Cretaceous Research 135 (2022) 105177

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Ontogenetic dietary shifts in North American hadrosaurids (Dinosauria: Ornithischia)

Taia Wyenberg-Henzler [a, *], R. Timothy Patterson [a], Jordan C. Mallon [a, b]

[a] *Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario K1S 5B6, Canada*
[b] *Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, Ontario, K1P 6P4, Canada*

ARTICLE INFO

Article history:
Received 3 October 2021
Received in revised form
20 January 2022
Accepted in revised form 14 February 2022
Available online 23 February 2022

Keywords:
Ontogeny
Hadrosauridae
Ontogenetic niche shift
Late Cretaceous
Diet
Allometry
Dental microwear

ABSTRACT

Ontogenetic niche shifts, the phenomenon whereby animals change their resource use with growth, were probably widespread in dinosaurs, but most studies of duck-billed dinosaur ontogeny have so far focused mainly on the development of the cranial ornamentation. Here, we quantify allometry of 13 ecomorphological variables of the skull and examine tooth microwear in a sample of North American hadrosaurids to better understand their ecological functioning with growth. Our results indicate that, consistent with the Jarman-Bell principle relating body size to fibre intake and feeding selectivity, juvenile hadrosaurids were relatively more selective than their adult counterparts and subsisted on softer, low-growing browse cropped using lateral rotations of the neck. Chewing movements of the jaw probably did not differ greatly between growth stages. Our findings invite further investigation relating to cranial ontogenetic allometry in hadrosauromorphs more broadly, and to the possible role of ontogenetic niche shifts in the size structuring of Late Cretaceous herbivore communities.

1. Introduction

Many extant taxa that experience slow, multi-year growth and a change in body size over several orders of magnitude during ontogeny also tend to undergo changes in niche occupation (Werner and Gilliam, 1984; Schellekens et al., 2010; ten Brink and de Roos, 2018). Such ontogenetic niche shifts (ONSs) can have important implications for community dynamics, because a single taxon can occupy multiple niches throughout life, thereby altering the types and number of interspecific interactions that occur (Werner and Gilliam, 1984; Ebenman, 1992; Claessen and Dieckmann, 2002). Individual growth rates, and consequently birth and death rates, are also impacted by ONSs, as intraspecific niche partitioning reduces the amount of competition for resources. Changes in niche occupation during ontogeny can also facilitate the segregation of different growth stages due to differences in resource requirements and intraspecific aggression (e.g., Keren-Rotem et al., 2006; Ramirez et al., 2017).

Ontogenetic shifts in diet occur across a wide range of vertebrate taxa including fish, amphibians, reptiles and some birds, and can be accompanied by changes in habitat (Dodson, 1975a; Durtsche, 2000; Blackburn and Moreau, 2006; Platt et al., 2006; Eskew et al., 2008; McLeay et al., 2009; Mendoza-Carranza and Paes Vieira, 2009; Ramirez et al., 2017). In some animals, such as crocodilians or the white sea catfish (*Genidens barbus*), these dietary shifts involve the gradual incorporation of increasingly larger food items, such that dietary breadth overlaps between neighbouring ontogenetic stages (Dodson, 1975a; Platt et al., 2006; Mendoza-Carranza and Paes Vieira, 2009). In other taxa, these dietary shifts involve a more dramatic change in diet such that dietary breadth, and even habitat, do not overlap between growth stages (Eskew et al., 2008; Ramirez et al., 2017). For instance, loggerhead sea turtles (*Carretta carretta*) primarily inhabit and feed upon *Sargassum* matts for the first 10 years of life prior to shifting to occupy a neritic habitat where they feed upon benthic prey (Ramirez et al., 2017). In this example, the niche shift is facilitated by body size, either in relation to decreasing predation risk, increasing energetic requirements or a mixture of both. Other shifts can be facilitated by non-size related factors. In Eastern cottonmouths (*Agkistrodon piscivorous*), for example, snakes shift from inhabiting muddy, sparsely vegetated habitats and primarily consuming salamanders to hunting a variety of prey in numerous different microhabitats following the loss of yellow coloration at

---

* Corresponding author.
E-mail address: taiawh626@gmail.com (T. Wyenberg-Henzler).

https://doi.org/10.1016/j.cretres.2022.105177

the tail tip, which is used to lure prey (Eskew et al., 2008). Perhaps one of the more dramatic ONSs observed is that of the Mexican spiny-tailed iguana (*Ctenosaura pectinata*), which is primarily herbivorous as an adult but begins life as an insectivore. Although, the exact reason is unknown, such a drastic dietary shift may relate to differences in nutrition requirements: juveniles consume insects due to their relatively higher nitrogen content compared to plants, thus potentially preventing slowed growth and reduced protein synthesis in young lizards (Durtsche, 2000).

The widespread occurrence of ONSs in modern taxa has led an increasing number of researchers to suspect that ONSs were also widespread in extinct taxa, including non-avian dinosaurs (hereafter, simply 'dinosaurs') (Varricchio, 2011; Codron et al., 2013; Erickson and Zelenitsky, 2014; Wang et al., 2017; Woodruff et al., 2018; Lakin and Longrich, 2019; Frederickson et al., 2020; Rowe and Snively, 2022; Therrien et al., 2021; Schroeder et al., 2021; Wyenberg-Henzler et al., 2021). The occurrence of dietary shifts in taxa comprising the extant phylogenetic bracket of dinosaurs (crocodylians and birds), in conjunction with the large change in sizes and multi-year growth observed across many dinosaur growth series (particularly those of larger taxa), make a particularly compelling case for the occurrence of dietary shifts in dinosaurs (Dodson, 1975a; Carpenter, 1999; Varricchio, 2011; Codron et al., 2013; Vanderveen et al., 2014; Woodward et al., 2015).

Despite the likelihood of ONSs in large dinosaurs, studies identifying the presence and nature of these ONSs are relatively absent from the literature until ~10 years ago, partly due to a lack of suitable juvenile material for study (Erickson and Zelenitsky, 2014; Wang et al., 2017; Woodruff et al., 2018; Lakin and Longrich, 2019; Frederickson et al., 2020; Rowe and Snively, 2022; Therrien et al., 2021; Knapp et al., 2021; Wyenberg-Henzler et al., 2021). Historically, most studies of cranial ontogeny in dinosaurs have focused on quantifying morphological variation for taxonomic purposes, and in the case of megaherbivorous ceratopsids and hadrosaurids, this was primarily centered on changes in cranial ornamentation (e.g., Dodson, 1975b; Goodwin et al., 2006; Horner and Goodwin, 2006, 2008; Evans, 2010; Longrich and Field, 2012; Farke et al., 2013; McGaritty et al., 2013; Frederickson and Tumarkin-Deratzian, 2014; Konishi, 2015; Mallon et al., 2015; Campbell et al., 2016). The hadrosaurids, in particular, constitute one of the best groups to investigate and characterize ONSs among dinosaurs because they are well-represented by growth series showing variation in occlusal morphology of the complex tooth battery (Erickson et al., 2012; Erickson and Zelenitsky, 2014). Given the relative importance of size in community structuring and previous research into dinosaur community body size distributions, ONSs in hadrosaurids and other large dinosaurs are thought to have played an important role in the shaping of dinosaur ecosystems (Codron et al., 2013; Schroeder et al., 2021; Wyenberg-Henzler et al., 2021). A more complete understanding of the niches occupied by hadrosaurids through life can elucidate the ecological roles of these animals filled in their respective communities.

We refer to the Jarman-Bell principle to derive a testable hypothesis about the expected niche shift between young and mature hadrosaurids. Briefly, the principle maintains that smaller herbivores meet their relatively higher metabolic needs by feeding on higher quality, more easily digestible vegetation (Bell, 1971; Jarman, 1974). In that case, we predict that younger hadrosaurids should exhibit craniodental features that correspond to low-fibre herbivory, particularly compared to their more mature counterparts.

1.1. *Institutional abbreviations*

AMNH, American Museum of Natural History, New York, New York; CMN, Canadian Museum of Nature, Ottawa, Ontario; GPDM, Great Plains Dinosaur Museum, Malta, Montana; MOR, Museum of the Rockies, Bozeman, Montana; ROM, Royal Ontario Museum, Toronto, Ontario; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UALVP, University of Alberta, Edmonton, Alberta; USNM, Smithsonian Institution, National Museum of Natural History, Washington, D.C.

2. Materials and methods

Our investigation into the ONSs of hadrosaurids was conducted using specimens from the Upper Cretaceous of North America, summarized in Table 1. Taxa chosen for study, representing the subfamilies Hadrosaurinae (sensu Xing et al., 2014) and Lambeosaurinae, were selected for their good preservation and representation of ontogenetic size classes, in some cases spanning perinates to skeletally mature adults.

2.1. *Comment on ontogenetic assignment*

Among fossil vertebrates, ontogenetic maturity can be gauged in many ways (e.g., relative size, histology, osteology, bone surface texture, etc.) (Hone et al., 2016). For our purposes, we classified a specimen as either 'immature' (juvenile or subadult) or 'mature' with reference to the degree of suture closure between bones of the dermal skull roof, cranial crest development, bone texture, and size (Dodson, 1975b; Tumarkin-Deratzian, 2009; Evans, 2010; Brink et al., 2011; McGarrity et al., 2013; Hone et al., 2016) (Fig. 1).

