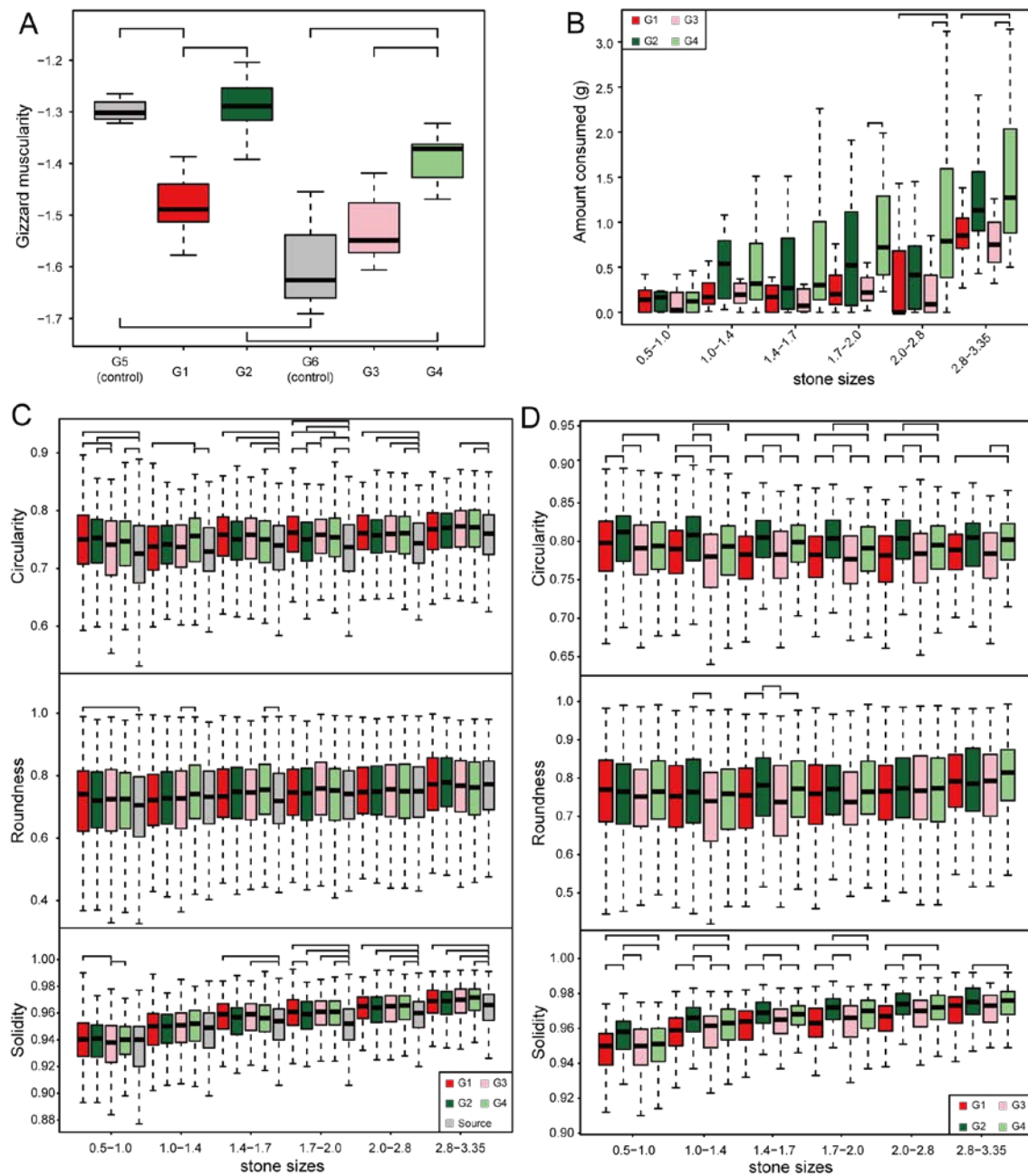


Figure 3 - 2. Results of the statistical analyses. (A) Boxplots showing gizzard muscularities by experimental groups. (B) Boxplots showing amount of stone consumed by experimental groups, shown per stone size categories. (C) Boxplots comparing shapes of the stones provided and the stones left uneaten by each

experimental group, shown per stone size categories. (D) Boxplots comparing shapes of the stones by the experimental groups, shown per stone size categories. The brackets represent p-values < 0.05.

3.3.2 Initial stone selection

Stones larger than 2.8mm were consumed significantly more than the smaller stones (Table S3-3), and the stones larger than 2.0 mm constitute more than half of the stones consumed in all groups. The amount of stone consumed were generally greater in the herbivorous groups than in the non-herbivorous groups (Fig. 3-2B). The trend is statistically significant between the groups with less initial gizzard muscularity (G3, G4) for the stones larger than 2.0 mm (Table S3-4). Within the herbivorous groups, the group with low initial gizzard muscularity (G4) consumed more stones than the group with high initial gizzard muscularity (G2), though not statistically significant.

The stones left uneaten generally had higher Circularity and Solidity values than the stones initially provided (Fig. 3-2C, Table S3-5). This trend for Circularity is statistically supported for nearly all of the size groups other than 1.0 – 1.4 mm stones in all groups. The trend for Solidity is statistically supported for the stones larger than 1.7 mm in all groups. On the other hand, there was generally no difference in Roundness

values of the provided stones and the leftover stones. The results suggest that all of the chicks selectively consumed angular stones with low Circularity and Solidity values. There is no general stone shape preference between different dietary types or initial gizzard muscularity.

3.3.3 Grit retention and abrasion

Herbivorous groups retain grits inside gizzards significantly more than in non-herbivorous groups in weights relative to the body mass (Table S3-6). The average sizes of the grits collected from the gizzard, normalized by cubic root of the body mass, are significantly larger in the herbivorous groups than in the non-herbivorous groups (Table S3-7). Groups with less initial gizzard muscularities contained larger grits in respect to their body mass, although statistically supported only between non-herbivorous groups (G1, G3). For grit shape, Circularity and Solidity values of the grits collected from chick gizzards are significantly larger than the stones provided under all conditions (Table S3-8). Roundness of the grits is also higher than the stones provided, which is statistically supported in herbivorous groups. Among the grits collected from chick gizzards, Circularity and Solidity values are higher in herbivorous groups than in the non-herbivorous groups (Fig. 2D; Table S3-9). The groups with

higher initial gizzard muscularity generally contain grits with higher Circularity and Solidity values under herbivorous diets, although the trend is not supported statistically in several grit size groups. Circularity values of non-herbivorous groups also demonstrate the same trend, although the differences are less supported statistically.

3.3.4 Stone excretion

The chicks with non-herbivorous diet excreted more grits than the chicks with herbivorous diets in number (G1: 269, G2: 91, G3: 292, G4: 52) and weight (G1: 0.83 g, G2: 0.26 g, G3: 1.34 g, G4: 0.09 g). The average stone sizes are significantly smaller in the herbivorous groups than in the non-herbivorous groups (Table S3-10). The groups with smaller initial gizzard muscularity also tend to excrete smaller stones, although statistically supported only between the non-herbivorous groups. The shapes of the excreted stones do not differ among different dietary and initial gizzard muscularity groups (Table S3-10). Compared to the grits collected from the gizzards, average sizes of the excreted stones were significantly smaller in all groups (Table S3-11). The average Solidity values of the excreted stones are also significantly smaller than the grits collected from the gizzards of the corresponding groups except in G1 which is not supported statistically. The average Circularity values are also smaller in the excreted

stones than in the gizzard grits, although there is no statistical support. At the same time, however, the Circularity and Solidity values of the excreted grits are still higher than the grits initially provided and consumed by the chicks.

3.4 Discussion

The present study is the first attempt to investigate regulatory factor of chicken grit characteristics through ingestion, internal abrasion, and excretion processes among different dietary and gizzard muscularity groups. Although the significant change in gizzard muscularity associated with diet change resulted in insignificant gizzard muscularity difference between the non-herbivorous groups at the end of the experiments (Fig. 3-2A, Table S3-2), the different initial gizzard muscularities are still expected to affect grit regulations.

3.4.1 Initial stone consumption

The active consumptions of large stones (Table S3-3) are less likely to be related to functional purposes but might simply be due to ease to pick since grit size difference is unlikely to affect digestion efficiency in domestic chickens (Smith, 1960). Absence of grit size preference by diet and gizzard muscularity also supports non-functional stone

size preferences. Difference in amount of grit consumption among different diet is in accordance with the previous wisdom (comprehensive review done in Gionfriddo and Best, 1999). At the same time, present experiments further suggest that gizzard muscularity also influence amount of grit consumption (Fig. 3-2B, Table S3-4). Since larger amount of grit improves digestive performance in domestic chickens (Bale-Therik et al., 2012) as long as the amount is not excessive (Moore, 1998b), the active stone consumption by less muscular gizzard group may be a regulation to supplement digestion ability.

Active consumption of angular grits (Fig. 3-2C, Table S3-5) is consistent with previous knowledge in domestic chickens (Smith, 1960) as well as in House Sparrows and Northern Bobwhite (Best and Gionfriddo, 1994). Since angular grits work as “blades” inside gizzards (Moore, 1998c), this selection would increase digestion efficiency. The active consumptions of angular grits in all of the experimental groups indicate that it is a congenital behavior rather than a regulation upon demands.

3.4.2 Grits inside gizzards

Possession of larger amounts and sizes of grits in herbivorous groups than in non-herbivorous groups is concordant with the majority of previous works (Hoskin et

al., 1970; May and Braun, 1973; Norris et al., 1975; Thomas et al., 1977; Soler et al., 1993; Gionfriddo and Best, 1999) as well as the trend in the initial stone consumption in the present experiments (Tables S3-6, S3-7). Grits retained inside gizzards being more rounded in average than the stones provided (Table S3-8) contradicts with the selective consumption of angular stones. Since the stones excreted are also more rounded in average than the stones initially provided (Table S3-11), the best explanation is that the grits were severely abraded inside gizzards. The dominance of rounded grits in gizzards of herbivorous groups than of non-herbivorous groups, as well as in gizzards of higher initial muscularity than of lower initial muscularity (Fig. 3-2D, Table S3-9), strongly suggest that diet and gizzard muscularity determines degree of grit abrasions. Since dietary structure largely affect gizzard muscularity in neornithines including domestic chickens (Dekinga et al., 2001; Hetland et al., 2003; Sacranie et al., 2012), gizzard muscularity may be the primary factor determining degree of grit abrasion. Correlations between grit shapes (average values of Circularity, Roundness, and Solidity) and gizzard muscularity ($p < 0.05$) further support the assumption. The severe grit abrasions inside gizzards suggest that grit shapes do not reflect stone selection patterns in domestic chickens and possibly in other neornithines unlike previously presumed (Best and Gionfriddo, 1991; Gionfriddo and Best, 1996). The present experiments suggest

that the differences in neornithine grit shapes may in fact reflect their different dietary structures and gizzard muscularities, although investigations in broader taxonomic sets are essential to test the assumption.

3.4.3 Grit excretion

Active excretion of smaller grits is controversial with Gionfriddo and Best (1995) and Tagami et al. (1969), but agrees Smith (1960). While these prior studies conducted experiments using narrow size range of grits, this study is much closer to the conditions in free-ranging birds (Gionfriddo and Best, 1999), thus expected to reflect nature of grit excretion. Excreted stones being more angular than the grits inside gizzards contradicts with the trend in House Sparrows (Gionfriddo and Best, 1999). However, the angular stones in this study are likely to represent the small stones chipped off from larger grits upon abrasion whereas the ones in Gionfriddo and Best (1999) represent one of the two extremities, thus direct comparison is not appropriate. Excretion of smaller sized, fewer stones by herbivorous groups than non-herbivorous groups contradicts with the trend in Mallards (Trost, 1981) and Ptarmigans (Norris et al., 1975) in which stone excretion is enhanced in softer diets. The differences may originate from differences in taxonomy or dietary structures (grass vs fish in this study whereas plants vs pellets in the previous

studies), although the physiological backgrounds causing the differences are unknown at this point. However, the trend shown in the present experiments may indicate that domestic chickens can improve ability to retain grits in their gizzard upon requirements of higher digestion ability for breaking down tough plant fibers. The significantly smaller stones in feces compared to the grits in gizzards (Table S3-11) suggests that grit excretion is screened primarily by grit size.

3.4.4 Regulatory system of grit use and implication on behavioral flexibility

The present experiments demonstrate that chicks have selection on size, amount, and shape of stones upon consumption and excretion (Fig. 3-3, Table 3-1). The features of the grits retained inside gizzards also differ among experimental groups. Size and shape of stones consumed and shape of stones excreted are not regulated by diet or gizzard muscularity, but the preferences are congenial. On the other hand, the amount of stones consumed, size and shape of the grits retained in gizzard, and size of the stones excreted are differentiated by different diet and gizzard muscularity. Amount of stones retained in gizzard and excreted are differentiated by diet but not by gizzard muscularity.

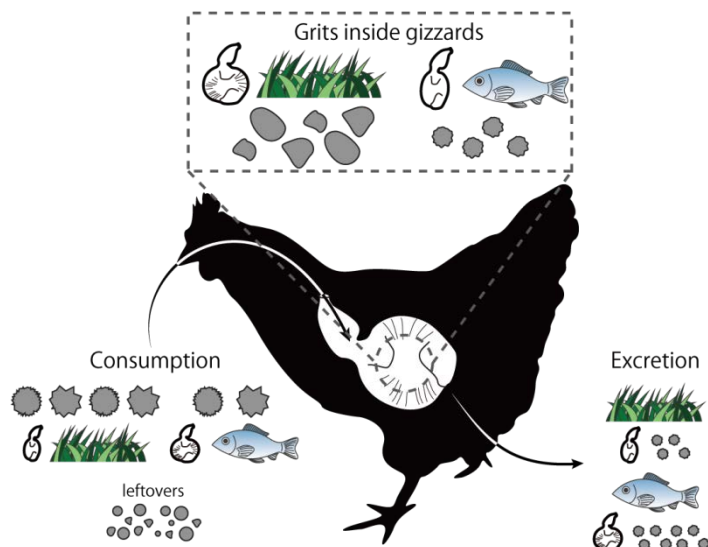


Figure 3 - 3. Schematic summary of the results obtained from the present experiments.

Table 3 - 1. Summarized results of the experiments.

Selection	
Consumed stones	
Size	Constantly large
Amount	Greater under herbivorous diet, low gizzard muscularity
Shape	Constantly angular
Gizzard grits	
Size	Larger under herbivorous diet, low gizzard muscularity
Amount	Greater under herbivorous diet
Shape	Constantly more rounded than consumed, especially under herbivorous diet and high gizzard muscularity
Excreted stones	
Size	Smaller under herbivorous diet, low gizzard muscularity
Amount	Greater under non-herbivorous diet
Shape	Constantly more angular than grits inside gizzards

The result suggests that both diet and gizzard muscularity regulate grit use for chicks and possibly other modern birds. The flexibility to regulate amount of stones consumed and excreted upon demands is likely to benefit energy consumption efficiency because

amount of grits retained in gizzard have a trade-off relationship with the amount of feed at one time: under a condition that allows efficient digestion without large amount of grits, consuming larger amount of food instead of stones would benefit chicks more. Paradoxically, the constant consumption of angular stones might be a congenial behavior acquired for higher digestion efficiency without restriction.

Behavioral flexibility is a key factor for animals to adapt environment changes along with time and space (Lefebvre et al., 1997; Chow et al., 2016). Although further study is essential to test if the behavioral flexibility demonstrated in this study is common among Neornithes or limited to chicks, the behavioral flexibility on amount of grit use might have supported the significantly high ability of neornithines to adapt to the environmental changes accompanying with changes in time (seasonal) and space (migration), together with the gizzard phenotypic flexibility (Starck, 1999; Dekinga et al., 2001; van Gils et al., 2005).

3.5 Acknowledgements

We thank Y. Deguchi and F. Kobari for allowing access to the experimental rooms and loan of experimental equipment, and T. Matsushima to detailed advises on chick management and experimental designs. We also thank K. Inada, M. Iijima, Junki

Yoshida, Chinzorig Tsogtbaatar, and A. R. Fiorillo for their helpful discussions and valuable insights.

CHAPTER 4: EVOLUTIONARY HISTORY OF AVIAN STOMACH AND THEIR GASTROLITHS USES

Abstract

Neornithes is the most diversified tetrapod group. They have extremely wide range of dietary habits, supported by numerous morphological and physiological adaptations. While relationships between neornithine diets and osteological variations have been intensely studied, study on stomach morphology is limited. Through comprehensive comparisons, this study demonstrates that neornithine stomachs can be categorized into at least four types, which are primarily determined systematically. Since strongly herbivorous diet (plant + seed) is present only in taxa with strongly muscular stomach type, neornithine stomach types are likely to give limitations to their dietary habits. At the same time, ancestral state reconstructions suggest that neornithine stomach types and dietary habits experienced largely different evolutionary histories, suggesting that the limitations by stomach types are not strict. Large variations in gizzard muscularity and occurrences of gastroliths regardless of stomach types might be mitigating diet limitations by stomach types. The present work also demonstrates that gastroliths

shapes could be used to predict dietary habits with high discriminance accuracies (up to 77%), providing a potential new method for predicting extinct archosaur diets.

4.1 Introduction

Neornithines, the least inclusive clade of living birds, is the most diversified tetrapod group represented by approximately 10,000 known living species. They are known to have wide range of dietary habits (Gill, 1995) that are supported by numerous morphological (Grant, 1999; Jonsson et al., 2012; Olsen and Gremillet, 2017) and physiological adaptations (Martínez del Río et al., 1992; Bairlein F. and Simons, 1995; Bosque, 2000). Neornithine digestive tract is one of those organs that show strong dietary adaptations (Klasing, 1998), with stomach showing the greatest range of variation among all internal organs (Ziswiler and Farner, 1972). Neornithine stomachs generally consists two distinct chambers, glandular stomach proventriculus and muscular stomach ventriculus. Proventriculus is located orad to the ventriculus and principally serves for secretion of mucus, HCl, and pepsin. The other stomach chamber ventriculus, which is also called gizzard, functions as the only place for mechanical digestion (Moore, 1999). It is widely accepted that neornithine stomach morphology has two extremities that are strongly related with their diet (Ziswiler and Farner, 1972; Klasing, 1998; Denbow, 2015). Birds that consume soft food, such as carnivorous and piscivorous taxa, generally have large proventriculus and less muscular ventriculus that together serve as a food storage, while birds that feed on coarse food items, such as

graminivorous taxa, generally have small proventriculus and highly muscular ventriculus for mechanical digestion of ingesta (Owen, 1866b; Swenander, 1901; Pernkopf, 1929; Ziswiler and Farner, 1972). In addition to the anatomical variations, neornithines are known to contain gastroliths inside their ventriculus in order to further facilitate mechanical digestions (Fritz, 1937; Gionfriddo and Best, 1999; Jin et al., 2014). Although gastroliths are mainly known from granivorous taxa (Best and Gionfriddo, 1991; Gionfriddo and Best, 1996), there are multiple reports from carnivorous and piscivorous taxa (Rôrig, 1907; Lambrecht, 1933; Beaune et al., 2008).

While the general trends strongly suggest that neornithine stomach morphology and use of gastroliths are associated with their diet, little attention has been given to the impacts of adaptive evolution of these features, unlike osteological variations which are intensely studied (Grant, 1999; Bright et al., 2016). One factor that hinders understandings of evolutionary history of neornithine stomach is insufficient generalizations of their morphological traits. Although multiple reports show that avian stomach variations cannot be fully explained by simple enlargement and reduction of ventriculus muscularities (Desselberger, 1931; Jackson and Place, 1990; Degen et al., 1994), these variations have not been incorporated into categorizations of avian stomach morphologies. The present study therefore attempts to establish a basic framework of

avian stomach morphology evaluations through comparisons of morphological features of major orders of neornithines that represent various dietary habits. Using the constructed framework, adaptive evolution of neornithine stomach is investigated. Occurrence frequencies and shape of gastroliths are also evaluated in order to test evolutionary associations between neornithine diet and their gastroliths use. This study is expected to establish a basis of avian stomach classification and shed light on impacts of gastric apparatus on neornithine diet diversification.

4.2 Material and method

Internal organs of wild and captive neornithines are dissected in order to observe morphological variations among neornithines. The observed specimens are stored in the Hokkaido University Museum (HoUMVC) and the Botanic Garden of Hokkaido University (HUNHM). All of the HUNHM specimens are fixed and stored in 10% neutral formalin, and the HoUMVC specimens are fixed with 10 % neutral formalin and stored in 70% ethanol. Stomach and gastroliths of crocodylians are also observed as outgroup. The observed crocodylian specimens are provided by Koike Wani Sohonpo Co. Ltd, Shizuoka Prefecture, Japan, Atagawa Tropical & Alligator Garden, Shizuoka Prefecture, Japan, and the Crocodylus Park, NT, Australia. None of the crocodylian

stomachs are preserved or catalogued. The final dataset includes 382 specimens (Data S4-1) from 368 modern bird individuals (115 species) and 14 modern crocodile individuals (4 species).

In order to investigate how differences in dietary structures affected neornithine stomach evolution, stomach types and muscularities are evaluated. The neornithine stomachs are categorized into 4 morphotypes based on their external morphologies. Stomach muscularity is evaluated as a ventriculus mass - body mass ratio in neornithines and stomach mass – body mass ratio in crocodylians. The body mass of several captured specimens were unavailable due to partial loss or drying of the organs prior to the dissection. Diet categories of avian taxa follow Wilman et al. (2014). All of the crocodylians are categorized as vertebrate feeder herein.

One-hundred time-calibrated phylogenetic trees of the neornithine taxa observed herein are obtained from BirdTree.org (Jetz et al., 2012; Rubolini et al., 2015), based on the phylogenetic reconstructions with Ericson backbone (Ericson et al., 2006). In order to incorporate the phylogenetic uncertainties, statistical analyses incorporating phylogenetic relationships are repeated for all of the 100 subsets. Stomach muscularities are averaged per taxa and log₁₀-transformed prior to analyses. Phylogenetic signals of neornithine diet, stomach type, and stomach muscularity are evaluated using R package

geiger version 2.0.6.2 (Pennell et al., 2014). Ancestral state reconstructions of neornithine diet, stomach type, and stomach muscularity are conducted using R package ape version 5.3 (Paradis and Schliep, 2019). Correlations between stomach type and stomach muscularity, and diet and stomach muscularity are inferred through phylogenetic generalized least squares (PGLS) using R package caper version 1.0.1 (Orme et al., 2018).

Phylogenetic signal of gastroliths occurrence frequency is tested using R package geiger version 2.0.6.2 (Pennell et al., 2014). Occurrence frequency of gastroliths is averaged per taxa. Correlations between diet and gastroliths occurrence frequency, stomach type and gastroliths occurrence frequency, and gizzard muscularity and gastroliths occurrence frequency are inferred through PGLS using R package caper version 1.0.1 (Orme et al., 2018). Area, minor axis, Circularity, Roundness, and Solidity of the gastroliths larger than 0.5 mm in minor axis are evaluated using software ImageJ version 1.8.0 (Schneider et al., 2012) following the method by Takasaki et al. (under prep.). Circularity, Roundness, and Solidity of the gastroliths are averaged per individual prior to analyses. In order to test if gastroliths shapes reflect neornithine diet, discriminant analysis is conducted using R package MASS version 7.3-51.4 (Venables and Ripley, 2013). Discriminant analysis is repeated for six times for individuals

containing more than 1, 10, 20, 30, 40, and 50 gastroliths in order to evaluate how differences in number of gastroliths per individual affect uncertainties in discriminations. Discriminant analyses are also performed on stomach types to test impact of different stomach types on gastroliths shapes. Principal component analysis is conducted on Circularity, Roundness, and Solidity of the gastroliths to reduce dimensionality. Correlation between the resultant PC1 and stomach muscularity is tested using ordinary least square regression.

All statistical analyses are conducted using R version 3.6.1 (R Core Team, 2019). Results of the statistical analyses are visualized using basic R functions and R packages phytools version 0.6-99 (Revell, 2012) and caret version 6.0-84 (Kuhn, 2008).

4.3 Results

4.3.1 Stomach description

Type A stomach is the “classic” neornithine stomach represented by Anseriformes, Charadriiformes, Columbiformes, Galliformes, Gruiformes, Passeriformes, Podicipediformes, and Palaeognathae (Figure 4-1). Proventriculus of type A stomach is generally smaller than its gizzard, which is generally positioned posteroventral to the proventriculus. The junction between the proventriculus and the gizzard is strongly

constricted and the gastric isthmus is well distinctive externally. The type A gizzard is characterized with the well-developed *M. crassus cranioventralis* and *M. crassus caudodorsalis*. The two large muscles are separated from the small muscles *M. tenuis craniodorsalis* and *M. tenuis cranioventralis* by *sulcus cranialis* and *sulcus caudalis*, respectively. The *sulcus cranialis* and *sulcus caudalis* are likely to make extra space for storage and possibly for contraction of the rigid gizzard. Both sides of the gizzards are covered with tendinous aponeuroses (*centrum tendineum*), which tend to be thicker and larger in individuals with more muscular gizzards. The gizzard opening for the duodenum is located on the lateral side of the gizzard, at the ventral margin of the *M. tenuis craniodorsalis*. The pyloric region between the gizzard and the duodenum is short. A distinct chamber at the pyloric region, *portio pylorica* (Stannius, 1846), was not observed in the type A stomachs unlike previously mentioned in some ducks, geese, and rails (Ziswiler and Farner, 1972; Klasing, 1998). The pyloric region of the type A stomachs are directly continuous with a deep groove of gizzard lumen, formed of two large longitudinal gastric folds, have no isthmus or valve to distinguish two regions unlike in type C stomachs (Figure 4-1D).

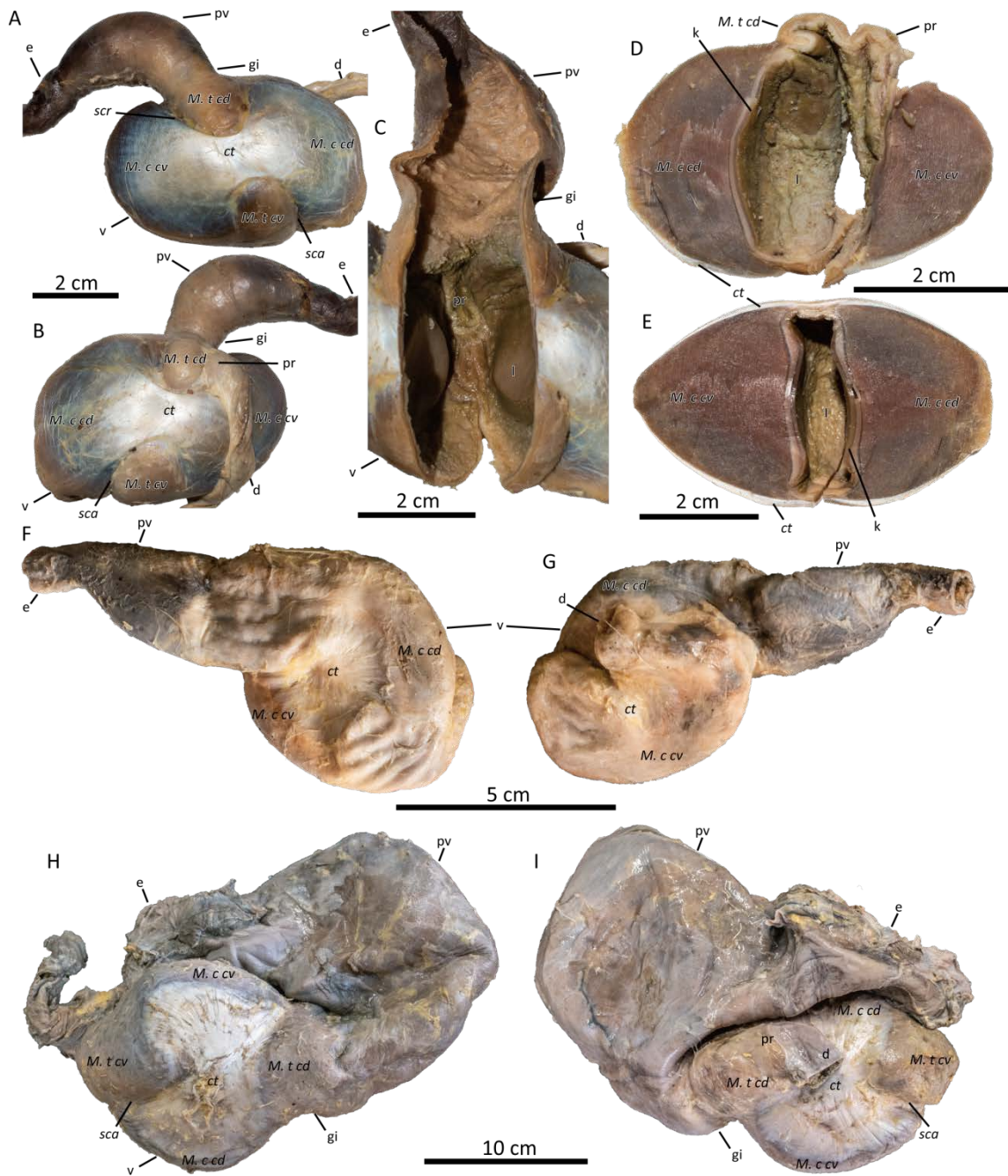


Figure 4 - 1. Representatives of type A stomachs. Stomach of *Anas acuta* in (A) left

and (B) right lateral views. (C) Internal cavity of the *Anas acuta* stomach. (D)

Transverse section of the ventriculus at the level of the pyloric region. Note that

the pyloric region does not form a distinct chamber but is a groove in between two

large gastric folds. (E) Transverse section of the ventriculus at its maximum width.

F-G, Stomach of *Dromaius novaehollandiae* in (F) left and (G) right lateral views.

Stomach of *Struthio camelus* in (H) left and (I) right lateral views. Abbreviations:

ct, *centrum tendineum*; d, duodenum; e, esophagus; gi, gastric isthmus; k, koilin

layer; l, lumen; *M. c cd*, *M. crassus caudodorsalis*; *M. c cv*, *M. crassus*

cranioventralis; *M. t cd*, *M. tenuis craniodorsalis*; *M. t cv*, *M. tenuis cranioventralis*;

pr, proventriculus; pv, proventriculus; *sca*, *sulcus caudalis*; *scr*, *sulcus cranialis*; v,

ventriculus.

The type A gizzard observed herein generally retain more muscular gizzard than in the other groups regardless of their diet, despite of the fact that gizzard muscularity is known to vary intraspecifically by diet type and amount of insoluble fiber consumed (Hetland et al., 2003; van Gils, 2003; Sacranie et al., 2012)(Takasaki et al., under prep.).

An exception is diving duck *Mergus*, which mainly feed on fish. *M. crassus*

cranioventralis and *M. crassus caudodorsalis* of *Mergus* is reduced and form stomach

wall as thin as that of proventriculus, therefore the gizzard is unlikely to serves as a cite

for mechanical digestion. On the other hand, other piscivorous taxa such as *Cerorhinca*

have enlarged proventriculus instead of modifying gizzard as a storage and retain

somewhat muscular gizzard. Another exception is a palaeognath *Dromaius* (Figure 4-1F, G), although the less muscular gizzard of *Dromaius* may originate from captive nature. Gizzard morphology of *Struthio*, the other palaeognath observed herein, is of typical type A. However, *Struthio* stomach is unique in the anteroventral positioning of gizzard relative to the proventriculus (Figure 4-1 H, I), while the ventriculus of the other type A stomachs are positioned posteroventral to the proventriculus. Instead, the gizzard location of *Struthio* resembles to those of type D stomach. Since stomachs of *Struthio* and type D also share enlarged proventriculus, the relocation of gizzard might be an adaptation associated with enlarged proventriculus for storage.

Type B stomach is represented by Accipitriformes, Camprimulgiformes, Coraciiformes, Cuculiformes, Falconiformes, Piciformes, and Strigiformes (Figure 4-2G-J). Proventriculus of type B stomach is smaller than its gizzard, although the proportion is generally larger than in type A stomach. The gastric isthmus between the proventriculus and the ventriculus is externally discernable although it is less distinctive than in type A stomachs, giving the type B stomachs spindle-shaped outline. Gizzard of type B stomach differs from type A in its thin gizzard wall and absence of *sulcus cranialis* and *sulcus caudalis* (Figure 4-2G, H). Although *M. crassus* of type B stomachs are generally less developed than in type A stomachs, muscle thickness vary

largely among type B stomachs from *M. crassus* being thick in *Picus awokera* and thin in *Milvus migrans* (Figure 4-2I, J). The differences in muscle thickness may reflect diet differences. Because *sulcus cranialis* and *sulcus caudalis* are absent, *M. crassus* and *M. tenuis* merge cranially and caudally therefore the two muscles cannot be distinguished externally. *Centrum tendineum* of type B stomach is generally thin and less developed than in type A stomachs, and do not reach the caudodorsal or cranioventral margin of the gizzard. The internal koilin layer is thin or absent. The opening for the duodenum is located on the anteroventral margin of the left lateral side of the gizzard next to the opening for the proventriculus. The pyloric region does not form a distinct chamber (*portio pylorica*) in most specimens observed herein. However, the pyloric region of *Milvus migrans* (HoUMVC 30018) has a distinct *portio pylorica* distinguished by two isthmuses, which agrees with previous inferences (Ziswiler and Farner, 1972; Klasing, 1998). However, *portio pylorica* was not observed in another *Milvus migrans* specimen (HoUM 30112) as well as other members of Accipitriformes dissected in this study, therefore the structure is not common among type B stomachs.

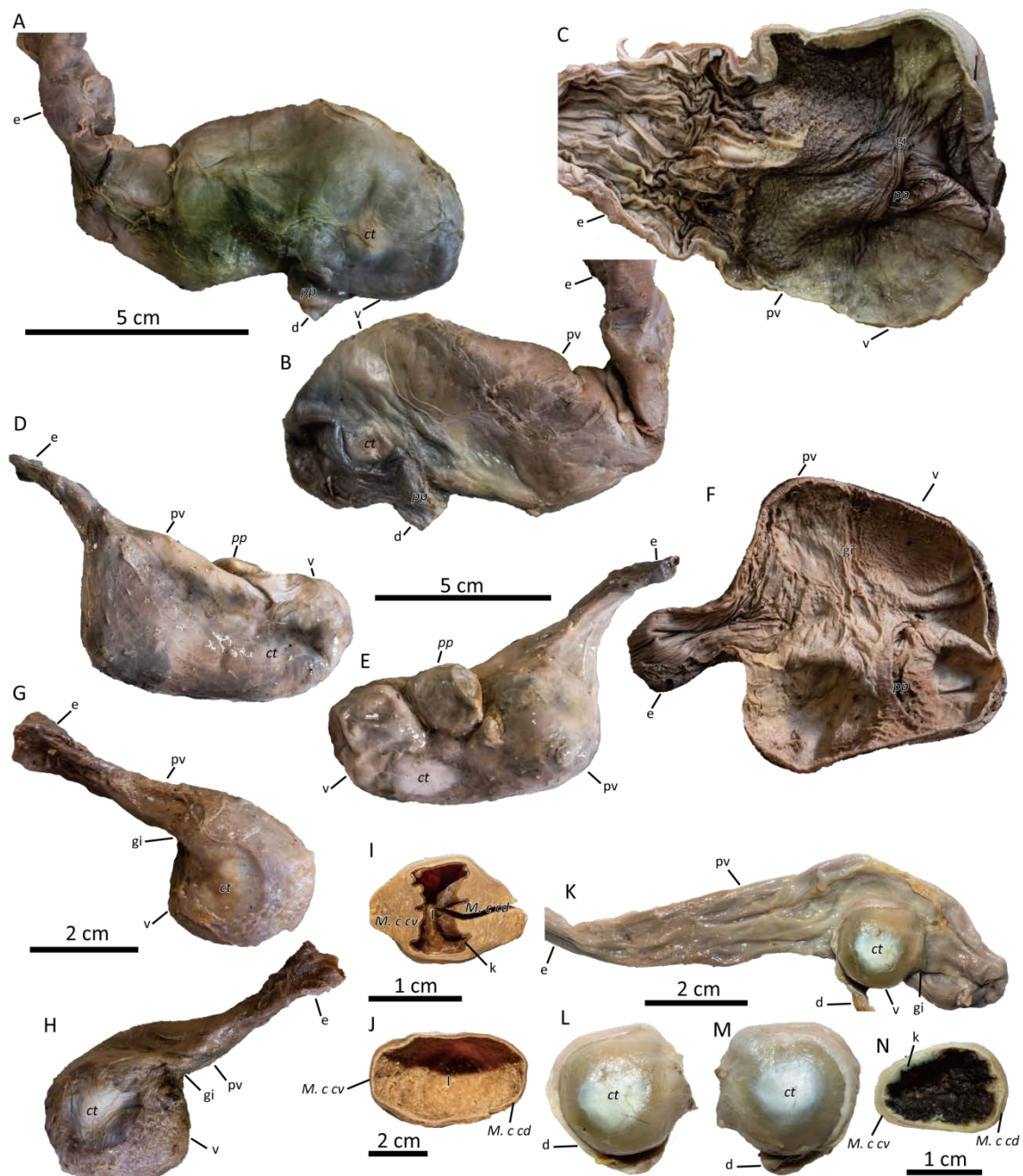


Figure 4 - 2. Type C stomachs (A-E). Stomach of *Phalacrocorax carbo* in (A) left and (B) right lateral views. (C) Internal cavity of the *Phalacrocorax carbo* stomach. Stomach of *Ardea cinerea* in (D) left and (E) right lateral views. (F) Internal cavity of the *Ardea cinerea* stomach. Type B stomachs (G-J). Stomach of *Strix uralensis* in

left (G) and right (H) lateral views. Transverse sections of *Picus awokera* (I) and *Milvus migrans* (J) ventriculus. Type D stomach *Puffinus tenuirostris* (K-N). Left lateral view of the whole stomach (K). *Puffinus tenuirostris* ventriculus in left lateral, (L) right lateral, (M) and transverse views.

