Hadrosaurs as ungulate parallels: Lost lifestyles and deficient data

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Hadrosaur dinosaurs (Ornithischia: Hadrosauridae) were abundant in Late Cretaceous terrestrial environments of North America and Asia. Their derived dental and postcranial specializations for herbivory have led to the suggestion that these dinosaurs were analogous to modern ungulates in lifestyle. Ungulates display a suite of morphological features that are correlated with diet, habitat preference, and sexual dimorphism. In this paper we examine several of these same features in hadrosaurs in order to determine whether they display similar patterns under multivariate analysis. Initial results confirm the resemblances between hadrosaurs and ungulates but suggest that missing data may considerably affect the outcomes of statistical analyses. Using the hadrosaur dataset as a template, we artificially degrade the (previously complete) ungulate datasets and perform the same analyses. Results are consistent with earlier results and provide an opportunity to assess the impact of missing data on the original multivariate structure. Our results support the hypothesis that hadrosaurs were similar to ungulates in patterns of ecomorphology.

Key words: Dinosauria, Ornithischia, Ornithopoda, multivariate statistics, paleoecology, Mammalia, NMDS.

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Introduction

The behavioral ecology of dinosaurs has often been inferred from their fossil remains through morphological analysis and analogy with extant reptiles, mammals and birds (e.g., Dodson 1975; Farlow 1976, 1987; Molnar 1977; Weishampel 1985; Carrano

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1998, 1999). Several previous hypotheses have compared the behavior of hadrosaurid dinosaurs to that of ungulate (hoofed) mammals because both groups are large, sexually dimorphic, terrestrial herbivores (Dodson 1975; Molnar 1977; Weishampel 1985). In this study, we use multivariate analyses of hadrosaur and ungulate morphology to evaluate these hypotheses, make further inferences concerning the behavioral ecology of these dinosaurs, and explore methodological problems imposed by the typically incomplete postcranial data for dinosaur specimens.

Hadrosauridae (Reptilia: Ornithischia) include two subfamilies, Lambeosaurinae and Hadrosaurinae (*sensu* Forster 1997a, Sereno 1997), both of which were abundant in the terrestrial faunas of western North America and east-central Asia from Cenomanian through Maastrichtian times (Brett-Surman 1979; Weishampel & Horner 1990; Forster 1997b). Hadrosaurs and ungulates appear to have paralleled each other in the development of several similar morphological features. The tooth-supported dental batteries of hadrosaurs are analogous to the complex cheek teeth of certain ungulates (Janis & Fortelius 1988), suggesting a similarly abrasive diet of coarse vegetation. Skull kineticism may have permitted transverse jaw motion during mastication, much as anisognathy does in the mammalian skull (Weishampel 1983, 1984, 1985; Norman & Weishampel 1985; Sereno 1997). Finally, both ungulate and hadrosaur species sometimes exhibit sexual dimorphism of their cranial appendages. Among hadrosaurs, dimorphism apparently occurred in lambeosaurines but has not been demonstrated convincingly in hadrosaurines (Dodson 1975; Hopson 1975; Molnar 1977; Chapman *et al.* 1997).

Among ungulates, patterns of sexual dimorphism (in terms of possession of horns and analogous structures) are strongly correlated with habitat preference. Species in open habitats (e.g., plains or savannah) are usually herd-forming with both sexes being horned and males not maintaining permanent territories. Ungulate species in closed habitats (e.g., woodland or forest), on the other hand, are more often solitary with horns usually found only on males, and these males may maintain permanent reproductive territories (Jarman 1974). Other morphological features, such as limb proportions (Scott 1985), muzzle dimensions (Janis & Ehrhardt 1988), and patterns of dental wear (Janis 1990a) also reflect these habitat differences. These combinations of morphological features act as signatures of habitat preference and are not tightly correlated with phylogenetic groupings. Rather, they reflect environmental influences on patterns of food dispersal and types of food available, which influence habitat-related grouping patterns and behavioral ecology.

If such suites of morphological features in modern large herbivorous mammals are indeed related to habitat preferences and are independent of phylogenetic affinities, then we might ask whether they also occurred in ancient large tetrapods, such as herbivorous dinosaurs. In this paper, we present a quantitative analysis of the hypothesis that patterns of sexual dimorphism in hadrosaurs cluster with other morphological indicators of habitat preference in the same pattern as occurs in present-day ungulates. A positive result from this analysis would imply that sexual dimorphism in dinosaurian herbivores was related to differences in reproductive behavioral ecology and habitat preference in a manner similar to that seen in large mammalian herbivores today.

In testing this hypothesis, however, we must confront the problem of missing data. Complete skeletal specimens of dinosaurs are comparatively rare (even for abundant taxa such as hadrosaurs), and so incomplete materials must inevitably be included in any analysis in order to provide a sufficient statistical sample. This problem applies to many other fossil groups as well and can be quite serious because missing data may affect the results of statistical tests or even prevent their use altogether. Here we utilize a method (non-metric multidimensional scaling, NMDS) that can accommodate a relatively large amount of missing data and test its effectiveness on a series of complete datasets that have been made artificially depauperate.

Hadrosaurs as 'Mesozoic ungulates'

Hadrosaurs are characterized by the development of dental batteries with a masticatory system well suited to a diet of terrestrial herbage (Sereno 1986, 1997; Forster 1998b). Although somewhat comparable dental systems exist in other ornithopods and in ceratopsians, hadrosaurs arguably show the most sophisticated development of these features (Weishampel 1984; Norman & Weishampel 1985; Ostrom 1986; Coe *et al.* 1987). Morphological adaptations for such extensive mastication are unknown among other reptiles but are present in a variety of herbivorous mammalian groups, including ungulates.

Hadrosaurid remains have been recovered from Mexico to Alaska, indicating that these dinosaurs lived within all of the broad climatic zones of Late Cretaceous western North America (Kauffman 1977; Batten 1984; Davies 1987; Wolfe & Upchurch 1987). This range included high-paleolatitude broadleaf deciduous forests (Parrish 1987; Upchurch & Wolfe 1987) and extended into South America and Antarctica, almost certainly crossing into still different climatic zones (Brett-Surman 1979; Bonaparte & Rougier 1987; Case *et al.* 1998). Hadrosaur tracks and skeletal materials are known from environments that consisted of heavily vegetated lowlands (Estes & Berberian 1970; Lockley 1987; Currie 1989; Lockley & Conrad 1989; Parker & Rowley 1989; Pittman 1989), although skeletal remains are also known from more arid floodplain deposits (Rogers 1990).