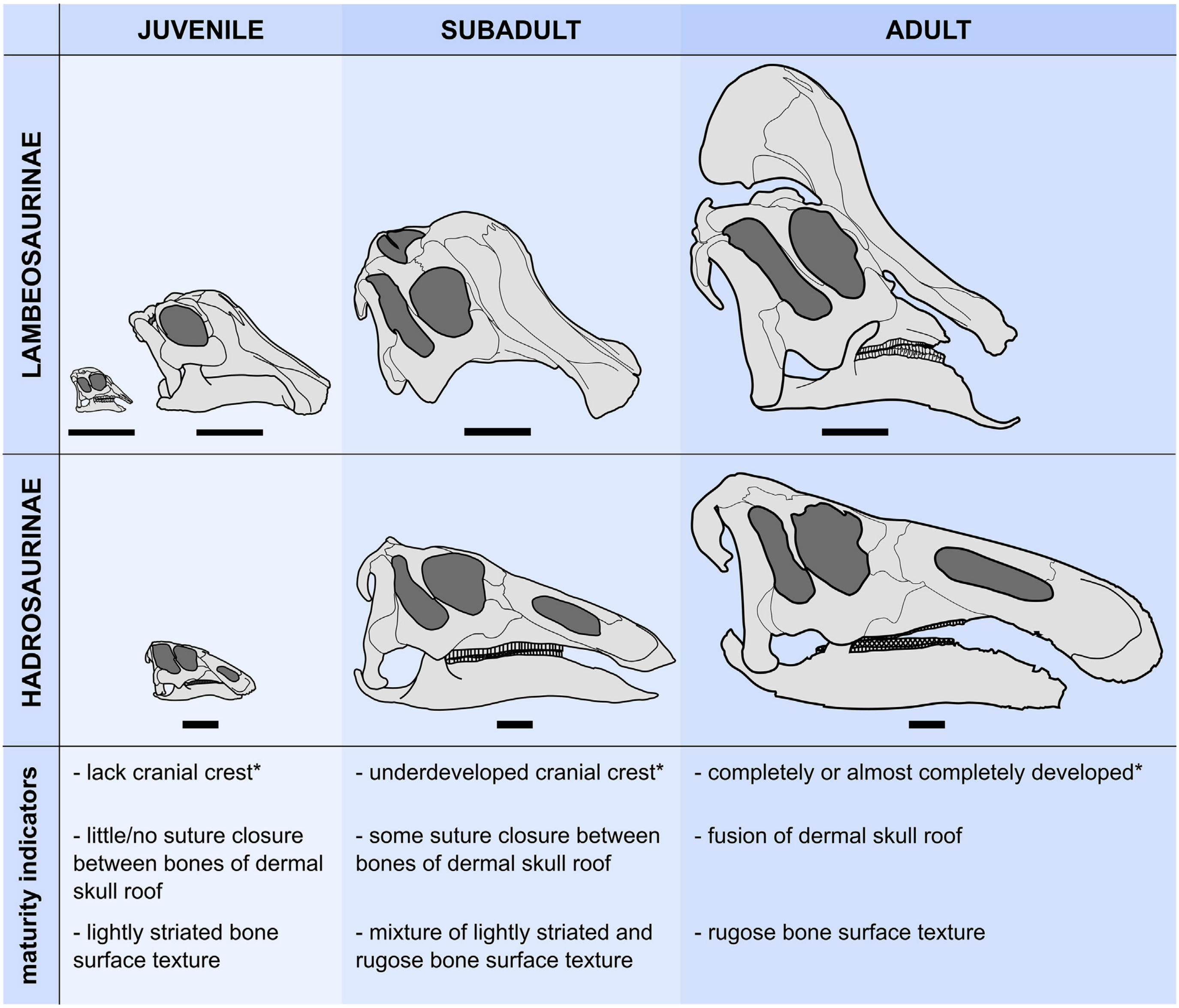
2.2. *Skull allometry*

Ontogenetic niche shifts in modern taxa are facilitated by changes in overall size that may or may not be accompanied by changes in shape (Werner and Gilliam, 1984). While shape change is not necessary for an ONS to occur, allometric growth (disproportional increases/decreases in morphology relative to size sensu Gould, 1966) of one or more features can provide more compelling evidence for the presence of an ONS. To investigate the potential ecological consequences of ontogenetic change in the skull, we considered 13 ecomorphological correlates (Supplementary File 1) known in modern vertebrate herbivores to reflect differences in the mechanical properties of the plants they eat, feeding height and feeding behaviour (Dodson, 1975a; Janis and Ehrhardt, 1988; Solounias et al., 1988; Janis, 1990, 1995; Spencer, 1995; Dompierre and Churcher, 1996; Mendoza et al., 2002; Herrel et al., 2006). These correlates have previously been used to describe the groups examined here (Mallon and Anderson, 2013; Wyenberg-Henzler, 2020; Wyenberg-Henzler et al., 2021). The rarity of juvenile hadrosaurids, especially at the smallest body sizes, necessitated the use of composite specimens produced by scaling and combining elements from various individuals. While a potential source of error in our dataset, we deemed it reasonable to include these composites because they are based on real fossil material and are accurate enough for our purposes.

We investigated allometric growth within the skull by using the log-transformed values of these ecomorphological correlates in a reduced major axis regression (RMA) against log-transformed skull length, which has previously been used as a proxy for body size (e.g., Dodson, 1975b; Evans, 2010; Campione and Evans, 2011).

Table 1
Sample sizes by family, subfamily and genus for analyses of skull ecomorphology and dental microwear in the present study.

Classification	Skull morphometrics			Dental microwear		
	juvenile	subadult	adult	juvenile	subadult	adult
Hadrosauridae	15	20	70	3	12	6
Hadrosaurinae	5	11	35	0	3	4
Brachylophosaurus	0	0	3	0	0	0
Edmontosaurus	1	6	20	0	1	3
Gryposaurus	1	2	4	0	0	0
Maiasaura	3	1	3	0	0	0
Prosaurolophus	0	2	5	0	2	1
Lambeosaurinae	10	9	35	3	9	2
Lambeosaurinae indet.	2	0	0	0	0	0
Corythosaurus	1	4	17	1	3	2
Hypacrosaurus	5	2	3	2	4	0
Lambeosaurus	2	2	14	0	0	0
Parasaurolophus	0	1	1	0	2	0



maturity indicators	JUVENILE	SUBADULT	ADULT
	- lack cranial crest*	- underdeveloped cranial crest*	- completely or almost completely developed*
	- little/no suture closure between bones of dermal skull roof	- some suture closure between bones of dermal skull roof	- fusion of dermal skull roof
	- lightly striated bone surface texture	- mixture of lightly striated and rugose bone surface texture	- rugose bone surface texture

Fig. 1. Determination of basic ontogenetic classifications in hadrosaurids. Scale bars = 10 cm. *Maturity indicators do not apply to some crestless hadrosaurine taxa (e.g., *Edmontosaurus*).

Reduced major axis regression was used because, unlike the more commonly used ordinary least squares regression, RMA assumes error in both the predictor and response variables (Hammer and Harper, 2006). We also conducted an ANCOVA for each variable to identify potential differences in slope and intercept between regression lines fitted for hadrosaurines and lambeosaurines using a likelihood and Wald test statistic, respectively, as these statistics are less sensitive to unequal residual variances (Warton et al., 2006). To control for inflation of family-wise error rates, the p-values from all of the regressions for a given clade were adjusted using the Holm-correction method (Holm, 1979; McDonald, 2014). If no significant differences in slope and intercept were identified (i.e., a p-value > 0.05), then the regression for that variable was rerun on the combined hadrosaurid dataset. As in other allometric studies, a relationship was deemed isometric if the confidence intervals for the slope of the regression line included a value of 1, positively allometric if values above 1 were included and negatively allometric if values below 1 were included (Klingenberg, 2016). Because small sample sizes can make it difficult to determine if recovered isometry is due to poor sampling or is reflective of a true developmental signal, some or all instances of isometry reported here may actually reflect instances of "soft" isometry (i.e., isometry due to low statistical power) (see Brown and Vavrek, 2015). These analyses and those that follow were conducted in R version 4.1.0 (R Core Team, 2019).

2.3. Dental microwear analysis

The microscopic damage inflicted on teeth during tooth-on-tooth, tooth-on-food and tooth-on-grit interactions (dental microwear) (Whitlock, 2011) has been previously used to identify chewing and dietary differences between taxa, both extant (Solounias and Semprebon, 2002; Semprebon et al., 2004; Nelson, 2005; Rivals and Semprebon, 2011) and extinct (Fiorillo, 1998; Goillot et al., 2009; Williams et al., 2009; Whitlock, 2011; Mallon and Anderson, 2014; DeSantis, 2016). For our purposes, we separated microwear features into two categories based on relative length and width: scratches (linear features with a length four or more times greater than the width) and pits (deep, circular to ovate features) (Nelson, 2005). To obtain casts of teeth for dental microwear analysis, we applied the methodology described by Mallon and Anderson (2014) to teeth from both maxillae and dentaries (to maximize sample size) using President Regular body polyvinylsiloxane for tooth surface impressions and Epotek 301 two-part epoxy for casting. Casts identified as potentially containing dental microwear using an Olympus SZX12 stereo light microscope were sputter coated using a Denton Vacuum Desk II at 50 atm for 30 s under a 40 mA current in preparation for imaging with a FEI scanning electron microscope. At a chamber pressure of 50 Pa, voltage of 5.00 kV and beam current of 0.10 nA, overlapping micrographs of the tooth surface were taken at 100× magnification and then manually overlaid and then rotated to orient the tooth apex upwards in InkScape v.1.1 (Caldwell et al., 2004–2021). Following the methodology of Fraser et al. (2009), images were loaded into ImageJ v.1.52a (Rasband et al., 1997-2018), a 0.4 × 0.4 mm bounding box was drawn around the area with the best preserved microwear, and the lengths, widths and orientations of features were measured and recorded.

2.3.1. Comparison of scratch orientation

Microwear scratch length and orientation can be used to infer primary and secondary jaw movements during feeding (e.g., power stroke and repositioning motions), and has been successfully used on adult hadrosaurids (Weishampel, 1983; Williams et al., 2009; Mallon and Anderson, 2014). To investigate potential changes in jaw motion during ontogeny, we conducted quantitative and qualitative comparisons of scratch orientation. Such an analysis requires standardization to one side of the skull, in this case, the

Table 2
Results for tests of equivalent slopes and intercepts for regressions against skull length conducted in hadrosaurids.

Log-transformed Y-variables	sample size	LR statistic (slope)	p-value (slope)	Wald statistic (intercept)	p-value (intercept)
beak length	La: 51 Ha: 47	0.007	1	2.043	1
diastema length	La: 49 Ha: 47	2.934	1	0.72	1
tooth row length	La: 51 Ha: 47	2.984	1	9.469	**0.023**
distal tooth row to mid-quadrate	La: 51 Ha: 43	0.448	1	0.405	1
snout width	La: 42 Ha: 34	0.158	1	0.002	1
dentary height	La: 51 Ha: 46	1.664	1	1.707	1
paroccipital process breadth	La: 32 Ha: 33	1.231	1	0.77	1
occiput height	La: 26 Ha: 27	1.925	1	10.079	**0.018**
coronoid process jaw joint	La: 47 Ha: 44	0.131	1	6.327	0.119
snout depression	La: 50 Ha: 44	0.048	1	4.549	0.296
skull height	La: 50 Ha: 45	3.521	0.788	15.436	**0.001**
quadrate breadth	La: 36 Ha: 34	0.244	1	0.643	1
SSI	La: 43 Ha: 28	0.155	1	0.039	1

Reported p-values are the Holm-corrected values. Significant p-values are in bold.
Abbreviations: LR, likelihood ratio; La, Lambeosaurinae; Ha, Hadrosaurinae; SSI, snout shape index.