Type C stomach is represented by Pelecaniformes and Suliformes (Figure 4-2A-F). It has enlarged proventriculus that is larger than its gizzard. The gastric isthmus is faint and indistinguishable externally. The stomach wall of the type C gizzard is extremely reduced, being thinner than the stomach wall of its proventriculus. Therefore, the gizzard of type C stomach is unlikely to serve for mechanical digestion. *Sulcus cranialis* and *sulcus caudalis* are completely absent as in type B stomach, resulting in union of *M. crassus* and *M. tenuis*. *Centrum tendineum* is extremely reduced and occupies less than 30% of the external surface of the gizzard. Koilin layer is absent in all of the observed specimens. The pyloric region of the stomach is located on the anteroventral margin of the left side of the gizzard in the observed Suliformes, whereas it is located on the anterodorsal margin in the observed Pelecaniformes. The pyloric region of the type C stomach is unique other than *Milvus migrans* (HoUMVC 30018) in forming *portio pylorica* separated by two isthmuses, as previously reported in Ardeidae (Svenander,

1899; Ziswiler and Farner, 1972). The *portio pylorica* of *Ardea cinerea* is sphere shaped and its gastric wall is as thick as the gizzard. On the other hand, the *portio pylorica* of *Phalacrocorax carbo* is tubular as in *Milvus migrans* and internally bear longitudinal gastric folds. It should be emphasized that although the third stomach chamber *portio pylorica* is previously referred as pyloric stomach (Ziswiler and Farner, 1972), it is not homologous with crocodylian pyloric stomach. Instead, crocodylian pyloric stomach is considered homologous with neornithine ventriculus (Pernkopf, 1929)(Takasaki and Kobayashi, under prep.)

Type D stomach is represented wholly by Procellariiformes (Figure 4-2K-N). Proventriculus of type D stomach is unique in its extreme longitudinal elongation, which is at least three times as long as its gizzard. The posterior end of the proventriculus is recurved anteriorly, therefore the gizzard of type D stomach is positioned ventrolateral to the proventriculus. This feature is unique among the observed specimens except for *Struthio*. The gastric isthmus is narrow and distinctive externally unlike in type C stomach. *M. crassus cranioventralis* and *M. crassus caudodorsalis* of the type D gizzard is much less developed than those of type A gizzard, but thicker than all type C and some type B specimens. *Sulcus cranialis* and *sulcus caudalis* are completely absent and the *centrum tendineum* is thin and undeveloped

unlike in type A stomach. Koilin layer is present in some specimens (Figure 4-2N), although it is much thinner than the koilin layer of type A stomach. The junction with the duodenum is located at the posterodorsal margin of the right side of the gizzard. Although the orientation of the gizzard is inverted, this is typical position of the gizzard-duodenum junction. Although the pyloric region is large relative to the gizzard, it does not have an extra isthmus therefore not forming *portio pylorica*. The features of type D stomach resemble to the stomach of crocodylians (Owen, 1866a; Richardson et al., 2002) (Takasaki and Kobayashi, submitted), although these features are clearly obtained distinctly.

4.3.2 Diet, stomach type, gizzard muscularity, and gastroliths

The present analyses suggest that differences in neornithine stomach types could be explained phylogenetically, whereas phylogenetic signals of diet and gizzard muscularity are smaller (Figure 4-3, Table 4-1). Strong herbivorous diet (Fruits + Nectar and Plant + Seed) is observed only from taxa with type A stomachs (Figure 4-4A). Vertebrate and invertebrate diets are present in all of the stomach types, with vertebrate diet occupying the largest proportion in the stomach type C, and invertebrate diet in the stomach type B. Omnivorous diet is most common in the stomach type D

while the stomach type C is suggested to have no omnivorous diet taxa. Fisher's exact test suggests that avian stomach types and diet is associated with each other ($p < 0.05$), although the current result may be phylogenetically biased. Gizzard muscularity of neornithines are different by both stomach types and diet (Figure 4-4B and C, Table 4-2). Differences are statistically significant among all stomach types other than between type B and C. Among different diet groups, vertebrate feeders have significantly low gizzard muscularity other than fruit + nectar feeders. PGLS also suggest that neornithine gizzard muscularity is correlated with both stomach types and diet (Table 4-3).

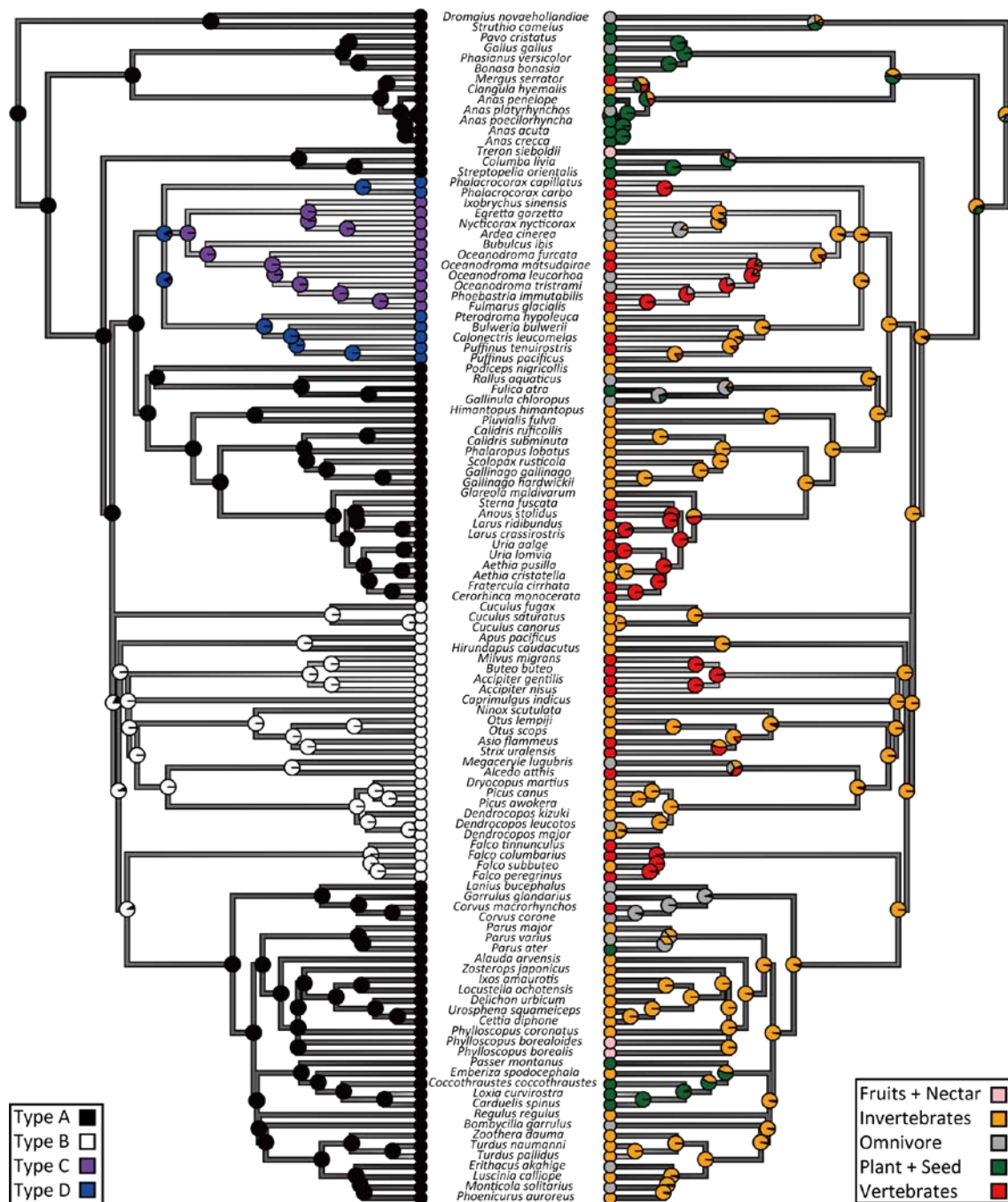


Figure 4 - 3. Evolutionary history of stomach type (left) and diet type (right) along the majority-rule consensus tree of the 100 trees analyzed. The branch color represents transition of gizzard muscularity.

Table 4 - 1. Phylogenetic signals of neornithine dietary habits, stomach types, and stomach muscularities.

	lambda (mean)	lambda (median)	lnL (mean)	lnL (median)	AIC (mean)	AIC (median)
Diet	0.70	0.90	-149.67	-144.35	303.35	292.69
Stomach types	1.00	1.00	-29.92	-29.90	63.85	63.79
Stomach muscularity	0.74	0.74	-12.89	-12.92	31.78	31.84

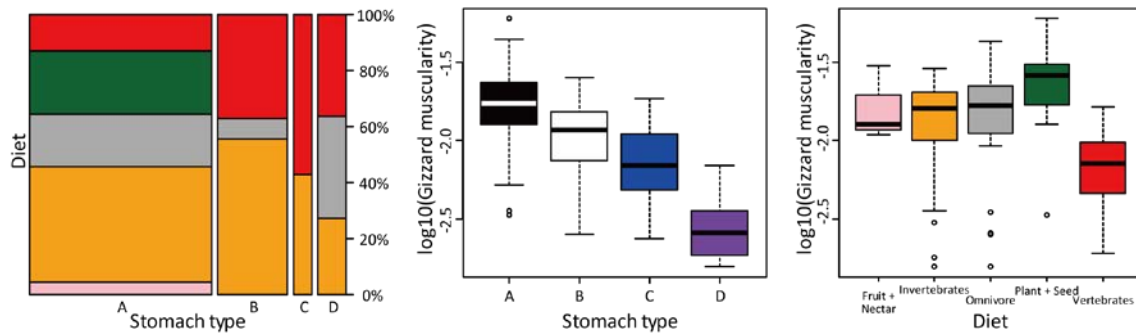


Figure 4 - 4. (A) Mosaic plot of diet against stomach type. Box plots of gizzard muscularity against stomach type (B) and diet (C).

Table 4 - 2. P-values obtained from multiple comparisons on gizzard muscularity by stomach type and dietary habits.

	A	B	C	—
B	0.0016	NA	NA	—
C	0.0006	0.0987	NA	—
D	0.0000	0.0000	0.0016	—
	Fruits + Nectar	Invertebrate	Omnivore	Plant + Seed
Invertebrate	1.0000	NA	NA	NA
Omnivore	1.0000	1.0000	NA	NA
Plant + Seed	1.0000	0.1710	0.2055	NA
Vertebrates	0.2055	0.0005	0.0130	0.0000

Table 4 - 3. Results of PGLS of stomach type and diet type against gizzard

muscularity in mean (top) and median (bottom) values of the 100 iterations

performed.

(mean)	lambda	r2	adj.r2	AIC	AICc	logL	p.value
Stomach Type	0.29	0.37	0.35	1.62	2.01	3.19	0.0000
Diet Type	0.74	0.15	0.12	18.43	19.03	-4.22	0.0023
Stomach+Diet	0.15	0.47	0.44	3.30	4.77	6.35	0.0000
(median)	lambda	r2	adj.r2	AIC	AICc	logL	p.value
Stomach Type	0.29	0.37	0.35	1.62	2.01	3.19	0.0000
Diet Type	0.73	0.15	0.12	18.61	19.20	-4.31	0.0022
Stomach+Diet	0.20	0.46	0.42	4.52	5.99	5.74	0.0000

At least one gastrolith is collected from stomachs of 90 neornithines among the 382 specimens observed (Data S4-1). Gastroliths occurrence frequencies are nearly constant among different stomach types at around 25% in average (Figure 4-5A, Table 4-4), suggesting that gastroliths occurrence frequency and stomach types are not associated to each other ($p = 0.30$). On the other hand, occurrence frequencies of neornithine gastroliths is associated with diet ($p < 0.001$), varying from 0% of fruit + nectar group to 60% of plant + seed group (Figure 4-5B, Table 4-4). The association with diet is concordant with prior works (Best and Gionfriddo, 1991; Gionfriddo and Best, 1996; Gionfriddo and Best, 1999). PGLS also support correlation between occurrence frequencies of gastroliths and different diet groups, while stomach type and gizzard

muscularity are suggested to have no correlation with gastroliths occurrences (Table 4-5).

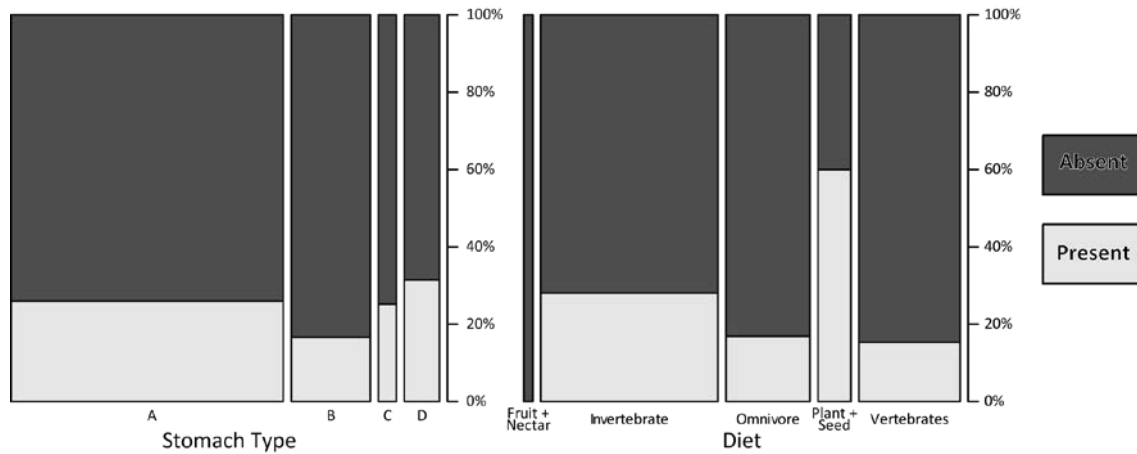


Figure 4 - 5. Mosaic plots of gastroliths occurrence frequencies against stomach type (A) and diet (B).

Table 4 - 4. Gastroliths occurrence frequencies by stomach type and diet.

	Stomach type				Diet				
	A	B	C	D	Fruit + Nectar	Invertebrate	Omnivore	Plant + Seed	Vertebrates
Present	64	12	4	10	0	45	13	18	14
Absent	184	60	12	22	8	116	64	12	78
Total	248	72	16	32	8	161	77	30	92
Ratio present	25.81%	16.67%	25.00%	31.25%	0.00%	27.95%	16.88%	60.00%	15.22%

Table 4 - 5. Results of PGLS of stomach type, diet type, and gizzard muscularity on gastroliths occurrence frequencies.

	lambda	r ²	adj.r ²	AIC	AICc	logL	p-value
Stomach type	0.24	0.00	-0.02	91.93	92.32	-41.96	0.9254
Diet type	0.15	0.10	0.06	84.13	84.73	-37.07	0.0333
Gizzard muscularity	0.26	0.01	0.00	87.50	87.62	-41.75	0.4296

Gastrolith shapes of 90 neornithines (42 species) and 14 crocodylians (4 species) are listed in Data S4-2. Discriminant analyses on archosaur gastroliths shapes, including those of crocodylians, show high discriminance accuracy for discriminating type A stomach and low accuracy on other stomach types (Figure 4-6A, B, Table 4-6).

Although number of gastroliths largely affects discriminant accuracies of stomach types C and D, overall accuracy is nearly constant independent of number of gastroliths.

Archosaur gastroliths shapes could better differentiate plant + seed feeders and invertebrate feeders from other dietary groups (Figure 4-6C, D, Table 4-6).

Discriminant accuracy of vertebrate feeders is also high when only the individuals with more than 30 gastroliths are considered. Unlike in stomach types, discriminant accuracy of diet based on gastroliths shapes gently increase along with increase in the minimum number of gastroliths an individual contains, owing to the increase in the accuracy of vertebrate feeders. Although the failure to identify omnivorous feeders decreases overall

discriminant accuracy, the result is appropriate since the “omnivorous” group is an aggregate of taxa which cannot be appropriately categorized to a certain diet category Wilman et al. (2014).

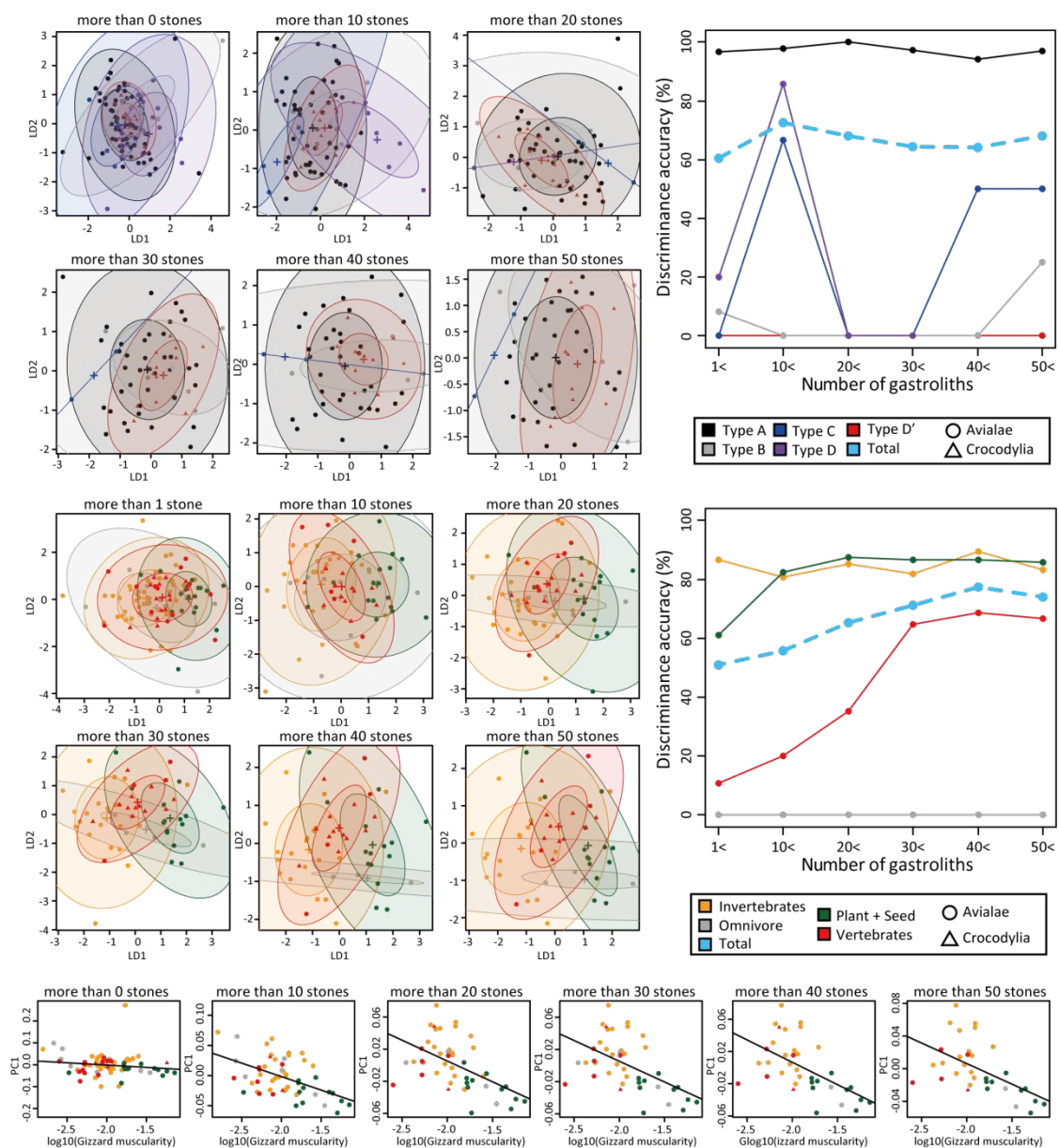


Figure 4 - 6. (A) Bivariate plots of LD1 and LD2 values obtained from the discriminant analyses grouped by stomach types. The inner ellipse and the outer ellipses represent 50% and 95% confidences, respectively. (B) Discrimination accuracies in each stomach type in the analyses with different minimum gastroliths numbers. (C) Bivariate plots of LD1 and LD2 values obtained from the

discriminant analyses grouped by dietary habits. The inner ellipse and the outer ellipses represent 50% and 95% confidences, respectively. (D) Discriminance accuracies in each dietary habit in the analyses with different minimum gastroliths numbers. (E). results of the regression analyses of PC1 values of gastroliths shapes against stomach muscularities in the analyses with different minimum gastroliths numbers.

Table 4 - 6. Summarized discriminant accuracies on stomach type and diet type by gastroliths shapes in the six analyses performed by different minimum number of gastroliths. Detail is provided in the Supplementary Table 4-4.

	Stomach type					Diet					
	A	B	C	D	D'	Overall	Invertebrate	Omnivore	Plant + seed	Vertebrate	Overall
All	96.77%	8.33%	0.00%	20.00%	0.00%	60.58%	86.67%	0.00%	61.11%	10.71%	50.96%
>10	97.96%	0.00%	66.67%	85.71%	0.00%	72.73%	80.65%	0.00%	82.35%	20.00%	55.84%
>20	100.00%	0.00%	0.00%	0.00%	0.00%	68.18%	85.19%	0.00%	87.50%	35.29%	65.15%
>30	97.44%	0.00%	0.00%	0.00%	0.00%	64.41%	81.82%	0.00%	86.67%	64.71%	71.19%
>40	94.29%	0.00%	50.00%	NA	0.00%	64.15%	89.47%	0.00%	86.67%	68.75%	77.36%
>50	96.97%	25.00%	50.00%	NA	0.00%	68.00%	83.33%	0.00%	85.71%	66.67%	74.00%

Principal component analyses successfully reduced dimensionality of gastroliths shape data with PC1 and PC2 explaining at least 95% of the variances in all analyses under different minimum gastroliths numbers (Table S4-1). Gastrolith Circularity generally has the highest eigenvector of PC1 with exception of the analysis without

gastroliths number limitation, in which Roundness has the highest eigenvector.

Eigenvector of PC2 is generally occupied by Roundness other than the analysis without gastroliths number limitation. Ordinary least square regressions suggest correlations between PC1 and archosaur stomach muscularity other than in the analysis including individuals with less than 10 gastroliths (Figure 4-6E, Table 4-7).

Table 4 - 7. Results of regression analyses of PC1 value of gastroliths shapes against gizzard muscularity in the six analyses performed by different minimum number of gastroliths.

	Slope	Intercept	R2	adj-R2	p-value
All	-0.02	-0.04	0.02	0.01	0.2050
>10	-0.04	-0.09	0.26	0.25	0.0001
>20	-0.05	-0.10	0.28	0.27	0.0001
>30	-0.05	-0.10	0.28	0.26	0.0003
>40	-0.06	-0.10	0.31	0.29	0.0004
>50	-0.05	-0.09	0.30	0.27	0.0011

4.4 Discussion

4.4.1 Evolutionary history of avian stomachs

This study is the first work which investigates evolutionary history of neornithine stomach comprehensively and systematically. While neornithine stomachs had been categorized primarily based on diets (less-muscular soft food feeder vs more-muscular

hard food feeder) (McLelland, 1979; Denbow, 2015), the present work demonstrates that neornithine stomachs can be grouped into four categories based on external morphology. It should be noted that there are some degree of variations within each categories, such as relocation of ventriculus in ostrich (Figure 4-1H, I), and even intraspecifically such as presence and absence of *portio pylorica* in *Milvus migrans*. Additionally, Desselberger (1931) reported a reduced ventriculus that is actually a diverticulum at the junction of the proventriculus and duodenum in several species of *Dicaeum*, suggesting presence of at least one additional stomach morphotype. Since the present study covers only a small part of approximately 10,000 neornithine species present today, further investigations on larger dataset is expected to reveal larger variations in neornithine stomach morphology. Despite of these problems, however, the groupings proposed herein is still the most comprehensive at this point and forms the basic framework of neornithine stomach morphotypes that allows systematic investigations on evolutionary history of neornithine stomach and its associations with neornithine ecologies including diets and use of gastroliths.

The neornithine stomach types are suggested to be primarily determined systematically (Figure 4-3, Table 4-4), although it is also associated with diets (Figure 4-4A) as previously suggested (Owen, 1866b; Ziswiler and Farner, 1972; McLelland,

1979; Denbow, 2015). The association of neornithine stomach types and diets suggest that stomach type give limits to avian dietary habits. Presence of strongly herbivorous taxa (plant + seed feeders and fruits + nectar feeders) only from type A stomachs strongly suggest that herbivorous diet in Neornithes require highly muscular stomachs that facilitate mechanical digestion of ingesta. The association between stomach type and diet is less significant in stomach types B, C, and D. These three types provide large food storage space in exchange for ability to break down the food mechanically. The large storage space is likely to allow swallowing preys as a whole in some strongly carnivorous taxa as such as owls and cormorants. Interestingly, a strongly piscivorous taxon of stomach type A, *Cerorhinca monocerata* is known to load preys on its beak to feed chicks (Wilson, 1977; Gaston and Jones, 1998), while cormorants feed chicks from the food stored in their stomachs (del Hoyo et al., 1992). The difference may indicate that stomach types affect neornithine foraging strategies, in addition to dietary habits.

While stomach types give limitations to diet, it is evident that evolutionary history of neornithine diet is much more complex than that of stomach type (Figure 4-3). The large diet variations within each stomach types (Figure 4-4A) further suggest that diet limitation by stomach types is not strict. One factor that is likely to contribute to the complex evolutionary history and the variations of neornithine diets is the high

evolutionary flexibility of neornithine digestive enzymes (Chen and Zhao, 2019). At the same time, differences in gizzard muscularity are also likely to contribute to the diet variations within each stomach types. While neornithine gizzard muscularity is largely affected by their stomach types, gizzard muscularity also varies among different dietary groups (Figure 4-4B, C, Table 4-5). Associations of diet type and gizzard muscularity are especially evident in stomach types A and B. While gizzard muscularities of invertebrate feeders, especially those feed on hard-shelled animals such as crustaceans and beetles, have high gizzard muscularities, vertebrate feeders have low gizzard muscularities. The trend can be seen in between closely related taxa (e.g., invertebrate feeding *Falco subbuteo* vs vertebrate feeding *Falco peregrinus*), suggesting that neornithine gizzard muscularity have high evolutionary flexibility. In addition, the association of gastroliths occurrence frequency with diet but not with stomach type (Figure 4-5) is likely to suggest that regardless of stomach types, neornithine consume gastroliths to aid mechanical digestion depending on demands of their diets. The supplements of mechanical digestion ability by gastroliths consumption upon need of diets, as well as the flexibility of neornithine gizzard to switch its function between food storage space and mechanical digestion cite, are likely to have allowed diet variations

within each stomach types and further facilitated avian dietary diversification, together with digestive enzymes (Chen and Zhao, 2019).

4.4.2 Gastroliths as a proxy for archosaur diet

The discriminant analyses on archosaur gastroliths shapes by stomach types show high overall discriminant accuracies at around 65% (Figure 4-6B, Table 4-6). However, the accuracy is likely to be an artefact caused by large sample size and distribution of gastroliths shapes of stomach type A. Although it is true that most of the gastroliths from stomach type A is correctly predicted to belong to stomach type A, most of the gastroliths from the other stomachs are incorrectly predicted to belong to stomach type A as well (Table S4-2). Note that crocodylian gastroliths (from stomach type D') are incorrectly predicted to belong to stomach type A. The present results highly suggest that despite of the “high” discriminant accuracies, gastroliths shapes are unlikely to be a good indicator of archosaur stomach types. The only possible exception is the discriminance among stomach types A, C, and D suggested under the analysis using individuals with more than 10 gastroliths. However, further investigations with larger sample sizes are mandatory to test if the discrimination is truly reflecting stomach type or not.

The discriminant analyses on archosaur gastroliths shapes by diet successfully differentiate plant + seed feeders from invertebrate feeders (Figure 4-6C, D, Table 4-6). Although the gastroliths morphospaces overlap with each other, 50% confidence intervals of plant + seed feeders and invertebrate feeders are reasonably apart from each other. The analyses on individuals with more than 30 gastroliths further discriminates vertebrate feeders from plant + seed and invertebrate feeders. The improvement of discriminance accuracy along with increase in minimum number of gastroliths is likely to be associated with removal of extreme values. Unlike in the analyses by stomach types, the archosaur gastroliths shapes successfully predict archosaur diet except for the omnivores. While the mispredictions of omnivores are lowering the overall discriminance accuracy, the center of their morphospace located amongst other diet types (Figure 4-6C) is in fact representing the nature as intermediate feeders. Although Gionfriddo and Best (1996) found no difference in gastroliths shapes by diet in North American neornithines, the present results strongly suggest that archosaur gastrolith shapes reflect their dietary habits. The relationship between diet and gastrolith shape is concordant with the trend observed in domestic chicks under experimental conditions (Chapter 3). The correlations between gizzard muscularity and gastrolith shape (Figure 4-6E, Table 4-7) are also consistent with the experiment (Chapter 3), suggesting that the

severe abrasions within muscular stomachs of herbivorous neornithines cause the differences in gastroliths shapes as previously demonstrated in domestic chicks (Chapter 3) and Ostrich (Wings and Sander, 2007).

Although diet of modern animals could be accurately investigated through various methods including field observations and analyzing stomach contents, the present results have significant importance in inferring diets of extinct animals. Presence of gastroliths have been considered as a definite evidence of herbivory in extinct dinosaurs (Wings and Sander, 2007; Zanno and Makovicky, 2011) and multiple studies use presence of gastroliths as one of the basis of herbivory (Kobayashi et al., 1999; Cerda, 2008; Makovicky et al., 2011; Lee et al., 2014). However, previous wisdom (Rôrig, 1907; Lambrecht, 1933; Siegel-Causey, 1990; Gionfriddo and Best, 1999) as well as the present study shows that presence of gastroliths by itself does not indicate herbivory in present-day archosaurs. Instead, this study proposes gastroliths shapes as better proxy for inferring extant archosaur diet. Application of this study therefore is expected to contribute to better understandings on extant archosaur diet and evolutionary history of gastrolith uses.

4.5 Acknowledgements

I deeply appreciate Dr. Masaki Eda (Hokkaido University Museum) and his volunteers, especially Kaoru Inada, Miu Tanaka, Takumi Sakakiyama, and Tomonori Tanaka, for collecting and managing the immersion specimens at the Hokkaido University Museum. Mr. Fumihito Takaya (Botanic Garden, Hokkaido University) kindly allowed me to work on the immersion specimens at the Botanic Garden. I would like to express my gratitude to Dr. Grahame Webb and Dr. Charlie Manolis at the Wildlife Management International Australia for managing access to the Australian crocodylian gastroliths and allowing me to dissect several captive crocodiles.

CHAPTER 5: A NOVEL NEW METHOD OF ARCHOSAUR DIET PREDICTION WITH IMPLICATIONS ON EVOLUTIONARY HISTORY OF ARCHOSAUR STOMACH

Abstract

Gastroliths (geo-gastroliths) are stones consumed and retained inside animal digestive tracts, often referred as “stomach stones” in archosaurs (crocodylians and dinosaurs including birds). Since gastroliths are especially common in modern herbivorous birds, presence of large amount of gastroliths in extinct archosaurs had been considered as a strong evidence of herbivory. However, recent works suggest that multiple non-herbivorous archosaurs often contain large amount of gastroliths, therefore the feature is unlikely a definitive evidence of herbivory. Instead, shapes of gastroliths are suggested to reflect dietary habits of archosaurs. The present study constructs a method to predict extinct archosaur dietary habits through comprehensive comparisons of extant archosaur gastroliths shapes. The new method establishes discriminant accuracy up to 78% in extant archosaurs. Diet predictions of extinct archosaurs based on gastroliths shapes are generally concordant with the previous assumptions based on osteological features in theropods, but are conflicting in non-theropod dinosaurs. While the conflicts may originate from prediction error, it may indicate that gastroliths shapes

reflect how intensely the gastroliths are used for aiding gastric mechanical digestion. Then, the diet prediction conflicts are likely to suggest that non-theropod dinosaurs did not have “gastric mill” that has high ability for gastric mechanical digestion. The ancestral state reconstructions suggest that “gastric mill” was acquired by the ancestral node of Coelurosauria, at the latest. Since this precedes appearances of edentulous theropods, acquisition of “gastric mill” might have been a key innovative factor allowing theropod edentulism. Furthermore, the intraspecific gastroliths shape variations in a Mesozoic bird *Archaeorhynchus spathula* may be capturing seasonal diet change and associated stomach phenotypic plasticity, which might have allowed them long distance migrations.

5.1 Introduction

Geo-gastroliths (hereafter called gastroliths) are sediment particles swallowed and retained inside animal digestive tracts. Among vertebrates, members of Archosauria (crocodylians and dinosaurs including birds) often contain gastroliths inside their stomachs (Cott, 1961; Gionfriddo and Best, 1999; Whittle and Everhart, 2000). Since consumption of gastroliths is especially common in herbivorous and granivorous birds (Gionfriddo and Best, 1999), presence of gastroliths have been considered as an evidence of herbivory in dinosaurs (Kobayashi et al., 1999; Zanno and Makovicky, 2011). Based on body mass – gastroliths mass relationship of herbivorous birds, Wings and Sander (2007) suggested that not simply presence of gastroliths, but having large amount of gastroliths which is about 1% of the body mass represent herbivory of dinosaurs. Following the definition, several taxa are considered herbivorous (Cerdeña, 2008; Makovicky et al., 2011; Lee et al., 2014).

However, it should be noted that gastroliths are widely reported from gizzards of insectivorous (Barlow et al., 1963; Jenkinson and Mengel, 1970; Brown, 1976; Barrentine, 1980; Potter, 1983), piscivorous (Lambrecht, 1933; McKeown, 1934; Siegel-Causey, 1990; Beaune et al., 2008), and even carnivorous birds (Rôrig, 1907; Lambrecht, 1933). Furthermore, Takasaki and Kobayashi (under prep.) demonstrated

that the body mass – gastroliths mass relationship of crocodylia is nearly identical with that of herbivorous birds. Furthermore, a strongly carnivorous non-avian dinosaur *Tarbosaurus baatar* also contain a huge amount of gastroliths in its gastric cavity (Currie, 1997). Therefore, presence of gastroliths is unlikely to be a reliable proxy for archosaur herbivory, regardless of the amount.

Chapter 4 demonstrated that gastroliths shapes can predict extant archosaur dietary habits. Although the method is not perfect, Chapter 4 demonstrated that gastroliths shape can predict diets of plant + seed feeders and invertebrate feeders in high accuracy and of vertebrate feeders in moderate accuracy. Application of this method to extant archosaur gastroliths is expected to lead to better understandings of extinct archosaur dietary habits. However, the method provided in Chapter 4 cannot be directly applied on majority of extinct archosaur gastroliths. While Chapter 4 evaluated gastroliths shapes using image analyses on completely segregated gastroliths, gastroliths of extant archosaurs are often unprepared and preserved in a mass therefore image analyses cannot be conducted. Therefore, gastroliths shape must be evaluated without using image analyses in order to predict extinct archosaur diets from gastroliths.

The present study evaluates gastroliths shapes of extant archosaurs qualitatively following Best and Gionfriddo (1991) and tests if the qualitative shape evaluation can

substitute the quantitative shape evaluation upon diet prediction. Then, gastroliths of extant archosaurs are reviewed and their shapes are evaluated qualitatively. Dietary habits of the extinct archosaurs are predicted through the comparisons with the qualitatively evaluated gastroliths shapes of extant archosaurs. Thereby, the present work attempts to establish a novel new method for inferring dietary habits of extant archosaurs. In addition to the diet predictions, gastroliths shape evaluations and thorough comparisons with gastroliths of extant birds is further expected to provide implications on evolutionary history of archosaur stomach, since gastroliths shapes reflect stomach muscularity in extant archosaurs (chapter 4).

5.2 Material and method

Since majority of gastroliths of extinct taxa are embed within the matrix, the quantitative method for evaluating gastroliths shape (chapter 4) is unavailable for extinct taxa. Therefore, gastroliths shapes of the 104 extant archosaur specimens (14 crocodylia and 90 Avialae) are re-evaluated qualitatively following Best and Gionfriddo (1991): Angular, sharp and irregular corners; Sub-angular, corners slightly rounded and inlets sharp; Sub-rounded, corners rounded and inlets more or less smooth; Rounded, corners well-rounded and only a few inlets; Well-rounded, Smoothly rounded with no

corners or inlets. Although generally all of the gastroliths shapes are evaluated, around 1,000 randomly selected gastroliths are 1,000 evaluated on specimens containing much over 1,000 gastroliths (Data S5-1). Dietary habitats of the extant birds are categorized based on (Wilman et al., 2014). Gastroliths of 38 extinct archosaur specimens are evaluated qualitatively using the same method under direct observations, high-resolution photographs, and published figures (Data S5-2). The specimens evaluated based on published figures are not incorporated into statistical analyses since shape evaluations based on single low-resolution figure are likely to produce unreliable results.