Late Cretaceous floral environments in North America were characterized by a mosaic of closed-canopy sparse forests on mesic soils and open-canopy vegetation on well-drained soils. Much of North America was wooded with large trees, but these trees were widely spaced, creating a habitat suitable for the movement of large animals (Upchurch & Wolfe 1987; Wolfe & Upchurch 1987). Angiosperms formed a lower canopy of vegetation, with the larger trees being mostly coniferous gymnosperms (Crane 1987). Open habitats were populated largely by ferns and low angiosperms (Wing & Tiffney 1987). Thus, Cretaceous terrestrial habitats included analogs to modern open and closed habitats, although the specific floral composition obviously differed markedly. The Cretaceous woodlands may have been more open than most modern forest environments, but the hadrosaurs themselves were larger animals than most modern forest ungulates. (The distinction between 'closed' and 'open' habitats is somewhat relative and must be considered from the perspective of the size of the specific animals involved.)

Because hadrosaurs seem to have been likely inhabitants of both open and closed environments based on the distribution of their fossil remains, one might infer that they were subject to the same basic physical and biological constraints as ungulates in similar habitats, which in turn might be manifested as similar morphological and behavioral adaptations. The differentiation of hadrosaurs into monomorphic and dimorphic species is one such similarity: hadrosaurines are larger (on average) and monomorphic (Dodson 1975), which suggests that they might have been open-habitat animals, whereas lambeosaurines are smaller (on average) and dimorphic (Dodson 1975), which suggests that they might have been closed-habitat animals. We test this below by examining whether other aspects of hadrosaur morphology are differentiated similarly to ungulates.

Material and methods

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY; FMNH, Field Museum of Natural History, Chicago, IL; GRIPS, Greater Rhode Island Paleontological Society; MOR, Museum of the Rockies, Bozeman, MT; NMC, Canadian Museum of Nature (formerly National Museum of Canada), Ottawa, ON; ROM, Royal Ontario Museum, Toronto, ON; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, AB; USNM, United States National Museum of Natural History, Washington, DC; YPM, Yale Peabody Museum, New Haven, CT.

Species	**Specimen**
Hadrosaurinae	
Anatotitan copei	AMNH 5730 (*Diclonius mirabilis*)•
Edmontosaurus annectens	YPM 2182 USNM 2414
Edmontosaurus edmontoni	ROM 867 NMC 8399 (*Thespesius edmontoni*)
Edmontosaurus regalis	NMC 2288• NMC 2289• ROM 658 ROM 5167cf
Edmontosaurus saskatchewanensis	NMC 8509 (*Thespesius saskatchewanensis*)
Gryposaurus incurvimanus	ROM 764 TMP 80.22.1
Prosaurolophus blackfeetensis	MOR 447 MOR 454
Prosaurolophus maximus	ROM 7871 ROM 1928 TMP 84.1.1
Saurolophus osborni	AMNH 5220*

Lambeosaurinae

Corythosaurus casuarius	AMNH 5240* USNM 011893 ROM 845 (*Corythosaurus excavatus*) NMC 8532* NMC 8676 (*Corythosaurus excavatus*)• TMP 80.40.1
Hypacrosaurus altispinus	AMNH 5217 AMNH 5357 USNM 7948 ROM 702 NMC 8501 TMP 82.10.1
Hypacrosaurus stebingeri	MOR 549
Lambeosaurus lambei	ROM 6474/1218 NMC 2869 NMC 8703 (*Lambeosaurus clavinitalis*)* NMC 0351 (*Lambeosaurus clavinitalis*) TMP 82.38.1

An asterisk (*) indicates that the data were taken entirely from the literature; a circle (•) indicates that measured data were supplemented by data from the literature. Names in parentheses indicate original taxonomic assignments (Glut 1982; Olshevsky 1992). Classification from Weishampel & Horner (1990).

Morphology and ecology in ungulates

The correlations between certain morphological characteristics and behavioral ecology in ungulates are quite specific (Geist 1974). Open-habitat ungulates are usually large, sexually monomorphic, and tend to live in herds (Jarman 1974). Additionally, they have longer distal limb elements (Scott 1985), wider muzzles (Janis & Ehrhardt 1988), and higher-crowned cheek teeth with a greater percentage of the tooth surface dedicated to shearing wear (Janis 1990a). Conversely, closed-habitat ungulates are usually smaller, sexually dimorphic, and exhibit male territoriality (Jarman 1985). They have shorter distal limb elements (Scott 1985), narrower muzzles (Janis & Ehrhardt 1988), and more low-crowned cheek teeth with a greater percentage of the tooth area exhibiting crushing wear (Janis 1988, 1990a).

The ratio of shearing to crushing gross dental wear in herbivorous mammals is strongly indicative of diet, with higher values (i.e. a greater amount of shear) characteristic of mammals with more fibrous diets; these, in turn, are usually open-habitat taxa (Janis 1990a). Relative muzzle width is also strongly correlated with diet in ungulates. Relatively broad muzzles are present in taxa that feed on more fibrous food, whereas narrower muzzles are present in taxa that feed on more succulent food (Janis

& Ehrhardt 1988; Solounias *et al.* 1988). The former tend to be open-habitat animals and the latter are usually closed-habitat. Interestingly, relative muzzle width is unrelated to specific food type but is instead related to whether the food is taken in a less selective or more selective fashion (Janis & Ehrhardt 1988; Janis 1990b). Among ungulates, relatively wider muzzles are present in taxa that feed on grass (less selective), and narrower muzzles in those that feed on other plant materials (more selective). However, grazing kangaroos feed selectively on grasses, and in fact have narrower muzzles than browsing kangaroos (Janis 1990b).

Relative distal hindlimb length is also correlated with habitat type, with more open-habitat taxa exhibiting relatively longer metatarsals (Scott 1985, 1987), perhaps related to a larger home range size (Janis & Wilhelm 1993). However, metatarsal length scales with strong negative allometry in Mammalia, meaning that larger taxa are usually relatively shorter-legged than smaller ones (Scott 1985; Bertram & Biewener 1990; Steudel and Beattie 1993). While deviations around the regression are seen in small and medium-sized ungulates (usually related to habitat type), few meaningful deviations are apparent in larger taxa (body mass > 200 kg). In fact, the regression appears to flatten at this point, such that absolute metatarsal length changes little with increasing size (Scott 1985).

Dimorphism has also been correlated with behavior and ecology, inasmuch as dimorphic taxa tend to exhibit male territoriality, or at least separation of the sexes for most of the year (with solitary males and small groups of females), and correspondingly maintain small home ranges in more closed habitats. Monomorphic forms tend to live in open habitats where they require larger home ranges and maintain a more gregarious lifestyle, with year-round association of the sexes (Jarman 1974). In dimorphic ungulates, males possess considerably larger cranial appendages (horns, antlers, etc.) than females, or females lack them entirely. In monomorphic ungulates, both sexes may have appendages of approximately equal size, or both may lack them entirely. This definition is not rigid but applies broadly across most ungulate groups.

Ungulate and hadrosaur data

The morphologic correlations with habitat in ungulates must be quantified in a manner that permits more direct statistical comparison to hadrosaurs. In devising a set of morphological variables that would sort out extant ungulates by habitat type, it was necessary to identify morphological features that could also be measured on hadrosaurs. For example, the most useful morphological index for distinguishing open-habitat ungulates (generally with more fibrous diets) from closed-habitat ungulates (usually with more succulent diets) is probably the hypsodonty index: the height of the unworn crown molar divided by a linear dimension of the crown surface such as length or width (Van Valen 1960; Janis 1988, 1990b). In comparison with the continually replacing dental battery of hadrosaurs, however, the hypsodonty index merely represents a constraint of the mammalian system of diphyodont tooth replacement (Janis & Fortelius 1988) and thus cannot be used for comparison.