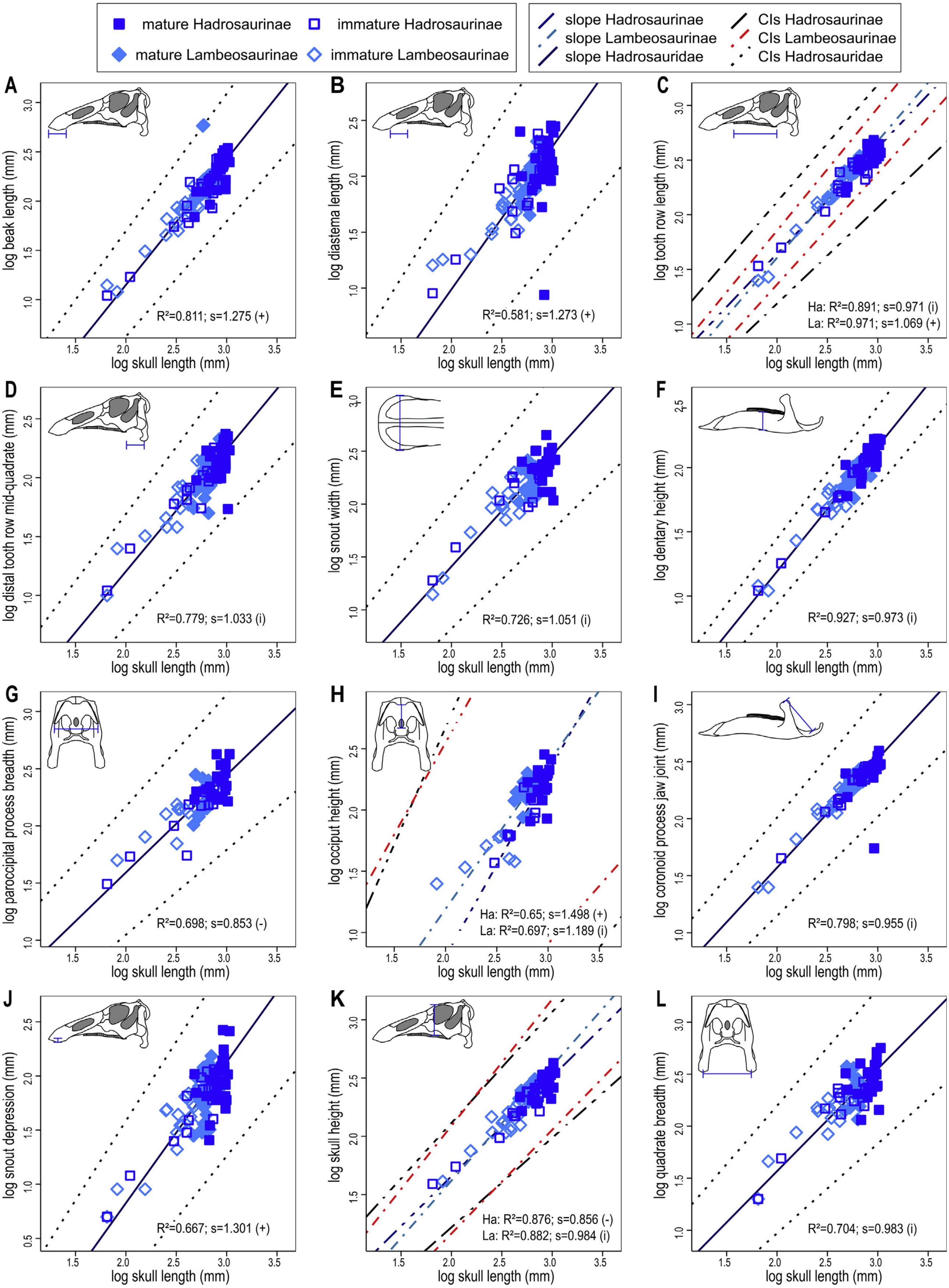


Fig. 2. Reduced major axis regression plots for various variables against log-transformed skull length for hadrosaurids. Abbreviations: Ha, Hadrosaurinae; La, Lambeosaurinae; s, slope; (+), positive allometry; (−), negative allometry; (i), isometry. Model parameters and subfamily-level comparisons of slope and intercept in Table 2 and 3.

Table 3
Results of reduced major axis regression of various variables against skull length for hadrosaurids.

Log-transformed Y-variables	grp	n	R^2	p-value	intercept	95% CI intercept	slope	95% CI slope	trend
beak length	H	98	0.811	**2.2E-35**	−1.4	−1.71 to −1.089	1.275	1.168 to 1.393	+
diastema length	H	96	0.581	**9.48E-19**	−1.557	−2.024 to −1.091	1.273	1.116 to 1.453	+
tooth row length	Ha	47	0.891	**2.41E-22**	−0.299	−0.572 to −0.026	0.971	0.879 to 1.072	i
	La	51	0.971	**4.76E-38**	−0.532	−0.674 to −0.391	1.069	1.018 to 1.123	+
distal tooth row to mid-quadrate	H	94	0.779	**7.6E-31**	−0.862	−1.139 to −0.584	1.033	0.937 to 1.138	i
snout width	H	76	0.726	**1.32E-21**	−0.692	−1.042 to −0.343	1.051	0.932 to 1.186	i
dentary height	H	97	0.927	**1.03E-54**	−0.755	−0.902 to −0.607	0.973	0.921 to 1.028	i
paroccipital process breadth	H	65	0.698	**2.01E-17**	−0.114	−0.439 to 0.211	0.853	0.743 to 0.979	−
occiput height	Ha	27	0.65	**7.8E-07**	−2.191	−3.242 to −1.141	1.498	1.176 to 1.907	+
	La	26	0.697	**3.44E-07**	−1.186	−1.927 to −0.445	1.189	0.945 to 1.497	i
coronoid process jaw joint	H	91	0.798	**1.6E-31**	−0.34	−0.59 to −0.089	0.955	0.869 to 1.05	i
snout depression	H	94	0.667	**1.11E-22**	−1.776	−2.205 to −1.347	1.301	1.155 to 1.466	+
skull height	Ha	45	0.876	**2.8E-20**	−0.055	−0.318 to 0.208	0.856	0.768 to 0.953	−
	La	50	0.882	**7.75E-23**	−0.349	−0.615 to −0.083	0.984	0.89 to 1.087	i
quadrate breadth	H	70	0.704	**7.03E-19**	−0.399	−0.753 to −0.045	0.983	0.862 to 1.12	i
SSI	H	71	0.006	0.514	1.707	1.138 to 2.276	−0.866	−1.098 to −0.683	NS

Reported p-values are Holm-corrected. Significant p-values are in bold. All variables showing a non-significant slope were not graphed with the other variables.
Abbreviations: grp, grouping; n, sample size; H, Hadrosauridae; Ha, Hadrosaurinae; La, Lambeosaurinae; NS, non-significant slope; +, positive allometry; −, negative allometry; I, isometry.

right dentary as in previous studies (e.g., Mallon and Anderson, 2014). This was achieved by first flipping composite micrographs of the right dentary and left maxilla on the vertical axis to standardize to the left dentary. The measured angles were then standardized to equivalent, positive angle values between 0° and 180° by adding 180° to all negative values (e.g., −30°+180° = 150°) before subtracting all angles from 180° to standardize them to the right dentary (e.g., 180°-150° = 30°). Qualitative comparisons between ontogenetic stages were conducted at the genus level by constructing rose diagrams. To obtain preferred scratch orientation(s), we pooled observations along the tooth row into a single diagram, separating binned scratch lengths (Mallon and Anderson, 2014). In some instances, it was not possible to fully sample the tooth row for each individual because not all teeth were present in the jaw, some teeth did not preserve any microwear, or the microwear preserved was taphonomically overprinted by 'acid

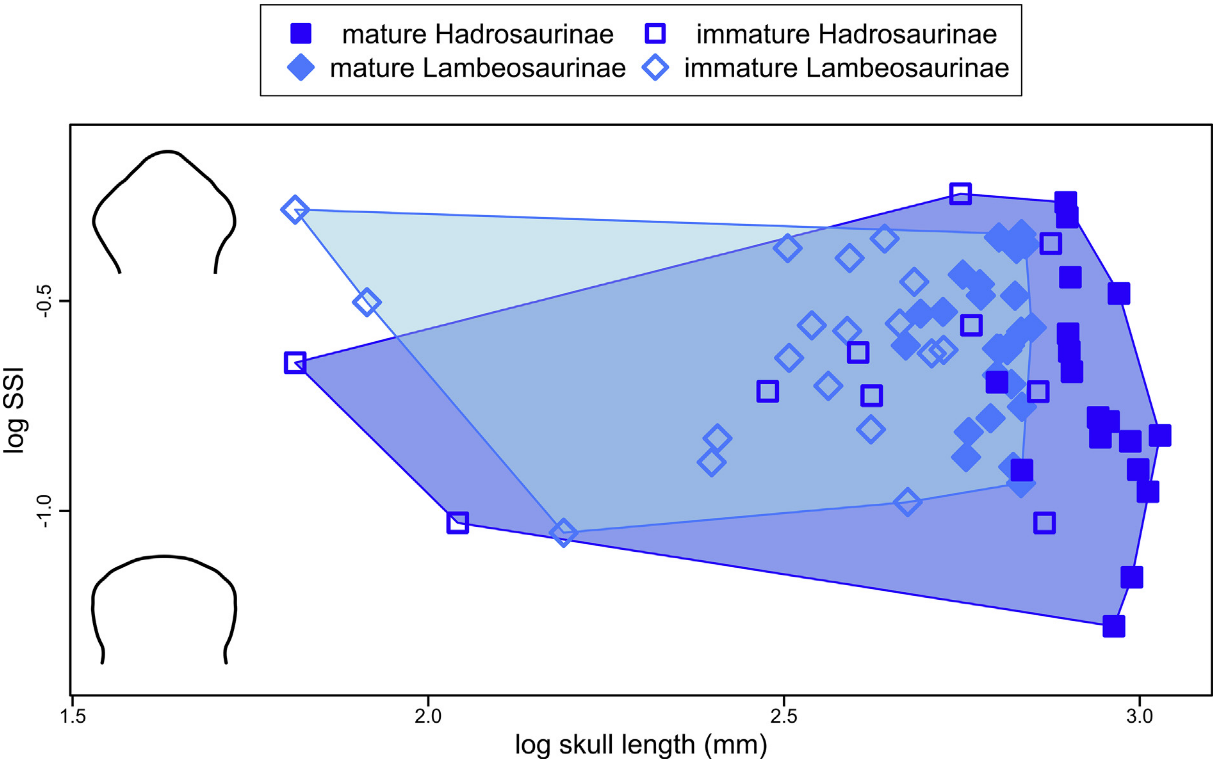


Fig. 3. Plots of log snout shape index against log skull length for hadrosaurids. Snout shape index was not plotted on regression plots with other variables as the estimated slope was not significant (see Tables 1 and 2).