Ratios of the five gastrolith shape categories are arcsine-transformed prior to the analyses. Principal component analysis is conducted on the transformed gastrolith shape categories to reduce the dimensionality. Correlation between the present qualitative shape evaluation and the previously performed quantitative shape evaluation (chapter 4) is confirmed through regression analysis between PC1 of the quantitative and qualitative gastrolith shape proxies. Dietary habits of extinct dinosaurs are predicted through linear discriminant analyses using the extant dataset (Data S5-2) for the training data. The discriminant analysis is conducted using R package MASS version 7.3-51.4 (Venables and Ripley, 2013). The stomach muscularity – gastroliths shape relationship

is tested through regression analyses between stomach muscularity and LD1 obtained from the discriminant analyses. The evolutionary transition of archosaur gastroliths shape, which is expected to reflect stomach muscularity (chapter 4), is inferred through ancestral state reconstruction conducted using R package ape version 5.3 (Paradis and Schliep, 2019) and visualized using R package phytools version 0.6-99 (Revell, 2012). The supertree used for the ancestral state reconstruction is constructed based on Boyd (2015), Sander et al. (2011), Hendrickx et al. (2015), and O'Connor (2019). Since specimens with small number of gastroliths cause inconsistency and unreliable results (chapter 4), the statistical analyses are repeated for datasets limited to specimens with more than 0 (all), 10, 20, 30, 40, and 50 gastroliths.

5.3 Results

5.3.1 Review and description of dinosaur gastroliths

Dinosaur gastroliths are reviewed and brief supplementary descriptions are provided. Since Wings (2014) provides detailed descriptions of sauropods gastroliths, the present descriptions focus on gastroliths of ornithischians and theropods.

5.3.1.1 *Ornithischia*

Ornithischian gastroliths are best represented by *Psittacosaurus*, a basal ceratopsian dinosaur. Multiple species of *Psittacosaurus* are known for gastroliths possessions: *Psittacosaurus mazongshanensis* (Xu, 1997), *Psittacosaurus mongoliensis* (Osborn, 1924), *Psittacosaurus sibiricus* (Averianov et al., 2006), and *Psittacosaurus* sp. (Mayr et al., 2002). The gastroliths mass of *Psittacosaurus mongoliensis* (AMNH FARB 6253) is dorsoventrally compressed and is anteroposteriorly as long as transversely wide (Figure 5-1A). Their gastroliths mass is located further anterior to the anterior end of the pubis. The gastroliths mass of AMNH FARB 6253 is slightly off the center toward left side of the abdominal cavity, although it could be a result of sinuous arrangements of the dorsal vertebrae. Although detail observation of AMNH FARB 6253 is unavailable since the specimen is currently under display, its gastroliths on the right side of the abdominal cavity seem to be slightly smaller than those on the left side. The gastroliths are generally angular in *Psittacosaurus mongoliensis* (AMNH FARB 6253; roundness index = 2.63), as well as in *Psittacosaurus mazongshanensis* (roundness index = 2.55). Detailed description of gastroliths of *Psittacosaurus mazongshanensis* is provided in Xu (1997).

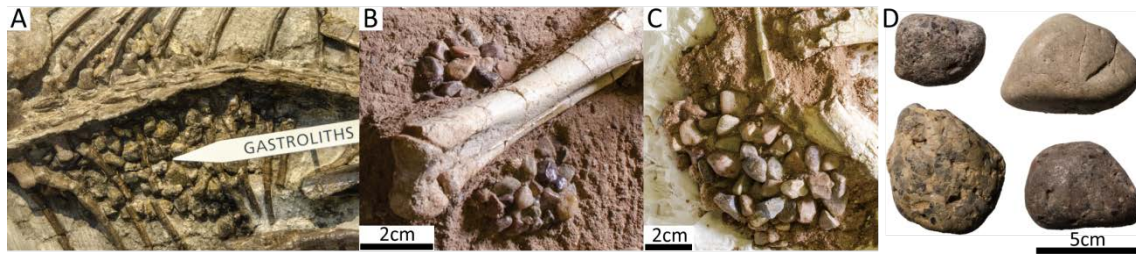


Figure 5 - 1. Ornithischian gastroliths. A, *Psittacosaurus mongoliensis* (AMNH FARB 6253); *Haya griva* (B, IGM 100/2015; C, IGM 100/3182); and D, *Edmontosaurus* (AMNH FARB 5863).

Aside from *Psittacosaurus*, a few basal ornithopods including *Haya griva* (Makovicky et al., 2011) are known to have gastroliths. In addition to IGM 100/2015 originally described, IGM 100/3182 also possesses tightly packed gastroliths mass (Figure 5-1B, C). The gastroliths mass of IGM 100/3182 is located anteromedial to the proximal end of the left tibia, suggesting less relocation than IGM 100/2015 which is located medial to the distal shaft of the tibia (Makovicky et al., 2011). The exposed gastroliths mass of IGM 100/3182 is 90 mm long anteroposteriorly, 55 mm high dorsoventrally, and 25 mm deep transversely. At least 43 gastroliths are exposed in IGM 100/3182. The minor axis of the largest gastrolith of IGM 100/3182 is 10.47 mm, which is slightly larger than that of IGM 100/2015 (8.9 mm). The size distributions of gastroliths are uniform in both specimens. The gastroliths are generally subrounded

with multiple stones retaining sharp edges in both specimens, resulting in low roundness indexes (2.69 in IGM 100/2015 and 2.70 in IGM 100/3182). Three specimens of another basal ornithopod *Gasparinisaura cincosaltensis* (MUCPv 213, MCSPv 111, MCSPv 112) also possess large number of gastroliths (Cerdeña, 2008). Cerdeña (2008) provides detailed descriptions of each specimen. It may be worth noting that shape of gastrolith largely vary individually, being more rounded in MUCPv 213 (roundness index = 3.17) and more angular in MCSPv 111 (roundness index = 2.43), although re-evaluation based on direct observation would be mandatory for further details. Gastroliths had also been reported from derived ornithopods *Iguanodon* (Rivett, 1956) and *Edmontosaurus* (AMNH FARB 5863) which was previously identified as *Claosaurus* (Brown, 1907). Although Brown (1907) noted only three pebbles from the *Edmontosaurus*, the catalogue number is given to four stones today (Figure 5-1D). Kobayashi et al. (2019) recently reported four pebbles as probable gastroliths of *Kamuysaurus japonicus*, a close relative of *Edmontosaurus*. However, rare occurrences, small number of gastroliths, and lack of details of the early records hinders further discussions of derived ornithopod gastroliths.

Other than ceratopians and ornithopods, gastroliths are rarely reported from ornithischian dinosaurs. Brown (1907) noted polished quartz pebbles near stegosaurid

bones, which is the only possible gastroliths record from the group. Two gastroliths records are present in ankylosaurs. One is the 38 gastroliths collected with *Panoplosaurus mirus* (ROM 1215), a completely disarticulated skeleton (Carpenter, 1990). Another ankylosaur gastroliths record is reported from an indeterminate ankylosaur found from the Luohandong Formation of Inner Mongolia (Ji et al., 2016). At least 22 gastroliths are located anteroventral to the synsacrum. The largest gastrolith is 23.4 mm wide in exposed minor axis and multiple large gastroliths of comparable sizes are present. The gastroliths are well-rounded (roundness index = 3.42) and flat, resembling to plesiosaur gastroliths. Although Wings (2004) also listed CEUM *Galtonia* as having gastroliths, none could be confirmed in the collection.

5.3.1.2 Non-avian theropods

Among all non-avian dinosaurs, *Sinornithomimus dongi* provides the best gastroliths records in terms of sample size and preservation status. Nearly all of the well-preserved skeletons within a bonebed possess gastroliths mass in their abdominal regions (Kobayashi et al., 1999; Kobayashi and Lu, 2003; Varricchio et al., 2008). The gastroliths masses are positioned anterior to the pubic boot of the pubis. Gastroliths masses of IVPP V11797-11, IVPP V11797-12, and one large uncatalogued specimen

are located on the left side of the abdominal cavity, while gastroliths mass of a smaller uncatalogued specimen is located on the right side of the abdominal cavity. The gastroliths masses are anteroposteriorly long and mediolaterally flat. Since the two skeletons which are dorsoventrally compressed (IVPP V11797-11, IVPP V11797-12) also show the same trend in gastroliths positioning, the anteroposteriorly long and mediolaterally flat gastroliths mass may be reflecting the shapes of *Sinornithomimus* gastric cavity. Kobayashi et al. (1999) reported over a 1,000 gastroliths from a juvenile *Sinornithomimus*. A larger uncatalogued specimen also has at least 1,070 gastroliths that are larger than 0.5 mm in minor axis exposed (Figure 5-2A). Gastroliths sizes of the large uncatalogued specimen reach up to 6.41 mm in diameter and clearly show anteroventral degradation (Figure 5-2A, B). Computed tomography image of a smaller uncatalogued specimen also suggest presence of smaller gastroliths cranioventrally (Figure 5-2C, D). *Sinornithomimus* gastroliths are well rounded in all specimens observed. Roundness index of the large uncatalogued specimen is 3.29 and is lowest cranioventrally.

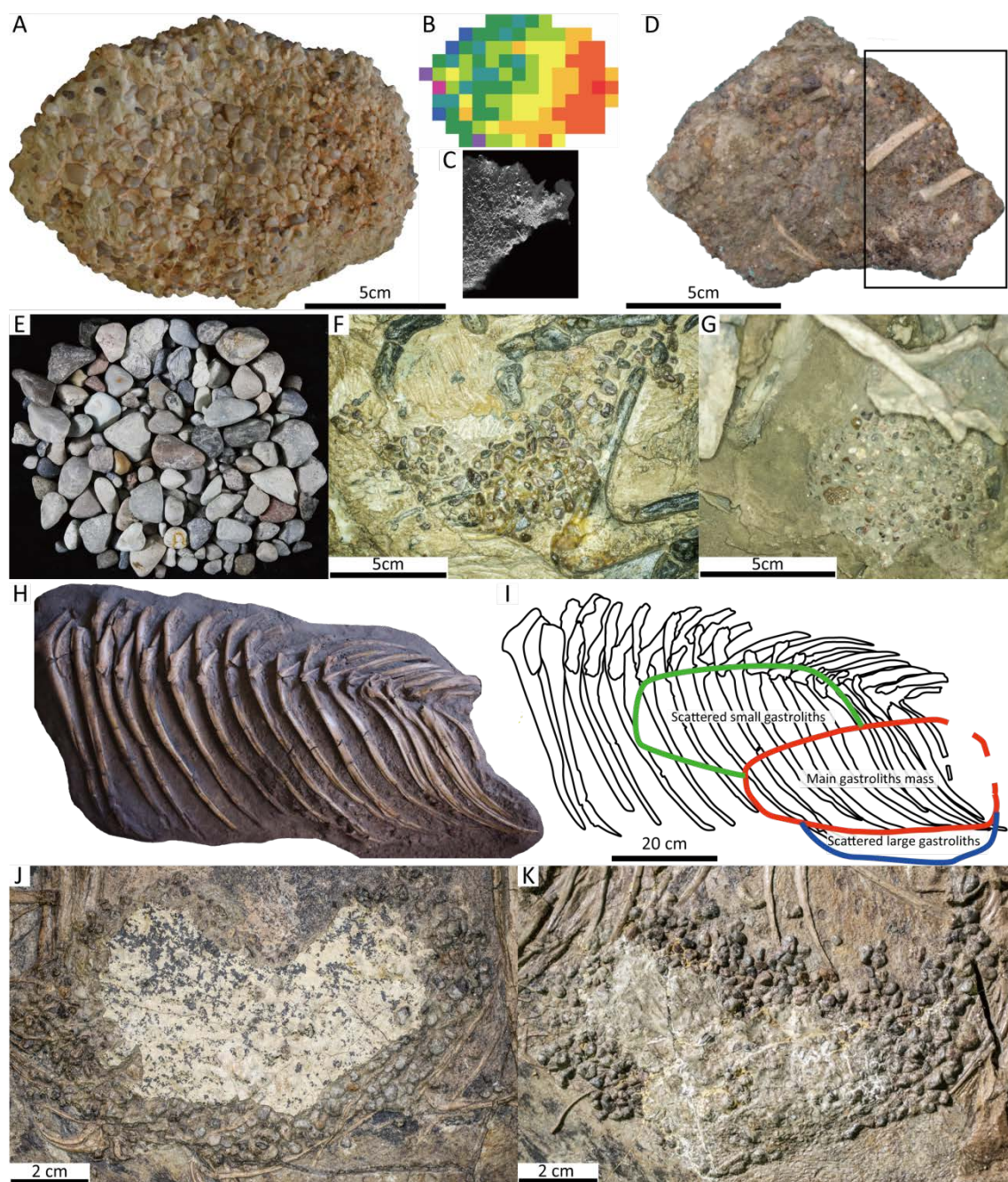


Figure 5 - 2. Theropod gastroliths. A, large *Sinornithomimus dongi* (uncatalogued) in right lateral view; B, heat map representing sizes of the gastroliths, warm color representing small and cold color representing large sizes; C, sagittal CT-image of the gastroliths mass of the small *Sinornithomimus dongi* (uncatalogued); D, small

Sinornithomimus dongi (uncatalogued) in right lateral view; E, *Deinocheirus mirificus* (MPC-D 100/127); F, *Limusaurus inextricabilis* (IVPP V15297) in left lateral view; G, *Limusaurus inextricabilis* (IVPP V15293) in right lateral view; H, *Tarbosaurus bataar* (MPC-D 552-1) in ventrolateral view; I, schematic drawing of the *Tarbosaurus* gastralium and positions of the gastroliths; J, *Caudipteryx dongi* (IVPP V12344) in left lateral view; K, *Caudipteryx* sp. (IVPP V12430) in left lateral view.

Gastroliths are present in three more ornithomimosaur taxa. At least 12 gastroliths are found associated with the semi-articulated skeleton of a basal ornithomimosaur *Nqwebasaurus thwazi* (De Klerk et al., 2000; Choiniere et al., 2012). Although the gastroliths are obviously relocated, majority of them are found close to the gastralium of *Nqwebasaurus* skeleton. *Shenzhousaurus orientalis* contains much more gastroliths than *Nqwebasaurus* does in its abdominal region (Ji et al., 2003). The gastroliths are concentrated at anterior to the anteriormost gastralium preserved, and are sparsely scattered throughout the thoracic cavity. Sizes of the gastroliths vary from less than 1 mm to 5.5mm, and the larger gastroliths are concentrated anteriorly. The gastroliths of *Shenzhousaurus* are generally angular, although majority of the stones lack sharp edges.

The RI of *Shenzhousaurus* gastroliths evaluated based on the gastroliths available from figures of Ji et al. (2003) is 2.81. Another ornithomimosaur *Deinocheirus mirificus* (MPC-D 100/127) is reported to have more than 1,400 gastroliths from the abdominal cavity (Lee et al., 2014). Majority of the gastroliths are segregated during preparation thus the original configurations of the gastroliths mass is unavailable today (Figure 5-2E). However, the partial remaining of gastrolith mass at the proximal end of the tibia indicates that the position of *Deinocheirus* do not differ largely from those in *Sinornithomimus*. Sizes of the observable 959 gastroliths vary from 1.37 mm to 60.92 mm in the intermediate axis. This is by far the largest gastroliths among the observed theropod gastroliths and is only slightly smaller than those of sauropods. The gastroliths of *Deinocheirus* are well-rounded (roundness index = 3.68).

An edentulous ceratosaur *Limusaurus inextricabilis* have gastroliths in adult specimens (e.g., IVPP V15293, IVPP V15297) but not in juvenile specimens (e.g., IVPP V20298), which may be reflecting ontogenetic diet change (Xu et al., 2009; Wang et al., 2017). The gastroliths masses of IVPP V15293 and IVPP V15297 are located anterodorsal to the pubis. The gastroliths of IVPP V15293 are arranged in a ventrally convex kidney-shape (Figure 5-2F). Larger stones are concentrated on the anteroventral region and smaller stones are concentrated on the anterodorsal region of the gastroliths

mass. Multiple gastroliths are overlapping the left pubis laterally. While this may be a result of gastroliths relocation after death, it may be reflecting life position of the stomach. The gastroliths of IVPP V15297 are accumulated in a semicircular region that is approximately 100 mm long and 70 mm high. The sizes of the gastroliths are nearly uniform within the region unlike in IVPP V15293. The gastroliths are generally less than 5 mm wide except for the largest stone in which the exposed minor axis is 10.1 mm. The gastroliths mass is located slightly left to the midline of the dorsal vertebrae. The gastroliths of both large *Limusaurus* are moderately rounded with roundness index of 2.96.

Although presence of gastroliths is often considered as a proxy for herbivory, there are multiple occurrences are known from supposed carnivorous theropods. The first record is the eight to ten pebbles found among the bones of a megalosaurid *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1838). A rounded 10 mm long quartz pebble found among the ribs a coelophysoid *Podokesaurus holyokensis* is also considered as a gastrolith (Tarlbot, 1911). Another coelophysoid taxon *Syntarsus* (*Coelophysis*) is also reported to be associated with gastroliths associated, but detail is not provided (Whittle and Everhart, 2000). A compsognathid *Sinocallipteryx* sp. contains four large gastroliths (minor axis of largest gastroliths = 12 mm) within its

abdominal cavity, associated with undigested stomach contents. The gastroliths of *Sinocallipteryx* are located anterior to the pubis along the ventral margin of the gastralium. A gastrolith of a spinosaurid *Baryonix walkeri* is found within its rib-cage, associated with fish and *Iguanodon* remains (Charig and Milner, 1997). While the theropods listed above have only less than 10 gastroliths, an allosauroid *Lourinhanosaurus antunesi* is unique in having 32 gastroliths and negative imprints of three more gastroliths within its rib cage (Mateus, 1998).

Although Suzuki and Watabe (2000) reported gastroliths from small-sized *Tarbosaurus bataar* based on field identifications, the specimen was later re-identified as an ornithomimosaur after preparation. However, a *Tarbosaurus bataar* skeleton (MPC-D 552-1, formerly PIN 552-1) in which femur length is 995 mm actually contains a large number of gastroliths in its abdominal region (Figure 5-2H, I). Since the skeleton has at least 17 pairs of gastralium while a *Tyrannosaurus rex* is known for at least 14 pairs (Brochu, 2003), the abdominal cage of this *Tarbosaurus* is expected to be nearly complete. Nearly all of the stones are retained medial to the rib and gastralium of the skeleton, which is filled with fine to medium sandstone. Although Currie (1997) considered these stones were acquired after death during burial, nearly complete inclusion of the stones medial to the abdominal cage and the large sizes of the stones

compared to the matrix strongly suggest the stones were acquired during prior to the death of the animal, regardless of the function. At least 682 stones are laterally exposed and the transverse section at the posterior end shows that the gastroliths mass is at least 3 cm thick. The gastroliths are present in the left lateral abdominal cavity from the 5th gastralium to the 17th gastralium. The position of the gastroliths at the posteroventral end of the abdominal cage is concordant with those known in *Sinornithomimus dongi* (Kobayashi and Lu, 2003). Within the abdominal cavity, gastroliths are small and their density is low anteroventrally. The gastroliths are densely compacted in the posteroventral abdominal cavity, while they are scarce but large in the posterodorsal abdominal cavity. Sizes of the gastroliths vary from less than 1 mm to 17.6 mm wide. The gastroliths are generally angular and have roundness index of 2.49. Roundness index are uniform anteroposteriorly except for the region anterior to the 8th gastralium in which the roundness index is much lower than the average (2.18).

Feathered oviraptorosaur *Caudipteryx* is one of the first non-avian theropod dinosaurs in which gastroliths possession is reported (Ji et al., 1998). In addition to the two *Caudipteryx zoui* specimens (NGMC 97-4-A, NGMC 97-9-A) described by Ji et al. (1998), Talori et al. (2018) recently reported two more *Caudipteryx* specimens having gastroliths (*Caudipteryx dongi* IVPP V12344, *Caudipteryx* sp. IVPP V12430). The left

lateral surfaces of the gastroliths masses are unprepared for preservational purpose thus the details in this region are unavailable. However, margins of the gastroliths masses are fully exposed thus approximately 200 gastroliths are observable in both specimens (Figure J, K). The gastroliths mass of IVPP V12430 is densely compacted and has ventrally convex kidney-shaped outline. IVPP V12344 has slightly more scattered gastroliths mass that pinches off posteriorly as in *Caudipteryx zoui* NGMC 97-9-A (Ji et al., 1998). Gastroliths of the two *Caudipteryx* are generally larger than 1 mm in minor axis, with the largest being 4.5 mm in IVPP 12430 and 6.5 mm in IVPP V12344. The size and roundness distributions of the gastroliths are nearly uniform anteroposteriorly and dorsoventrally in both *Caudipteryx* specimens observed. Roundness indexes are high in both specimens (3.23 in IVPP V12344 and 3.30 in IVPP V12430).

5.3.1.3 Mesozoic birds

Gastroliths are known from a large number of Mesozoic birds, all of which occurring from Cretaceous deposits of China. At least five individuals of seed eating bird *Jeholornis prima* (Zhou and Zhang, 2002) are found associated with gastroliths (O'Connor et al., 2017; O'Connor, 2019). The gastroliths masses of STM 2-15 and STM 2-31 are preserved nearly in situ at their abdominal regions. The gastroliths mass of

STM 3-31 is also positioned near the abdominal region but is out of the bird's gastral basket. At least 40 stones are identifiable externally in these gastroliths masses and they are tightly compacted and form subcircular blocks. The gastroliths sizes vary from less than 0.5 mm up to 3 mm in minor axis. Roundness indexes of these gastroliths masses are moderately high at around 3.1. The gastroliths of the other two *Jeholornis* specimens (STM 3-19, STM 3-28) are largely relocated out of the abdominal cavity and are smaller in number and size. Another seed eating bird *Sapeornis chaoyangensis* also have reports of gastroliths from multiple individuals (Zheng et al., 2011; O'Connor, 2019), although their details are unavailable at this point. An enantiornithean *Bohaiornis guoi* is associated with several stones in the abdominal region, which were initially interpreted as gastroliths (Li et al., 2014). However, they had recently been recognized as a type of mineral precipitation therefore the stones are not actually gastroliths (O'Connor, 2019).

Five individuals of an ornithuromorph *Archaeorhynchus spathula* are associated with gastroliths (Zhou and Zhang, 2006; Zhou et al., 2013; Wang and Zhou, 2016; O'Connor, 2019). The gastroliths are preserved in situ and are tightly compacted to form semicircular gastroliths masses in four specimens (IVPP V17075, IVPP V 17091, IVPP V 20312, and STM 7-11) and are scattered but still within its abdominal cavity in

IVPP V14287 (Figure 5-3A-D). The gastroliths are generally large in IVPP V14287 and IVPP V 17091 (minor axis >1.5 mm) whereas they are generally small in IVPP V17075 and IVPP V20312 (minor axis < 1.0 mm). The gastroliths roundness index of *Archaeorhynchus spathula* largely varies from 2.65 in IVPP V17963 and high 3.53 in IVPP V14287. Gastroliths of *Bellulornis rectusunguis* (IVPP V17970) are located in the abdominal region anteroventral to the synsacrum as a mass (Wang et al., 2016b). More than half of *Bellulornis* gastroliths are larger than 2 mm in minor axis, and the largest gastrolith is 5.5 mm wide (Figure 5-3E). *Eogranivora edentulata* (STM 35-3) retains its gastroliths anteroventral to synsacrum (Zheng et al., 2018). The gastroliths are preserved in both the main (12) and the counter slabs (approximately 100). In exchange to the large number, the gastroliths are generally small and barely reach 1 mm in minor axis. The gastroliths of *Eogranivora* are moderately rounded (RI = 3.19). A long beaked ornithuromorph *Changzuornis ahgm* (AGB 5840) has six gastroliths in its abdominal region (Huang et al., 2016). The semicircular depression that separates the gastroliths anteroposteriorly is highly indicates that the specimen had more gastroliths in life (Figure 5-3F). The remaining gastroliths are large (minor axis < 3.3. mm) and are moderately rounded. Another long beaked ornithuromorph *Dingavis longimaxilla* (IVPP V20284) retains approximately 40 gastroliths ventral to the synsacrum (O'Connor et al.,

2016). They are less densely compacted than in gastroliths masses of *Jeholornis prima*, *Archaeorhynchus spathula*, *Bellulornis rectusunguis*, *Gansus yumenensis*, and *Iteravis huchzemeyeri*, although that could simply be preservational. The minor axes of *Dingavis longimaxilla* gastroliths range from 1.4 mm to 3.4 mm. *Hongshanornis longicreta* (DNHM D2945) retains five gastroliths and six gastrolith imprints in its abdominal region (Chiappe et al., 2014). The gastroliths and the imprints are not as tightly compacted as in most of the other birds describe above. The largest gastrolith imprint is 1.9 mm wide in minor axis.

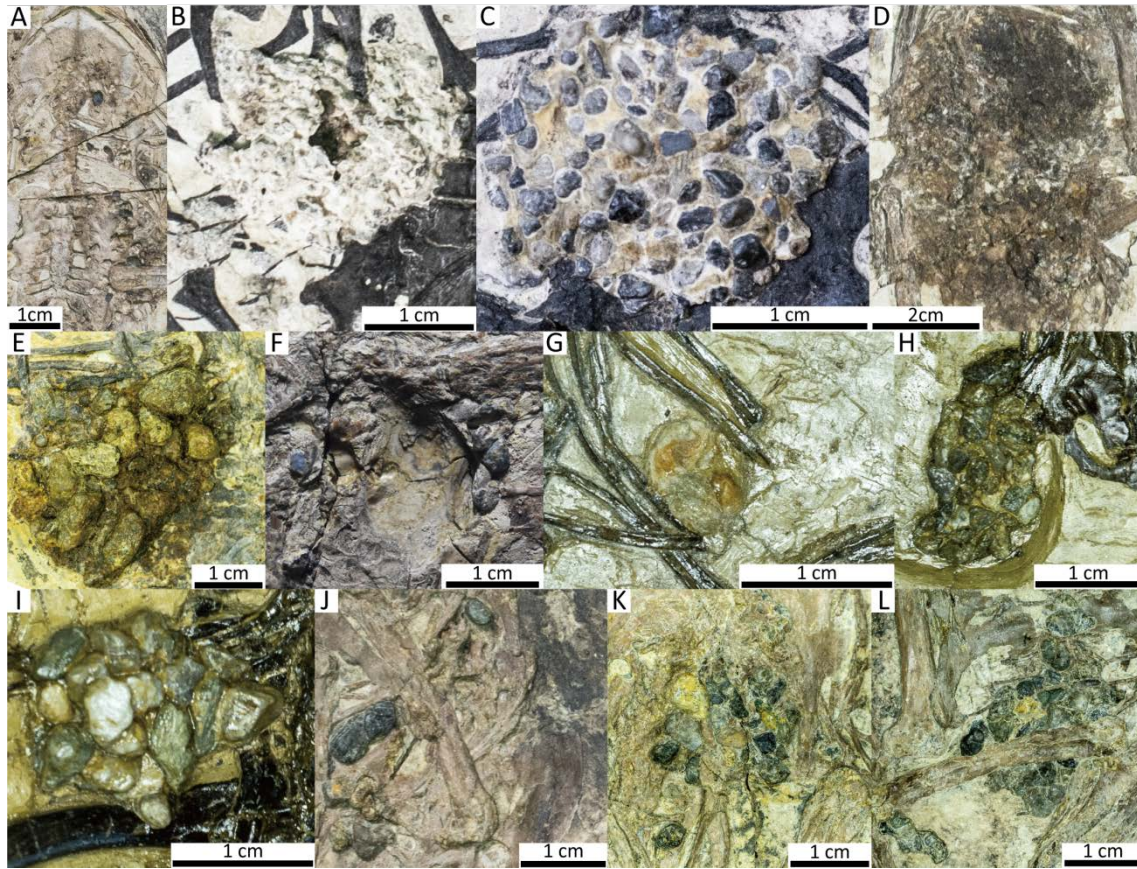


Figure 5 - 3. Mesozoic bird gastroliths. *Archaeorhynchus spathula* (A, IVPP V14287; B, IVPP V17075; C, IVPP V17091; D, IVPP V20312); E, *Bellulornis rectusunguis* (IVPP V17970); F, *Changzuiornis ahgm* (AGB 5840); *Gansus yumenensis* (G, CGCS 05-CM-014; H, CGCS 06-CM-011; I, CGCS 07-CM-001); *Iteravis huchzermeyeri* (J, IVPP V18958; K, V20133; L, IVPP V20134).

Gastroliths mass of a piscivorous bird *Yanornis martini* (IVPP V13358) are concentrated in the posteroventral abdominal region and is dorsoventrally elongated

(Zhou et al., 2004). While the largest gastrolith is as wide as 2.2 mm in minor axis, majority of the gastroliths are less than 0.5 mm wide. The *Yanornis* gastroliths were initially considered as an evidence of herbivory and possible indicator of seasonal diet change (Zhou et al., 2004). However, Zheng et al. (2014) later concluded that the gastroliths represent sand impacted in intestines rather than stomach stones that aid grinding fibrous food, based on the position of the gastroliths mass and the rarity of gastroliths occurrence from *Yanornis*. Gastroliths in another *Yanornis* specimen (STM 9-51) are considered to be ingested accidentally. Three specimens of aquatic bird *Gansus yumenensis* (CGCS 05-CM-014, CGCS 06-CM-011, CGCS 07-CM-001) are associated with gastroliths (Wang et al., 2015). While only three gastroliths are preserved in semi-articulated skeleton CGCS 05-CM-014, at least 34 (CGCS 06-CM-011) and 18 (CGCS 07-CM-001) gastroliths are preserved in a mass (Figure 5-3G-I). The gastroliths masses are located posterior to the sternum and are slightly displaced to the right side of the abdominal cavity in both specimens. The gastroliths are generally larger than 2 mm in minor axis in both specimens. The gastroliths of *Gansus yumenensis* are generally angular (RI = 2.32 in CGCS 06-CM-011 and 2.94 in CGCS 07-CM-001) and bear multiple pits and grooves on the surfaces. Another aquatic ornithuromorph *Iteravis huchzermeyeri*, including those previously named *Gansus zheni*,

also have gastroliths (Liu et al., 2014; Zhou et al., 2014; Wang et al., 2018; O'Connor, 2019). Although the type specimen IVPP V18958 has only 6 gastroliths scattered near the pelvic girdle, gastroliths of other specimens (AGB 5841, BMNHC-Ph 1318, BMNHC-Ph 1342, IVPP V20133, IVPP V20134) form compact gastroliths masses that are located in the left side of their abdominal regions (Figure 5-3J-L). The gastroliths are generally large and the largest gastroliths of each specimen are at least 3 mm wide in minor axis. The gastroliths of *Iteravis huchzermeyeri* are generally angular with roundness index less than 3.0 in all known individuals.

The 19 gastroliths of *Chongmingia zhengix* (STM 9-9) are scattered widely in the anterior thoracic region instead of forming a mass in abdominal region (Wang et al., 2016a). The gastrolith roundness evaluated based on Figure 1 of Wang et al. (2016a) are generally low (RI = 2.89), although direct observation is preferred for accurate evaluation.

5.3.2 Statistical analyses

The principal component analyses successfully reduced the dimensionalities of the gastroliths shape proxies. PC1 explains more than 70% of the variance in all of the analyses except for the analysis including all specimens (Table S5-1). The PC1 of

qualitative gastroliths shape proxy is generally correlated with the PC1 of the quantitative gastroliths shape proxy (Figure 5-4, Table 5-1), suggesting that the qualitative method utilized herein can substitute the quantitative method presented in the previous chapter. The discriminant analyses on the extant archosaur gastroliths shapes resulted in overall discriminant accuracies higher than 60% in all analyses (Figure 5-5, Table 5-2, Table S5-2). The discriminant accuracies are generally high for invertebrates and plant + seed feeders, whereas they are generally low in omnivores. The discriminant accuracies of vertebrate feeders and omnivores are significantly low in the analyses incorporating all specimens than the analyses incorporating specimens containing more than 10 gastroliths, suggesting that at least 10 gastroliths, preferably more than 30 gastroliths, are mandatory to obtain reliable predictions. With the exception of the analysis incorporating all specimens, LD1 explains relative proportions of angular + sub-angular gastroliths vs sub-rounded + rounded + well-rounded gastroliths. Invertebrate and vertebrate feeders tend to have more angular gastroliths than the plant + seed feeders, which is concordant with the analyses based on quantitative method (chapter 4).

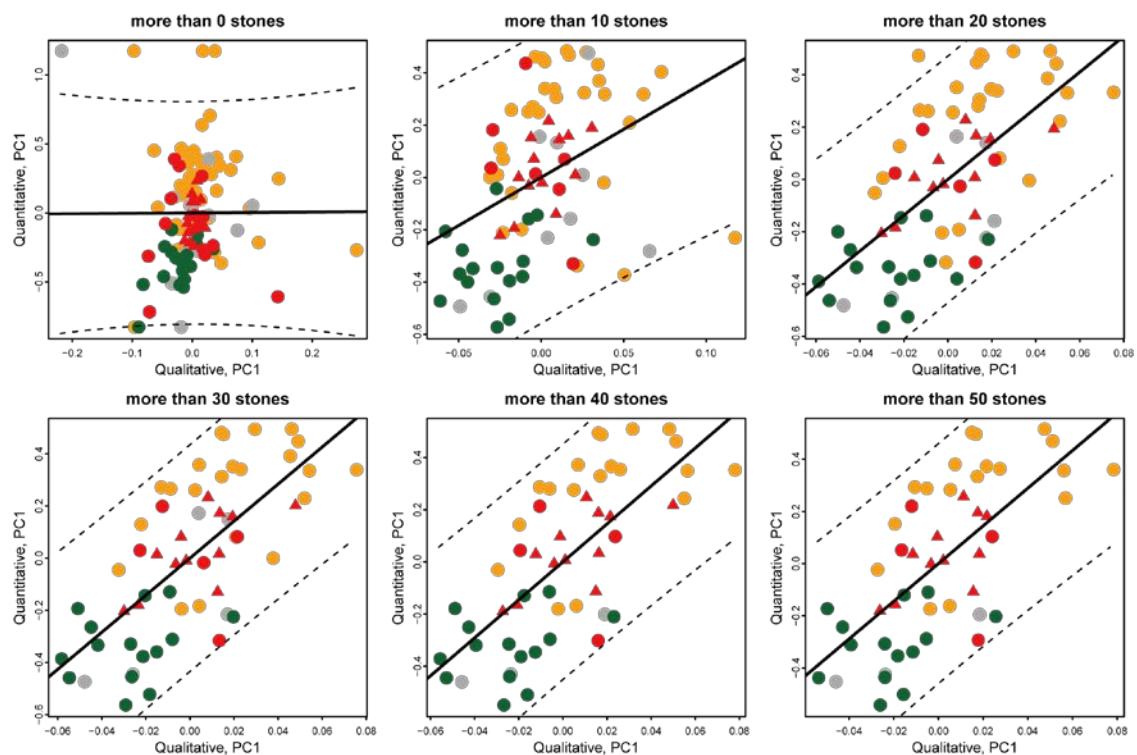


Figure 5 - 4. Results of the regression analyses between the PC1 of the quantitative gastroliths shape proxies and the PC1 of the qualitative gastroliths shape proxies.

Solid lines are the regression lines and the dotted lines represent the 95% prediction intervals.