Three relevant morphological variables in ungulates can be directly compared with hadrosaurs: (1) the ratio of shearing to crushing wear on the cheek teeth (SCR); (2) rel-

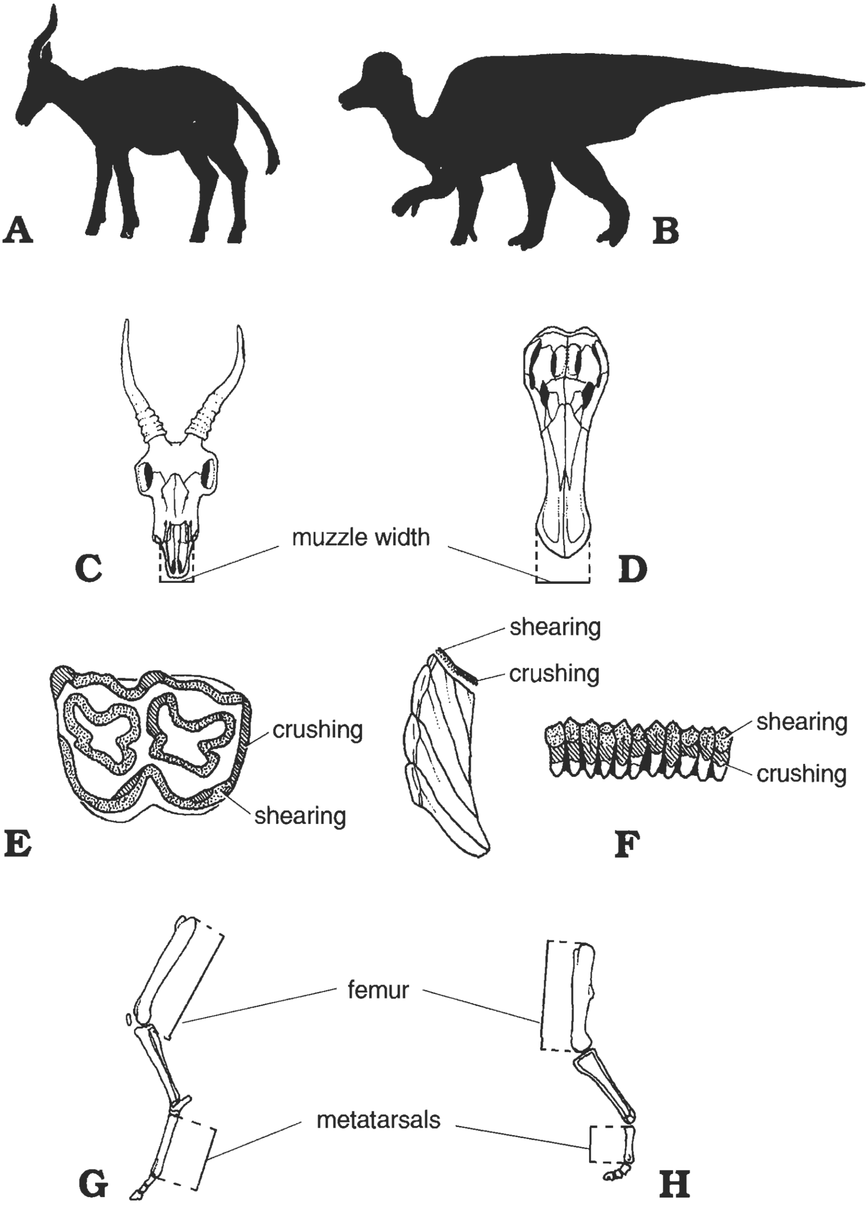

Fig. 1. Measurements for ungulates and hadrosaurs used in this study. These measurements were chosen to record analogous morphological features in the two groups. Ungulates are represented by the topi, *Damaliscus lunatus* (**A**), and hadrosaurs by the lambeosaurine *Corythosaurus casuarius* (**B**). Muzzle width (MW) in ungulates is measured at premaxilla-maxilla boundary in ungulates (**C**), and at the maximal width of premaxilla in hadrosaurs (**D**) (skulls in dorsal view). Shearing (stipple) and crushing (hatching) wear are measured on the occlusal surface of M2 in ungulates (**E**: occlusal view; modified from Janis 1990a), and on the occlusal surface of the dental battery in hadrosaurs (**F**: anterior section, left; occlusal view, right; modified from Lull & Wright 1942). Relative distal hindlimb length is calculated from the lengths of the femur and metatarsal III in both ungulates (**G**) and hadrosaurs (**H**) (lateral view of left hindlimbs).

Table 1. Data for ungulate mammals. Abbreviations: (BM), body mass (averaged male and female values in kilograms); SCR, dental shear/crush ratio; RMW, relative muzzle width; RDL, relative distal limb length. Families: (B), Bovidae; (C), Cervidae; (E), Equidae; (M), Moschidae; (T), Tragulidae. Data obtained primarily from the Museum of Comparative Zoology (Harvard University) and the American Museum of Natural History. Only wild shot (rather than zoo) specimens were measured (see Janis & Ehrhardt 1988; Janis 1990b; Janis & Wilhelm 1993 for details).

Case taxon (Family)	**(BM)**	**SCR**	**RMW**	**RDL**
I. Monomorphic, open-habitat				
A. common zebra (*Equus burchelli*) (E)	(235)	7.57	0.95	0.74
B. hartebeest (*Acelaphus buselaphus*) (B)	(136)	1.09	1.09	0.92
C. American bison (*Bison bison*) (B)	(865)	6.11	1.00	0.68
D. eland (*Taurotragus oryx*) (B)	(511)	1.29	0.85	0.81
E. African buffalo (*Syncerus caffer*) (B)	(620)	1.93	1.19	0.57
F. topi (*Damaliscus lunatus*) (B)	(136)	2.00	1.10	1.16
G. caribou (*Rangifer tarandus*) (C)	(95)	1.65	1.02	0.95
H. wildebeest (*Connochaetes taurinus*) (B)	(216)	4.87	1.11	0.82
II. Dimorphic, closed-habitat (forest)				
I. pudu (*Pudu pudu*) (C)	14	1.38	0.57	0.64
J. lesser mouse deer (*Tragulus javanicus*) (T)	2	1.50	0.79	0.82
K. bay duiker (*Cephalophus dorsalis*)* (B)	20	1.37	0.75	0.66
L. bushbuck (*Tragelaphus scriptus*) (B)	58	1.25	0.84	0.78
III. Dimorphic, closed-habitat (woodland)				
I. kudu (*Tragelaphus strepsiceros*) (B)	215	0.53	0.89	0.86
J. musk deer (*Moschus moschiferus*) (M)	11	1.74	0.87	1.00
K. white-tailed deer (*Odocoileus virginianus*) (C)	57	1.69	0.80	1.00
L. Reeves' muntjac (*Muntiacus reevesi*) (C)	13	1.12	0.74	1.10