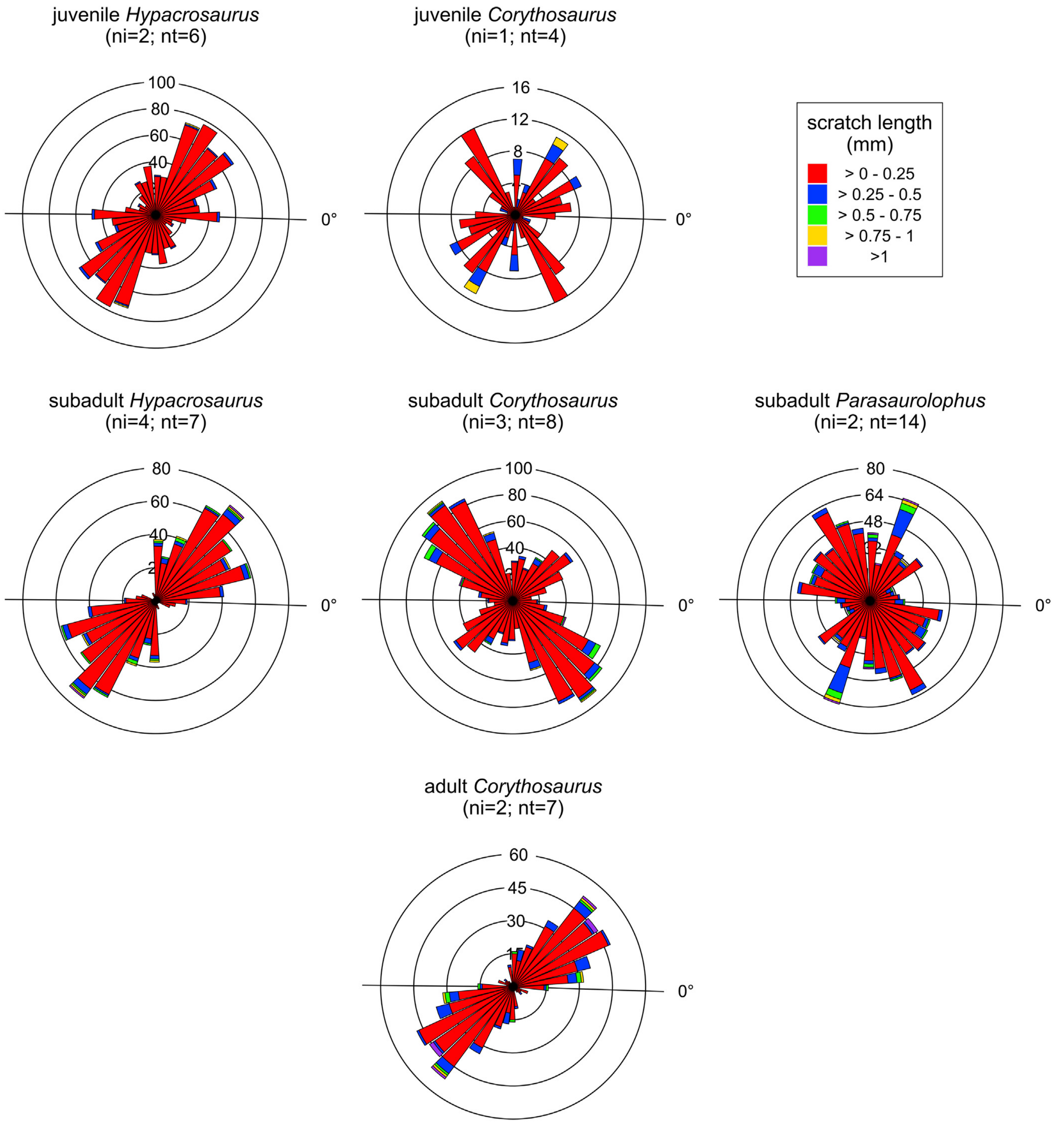


Fig. 4. Pooled rose diagrams for each genus and ontogenetic stage for lambeosaurines. Plots are produced by pooling results from multiple individuals and multiple teeth. All teeth standardized to the right dentary. Abbreviations: ni, number of individuals used; nt, number of teeth used total. Orientation: 0° = mesial, 180° = distal, and 270° = basal/ventral (bottom). Rose diagrams pooled across multiple teeth for each individual are available in Supplementary materials.

etching'. Because of this, it was sometimes necessary to combine observations of multiple individuals of the same ontogenetic stage in a single rose diagram to generate a composite tooth row.

Quantitative comparisons were made between ontogenetic stages at the subfamily level for hadrosaurids because sample sizes for each stage were too small to be made at the genus level. We used the circle_mle() function (Fitak and Johnsen, 2020) to estimate mean angle(s) (q) and concentration parameter(s) (k) for each specimen over 1000 iterations and requiring a minimum of 30° separation between angle groupings. This value was chosen because it represents a reasonable trade-off between allowing for variance in scratch orientation and the identification of subtle angle groupings, if present. The circle_mle() function employs a likelihood-based approach to calculate the mean angle(s) and

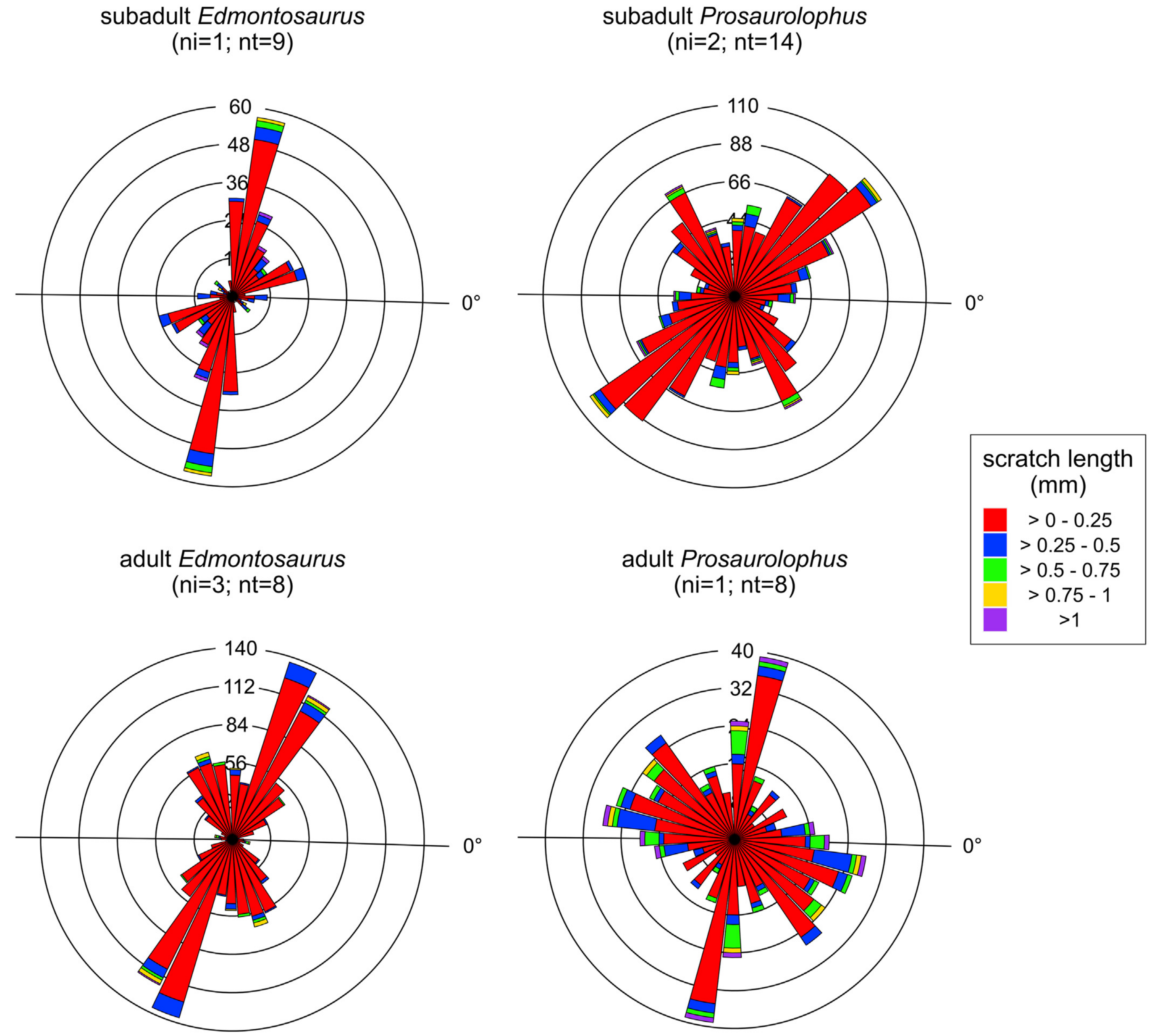


Fig. 5. Pooled rose diagrams for each genus and ontogenetic stage for hadrosaurines. Plots are produced by pooling results from multiple individuals and multiple teeth. All teeth standardized to the right dentary. Abbreviations: ni, number of individuals used; nt, number of teeth used total. Orientation: 0° = mesial, 180° = distal, and 270° = basal/ventral (bottom). Rose diagrams pooled across multiple teeth for each individual are available in Supplementary materials.

concentration parameter(s) for one or more models (selected by the user) that assume uniform, and several different unimodal and bimodal distributions (Fitak and Johnsen, 2017). The function then returns the estimated values with the lowest Akaike Information Criterion (AIC) value. For our purposes, we considered five of the ten possible models (uniform, homogeneous symmetrical bimodal, symmetrical bimodal, homogeneous bimodal, and bimodal). We excluded symmetric modified unimodal and modified unimodal models because these models assume a combination of a preferred direction and a component of random directions (Schnute and Groot, 1992) into model construction – randomness that is not compatible under the framework of dental microwear. We also excluded all axial bimodal models because these models assume that the two direction groupings are exactly 180 degrees apart. The mean angle(s) (q) can indicate the average direction for each scratch distribution while the concentration parameter(s) (k) indicate the homogeneity of scratch orientations within each distribution where large values of k indicate tight clustering of angles (Schnute and Groot, 1992; Fitak and Johnsen, 2017).

2.3.2. Feature counts and dimensions

The relative number of pits to scratches and the relative size of features have previously been used in extant taxa to distinguish dietary categories (Solounias and Semprebon, 2002; Semprebon et al., 2004; Rivals and Semprebon, 2011). Browsing ungulates (i.e., those selecting for low-fibre plants or plant parts) generally exhibit a higher ratio of microscopic pits to scratches on their occlusal surfaces than their grazing counterparts (consuming a higher fibre content). Feature size (e.g., coarse scratches, large pits) can be used to further subdivide these groups. For example, elephants consume bark, coarse stems, and leaves, and their dental microwear is characterized by a high percentage of coarse scratches and large pits (Solounias and Semprebon, 2002). Here, we considered pit scratch count ratio, scratch width, scratch length and pit area. Because of small sample sizes, these comparisons were conducted with non-parametric tests. A Kruskal-Wallis test was used to conduct the omnibus test and, if the results returned a p-value > 0.05, a follow-up pairwise Mann-Whitney U test with Holm-corrected p-values was conducted (Holm, 1979; McDonald, 2014). Boxplots of each of these microwear variables were also constructed to facilitate qualitative comparisons between stages.

3. Results

3.1. Morphometrics

Statistical comparisons of slope and intercept between subfamilies indicate significant differences between regression lines for Hadrosaurinae and Lambeosaurinae in tooth row length, occiput height and skull height (Table 2).

Three of the 13 variables are positively allometric (beak length, diastema length, snout depression) and one variable is negatively allometric (paroccipital process breadth) for all hadrosaurids (Fig. 2; Table 3). Tooth row length and occiput height are also positively allometric for lambeosaurines and hadrosaurines, respectively. Skull height is negatively allometric for hadrosaurines. ‘Strong’ allometry (slope >1.1 or slope <0.9) is observed for all these variables except for tooth row length. All other measurements show an isometric relationship with skull length.

Snout shape index shows no linear relationship with skull length and so is plotted separately from the other variables for both hadrosaurid subfamilies (Fig. 3). Overlap along the y-axis is relatively consistent through ontogeny and no significant differences are returned ($n_{\text{immature}} = 28$, $n_{\text{mature}} = 43$, df = 1, rank sum statistic = 0.05, p-value = 0.823).

3.2. Dental microwear

Specimens sampled for each genus and ontogenetic stage, and the number of teeth sampled for each specimen, are provided in the Supplementary materials. Mean angles and concentration parameters estimated from model construction, and mean scratch length, scratch width, pit area and pit/scratch ratio for each individual specimen, are also provided in the Supplementary materials.