Table 5 - 1. Results of the regression analyses between PC1 scores of gastroliths shapes evaluated based on qualitative and quantitative methods

		Predicted				
		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	0<	Invertebrate	37	0	4	4
		Omnivore	6	0	5	2
		Plant + Seed	0	0	15	3
		Vertebrate	14	1	3	10
	10<	Invertebrate	21	0	3	7
		Omnivore	2	3	3	1
		Plant + Seed	0	1	13	3
		Vertebrate	4	1	1	14
	20<	Invertebrate	20	0	1	6
		Omnivore	1	1	3	1
		Plant + Seed	0	1	13	2
		Vertebrate	5	0	2	10
	30<	Invertebrate	17	0	0	5
		Omnivore	0	1	2	2
		Plant + Seed	0	0	13	2
		Vertebrate	1	1	2	13
	40<	Invertebrate	16	0	0	3
		Omnivore	0	1	2	0
		Plant + Seed	0	0	12	3
		Vertebrate	2	0	2	12
	50<	Invertebrate	15	0	0	3
		Omnivore	0	1	2	0
		Plant + Seed	0	0	11	3
		Vertebrate	1	0	2	12

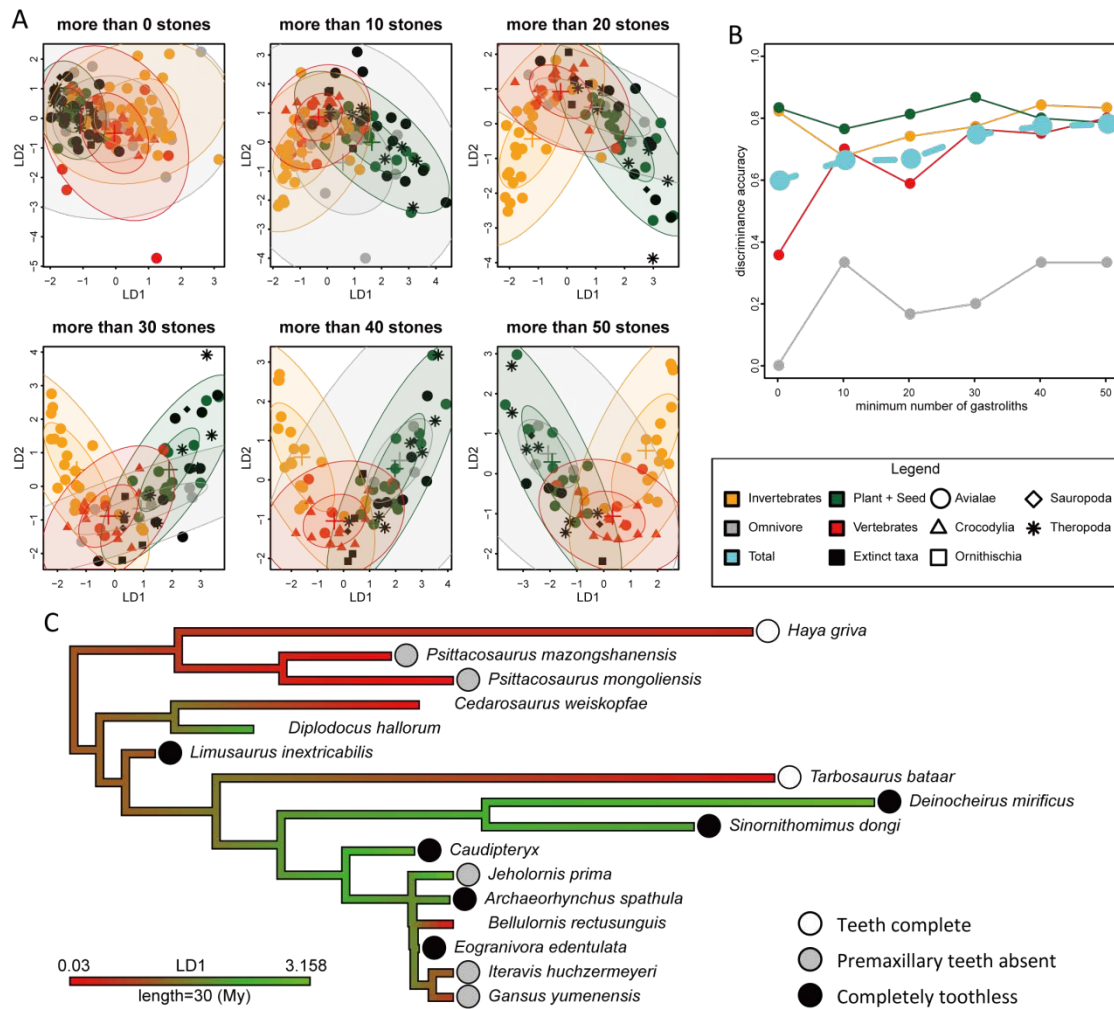


Figure 5 - 5. (A) Bivariate plots of LD1 and LD2 scores obtained from the discriminant analyses under six different minimum gastroliths numbers. Inner and outer ellipses represent 50% and 95% confidences for each diet categories, respectively. (B) Discriminance accuracies of diet types in the six analyses under different minimum gastroliths numbers. (C) Hypothetical evolutionary history of archosaur stomach muscularity, represented by gastrolitshs shape (LD1 value).

Table 5 - 2. Summary of the diet type discriminance accuracies by gastroliths shapes in the six analyses performed by different minimum number of gastroliths. Detail is provided in the Table S5-2.

	Invertebrate	Omnivore	Plant + Seed	Vertebrate	Overall
All	0.82	0.00	0.83	0.36	0.60
>10	0.68	0.33	0.76	0.70	0.66
>20	0.74	0.17	0.81	0.59	0.67
>30	0.77	0.20	0.87	0.76	0.75
>40	0.84	0.33	0.80	0.75	0.77
>50	0.83	0.33	0.79	0.80	0.78

The predicted dietary habits of the extinct archosaurs are generally consistent among the analyses other than the one incorporating all specimens regardless of gastroliths number (Table 5-3), which produce sub-equal posterior probabilities among all of the diet categories (Table S5-3). The ornithischians *Haya griva* and *Psittacosaurus* are predicted as omnivore or vertebrate feeders, despite that they are previously considered as herbivorous (Serenio et al., 2010; Makovicky et al., 2011). A sauropod *Diplodocus hallorum* is as predicted as plant + seed feeder, as sauropods are suggested to be (Sander et al., 2011). However, the other sauropod analyzed herein *Cedarosaurus weiskopfae* is predicted as a vertebrate feeder based on its gastroliths shape. Diet predictions by gastroliths shapes are more consistent with the diet previously suggested by osteological features in non-avian theropods than in ornithischians and sauropods.

The only exceptions are *Limusaurus inextricabilis* specimens which generally have low supports for the predictions (posterior probabilities <50%) and are predicted as vertebrate feeders under several conditions. Mesozoic birds *Eogranivora edentulata* and *Jeholornis prima* are predicted as plant + seed feeders with strong supports. *Archaeorhynchus spathula* is generally predicted as plant + seed feeder. However, it should be noted that while the prediction is strongly supported in IVPP V14287 and IVPP V 17091, the posterior probabilities are much lower in IVPP V17075 and V20312, which are occasionally predicted as omnivore or vertebrate feeder under several conditions. Aquatic ornithuromorph *Gansus yumenensis* and *Iteravis huchzermeyeri* are predicted as vertebrate feeders. Another ornithuromorph *Bellulornis rectusunguis* is also predicted to be a vertebrate feeder.

Table 5 - 3. Predicted diets of extant archosaurs based on gastroliths shapes under six analyses performed under different minimum gastroliths numbers. Refer Table S5-3 for posterior probabilities.

ID	Taxa	Group	Predicted diet					
			0<	10<	20<	30<	40<	50<
IGM 100/2015	<i>Haya griva</i>	Ornithischia	<i>Vertebrate</i>	Omnivore	Omnivore	Omnivore	Omnivore	–
IGM 100/3182	<i>Haya griva</i>	Ornithischia	<i>Plant + seed</i>	Vertebrate	Vertebrate	Vertebrate	Vertebrate	–
IVPP V12165	<i>Psittacosaurus mazongshanensis</i>	Ornithischia	<i>Vertebrate</i>	Vertebrate	Vertebrate	Vertebrate	Vertebrate	Vertebrate
AMNH 6253	<i>Psittacosaurus mongoliensis</i>	Ornithischia	<i>Invertebrate</i>	Vertebrate	Vertebrate	Vertebrate	Vertebrate	–
DMNH 39045	<i>Cedarosaurus weiskopfae</i>	Sauropoda	<i>Vertebrate</i>	Vertebrate	Vertebrate	Vertebrate	Vertebrate	Vertebrate
NMMNH 3690	<i>Diplodocus hallorum</i>	Sauropoda	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
IVPP V12344	<i>Caudipteryx dongi</i>	Theropoda	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
IVPP V12430	<i>Caudipteryx</i> sp.	Theropoda	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
MPC-D 100/127	<i>Deinocoelurus mirificus</i>	Theropoda	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
IVPP V15293	<i>Limusaurus inextricabilis</i>	Theropoda	<i>Plant + seed</i>	<i>Plant + seed</i>	<i>Plant + seed</i>	Plant + seed	Plant + seed	Vertebrate
IVPP V15297	<i>Limusaurus inextricabilis</i>	Theropoda	<i>Vertebrate</i>	<i>Plant + seed</i>	<i>Vertebrate</i>	<i>Plant + seed</i>	Plant + seed	Vertebrate
uncatalogued	<i>Sinornithomimus dongi</i>	Theropoda	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
MPC-D 552-1	<i>Tarbosaurus bataar</i>	Theropoda	<i>Invertebrate</i>	Vertebrate	Vertebrate	Vertebrate	Vertebrate	Vertebrate
IVPP V14287	<i>Archaeorhynchus spathula</i>	Avialae	Plant + seed	Plant + seed	Plant + seed	Plant + seed	–	–
IVPP V17075	<i>Archaeorhynchus spathula</i>	Avialae	<i>Vertebrate</i>	Plant + seed	<i>Plant + seed</i>	Omnivore	Omnivore	Omnivore
IVPP V17091	<i>Archaeorhynchus spathula</i>	Avialae	<i>Plant + seed</i>	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
IVPP V20312	<i>Archaeorhynchus spathula</i>	Avialae	<i>Plant + seed</i>	<i>Plant + seed</i>	<i>Plant + seed</i>	<i>Vertebrate</i>	<i>Plant + seed</i>	–
IVPP V17970	<i>Bellulornis rectusunguis</i>	Avialae	<i>Vertebrate</i>	Vertebrate	–	–	–	–
CGCS 06-CM-011	<i>Gansus yumenensis</i>	Avialae	<i>Vertebrate</i>	Vertebrate	Vertebrate	Vertebrate	–	–
CGCS 07-CM-011	<i>Gansus yumenensis</i>	Avialae	<i>Vertebrate</i>	Omnivore	–	–	–	–
IVPP V18958	<i>Iteravis huchzermeyeri</i>	Avialae	<i>Invertebrate</i>	–	–	–	–	–
IVPP V20133	<i>Iteravis huchzermeyeri</i>	Avialae	<i>Vertebrate</i>	Vertebrate	–	–	–	–
IVPP V20134	<i>Iteravis huchzermeyeri</i>	Avialae	Vertebrate	Vertebrate	–	–	–	–
STM35-3	<i>Eogranivora edentulata</i>	Avialae	Plant + seed	Plant + seed	Plant + seed	Plant + seed	–	–
STM2-15	<i>Jeholornis prima</i>	Avialae	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	–
STM2-31	<i>Jeholornis prima</i>	Avialae	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed
STM3-19	<i>Jeholornis prima</i>	Avialae	Plant + seed	–	–	–	–	–
STM3-28	<i>Jeholornis prima</i>	Avialae	Plant + seed	Plant + seed	–	–	–	–
STM3-31	<i>Jeholornis prima</i>	Avialae	Plant + seed	Plant + seed	Plant + seed	Plant + seed	Plant + seed	–

Bold: posterior probability > 90%
Italic: posterior probability < 50%

5.4 Discussion

The present work proposes a novel new method for inferring extinct archosaur dietary habits using gastroliths shapes. Although it should be kept in mind that this method is not perfect (maximum discriminant accuracy 78%), the present method is expected to serve as a new option for inferring extant archosaur dietary habits, in addition to previously used methods (e.g., osteological features, stable isotopes, stomach contents).

While the discriminant analyses on the extant archosaurs demonstrate moderately high discriminant accuracies (Table 5-2), dietary habit predictions for multiple ornithischians and sauropods contradict with previous assumptions: *Haya griva* is predicted as omnivorous and vertebrate feeder and *Psittacosaurus* and *Cedarosaurus weiskopfae* are predicted as vertebrate feeders, although all of them had previously been considered as herbivores. Since herbivory of *Haya griva* is inferred solely from presence of large amount of gastroliths, which is does not always represent herbivory (Chapter 4), the prediction may reflect actual dietary habit of *Haya griva*. However, it is less likely in *Psittacosaurus* since multiple osteological features of *Psittacosaurus* strongly suggest herbivorous diet of the taxa (Serenio et al., 2010). *Cedarosaurus weiskopfae* is also unlikely to be a vertebrate feeder since the animal is too huge to hunt another vertebrate for feeding and sauropods have multiple adaptations toward herbivory such as oral processing and gut fermentations (Hummel and Clauss, 2011).

While the conflicts may suggest that the diet predictions using gastroliths shapes are only applicable to theropods, it also indicates that the archosaur gastroliths shapes actually reflect how intensely the gastroliths are used for aiding gastric mechanical digestion. In fact, chapter 3 demonstrated that gastroliths shapes are determined by abrasions within stomach upon aiding mechanical digestion, suggesting that the angular

gastroliths had less contribution for gastroliths mechanical digestion. Since the gastric mechanical digestion is supported by muscular stomachs (Moore, 1999), the correlations between the stomach muscularity and gastroliths shapes in extant archosaurs in both quantitative (chapter 4) and qualitative (Table 5-4) methods further support the assumption. Then, the angular gastroliths masses of *Haya griva*, *Psittacosaurus*, and *Cedarosaurus weiskopfae* indicate that these taxa did not have strong muscular gastric mill and that their gastroliths did not aid gastric digestion as much as in modern granivorous birds. The relatively rounded gastroliths of *Diplodocus hallorum* may be reflecting the initial shapes of the stones consumed, since sauropods are considered to have no gastric mill (Wings and Sander, 2007) therefore their gastroliths are unlikely to have experienced severe abrasions within stomach.

Table 5 - 4. Results of the regression analyses on PC1 values of gastroliths shapes against archosaur stomach muscularities.

	Slope	Intercept	R2	p-value
All	-1.03	-1.95	0.08	0.0159
>10	2.23	4.32	0.27	0.0001
>20	3.43	6.46	0.39	0.0000
>30	3.53	6.71	0.43	0.0000
>40	4.02	7.55	0.44	0.0000
>50	-3.78	-7.07	0.41	0.0001

The assumption that gastroliths shapes reflect adaptation for gastric mechanical digestion provides implications on archosaur stomach evolutionary history. Although the incompleteness of the fossil records strongly limits the taxa to be analyzed, the ancestral state reconstructions suggest that high ability for gastric mechanical digestion was accomplished by the ancestral node of Coelurosauria, at the latest (Figure 5-5B). The anteroventral concentrations of smaller gastroliths in *Tarbosaurus* and *Sinornithomimus* may further indicate presence of two-chambered stomach in Coelurosauria, although further observations in both extant and extinct archosaurs are mandatory to test the assumption. The moderate LD1 value of *Limusaurus inextricabilis* gastroliths indicate that stomach of this taxa was not highly adapted for gastric mechanical digestion, despite of the large amount and consistent occurrences of gastroliths from multiple adult specimens (Wang et al., 2017). Therefore, *Limusaurus inextricabilis* may represent a transitional stage from basal archosaur stomach incapable of gastric mechanical digestion to avian style stomachs that are capable of, though not always, mechanically digesting ingesta inside their stomach. Since stomach types limit dietary habits in extant birds (chapter 4) which completely lack oral mastication ability (Moore, 1998a), the acquisition of the basis for gastric mechanical digestion might had been a key factor that triggered edentulism that independently occurred multiple times

in Maniraptoriformes (ornithomimosaurs, therizinosaurs, oviraptors, and aves). The associations between the relatively rounded gastroliths and the edentulism further support that acquisition of “gastric mill” is a key to allow tooth loss in archosaurs (Figure 5-5)

Among the Mesozoic birds, O’Connor (2019) dismissed granivory of the aquatic ornithuromorphs *Gansus yumenensis* and *Iteravis huchzermeyeri* and questioned their herbivory primarily based on presence of teeth. The present analyses agree with O’Connor (2019) that *Gansus yumenensis* and *Iteravis huchzermeyeri* and further suggest they were primarily vertebrate feeders. The anatomical similarities of *Gansus yumenensis* with foot-propelled diving birds (You et al., 2006) may suggest that *Gansus yumenensis* were foraging on water and had piscivorous diet. Strong supports for plant + seed diet in *Jeholornis prima* is concordant with common seed occurrences from their stomach contents (Zhou and Zhang, 2002; O’Connor, 2019). The well-rounded gastroliths of *Jeholornis prima* and presence of teeth together suggest that stomach adaptation is more important for herbivory than tooth loss. Unlike in *Jeholornis prima*, the supports for plant + seed diet based on gastroliths shapes are inconsistent in *Archaeorhynchus spathula* (Table 5-3, Table S5-3). If the inconsistency does not derive from the prediction uncertainties, plant + seed feeding in two individuals and possible

omnivory and vertebrate feeding in the other individuals may represent diet change often associated with breeding seasons in extant birds (e.g., del Hoyo et al., 2005). Although the dynamic seasonal diet change of *Yanornis* proposed in Zhou et al. (2004) is now considered unlikely (Zheng et al., 2014), the present result supports that Ornithuromorpha had diet switching behavior. The gastroliths shape variations and the associated diet shifts among *Archaeorhynchus spathula* further indicate stomach phenotypic plasticity (Starck, 1999; Dekinga et al., 2001). Since the stomach phenotypic plasticity is an important factor determining long distance migration strategies (van Gils et al., 2005), ornithuromorphs might have been capable of traveling extremely long distances as modern day migratory birds do, although discoveries of same taxa from different continents would be desirable to test it.

5.5 Acknowledgements

Observations of fossil archosaur gastroliths were established with kind help of Carl Mehling (American Museum of Natural History), Jingmai O'Connor (Institute of Vertebrate Paleontology and Paleoanthropology, China), Kristen MacKenzie (Denver Museum of Nature and Science), Nicole Ridgwell (New Mexico Museum of Natural History and Sciences), Tsogtbaatar Chinzorig (IP-MAS), and Xu Xing (Institute of

Vertebrate Paleontology and Paleoanthropology, China). I deeply appreciate Dr. Masaki Eda (Hokkaido University Museum), Mr. Fumihito Takaya (Botanic Garden, Hokkaido University), Dr. Grahame Webb and Dr. Charlie Manolis (Wildlife Management International Australia) for access to extant archosaur gastroliths. I would also like to thank Jingmai O'Connor and the lab members at the Hokkaido University, especially Junki Yoshida, Atsushi Hori, Masaya Iijima, Tomonori Tanaka, and Tsogtbaatar Chinzorig for their help and comments to improve the present study.

SUPPLEMENTARY INFORMATION

Data S1.2 - 1. ROM specimens used for phylogenetic analysis

ID	Element
ROM 53493	Parietal
ROM 53494	Supraoccipital
ROM 53499	Prefrontal
ROM 53500	Prefrontal
ROM 53501	Frontal
ROM 53502	Frontal
ROM 53503	Exoccipital
ROM 53504	Exoccipital
ROM 53509	Squamosal
ROM 53510	Squamosal
ROM 53511	Lacrima
ROM 53512	Lacrima
ROM 53513	Postorbital
ROM 53514	Postorbital
ROM 53515	Quadratojugal
ROM 53516	Quadratojugal
ROM 53518	Jugal
ROM 53519	Jugal
ROM 53520	Jugal
ROM 53521	Quadrate
ROM 53522	Quadrate
ROM 53523	Nasal
ROM 53524	Nasal
ROM 53525	Premaxilla
ROM 53526	Premaxilla
ROM 53527	Maxilla
ROM 53528	Maxilla
ROM 53529	Dentary
ROM 53530	Dentary
ROM 53535	Surangular
ROM 53536	Surangular
ROM 53537	Prootic
ROM 53538	Basioccipital (cast)
ROM 53539	Pterygoid

Data S1.2 - 2. Character-taxon matrix used for the phylogenetic analyses

[illegible]

[illegible]

Text S1.2 - 1. Additional phylogenetic characters

351. Posteroventral margin of the quadratojugal (**New character**): Posterior and ventral margins are acutely angled, forming a small projection (0); Posterior and ventral margins are acutely angled, forming a large hook-like process (1); Posterior and ventral margins are widely angled, forming a gentle curvature (2).
352. Mid-dorsal vertebra: columnar shaped centrum (**New character**) (0); heart-shaped centrum formed by combination of ventrally positioned neural canal , expanded laterodorsal margins, and ventral keel (1).
353. Prenarial region anterior to the circumnarial ridge (**New character**; after Xing et al. (2014); Xing et al. (2017): short (0); elongated (1).
354. Postorbital process of jugal (**New character**; after Xing et al. (2014); Xing et al. (2017): smooth (0); horizontal shelf present (1).

Table S1.2 - 1. Hadrosaurine maxilla measurements.

Taxa	ID	Length	Height
<i>Prosaurolophus maximus</i>	MOR 454	348	120
<i>Probrachylophosaurus bergei</i>	MOR 2919	372	144
<i>Naashoibitosaurus ostromi</i>	NMMNH P-16106	389	139
<i>Laiyangosaurus youngi</i>	IVPP V 23401.1	318	101
<i>Laiyangosaurus youngi</i>	IVPP V 23405.1	151	56
<i>Laiyangosaurus youngi</i>	IVPP V 23403.1	157	55
<i>Laiyangosaurus youngi</i>	IVPP V 23402.1	146	56
<i>Gryposaurus latidens</i>	MOR 478-5-28-8-1	294	120
<i>Edmontosaurus regalis</i>	CMN 2289	447	176
<i>Edmontosaurus annectens</i>	DMNH EPV.127418	314	119
<i>Edmontosaurus annectens</i>	ROM 53527	240	96
<i>Edmontosaurus annectens</i>	ROM 64083	457	175
<i>Edmontosaurus annectens</i>	DMNH EPV 127415	321	105
<i>Edmontosaurus annectens</i>	DMNH EPV 127418	323	121
<i>Edmontosaurus annectens</i>	LACM 23504	172	75
<i>Brachylophosaurus canadensis</i>	MOR 1071-7-6-98-79	320	117
<i>Brachylophosaurus canadensis</i>	MOR 1071-8-13-98-559	330	126
<i>Acristavus gagslarsoni</i>	MOR 1155	341	132
Liscomb hadrosaurine	UAMES 4250	156	53
Liscomb hadrosaurine	UAMES 7662	140	47
Liscomb hadrosaurine	UAMES 4327	155	49

Data S2 - 1. List of the hadrosaurid skulls analyzed

Taxa	ID	Subfamily	Skull_length	Quad_length	Environment
<i>Brachylophosaurus canadensis</i>	CMN_8893	Hadrosaurinae	848	343	Terrestrial + Marginal
<i>Edmontosaurus annectens</i>	CMN_8509	Hadrosaurinae	835	331	Terrestrial + Marginal
<i>Edmontosaurus annectens</i>	USNM_3814	Hadrosaurinae	1129	410	Terrestrial + Marginal
<i>Edmontosaurus regalis</i>	CMN_2288	Hadrosaurinae	1100	415	Terrestrial
<i>Edmontosaurus regalis</i>	NHM_R8927	Hadrosaurinae	875	341	Terrestrial
<i>Edmontosaurus regalis</i>	USNM_12711	Hadrosaurinae	1137	421	Terrestrial
<i>Gryposaurus notabilis</i>	CMN_2278	Hadrosaurinae	980	420	Terrestrial
<i>Gryposaurus notabilis</i>	ROM_873	Hadrosaurinae	965	439	Terrestrial
<i>Prosaurolophus maximus</i>	CMN_2277	Hadrosaurinae	915	330	Terrestrial + Marginal
<i>Prosaurolophus maximus</i>	CMN_2870	Hadrosaurinae	925	372	Terrestrial + Marginal
<i>Prosaurolophus maximus</i>	USNM_12712	Hadrosaurinae	1149	435	Terrestrial + Marginal
<i>Saurolophus osborni</i>	CMN_8796	Hadrosaurinae	1030	391	Terrestrial + Marginal
<i>Corythosaurus casuarius</i>	CMN_34825	Lambeosaurinae	492	221	Terrestrial
<i>Corythosaurus casuarius</i>	CMN_8633	Lambeosaurinae	532	222	Terrestrial
<i>Corythosaurus casuarius</i>	ROM_1933	Lambeosaurinae	749	NA	Terrestrial
<i>Corythosaurus casuarius</i>	ROM_776	Lambeosaurinae	786	277	Terrestrial
<i>Corythosaurus casuarius</i>	ROM_777	Lambeosaurinae	NA	291	Terrestrial
<i>Corythosaurus casuarius</i>	ROM_845	Lambeosaurinae	776	291	Terrestrial
<i>Corythosaurus casuarius</i>	ROM_868	Lambeosaurinae	830	309	Terrestrial
<i>Corythosaurus casuarius</i>	UALVP_52826	Lambeosaurinae	862	307	Terrestrial
<i>Corythosaurus casuarius</i>	USNM_16600	Lambeosaurinae	412	169	Terrestrial
<i>Lambeosaurus lambei</i>	CMN_2759	Lambeosaurinae	563	236	Terrestrial + Marginal
<i>Lambeosaurus lambei</i>	CMN_8703	Lambeosaurinae	759	279	Terrestrial + Marginal
<i>Lambeosaurus lambei</i>	ROM_1218	Lambeosaurinae	764	279	Terrestrial + Marginal
<i>Lambeosaurus lambei</i>	ROM_794	Lambeosaurinae	902	316	Terrestrial + Marginal
<i>Lambeosaurus magnicristatus</i>	CMN_8705	Lambeosaurinae	776	296	Terrestrial + Marginal
<i>Parasaurolophus walkeri</i>	ROM_768	Lambeosaurinae	783	262	Terrestrial

Data S2 - 2. Measurements of the hadrosaurid limbs analyzed. Bolds represent estimated measurements.

Genus	Species	ID	Subfamily	HL	RL	McL	FL	TL	MTL	Environments	Source
<i>Brachylophosaurus</i>	<i>canadensis</i>	MOR 794	Hadrosaurinae	595	709	280	1290	1098	440	Terrestrial + Marginal	Prieto-Márquez (2001)
<i>Corythosaurus</i>	<i>casuarius</i>	AMNH 5338	Lambeosaurinae	546	577	242	987	924	378	Terrestrial	Lull and Wright (1942)
<i>Corythosaurus</i>	<i>casuarius</i>	CMN 8676	Lambeosaurinae	450	535	215	890	813	320	Terrestrial	Sternberg (1935)
<i>Corythosaurus</i>	<i>casuarius</i>	TMP 1984.121.0001	Lambeosaurinae	560	540	261	1045	895	349	Terrestrial	Sternberg (1935), Mallon et al. (2013)
<i>Corythosaurus</i>	<i>casuarius</i>	TMP 1980.040.0001	Lambeosaurinae	570	629	254	1070	949	394	Terrestrial	Mallon et al. (2013)
<i>Corythosaurus</i>	<i>intermedius</i>	ROM 845	Lambeosaurinae	530	640	270	1055	925	390	Terrestrial	Mallon et al. (2013)
<i>Edmontosaurus</i>	<i>annectens</i>	AMNH 5730	Hadrosaurinae	501	440	220	1040	870	340	Terrestrial + Marginal	Brett-Surman (1989)
<i>Edmontosaurus</i>	<i>annectens</i>	LACM 23504	Hadrosaurinae	292	270	153	568	507	203	Terrestrial + Marginal	Prieto-Márquez (2010)
<i>Edmontosaurus</i>	<i>annectens</i>	USNM 2414	Hadrosaurinae	501	440	220	1025	870	340	Terrestrial + Marginal	Brown (1913)
<i>Edmontosaurus</i>	<i>annectens</i>	YPM 2182	Hadrosaurinae	590	555	273	1053	947	346	Terrestrial + Marginal	Brett-Surman (1989)
<i>Edmontosaurus</i>	<i>regalis</i>	CMN 2289	Hadrosaurinae	690	673	308	1280	1174	426	Terrestrial	Campione (2015)
<i>Edmontosaurus</i>	<i>regalis</i>	CMN 8399	Hadrosaurinae	587	610	272	1118	930	345	Terrestrial	Lull and Wright (1942)
<i>Edmontosaurus</i>	<i>regalis</i>	ROM 801	Hadrosaurinae	650	600	310	1240	1000	410	Terrestrial	Lull and Wright (1942)
<i>Gryposaurus</i>	<i>notabilis</i>	MSNM V345	Hadrosaurinae	740	664	269	1105	1003	395	Terrestrial	Bertoza et al. (2017), Mallon et al. (2013)
<i>Gryposaurus</i>	<i>notabilis</i>	ROM 764	Hadrosaurinae	630	555	226	1045	943	363	Terrestrial	Parks (1920), Mallon et al. (2013)
<i>Gryposaurus</i>	<i>notabilis</i>	TMP 1980.022.0001	Hadrosaurinae	540	502	224	955	860	316	Terrestrial	Mallon et al. (2013)
<i>Kanabosaurus</i>	<i>japonicus</i>	HMG-1219	Hadrosaurinae	620	607	285	1060	1035	366	Marginal	Kobayashi et al. (2019)
<i>Lambeosaurus</i>	<i>lambei</i>	AMNH 5340	Lambeosaurinae	305	320	151	590	550	210	Terrestrial + Marginal	Lull and Wright (1942)
<i>Lambeosaurus</i>	<i>lambei</i>	CMN 8703	Lambeosaurinae	520	616	265	1020	1000	366	Terrestrial + Marginal	Sternberg (1935), Mallon et al. (2013)
<i>Lambeosaurus</i>	<i>lambei</i>	ROM 1218	Lambeosaurinae	500	600	250	1070	925	385	Terrestrial + Marginal	Mallon et al. (2013)
<i>Lambeosaurus</i>	<i>magnicristatus</i>	TMP 1966.004.0001	Lambeosaurinae	504	630	275	1063	1020	365	Terrestrial + Marginal	Evans (2007), Mallon et al. (2013)
<i>Lambeosaurus</i>	<i>sp</i>	FMNH UC 1479	Lambeosaurinae	515	580	247	1045	955	385	Terrestrial + Marginal	Personal observation
<i>Parasaurolophus</i>	<i>cyrtocristatus</i>	FMNH p27393	Lambeosaurinae	538	584	246	1035	949	382	Terrestrial + Marginal	Personal observation
<i>Parasaurolophus</i>	<i>walkeri</i>	ROM 768	Lambeosaurinae	520	485	208	1032	909	424	Terrestrial	Sternberg (1935), Mallon et al. (2013)
<i>Saurolophus</i>	<i>maximus</i>	ROM 787	Hadrosaurinae	525	510	230	983	826	315	Terrestrial + Marginal	Personal observation
<i>Saurolophus</i>	<i>angustirostris</i>	PIN 551-8	Hadrosaurinae	600	530	280	1200	1000	330	Terrestrial	Rozhdvestvensky (1957), Maryńska and Osmólska (1984)
<i>Saurolophus</i>	<i>osborni</i>	AMNH 5220	Hadrosaurinae	500	600	293	1170	1000	370	Terrestrial + Marginal	Brown (1913)

Table S2 - 1. Results of the regression analyses between beak shape and skull size proxies.

All specimens									
	Skull			Quadrate			Centroid size		
	Slope	P-value	R-sq	Slope	P-value	R-sq	Slope	P-value	R-sq
PC 1	-1.639	<0.001	0.477	-1.737	<0.001	0.645	-1.241	<0.001	0.371
PC 2	0.849	0.164	0.079	0.899	0.242	0.057	0.646	0.118	0.095
PC 3	0.636	0.738	0.005	0.677	0.813	0.002	0.479	0.924	0.000
PC 4	0.523	0.521	0.017	0.561	0.476	0.021	0.398	0.791	0.003
PC 5	-0.420	0.364	0.034	-0.451	0.441	0.025	-0.317	0.131	0.089
Hadrosaurinae									
	Slope	P-value	R-sq	Slope	P-value	R-sq	Slope	P-value	R-sq
PC 1	2.802	0.991	<0.001	-2.978	0.671	0.019	1.671	0.441	0.060
PC 2	1.574	0.621	0.025	1.673	0.836	0.005	0.939	0.441	0.061
PC 3	1.281	0.173	0.177	1.362	0.762	0.010	0.764	0.270	0.120
PC 4	-0.888	0.690	0.017	-0.944	0.382	0.077	-0.530	0.792	0.007
Lambeosaurinae									
	Slope	P-value	R-sq	Slope	P-value	R-sq	Slope	P-value	R-sq
PC 1	-1.160	0.092	0.218	-1.593	0.015	0.401	-0.855	0.151	0.152
PC 2	0.946	0.778	0.007	1.206	0.824	0.004	0.705	0.568	0.026
PC 3	-0.661	0.433	0.052	-0.897	0.395	0.061	-0.483	0.347	0.068
PC 4	0.470	0.437	0.051	0.642	0.398	0.060	0.345	0.098	0.197
PC 5	-0.422	0.225	0.120	-0.555	0.282	0.096	-0.321	0.407	0.053

Table S2 - 2. P-values of student's t-test on beak shapes categorized by environment and subfamily.

PC axes	All specimens		Hadrosaurinae	Lambeosaurinae
	Environment	Subfamily	Environment	Environment
PC 1	0.047	<0.001	0.359	0.053
PC 2	0.263	0.919	0.221	0.961
PC 3	0.676	0.314	0.937	0.662
PC 4	0.201	0.238	0.009	0.746
PC 5	0.286	0.132	-	0.668

Table S2 - 3. P-values of student's t-test on relative fore- hind-limb lengths categorized by environment and subfamily.

	Hadrosauridae		Hadrosaurinae	Lambeosaurinae
	By subfamily	By environments		
w/o estimates	0.258	0.004	0.054	0.001
w/ estimates	0.874	0.060	0.078	0.522

Table S2 - 4. Factor loadings of the PCA on the normalized limb segments with and without estimated measurements.

	w/o estimates						w/ estimates					
	PC1	PC2	PC3	PC4	PC5	PC6	PC1	PC2	PC3	PC4	PC5	PC6
HL	-0.664	0.034	-0.694	-0.023	0.275	0.014	-0.123	-0.308	-0.901	0.278	-0.032	0.024
RL	0.863	0.205	-0.162	-0.351	-0.252	0.016	0.912	0.127	0.210	-0.008	0.327	0.023
McL	-0.212	0.711	0.624	0.138	0.200	0.011	0.021	-0.777	0.523	-0.153	-0.315	0.020
FL	-0.801	-0.196	0.150	0.172	-0.517	0.009	-0.841	-0.082	0.119	-0.360	0.378	0.014
TL	-0.258	-0.651	0.470	-0.502	0.192	0.006	-0.410	0.246	0.527	0.702	0.032	0.010
MtL	0.580	-0.568	0.091	0.561	0.135	0.011	-0.117	0.911	-0.019	-0.257	-0.300	0.020

Table S3 - 1. Differences in body mass among experimental groups. Bolds represent p-values less than 0.05.

	difference	p-value
G1-G5	-0.0001	1.0000
G2-G1	-0.2132	0.0000
G2-G5	-0.2133	0.0089
G3-G1	-0.0547	0.6852
G3-G2	0.1585	0.0023
G3-G5	-0.0547	0.9328
G3-G6	-0.0694	0.8353
G4-G1	-0.1378	0.0071
G4-G2	0.0753	0.4249
G4-G3	-0.0832	0.2374
G4-G5	-0.1379	0.1846
G4-G6	-0.1526	0.1083
G6-G1	0.0148	0.9998
G6-G2	0.2280	0.0042
G6-G5	0.0147	1.0000

Table S3 - 2. Differences in gizzard muscularity among experimental groups. Bolds represent p-values less than 0.05.

	difference	p-value
G1-G5	-0.1861	0.0000
G1-G6	0.1158	0.0083
G2-G1	0.1921	0.0000
G2-G5	0.0060	1.0000
G2-G6	0.3080	0.0000
G3-G1	-0.0456	0.2467
G3-G2	-0.2377	0.0000
G3-G5	-0.2317	0.0000
G3-G6	0.0703	0.2557
G4-G1	0.0972	0.0003
G4-G2	-0.0949	0.0009
G4-G3	0.1428	0.0000
G4-G5	-0.0889	0.0787
G4-G6	0.2131	0.0000
G5-G6	0.3020	0.0000

Table S3 - 3. Differences in average amount of stones consumed among the different sizes of the stone provided. Bolds represent p-values less than 0.05.

	G1		G2		G3		G4	
	difference	p-value	difference	p-value	difference	p-value	difference	p-value
1.0-1.4 - 0.5-1.0	0.0840	0.9901	0.2850	0.7688	0.1531	0.5909	0.3053	0.8269
1.4-1.7 - 0.5-1.0	0.0873	0.9882	0.2433	0.8656	0.0694	0.9775	0.3960	0.6141
1.4-1.7 - 1.0-1.4	0.0033	1.0000	-0.0417	1.0000	-0.0837	0.9496	0.0907	0.9992
1.7-2.0 - 0.5-1.0	0.2113	0.6447	0.4492	0.3040	0.2250	0.1769	0.7153	0.0588
1.7-2.0 - 1.0-1.4	0.1273	0.9395	0.1642	0.9724	0.0719	0.9737	0.4100	0.5778
1.7-2.0 - 1.4-1.7	0.1240	0.9457	0.2058	0.9291	0.1556	0.5737	0.3193	0.7983
2.0-2.8 - 0.5-1.0	0.1820	0.7735	0.3350	0.6270	0.1088	0.8602	0.8280	0.0171
2.0-2.8 - 1.0-1.4	0.0980	0.9802	0.0500	0.9999	-0.0444	0.9971	0.5227	0.3052
2.0-2.8 - 1.4-1.7	0.0947	0.9830	0.0917	0.9981	0.0394	0.9984	0.4320	0.5206
2.0-2.8 - 1.7-2.0	-0.0293	0.9999	-0.1142	0.9947	-0.1163	0.8230	0.1127	0.9976
2.8-3.35 - 0.5-1.0	0.7293	0.0000	1.1042	0.0000	0.6519	0.0000	1.2960	0.0000
2.8-3.35 - 1.0-1.4	0.6453	0.0002	0.8192	0.0039	0.4988	0.0000	0.9907	0.0022
2.8-3.35 - 1.4-1.7	0.6420	0.0002	0.8608	0.0021	0.5825	0.0000	0.9000	0.0071
2.8-3.35 - 1.7-2.0	0.5180	0.0042	0.6550	0.0370	0.4269	0.0003	0.5807	0.1992
2.8-3.35 - 2.0-2.8	0.5473	0.0020	0.7692	0.0081	0.5431	0.0000	0.4680	0.4296

Table S3 - 4. Differences in average amount of stones consumed among the experimental groups. Bolds represent p-values less than 0.05.

	0.5-1.0		1.0-1.4		1.4-1.7		1.7-2.0		2.0-2.8		2.8-3.35	
	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value
G2-G1	0.0360	0.9849	0.2370	0.3407	0.1920	0.7161	0.2738	0.6117	0.1890	0.8388	0.4108	0.2474
G3-G1	-0.0588	0.9253	0.0103	0.9998	-0.0767	0.9682	-0.0451	0.9963	-0.1320	0.9230	-0.1363	0.9069
G3-G2	-0.0948	0.7833	-0.2267	0.3676	-0.2688	0.4433	-0.3190	0.4737	-0.3210	0.4840	-0.5471	0.0645
G4-G1	0.0480	0.9592	0.2693	0.1889	0.3567	0.1710	0.5520	0.0530	0.6940	0.0106	0.6147	0.0213
G4-G2	0.0120	0.9994	0.0323	0.9957	0.1647	0.8009	0.2782	0.5996	0.5050	0.1296	0.2038	0.7867
G4-G3	0.1068	0.6755	0.2590	0.2059	0.4334	0.0600	0.5971	0.0278	0.8260	0.0014	0.7509	0.0027

Table S3 - 5. Differences in average shapes of the stones initially provided and stones left uneaten. Bolds represent p-values less than 0.05.