* dental wear data from the related *C. nigrifrons*.

ative muzzle width (RMW); and (3) relative distal hindlimb length (RDL) (Fig. 1, Table 1). (Because the data were used to generate ratios, they were not log-transformed prior to analysis.) Ungulate shear/crush ratio measurements were taken from the upper second molars of single individuals from each taxon. All were at the same relative wear stage (because gross dental wear is cumulative), in which the third molars had erupted but were not yet worn. The mode of quantification, and the functional relevance of this ratio, is discussed in Janis (1990a). Hunter & Janis (1988) determined that the dental batteries of hadrosaurine hadrosaurids can be coded for shear/crush ratio by measuring the mediolateral width of shearing and crushing surfaces on the maxillary and dentary tooth batteries. The values obtained for adults of this group are similar to those in ungulates with fibrous diets. Lambeosaurines are nearly identical to hadrosaurines in gross dental morphology and were similarly coded. Since individual animals often exhibit some variation in shear/crush ratio depending on whether it was measured on the maxillary or the dentary battery, we averaged the two values whenever possible.

Table 2. Data for hadrosaur dinosaurs. Dashes indicate missing values, or gaps, in the data. Abbreviations: (BM), body mass (averaged male and female values in kilograms); SCR, dental shear/crush ratio; RMW, relative muzzle width; RDL, relative distal limb length. An asterisk indicates a taxon with shear/crush ratio obtained from maxillary data only. Data were taken with vernier calipers (< 200 mm) and measuring tape (> 200 mm) from a total of 32 adult individuals (11 species, seven genera), and validated with photographs taken at the time of measurement. These were supplemented with data from the literature (Marsh 1896; Brown 1912, 1913a, b, 1914, 1916; Gilmore 1924a, b, c, 1933; Lull & Wright 1942), yielding a total of 36 individuals (12 species, eight genera).

Case taxon	SCR	RMW	RDL
I. Hadrosaurines (monomorphic)			
A. *Saurolophus osborni**	3.33	0.84	0.32
B. *Anatotitan copei**	1.20	0.75	0.35
C. *Prosaurolophus blackfeetensis*	2.25	–	–
D. *Prosaurolophus maximus*	1.75	0.48	0.31
E. *Edmontosaurus regalis*	1.43	0.84	0.34
F. *Edmontosaurus edmontoni*	–	–	0.35
G. *Edmontosaurus saskatchewanensis**	2.00	0.60	–
H. *Gryposaurus incurvimanus*	1.41	0.57	0.35
II. Lambeosaurines (dimorphic)			
I. *Corythosaurus casuarius*	1.74	0.36	0.35
J. *Hypacrosaurus altispinus*	1.78	0.53	0.32
K. *Hypacrosaurus stebingeri*	1.80	0.41	0.39
L. *Lambeosaurus lambei*	1.75	0.49	0.33

Muzzle width in ungulates was measured at the premaxillary/maxillary boundary. The data used in this study represent values averaged from three and ten male individuals in each taxon (for further details see Janis & Ehrhardt 1988). Hadrosaurs probably used their muzzles for cropping vegetation similarly: they possessed tooth-like denticles at the front of the premaxillae and predentary analogous to the incisors of ungulates (Morris 1970). For hadrosaurs, we measured the maximum bilateral width of the premaxillae, generally from one to three individuals. We eliminated the size factor in the analyses by dividing muzzle width by femur circumference (since it scales with slight positive allometry in ungulates), resulting in a ratio of relative muzzle width (Janis 1990b).

Relative distal hindlimb length in both ungulates and hadrosaurs is defined as the maximal articular length of the metatarsal divided by the maximal articular length of the femur. The measurements used in this study represent single individuals or an average of two to three individuals (for details see Janis & Wilhelm 1993). Relative hindlimb (rather than relative forelimb) length was chosen here to facilitate direct comparison with (at least facultatively) bipedal hadrosaurs. Although the elements representing the functional distal limb differ somewhat between the digitigrade hadrosaurs and the unguligrade ungulates, lever theory predicts a lengthening of the most distal limb elements (here, the metatarsals) in order to maximize efficiency at the expense of power (e.g., Gregory 1912; Maynard Smith & Savage 1955). As a result, lengthening of the metatarsals in association with open habitats (Janis & Wilhelm

1993) or high-speed locomotion (Garland & Janis 1992) should occur regardless of posture. Note that the negatively allometric scaling pattern of the metatarsals (Martin 1990; McNab 1990; Scott 1990) will tend to bias the ungulate data (which included a mix of taxa both above and below the 200 kg size limit) relative to the hadrosaurs (all of which would have had a body mass considerably greater than 200 kg; Anderson *et al.* 1985).

Lastly, we characterized the ungulates as either dimorphic or monomorphic, and noted the presence or absence of a presumably sexually dimorphic crest in hadrosaurs (see Hopson 1975; Dodson 1975). Our definition of monomorphism in ungulates includes taxa where both sexes are alike in the possession (or lack) of cranial appendages (horns or antlers). This was to facilitate comparison between the hadrosaurine and lambeosaurine dinosaurs, where both sexes in monomorphic forms lacked cranial structures (or possessed identical structures, e.g., *Saurolophus*, *Prosaurolophus*) and in dimorphic forms had cranial structures that differed in shape (Dodson 1975; Hopson 1975; Molnar 1977). Cranial appendage dimorphism usually (but not invariably) reflects body size dimorphism, but we did not consider this aspect of sexual dimorphism in our analyses directly. Morphological variables were thus designed to be comparable in both mammal and dinosaur data in terms of both the number and types of measurements possible, and the numbers of monomorphic and dimorphic taxa involved.

Two sets of mammal data were created: (1) seven monomorphic, open-habitat ungulates were compared with four dimorphic, closed-habitat ungulates with a preference for forest habitats; and (2) the same monomorphic taxa were compared with four dimorphic, closed-habitat ungulates with a preference for more open woodlands. Although no attempt was made to quantitatively assess the influence of phylogeny among the ungulates (e.g., Harvey & Pagel 1991), we selected ungulates from as wide a phylogenetic distribution as possible for each grouping. Although most open-habitat ungulates belong to the artiodactyl family Bovidae, we also included the caribou (Cervidae) and zebra (Perissodactyla: Equidae). The closed-habitat ungulates (woodland and forest) were all ruminant artiodactyls from the families Bovidae, Cervidae, Moschidae, and Tragulidae (Table 1). Phylogeny is more likely to be a direct influence in the case of the hadrosaurs, where the presence or absence of sexual dimorphism corresponds to the group's division into lambeosaurines and hadrosaurines, respectively. Genus-level phylogeny within these subfamilies is currently in flux (see Horner & Weishampel 1990; Forster 1997a), and so the effects of such potential bias cannot be evaluated directly.