Rose diagrams do not show any consistent differences in scratch orientation or variability between ontogenetic stages (Figs. 4, 5; Supplementary Figs. S1–5). Only one specimen, the juvenile *Corythosaurus* specimen (USNM 16600), exhibits a noticeably greater variability in scratch orientation compared to other more mature individuals (Fig. 4). Generally, hadrosaurids exhibit a bimodal scratch distribution with a primary mode of scratches in the dorsomesial-ventrodistal direction and a second mode of scratches in the dorsodistal-ventromesial direction, regardless of ontogenetic stage. However, some specimens show a primary mode of dorsodistal-ventromesial scratches and secondary mode of dorsomesial-ventrodistal scratches (e.g., subadult *Corythosaurus* [ROM 759, USNM 11839]; adult *Edmontosaurus* [USNM 4808, MOR 003]) (Figs. 4, 5; Supplementary Figs. S1–5). No clear pattern in modality was observed for any ontogenetic stage because both unimodal models and bimodal models best fit different individuals of the same ontogenetic stage (e.g., subadult *Hypacrosaurus* [ROM 61784 unimodal, USNM 11950 bimodal]) (Supplementary Table S3).

No significant differences are observed between ontogenetic stages for any of the statistical tests conducted (Table 4). Comparisons of constructed boxplots also indicate very little difference in descriptive parameters (Fig. 6). Mean pit/scratch count ratio is slightly higher for juveniles and the scratches are slightly shorter than those of subadults and adults, on average (Fig. 6).

4. Discussion

4.1. Jaw mechanics

The weakly constructed skulls of immature hadrosaurids, characterized by cartilaginous joints and weakly interdigitated sutures (Horner and Currie, 1994; Bailleul et al., 2012, 2016), might lead one to predict that variation in dental microstriation orientation should be higher in these forms, reflective of a more poorly constrained chewing mechanism. However, we find no evidence that this is the case; there is no obvious progression from highly variable

Table 4
Results of Mann-Whitney-U tests conducted on various feature measurements between ontogenetic stages for each hadrosaurid subfamily.

variable	subfamily	sample size	chi-squared statistic	degrees of freedom	p-value

scratch/pit count ratio	Lambeosaurinae	juvenile (n = 2);
		subadult (n = 6);
		adult (n = 2)
			0.182	2	0.913

	Hadrosaurinae	juvenile (n = 1);
		subadult (n = 2);
		adult (n = 2)
			0.6	2	0.741

scratch length (mm)	Lambeosaurinae	juvenile (n = 2);
		subadult (n = 7);
		adult (n = 2)
			1.149	2	0.563

	Hadrosaurinae	juvenile (n = 1);
		subadult (n = 5);
		adult (n = 4)
			2.455	2	0.293

scratch width (mm)	Lambeosaurinae	juvenile (n = 2);
		subadult (n = 7);
		adult (n = 2)
			0.671	2	0.715

	Hadrosaurinae	juvenile (n = 1);
		subadult (n = 5);
		adult (n = 4)
			0.53	2	0.767

pit area (mm^2)	Lambeosaurinae	juvenile (n = 2);
		subadult (n = 7);
		adult (n = 2)
			0.506	2	0.776

	Hadrosaurinae	juvenile (n = 1);
		subadult (n = 4);
		adult (n = 3)
			1.833	2	0.4

Sample sizes for each ontogenetic stage are provided in brackets.

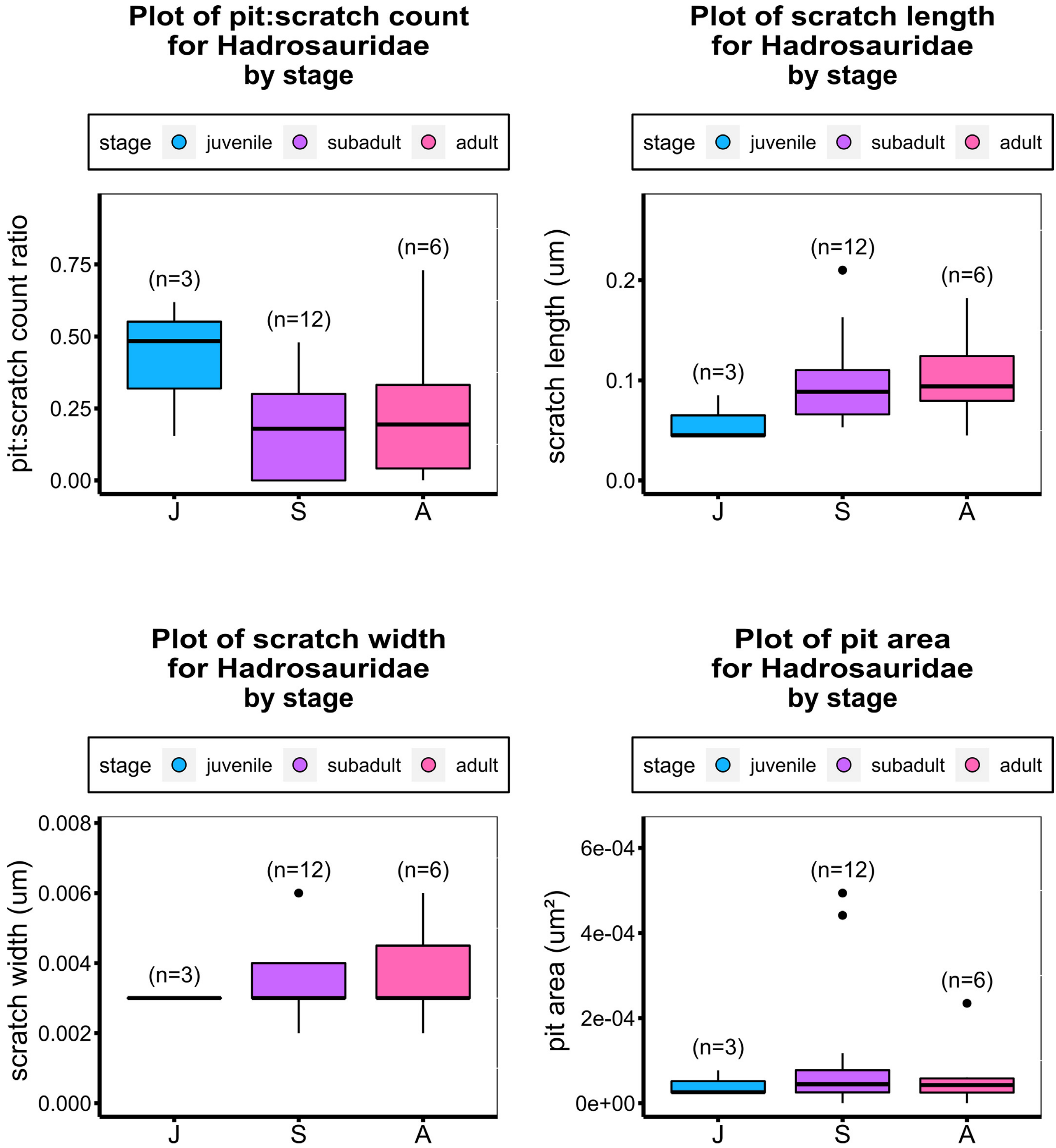


Fig. 6. Boxplots of mean feature dimensions for ontogenetic stages for the Hadrosauridae. For boxplots of each genus see Supplementary materials. Abbreviations: n, number of individuals; J, juvenile; S, subadult; A, adult.

microstriation orientation in juveniles to a more tightly constrained pattern in adults. Perhaps the neuromuscular mechanisms of the juveniles were well-canalized and not dependent on the tightness of the cranial joints. The exceptionally high variation in young *Corythosaurus* (Fig. 4) is plausibly attributable to random sampling of just a highly variable individual. With new fossil discoveries, sampling of more individuals at this ontogenetic stage will likely constrain the resultant signal.

Our microwear data are consistent with previous studies finding multiple (typically two) scratch orientation modes (e.g., Weishampel, 1983; Williams et al., 2009; Mallon and Anderson, 2014; Rivera-Sylva et al., 2019). However, whereas those previous

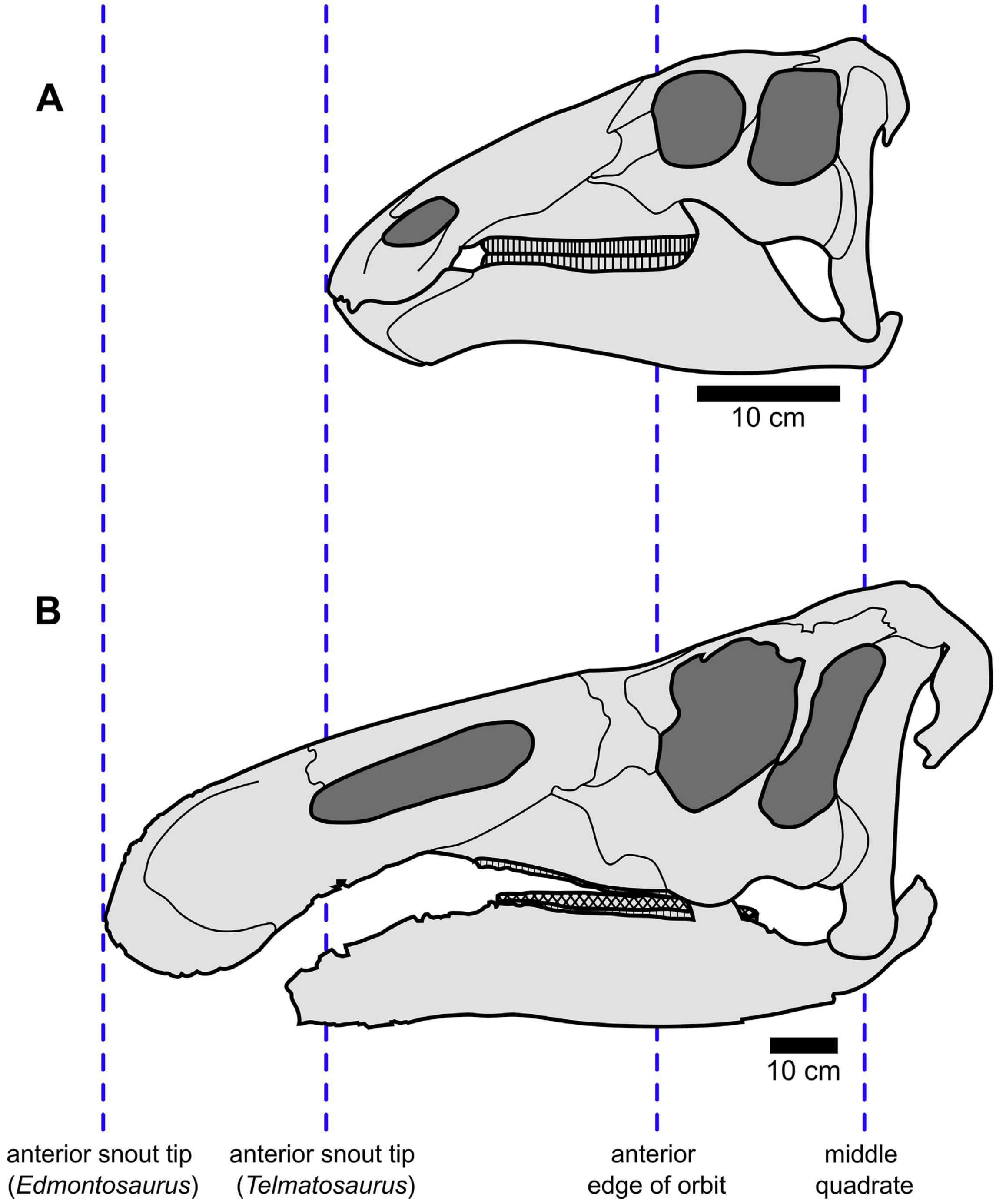


Fig. 7. Differences in relative facial length between adults of large and small hadrosauromorph taxa. A) *Telmatosaurus* composite reconstruction modified from Weishampel et al. (1993). B) Large adult *Edmontosaurus* skull (MOR 003) (jugal, quadratojugal, distal end of the quadrate and parts of the orbit and postorbital fenestra have been drawn in). Note: skulls have been scaled so that the distance between the anterior edge of the orbit to the middle of the quadrate is the same to facilitate comparison of snout length.