	0.5-1.0		1.0-1.4		1.4-1.7		1.7-2.0		2.0-2.8		2.8-3.35		
	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	
Circularity	G2-G1	-0.0068	0.5432	0.0017	0.9905	-0.0070	0.2753	-0.0149	0.0001	-0.0068	0.1773	-0.0005	0.9998
	G3-G1	-0.0192	0.0002	0.0005	0.9999	-0.0029	0.9258	-0.0045	0.6532	-0.0019	0.9745	0.0010	0.9978
	G3-G2	-0.0124	0.0425	-0.0012	0.9977	0.0041	0.7711	0.0104	0.0133	0.0050	0.4954	0.0015	0.9880
	G4-G1	-0.0095	0.2089	0.0101	0.0465	-0.0083	0.1299	-0.0091	0.0445	-0.0031	0.8604	0.0029	0.8745
	G4-G2	-0.0027	0.9755	0.0084	0.1479	-0.0013	0.9961	0.0058	0.3977	0.0038	0.7410	0.0034	0.7902
	G4-G3	0.0098	0.1833	0.0096	0.0684	-0.0054	0.5406	-0.0046	0.6201	-0.0012	0.9953	0.0019	0.9689
	Source-G1	-0.0256	0.0000	-0.0069	0.3268	-0.0216	0.0000	-0.0265	0.0000	-0.0188	0.0000	-0.0076	0.0959
	Source-G2	-0.0188	0.0003	-0.0086	0.1305	-0.0146	0.0003	-0.0116	0.0037	-0.0119	0.0011	-0.0070	0.1439
	Source-G3	-0.0063	0.6118	-0.0074	0.2534	-0.0188	0.0000	-0.0220	0.0000	-0.0169	0.0000	-0.0085	0.0415
Source-G4	-0.0161	0.0028	-0.0170	0.0000	-0.0134	0.0015	-0.0174	0.0000	-0.0157	0.0000	-0.0105	0.0054	
Roundness	G2-G1	-0.0080	0.8848	0.0059	0.9403	-0.0029	0.9949	-0.0036	0.9876	0.0024	0.9976	0.0036	0.9859
	G3-G1	-0.0085	0.8575	-0.0081	0.8311	-0.0034	0.9902	0.0098	0.6627	0.0019	0.9990	-0.0089	0.7114
	G3-G2	-0.0006	1.0000	-0.0139	0.3635	-0.0005	1.0000	0.0134	0.3493	-0.0005	1.0000	-0.0125	0.3841
	G4-G1	-0.0084	0.8631	0.0181	0.1270	0.0103	0.6211	-0.0010	0.9999	-0.0003	1.0000	-0.0139	0.2714
	G4-G2	-0.0004	1.0000	0.0122	0.5019	0.0131	0.3706	0.0026	0.9963	-0.0027	0.9960	-0.0175	0.0899
	G4-G3	0.0001	1.0000	0.0261	0.0059	0.0137	0.3293	-0.0108	0.5752	-0.0022	0.9981	-0.0051	0.9514
	Source-G1	-0.0266	0.0162	0.0025	0.9975	-0.0172	0.1261	-0.0048	0.9646	0.0011	0.9999	-0.0078	0.7996
	Source-G2	-0.0187	0.1882	-0.0034	0.9924	-0.0143	0.2824	-0.0012	0.9998	-0.0012	0.9998	-0.0114	0.4792
	Source-G3	-0.0181	0.2143	0.0106	0.6405	-0.0138	0.3205	-0.0146	0.2632	-0.0008	1.0000	0.0011	0.9999
Source-G4	-0.0182	0.2090	-0.0156	0.2516	-0.0274	0.0016	-0.0038	0.9848	0.0015	0.9996	0.0061	0.9057	
Solidity	G2-G1	-0.0028	0.2918	-0.0003	0.9992	-0.0029	0.0727	-0.0035	0.0060	-0.0022	0.2133	-0.0002	0.9994
	G3-G1	-0.0059	0.0003	0.0004	0.9972	-0.0013	0.8003	-0.0016	0.5239	-0.0013	0.6783	0.0004	0.9931
	G3-G2	-0.0031	0.1837	0.0007	0.9776	0.0017	0.5777	0.0019	0.3457	0.0008	0.9320	0.0006	0.9668
	G4-G1	-0.0025	0.4133	0.0004	0.9984	-0.0027	0.1134	-0.0017	0.4776	-0.0009	0.8889	0.0018	0.3212
	G4-G2	0.0003	0.9995	0.0007	0.9831	0.0002	0.9998	0.0018	0.3873	0.0012	0.7541	0.0020	0.2133
	G4-G3	0.0034	0.1141	-0.0001	1.0000	-0.0015	0.6937	-0.0001	1.0000	0.0004	0.9946	0.0014	0.5840
	Source-G1	-0.0045	0.0161	-0.0012	0.8900	-0.0057	0.0000	-0.0110	0.0000	-0.0062	0.0000	-0.0034	0.0031
	Source-G2	-0.0017	0.7718	-0.0009	0.9625	-0.0028	0.0978	-0.0075	0.0000	-0.0040	0.0008	-0.0032	0.0068
	Source-G3	0.0015	0.8435	-0.0016	0.7190	-0.0045	0.0008	-0.0094	0.0000	-0.0048	0.0000	-0.0038	0.0006
Source-G4	-0.0020	0.6409	-0.0015	0.7444	-0.0030	0.0619	-0.0093	0.0000	-0.0052	0.0000	-0.0052	0.0000	

Table S3 - 6. Differences in average amount of grits recovered from gizzards. Bolds represent p-values less than 0.05.

	difference	p-value
G2-G1	0.0038	0.0129
G3-G1	0.0000	1.0000
G3-G2	-0.0038	0.0110
G4-G1	0.0039	0.0054
G4-G2	0.0001	0.9996
G4-G3	0.0039	0.0045

Table S3 - 7. Differences in average size of grits recovered from gizzards. Bolds represent p-values less than 0.05.

	difference	p-value
G2-G1	0.0687	0.0000
G3-G1	0.0542	0.0000
G3-G2	-0.0145	0.0084
G4-G1	0.0741	0.0000
G4-G2	0.0053	0.5746
G4-G3	0.0199	0.0001

Table S3 - 8. Differences in average shapes of the stones initially provided and the grits recovered from gizzards. Bolds represent p-values less than 0.05.

		0.5-1.0		1.0-1.4		1.4-1.7		1.7-2.0		2.0-2.8		2.8-3.35	
		difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value
Circularity	Source-G1	-0.0683	0.0000	-0.0543	0.0000	-0.0450	0.0000	-0.0427	0.0000	-0.0342	0.0000	-0.0257	0.0000
	Source-G2	-0.0805	0.0000	-0.0742	0.0000	-0.0698	0.0000	-0.0682	0.0000	-0.0593	0.0000	-0.0361	0.0000
	Source-G3	-0.0660	0.0000	-0.0433	0.0000	-0.0485	0.0000	-0.0412	0.0000	-0.0357	0.0000	-0.0253	0.0000
	Source-G4	-0.0695	0.0000	-0.0588	0.0000	-0.0623	0.0000	-0.0544	0.0000	-0.0506	0.0000	-0.0399	0.0000
Roundness	Source-G1	-0.0645	0.0000	-0.0230	0.0248	-0.0218	0.0861	-0.0190	0.2882	-0.0128	0.5414	-0.0275	0.0584
	Source-G2	-0.0627	0.0000	-0.0370	0.0000	-0.0489	0.0000	-0.0273	0.0138	-0.0222	0.0481	-0.0276	0.0841
	Source-G3	-0.0520	0.0000	-0.0012	0.9999	-0.0153	0.4148	-0.0086	0.8667	-0.0161	0.2755	-0.0225	0.2503
	Source-G4	-0.0665	0.0000	-0.0223	0.0360	-0.0403	0.0000	-0.0289	0.0066	-0.0205	0.0448	-0.0379	0.0002
Solidity	Source-G1	-0.0113	0.0000	-0.0111	0.0000	-0.0103	0.0000	-0.0127	0.0000	-0.0075	0.0000	-0.0057	0.0006
	Source-G2	-0.0189	0.0000	-0.0182	0.0000	-0.0168	0.0000	-0.0210	0.0000	-0.0156	0.0000	-0.0093	0.0000
	Source-G3	-0.0130	0.0000	-0.0114	0.0000	-0.0123	0.0000	-0.0153	0.0000	-0.0098	0.0000	-0.0074	0.0000
	Source-G4	-0.0141	0.0000	-0.0151	0.0000	-0.0159	0.0000	-0.0174	0.0000	-0.0136	0.0000	-0.0103	0.0000

Table S3 - 9. Differences in average shapes of the grits recovered from gizzards

among the experimental groups. Bolds represent p-values less than 0.05.

		0.5-1.0		1.0-1.4		1.4-1.7		1.7-2.0		2.0-2.8		2.8-3.35	
		difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value
Circularity	G2-G1	0.0122	0.0005	0.0199	0.0000	0.0249	0.0000	0.0255	0.0000	0.0251	0.0000	0.0104	0.2054
	G3-G1	-0.0023	0.9301	-0.0109	0.0269	0.0036	0.8001	-0.0015	0.9880	0.0015	0.9767	-0.0004	0.9998
	G3-G2	-0.0145	0.0023	-0.0308	0.0000	-0.0213	0.0000	-0.0269	0.0000	-0.0236	0.0000	-0.0108	0.2087
	G4-G1	0.0013	0.9759	0.0046	0.5739	0.0173	0.0000	0.0117	0.0419	0.0164	0.0000	0.0141	0.0126
	G4-G2	-0.0110	0.0071	-0.0153	0.0001	-0.0075	0.1475	-0.0138	0.0039	-0.0087	0.0460	0.0038	0.8649
	G4-G3	0.0036	0.8137	0.0155	0.0005	0.0138	0.0017	0.0132	0.0079	0.0149	0.0001	0.0146	0.0163
Roundness	G2-G1	-0.0018	0.9932	0.0140	0.3065	0.0271	0.0210	0.0083	0.8595	0.0093	0.7478	0.0001	1.0000
	G3-G1	-0.0124	0.4049	-0.0219	0.0679	-0.0065	0.9134	-0.0104	0.7638	0.0033	0.9851	-0.0050	0.9804
	G3-G2	-0.0107	0.6031	-0.0359	0.0004	-0.0336	0.0025	-0.0186	0.2241	-0.0060	0.9103	-0.0051	0.9811
	G4-G1	0.0021	0.9883	-0.0007	0.9997	0.0185	0.2105	0.0099	0.7785	0.0076	0.8180	0.0104	0.7931
	G4-G2	0.0038	0.9503	-0.0147	0.2699	-0.0086	0.7775	0.0016	0.9983	-0.0017	0.9970	0.0103	0.8194
	G4-G3	0.0145	0.3193	0.0212	0.0872	0.0250	0.0478	0.0203	0.1569	0.0043	0.9565	0.0154	0.5680
Solidity	G2-G1	0.0075	0.0000	0.0071	0.0000	0.0065	0.0000	0.0083	0.0000	0.0081	0.0000	0.0036	0.1275
	G3-G1	0.0017	0.4771	0.0003	0.9903	0.0020	0.3124	0.0026	0.1775	0.0023	0.1289	0.0017	0.7257
	G3-G2	-0.0059	0.0000	-0.0068	0.0000	-0.0045	0.0002	-0.0057	0.0000	-0.0058	0.0000	-0.0019	0.6960
	G4-G1	0.0027	0.0158	0.0040	0.0007	0.0055	0.0000	0.0047	0.0010	0.0061	0.0000	0.0046	0.0087
	G4-G2	-0.0048	0.0000	-0.0031	0.0136	-0.0009	0.8095	-0.0036	0.0080	-0.0020	0.1428	0.0010	0.9211
	G4-G3	0.0011	0.8149	0.0036	0.0083	0.0036	0.0062	0.0021	0.2692	0.0038	0.0005	0.0029	0.2475

Table S3 - 10. Differences in average size and shapes of the stones excreted among the experimental groups. Bolds represent p-values less than 0.05.

	Size		Circularity		Roundness		Solidity	
	difference	p-value	difference	p-value	difference	p-value	difference	p-value
G2-G1	-0.0721	0.0048	0.0061	0.7336	0.0105	0.8699	0.0024	0.6449
G3-G1	0.0489	0.0065	-0.0030	0.8846	0.0094	0.7587	0.0025	0.2875
G3-G2	0.1210	0.0000	-0.0091	0.4070	-0.0011	0.9998	0.0001	0.9999
G4-G1	-0.0653	0.0734	-0.0034	0.9667	0.0073	0.9746	-0.0037	0.4516
G4-G2	0.0068	0.9963	-0.0095	0.6765	-0.0033	0.9984	-0.0061	0.1524
G4-G3	-0.1142	0.0001	-0.0004	0.9999	-0.0022	0.9993	-0.0062	0.0636

Table S3 - 11. Differences in average size and shapes of the stones excreted and the grits recovered from gizzards. Bolds represent p-values less than 0.05.

Gizzard grits – excreted stones	Size		Circularity		Roundness		Solidity	
	difference	p-value	difference	p-value	difference	p-value	difference	p-value
G1	0.2010	0.0007	0.0034	0.9694	-0.0010	1.0000	0.0028	0.2205
G2	0.5299	0.0000	0.0155	0.0755	0.0005	1.0000	0.0105	0.0000
G3	0.3672	0.0000	0.0021	0.9984	-0.0168	0.2781	0.0060	0.0000
G4	0.6220	0.0000	0.0153	0.3648	0.0019	1.0000	0.0141	0.0000

Data S4 - 1. List of the stomachs observed.

ID	Taxa	Order	Clade	Stomach type	Proventriculus	Ventriculus	Body mass	DurCut	M. crassus	Succus cranialis/caudalis	Gastric intubus	Ventriculus position	Perito phoria	Gastroliths
(H4.M 0005)	<i>Podiceps nigricollis</i>	Podicipediformes	Avialae	A	0.3	4	180	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0007)	<i>Puffin montanus</i>	Procellariiformes	Avialae	A	0.1	0.4	21	PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0008)	<i>Randallia garmani</i>	Passeriformes	Avialae	A	0.1	1.3	2	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0011)	<i>Anas penelope</i>	Anseriformes	Avialae	A	2.3	28	630	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0012)	<i>Zonotrichia diemina</i>	Passeriformes	Avialae	A	0.2	1.7	62	Invertebrate	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0014)	<i>Larus californicus</i>	Chondriiformes	Avialae	A	0.9	3.6	60	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0015)	<i>Fregata acaudata</i>	Columbiformes	Avialae	A	1.6	6.3	273	FruiNect	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0017)	<i>Phaethon venustus</i>	Caprimulgiformes	Avialae	A	2.6	21.3	125	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0018)	<i>Elanus nigripes</i>	Cathartiformes	Avialae	B	4	9.4	497	VertiIscasco	Thin	Absent	Evident	Normal	Present	Absent
(H4.M 0019)	<i>Accipiter gentilis</i>	Accipitriformes	Avialae	B	1.9	2	667	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0020)	<i>Streptopelia risoria</i>	Columbiformes	Avialae	A	0.4	5.4	199	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0022)	<i>Thresornis sinuatus</i>	Podicipediformes	Avialae	A	8.36	36.95	1305	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0025)	<i>Neotoma neotoma</i>	Pelecaniformes	Avialae	C				VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0026)	<i>Neotoma neotoma</i>	Pelecaniformes	Avialae	C	2.65	2.35	488	VertiIscasco	Thin	Absent	Obscure	Normal	Present	Present
(H4.M 0034)	<i>Neotoma neotoma</i>	Pelecaniformes	Avialae	C	2.51	1.99		VertiIscasco	Thin	Absent	Obscure	Normal	Absent	Absent
(H4.M 0037)	<i>Falco suburus</i>	Falconiformes	Avialae	B	0.54	2.3	158	Invertebrate	Thin	Absent	Evident	Normal	Absent	Present
(H4.M 0044)	<i>Aluco arcticus</i>	Cathartiformes	Avialae	B	0.96	0.39	27	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0049)	<i>Zenaidura macroura</i>	Passeriformes	Avialae	A	0	0.2		FruiNect	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0050)	<i>Glareola melanocephala</i>	Chondriiformes	Avialae	A	0.2	1.1	47	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0051)	<i>Melospiza cinerea</i>	Passeriformes	Avialae	A	0.2	1	60	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0052)	<i>Icterus americanus</i>	Passeriformes	Avialae	A	0.1	1.2		FruiNect	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0053)	<i>Phoenicurus phoenicurus</i>	Passeriformes	Avialae	A	0.1	0.4	18	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0054)	<i>Catharus ustulatus</i>	Chondriiformes	Avialae	A	0.1	0.1	14	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0055)	<i>Geothlypis trichas</i>	Chondriiformes	Avialae	A	0.3	1.2	88	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0056)	<i>Coccyzus erythrophthalmus</i>	Chondriiformes	Avialae	A	0.2	0.8		PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0057)	<i>Turdus migratorius</i>	Pelecaniformes	Avialae	C	0.5	0.6	85	Invertebrate	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0058)	<i>Anas platyrhynchos</i>	Scolopaciformes	Avialae	B	0.6	2.1	202	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0059)	<i>Falco tinnunculus</i>	Falconiformes	Avialae	B	1	2.6	128	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0060)	<i>Picus canadensis</i>	Psittaciformes	Avialae	B	0.5	1.5	115	Invertebrate	Thin	Absent	Evident	Normal	Absent	Present
(H4.M 0061)	<i>Phalacrocorax carolinensis</i>	Chondriiformes	Avialae	A	0.3	2.1	115	Invertebrate	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0062)	<i>Leucosticte tinnunculus</i>	Procellariiformes	Avialae	D	0.1	0.1	29	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0063)	<i>Oenanthe isabellina</i>	Procellariiformes	Avialae	D	0.1	0.1	56	Invertebrate	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0064)	<i>Aluco arcticus</i>	Cathartiformes	Avialae	B	0.08	0.36	28	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0065)	<i>Anas platyrhynchos</i>	Chondriiformes	Avialae	A	0.2	0.9	158	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0066)	<i>Himantopus himantopus</i>	Chondriiformes	Avialae	A	0.5	2.3	143	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0067)	<i>Bubulcus ibex</i>	Pelecaniformes	Avialae	C	1.3	2.6	178	Invertebrate	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0068)	<i>Puffinus pacificus</i>	Procellariiformes	Avialae	D	4.8	4.8	373	VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0069)	<i>Egretta garzetta</i>	Pelecaniformes	Avialae	C	2.3	1.8	422	Invertebrate	Thin	Absent	Obscure	Normal	Present	Present
(H4.M 0070)	<i>Myristicivora myristicivora</i>	Procellariiformes	Avialae	C	1.1	6.1	64	Invertebrate	Thin	Absent	Relevant	Absent	Absent	
(H4.M 0071)	<i>Anas platyrhynchos</i>	Anseriformes	Avialae	A	0.9	1.6	400	PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0072)	<i>Turdus pallidus</i>	Passeriformes	Avialae	A	1.9	0.3	88	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0073)	<i>Sceloporus roosevelti</i>	Chondriiformes	Avialae	A	0.2	0.5	308	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0074)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	1.5	0.4	120	VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0075)	<i>Falco arcticus</i>	Falconiformes	Avialae	A	0.6	18.8	378	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0077)	<i>Gallinula chloropus</i>	Chondriiformes	Avialae	A	0.2	0.8	160	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0078)	<i>Turdus naumanni</i>	Passeriformes	Avialae	A	0.1	0.8	52	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0079)	<i>Accipiter americanus</i>	Accipitriformes	Avialae	A	0.4	0.4	150	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0080)	<i>Sterna bergii</i>	Chondriiformes	Avialae	A	1.2	0.9	111	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0081)	<i>Larus argentatus</i>	Chondriiformes	Avialae	A	2.37	4.33	362	VertiIscasco	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0082)	<i>Colaptes auratus</i>	Procellariiformes	Avialae	D	5.2	1.5	428	Omnivore	Thin	Absent	Evident	Relevant	Absent	Present
(H4.M 0083)	<i>Zonotrichia leucophrys</i>	Passeriformes	Avialae	A	0.4	0.4	19	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0084)	<i>Ardea herodias</i>	Pelecaniformes	Avialae	C	6.03	5.73	1090	VertiIscasco	Thin	Absent	Obscure	Normal	Present	Present
(H4.M 0085)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	0.3	0.6	49	Invertebrate	Thick	Present	Evident	Relevant	Absent	Absent
(H4.M 0088)	<i>Falco arcticus</i>	Falconiformes	Avialae	A	0.63	17.03	297	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0089)	<i>Zonotrichia diemina</i>	Passeriformes	Avialae	A	0.23	2.67	125	Invertebrate	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0090)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	0.62	1.43	142	Invertebrate	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0091)	<i>Zonotrichia diemina</i>	Passeriformes	Avialae	A	0.18	2.4	153	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0094)	<i>Circus hudsonius</i>	Accipitriformes	Avialae	B	0.42	1.82	120	Invertebrate	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0095)	<i>Phalaropus lobatus</i>	Scolopaciformes	Avialae	B	0.25	1.77	175	VertiIscasco	Thin	Absent	Obscure	Normal	Absent	Absent
(H4.M 0096)	<i>Zonotrichia diemina</i>	Passeriformes	Avialae	A	0.26	1.73	135	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0097)	<i>Zonotrichia diemina</i>	Passeriformes	Avialae	A	0.24	1.47	115	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0098)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	0.04	0.53	173	VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0099)	<i>Puffinus pacificus</i>	Procellariiformes	Avialae	D	2.29	0.74	381	VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0100)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	0.94	0.49	109	VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Present
(H4.M 0101)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	0.09	0.4	109	Invertebrate	Thick	Present	Evident	Relevant	Absent	Present
(H4.M 0102)	<i>Himantopus himantopus</i>	Chondriiformes	Avialae	A	0.2	1.59	93	Invertebrate	Thick	Present	Evident	Normal	Absent	Present
(H4.M 0103)	<i>Myristicivora myristicivora</i>	Procellariiformes	Avialae	C	0.65	3.6	148	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0104)	<i>Falco arcticus</i>	Falconiformes	Avialae	A	0.65	23.85	332	PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0105)	<i>Phalaropus lobatus</i>	Scolopaciformes	Avialae	C	7.46	4.84	966	VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0106)	<i>Phalaropus lobatus</i>	Scolopaciformes	Avialae	C	0.43	4.8	738	VertiIscasco	Thin	Absent	Evident	Normal	Absent	Absent
(H4.M 0107)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49	0.57		VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0108)	<i>Uria lomvia</i>	Chondriiformes	Avialae	A				VertiIscasco	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0109)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	1.1	0.36		VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0110)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.13			Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0111)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.13			Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0112)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	2.18	4.32	271	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
(H4.M 0113)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	1.1	0.36		VertiIscasco	Thin	Absent	Evident	Relevant	Absent	Absent
(H4.M 0114)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0115)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0116)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0117)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0118)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0119)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0120)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0121)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0122)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0123)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0124)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0125)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0126)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0127)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0128)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0129)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0130)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0131)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0132)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	Absent
(H4.M 0133)	<i>Phalaropus lobatus</i>	Procellariiformes	Avialae	D	3.49			VertiIscasco	Thin	Absent	Obscure	Normal	Present	

237

ID	Taxa	Order	Clade	Stomach type	Proventriculus	Ventriculus	Body mass	Diet/Cat	M. crassus	Succus cranialis/caudalis	Gastric isthmus	Ventriculus position	Portio pylorica	Gastroliths
HUNIM 60509	<i>Phylloscopus coronatus</i>	Passeriformes	Avialae	A	0.02	0.15	9	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60510	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.04	0.37	15	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60511	<i>Dendroscopus major</i>	Piciformes	Avialae	B	0.12	1.1	61	Omnivore	Thin	Absent	Evident	Normal	Absent	Present
HUNIM 60512	<i>Sitta uralensis</i>	Strigiformes	Avialae	B				VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 60516	<i>Bombicilla garrulus</i>	Passeriformes	Avialae	A				Omnivore	Thick	Present	Evident	Normal	Absent	Present
HUNIM 60521	<i>Oculus saturatus</i>	Cuculiformes	Avialae	B	0.15	0.88	58	Invertebrate	Thin	Absent	Evident	Normal	Absent	Present
HUNIM 60522	<i>Anas platyrhynchos</i>	Anseriformes	Avialae	A	1.83	27.08	1633	PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60523	<i>Anas crecca</i>	Anseriformes	Avialae	A	0.5	6.19	208	PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60525	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.86	7.11	885	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60526	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.42	3.53	482	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60527	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.86	4.49	610	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60528	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.4	3.53	360	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60529	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.95	4.94	509	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60530	<i>Corvus corone</i>	Passeriformes	Avialae	A	0.65	10.09	478	VertFishScav	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60531	<i>Corvus corone</i>	Passeriformes	Avialae	A	0.36	3.48	314	VertFishScav	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60532	<i>Garrulus glandarius</i>	Passeriformes	Avialae	A	0.24	3.42	120	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60533	<i>Garrulus glandarius</i>	Passeriformes	Avialae	A	0.21	3.62	128	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 60534	<i>Dendroscopus major</i>	Piciformes	Avialae	B	0.12	1.08	69	Omnivore	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 60967	<i>Coccothraustes coccothraustes</i>	Passeriformes	Avialae	A	0.19	0.6		PlantSeed	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61147	<i>Bombicilla garrulus</i>	Passeriformes	Avialae	A	0.12	1.24	63	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61348	<i>Bombicilla garrulus</i>	Passeriformes	Avialae	A	0.11	1.1	71	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61373	<i>Dendroscopus major</i>	Piciformes	Avialae	B	0.11	0.86	71	Omnivore	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61388	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.04	0.35	19	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61389	<i>Urosphena squameiceps</i>	Passeriformes	Avialae	A	0.3	0.3	10	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61390	<i>Phylloscopus borealis</i>	Passeriformes	Avialae	A	0.01	0.1	7	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61392	<i>Phylloscopus coronatus</i>	Passeriformes	Avialae	A	0.01	0.12	5	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61398	<i>Parus varius</i>	Passeriformes	Avialae	A	0.09	0.24	19	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61401	<i>Anas platyrhynchos</i>	Anseriformes	Avialae	A	2.65	33.71	960	Omnivore	Thick	Present	Evident	Normal	Absent	Present
HUNIM 61590	<i>Parus major</i>	Passeriformes	Avialae	A	0.03	0.17	12	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61591	<i>Parus major</i>	Passeriformes	Avialae	A	0.03	0.15	11	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61592	<i>Parus major</i>	Passeriformes	Avialae	A	0.02	0.13	15	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61596	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.02	0.2	7	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61597	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.02	0.25	7	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61601	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.03	0.27	12	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61603	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.04	0.31	13	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61604	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.02	0.26	12	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61606	<i>Phylloscopus borealoides</i>	Passeriformes	Avialae	A	0.01	0.11	5	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61607	<i>Phylloscopus borealoides</i>	Passeriformes	Avialae	A	0.01	0.17	9	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61608	<i>Phylloscopus borealis</i>	Passeriformes	Avialae	A	0.02	0.13	9	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61609	<i>Phylloscopus borealis</i>	Passeriformes	Avialae	A	0.02	0.17	11	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61610	<i>Zosterops japonica</i>	Passeriformes	Avialae	A	0.005	0.065	4	FruitBee	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61616	<i>Urosphena squameiceps</i>	Passeriformes	Avialae	A	0.02	0.17	10	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61651	<i>Alcedo amba</i>	Coraciiformes	Avialae	B	0.04	0.38	26.8	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61652	<i>Alcedo amba</i>	Coraciiformes	Avialae	B	0.04	0.27	16.2	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61653	<i>Dryocopus martius</i>	Piciformes	Avialae	B	0.29	1.35	198	Invertebrate	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61654	<i>Accipiter nisus</i>	Accipitriformes	Avialae	B	0.32	0.3	91	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61655	<i>Accipiter nisus</i>	Accipitriformes	Avialae	B	0.46	0.39	142	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61656	<i>Sitta uralensis</i>	Strigiformes	Avialae	B	5.65	6.77	660	VertFishScav	Thin	Absent	Evident	Normal	Absent	Present
HUNIM 61657	<i>Sitta uralensis</i>	Strigiformes	Avialae	B	0.84	3.83	446	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61658	<i>Bonasa bonasia</i>	Galliformes	Avialae	A	1.05	6.68	435.9	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
HUNIM 61659	<i>Myrica carinata</i>	Anseriformes	Avialae	A	1.44	4.5	365	VertFishScav	Thick	Present	Evident	Normal	Absent	Present
HUNIM 61660	<i>Caprimulgus indicus</i>	Caprimulgiformes	Avialae	B			1200	Invertebrate	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61661	<i>Accipiter nisus</i>	Accipitriformes	Avialae	B	0.88	0.86	335	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61662	<i>Sitta uralensis</i>	Strigiformes	Avialae	B	1.62	5.96	438	VertFishScav	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61664	<i>Streptopelia orientalis</i>	Columbiformes	Avialae	A	0.69	6.83	270	PlantSeed	Thick	Present	Evident	Normal	Absent	Present
HUNIM 61665	<i>Oculus saturatus</i>	Cuculiformes	Avialae	B	0.74	1.65	102	Invertebrate	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61667	<i>Falco subbuteo</i>	Falconiformes	Avialae	B	0.73	1.98	144	Invertebrate	Thin	Absent	Evident	Normal	Absent	Absent
HUNIM 61668	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.91	10.6	600	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61669	<i>Corvus macrorhynchos</i>	Passeriformes	Avialae	A	0.86	4.9	520	Omnivore	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61674	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.03	0.33	22	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61675	<i>Cettia diphone</i>	Passeriformes	Avialae	A	0.03	0.35	10	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61676	<i>Urosphena squameiceps</i>	Passeriformes	Avialae	A	0.02	0.17	10	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61677	<i>Phylloscopus borealoides</i>	Passeriformes	Avialae	A	0.01	0.16	9	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
HUNIM 61678	<i>Phylloscopus coronatus</i>	Passeriformes	Avialae	A	0.01	0.18	7	Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
uncataloged01	<i>Uromyza himantopus</i>	Charadriiformes	Avialae	A				Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
uncataloged02	<i>Struthio camelus</i>	Palaeognathae	Avialae	A				PlantSeed	Thick	Present	Evident	Relocated	Absent	Present
uncataloged03	<i>Struthio camelus</i>	Palaeognathae	Avialae	A				Invertebrate	Thick	Present	Evident	Relocated	Absent	Present
uncataloged04	<i>Zoothera dauma</i>	Passeriformes	Avialae	A	0.32	1.63		Invertebrate	Thick	Present	Evident	Normal	Absent	Absent
Darwin 01	<i>Crocodylus johnstoni</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
Darwin 02	<i>Crocodylus johnstoni</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
Darwin 03	<i>Crocodylus johnstoni</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
Darwin 04	<i>Crocodylus porosus</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 01	<i>Gavialis gangeticus</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 02	<i>Gavialis gangeticus</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 03	<i>Crocodylus siamensis</i>	Crocodylia	Eusuchia	D			2300	VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 04	<i>Crocodylus siamensis</i>	Crocodylia	Eusuchia	D			3445	VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 05	<i>Crocodylus siamensis</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 06	<i>Crocodylus siamensis</i>	Crocodylia	Eusuchia	D			3310	VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 07	<i>Crocodylus porosus</i>	Crocodylia	Eusuchia	D		172	3000	VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 08	<i>Crocodylus porosus</i>	Crocodylia	Eusuchia	D		861	120000	VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 09	<i>Crocodylus porosus</i>	Crocodylia	Eusuchia	D		1236	120000	VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present
TEMP erc 10	<i>Gavialis gangeticus</i>	Crocodylia	Eusuchia	D				VertFishScav	Thin	Absent	Evident	Relocated	Absent	Present

Data S4 - 2. Summary of gastroliths features observed.