Few of the measured dinosaur specimens were complete, a problem common in vertebrate paleontology but exaggerated by the poor fossil record of dinosaurs (Dodson 1990). Initial statistical analyses of the raw data indicated that the amount of missing data was too great to allow processing by standard multivariate procedures. Therefore, a second data set of composite taxa was created with 16 species among eight genera (Table 2). These taxa were assembled from multiple specimens of a given species, using the average ratio values of all available individuals of that species. Only relative measurements were used; specific linear measurements were not extrapolated because of the high probability for error. The variance of these ratios was small within each species relative to the variance among species. This composite dataset was ultimately used in the multivariate analyses.

Ordination analyses

In order to ordinate the data, it is first necessary to identify an appropriate statistical technique and justify its application here. With only three morphometric variables, it is usually an easy task to search for patterns of differentiation among the taxa: construct a three-dimensional scatter plot (or a series of three bivariate plots), and examine the resultant patterns. Here, however, the problem of missing data is such that certain taxa simply do not exist in the one or more dimensions where information is lacking.

Alternative representations can be produced by reducing the data into one or two composite dimensions using multivariate ordination techniques. In this manner, missing data are accommodated on the basis of statistical relationships among the taxa that have been determined by the data available. Although standard ordination techniques, such as principal components analysis (PCA) and canonical variates analysis (e.g., Reyment 1991), do not permit missing data, there are several less widely utilized techniques in morphometrics that do. We chose to use non-metric multidimensional scaling (NMDS) (Kruskal 1964a, 1964b; see also Sneath & Sokal 1973; Gauch 1982; Wilkinson 1989). NMDS ordinates taxa based upon the ranked values of distances between them and therefore has a relationship to PCA that is analogous to the relationship of rank correlation to product-moment correlation. NMDS tends to behave well with data that (like ours) have strange, non-normal distributions. Because of this property, NMDS has been used more for ecological applications within the natural sciences (e.g., Kammer & Ausich 1987; see also Gauch 1982), but there is no reason why it cannot be applied to morphometric data, even when well behaved (Sneath & Sokal 1973).

We used the SYSAT computer package (Wilkinson 1989) to compute NMDS ordinations; this package has the additional benefit of allowing missing values in the input distance matrix. These occur when two taxa share no variables in common because of respective missing data. (It might seem as though such taxa could not be ordinated, but their distances from other taxa with more complete data constrain their positions in the ordination space.) Before computing the NMDS ordinations, the three variables were first standardized to zero mean and unit variance in order to equalize their weights. (Experiments with other equalizing methods, such as logarithmic transformations, produced very similar final ordinations.) A matrix of Euclidean distances between taxa was then computed; when missing data were encountered, the affected values were simply ignored in the distance computation. The distance matrix was then entered into the MDS routine of SYSTAT, and two NMDS axes were computed.

As presented below, generally only the first NMDS axis was consistently meaningful. Therefore, we measured differentiation between groups only along this axis. With one axis and two groups, we used the standard *t*-test for unpaired samples as the measure of differentiation. Because we are dealing with groups of the same sizes in both the ungulate and hadrosaur data sets, the measured *t*-statistic can be compared between ordinations.

The question of which variables might be influencing any differentiation along an axis can be solved rather simply. Although NMDS produces nothing comparable to variable loadings in PCA or variable coordinates in correspondence analysis (Reyment 1991), the relationships of variables to axes can be determined by correlation. If taxa with high coordinates on an axis consistently have high values of a variable, and taxa low on the axis consistently have low values, then that variable will have a high positive correlation with the axis. Thus, it can be inferred that the distribution of taxa along the axis is in part influenced by that variable. Since NMDS is a technique based on ranks, and because our data are not normally distributed, rank correlation coefficients are appropriate for measuring relationships between variables and axes. We used Kendall's tau (Sokal & Rohlf 1995) for this purpose.

Results

We present the ordinations for ungulates first, so that these can provide a model for the hadrosaur analysis. Both will be considered in some detail, following which we will examine the problem of missing data in the hadrosaur dataset.

Ungulates. — The ungulate data are presented in Table 1. In general, these data exhibit the proposed differences in morphology based on the differences in sexual dimorphism and correlated habitat type. For example, the shear/crush ratio for the monomorphic taxa is much greater than for the dimorphic taxa, corresponding with their more fibrous diets. Exceptions do exist, as in the cases of the eland and caribou, both of which have shear/crush ratios that fall within the range of dimorphic ungulates. In contrast to other monomorphic ungulates, these taxa are mixed feeders rather than strict grazers (see Janis 1990a, b for references on ungulate diets); they would thus be expected to have lower shear/crush ratios. A problematical exception exists in the case of the hartebeest, which has a surprisingly low ratio despite being a grazer. However, this may represent something of an artifact: the hartebeest's low shear/crush ratio stems from its high values of 'shearing crush' wear, which should perhaps be considered as a type of shearing wear (see Janis 1990a).

Monomorphic ungulates have almost uniformly higher relative muzzle width values (i.e. relatively broader muzzles) than dimorphic ungulates, with the eland again as an exception, probably for the same reasons as discussed above. With regard to relative distal hindlimb length, the monomorphic ungulates are generally larger than the dimorphic forms, mostly with body masses above the critical value of 200 kg, and so have relatively short metatarsals. Note that the topi, an open-habitat taxon that is also of fairly low body mass, has the relatively longest metatarsals. Note also that the monomorphic ungulates have higher mean relative distal hindlimb lengths than those found in the forest habitats (0.83 vs. 0.73), despite their much larger size.

Ordination of open-habitat and forest-dwelling ungulates in two dimensions (Fig. 2A) yielded a Kruskal stress value of 0.090, which is considered 'excellent' (Kruskal 1964a). This is hardly surprising – only three variables were used. Axis one in the ordination exhibits a significant separation of the two ungulate groups ($t = 4.35$, 10 df; $p < 0.01$), with closed-habitat ungulates falling at the positive end of the axis and open-habitat ungulates tending toward the negative end. There is no overlap between the two groups, although there is also no gap between them. The correlation of variables with axis one (Table 3) fall out as might be predicted, with negative values for the shear/crush ratio ($p < 0.01$) and relative muzzle width ($p < 0.01$), and a positive value