studies found the dominant scratch mode as angled dorsodistally-ventromesially (the inferred axis of the power stroke), our findings usually recover the dominant mode as angled dorsomesially-ventrodistally. (The secondary or sub-dominant mode, if present, tends to be oriented approximately normal to the dominant mode, consistent with previous findings.) The reasons for this discrepancy are not immediately obvious. Our study includes some genera not examined before (e.g., *Hypacrosaurus*, *Parasaurolophus*), so it is possible that these taxa had a chewing mechanism that differed from other hadrosaurids. However, most taxa included in the present study were also examined elsewhere (*Edmontosaurus*: Williams et al., 2009; *Corythosaurus*, *Prosaurolophus*: Mallon and Anderson, 2014), so an alternative explanation for the discrepancy is required. Mallon and Anderson (2014) showed that poor sampling along the tooth row (which is most significantly limited by preservational factors in dinosaurs) can affect signal recovery (contra Williams et al., 2009), which may account for some of the conflict detected here. It is also possible that differences in working magnification (100× in this study vs. 35× in Mallon and Anderson, 2014 and Rivera-Sylva et al., 2019 vs. 300× in Williams et al., 2009) produced the inconsistent results. For this to be true, different sets of scratch orientations would need to be visible at different magnifications. Whether this is the case for hadrosaurids requires further investigation. Mihlbachler and Beatty (2012) showed that raw frequency microwear data tend to vary with image resolution in a way that proportional data do not, but they did not consider scratch orientation.

4.2. *Diet and feeding behaviour*

The Jarman-Bell principle maintains that, because of their higher size-relative metabolic needs, smaller animals require higher quality, low fibre foods than larger ones (Bell, 1971; Jarman, 1974). Accordingly, we might expect that adult hadrosaurids were able to tolerate more fibrous diets than the young.

In their characterization of hadrosaurid dental morphology with age, Erickson and Zelenitsky (2014) showed that, as juveniles, *Hypacrosaurus stebingeri* possessed cup-like occlusal surfaces, and that shearing occlusal surfaces typical of ungulates having fibrous diets were only expressed later in life (these echo earlier findings for *Maiasaura peeblesorum* in a preliminary study by Hunter and Janis, 1988). This hypothesized ontogenetic niche shift in hadrosaurids, from low- to high-fiber herbivory, is consistent with the Jarman-Bell principle (Bell, 1971; Jarman, 1974) and supported by our findings here (to focus our discussion, we will consider only those variables exhibiting ‘strong’ allometry, defined above).

Our cranial allometric results reveal strong, positive allometry in snout (beak + diastema) length and depression below the tooth row among hadrosaurids. Thus, juvenile hadrosaurids possessed relatively shorter snouts than adults, with a beak that terminated at or near the level of the occlusal plane. Juvenile hadrosaurid beaks were also narrower than those of adults by virtue of their smaller size, which would have made them comparatively selective foragers. Similar cranial features are frequently observed in modern browsing ungulates that feed among trees or shrubs, selecting for soft, nutrient-rich vegetation such as shoots or fruits (Janis, 1990, 1995; Spencer, 1995; Mendoza, 2002). A higher incidence of microwear pits also characterize the teeth of browsing ungulates (Semprebon et al., 2011), and may likewise typify those of juvenile hadrosaurids (Fig. 6), but more data are needed. As the face elongated (thereby accommodating more teeth in the dental battery) and the beak depressed and widened with age, adult hadrosaurids may have foraged at a wider range of levels in the canopy (high and low) and on tougher, more fibrous vegetation (Mallon et al., 2013). Other aspects of cranial allometry in hadrosaurids are plausibly explained by ontogenetic differences in feeding behaviour. In modern ungulates, larger paroccipital processes are associated with increased surface area for the attachment of larger cervical musculature and interpreted as reflecting the greater use of head movements to sever vegetation during feeding (Janis, 1990, 1995; Spencer, 1995). In hadrosaurids, the paroccipital processes served as the insertion sites for the obliquus capitis magnus and pars transversalis capitis musculature (Ostrom, 1961), which pivoted the head laterally about the occipital condyle when flexed. Thus, negative allometric growth of the paroccipital processes in hadrosaurids plausibly suggests that juveniles more frequently used lateral head movements to sever vegetation gripped by the beak compared to adults.

Our study does not recover some previously noted differences between hadrosaurines and lambeosaurines. For example, lambeosaurines are reported elsewhere as having smaller skulls (notwithstanding the crest) with shorter snouts and narrower, more ventrally deflected beaks compared to hadrosaurines (Chapman and Brett-Surman, 1990; Carrano et al., 1999; Mallon and Anderson, 2013). These incongruities are plausibly owed to taxonomic sampling and methodological differences (e.g., linear vs. geometric morphometrics; bivariate vs. multivariate statistics). Interestingly, our observation that positive allometry in occiput height only occurs in hadrosaurines and not lambeosaurines is unique and may be explained with recourse to feeding behaviour. In hadrosaurids, that area of the occiput between the foramen magnum and skull roof forms the insertion areas for the rectus capitis posterior and spinalis capitis muscles (Ostrom, 1961), which, when contracted, served to rotate the head upwards about the occipital condyle. The relatively greater size of these muscles in adult hadrosaurines may indicate a proportional age-related increase in their use during feeding. Based on various aspects of skeletal and dental ecomorphology, Carrano et al. (1999) suggested that hadrosaurines may have preferentially fed within the herb layer of open environments. Such extensions of the head would therefore have served well for cropping low-growing vegetation. This proposed behaviour likewise comports with the known dental microwear evidence (Mallon and Anderson, 2014).

4.3. *Cranial evolutionary allometry*

Although the longer snouts of adult hadrosaurids may well have facilitated their exploitation of a wider variety of plant resources (particularly via accommodation of the highly specialized dental battery), it is not clear that the snout was specifically adapted for such a purpose. The phenomenon of conserved cranial evolutionary allometry has been well-documented in a wide variety of mammals and posits that facial length is strongly constrained by adult body size, such that larger animals experience greater facial lengthening (Cardini and Polly, 2013; Cardini et al., 2015). Comparing the skulls of smaller hadrosauromorphs, such as *Telmatosaurus*, to those of the largest members of the clade (e.g., *Edmontosaurus*), the smaller animals exhibit relatively shorter faces, consistent with this hypothesis (Fig. 7). By contrast, tyrannosauroids exhibit much the opposite pattern (Currie, 2003), whereby smaller forms (e.g., *Alioramus*) exhibit relatively longer faces than larger forms (e.g., *Tyrannosaurus*). Dinosaurs thus display a variety of cranial evolutionary allometric trends, and will undoubtedly make for an interesting non-mammalian case study.

5. Conclusion

Despite the numerous studies investigating hadrosaurid cranial ontogeny (e.g., Dodson, 1975b; Evans, 2010; Campione and Evans, 2011; Farke et al., 2013; McGaritty et al., 2013), these tend to be focused on the development of the cranial crests and rarely on aspects of ecomorphology. Our examination of cranial allometry and dental microwear in hadrosaurids finds evidence to support the ontogenetic niche shift hypothesis. Consistent with the Jarman-Bell principle, we argue that young hadrosaurids fed on soft, nutrient-rich vegetation at low feeding heights, cropped using lateral rotations of the head. Adults, by contrast, fed on tougher vegetation that grew at a range of feeding heights. Large hadrosaurines likely emphasized neck extension to crop vegetation. Jaw motions produced during feeding appear not to have differed significantly between immature and adult hadrosaurids, despite the greater development of the tooth battery in the latter age group.

Our findings are most limited by the availability of juvenile hadrosaurid material, particularly for the purposes of microwear study. Extension of our methods to the Asian fossil record, which does not suffer from the same fluvially-derived taphonomic size biases of the North American record (Brown et al., 2013, 2021;

Mallon et al., 2018), may offer a needed test of our findings and of their broader applicability. The pattern of facial elongation among hadrosauromorphs recalls a similar pattern of cranial evolutionary allometry among mammals and likewise invites further investigation. Ontogenetic niche shifts are thought by some to have played an important role in the size structuring of Late Cretaceous carnivorous dinosaur communities (Holtz, 2021; Schroeder et al., 2021). Our study gives reason to think this might also have been the case in contemporaneous herbivore communities (cf. Wyenberg-Henzler et al., 2021).

Acknowledgments

Constructive criticism of early drafts of this paper were provided by G. Blouin-Demers, D. Evans, M. Ryan, and A. Simons. Helpful conversations and methodological support were offered by B. Arnaout, J. Farlow, D. Fraser, and N. Campione. Thanks to curators and their assistants at AMNH, CMN, GPDM, MOR, ROM, TMP, USNM, and UALVP for access to materials and models. Thanks to P. Dodson for his helpful review and to E. Koutsoukos for editorial assistance. This work was funded by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to JCM (RGPIN-2017-06356), and by grants from the Dinosaur Research Institute and Jurassic Foundation to TWH.

References

Bailleul, A.M., Hall, B.K., Horner, J.R., 2012. First evidence of dinosaurian secondary cartilage in the post-hatching skull of *Hypacrosaurus stebingeri* (Dinosauria, Ornithischia). PLoS One 7 (4), e36112. https://doi.org/10.1371/journal.pone.0036112.

Bailleul, A.M., Nyssen-Behets, C., Lengelé, B., Hall, B.K., Horner, J.R., 2016. Chondroid bone in dinosaur embryos and nestlings (Ornithischia: Hadrosauridae): insights into the growth of the skull and the evolution of skeletal tissues. Comptes Rendus Palevol 15 (1–2), 49–64. https://doi.org/10.1016/j.crpv.2014.12.004.

Bell, R., 1971. A grazing ecosystem in the Serengeti. Scientific American 225, 86–93. https://doi.org/10.1038/scientificamerican0771-86.

Blackburn, D.C., Moreau, C.S., 2006. Ontogenetic diet change in the arthroleptid frog *Schoutedenella xenodactyloides*. Journal of Herpetology 40 (3), 388–394. https://doi.org/10.1670/0022-1511(2006)40[388:ODCITA]2.0.CO;2.

Brink, K.S., Zelenitsky, D.K., Evans, D.C., Therrien, F., Horner, J.R., 2011. A sub-adult skull of *Hypacrosaurus stebingeri* (Ornithischia: Lambeosaurinae): anatomy and comparison. Historical Biology 23 (1), 63–72. https://doi.org/10.1080/08912963.2010.499169.

Brown, C.M., Vavrek, M.J., 2015. Small sample sizes in the study of ontogenetic allometry: implications for palaeobiology. PeerJ 3, e818. https://doi.org/10.7717/PeerJ.818.

Brown, C.M., Evans, D.C., Campione, N.E., O'Brien, L.J., Eberth, D.A., 2013. Evidence for taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial alluvial-paralic system. Palaeogeography, Palaeoclimatology, Palaeoecology 372, 108–122. https://doi.org/10.1016/j.palaeo.2012.06.027.