ID	Taxa	Order	Group	Number of gastroliths	Area	Minor axis	Circularity	Roundness	Solidity
Darwin 01	<i>Crocodylus johnsoni</i>	Crocodylia	Crocodylia	13	16.98	3.87	0.752	0.745	0.955
Darwin 02	<i>Crocodylus johnsoni</i>	Crocodylia	Crocodylia	171	14.21	3.04	0.74	0.719	0.947
Darwin 03	<i>Crocodylus johnsoni</i>	Crocodylia	Crocodylia	737	14.17	2.74	0.753	0.735	0.946
Darwin 04	<i>Crocodylus porosus</i>	Crocodylia	Crocodylia	891	389.71	8.68	0.772	0.737	0.961
TEMP croc 01	<i>Gavialis gangeticus</i>	Crocodylia	Crocodylia	406	4.95	1.93	0.735	0.729	0.962
TEMP croc 02	<i>Gavialis gangeticus</i>	Crocodylia	Crocodylia	1416	0.64	0.75	0.741	0.742	0.949
TEMP croc 03	<i>Crocodylus siamensis</i>	Crocodylia	Crocodylia	1016	3.08	1.55	0.735	0.741	0.957
TEMP croc 04	<i>Crocodylus siamensis</i>	Crocodylia	Crocodylia	278	5.53	1.96	0.727	0.747	0.957
TEMP croc 05	<i>Crocodylus siamensis</i>	Crocodylia	Crocodylia	424	7.22	2.26	0.755	0.744	0.953
TEMP croc 06	<i>Crocodylus siamensis</i>	Crocodylia	Crocodylia	5977	1.13	0.91	0.756	0.74	0.939
TEMP croc 07	<i>Crocodylus porosus</i>	Crocodylia	Crocodylia	7	374.03	18.6	0.719	0.741	0.962
TEMP croc 08	<i>Crocodylus porosus</i>	Crocodylia	Crocodylia	45	26.17	3.85	0.699	0.75	0.947
TEMP croc 09	<i>Crocodylus porosus</i>	Crocodylia	Crocodylia	678	23.46	2.51	0.779	0.743	0.955
TEMP croc 10	<i>Gavialis gangeticus</i>	Crocodylia	Crocodylia	466	6.12	1.68	0.766	0.742	0.944
HoUM 30011	<i>Anas penelope</i>	Anseriformes	Extant bird	1660	0.59	0.73	0.773	0.756	0.959
HoUM 30012	<i>Zoothera dauma</i>	Passeriformes	Extant bird	82	0.76	0.81	0.737	0.742	0.94
HoUM 30017	<i>Phasianus versicolor</i>	Galliformes	Extant bird	1048	2.97	1.63	0.775	0.751	0.956
HoUM 30020	<i>Streptopelia orientalis</i>	Columbiformes	Extant bird	362	1.17	0.94	0.763	0.73	0.942
HoUM 30030	<i>Nycticorax nycticorax</i>	Pelecaniformes	Extant bird	2	0.48	0.69	0.807	0.8	0.955
HoUM 30037	<i>Falco subbuteo</i>	Falconiformes	Extant bird	1	37.88	4.76	0.704	0.47	0.99
HoUM 30061	<i>Pluvialis fulva</i>	Charadriiformes	Extant bird	32	1.08	0.95	0.714	0.723	0.95
HoUM 30069	<i>Egretta garzetta</i>	Pelecaniformes	Extant bird	118	0.47	0.65	0.742	0.767	0.947
HoUM 30071	<i>Anas acuta</i>	Anseriformes	Extant bird	1272	0.98	0.92	0.776	0.749	0.964
HoUM 30075	<i>Fulica atra</i>	Gruiformes	Extant bird	902	1.75	1.29	0.799	0.776	0.959
HoUM 30082	<i>Calonectris leucomelas</i>	Procellariiformes	Extant bird	37	0.95	0.88	0.745	0.747	0.95
HoUM 30084	<i>Ardea cinerea</i>	Pelecaniformes	Extant bird	187	0.7	0.74	0.761	0.774	0.933
HoUM 30088	<i>Fulica atra</i>	Gruiformes	Extant bird	3046	0.62	0.74	0.79	0.757	0.953
HoUM 30089	<i>Zoothera dauma</i>	Passeriformes	Extant bird	6	0.58	0.66	0.771	0.703	0.946
HoUM 30090	<i>Zoothera dauma</i>	Passeriformes	Extant bird	1	0.34	0.6	0.769	0.835	0.931
HoUM 30107	<i>Pterodroma hypoleuca</i>	Procellariiformes	Extant bird	3	0.52	0.65	0.736	0.774	0.904
HoUM 30110	<i>Himantopus himantopus</i>	Charadriiformes	Extant bird	1	6.66	2.48	0.736	0.728	0.966
HoUM 30113	<i>Fulica atra</i>	Gruiformes	Extant bird	7114	0.78	0.82	0.791	0.765	0.957
HoUM 30144	<i>Clangula hyemalis</i>	Anseriformes	Extant bird	439	2.49	1.4	0.783	0.728	0.963
HoUM 30148	<i>Phoebeastria immutabilis</i>	Procellariiformes	Extant bird	16	30	4.58	0.707	0.678	0.952
HoUM 30152	<i>Corvus macrorhynchos</i>	Passeriformes	Extant bird	19	0.89	0.82	0.735	0.716	0.931
HoUM 30158	<i>Aethia cristatella</i>	Charadriiformes	Extant bird	2	6.49	2.43	0.714	0.713	0.949
HoUM 30164	<i>Ardea cinerea</i>	Pelecaniformes	Extant bird	20	0.38	0.59	0.743	0.765	0.927
HoUM 30171	<i>Loxia curvirostra</i>	Passeriformes	Extant bird	14	0.59	0.74	0.754	0.776	0.952
HoUM 30180	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	200	0.74	0.8	0.772	0.753	0.945
HoUM 30181	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	1	2.57	1.67	0.74	0.846	0.941
HoUM 30205	<i>Anas acuta</i>	Anseriformes	Extant bird	214	1.42	1.09	0.754	0.75	0.964
HoUM 30235	<i>Bonasa bonasia</i>	Galliformes	Extant bird	54	4.24	1.91	0.764	0.74	0.959
HoUM 30239	<i>Buteo buteo</i>	Accipitriformes	Extant bird	337	2.12	1.28	0.777	0.714	0.955
HoUM 30288	<i>Pavo cristatus</i>	Galliformes	Extant bird	1295	6.38	2.03	0.771	0.726	0.963
HoUM 30331	<i>Gallinago gallinago</i>	Charadriiformes	Extant bird	24	1.26	0.98	0.768	0.693	0.958
HoUM 30333	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	85	1.86	1.07	0.735	0.758	0.933
HoUM 30356	<i>Columba livia</i>	Columbiformes	Extant bird	78	3.06	1.34	0.796	0.775	0.955
HoUM 31130	<i>Bonasa bonasia</i>	Galliformes	Extant bird	41	6.61	2.38	0.805	0.742	0.975
HUNHM 46079	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	33	0.83	0.86	0.717	0.812	0.948
HUNHM 46965	<i>Phalaropus lobatus</i>	Suliformes	Extant bird	2	1.42	1.18	0.733	0.814	0.957
HUNHM 46970	<i>Phalaropus lobatus</i>	Suliformes	Extant bird	4	1.37	1	0.755	0.64	0.967
HUNHM 46984	<i>Bombicilla garrulus</i>	Passeriformes	Extant bird	21	0.38	0.58	0.731	0.736	0.939
HUNHM 47000	<i>Oceanodroma furcata</i>	Procellariiformes	Extant bird	11	2.84	1.57	0.715	0.702	0.958
HUNHM 47001	<i>Oceanodroma furcata</i>	Procellariiformes	Extant bird	6	1.62	1.2	0.704	0.738	0.941
HUNHM 47002	<i>Oceanodroma furcata</i>	Procellariiformes	Extant bird	20	3.02	1.56	0.672	0.65	0.951
HUNHM 47003	<i>Oceanodroma furcata</i>	Procellariiformes	Extant bird	23	2.31	1.33	0.753	0.702	0.963
HUNHM 47454	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	5	0.98	0.88	0.735	0.74	0.946
HUNHM 47455	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	44	0.55	0.7	0.719	0.752	0.944
HUNHM 47456	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	5	1.57	0.9	0.631	0.627	0.938
HUNHM 48086	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	11	0.69	0.73	0.763	0.765	0.952
HUNHM 48087	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	54	0.57	0.68	0.703	0.713	0.94
HUNHM 48089	<i>Larus crassirostris</i>	Charadriiformes	Extant bird	2	9.38	2.93	0.776	0.809	0.975
HUNHM 48398	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	39	1.45	0.97	0.704	0.739	0.947
HUNHM 48401	<i>Calidris subminuta</i>	Charadriiformes	Extant bird	26	0.81	0.83	0.778	0.755	0.952
HUNHM 48405	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	204	0.61	0.74	0.733	0.75	0.928
HUNHM 48406	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	222	0.62	0.74	0.764	0.753	0.938
HUNHM 48407	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	28	0.41	0.61	0.736	0.753	0.944
HUNHM 48408	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	186	0.9	0.87	0.75	0.744	0.936
HUNHM 48409	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	304	0.58	0.72	0.696	0.744	0.938
HUNHM 48410	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	10	1.36	1.07	0.698	0.709	0.937
HUNHM 48411	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	235	0.78	0.8	0.762	0.74	0.937
HUNHM 48412	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	119	1.02	0.94	0.703	0.753	0.937
HUNHM 48413	<i>Gallinago hardwickii</i>	Charadriiformes	Extant bird	346	0.61	0.74	0.7	0.745	0.943
HUNHM 60093	<i>Anas platyrhynchos</i>	Anseriformes	Extant bird	1076	1.07	0.94	0.729	0.757	0.954
HUNHM 60094	<i>Oceanodroma leucorhoa</i>	Procellariiformes	Extant bird	16	1.99	1.23	0.721	0.672	0.96
HUNHM 60095	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	24	0.61	0.72	0.735	0.766	0.938
HUNHM 60099	<i>Dendrocopos major</i>	Piciformes	Extant bird	35	0.5	0.66	0.732	0.746	0.946

ID	Taxa	Order	Group	Number of gastroliths	Area	Minor axis	Circularity	Roundness	Solidity
HUNHM 60101	<i>Dendrocopos major</i>	Piciformes	Extant bird	4	0.61	0.77	0.728	0.78	0.937
HUNHM 60104	<i>Dendrocopos leucotos</i>	Piciformes	Extant bird	7	0.54	0.7	0.752	0.726	0.957
HUNHM 60163	<i>Buteo buteo</i>	Accipitriformes	Extant bird	5	0.48	0.64	0.724	0.713	0.949
HUNHM 60164	<i>Bonasa bonasia</i>	Galliformes	Extant bird	75	6.47	2.14	0.763	0.752	0.97
HUNHM 60167	<i>Cuculus canorus</i>	Cuculiformes	Extant bird	51	0.94	0.86	0.729	0.724	0.95
HUNHM 60168	<i>Otus lempiji</i>	Strigiformes	Extant bird	81	0.5	0.68	0.748	0.777	0.95
HUNHM 60169	<i>Strix uralensis</i>	Strigiformes	Extant bird	8	1.76	1.24	0.771	0.716	0.966
HUNHM 60323	<i>Cerorhinca monocerata</i>	Charadriiformes	Extant bird	1	57.78	6.61	0.748	0.594	0.99
HUNHM 60326	<i>Cerorhinca monocerata</i>	Charadriiformes	Extant bird	37	0.85	0.83	0.746	0.728	0.949
HUNHM 60327	<i>Cerorhinca monocerata</i>	Charadriiformes	Extant bird	17	0.46	0.66	0.747	0.789	0.95
HUNHM 60329	<i>Cerorhinca monocerata</i>	Charadriiformes	Extant bird	5	0.87	0.88	0.679	0.746	0.935
HUNHM 60332	<i>Oceanodroma leucorhoa</i>	Procellariiformes	Extant bird	12	2.54	1.45	0.734	0.718	0.964
HUNHM 60333	<i>Oceanodroma leucorhoa</i>	Procellariiformes	Extant bird	8	3.98	1.63	0.653	0.666	0.942
HUNHM 60340	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	646	1.08	0.93	0.676	0.731	0.938
HUNHM 60341	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	489	0.74	0.81	0.732	0.766	0.946
HUNHM 60478	<i>Scolopax rusticola</i>	Charadriiformes	Extant bird	67	0.7	0.77	0.748	0.74	0.94
HUNHM 60479	<i>Anas platyrhynchos</i>	Anseriformes	Extant bird	1257	0.88	0.85	0.773	0.76	0.953
HUNHM 60511	<i>Dendrocopos major</i>	Piciformes	Extant bird	1	2.2	1.46	0.744	0.763	0.957
HUNHM 60516	<i>Bombycilla garrulus</i>	Passeriformes	Extant bird	1	2.46	1.74	0.771	0.963	0.943
HUNHM 60521	<i>Cuculus saturatus</i>	Cuculiformes	Extant bird	4	2.54	1.37	0.71	0.687	0.957
HUNHM 61401	<i>Anas platyrhynchos</i>	Anseriformes	Extant bird	658	1.31	1.04	0.791	0.765	0.972
HUNHM 61656	<i>Strix uralensis</i>	Strigiformes	Extant bird	415	2.85	1.5	0.735	0.725	0.969
HUNHM 61658	<i>Bonasa bonasia</i>	Galliformes	Extant bird	22	7.01	2.59	0.731	0.834	0.963
HUNHM 61659	<i>Mergus serrator</i>	Anseriformes	Extant bird	774	0.89	0.86	0.727	0.744	0.952
HUNHM 61664	<i>Streptopelia orientalis</i>	Columbiformes	Extant bird	1	7.36	2.78	0.79	0.823	0.967
TEMP Bird_0001	<i>Struthio camelus</i>	Palaeognathae	Extant bird	978	30.21	3.62	0.767	0.747	0.97
TEMP Bird_0002	<i>Struthio camelus</i>	Palaeognathae	Extant bird	15740	2.54	0.98	0.737	0.708	0.941

Table S4 - 1. Proportion of variance and factor loadings obtained from the six PCA with different minimum gastroliths numbers.

	All			<10			<20			<30			<40			<50		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Variance (%)	0.75	0.22	0.03	0.60	0.34	0.05	0.59	0.35	0.06	0.70	0.24	0.06	0.74	0.19	0.07	0.72	0.21	0.08
Circularity	-0.31	0.92	0.23	-0.74	-0.64	-0.20	-0.97	0.12	0.21	-0.97	0.14	0.21	-0.96	0.14	0.24	-0.95	-0.21	-0.24
Roundness	-0.95	-0.28	-0.13	-0.66	0.74	0.09	-0.12	-0.99	-0.02	-0.16	-0.98	-0.08	-0.18	-0.97	-0.16	-0.25	0.96	0.16
Solidity	0.05	0.26	-0.96	-0.09	-0.20	0.98	-0.20	0.05	-0.98	-0.20	0.11	-0.97	-0.21	0.20	-0.96	-0.20	-0.21	0.96

Table S4 - 2. Results of the discriminant analyses grouped by stomach type and dietary habits.

Stomach type							Diet				
Predicted							Predicted				
all	A	B	C	D	D'		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	A	60	1	0	1	0	Invertebrate	39	0	1	5
	B	11	1	0	0	0	Omnivore	10	0	2	1
	C	6	0	0	0	0	Plant + Seed	3	1	11	3
	D	8	0	0	2	0	Vertebrate	21	0	4	3
	D'	14	0	0	0	0					
more than 10 stones											
	A	B	C	D	D'		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	A	48	0	0	1	0	Invertebrate	25	0	2	4
	B	4	0	0	1	0	Omnivore	6	0	2	1
	C	1	0	2	0	0	Plant + Seed	2	0	14	1
	D	1	0	0	6	0	Vertebrate	13	0	3	4
	D'	13	0	0	0	0					
more than 20 stones											
	A	B	C	D	D'		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	A	45	0	0	0	0	Invertebrate	23	0	2	2
	B	5	0	0	0	0	Omnivore	4	0	2	0
	C	2	0	0	0	0	Plant + Seed	2	0	14	0
	D	2	0	0	0	0	Vertebrate	9	0	2	6
	D'	12	0	0	0	0					
more than 30 stones											
	A	B	C	D	D'		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	A	38	0	1	0	0	Invertebrate	18	0	1	3
	B	5	0	0	0	0	Omnivore	2	0	2	1
	C	2	0	0	0	0	Plant + Seed	0	0	13	2
	D	1	0	0	0	0	Vertebrate	4	0	2	11
	D'	12	0	0	0	0					
more than 40 stones											
	A	B	C	D	D'		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	A	33	0	0	0	2	Invertebrate	17	0	1	1
	B	3	0	0	0	1	Omnivore	1	0	2	0
	C	1	0	1	0	0	Plant + Seed	0	0	13	2
	D	0	0	0	0	0	Vertebrate	3	0	2	11
	D'	12	0	0	0	0					
more than 50 stones											
	A	B	C	D	D'		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	A	32	0	0	0	1	Invertebrate	15	0	1	2
	B	2	1	0	0	1	Omnivore	1	0	2	0
	C	1	0	1	0	0	Plant + Seed	0	0	12	2
	D	0	0	0	0	0	Vertebrate	3	0	2	10
	D'	11	0	0	0	0					

Data S5 - 1. List of extant archosaurs examined

ID	Taxa	Order	Group	BM	Number evaluat	Largest minor a	Angular	Sub-angular	Sub-rounded	Rounded	Well-rounded	Diet
HoUM 30011	<i>Anas_penelope</i>	Anseriformes	Extant bird	630	1660	2.81	69	177	1009	341	64	PlantSeed
HoUM 30012	<i>Zoothera_dauma</i>	Passeriformes	Extant bird		80	2.37	27	30	23	0	0	Invertebrate
HoUM 30017	<i>Phasianus_versicolor</i>	Galliformes	Extant bird	1285	1048	4.04	99	203	424	251	71	PlantSeed
HoUM 30020	<i>Streptopelia_orientalis</i>	Columbiformes	Extant bird	199	362	3.25	68	70	173	49	2	PlantSeed
HoUM 30030	<i>Nycticorax_nycticorax</i>	Pelecaniformes	Extant bird	488	2	0.95	0	1	0	1	0	VentFishScav
HoUM 30037	<i>Falco_subbuteo</i>	Falconiformes	Extant bird	158	1	1.01	0	1	0	0	1	Invertebrate
HoUM 30061	<i>Pluvialis_fulva</i>	Charadriiformes	Extant bird	115	32	4.76	9	9	8	5	1	Invertebrate
HoUM 30069	<i>Egretta_garzetta</i>	Pelecaniformes	Extant bird	422	118	4.52	17	28	52	19	2	Invertebrate
HoUM 30071	<i>Anas_acuta</i>	Anseriformes	Extant bird	400	1272	2.27	32	98	558	353	231	PlantSeed
HoUM 30075	<i>Fulica_atra</i>	Gruiformes	Extant bird	370	902	2.68	53	101	399	258	91	PlantSeed
HoUM 30082	<i>Calonectris_leucomelas</i>	Procellariiformes	Extant bird	428	37	1.77	11	14	10	2	0	Omnivore
HoUM 30084	<i>Ardea_cinerea</i>	Pelecaniformes	Extant bird	1090	187	4.52	69	54	54	10	0	VentFishScav
HoUM 30088	<i>Fulica_atra</i>	Gruiformes	Extant bird	297	1155	2.29	137	176	420	291	131	PlantSeed
HoUM 30089	<i>Zoothera_dauma</i>	Passeriformes	Extant bird	125	6	1.69	4	2	0	0	0	Invertebrate
HoUM 30090	<i>Zoothera_dauma</i>	Passeriformes	Extant bird	142	1	0.60	0	0	1	0	0	Invertebrate
HoUM 30107	<i>Pterodroma_hypoleuca</i>	Procellariiformes	Extant bird	109	3	0.93	2	0	1	0	0	VentFishScav
HoUM 30110	<i>Himantopus_himantopus</i>	Charadriiformes	Extant bird	93	1	2.48	1	0	0	0	0	Invertebrate
HoUM 30113	<i>Fulica_atra</i>	Gruiformes	Extant bird	332	1083	3.34	162	173	451	211	86	PlantSeed
HoUM 30144	<i>Clangula_hymelidis</i>	Anseriformes	Extant bird	439	334	3.34	105	110	164	51	9	Invertebrate
HoUM 30148	<i>Phoebastria_immutabilis</i>	Procellariiformes	Extant bird	1275	16	7.97	10	2	3	0	1	Invertebrate
HoUM 30152	<i>Corvus_macrorhynchos</i>	Anseriformes	Extant bird	435	19	2.06	10	6	3	0	0	Omnivore
HoUM 30158	<i>Aethya_cristatella</i>	Charadriiformes	Extant bird	2	2	2.58	2	0	0	0	0	Invertebrate
HoUM 30164	<i>Ardea_cinerea</i>	Pelecaniformes	Extant bird	1010	20	0.81	10	6	4	0	0	VentFishScav
HoUM 30171	<i>Loxia_curvirostra</i>	Passeriformes	Extant bird	30	14	1.29	3	4	5	2	0	PlantSeed
HoUM 30180	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	180	200	2.70	86	42	40	24	8	Invertebrate
HoUM 30181	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	195	1	1.67	1	0	0	0	0	Invertebrate
HoUM 30205	<i>Anas_acuta</i>	Anseriformes	Extant bird		214	2.29	25	38	76	40	35	PlantSeed
HoUM 30235	<i>Bonasa_bonasia</i>	Galliformes	Extant bird	285	54	3.66	5	8	23	16	2	PlantSeed
HoUM 30239	<i>Buteo_buteo</i>	Accipitriformes	Extant bird	655	337	3.64	99	90	104	37	7	VentFishScav
HoUM 30288	<i>Pavo_cristatus</i>	Galliformes	Extant bird	4500	1005	12.04	209	228	315	171	82	PlantSeed
HoUM 30331	<i>Gallinago_gallinago</i>	Charadriiformes	Extant bird	55	24	1.58	14	5	5	0	0	Invertebrate
HoUM 30333	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	255	85	3.16	54	18	11	2	0	Invertebrate
HoUM 30356	<i>Columba_livia</i>	Columbiformes	Extant bird		78	4.03	14	13	36	12	3	PlantSeed
HoUM 31130	<i>Bonasa_bonasia</i>	Galliformes	Extant bird	418	41	4.13	2	10	15	10	4	PlantSeed
HUNHM 46079	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	156	33	2.28	9	13	6	2	3	Invertebrate
HUNHM 46965	<i>Phalaropus_lobatus</i>	Suliformes	Extant bird		2	1.45	1	0	0	0	1	Invertebrate
HUNHM 46970	<i>Phalaropus_lobatus</i>	Suliformes	Extant bird		4	2.34	1	1	0	1	0	Invertebrate
HUNHM 46984	<i>Bombicilla_garrulus</i>	Passeriformes	Extant bird		21	0.78	3	4	12	2	0	Omnivore
HUNHM 47000	<i>Oceanodroma_furcata</i>	Procellariiformes	Extant bird		11	1.98	1	2	4	3	1	Invertebrate
HUNHM 47001	<i>Oceanodroma_furcata</i>	Procellariiformes	Extant bird		6	1.64	5	0	1	0	0	Invertebrate
HUNHM 47002	<i>Oceanodroma_furcata</i>	Procellariiformes	Extant bird		20	2.23	4	3	7	5	1	Invertebrate
HUNHM 47003	<i>Oceanodroma_furcata</i>	Procellariiformes	Extant bird		23	2.62	3	4	6	8	2	Invertebrate
HUNHM 47454	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird		5	1.27	2	1	2	0	0	Invertebrate
HUNHM 47455	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	132	44	1.22	24	13	7	0	0	Invertebrate
HUNHM 47456	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird		5	2.22	2	1	0	2	0	Invertebrate
HUNHM 48086	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	278	12	1.56	3	3	5	1	0	Invertebrate
HUNHM 48087	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird		298	54	1.74	23	14	13	4	Invertebrate
HUNHM 48089	<i>Larus_crassirostris</i>	Charadriiformes	Extant bird	520	2	4.45	0	0	1	1	0	VentFishScav
HUNHM 48398	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	242	39	4.02	23	8	6	2	0	Invertebrate
HUNHM 48401	<i>Gallinago_subminuta</i>	Charadriiformes	Extant bird	26	26	1.35	9	10	2	0	0	Invertebrate
HUNHM 48405	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	132	204	1.72	95	61	45	3	0	Invertebrate
HUNHM 48406	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	132	223	1.45	88	70	60	5	0	Invertebrate
HUNHM 48407	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	168	28	0.84	15	7	6	0	0	Invertebrate
HUNHM 48408	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	122	186	2.38	78	56	46	4	2	
HUNHM 48409	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	134	304	1.57	157	76	60	10	1	Invertebrate
HUNHM 48410	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	120	10	1.60	5	3	2	0	0	Invertebrate
HUNHM 48411	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	112	235	2.76	107	64	53	8	3	Invertebrate
HUNHM 48412	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	120	119	1.94	76	24	18	1	0	Invertebrate
HUNHM 48413	<i>Gallinago_hardwickii</i>	Charadriiformes	Extant bird	120	346	1.29	198	88	56	4	0	Invertebrate
HUNHM 60093	<i>Anas_platyrhynchos</i>	Anseriformes	Extant bird		1076	2.86	166	190	507	189	24	Omnivore
HUNHM 60094	<i>Oceanodroma_leucorhoa</i>	Procellariiformes	Extant bird	29	16	1.84	4	1	2	7	2	Omnivore
HUNHM 60095	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird		24	1.55	10	8	5	1	0	Invertebrate
HUNHM 60099	<i>Dendrocygus_majior</i>	Piciformes	Extant bird	58	35	1.26	12	9	12	2	0	Omnivore
HUNHM 60101	<i>Dendrocygus_majior</i>	Piciformes	Extant bird	61	4	1.01	1	2	1	0	0	Omnivore
HUNHM 60104	<i>Dendrocygus_leucotos</i>	Piciformes	Extant bird	79	7	0.90	3	2	2	1	0	Invertebrate
HUNHM 60163	<i>Buteo_buteo</i>	Accipitriformes	Extant bird	360	5	0.89	1	0	4	0	0	VentFishScav
HUNHM 60164	<i>Bonasa_bonasia</i>	Galliformes	Extant bird	356	75	5.35	4	5	28	30	8	PlantSeed
HUNHM 60167	<i>Cuculus_canorus</i>	Cuculiformes	Extant bird	96	51	1.93	27	14	7	2	1	Invertebrate
HUNHM 60168	<i>Otus_lempiji</i>	Strigiformes	Extant bird	122	81	0.80	11	19	36	14	1	Invertebrate
HUNHM 60169	<i>Strix_uralensis</i>	Strigiformes	Extant bird	450	8	1.72	1	1	5	0	1	VentFishScav
HUNHM 60323	<i>Cerorhinca_monocerata</i>	Charadriiformes	Extant bird		1	6.61	0	0	0	1	0	VentFishScav
HUNHM 60326	<i>Cerorhinca_monocerata</i>	Charadriiformes	Extant bird	354	37	1.93	8	12	9	8	0	VentFishScav
HUNHM 60327	<i>Cerorhinca_monocerata</i>	Charadriiformes	Extant bird	188	17	0.99	4	5	7	1	0	VentFishScav
HUNHM 60329	<i>Cerorhinca_monocerata</i>	Charadriiformes	Extant bird	164	5	1.49	2	2	1	0	0	VentFishScav
HUNHM 60332	<i>Oceanodroma_leucorhoa</i>	Procellariiformes	Extant bird	64	12	2.18	4	2	4	2	0	Omnivore
HUNHM 60333	<i>Oceanodroma_leucorhoa</i>	Procellariiformes	Extant bird	70	8	2.51	3	1	1	2	1	Omnivore
HUNHM 60340	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	340	646	2.43	328	169	118	31	0	Invertebrate
HUNHM 60341	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	298	489	1.85	327	91	58	12	1	Invertebrate
HUNHM 60478	<i>Scolopax_rusticola</i>	Charadriiformes	Extant bird	308	67	1.68	31	23	11	2	0	Invertebrate
HUNHM 60479	<i>Anas_platyrhynchos</i>	Anseriformes	Extant bird	680	1257	4.49	43	197	687	268	62	Omnivore
HUNHM 60511	<i>Dendrocygus_majior</i>	Piciformes	Extant bird	61	1	1.46	0	0	1	0	0	Omnivore
HUNHM 60516	<i>Bombicilla_garrulus</i>	Passeriformes	Extant bird		1	1.74	1	0	0	0	0	Omnivore
HUNHM 60521	<i>Cuculus_saturatus</i>	Cuculiformes	Extant bird		4	1.68	2	1	1	0	0	Invertebrate
HUNHM 61401	<i>Anas_platyrhynchos</i>	Anseriformes	Extant bird	960	658	4.13	19	110	279	225	25	Omnivore
HUNHM 61656	<i>Strix_uralensis</i>	Strigiformes	Extant bird	660	415	5.19	51	71	138	98	57	VentFishScav
HUNHM 61658	<i>Bonasa_bonasia</i>	Galliformes	Extant bird	435.9	22	4.78	1	2	17	2	0	PlantSeed
HUNHM 61659	<i>Mergus_serrator</i>	Anseriformes	Extant bird	865	774	2.64	214	242	269	43	6	VentFishScav
HUNHM 61664	<i>Streptopelia_orientalis</i>	Columbiformes	Extant bird		1	2.78	0	0	1	0	0	PlantSeed
TEMP Bird_0001	<i>Struthio_camelus</i>	Palaeognathae	Extant bird		978	25.54	61	226	314	291	86	PlantSeed
TEMP Bird_0002	<i>Struthio_camelus</i>	Palaeognathae	Extant bird		1099	29.73	157	251	415	189	87	PlantSeed
Darwin 01	<i>Crocodylus_johnsoni</i>	Crocodylia	Crocodylia		13	5.27	3	4	6	0	0	VentFishScav
Darwin 02	<i>Crocodylus_johnsoni</i>	Crocodylia	Crocodylia		171	8.50	38	47	79	6	1	VentFishScav
Darwin 03	<i>Crocodylus_johnsoni</i>	Crocodylia	Crocodylia		737	15.54	165	200	320	46	6	VentFishScav
Darwin 04	<i>Crocodylus_porosus</i>	Crocodylia	Crocodylia		891	56.05	158	196	334	143	60	VentFishScav
TEMP croc 01	<i>Gavialis_gangeticus</i>	Crocodylia	Crocodylia		406	7.93	149	122	110	21	4	VentFishScav
TEMP croc 02	<i>Gavialis_gangeticus</i>	Crocodylia	Crocodylia		1416	2.26	489	584	275	62	6	VentFishScav
TEMP croc 03	<i>Crocodylus_siamesis</i>	Crocodylia	Crocodylia	2300	1016	6.06	144	295	463	100	14	VentFishScav
TEMP croc 04	<i>Crocodylus_siamesis</i>	Crocodylia	Crocodylia	3445	278	10.01	94	94	72	13	5	VentFishScav
TEMP croc 05	<i>Crocodylus_siamesis</i>	Crocodylia	Crocodylia		424	7.46	85	125	186	23	5	VentFishScav
TEMP croc 06	<i>Crocodylus_siamesis</i>	Crocodylia	Crocodylia	3210	1038	8.21	272	322	399	40	5	VentFishScav
TEMP croc 07	<i>Crocodylus_porosus</i>	Crocodylia	Crocodylia	3000	7	26.63	3	2	2	0	0	VentFishScav
TEMP croc 08	<i>Crocodylus_porosus</i>	Crocodylia	Crocodylia	120000	45	11.41	15	14	15	1	0	VentFishScav
TEMP croc 09	<i>Crocodylus_porosus</i>	Crocodylia	Crocodylia	120000	678	30.38	125	141	194	156	62	VentFishScav
TEMP croc 10	<i>Gavialis_gangeticus</i>	Crocodylia	Crocodylia		466	13.54	111	152	155	41	7	VentFishScav

Data S5 - 2. List of the extant archosaur gastroliths examined

ID	Taxa	Clade	Number evaluated	Largest minor axis	Angular	Sub-angular	Sub-rounded	Rounded	Well-rounded	RI	Data acquired from
MGSPv 111	<i>Gasparinisaura cincosaltensis</i>	Ornithischia	23	6.26	3	8	10	2	0	2.48	Cerda (2008)
MGSPv 112	<i>Gasparinisaura cincosaltensis</i>	Ornithischia	11		0	5	4	2	0	2.73	Cerda (2008)
MUCPv 213	<i>Gasparinisaura cincosaltensis</i>	Ornithischia	23			1	4	4	3	3.17	Cerda (2008)
IVPP V14287	<i>Archaeorhynchus spatula</i>	Avialae	38	2.1	1	3	16	11	7	3.53	Direct observation
IVPP V17075	<i>Archaeorhynchus spatula</i>	Avialae	64	1.1	2	13	39	9	1	2.91	Direct observation
IVPP V17091	<i>Archaeorhynchus spatula</i>	Avialae	79	2.39	9	14	39	13	4	2.86	Direct observation
IVPP V20312	<i>Archaeorhynchus spatula</i>	Avialae	44	2.87	5	9	22	7	1	2.77	Direct observation
IVPP V17970	<i>Bellulomis rectusunguis</i>	Avialae	17	5.5	2	6	6	2	1	2.65	Direct observation
CGCS 06-CM-011	<i>Gansus yumenensis</i>	Avialae	34	3.3	7	13	10	4	0	2.32	Direct observation
CGCS 07-CM-011	<i>Gansus yumenensis</i>	Avialae	18	3.1	1	3	10	4	0	2.94	Direct observation
IVPP V18958	<i>Iteravis huchzermeyeri</i>	Avialae	6	3	3	0	2	1	0	2.17	Direct observation
IVPP V20133	<i>Iteravis huchzermeyeri</i>	Avialae	17	4	1	6	8	1	1	2.71	Direct observation
IVPP V20134	<i>Iteravis huchzermeyeri</i>	Avialae	19	3.4	1	6	9	2	1	2.79	Direct observation
IGM 100/2015	<i>Haya griva</i>	Ornithischia	42	8.9	5	10	20	7	0	2.69	Direct observation
IGM 100/3182	<i>Haya griva</i>	Ornithischia	43	10.47	8	12	11	9	3	2.7	Direct observation
IVPP V12165	<i>Psittacosaurus mazongshanensis</i>	Ornithischia	55	19.88	7	20	20	7	1	2.55	Direct observation
AMNH 6253	<i>Psittacosaurus mongoliensis</i>	Ornithischia	48	20.6	8	15	15	7	3	2.63	Direct observation
DMNH 39045	<i>Cedarosaurus weiskopfiae</i>	Sauropoda	96	70.23	19	26	38	11	2	2.49	Direct observation
NMNH 3690	<i>Diplodocus hallorum</i>	Sauropoda	117	65.07	13	10	50	25	19	3.23	Direct observation
IVPP V12344	<i>Caudipteryx dongi</i>	Theropoda	196	6.5	6	27	95	51	17	3.23	Direct observation
IVPP V12430	<i>Caudipteryx</i> sp.	Theropoda	202	4.5	7	16	109	49	21	3.3	Direct observation
MPO-D 100/127	<i>Deinocoelurus mirificus</i>	Theropoda	959	60.92	45	73	238	387	216	3.68	Direct observation
IVPP V15293	<i>Limusaurus inextricabilis</i>	Theropoda	185		19	47	59	43	17	2.96	Direct observation
IVPP V15297	<i>Limusaurus inextricabilis</i>	Theropoda	201	10	11	58	74	45	13	2.96	Direct observation
uncatalogued	<i>Sinornithomimus dongi</i>	Theropoda	1070	6.41	63	166	366	352	123	3.29	Direct observation
MPO-D 552-1	<i>Tarbosaurus bataar</i>	Theropoda	882	17.6	147	188	269	81	17	2.49	Direct observation
NGMC 97-4-002	<i>Shenzhousaurus orientalis</i>	Theropoda	53	5.5	5	15	20	11	2	2.81	Ji et al. (2013)
-	<i>Indeterminate arkylosaur</i>	Ornithischia	19	23.4	1	1	9	5	3	3.42	Ji et al. (2016)
BMNH-C-Ph 1318	<i>Iteravis huchzermeyeri</i>	Avialae	14	4	3	5	3	2	1	2.5	Liu et al. (2014)
BMNH-C-Ph 1342	<i>Iteravis huchzermeyeri</i>	Avialae	29	4.3	2	11	12	2	2	2.69	Liu et al. (2014)
STM35-3	<i>Eogranivora edentulata</i>	Avialae	32	1	4	4	12	6	6	3.19	Photographs
STM2-15	<i>Jeholomis prima</i>	Avialae	49	5	4	5	28	9	3	3.04	Photographs
STM2-31	<i>Jeholomis prima</i>	Avialae	63	3.06	1	11	29	14	8	3.27	Photographs
STM3-19	<i>Jeholomis prima</i>	Avialae	6		0	0	2	3	1	3.83	Photographs
STM3-28	<i>Jeholomis prima</i>	Avialae	18	3.5	0	2	5	7	4	3.72	Photographs
STM3-31	<i>Jeholomis prima</i>	Avialae	43	2.27	3	3	19	13	5	3.33	Photographs
STM 9-9	<i>Chongmingia zhengxi</i>	Avialae	19	5.5	2	5	7	3	2	2.89	Wang et al. (2016)

Table S5 - 1. Results of the PCA under six different minimum gastroliths numbers.

	PC1	PC2	PC3	PC4	PC5
standard deviation	0.40	0.28	0.22	0.19	0.08
0< proportion of variance	0.49	0.24	0.15	0.11	0.02
cumulative proportion	0.49	0.73	0.87	0.98	1.00
standard deviation	0.30	0.14	0.08	0.07	0.03
10< proportion of variance	0.74	0.16	0.05	0.04	0.01
cumulative proportion	0.74	0.90	0.95	0.99	1.00
standard deviation	0.30	0.13	0.08	0.06	0.03
20< proportion of variance	0.78	0.13	0.05	0.03	0.01
cumulative proportion	0.78	0.91	0.96	0.99	1.00
standard deviation	0.30	0.11	0.07	0.06	0.03
30< proportion of variance	0.81	0.11	0.05	0.03	0.01
cumulative proportion	0.81	0.91	0.96	0.99	1.00
standard deviation	0.31	0.11	0.06	0.05	0.03
40< proportion of variance	0.83	0.10	0.04	0.02	0.01
cumulative proportion	0.83	0.94	0.97	0.99	1.00
standard deviation	0.30	0.11	0.06	0.05	0.03
50< proportion of variance	0.83	0.11	0.04	0.02	0.01
cumulative proportion	0.83	0.94	0.97	0.99	1.00

Table S5 - 2. Results of the discriminant analyses under six different minimum gastroliths numbers

		Predicted				
		Invertebrate	Omnivore	Plant + Seed	Vertebrate	
Observed	0<	Invertebrate	37	0	4	4
		Omnivore	6	0	5	2
		Plant + Seed	0	0	15	3
		Vertebrate	14	1	3	10
	10<	Invertebrate	21	0	3	7
		Omnivore	2	3	3	1
		Plant + Seed	0	1	13	3
		Vertebrate	4	1	1	14
	20<	Invertebrate	20	0	1	6
		Omnivore	1	1	3	1
		Plant + Seed	0	1	13	2
		Vertebrate	5	0	2	10
	30<	Invertebrate	17	0	0	5
		Omnivore	0	1	2	2
		Plant + Seed	0	0	13	2
		Vertebrate	1	1	2	13
	40<	Invertebrate	16	0	0	3
		Omnivore	0	1	2	0
		Plant + Seed	0	0	12	3
		Vertebrate	2	0	2	12
50<	Invertebrate	15	0	0	3	
	Omnivore	0	1	2	0	
	Plant + Seed	0	0	11	3	
	Vertebrate	1	0	2	12	

Table S5 - 3. Posterior probabilities of the archosaur diet predictions based on gastroliths shapes under six different minimum gastroliths numbers. Bolds represent the highest posterior probability for the individual in the analysis.