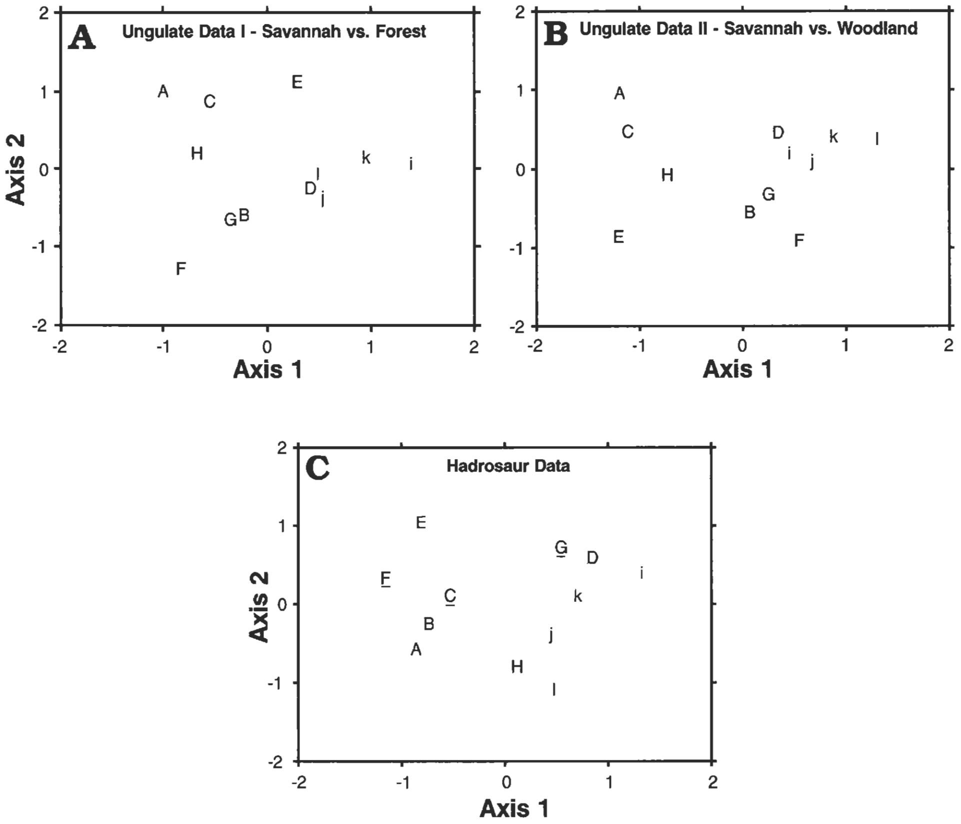

Fig. 2. Two-dimensional ordination plots, produced by non-metric multidimensional scaling (NMDS), for three datasets: ungulate mammals, savannah and forest taxa (**A**); ungulate mammals, savannah and woodland taxa (**B**); hadrosaur dinosaurs (**C**). Letters indicate the ordination positions of the taxa and correspond to the letters in Tables 1 and 2. In **A** and **B**, uppercase letters denote monomorphic, open-habitat ungulates, and lowercase letters denote dimorphic, closed-habitat ungulates. In **C**, uppercase letters denote monomorphic hadrosaurines, and lowercase letters denote dimorphic lambeosaurines; underlined letters indicate taxa with missing data.

for relative metatarsal length ($p < 0.05$). Thus, forest ungulates are sorting according to relatively short legs, relatively narrow muzzles, and more crushing wear on the teeth.

The only monomorphic taxa that were not clearly separated from the dimorphic taxa along axis one were the eland (case D) and buffalo (case E). The position of the eland was not unexpected: it is the sole open-habitat member of the bovid tribe Tragelaphini, which otherwise contains only closed-habitat species, and may represent a recent invader of open habitats. Its narrow muzzle may merely reflect its phylogenetic history. The buffalo has high values on axis one because of its large size, as its relatively low relative distal hindlimb length mimics those of closed-habitat taxa. Very low values along dimension one for the zebra (case A), bison (case C), wildebeest (case H), and topi (case F) probably result from their relatively high shear/crush ratios. There seems to be little phylogenetic effect on the clustering of monomorphic ungulates. The two monomorphic taxa that cluster together, the hartebeest (case B) and caribou (case

Table 3. Rank correlations (Kendall's tau) between variables and NMDS axes for three ordinations: ungulate mammals (including forest taxa); ungulate mammals (including woodland taxa); and hadrosaurian dinosaurs. Abbreviations as in Tables 1 and 2. Key: * $p < 0.05$; ** $p < 0.01$.

	Axis 1	**Axis 2**
Ungulates I		
SCR	-0.485**	0.303
RMW	-0.545**	0.000
RDL	0.364*	-0.667**
Ungulates II		
SCR	-0.424*	0.091
RMW	-0.545**	-0.455*
RDL	0.727**	-0.212
Hadrosaurs		
SCR	0.197	0.254
RMW	-0.648*	0.141*
RDL	-0.493*	-0.667

G), belong to different families, and there is no obvious clustering of the closely related acelaphine bovids – the hartebeest, topi (case F), and wildebeest (case H).

The ordination of open-habitat ungulates with woodland ungulates (Fig. 2B) also provided an 'excellent' stress value of 0.066 in two dimensions. The separation of groups along axis one is less pronounced than in the previous ordination, but still very significant ($t = 3.76$, 10 df; $p < 0.01$). However, variable correlations are somewhat different from those of the forest taxa. Although there are still high negative variable correlations for relative muzzle width ($p < 0.01$) and shear/crush ratio ($p < 0.01$), suggesting a separation according to diet as in the previous analysis, the direction of the variable correlations for relative distal hindlimb length shows high positive correlation with axis one ($p < 0.01$). Thus, in this particular analysis, where habitat difference is not as pronounced and monomorphic taxa are generally larger than the dimorphic taxa, relative distal hindlimb length appears to be acting to distinguish the groups on the basis of size. Note that variable correlations with axis two differ from those in the first ordination, indicating that this axis is not capturing consistent information. The eland (case D) is again placed close to the cluster of dimorphic, more closed-habitat taxa at the positive end of axis one. Again, no obvious clustering of acelaphines (cases B, F, and H) is apparent, suggesting little phylogenetic influence on the grouping of monomorphic ungulates.

Hadrosaurs. — The hadrosaur data are presented in Table 2. An initial glance at the data reveals a pattern similar to that observed in the ungulate data in the comparison between savannah and woodland taxa in Table 1. Hadrosaurines, for example, appear to have relatively wider muzzles (mean = 0.68 vs. 0.45) and higher shear/crush ratios (mean = 1.91 vs. 1.77) than lambeosaurines, although the relative distal limb pattern is more ambiguous. Note also the substantial overlap and great range of values for some of the variables: in hadrosaurines, shear/crush ratio ranges from 1.20 to 3.33 and relative muzzle width from 0.48 to 0.84. The amount of missing data is obviously substantial, so that we hesitate to make predictions based on the raw data alone.

Ordination was performed in the same way as with the ungulate data. The two-dimensional NMDS ordination (Fig. 2C), with 14% (or 5/36) missing data, resulted in a 'good' stress value of 0.13. This stress is greater than either of the datasets for ungulates and reflects distortion in the distance matrix inflicted by the missing data. Still, axis one separates the dimorphic lambeosaurines from the monomorphic hadrosaurines, although not as strongly as in the ordinations for the ungulates ($t = 2.64$, 10 df; $p < 0.10$). The ordination bears greatest resemblance to the mammal ordination with woodland ungulates (Fig. 1B), especially given that RDL exhibits a modest positive correlation, relative muzzle width a high negative correlation, and shear/crush ratio a modest negative correlation with axis one (Table 3). As before, axis two may not be meaningful, despite a moderately significant ($p < 0.05$) positive correlation with shear/crush ratio (see below).