Brown, C.M., Campione, N.E., Wilson Mantilla, G.P., Evans, D.C., 2021. Size-driven preservational and macroecological biases in the latest Maastrichtian terrestrial vertebrate assemblages of North America. Paleobiology 1–29. https://doi.org/10.1017/pab.2021.35.

Caldwell, I., da SilvaSanches, F.C., Conder Rueda, X., Suwalski, P., Petroff, M., Chyla, Z., De-Cooman, A., Baxter, B., Mathog, D., Belis, A., et al., 2004. Inkscape: Open Source Scalable Vector Graphics Editor (image analysis software). Version 1.1. from. http://www.inkscape.org/.

Campbell, J.A., Ryan, M.J., Holmes, R.B., Schröder-Adams, C.J., 2016. A re-evaluation of the chasmosaurine ceratopsid Genus *Chasmosaurus* (Dinosauria: Ornithischia) from the Upper Cretaceous (Campanian) Dinosaur Park Formation of Western Canada. PLoS One 11 (1), e0145805. https://doi.org/10.1371/journal.pone.0145805.

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 (9), e25186. https://doi.org/10.1371/journal.pone.0025186.

Cardini, A., Polly, P.D., 2013. Larger mammals have longer faces because of size-related constraints on skull form. Nature Communications 4 (2458). https://doi.org/10.1038/ncomms3458.

Cardini, A., Polly, D., Dawson, R., Milne, N., 2015. Why the long face? Kangaroos and wallabies follow the same 'rule' of cranial evolutionary allometry (CREA) as placentals. Evolutionary Biology 42, 169–176. https://doi.org/10.1007/s11692-015-9308-9.

Carpenter, K., 1999. The embryo and hatching. In: Carpenter, K. (Ed.), Eggs, Nests and Baby Dinosaurs: A Look at Dinosaur Reproduction. Indiana University Press, Bloomington, pp. 179–214.

Carrano, M.T., Janis, C.M., Sepkoski Jr., J.J., 1999. Hadrosaurs as ungulate parallels: lost lifestyles and deficient data. Acta Palaeontologica Polonica 44 (3), 237–261. https://www.app.pan.pl/article/item/app44-237.html.

Chapman, R., Brett-Surman, M.K., 1990. Morphometric observations on hadrosaurid ornithopods. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 163–177.

Claessen, D., Dieckmann, U., 2002. Ontogenetic niche shifts and evolutionary branching in size-structured populations. Evolutionary Ecology Research 4 (2), 189–217. https://repository.rothamsted.ac.uk/item/88y40/ontogenetic-niche-shifts-and-evolutionary-branching-in-size-structured-populations.

Codron, D., Carbone, C., Clauss, M., 2013. Ecological interactions in dinosaur communities: influences of small offspring and complex ontogenetic life histories. PLoS One 8 (10), e77110. https://doi.org/10.1371/journal.pone.0077110.

Currie, P.J., 2003. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. Canadian Journal of Earth Sciences 40 (4), 651–665. https://doi.org/10.1139/e02-083.

DeSantis, L.R.G., 2016. Dental microwear textures: reconstructing diets of fossil mammals. Surface Topography: Metrology and Properties 4 (2), 023002. https://iopScience.iop.org/article/10.1088/2051-672X/4/2/023002.

Dodson, P., 1975a. Functional and ecological significance of relative growth in *Alligator*. Journal of Zoology 175 (3), 315–355. https://doi.org/10.1111/j.1469-7998.1975.tb01405.x.

Dodson, P., 1975b. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. Systematic Zoology 24 (1), 37–54. https://doi.org/10.2307/2412696.

Dompierre, H., Churcher, C.S., 1996. Premaxillary shape as an indicator of the diet of seven extinct late Cenozoic new world camels. Journal of Vertebrate Paleontology 16, 141–148. https://www.jstor.org/stable/4523700.

Durtsche, R.D., 2000. Ontogenetic plasticity of food habits in the Mexican spiny-tailed iguana, *Ctenosaura pectinata*. Oecologia 124, 185–195. https://doi.org/10.1007/s004420050006.

Ebenman, B., 1992. Evolution in organisms that change their niches during the life cycle. American Naturalist 139 (5), 990–1021. https://doi.org/10.1086/285370.

Erickson, G.M., Zelenitsky, D.K., 2014. Osteohistology and occlusional morphology of *Hypacrosaurus stebingeri* teeth throughout ontogeny with comments on wear-induced form and function. In: Eberth, D.A., Evans, D.C. (Eds.), Hadrosaurs. Indiana University Press, Bloomington, pp. 422–432.

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 (6103), 98–101.

Eskew, E.A., Willson, J.D., Winne, C.T., 2008. Ambush site selection and ontogenetic shifts in foraging strategy in a semi-aquatic pit viper, the Eastern cottonmouth. Journal of Zoology 277 (2), 179–186. https://doi.org/10.1111/j.1469-7998.2008.00527.x.

Evans, D.C., 2010. Cranial anatomy and systematics of *Hypacrosaurus altispinus*, and a comparative analysis of skull growth in lambeosaurine hadrosaurids (Dinosauria: Ornithischia). Zoological Journal of the Linnean Society 159 (2), 398–434. https://doi.org/10.1111/j.1096-3642.2009.00611.x.

Farke, A.A., Chok, D.J., Herrero, A., Scolieri, B., Werning, S., 2013. Ontogeny in the tube-crested dinosaur *Parasaurolophus* (Hadrosauridae) and heterochrony in hadrosaurids. PeerJ 1, e182. https://doi.org/10.7717/PeerJ.182.

Fiorillo, A.R., 1998. Dental micro wear patterns of the sauropod dinosaurs *Camarasaurus* and *Diplodocus*: evidence for resource partitioning in the late Jurassic of North America. Historical Biology 13 (1), 1–16. https://doi.org/10.1080/08912969809386568.

Fitak, R.R., Johnsen, S., 2017. Bringing the analysis of animal orientation data full circle: model-based approaches with maximum likelihood. Journal of Experimental Biology 220 (21), 3878–3882. https://doi.org/10.1242/jeb.167056.

Fitak, R.R., Johnsen, S., 2020. CircMLE: Maximum Likelihood Analysis of Circular Data (R package). version 0.3.0. from. https://CRAN.R-project.org/package=CircMLE.

Fraser, D., Mallon, J.C., Furr, R., Theodor, J.M., 2009. Improving the repeatability of low magnification microwear methods using high dynamic range imaging. Palaios 24 (12), 818–825. https://doi.org/10.2110/palo.2009.p09-064r.

Frederickson, J.A., Tumarkin-Deratzian, A.R., 2014. Craniofacial ontogeny in *Centrosaurus apertus*. PeerJ 2, e252. https://doi.org/10.7717/peerj.252.

Frederickson, J.A., Engel, M.H., Cifelli, R.L., 2020. Ontogenetic dietary shifts in *Deinonychus antirrhopus* (Theropoda; Dromaeosauridae): insights into the ecology and social behavior of raptorial dinosaurs through stable isotope analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 552, 109780. https://doi.org/10.1016/j.palaeo.2020.109780.

Goillot, C., Blondel, C., Peigné, S., 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) — implications for the reconstruction of the diet of extinct taxa. Palaeogeography, Palaeoclimatology, Palaeoecology 271 (1–2), 13–23. https://doi.org/10.1016/j.palaeo.2008.09.004.

Goodwin, M.B., Clemens, W.A., Horner, J.R., Padian, K., 2006. The smallest known *Triceratops* skull: new observations on ceratopsid cranial anatomy and ontogeny. Journal of Vertebrate Paleontology 26 (1), 103–112. https://www.tandfonline.com/doi/abs/10.1671/0272-4634%282006%2926%5B103%3ATSKTSN%5D2.0.CO%3B2.

Gould, S.J., 1966. Allometry and size in ontogeny and phylogeny. Biological Reviews 41 (4), 587–638. https://doi.org/10.1111/j.1469-185x.1966.tb01624.x.

Hammer, Ø., Harper, D.A.T., 2006. Paleontological data analysis. Blackwell Publishing Ltd., Malden.

Herrel, A., Joachim, R., Vanhooydonck, B., Irschick, D.J., 2006. Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. Biological Journal of the Linnean Society 89 (3), 443–454. https://doi.org/10.1111/j.1095-8312.2006.00685.x.

Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6 (2), 65–70. https://www.jstor.org/stable/4615733.

Holtz, T.R., 2021. Theropod guild structure and the tyrannosaurid niche assimilation hypothesis: implications for predatory dinosaur macroecology and ontogeny in later Late Cretaceous Asiamerica. Canadian Journal of Earth Sciences 58 (9), 778–795. https://doi.org/10.1139/cjes-2020-0174.

Hone, D.W.E., Farke, A.A., Wedel, M.J., 2016. Ontogeny and the fossil record: what, if anything, is an adult dinosaur? Biology Letters 12 (2), 20150947. https://doi.org/10.1098/rsbl.2015.0947.

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, Cambridge, pp. 312–336.

Horner, J.R., Goodwin, M.B., 2006. Major cranial changes during *Triceratops* ontogeny. Proceedings of the Royal Society B: Biological Sciences 273 (1602), 2757–2761. https://doi.org/10.1098/rspb.2006.3643.

Horner, J.R., Goodwin, M.B., 2008. Ontogeny of cranial epi-ossifications in *Triceratops*. Journal of Vertebrate Paleontology 28 (1), 134–144. https://doi.org/10.1671/0272-4634(2008)28[134:OOCEIT]2.0.CO;2.

Hunter, J.P., Janis, C.M., 1988. Tooth wear in juvenile and adult hadrosaurs: implications for parental care. In: Horner, J.R., Elis, K. (Eds.), Abstracts with Program 23A. Presented at the International Symposium on Vertebrate Behavior as Derived from the Fossil Record, Bozeman.

Janis, C., 1990. A comparison of macropodoids and ungulates. Memoirs of the Queensland Museum 28, 349–366. https://biostor.org/reference/109946.

Janis, C., 1995. Correlation between craniodental morphology and feeding behaviour in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason, J. (Ed.), Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Cambridge, pp. 76–98.

Janis, C.M., Ehrhardt, D., 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zoological Journal of the Linnean Society 92 (3), 267–284. https://doi.org/10.1111/j.1096-3642.1988.tb01513.x.

Jarman, P.J., 1974. The social organisation of antelope in relation to their ecology. Behaviour 48, 215–267. https://doi.org/10.1163/156853974X00345.

Keren-Rotem, T., Bouskila, A., Geffen, E., 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behavioral Ecology and Sociobiology 59, 723–731. https://doi.org/10.1007/s00265-005-0102-z.

Klingenberg, C.P., 2016. Size, shape, and form: concepts of allometry in geometric morphometrics. Development Genes and Evolution 226 (3), 113–137. https://doi.org/10.1007/s00427-016-0539-2.

Knapp, A., Knell, R.J., Hone, D.W.E., 2021. Three-dimensional geometric morphometric analysis of the skull of *Protoceratops andrewsi* supports a socio-sexual signalling role for the ceratopsian frill. Proceedings of the Royal Society B: Biological Sciences 288 (1944), 20202938. https://doi.org/10.1098/rspb.2020.2938.