ID	Taxa	Group	0<				10<				20<			
			Invertebrate	Omnivore	Plant + seed	Vertebrate	Invertebrate	Omnivore	Plant + seed	Vertebrate	Invertebrate	Omnivore	Plant + seed	Vertebrate
IGM 100/2015	<i>Haya griva</i>	Ornithischia	0.21	0.19	0.16	0.44	0.09	0.62	0.15	0.15	0.03	0.84	0.03	0.11
IGM 100/3182	<i>Haya griva</i>	Ornithischia	0.29	0.14	0.80	0.26	0.33	0.04	0.11	0.52	0.23	0.03	0.09	0.66
IIPP V12165	<i>Psittacosaurus mazongshanensis</i>	Ornithischia	0.29	0.14	0.14	0.44	0.10	0.03	0.05	0.92	0.06	0.08	0.01	0.85
AMNH 6253	<i>Psittacosaurus mongoliensis</i>	Ornithischia	0.81	0.14	0.25	0.30	0.17	0.01	0.07	0.75	0.09	0.02	0.05	0.84
DMNH 39045	<i>Cedarosaurus weiskopfae</i>	Sauropoda	0.31	0.16	0.21	0.32	0.22	0.04	0.09	0.65	0.10	0.07	0.05	0.78
NMMNH 3690	<i>Diplodocus hallorum</i>	Sauropoda	0.11	0.11	0.70	0.09	0.01	0.01	0.97	0.01	0.00	0.00	1.00	0.00
IIPP V12344	<i>Caudipteryx dongi</i>	Theropoda	0.10	0.13	0.57	0.20	0.00	0.06	0.93	0.01	0.00	0.03	0.96	0.00
IIPP V12430	<i>Caudipteryx</i> sp.	Theropoda	0.08	0.12	0.87	0.13	0.00	0.02	0.97	0.00	0.00	0.00	1.00	0.00
MPC-D 100/127	<i>Deinocoelurus mirificus</i>	Theropoda	0.10	0.10	0.70	0.11	0.00	0.05	0.94	0.00	0.00	0.00	1.00	0.00
IIPP V15293	<i>Limusaurus inextricabilis</i>	Theropoda	0.21	0.14	0.41	0.25	0.13	0.06	0.41	0.40	0.07	0.06	0.45	0.41
IIPP V15297	<i>Limusaurus inextricabilis</i>	Theropoda	0.19	0.14	0.32	0.85	0.06	0.10	0.45	0.39	0.04	0.20	0.34	0.42
uncatalogued	<i>Sinornithomimus dongi</i>	Theropoda	0.12	0.12	0.99	0.17	0.02	0.12	0.84	0.02	0.01	0.03	0.95	0.01
MPC-D 552-1	<i>Tarbosaurus bataar</i>	Theropoda	0.30	0.17	0.24	0.28	0.27	0.04	0.11	0.58	0.12	0.06	0.08	0.74
IIPP V14287	<i>Archaeorhynchus spatula</i>	Avialae	0.08	0.10	0.70	0.12	0.00	0.01	0.98	0.00	0.00	0.00	1.00	0.00
IIPP V17075	<i>Archaeorhynchus spatula</i>	Avialae	0.14	0.17	0.30	0.39	0.01	0.13	0.78	0.08	0.00	0.47	0.48	0.05
IIPP V17091	<i>Archaeorhynchus spatula</i>	Avialae	0.17	0.16	0.47	0.21	0.07	0.05	0.68	0.22	0.01	0.08	0.75	0.16
IIPP V20312	<i>Archaeorhynchus spatula</i>	Avialae	0.19	0.17	0.35	0.29	0.09	0.12	0.48	0.31	0.03	0.27	0.40	0.30
IIPP V17970	<i>Bellulornis rectusunguis</i>	Avialae	0.30	0.13	0.20	0.37	0.07	0.01	0.07	0.86	–	–	–	–
CGCS 06-CM-011	<i>Gansus yumenensis</i>	Avialae	0.33	0.13	0.05	0.49	0.27	0.16	0.01	0.55	0.24	0.18	0.00	0.57
CGCS 07-CM-011	<i>Gansus yumenensis</i>	Avialae	0.13	0.20	0.24	0.43	0.01	0.77	0.21	0.01	–	–	–	–
IIPP V18958	<i>Iteravis huchzemeyeri</i>	Avialae	0.36	0.30	0.20	0.15	–	–	–	–	–	–	–	–
IIPP V20133	<i>Iteravis huchzemeyeri</i>	Avialae	0.27	0.12	0.16	0.45	0.02	0.00	0.16	0.81	–	–	–	–
IIPP V20134	<i>Iteravis huchzemeyeri</i>	Avialae	0.14	0.14	0.23	0.41	0.03	0.02	0.31	0.65	–	–	–	–
STM35-3	<i>Eggranivora edentulata</i>	Avialae	0.15	0.11	0.64	0.11	0.03	0.01	0.92	0.04	0.00	0.00	0.99	0.01
STM2-15	<i>Jeholornis prima</i>	Avialae	0.11	0.14	0.81	0.15	0.01	0.04	0.93	0.02	0.00	0.02	0.97	0.01
STM2-31	<i>Jeholornis prima</i>	Avialae	0.12	0.12	0.52	0.24	0.00	0.02	0.96	0.02	0.00	0.01	0.98	0.00
STM3-19	<i>Jeholornis prima</i>	Avialae	0.06	0.13	0.64	0.16	–	–	–	–	–	–	–	–
STM3-28	<i>Jeholornis prima</i>	Avialae	0.11	0.11	0.53	0.25	0.00	0.05	0.95	0.00	–	–	–	–
STM3-31	<i>Jeholornis prima</i>	Avialae	0.08	0.11	0.71	0.10	0.01	0.05	0.94	0.00	0.00	0.00	1.00	0.00

ID	Taxa	Group	30<				40<				50<			
			Invertebrate	Omnivore	Plant + seed	Vertebrate	Invertebrate	Omnivore	Plant + seed	Vertebrate	Invertebrate	Omnivore	Plant + seed	Vertebrate
IGM 100/2015	<i>Haya griva</i>	Ornithischia	0.01	0.87	0.02	0.11	0.02	0.86	0.04	0.08	–	–	–	–
IGM 100/3182	<i>Haya griva</i>	Ornithischia	0.15	0.03	0.16	0.66	0.05	0.00	0.16	0.78	–	–	–	–
IIPP V12165	<i>Psittacosaurus mazongshanensis</i>	Ornithischia	0.02	0.10	0.01	0.88	0.01	0.00	0.01	0.97	0.01	0.00	0.01	0.98
AMNH 6253	<i>Psittacosaurus mongoliensis</i>	Ornithischia	0.07	0.02	0.07	0.84	0.02	0.00	0.05	0.93	–	–	–	–
DMNH 39045	<i>Cedarosaurus weiskopfae</i>	Sauropoda	0.07	0.06	0.05	0.82	0.04	0.00	0.05	0.91	0.05	0.00	0.05	0.89
NMMNH 3690	<i>Diplodocus hallorum</i>	Sauropoda	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00
IIPP V12344	<i>Caudipteryx dongi</i>	Theropoda	0.00	0.05	0.95	0.00	0.00	0.15	0.85	0.00	0.00	0.17	0.83	0.00
IIPP V12430	<i>Caudipteryx</i> sp.	Theropoda	0.00	0.01	0.99	0.00	0.00	0.07	0.93	0.00	0.00	0.06	0.94	0.00
MPC-D 100/127	<i>Deinocoelurus mirificus</i>	Theropoda	0.00	0.00	1.00	0.00	0.00	0.01	0.99	0.00	0.00	0.01	0.98	0.00
IIPP V15293	<i>Limusaurus inextricabilis</i>	Theropoda	0.03	0.05	0.58	0.34	0.01	0.01	0.64	0.34	0.01	0.01	0.47	0.50
IIPP V15297	<i>Limusaurus inextricabilis</i>	Theropoda	0.01	0.23	0.39	0.37	0.00	0.08	0.55	0.38	0.00	0.09	0.33	0.57
uncatalogued	<i>Sinornithomimus dongi</i>	Theropoda	0.00	0.02	0.97	0.01	0.00	0.06	0.94	0.00	0.00	0.08	0.91	0.01
MPC-D 552-1	<i>Tarbosaurus bataar</i>	Theropoda	0.09	0.05	0.08	0.77	0.06	0.00	0.08	0.86	0.07	0.00	0.09	0.83
IIPP V14287	<i>Archaeorhynchus spatula</i>	Avialae	0.00	0.00	1.00	0.00	–	–	–	–	–	–	–	–
IIPP V17075	<i>Archaeorhynchus spatula</i>	Avialae	0.00	0.89	0.25	0.06	0.00	0.71	0.26	0.03	0.00	0.71	0.25	0.03
IIPP V17091	<i>Archaeorhynchus spatula</i>	Avialae	0.01	0.08	0.71	0.20	0.00	0.03	0.79	0.17	0.01	0.03	0.81	0.15
IIPP V20312	<i>Archaeorhynchus spatula</i>	Avialae	0.01	0.30	0.33	0.36	0.01	0.14	0.50	0.35	–	–	–	–
IIPP V17970	<i>Bellulornis rectusunguis</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
CGCS 06-CM-011	<i>Gansus yumenensis</i>	Avialae	–	0.08	0.24	0.00	0.68	–	–	–	–	–	–	–
CGCS 07-CM-011	<i>Gansus yumenensis</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
IIPP V18958	<i>Iteravis huchzemeyeri</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
IIPP V20133	<i>Iteravis huchzemeyeri</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
IIPP V20134	<i>Iteravis huchzemeyeri</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
STM35-3	<i>Eggranivora edentulata</i>	Avialae	0.00	0.00	0.99	0.00	–	–	–	–	–	–	–	–
STM2-15	<i>Jeholornis prima</i>	Avialae	0.00	0.03	0.86	0.01	0.00	0.06	0.93	0.00	–	–	–	–
STM2-31	<i>Jeholornis prima</i>	Avialae	0.00	0.02	0.97	0.00	0.00	0.04	0.98	0.00	–	–	–	–
STM3-19	<i>Jeholornis prima</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
STM3-28	<i>Jeholornis prima</i>	Avialae	–	–	–	–	–	–	–	–	–	–	–	–
STM3-31	<i>Jeholornis prima</i>	Avialae	0.00	0.00	0.99	0.00	0.00	0.04	0.98	0.00	0.00	0.06	0.94	0.01

BIBLIOGRAPHY

Adams, D., Collyer, M., Kaliontzopoulou, A., 2019. Geomorph: Software for geometric morphometric analyses. R package version 3.1.0.

Amerah, A.M., Ravindran, V., Lentle, R.G., Thomas, D.G., 2007. Feed particle size: Implications on the digestion and performance of poultry. *World's Poultry Science Journal* 63, 439-455.

Amiot, R., Lécuyer, C., Buffetaut, E., Fluteau, F., Legendre, S., Martineau, F., 2004. Latitudinal temperature gradient during the Cretaceous Upper Campanian–Middle Maastrichtian: $\delta^{18}\text{O}$ record of continental vertebrates. *Earth Planet Sci Lett* 226, 255-272.

Arsenault, R., Owen-Smith, N., 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos* 117, 1711-1717.

Averianov, A.O., Voronkevich, A.V., Leshchinskiy, S.V., Fayngertz, A.V., 2006. A Ceratopsian dinosaur *Psittacosaurus sibiricus* from the Early Cretaceous of West Siberia, Russia and its phylogenetic relationships. *J. Syst. Palaeontol.* 4, 359-395.

- Béland, P., Russell, D.A., 1978. Paleocology of Dinosaur Provincial Park (Cretaceous), Alberta, interpreted from the distribution of articulated vertebrate remains. *Can. J. Earth Sci.* 15, 1012-1024.
- Bairlein F., Simons, D., 1995. Nutritional adaptations in migrating birds. *Israel Journal of Ecology and Evolution* 41, 357-367.
- Bale-Therik, J.F., Sabuna, C., Jusoff, K., 2012. Influence of Grit on Performance of Local Chicken under Intensive Management System. *Global Veterinaria* 9, 248-251.
- Bapst, D.W., 2012. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution* 3, 803-807.
- Barker, R.T., 1971. Dinosaur physiology and the origin of mammals. *Evolution* 25, 636-658.
- Barlow, J., Klaas, E., Lenz, J., 1963. Sunning of bank swallows and cliff swallows. *Condor* 65, 438-440.
- Barrentine, C.D., 1980. The ingestion of grit by nestling barn swallows. *J. Field Ornithol.* 51, 368-371.
- Barrio, I.C., Bueno, C.G., Gartzia, M., Soininen, E.M., Christie, K.S., Speed, J.D.M., Ravolainen, V.T., Forbes, B.C., Gauthier, G., Horstkotte, T., Hoset, K.S., Høye,

- T.T., Jónsdóttir, I.S., Lévesque, E., Mörsdorf, M.A., Olofsson, J., Wookey, P.A., Hik, D.S., 2016. Biotic interactions mediate patterns of herbivore diversity in the Arctic. *Global Ecol. Biogeogr.* 25, 1108-1118.
- Barsbold, R., Osmólska, H., 1999. The skull of *Velociraptor* (Theropoda) from the late Cretaceous of Mongolia. *Acta Palaeontol. Pol.* 44, 189-219.
- Beaune, D., Le Bohec, C., Lucas, F., Gauthier-Clerc, M., Le Maho, Y., 2008. Stomach stones in king penguin chicks. *Polar Biol.* 32, 593-597.
- Bell, P.R., Fanti, F., Currie, P.J., Arbour, V.M., 2014. A mummified duck-billed dinosaur with a soft-tissue cock's comb. *Curr. Biol.* 24, 70-75.
- Bell, P.R., Snively, E., 2008. Polar dinosaurs on parade: a review of dinosaur migration. *Alcheringa: An Australasian Journal of Palaeontology* 32, 271-284.
- Bertozzo, F., Dal Sasso, C., Fabbri, M., Manucci, F., Maganuco, S., 2017. Redescription of a remarkably large *Gryposaurus notabilis* (Dinosauria: Hadrosauridae) from Alberta, Canada. *Mem Soc Ital Sci Nat Mus Civ Stor Nat Milano* XLIII.
- Best, L.B., Gionfriddo, J.P., 1991. Characterization of grit use by cornfield birds. *Wilson Bull.* 103, 68-82.

Best, L.B., Gionfriddo, J.P., 1994. Effects of surface texture and shape on grit selection by house sparrows and northern bobwhite. *The Wilson Bulletin*, 689-695.

Blakey, R., 2018. Global paleogeography and techtonics in deep time map.

Blix, A.S., 2005. Arctic animals and their adaptations to life on the edge. Tapir Academic Press.

Bolotsky, Y.L., Godefroit, P., 2004. A new hadrosaurine dinosaur from the Late Cretaceous of Far Eastern Russia. *J. Vert. Paleontol.* 24, 351-365.

Bonaparte, J., Franchi, M.R., Powell, J.E., Sepulveda, E., 1984. La Formación Los Alamitos (Campaniano-Maastrichtiano) del sudeste de Rio Negro, con descripcion de *Kritosaurus australis* n. sp. (Hadrosauridae). Significado paleogeografico de los vertebrados. *Rev. Asoc. Geol. Argent.* 39, 284-299.

Bosque, C., 2000. Dietary nitrogen as a limiting nutrient in frugivorous birds. *Rev. Chil. Hist. Nat.* 73, 441-450.

Boyd, C.A., 2015. The systematic relationships and biogeographic history of ornithischian dinosaurs. *PeerJ* 3, e1523.

Bramble, K., Currie, P.J., Tanke, D.H., Torices, A., 2017a. Reuniting the “head hunted” *Corythosaurus excavatus* (Dinosauria: Hadrosauridae) holotype skull with its dentary and postcranium. *Cretaceous Res.* 76, 7-18.

Bramble, K., LeBlanc, A.R.H., Lamoureux, D.O., Wosik, M., Currie, P.J., 2017b.

Histological evidence for a dynamic dental battery in hadrosaurid dinosaurs. *Sci Rep* 7, 15787.

Brett-Surman, M.K., 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. *Nature* 277, 560-562.

Brett-Surman, M.K., 1989. A Revision of the Hadrosauridae (Reptilia: Ornithischia) and Their Evolution During the Campanian and Maastrichtian, Graduate School of Arts and Sciences. George Washington University, Washington, DC, pp. 1-272.

Brett-Surman, M.K., Wagner, J.R., 2007. Discussion of character analysis of the appendicular anatomy in Campanian and Maastrichtian North American hadrosaurids—variation and ontogeny. Indiana University Press, Bloomington.

Bright, J.A., Marugan-Lobon, J., Cobb, S.N., Rayfield, E.J., 2016. The shapes of bird beaks are highly controlled by nondietary factors. *Proc Natl Acad Sci U S A* 113, 5352-5357.

Brochu, C.A., 2003. Osteology of *Tyrannosaurus Rex*: Insights from a nearly complete Skeleton and High-Resolution Computed Tomographic Analysis of the Skull. *J. Vert. Paleontol.* 22, 1-138.

- Brouwers, E.M., Clemens, W.A., Spicer, R.A., Ager, T.A., Carter, L.D., Sliter, W.V.,
1987. Dinosaurs on the North Slope, Alaska: high latitude, latest Cretaceous
environments. *Science* 237, 1608-1610.
- Brown, B., 1907. Gastroliths. *Science* 25, 392.
- Brown, B., 1912. A crested dinosaur from the Edmonton Cretaceous. *Bull. Am. Mus.
Nat. Hist.* 31, 131-136.
- Brown, B., 1913. A new trachodont dinosaur, *Hypacrosaurus*, from the Edmonton
Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.* 32, 395-406.
- Brown, B., 1916. *Corythosaurus casuarius*: skeleton, musculature and epidermis. *Bull.
Am. Mus. Nat. Hist.* 35, 709-716.
- Brown, C.M., Druckenmiller, P., Sues, H.-D., 2011. Basal ornithopod (Dinosauria:
Ornithischia) teeth from the Prince Creek Formation (early Maastrichtian) of
Alaska. *Can. J. Earth Sci.* 48, 1342-1354.
- Brown, C.R., 1976. Use of gravel by Purple Martins. *The Auk* 93, 842-842.
- Brusatte, S.L., Benton, M.J., Ruta, M., Lloyd, G.T., 2008. Superiority, competition, and
opportunism in the evolutionary radiation of dinosaurs. *Science* 321, 1485-1488.
- Buckner, G.D., Martin, J.H., Peter, A., 1926. Concerning the Growth of Chickens Raised
Without Grit. *Poult. Sci.* 5, 203-208.

- Campione, N.E., 2015. Postcranial anatomy of *Edmontosaurus regalis* (Hadrosauridae) from the Horseshoe Canyon Formation, Alberta, Canada, in: Eberth, D.A., Evans, D.C. (Eds.), *Hadrosaurs*. Indiana University Press, pp. 208-244.
- Campione, N.E., Brink, K.S., Freedman, E.A., McGarrity, C.T., Evans, D.C., 2013. ‘*Glishades ericksoni*’, an indeterminate juvenile hadrosaurid from the Two Medicine Formation of Montana: implications for hadrosauroid diversity in the latest Cretaceous (Campanian-Maastrichtian) of western North America. *Palaeobiodiversity and Palaeoenvironments*.
- Campione, N.E., Evans, D.C., 2011. Cranial growth and variation in *Edmontosaurs* (Dinosauria: Hadrosauridae): implications for latest Cretaceous megaherbivore diversity in North America. *PLoS ONE* 6, e25186.
- Carpenter, K., 1990. Ankylosaur systematics: example using *Panoplosaurus* and *Edmontonia* (Ankylosauria: Nodosauridae), in: Carpenter, K., Currie, P.J. (Eds.), *Dinosaur Systematics Approaches and Perspectives*. Cambridge University Press, Tyrrell Museum of Palaeontology, Alberta, pp. 281-298.
- Carpenter, K., Young, D.B., 2002. Late Cretaceous dinosaurs from the Denver Basin, Colorado. *Rocky. Mt. Geol* 37, 237-254.

Carrano, M.T., Janis, C.M., Sepkoski, J.J., Jr., 1999. Hadrosaurs as ungulate parallels:

lost lifestyles and deficient data. *Acta Palaeontol. Pol.* 44, 237-261.

Cerda, I.A., 2008. Gastroliths in an ornithopod dinosaur. *Acta Palaeontol. Pol.* 53,

351-355.

Charig, A.J., Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the

Wealden of Surrey. *Bull Nat Hist Mus Geol Ser* 53, 11-70.

Chen, Y.-H., Zhao, H., 2019. Evolution of digestive enzymes and dietary diversification

in birds. *PeerJ* 7, e6840.

Chiappe, L.M., Zhao, B., O'Connor, J.K., Chunling, G., Wang, X., Habib, M.,

Marugan-Lobon, J., Meng, Q., Cheng, X., 2014. A new specimen of the Early

Cretaceous bird *Hongshanornis longicresta*: insights into the aerodynamics and

diet of a basal ornithuromorph. *PeerJ* 2, e234.

Chinsamy, A., Thomas, D.B., Tumarkin-Deratzian, A.R., Fiorillo, A.R., 2012.

Hadrosaurs were perennial polar residents. *The Anatomical Record* 295,

610-614.

Choiniere, J.N., Forster, C.A., de Klerk, W.J., 2012. New information on *Nqwebasaurus*

thwazi, a coelurosaurian theropod from the Early Cretaceous Kirkwood

Formation in South Africa. *J Afr Earth Sci* 71-72, 1-17.

- Chow, P.K.Y., Lea, S.E.G., Leaver, L.A., 2016. How practice makes perfect: the role of persistence, flexibility and learning in problem-solving efficiency. *Anim. Behav.* 112, 273-283.
- Clemens, W.A., Nelms, L.G., 1993. Paleoeological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. *Geology* 21, 503.
- Conrad, J.E., McKee, E.H., Turrin, B.D., 1992. Age of tephra beds at the Ocean Point dinosaur locality, North Slope, Alaska, based on K-Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ analyses. U.S. Geological Survey Bulletin 1990C, C1-C12.
- Cott, B.H., 1961. Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *The Transactions of the Zoological Society of London* 29, 211-356.
- Cullen, T.M., Fanti, F., Capobianco, C., Ryan, M.J., Evans, D.C., 2016. A vertebrate microsite from a marine-terrestrial transition in the Foremost Formation (Campanian) of Alberta, Canada, and the use of faunal assemblage data as a paleoenvironmental indicator. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 444, 101-114.

- Currie, P., J., 1997. Gastroliths, in: Currie, P., J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, California, USA, p. 270.
- Currie, P.J., 2003. Cranial anatomy of tyrannosaurid dinosaurs from the late Cretaceous of Alberta, Canada. Acta Palaeontol. Pol. 48, 191-226.
- Currie, P.J., Holmes, R.B., Ryan, M.J., Coy, C., 2016. A juvenile chasmosaurine ceratopsid (Dinosauria, Ornithischia) from the Dinosaur Park Formation, Alberta, Canada. J. Vert. Paleontol. 36, e1048348.
- Currie, P.J., Zhao, X.-J., 1993. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. Can. J. Earth Sci. 30, 2231-2247.
- Cuthbertson, R.S., Holmes, R.B., 2010. The first complete description of the holotype of *Brachylophosaurus canadensis* Sternberg, 1953 (Dinosauria: Hadrosauridae) with comments on intraspecific variation. Zool. J. Linn. Soc. 159, 373-397.
- Cuthbertson, R.S., Tirabasso, A., Rybczynski, N., Holmes, R.B., 2012. Kinetic limitations of intracranial joints in *Brachylophosaurus canadensis* and *Edmontosaurus regalis* (Dinosauria: Hadrosauridae), and their implications for the chewing mechanics of hadrosaurids. Anat Rec (Hoboken) 295, 968-979.

- Davies, K.L., 1987. Duck-bill dinosaurs (Hadrosauridae, Ornithischia) from the North Slope of Alaska. *J. Paleontol.* 61, 198-200.
- De Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A., Ross, C.F., 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. *J. Vert. Paleontol.* 20, 324-332.
- Degen, A.A., Duke, G., E., Reynhout, J., K., 1994. Gastroduodenal motility and glandular stomach function in young ostriches. *The Auk* 111, 750-755.
- Dekinga, A., Dietz, M.W., Koolhaas, A., Piersma, T., 2001. Time course and reversibility of changes in the gizzards of red knots alternately eating hard and soft food. *J. Exp. Biol.* 204, 2167-2173.
- del Hoyo, J., Elliott, A., Christie, D., 2005. Handbook of the Birds of the World. Volume1: Cuckoo-shrikes to Thrushes. Lynx Edicions, Barcelona.
- del Hoyo, J., Elliott, A., Sargatal, J., 1992. Handbook of the Birds of the World. Volume1: Ostrich to Ducks. Lynx Edicions, Barcelona, Spain.
- Denbow, D.M., 2015. Gastrointestinal Anatomy and Physiology, in: Akers, R.M., Denbow, D.M. (Eds.), *Anatomy and Physiology of Domestic Animals*, 2nd Edition. Wiley-Blackwell, New Jersey, pp. 337-366.

- Desselberger, H., 1931. Der Verdauungskanal der Dicaeiden nach Gestalt und Funktion. *Journal für Ornithologie* 79, 353-370.
- Dodson, P., Forster, C.A., Sampson, S.D., 2004. Ceratopsidae, in: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria: Second Edition*, University of California Press, pp. 494-513.
- Edmund, A.G., 1957. On the foramina in the jaws of many ornithischian dinosaurs. *Contributions of the Royal Ontario Museum, Division of Zoology and Palaeontology* 48.
- Erickson, G.M., Krick, B.A., Hamilton, M., Bourne, G.R., Norell, M.A., Lilleodden, E., Sawyer, W.G., 2012. Complex dental structure and wear biomechanics in hadrosaurid dinosaurs. *Science* 338, 98-101.
- Erickson, G.M., Zelenitsky, D.K., 2015. Osteohistology and Occlusal Morphology of *Hypacrosaurus stebingeri* Teeth throughout Ontogeny with Comments on Wear-Induced Form and Function, *Hadrosaurs*. Indiana University Press, pp. 422-432.
- Ericson, P.G., Zuccon, D., Ohlson, J.I., Johansson, U.S., Alvarenga, H., Prum, R.O., 2006. Higher-level phylogeny and morphological evolution of tyrant flycatchers,

- cotingas, manakins, and their allies (Aves: Tyrannida). *Mol Phylogenet Evol* 40, 471-483.
- Eudes-Deslongchamps, A., 1838. Mémoire sur le *Poekilopleuron bucklandii*, grand saurien fossile, intermédiaire entre les crocodiles et les lézards, découvert dans les carrières de la Maladrerie, près Caen, au mois de juillet 1835
- Mémoires de la Société Linnéenne Normandie 6, 1-114.
- Evans, D.C., 2006. Nasal cavity homologues and cranial crest function in lambeosaurine dinosaurs. *Paleobiology* 32, 109-125.
- Evans, D.C., 2010. Cranial anatomy and systematics of *Hypacrosaurus altispinus*, and a comparative analysis of skull growth in lambeosaurine hadrosaurids (Dinosauria: Ornithischia). *Zool. J. Linn. Soc.* 159, 398-434.
- Evans, D.C., Ridgely, R., Witmer, L.M., 2009. Endocranial anatomy of lambeosaurine hadrosaurids (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. *Anat Rec (Hoboken)* 292, 1315-1337.
- Farlow, J.O., 1976. A Consideration of the Trophic Dynamics of a Late Cretaceous Large-Dinosaur Community (Oldman Formation). *Ecology* 57, 841-857.
- Festa-Bianchet, M., 2008a. *Ovis canadensis*, June 30, 2008 ed. The IUCN Red List of Threatened Species 2008, p. e.T15735A5075259.

- Festa-Bianchet, M., 2008b. *Ovis dalli*, June 30, 2008 ed. The IUCN Red List of Threatened Species 2008, p. e.T39250A10179389.
- Fiorillo, A., 1989. The vertebrate fauna from the Judith River Formation (Late Cretaceous) of Wheatland and Golden Valley Counties, Montana. The Mosasaur 4, 127-142.
- Fiorillo, A.R., 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, USA. Palaeogeogr., Palaeoclimatol., Palaeoecol. 81, 281-311.
- Fiorillo, A.R., 2008a. Dinosaurs of Alaska: Implications for the Cretaceous origin of Beringia. Geological Society of America Special Papers 442, 313-326.
- Fiorillo, A.R., 2008b. On the occurrence of exceptionally large teeth of *Troodon* (Dinosauria: Saurischia) from the late Cretaceous of Northern Alaska. Palaios 23, 322-328.
- Fiorillo, A.R., 2018. Alaska Dinosaurs: An ancient arctic world. CRC Press, Boca Raton.
- Fiorillo, A.R., Adams, T.L., 2012. A therizinosaur track from the Lower Cantwell Formation (Upper Cretaceous) of Denali National Park, Alaska. Palaios 27, 395-400.

- Fiorillo, A.R., Contessi, M., Kobayashi, Y., McCarthy, P.J., 2014a. Theropod tracks from the lower Cantwell Formation (Upper Cretaceous) of Denali National Park, Alaska, USA with comments on theropod diversity in an ancient, high-latitude terrestrial ecosystem. *New Mexico Museum of Natural History and Science* 62, 429-439.
- Fiorillo, A.R., Gangloff, R.A., 2000. Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on Arctic dinosaur paleoecology. *J. Vert. Paleontol.* 20, 675-682.
- Fiorillo, A.R., Gangloff, R.A., 2001. The caribou migration model for arctic hadrosaurs (Dinosauria: Ornithischia): A reassessment. *Hist. Biol.* 15, 323-334.
- Fiorillo, A.R., Hasiotis, S.T., Kobayashi, Y., 2014b. Herd structure in Late Cretaceous polar dinosaurs: A remarkable new dinosaur tracksite, Denali National Park, Alaska, USA. *Geology* 42, 719-722.
- Fiorillo, A.R., McCarthy, P.J., Flaig, P.P., 2010. Taphonomic and sedimentologic interpretations of the dinosaur-bearing Upper Cretaceous Strata of the Prince Creek Formation, Northern Alaska: Insights from an ancient high-latitude terrestrial ecosystem. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 295, 376-388.

- Fiorillo, A.R., McCarthy, P.J., Flaig, P.P., 2016. A multi-disciplinary perspective on habitat preferences among dinosaurs in a Cretaceous Arctic greenhouse world, North Slope, Alaska (Prince Creek Formation: lower Maastrichtian). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 441, 377-389.
- Fiorillo, A.R., McCarthy, P.J., Kobayashi, Y., Tomsich, C.S., Tykoski, R.S., Lee, Y.N., Tanaka, T., Noto, C.R., 2018. An unusual association of hadrosaur and therizinosaur tracks within Late Cretaceous rocks of Denali National Park, Alaska. *Sci. Rep.* 8, 11706.
- Fiorillo, A.R., Tykoski, R.S., 2012. A new Maastrichtian species of the centrosaurine ceratopsid *Pachyrhinosaurus* from the North Slope of Alaska. *Acta Palaeontol. Pol.* 57, 561-573.
- Fiorillo, A.R., Tykoski, R.S., 2013. An immature *Pachyrhinosaurus perotorum* (Dinosauria: Ceratopsidae) nasal reveals unexpected complexity of craniofacial ontogeny and integument in *Pachyrhinosaurus*. *PLoS ONE* 8, e65802.
- Fiorillo, A.R., Tykoski, R.S., 2014. A diminutive new tyrannosaur from the top of the world. *PLoS ONE* 9, e91287.

- Fiorillo, A.R., Tykoski, R.S., 2016. Small hadrosaur manus and pes tracks from the Lower Cantwell Formation (Upper Cretaceous) Denali National Park, Alaska: implications for locomotion in juvenile hadrosaurs. *Palaios* 31, 479-482.
- Fiorillo, A.R., Tykoski, R.S., Currie, P.J., McCarthy, P.J., Flaig, P., 2009. Description of two partial *Troodon* braincases from the Prince Creek Formation (Upper Cretaceous), North Slope Alaska. *J. Vert. Paleontol.* 29, 178-187.
- Flaig, P.P., Fiorillo, A.R., McCarthy, P.J., 2014. Dinosaur-bearing hyperconcentrated flows of Cretaceous Arctic Alaska: recurring catastrophic event beds on a distal paleopolar coastal plain. *Palaios* 29, 594-611.
- Flaig, P.P., Hasiotis, S.T., Fiorillo, A.R., 2017. A paleopolar dinosaur track site in the Cretaceous (Maastrichtian) Prince Creek Formation of Arctic Alaska: track characteristics and probable trackmakers. *Ichnos* 25, 208-220.
- Flaig, P.P., McCarthy, P.J., Fiorillo, A.R., 2013. Anatomy, Evolution, and Paleoenvironmental Interpretation of an Ancient Arctic Coastal Plain: Integrated Paleopedology and Palynology from the Upper Cretaceous (Maastrichtian) Prince Creek Formation, North Slope, Alaska, USA, in: Driese, S.G., Nordt, L.C. (Eds.), *New Frontiers in Paleopedology and Terrestrial Paleoclimatology*:

Paleosols and Soil Surface Analog Systems. SEPM Society for Sedimentary Geology.

Flores, R.M., Myers, M.D., Houseknecht, D.W., Stricker, G.D., Brizzolara, D.W.,

Ryherd, T.J., Takahashi, K.I., 2007. Stratigraphy and facies of Cretaceous

Schrader Bluff and Prince Creek Formations in Colville River Bluffs, North

Slope, Alaska. U.S. Geological Survey Professional Paper 1747, 1-52.

Foote, M., 1993. Contributions of individual taxa to overall morphological disparity.

Paleobiology 19, 403-419.

Ford, J.K.B., Ellis, G.M., Matkin, D.R., Balcomb, K.C., Briggs, D., Morton, A.B., 2005.

Killer Whale Attacks on Minke Whales: Prey Capture and Antipredator Tactics.

Mar. Mamm. Sci. 21, 603-618.

Fowler, D.W., Freedman, E.A., Scannella, J.B., Kambic, R.E., 2011. The predatory

ecology of *Deinonychus* and the origin of flapping in birds. PLoS ONE 6,

e28964.

Freedman Fowler, E.A., Horner, J.R., 2015. A new brachylophosaurin hadrosaur

(Dinosauria: Ornithischia) with an intermediate nasal crest from the Campanian

Judith River Formation of northcentral Montana. PLoS ONE 10, e0141304.

- Fritz, J., Kienzle, E., Hummel, J., Wings, O., Streich, W.J., Clauss, M., 2011. Gizzard vs. teeth, it's a tie: food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies. *Paleobiology* 37, 577-586.
- Fritz, J.C., 1937. The effect of feeding grit on digestibility in the domestic fowl. *Poult. Sci.* 16, 75-79.
- Gangloff, R., 1994. The record of Cretaceous dinosaurs in Alaska: an overview, 1992 Proceedings International Conference on Arctic Margins. Mineral Management Service, Outer Continental Shelf Study, pp. 399-404.
- Gangloff, R.A., 1995. *Edmontonia* sp., the first record of an ankylosaur from Alaska. *J. Vert. Paleontol.* 15, 195-200.
- Gangloff, R.A., 1998. Arctic dinosaurs with emphasis on the Cretaceous record of Alaska and the Eurasian-North American connection. Lower and Middle Cretaceous Terrestrial Ecosystems: New Mexico Museum of Natural History and Science Bulletin 14, 211-220.
- Gangloff, R.A., 2012. *Dinosaurs under the Aurora*. Indiana University Press.
- Gangloff, R.A., Fiorillo, A.R., 2010. Taphonomy and paleoecology of a bonebed from the Prince Creek Formation, North Slope, Alaska. *Palaios* 25, 299-317.

- Gangloff, R.A., Fiorillo, A.R., Norton, D.W., 2005. The first pachycephalosaurine (Dinosauria) from the paleo-Arctic of Alaska and its paleogeographic implications. *J. Paleontol.* 79, 997-1001.
- Gaston, A.J., Jones, I.L., 1998. *The Auks: Alcidae*. Oxford University Press, Oxford, England, UK.
- Gates, T.A., Horner, J.R., Hanna, R.R., Nelson, C.R., 2011. New unadorned hadrosaurine hadrosaurid (Dinosauria, Ornithopoda) from the Campanian of North America. *J. Vert. Paleontol.* 31, 798-811.
- Gates, T.A., Prieto-Marquez, A., Zanno, L.E., 2012. Mountain building triggered Late Cretaceous North American megaherbivore dinosaur radiation. *PLoS ONE* 7, e42135.
- Gates, T.A., Sampson, S.D., 2007. A new species of *Gryposaurus* (Dinosauria: Hadrosauridae) from the late Campanian Kaiparowits Formation, southern Utah, USA. *Zool. J. Linn. Soc.* 151, 351-376.
- Gill, F.B., 1995. *Ornithology*. Macmillan.
- Gill, P.G., Purnell, M.A., Crumpton, N., Brown, K.R., Gostling, N.J., Stampanoni, M., Rayfield, E.J., 2014. Dietary specializations and diversity in feeding ecology of the earliest stem mammals. *Nature* 512, 303-305.

- Gilmore, C.W., 1924. On the skull and skeleton of *Hypacrosaurus*, a helmet-crested dinosaur from the Edmonton Cretaceous of Alberta. Geol Surv Can Bull 38, 49-64.
- Gilmore, C.W., 1937. On the detailed skull structure of a crested hadrosaurian dinosaur. Proceedings of the United States National Museum 84, 481-491.
- Gionfriddo, J.P., Best, L.B., 1995. Grit Use by House Sparrows - Effects of Diet and Grit Size. Condor 97, 57-67.
- Gionfriddo, J.P., Best, L.B., 1996. Grit-use patterns in North American birds: the influence of diet, body size, and gender. The Wilson Bulletin, 685-696.
- Gionfriddo, J.P., Best, L.B., 1999. Grit Use by Birds: a Review, in: Nolan Jr., V., Ketterson, E.D., Thompson, C.F. (Eds.), Curr Ornithol. Kluwer Academic/Plenum Publishers, New York, pp. 89-148.
- Godefroit, P., Alifanov, V., Bolotsky, Y., 2004a. A re-appraisal of *Aralosaurus tuberiferus* (Dinosauria, Hadrosauridae) from the Late Cretaceous of Kazakhstan. Bulletin de L'institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 74, 139-154.

Godefroit, P., Bolotsky, Y.L., Bolotsky, I.Y., 2012a. Osteology and relationships of

Olorotitan arharensis, a hollow-crested hadrosaurid dinosaur from the latest

Cretaceous of Far Eastern Russia. *Acta Palaeontol. Pol.* 57, 527-560.

Godefroit, P., Bolotsky, Y.L., Lauters, P., 2012b. A new saurolophine dinosaur from the

latest cretaceous of Far Eastern Russia. *PLoS ONE* 7, e36849.

Godefroit, P., Bolotsky, Y.L., Van Itterbeeck, J., 2004b. The lambeosaurine dinosaur

Amurosaurus riabinini, from the Maastrichtian of Far Eastern Russia. *Acta*

Palaeontol. Pol. 49.

Godefroit, P., Dong, Z., Bultynck, P., Li, H., Feng, L., 1998. New *Bactrosaurus*

(Dinosauria: Hadrosauroidea) material from Iren Dabasu (Inner Mongolia, PR

China). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique,*

Sciences de la Terra 68, 3-70.

Godefroit, P., Escuillié, F., Bolotsky, Y.L., Lauters, P., 2012c. A new basal

hadrosauroid dinosaur from the upper Cretaceous of Kazakhstan, in: Godefroit,

P. (Ed.), *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems.*

Indiana University Press, Bloomington, pp. 335-358.