It is possible that low correlations between variables and axis one could result from the high incidence of missing data. To test for this possibility, we conducted a series of unpaired, one-sided t-tests on all available data for the hadrosaurs (as opposed to averages for each species) to determine if there was a differentiation that paralleled open-habitat versus woodland ungulates. Consistent with the correlation of relative metatarsal length to axis one, lambeosaurines have relatively longer third metatarsals ($t = 2.39$, 8 df; $p < 0.05$) and relatively narrower muzzles ($t = 4.388$, 16 df; $p < 0.001$). Also like the correlations, there is no significant difference in shear/crush ratio ($t = 0.972$, 15 df; $p > 0.30$), although the trends follow the same patterns as in ungulates. To test shear/crush ratio further, we computed separate ratios for the maxilla and dentary and again found no significant differences (maxilla: $t = 0.350$, 12 df; $p > 0.70$; dentary: $t = 1.06$, 18 df; $p > 0.30$). Thus, the differentiation between hadrosaurines and lambeosaurines reflected in the ordination (Fig. 1C) is a greater function of RDL and relative muzzle width than of shear/crush ratio.

The differentiation in Fig. 1C between the two hadrosaur groups is only partial. Four of the hadrosaurines, *Prosaurolophus maximus*, *P. blackfeetensis*, *Anatotitan copei* (case D) and *Edmontosaurus saskatchewanensis* (case G), cluster closely with the four lambeosaurines. *P. blackfeetensis* is represented by only one variable, the shear/crush ratio; since this value is close to that for most lambeosaurines, the taxon clusters with this group. Furthermore, the genus *Prosaurolophus* tends to have a narrower muzzle than other hadrosaurines, and in this respect is more similar to the lambeosaurines. *E. saskatchewanensis*, however, is characterized by two variables, relative muzzle width and shear/crush ratio. The muzzle is relatively narrow for the hadrosaurines and within the range exhibited by the lambeosaurines. Since relative muzzle width has a slightly higher correlation with axis one than does shear/crush ratio, this taxon clusters with the lambeosaurines. Although *Anatotitan* is represented by all three variables, it may be drawn towards the lambeosaurine cluster by its low shear/crush ratio.

Thus, the ordination of hadrosaurs partially separates monomorphic from dimorphic species in a manner visually similar to the ungulate ordinations, especially for that using woodland taxa. It is therefore tempting to conclude that the hadrosaurs are sorting on the basis of morphological correlates of habitat choice. However, here the similarity to the ungulates is less complete. The differentiation of the hadrosaurines and lambeosaurines is affected most strongly by relative distal hindlimb length, which correlates with size in large animals, and relative muzzle width, which correlates with diet. Dental ratios are much more poorly correlated with these groupings. For the ungulates, differentiation of open-habitat and woodland species was a stronger function of the diet-relative muzzle width (and also shear/crush ratio) correlation, as well as size-related relative distal hindlimb length (Table 3).

It is possible that these dissimilarities between hadrosaurs and ungulates are real. Alternatively, it is possible that they are a function of the differences in quality between the two datasets. We explore this latter possibility below.

Addressing the problem of missing data

At this stage, missing data present an important problem: how does the lack of information muddle or bias these (or, indeed, any) results? In order to test the robustness and reliability of these results, we used the 'holes' in the hadrosaur dataset as a template to artificially delete data from the mammal set. Because the results from the hadrosaur ordination were more similar to those of the second mammal analysis (open versus woodland) in terms of separation of groups and variable correlations, only the second mammal dataset was artificially degraded. This choice was also prompted by a desire to avoid a bias towards separation of groups, which were better differentiated in the first mammal dataset.

The procedure for degrading the dataset was simple. First, we deleted the occurrences in the original mammal data (Table 1) to correspond with the gaps in the dinosaur data (Table 2). For example, the third hadrosaur taxon, *P. blackfeetensis* (case C), is lacking data for the dental shear/crush ratio and the relative muzzle width. Accordingly, these same data were removed from case C (the bison) in the mammal dataset, and so on.

Three additional degraded datasets ('iterations') were generated by changing the position of the mammal taxa within each group, and overlaying the pattern of 'holes' from the dinosaur data. In each iteration, the taxon at the bottom of each group's list (for example, the wildebeest among the monomorphic ungulates, and the muntjac among the dimorphic taxa in iteration two) was moved to the top of its respective group, and the original first taxon moved to the second position. The number of iterations was limited to four because this was the number of taxa in the smaller (dimorphic) grouping for both mammal and dinosaur taxa. Still, ordination analysis of four artificially degraded datasets should ensure that any similarities in significance between the degraded mammal data and the dinosaur data were the result of technique robustness and not a chance occurrence resulting from the particular ordering of the mammal taxa.

NMDS ordinations of all four iterations (Fig. 3; Table 4) resemble each other: the dimorphic taxa cluster over the positive portion of axis one and are more or less separated from the monomorphic taxa, as in the ordination of the complete dataset. However, the separation generally is not as strong as in the complete ungulate dataset (average t-value = 2.04, in contrast to 2.64 for complete data), and various monomorphic taxa fall among the dimorphic taxa, similar to the pattern seen in the hadrosaur ordination. Some of the specifics of these patterns are outlined below:

Table 4. Rank correlations (Kendall's tau) between variables and NMDS axes for ordinations in which data for ungulates (with woodland taxa) were degraded by deleting as many values as were missing from the hadrosaur dataset. See text for further methodological details. Key: * $p < 0.05$; ** $p < 0.01$.

	Axis 1	Axis 2
Iteration 1		
SCR	-0.455*	-0.345
RMW	-0.733**	0.333
RDL	0.822**	-0.400
Iteration 2		
SCR	-0.636**	0.309
RMW	-0.600*	-0.200
RDL	0.800**	0.356
Iteration 3		
SCR	-0.382	-0.127
RMW	-0.422*	-0.867**
RDL	0.844**	0.089
Iteration 4		
SCR	-0.200	0.309
RMW	-0.289	-0.422*
RDL	0.711**	-0.400
Means (± standard deviation)		
SCR	-0.418 (± 0.180)	0.037 (± 0.327)
RMW	-0.487 (± 0.162)	-0.289 (± 0.499)
RDL	0.794 (± 0.058)	-0.089 (± 0.376)

Iteration 1. — ($t = 2.63$, 10 df; $p < 0.05$; Fig. 3A). Here the eland (case D), which corresponds in position to *P. maximus* in the dataset, now clusters within the grouping of the dimorphic ungulates on the basis of its relatively low shear/crush ratio (see Results). The topi (case F) also clusters with the dimorphic ungulates on axis one. In this iteration, it corresponds to *E. edmontoni*, which is represented only by relative distal hindlimb length. As the topi is a relatively small ungulate in comparison with the other monomorphic taxa, and is thus proportionally longer-legged, this single measurement now makes it cluster with the generally smaller dimorphic taxa.