Konishi, T., 2015. Redescription of UALVP 40, an unusual specimen of *Chasmosaurus* Lambe, 1914 (Ceratopsidae: Chasmosaurinae) bearing long postorbital horns, and its implications for ontogeny and alpha taxonomy of the genus. Canadian Journal of Earth Sciences 52 (8), 608–619. https://doi.org/10.1139/cjes-2014-0167.

Lakin, R.J., Longrich, N.R., 2019. Juvenile spinosaurs (Theropoda: Spinosauridae) from the middle Cretaceous of Morocco and implications for spinosaur ecology. Cretaceous Research 93, 129–142. https://doi.org/10.1016/j.cretres.2018.09.012.

Longrich, N.R., Field, D.J., 2012. *Torosaurus* is not *Triceratops*: ontogeny in chasmosaurine ceratopsids as a case study in dinosaur taxonomy. PLoS One 7, e32623. https://doi.org/10.1371/journal.pone.0032623.

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 (7), e67182. https://doi.org/10.1371/journal.pone.0067182.

Mallon, J.C., Anderson, J.S., 2014. The functional and palaeoecological implications of tooth morphology and wear for the megaherbivorous dinosaurs from the Dinosaur Park Formation (Upper Campanian) of Alberta, Canada. PLoS One 9 (6), e98605. https://doi.org/10.1371/journal.pone.0098605.

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 Ecology 13 (14). https://doi.org/10.1186/1472-6785-13-14.

Mallon, J.C., Ryan, M.J., Campbell, J.A., 2015. Skull ontogeny in *Arrhinoceratops brachyops* (Ornithischia: Ceratopsidae) and other horned dinosaurs: horned dinosaur skull growth. Zoological Journal of the Linnean Society 175, 910–929. https://doi.org/10.1111/zoj.12294.

Mallon, J.C., Henderson, D.M., McDonough, C.M., Loughry, W.J., 2018. A “bloat-and-float” taphonomic model best explains the upside-down preservation of ankylosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology 497, 117–127. https://doi.org/10.1016/j.palaeo.2018.02.010.

McDonald, J.H., 2014. Multiple comparisons. In: Handbook of Biological Statistics. Sparky House Publishing, Baltimore, pp. 254–260.

McGarrity, C.T., Campione, N.E., Evans, D.C., 2013. Cranial anatomy and variation in *Prosaurolophus maximus* (Dinosauria: Hadrosauridae). Zoological Journal of the Linnean Society 167 (4), 531–568. https://doi.org/10.1111/zoj.12009.

McLeay, L.J., Page, B., Goldsworthy, S.D., Ward, T.M., Paton, D.C., 2009. Size matters: variation in the diet of chick and adult crested terns. Marine Biology 156, 1765–1780. https://doi.org/10.1007/s00227-009-1211-4.

Mendoza, M., Janis, C.M., Palmqvist, P., 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. Journal of Zoology 258 (2), 223–246. https://doi.org/10.1017/S0952836902001346.

Mendoza-Carranza, M., Vieira, J.P., 2009. Ontogenetic niche feeding partitioning in juvenile of white sea catfish *Genidens barbus* in estuarine environments, southern Brazil. Journal of the Marine Biological Association of the United Kingdom 89 (4), 839–848. https://doi.org/10.1017/S0025315408002403.

Mihlbachler, M., Beatty, B., 2012. Magnification and resolution in dental microwear analysis using light microscopy. Palaeontologia Electronica 15 (2.25A), 1–15. https://doi.org/10.26879/317.

Nelson, S., Badgley, C., Zaken, E., 2005. Microwear in modern squirrels in relation to diet. Palaeontologica Electronica 8 (3:14A), 1–15. https://palaeo-electronica.org/2005_1/nelson14/issue1_05.htm.

Ostrom, J.H., 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. Bulletin of the American Museum of Natural History 122 (2), 39–186. http://hdl.handle.net/2246/1260.

Platt, S.G., Rainwater, T.R., Finger, A.G., Thorbjarnarson, J.B., Anderson, T.A., McMurry, S.T., 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. The Herpetological Journal 16 (3), 281–290. https://www.thebhs.org/publications/the-herpetological-journal/volume-16-number-3-july-2006/449-07-food-habits-ontogenetic-dietary-partitioning-and-observations-of-foraging-behaviour-of-morelet-s-crocodile-i-crocodylus-moreletii-i-in-northern-belize.

R Core Team, 2019. R: The R Project for Statistical Computing (data analysis software). version 4.1.0. from. https://www.R-project.org/.

Ramirez, M.D., Avens, L., Seminoff, J.A., Goshe, L.R., Heppell, S.S., 2017. Growth dynamics of juvenile loggerhead sea turtles undergoing an ontogenetic habitat shift. Oecologia 183, 1087–1099. https://doi.org/10.1007/s00442-017-3832-5.

Rasband, W.S., Avens, L., Seminoff, J., Goshes, L., Hepel, l S., 1997-2018. ImageJ (image analysis software). version 1.52a. from. https://imagej.nih.gov/ij/.

Rivals, F., Semprebon, G.M., 2011. Dietary plasticity in ungulates: insight from tooth microwear analysis. Quaternary International 245 (2), 279–284. https://doi.org/10.1016/j.quaint.2010.08.001.

Rivera-Sylva, H.E., Barrón-Ortíz, C.I., González, R.V., Rodríguez, R.L.N., Guzmán-Gutiérreza, J.R., Valdez, F.C., Dávila, C. de L., 2019. Preliminary assessment of hadrosaur dental microwear from the Cerro del Pueblo Formation (Upper Cretaceous: Campanian) of Coahuila, northeastern Mexico. Paleontología Mexicana 8 (1), 17–28. http://ojs-igl.unam.mx/index.php/Paleontologia/article/view/606.

Rowe, A.J., Snively, E., 2022. Biomechanics of juvenile tyrannosaurid mandibles and their implications for bite force: Evolutionary biology. Anatomical Record 305 (2), 373–392. https://doi.org/10.1002/ar.24602.

Schellekens, T., de Roos, A.M., Persson, L., 2010. Ontogenetic diet shifts result in niche partitioning between two consumer species irrespective of competitive abilities. American Naturalist 176 (3), 625–637. https://doi.org/10.1086/656488.

Schnute, J.T., Groot, K., 1992. Statistical analysis of animal orientation data. Animal Behaviour 43 (1), 15–33. https://doi.org/10.1016/S0003-3472(05)80068-5.

Schroeder, K., Lyons, S.K., Smith, F.A., 2021. The influence of juvenile dinosaurs on community structure and diversity. Science 371 (6532), 941–944. https://doi.org/10.1126/Science.abd9220.

Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? Journal of Human Evolution 47, 115–144. https://doi.org/10.1016/j.jhevol.2004.06.004.

Semprebon, G.M., Sise, P.J., Coombs, M.C., 2011. Potential bark and fruit browsing as revealed by stereomicrowear analysis of the peculiar clawed herbivores known as chalicotheres (Perissodactyla, Chalicotherioidea). Journal of Mammalian Evolution 18 (1), 33–55. https://doi.org/10.1007/s10914-010-9149-3.

Solounias, N., Teaford, M., Walker, A., 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. Paleobiology 14 (3), 287–300. https://doi.org/10.1017/S009483730001201X.

Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. American Museum Novitates 3366, 1–49. http://hdl.handle.net/2246/2855.

Spencer, L.M., 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. Journal of Mammalogy 76 (2), 448–471. https://doi.org/10.2307/1382355.

ten Brink, H., de Roos, A.M., 2018. Large-amplitude consumer-resource cycles allow for the evolution of ontogenetic niche shifts in consumer life history. Journal of Theoretical Biology 457, 237–248. https://doi.org/10.1016/j.jtbi.2018.08.035.

Therrien, F., Zelenitsky, D.K., Voris, J.T., Tanaka, K., 2021. Mandibular force profiles and tooth morphology in growth series of *Albertosaurus sarcophagus* and *Gorgosaurus libratus* (Tyrannosauridae: Albertosaurinae) provide evidence for an ontogenetic dietary shift in tyrannosaurids. Canadian Journal of Earth Sciences 58 (9), 812–828. https://doi.org/10.1139/cjes-2020-0177.

Tumarkin-Deratzian, A.R., 2009. Evaluation of long bone surface textures as ontogenetic indicators in centrosaurine ceratopsids. Anatomical Record 292 (9), 1485–1500. https://doi.org/10.1002/ar.20972.

Vanderven, E., Burns, M.E., Currie, P.J., 2014. Histologic growth dynamic study of *Edmontosaurus regalis* (Dinosauria: Hadrosauridae) from a bonebed assemblage of the Upper Cretaceous Horseshoe Canyon Formation, Edmonton, Alberta, Canada. Canadian Journal of Earth Sciences 51 (11), 1023–1033. https://doi.org/10.1139/cjes-2014-0064.

Varricchio, D.J., 2011. A distinct dinosaur life history? Historical Biology 23 (1), 91–107. https://doi.org/10.1080/08912963.2010.500379.

Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G., Clark, J.M., Xu, X., 2017. Extreme ontogenetic changes in a ceratosaurian theropod. Current Biology 27 (1), 144–148. https://doi.org/10.1016/j.cub.2016.10.043.

Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. Biological Reviews 81 (2), 259–291. https://doi.org/10.1017/S1464793106007007.

Weishampel, D.B., 1983. Hadrosaurid jaw mechanics. Acta Palaeontologica Polonica 28 (1–2), 271–280.

Weishampel, D.B., Norman, D.B., Grigorescu, D., 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. Palaeontology 236 (2), 361–385.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141.

Whitlock, J.A., 2011. Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses. PLoS One 6 (4), e18304. https://doi.org/10.1371/journal.pone.0018304.

Williams, V.S., Barrett, P.M., Purnell, M.A., 2009. Quantitative analysis of dental microwear in hadrosaurid dinosaurs, and the implications for hypotheses of jaw mechanics and feeding. Proceedings of the National Academy of Sciences 106 (27), 11194–11199. https://doi.org/10.1073/pnas.0812631106.

Woodruff, D.C., Carr, T.D., Storrs, G.W., Waskow, K., Scannella, J.B., Nordén, K.K., Wilson, J.P., 2018. The smallest diplodocid skull reveals cranial ontogeny and growth-related dietary changes in the largest dinosaurs. Scientific Reports 8, 14341. https://doi.org/10.1038/s41598-018-32620-x.

Woodward, H.N., Freedman Fowler, E.A., Farlow, J.O., Horner, J.R., 2015. *Maiasaura*, a model organism for extinct vertebrate population biology: a large sample statistical assessment of growth dynamics and survivorship. Paleobiology 41 (4), 503–527. https://doi.org/10.1017/pab.2015.19.

Wyenberg-Henzler, T., 2020. Ontogenetic niche shifts in megaherbivorous dinosaurs of Late Cretaceous North America and their ecological implications (M.Sc.). Carleton, Ottawa.

Wyenberg-Henzler, T., Patterson, R.T., Mallon, J.C., 2021. Size-mediated competition and community structure in a Late Cretaceous herbivorous dinosaur assemblage. Historical Biology. https://doi.org/10.1080/08912963.2021.2010191.

Xing, H., Zhao, X., Li, D., Chen, S., Mallon, J.C., Zhang, Y., 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 88 (6), 1801–1840.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2022.105177.