- Godefroit, P., Golovneva, L., Shchepetov, S., Garcia, G., Alekseev, P., 2009. The last polar dinosaurs: high diversity of latest Cretaceous arctic dinosaurs in Russia. *Naturwissenschaften* 96, 495-501.
- Godefroit, P., Shulin, H., Tingxiang, Y., Lauters, P., 2008. New hadrosaurid dinosaurs from the uppermost Cretaceous of northeastern China. *Acta Palaeontol. Pol.* 53, 47-74.
- Godefroit, P., Zan, S., Liyong, J., 2001. The maastrichtian (Late Cretaceous) lambeosaurine dinosaur *Charonosaurus jiyinensis* from North-Eastern China. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 71, 108-159.
- Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32, 221-238.
- Gordon, I.J., Illius, A.W., 1988. Incisor Arcade Structure and Diet Selection in Ruminants. *Funct. Ecol.* 2, 15-22.
- Grant, P.R., 1999. Ecology and evolution of Darwin's finches. Princeton University Press.
- Guenther, M., 2014. Comparative ontogenies (appendicular skeleton) for three hadrosaurids and a basal iguanodontian: divergent developmental pathways in

- Hadrosaurinae and Lambeosaurinae, *Hadrosaurs (Life of the Past)*. Indiana University Press Bloomington, pp. 398-415.
- Guenther, M.F., 2009. Influence of sequence heterochrony on hadrosaurid dinosaur postcranial development. *the Anatomical Record* 292, 1427-1441.
- Haq, B.U., 2014. Cretaceous eustasy revisited. *Global Planet. Change* 113, 44-58.
- Heaton, M.J., 1972. The palatal structure of some Canadian Hadrosauridae (Reptilia: Ornithischia). *Can. J. Earth Sci.* 9, 185-205.
- Hendrickx, C., Hartman, S.A., Mateus, O., 2015. An overview of non-avian theropod discoveries and classification. *PalArch's Journal of Vertebrate Palaeontology* 12, 1-73.
- Hetland, H., Svihus, B., Krogdahl, A., 2003. Effects of oat hulls and wood shavings on digestion in broilers and layers fed diets based on whole or ground wheat. *Br. Poult. Sci.* 44, 275-282.
- Higgins, R.W., Ruff, C.B., 2011. The effects of distal limb segment shortening on locomotor efficiency in sloped terrain: Implications for Neandertal locomotor behavior. *Am. J. Phys. Anthropol.* 146, 336-345.

- Horner, J.R., 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale (marine) of south-central Montana with a checklist of Upper Cretaceous dinosaur remains from marine sediments in North America. *J. Paleontol.*, 566-577.
- Horner, J.R., 1983. Cranial osteology and morphology of the type specimen of *Maiasaura peeblesorum* (Ornithischia: Hadrosauridae), with a discussion of its phylogenetic position. *J. Vert. Paleontol.* 3, 29-38.
- Horner, J.R., 1984. The nesting behavior of dinosaurs. *Sci. Am.* 250, 130-137.
- Horner, J.R., 1992. Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae) with descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relationships. *Museum of the Rockies Occasional Paper 2*, 1-119.
- Horner, J.R., Currie, P.J., 1994. Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta, in: Carpenter, K., Hirsch, K.F., Horner, J.R. (Eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York, pp. 312-336.
- Horner, J.R., Weishampel, D.B., Forster, C.A., 2004. Hadrosauridae, in: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria: Second Edition*. University of California Press, pp. 438-463.

- Hoskin, C.M., Guthrie, R.D., Hoffman, B.L., 1970. Pleistocene, Holocene and recent bird gastroliths from interior Alaska. *Arctic*, 14-23.
- Hu, C.-C., 1973. A new hadrosaur from the Cretaceous of Chucheng, Shantung. *Acta Geologica sinica* 2, 179-206.
- Huang, J., Wang, X., Hu, Y., Liu, J., Peteya, J.A., Clarke, J.A., 2016. A new ornithurine from the Early Cretaceous of China sheds light on the evolution of early ecological and cranial diversity in birds. *PeerJ* 4, e1765.
- Hummel, J., Clauss, M., 2011. Sauropod feeding and digestive physiology, in: Klein, N., Remes, K., Gee, C.T., Sander, P.M. (Eds.), *Biology of the sauropod dinosaurs. Understanding the life of giants*. Indiana University Press, Bloomington and Indianapolis, pp. 11-32.
- Jackson, S., Place, A.R., 1990. Gastrointestinal transit and lipid assimilation efficiencies in three species of sub-antarctic seabird. *J Exp Zool* 255, 141-154.
- Janis, C.M., 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. *Functional morphology in vertebrate paleontology*, 76-98.

- Janis, C.M., Ehrhardt, D., 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool. J. Linn. Soc.* 92, 267-284.
- Jenkinson, M.A., Mengel, R.M., 1970. Ingestion of stones by goatsuckers (Caprimulgidae). *Condor* 72, 236-237.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. *Nature* 491, 444-448.
- Ji, Q., Currie, P.J., Norell, M.A., Shu-An, J., 1998. Two feathered dinosaurs from northeastern china. *Nature* 393, 753-761.
- Ji, Q., Norell, M.A., Makovicky, P.J., Gao, K.-Q., Ji, S.A., Yuan, C., 2003. An Early Ostrich Dinosaur and Implications for Ornithomimosaur Phylogeny. *Am Mus Novit* 3420, 1.
- Ji, S.A., Jiang, S., Zhang, L., Hao, J., 2016. Discovery of the Early Cretaceous Ankylosaur Gastroliths and Scale Impressions from the Ordos Basin, Inner Mongolia, China. *Advances in Geosciences* 06, 355-360.
- Jin, L., Gao, Y.-y., Ye, H., Wang, W.-c., Lin, Z.-p., Yang, H.-y., Huang, S.-b., Yang, L., 2014. Effects of dietary fiber and grit on performance, gastrointestinal tract

development, lipometabolism, and grit retention of goslings. *J. Integr. Agr.* 13, 2731-2740.

Jonsson, K.A., Fabre, P.H., Fritz, S.A., Etienne, R.S., Ricklefs, R.E., Jorgensen, T.B., Fjeldsa, J., Rahbek, C., Ericson, P.G., Woog, F., Pasquet, E., Irestedt, M., 2012. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proc Natl Acad Sci U S A* 109, 6620-6625.

Kilbourne, B.M., Hoffman, L.C., 2013. Scale effects between body size and limb design in quadrupedal mammals. *PLoS ONE* 8, e78392.

Klasing, K.C., 1998. Comparative avian nutrition. CAB INTERNATIONAL, Wallingford.

Kobayashi, Y., Lu, J.-C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontol. Pol.* 48, 235-259.

Kobayashi, Y., Lu, J.-C., Dong, Z.-M., Barsbold, R., Azuma, Y., Tomida, Y., 1999. Herbivorous diet in an ornithomimid dinosaur. *Nature* 402, 480-481.

Kobayashi, Y., Nishimura, T., Takasaki, R., Chiba, K., Fiorillo, A.R., Tanaka, K., Chinzorig, T., Sato, T., Sakurai, K., 2019. A new hadrosaurine (Dinosauria: Hadrosauridae) from the marine deposits of the Late Cretaceous Hakobuchi Formation, Yezo Group, Japan. *Sci Rep* 9.

- Kuhn, M., 2008. Building Predictive Models in R Using the caret Package. Journal of Statistical Software 28.
- Lambe, L.M., 1914. On *Gryposaurus notabilis*, a new genus and species of trachodont dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Chasmosaurus belli*. Ottawa Naturalist 27, 144-155.
- Lambrecht, K., 1933. Handbuch der palaeornithologie. Gebrüder Borntraeger.
- Langston, W., 1960. The vertebrate fauna of the Selma Formation of Alabama: Part VI. The Dinosaurs. Fieldiana: Geology Memoirs 3, 313-361.
- LeBlanc, A.R., Reisz, R.R., Evans, D.C., Bailleul, A.M., 2016. Ontogeny reveals function and evolution of the hadrosaurid dinosaur dental battery. BMC Evol Biol 16, 152.
- Lee, Y.N., Barsbold, R., Currie, P.J., Kobayashi, Y., Lee, H.J., Godefroit, P., Escuillie, F., Chinzorig, T., 2014. Resolving the long-standing enigmas of a giant ornithomimosaur *Deinocheirus mirificus*. Nature 515, 257-260.
- Lefebvre, L., Whittle, P., Lascaris, E., Finkelstein, A., 1997. Feeding innovations and forebrain size in birds. Anim. Behav. 53, 549-560.

- Li, Z., Zhou, Z., Wang, M., Clarke, J.A., 2014. A New Specimen of Large-Bodied Basal Enantiornithine *Bohaiornis* from the Early Cretaceous of China and the Inference of Feeding Ecology in Mesozoic Birds. *J. Paleontol.* 88, 99-108.
- Liu, D., Chiappe, L.M., Zhang, Y., Bell, A., Meng, Q., Ji, Q., Wang, X., 2014. An advanced, new long-legged bird from the Early Cretaceous of the Jehol Group (northeastern China): insights into the temporal divergence of modern birds. *Zootaxa* 3884, 253-266.
- Lloyd, G.T., 2016. Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and future directions. *Biol. J. Linn. Soc.* 118, 131-151.
- Lloyd, G.T., Wang, S.C., Brusatte, S.L., 2012. Identifying heterogeneity in rates of morphological evolution: discrete character change in the evolution of lungfish (*Sarcopterygii*; *Dipnoi*). *Evolution* 66, 330-348.
- Lockley, M.G., Young, B.H., Carpenter, K., 1983. Hadrosaur locomotion and herding behavior: Evidence from footprints in the Mesaverde Formation, Grand Mesa Coal Field, Colorado. *Mt Geol* 20, 5-14.
- Lull, R.S., Wright, N.E., 1942. Hadrosaurian Dinosaurs of North America. Geological Society of America Special Papers 40, 1-272.

- Lund, E.K., Gates, T.A., 2006. A historical and biogeographical examination of hadrosaurian dinosaurs. New Mexico Museum of Natural History and Science Bulletin 35, 263-276.
- Makovicky, P.J., Kilbourne, B.M., Sadleir, R.W., Norell, M.A., 2011. A new basal ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. J. Vert. Paleontol. 31, 626-640.
- Mallon, J.C., Anderson, J.S., 2013. Skull ecomorphology of megaherbivorous dinosaurs from the dinosaur park formation (upper campanian) of Alberta, Canada. PLoS ONE 8, e67182.
- Mallon, J.C., Anderson, J.S., 2014. Implications of beak morphology for the evolutionary paleoecology of the megaherbivorous dinosaurs from the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. Palaeogeogr., Palaeoclimatol., Palaeoecol. 394, 29-41.
- Mallon, J.C., Evans, D.C., Ryan, M.J., Anderson, J.S., 2013. Feeding height stratification among the herbivorous dinosaurs from the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. BMC Ecol 13, 14.

- Martínez del Río, C., Baker, H.G., Baker, I., 1992. Ecological and evolutionary implications of digestive processes: Bird preferences and the sugar constituents of floral nectar and fruit pulp. *Experientia* 48, 544-551.
- Maryańska, T., Chapman, R.E., Weishampel, D.B., 2004. Pachycephalosauria, in: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria: Second Edition*. University of California Press, pp. 464-477.
- Maryańska, T., Osmólska, H., 1984. Postcranial anatomy of *Saurolophus angustirostris* with comments on other hadrosaurs. *Palaeontol. Pol.* 46, 119-141.
- Mateus, O., 1998. *Lourinhanosaurus antunesi*, A New Upper Jurassic Allosauroid (Dinosauria: Theropoda) from Lourinhã, Portugal. *Memórias da Academia de Ciências de Lisboa* 37, 111-124.
- May, T.A., Braun, C.E., 1973. Gizzard stones from adult white-tailed ptarmigan (*Lagopus leucurus*) in Colorado. *Arct. Alp. Res.*, 49-57.
- Mayr, G., Peters, D.S., Plodowski, G., Vogel, O., 2002. Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften* 89, 361-365.

- McDonald, A.T., Bird, J., Kirkland, J.I., Dodson, P., 2012. Osteology of the basal hadrosauroid *Eolambia caroljonesa* (Dinosauria: Ornithopoda) from the Cedar Mountain Formation of Utah. PLoS ONE 7, e45712.
- McIlhenny, E., 1932. The blue goose in its winter home. The Auk 49, 279-306.
- McKee, E.H., Conrad, J.E., Turin, B.D., 1989. Better dates for Arctic dinosaurs. Eos, Transactions American Geophysical Union 70, 74.
- McKeown, K.C., 1934. The food of birds from south-western New South Wales. Rec. Aust. Mus. 19, 113-135.
- McLelland, J., 1979. Digestive system, in: King, A.S., McLelland, J. (Eds.), Form and Function in Birds. Academic Press, London, pp. 69-181.
- Mendoza, M., Janis, C.M., Palmqvist, P., 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. J. Zool. 258, 223-246.
- Montuelle, S.J., Kane, E.A., 2019. Food Capture in Vertebrates: A Complex Integrative Performance of the Cranial and Postcranial Systems, in: Bels, V., Whishaw, I.Q. (Eds.), Feeding in Vertebrates: Evolution, Morphology, Behavior, Biomechanics. Springer International Publishing, Cham, pp. 71-137.

- Moore, S., 1998a. The gizzard morphology of an avian herbivore: the domestic goose, *Anser anser*. *Aust. J. Zool.* 46, 345-357.
- Moore, S.J., 1998b. The comparative functional gizzard morphology of several species of birds. *Aust. J. Zool.* 46, 359.
- Moore, S.J., 1998c. Use of an artificial gizzard to investigate the effect of grit on the breakdown of grass. *J. Zool.* 246, 119-124.
- Moore, S.J., 1999. Food breakdown in an avian herbivore: who needs teeth? *Aust. J. Zool.* 47, 625.
- Mori, H., Druckenmiller, P., Erickson, G., 2016. A new Arctic hadrosaurid (Dinosauria: Hadrosauridae) from the Prince Creek Formation (lower Maastrichtian) of northern Alaska. *Acta Palaeontol. Pol.* 61, 15-32.
- Mull, C.G., Houseknecht, D.W., Bird, K.J., 2003. Revised Cretaceous and Tertiary stratigraphic nomenclature in the Colville Basin, Northern Alaska. U.S. Geological Survey Professional Paper 1973, 426.
- Nabavizadeh, A., 2015. Hadrosauroid Jaw Mechanics and the Functional Significance of the Predentary Bone, in: Eberth, D.A., Evans, D.C., Ralrick, P.E. (Eds.), *Hadrosaurs*. Indiana University Press, pp. 467-483.

Nakajima, J., Kobayashi, Y., Chinzorig, T., Tanaka, T., Takasaki, R., Tsogtbaatar, K.,

Currie, P.J., Fiorillo, A.R., 2018. Dinosaur tracks at the Nemegt locality:

Paleobiological and paleoenvironmental implications. *Palaeogeogr.*,

Palaeoclimatol., *Palaeoecol.* 494, 147-159.

Nelms, L., 1989. Late Cretaceous dinosaurs from the North Slope of Alaska. *J. Vert.*

Paleontol. 9, 34.

Norman, D.B., 2002. On Asian ornithopods (Dinosauria: Ornithischia). 4.

Probactrosaurus Rozhdestvensky, 1966. *Zool. J. Linn. Soc.* 136, 113-144.

Norman, D.B., Sues, H.D., Witmer, L.M., Coria, R.A., 2004. Basal Ornithopoda, in:

Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria: Second*

Edition. University of California Press, pp. 393-412.

Norris, E., Norris, C., Steen, J.B., 1975. Regulation and Grinding Ability of Grit in the

Gizzard of Norwegian Willow Ptarmigan (*Lagopus Lagopus*). *Poult. Sci.* 54,

1839-1843.

O'Connor, J., Wang, X., Sullivan, C., Wang, Y., Zheng, X., Hu, H., Zhang, X., Zhou, Z.,

2017. First report of gastroliths in the Early Cretaceous basal bird *Jeholornis*.

Cretaceous Res.

- O'Connor, J.K., Wang, M., Hu, H., 2016. A new ornithuromorph (Aves) with an elongate rostrum from the Jehol Biota, and the early evolution of rostralization in birds. *J. Syst. Palaeontol.* 14, 939-948.
- O'Connor, J., 2019. The trophic habits of early birds. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*
- Olsen, A.M., Gremillet, D., 2017. Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Funct. Ecol.* 31, 1985-1995.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., Pearse, W., 2018. Caper: comparative analyses of phylogenetics and evolution in R. R package version 1.0.1.
- Osborn, H.F., 1924. *Psittacosaurus and Protiguanodon: Two Lower Cretaceous Iguanodonts from Mongolia.*
- Ostrom, J.H., 1961. *Cranial morphology of the hadrosaurian dinosaurs of North America.* American Museum of Natural History.
- Owen, R., 1866a. *Anatomy of Vertebrates. Volume 1: Fishes and Reptiles.* Longmans, Green, and Co.
- Owen, R., 1866b. *On the Anatomy of Vertebrates. Volume 2: Birds and Mammals.* Longmans, Green and Company.

- Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526-528.
- Parks, W.A., 1920. The osteology of the trachodont dinosaur *Kritosaurus incurvimanus*. University of Toronto Studies (Geological series) 11, 1-74.
- Pennell, M.W., Eastman, J.M., Slater, G.J., Brown, J.W., Uyeda, J.C., FitzJohn, R.G., Alfaro, M.E., Harmon, L.J., 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30, 2216-2218.
- Pernkopf, E., 1929. Beiträge zur vergleichenden Anatomie des Vertebratenmagens. *Zeitschrift für Anatomie und Entwicklungsgeschichte* 91, 329-390.
- Pontzer, H., 2005. A new model predicting locomotor cost from limb length via force production. *J Exp Biol* 208, 1513-1524.
- Pontzer, H., 2007. Predicting the energy cost of terrestrial locomotion: a test of the LiMb model in humans and quadrupeds. *J Exp Biol* 210, 484-494.
- Potter, E.F., 1983. Ingestion of grit by wood warblers. *The Chat* 47, 103-104.
- Potter, M.A., Lentle, R.G., Minson, C.J., Birtles, M.J., Thomas, D., Hendriks, W.H., 2006. Gastrointestinal tract of the brown kiwi (*Apteryx mantelli*). *J. Zool.* 270, 429-436.

Prestrud, P., 1991. Adaptation by the Arctic Fox (*Alopex lagopus*) to the Polar Winter.

Arctic 44, 132-138.

Prieto-Márquez, A., 2001. Osteology and variation of *Brachylophosaurus canadensis*

(Dinosauria, Hadrosauridae) from the Upper Cretaceous Judith River Formation

of Montana, Department of Earth Sciences. Montana State University, Bozeman,

Montana, p. xvii+390.

Prieto-Márquez, A., 2005. New information on the cranium of *Brachylophosaurus*

canadensis (Dinosauria, Hadrosauridae), with a revision of its phylogenetic

position. J. Vert. Paleontol. 25, 144-156.

Prieto-Márquez, A., 2010a. The braincase and skull roof of *Gryposaurus*

notabilis (Dinosauria, Hadrosauridae), with a taxonomic revision of the genus. J.

Vert. Paleontol. 30, 838-854.

Prieto-Márquez, A., 2010b. Global historical biogeography of hadrosaurid dinosaurs.

Zool. J. Linn. Soc. 159, 503-525.

Prieto-Márquez, A., 2010c. Global phylogeny of Hadrosauridae (Dinosauria:

Ornithopoda) using parsimony and Bayesian methods. Zool. J. Linn. Soc. 159,

435-502.

- Prieto-Márquez, A., 2011. Cranial and appendicular ontogeny of *Bactrosaurus johnsoni*, a hadrosauroid dinosaur from the Late Cretaceous of northern China. *Palaeontology* 54, 773-792.
- Prieto-Márquez, A., 2014. A juvenile *Edmontosaurus* from the late Maastrichtian (Cretaceous) of North America: Implications for ontogeny and phylogenetic inference in saurolophine dinosaurs. *Cretaceous Res.* 50, 282-303.
- Prieto-Márquez, A., Erickson, G.M., Ebersole, J.A., 2016. Anatomy and osteohistology of the basal hadrosaurid dinosaur *Eotrachodon* from the uppermost Santonian (Cretaceous) of southern Appalachia. *PeerJ* 4, e1872.
- Prieto-Márquez, A., Fondevilla, V., Sellés, A.G., Wagner, J.R., Galobart, À., 2019. *Adynomosaurus arcanus*, a new lambeosaurine dinosaur from the Late Cretaceous Ibero-Armorican Island of the European archipelago. *Cretaceous Res.* 96, 19-37.
- Prieto-Márquez, A., Gutarra, S., 2016. The ‘duck-billed’ dinosaurs of Careless Creek (Upper Cretaceous of Montana, USA), with comments on hadrosaurid ontogeny. *J. Paleontol.* 90, 133-146.

- Prieto-Márquez, A., Wagner, J.R., 2009. *Pararhabdodon isonensis* and *Tsintaosaurus spinorhinus*: a new clade of lambeosaurine hadrosaurids from Eurasia. Cretaceous Res. 30, 1238-1246.
- Prieto-Márquez, A., Weishampel, D.B., Horner, J.R., 2006. The dinosaur *Hadrosaurus foulkii*, from the Campanian of the east coast of North America, with a reevaluation of the genus. Acta Palaeontol. Pol. 51.
- Prieto-Marquez, A., 2007. Postcranial osteology of the hadrosaurid dinosaur *Brachylophosaurus canadensis* from the Late Cretaceous of Montana, in: Carpenter, K. (Ed.), Horns and beaks. Ceratopsian and ornithopod dinosaurs. Indiana University Press, Bloomington & Indianapolis, Indiana, pp. 91-115.
- Proctor, N.S., Lynch, P.J., 1993. Manual of ornithology: avian structure & function. Yale University Press.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rôrig, G., 1907. Magenuntersuchungen heimischer Raub-vogel. Arb. Kais. Biol. Anst. Land-u. Forstw 5, 237-265.

Ram, xed, rez-Velasco, A.A., Hern, xe, ndez-Rivera, R., xe, Servin-Pichardo, R., 2015.

The Hadrosaurian Record from Mexico, *Hadrosaurs*. Indiana University Press,
pp. 340-360.

Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and
other things). *Methods in Ecology and Evolution* 3, 217-223.

Rich, T.H., Gangloff, R.A., Hammer, W.R., 1997. Polar Dinosaurs, in: Currie, P.J.,
Padian, K. (Eds.), *Encyclopedia of Dinosaurs*. Academic Press, pp. 562-573.

Richardson, K.C., Webb, G., Manolis, S.C., 2002. *Crocodiles: Inside Out: A Guide to
the Crocodilians and Their Functional Morphology*. Surrey Beatty & Sons, Ltd.,
Sydney.

Rivett, W.H.E., 1956. Reptilian bones from the Weald Clay. *Proceedings of the
Geological Society of London* 1540, 110-111.

Rozhdestvensky, A., 1952. A new representative of the duck-billed dinosaurs from the
Upper Cretaceous deposits of Mongolia. *Doklay Akademii Naukk SSSR* 86,
405-408.

Rozhdestvensky, A., 1957. saurolophus hadrosaur from mongolia.

Rozhdestvensky, A., 1968. *Hadrosaurs of Kazakhstan. Upper Paleozoic and Mesozoic
Amphibians and Reptiles*. Moscow: Akademia Nauk SSSR, 97-141.

- Rubolini, D., Liker, A., Garamszegi, L.Z., Møller, A.P., Saino, N., 2015. Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: A primer. *Current Zoology* 61, 959-965.
- Russell, D.A., 1988. A checklist of North American marine Cretaceous vertebrates including fresh water fishes. *Occas Pap Tyrrell Mus Palaeontol* 4, 1-58.
- Russell, D.A., 1990. Mesozoic vertebrates of Arctic Canada, in: Harington, C.R. (Ed.), *Canada's missing dimension: science and history in the Canadian Arctic Island*. Canadian Museum of Nature, Ottawa, Canada, pp. 81-90.
- Sacranie, A., Svihus, B., Denstadli, V., Moen, B., Iji, P.A., Choct, M., 2012. The effect of insoluble fiber and intermittent feeding on gizzard development, gut motility, and performance of broiler chickens. *Poult Sci* 91, 693-700.
- Sander, P.M., Christian, A., Clauss, M., Fechner, R., Gee, C.T., Griebeler, E.M., Gunga, H.C., Hummel, J., Mallison, H., Perry, S.F., 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews* 86, 117-155.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671-675.

- Scholander, P.F., Hock, R., Walters, V., Irving, L., 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *The Biological Bulletin* 99, 259-271.
- Sereno, P.C., Xijin, Z., Lin, T., 2010. A new psittacosaur from Inner Mongolia and the parrot-like structure and function of the psittacosaur skull. *Proc Biol Sci* 277, 199-209.
- Siegel-Causey, D., 1990. Gastroliths assist digestion in shags. *Notornis* 37, 70-72.
- Smith, R., 1960. The influence of size and surface condition of grit upon the digestibility of feed by the domestic fowl. *Can J Anim Sci* 40, 51-56.
- Smith, R., MacIntyre, T., 1959. The influence of soluble and insoluble grit upon the digestibility of feed by the domestic fowl. *Can J Anim Sci* 39, 164-169.
- Soler, J.J., Soler, M., Martinez, J.G., 1993. Grit ingestion and cereal consumption in five corvid species. *ARDEA-WAGENINGEN*- 81, 143-143.
- Solounias, N., Moelleken, S.M.C., 1993. Dietary Adaptation of Some Extinct Ruminants Determined by Premaxillary Shape. *J. Mammal.* 74, 1059-1971.
- Spencer, L.M., 1995. Morphological Correlates of Dietary Resource Partitioning in the African Bovidae. *J. Mammal.* 76, 448-471.

Stannius, F.H., 1846. Lehrbuch der vergleichenden Anatomie der Wirbelthiere. Veit & Co., Berlin.

Starck, J.M., 1999. Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Biol.* 202, 3171-3179.

Sternberg, C.M., 1935. Hooded hadrosaurs of the Belly River Series of the Upper Cretaceous. Canada Department of Mines Bulletin (Geological Series) 77, 1-37.

Strickson, E., Prieto-Marquez, A., Benton, M.J., Stubbs, T.L., 2016. Dynamics of dental evolution in ornithopod dinosaurs. *Sci Rep* 6, 28904.

Stubbs, T.L., Benton, M.J., Elsler, A., Prieto-Márquez, A., 2019. Morphological innovation and the evolution of hadrosaurid dinosaurs. *Paleobiology* 45, 347-362.

Sullivan, R.M., 2006. A taxonomic review of the Pachycephalosauridae (Dinosauria: Ornithischia). *New Mexico Museum of Natural History and Science* 35, 347-365.

Suzuki, S., Watabe, M., 2000. Report on the Japan-Mongolia joint paleontological expedition to the Gobi desert, 1998. *Hayashibara Mus Nat Hist Res Bull* 1, 83-98.

- Swenander, G., 1899. Beiträge zur kenntnis des kropfes der vogel. Zool. Anz. 22, 140-142.
- Swenander, G., 1901. Studien über den Bau des Schlundes und des Magens der Vögel. Det Kongelige Norske Videnskabers Selskabs Skrifter 6, 1-240.
- Tagami, S., Nakaya, T., Kuchii, T., Tarumoto, Y., Tamai, S., Kawamura, K., 1969. Effects of grit on chick growth with morphological study of alimentary canal. Japanese poultry science 6, 171-178.
- Takasaki, R., Chiba, K., Kobayashi, Y., Currie, P.J., Fiorillo, A.R., 2017. Reanalysis of the phylogenetic status of *Nipponosaurus sachalinensis* (Ornithopoda: Dinosauria) from the Late Cretaceous of southern Sakhalin. Hist. Biol. 30, 694-711.
- Takasaki, R., Fiorillo, A.R., Kobayashi, Y., Tykoski, R.S., McCarthy, P.J., 2019. The First Definite Lambeosaurine Bone From the Liscomb Bonebed of the Upper Cretaceous Prince Creek Formation, Alaska, United States. Sci Rep 9, 5384.
- Talori, Y.S., Liu, Y.F., Zhao, J.S., Sullivan, C., O'Connor, J.K., Li, Z.H., 2018. Winged forelimbs of the small theropod dinosaur Caudipteryx could have generated small aerodynamic forces during rapid terrestrial locomotion. Sci Rep 8, 17854.

- Tarbot, M., 1911. *Podokesaurus holyokensis*, a new dinosaur from the Triassic of the Connecticut Valley. *Am. J. Sci.* 31, 469-479.
- Taylor, M.A., 1993. Stomach stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods. *Philos. T. R. Soc. B.* 341, 163-175.
- Thomas, G., Owen, M., Richards, P., 1977. Grit in waterfowl at the Ouse Washes, England. *Wildfowl* 28, 3.
- Thulborn, T., 1990. *Dinosaur Tracks*. Chapman and Hall, London.
- Trost, R.E., 1981. Dynamics of Grit Selection and Retention in Captive Mallards. *The Journal of Wildlife Management* 45, 64.
- Tykoski, R.S., Fiorillo, A.R., Chiba, K., 2019. New data and diagnosis for the Arctic ceratopsid dinosaur *Pachyrhinosaurus perotorum*. *J. Syst. Palaeontol.* 17, 1177-1196.
- Van der Meulen, J., Kwakernaak, C., Kan, C.A., 2008. Sand intake by laying hens and its effect on egg production parameters. *J Anim Physiol Anim Nutr (Berl)* 92, 426-431.
- van Gils, J.A., 2003. Cost-benefit analysis of mollusc-eating in a shorebird II. Optimizing gizzard size in the face of seasonal demands. *J. Exp. Biol.* 206, 3369-3380.

- van Gils, J.A., Battley, P.F., Piersma, T., Drent, R., 2005. Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proc Biol Sci* 272, 2609-2618.
- Varricchio, D.J., 1995. Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 114, 297-323.
- Varricchio, D.J., Sereno, P.C., Xijin, Z., Lin, T., Wilson, J.A., Lyon, G.H., 2008. Mud-Trapped Herd Captures Evidence of Distinctive Dinosaur Sociality. *Acta Palaeontol. Pol.* 53, 567-578.
- Venables, W.N., Ripley, B.D., 2013. Modern applied statistics with S-PLUS. Springer Science & Business Media.
- Wang, M., Lloyd, G.T., 2016. Rates of morphological evolution are heterogeneous in Early Cretaceous birds. *Proc Biol Sci* 283.
- Wang, M., Wang, X., Wang, Y., Zhou, Z., 2016a. A new basal bird from China with implications for morphological diversity in early birds. *Sci Rep* 6, 19700.
- Wang, M., Zhou, Z., 2016. A new adult specimen of the basalmost ornithuromorph bird *Archaeorhynchus spathula* (Aves: Ornithuromorpha) and its implications for early avian ontogeny. *J. Syst. Palaeontol.* 15, 1-18.

- Wang, M., Zhou, Z., Zhou, S., 2016b. A new basal ornithuromorph bird (Aves: Ornithothoraces) from the Early Cretaceous of China with implication for morphology of early Ornithuromorpha. *Zool. J. Linn. Soc.* 176, 207-223.
- Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G.H., Clark, J.M., Xu, X., 2017. Extreme Ontogenetic Changes in a Ceratosaurian Theropod. *Curr Biol* 27, 144-148.
- Wang, X., Huang, J., Hu, Y., Liu, X., Peteya, J., Clarke, J.A., 2018. The earliest evidence for a supraorbital salt gland in dinosaurs in new Early Cretaceous ornithurines. *Sci Rep* 8, 3969.
- Wang, Y.-M., O'Connor, J.K., Li, D.-Q., You, H.-L., 2015. New information on postcranial skeleton of the Early Cretaceous *Gansus yumenensis* (Aves: Ornithuromorpha). *Hist. Biol.* 28, 666-679.
- Warton, D.I., Duursma, R.A., Falster, D.S., Taskinen, S., 2012. smatr 3- an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3, 257-259.
- Watanabe, A., Erickson, G.M., Druckenmiller, P.S., 2013. An ornithomimosaurian from the Upper Cretaceous Prince Creek Formation of Alaska. *J. Vert. Paleontol.* 33, 1169-1175.

- Weishampel, D.B., 1981. The nasal cavity of lambeosaurine hadrosaurids (Reptilia: Ornithischia): comparative anatomy and homologies. *J. Paleolimnol.* 55, 1046-1057.
- Weishampel, D.B., 1983. Hadrosaurid jaw mechanics. *Acta Palaeontol. Pol.* 28, 271-280.
- Weishampel, D.B., 1984. Evolution of jaw mechanisms in ornithomimid dinosaurs. *Adv Anat Embryol Cell Biol* 87.
- Weishampel, D.B., Barrett, P.M., Coria, R.A., Loeuff, J.L., Xing, X., Xijin, Z., Sahni, A., Gomani, E.M.P., Noto, C.R., 2004. Dinosaur distribution, in: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria: Second Edition*, 2nd ed. University of California Press, pp. 515-606.
- Whittle, C.H., Everhart, M.J., 2000. Apparent and implied evolutionary trends in lithophagid vertebrates from New Mexico and elsewhere. *Dinosaurs of New Mexico: Bulletin* 17 17, 75.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95, 2027-2027.

- Wilson, U.W., 1977. A study of the biology of the *Rhinoceros Auklet* on Protection Island, Washington. Univ. of Washington, Seattle.
- Wings, O., 2004. Identification, distribution, and function of gastroliths in dinosaurs and extant birds with emphasis on ostriches (*Struthio camelus*),
Mathematisch-Naturwissenschaftlichen Fakultät Rheinischen
Friedrich-Wilhelms-Universität Bonn
- Wings, O., 2014. The rarity of gastroliths in sauropod dinosaurs - a case study in the Late Jurassic Morrison Formation, western USA. *Foss Rec* 18, 1-16.
- Wings, O., Sander, P.M., 2007. No gastric mill in sauropod dinosaurs: new evidence from analysis of gastrolith mass and function in ostriches. *P. R. Soc. B* 274, 635-640.
- Witte, W.K., Stone, D.B., Mull, C., 1987. Paleomagnetism, paleobotany, and paleogeography of the Cretaceous, North Slope, Alaska, in: Tailleux, I., Weimer, P. (Eds.), *Alaskan North Slope Geology*. Society of Economic Paleontologists and Mineralogists, Pacific Section, Bakersfield, pp. 571-579.
- Wosik, M., Goodwin, M.B., Evans, D.C., 2019. Nestling-sized hadrosaurine cranial material from the Hell Creek Formation of northeastern Montana, USA, with an analysis of cranial ontogeny in *Edmontosaurus annectens*. *Paleobios* 36, 1-18.

Xing, H., Mallon, J.C., Currie, M.L., 2017. Supplementary cranial description of the types of *Edmontosaurus regalis* (Ornithischia: Hadrosauridae), with comments on the phylogenetics and biogeography of Hadrosaurinae. PLoS ONE 12, e0175253.

Xing, H., Zhao, X.J., Wang, K.B., Li, D.J., Chen, S.Q., Mallon, J.C., Zhang, Y.X., Xu, X., 2014. Comparative osteology and phylogenetic relationship of *Edmontosaurus* and *Shantungosaurus* (Dinosauria: Hadrosauridae) from the Upper Cretaceous of North America and East Asia. Acta Geologica Sinica-English Edition 88, 1623-1652.

Xu, X., 1997. A new psittacosaur (*Psittacosaurus mazongshanensis* sp. nov.) from Mazongshan area, Gansu Province, China, in: Dong, Z. (Ed.), Sino-Japanese Silk Road Dinosaur Expedition. China Ocean Press, pp. 48-67.

Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C.K., Han, F.L., Guo, Y., 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature 459, 940-944.

You, H.L., Lamanna, M.C., Harris, J.D., Chiappe, L.M., O'Connor, J., Ji, S.A., Lu, J.C.,

Yuan, C.X., Li, D.Q., Zhang, X., Lacovara, K.J., Dodson, P., Ji, Q., 2006. A
298

- nearly modern amphibious bird from the Early Cretaceous of northwestern China. *Science* 312, 1640-1643.
- Zanno, L.E., Makovicky, P.J., 2011. Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. *Proc Natl Acad Sci U S A* 108, 232-237.
- Zhang, J., Wang, X., Wang, Q., Jiang, S., Cheng, X., Li, N., Qiu, R., 2017. A new saurolophine hadrosaurid (Dinosauria: Ornithopoda) from the Upper Cretaceous of Shandong, China. *An. Acad. Bras. Cienc.* 91, 1-19.
- Zheng, X., Martin, L.D., Zhou, Z., Burnham, D.A., Zhang, F., Miao, D., 2011. Fossil evidence of avian crops from the Early Cretaceous of China. *Proc Natl Acad Sci U S A* 108, 15904-15907.
- Zheng, X., O'Connor, J.K., Huchzermeyer, F., Wang, X., Wang, Y., Zhang, X., Zhou, Z., 2014. New specimens of *Yanornis* indicate a piscivorous diet and modern alimentary canal. *PLoS ONE* 9, e95036.
- Zheng, X., O'Connor, J.K., Wang, X., Wang, Y., Zhou, Z., 2018. Reinterpretation of a previously described Jehol bird clarifies early trophic evolution in the Ornithuromorpha. *Proc Biol Sci* 285.

- Zhou, S., O'Connor, J.K., Wang, M., 2014. A new species from an ornithuromorph (Aves: Ornithothoraces) dominated locality of the Jehol Biota. *Chin. Sci. Bull.* 59, 5366-5378.
- Zhou, S., Zhou, Z., O'Connor, J.K., 2013. Anatomy of the basal ornithuromorph bird *Archaeorhynchus spathula* from the Early Cretaceous of Liaoning, China. *J. Vert. Paleontol.* 33, 141-152.
- Zhou, Z., Clarke, J., Zhang, F., Wings, O., 2004. Gastroliths in *Yanornis*: an indication of the earliest radical diet-switching and gizzard plasticity in the lineage leading to living birds? *Naturwissenschaften* 91, 571-574.
- Zhou, Z., Zhang, F., 2002. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* 418, 405.
- Zhou, Z., Zhang, F., 2006. A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China. *Zool. Scr.* 35, 363-373.
- Ziswiler, V., Farner, D.S., 1972. Digestion and the digestive system. *Avian Biol.* 2, 343-430.