Iteration 2. — ($t = 2.14$, 10 df; $p < 0.1$; Fig. 3B). These results bear the greatest resemblance to those from the complete dataset, and accordingly are the most significant. The eland (case D) now corresponds to *E. regalis*, which has a full set of measurements and no longer clusters with the dimorphic ungulates. In fact, with the eland constrained in this fashion, the analysis shows a similar degree of separation between the two groups to the analyses with complete data. Only the hartebeest (case B), now clusters with the dimorphic forms. The hartebeest now corresponds to *P. blackfeetensis* and is represented only by its low shear/crush ratio (see Results), causing it to cluster with the mixed-feeding dimorphic taxa.

Iteration 3. — ($t = 1.27$, 10 df; $p > 0.05$). In this iteration (Fig. 3C), the eland (case D) now corresponds to *E. edmontoni*, and hence is only represented by RDL. It now clus-

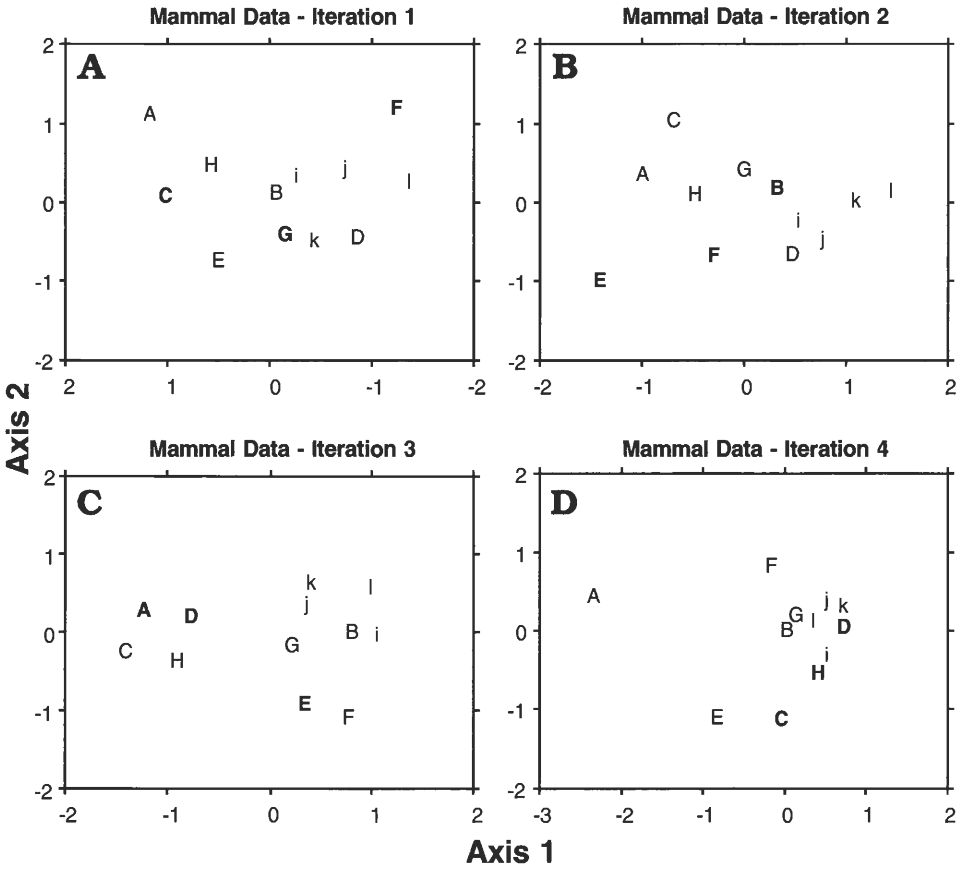

Fig. 3. **A–D**. Two-dimensional ordination plots, produced by non-metric multidimensional scaling (NMDS), for the ungulate data (including woodland taxa) after being degraded to the level of the hadrosaur data in four different ways ('iterations'), as described in the text. As in Fig. 2, letters indicate the ordination positions of taxa and correspond to the letters in Table 1. Capital letters denote open-habitat ungulates, and lowercase letters denote woodland ungulates; boldface letters indicate taxa with missing data.

ters with the other large, proportionally shorter-legged monomorphic ungulates. The hartebeest (case B) now corresponds to *P. maximus* and is represented by all three variables, and thus appears to cluster less strongly with the dimorphic forms. Two other taxa, the topi (case F) and caribou (case G) now cluster with the dimorphic forms. Since both these taxa correspond to hadrosaurs with the full complement of measurements (*Gryposaurus* and *Corythosaurus*, respectively), it is not clear why this grouping should occur, but the relatively low shear/crush ratio values for both taxa may be responsible.

Iteration 4. — ($t = 2.14$, 10 df; $p < 0.1$). Here (Fig. 3D) the eland (case D) occupies the position of *E. saskatchewanensis* in the dinosaur dataset, which is missing data for relative distal hindlimb length. Without this clue that it is a relatively short-legged large animal, it clusters within the grouping of dimorphic ungulates. The topi (case F) and caribou (case G) also cluster with the dimorphic ungulates as in the previous iteration.

Here they occupy the positions of *Corythosaurus* and *H. altispinus*, respectively, and are thus represented by all three variables; again, low shear/crush ratio values may be affecting their positions (see above). Finally, the same factor may underlie the grouping of the hartebeest (case B, here corresponding to *Anatotitan*) with the dimorphic ungulates. Notably, although this is the only iteration with a non-significant separation along axis 1, the general trends remain similar to those in the first three iterations.

The rank correlation coefficients between the three degraded variables and the ordination axes in each iteration (Table 4) very importantly show that axis one maintains the same general relationship with the variables as in the full ungulate dataset despite the degradation of the data (Table 3). In particular, the signs of the correlations remain the same in all four iterations even though their statistical significances vary. The correlations between shear/crush ratio and axis 1 are most variable, as documented by their standard deviations (Table 4). In fact, two standard deviations about the mean for shear/crush ratio include zero, which suggests that a lack of correlation (or even weak positive correlation) with this variable in an ordination could be more a function of missing data than of true relationships among the taxa. Two standard deviations about the mean correlations for relative muzzle width and relative distal hindlimb length do not include zero, and therefore the signs of these correlations in the deficient hadrosaurian data may be more trustworthy. However, the variability of the correlations in the degraded ungulate datasets suggests that statistical significance cannot be expected with missing data even if there is a true correspondence between the morphologic variables and habitat. For axis two, the rank correlations with all variables show even higher variability, and two standard deviations about the mean always include zero. This suggests that axis two cannot be trusted to be encapsulating meaningful morphometric relationships among the taxa in situations with as much missing information as the hadrosaurian dataset.

The experiments with degraded ungulate data indicate that the separation between monomorphic and dimorphic hadrosaurs on axis one of the NMDS ordination is probably not an artifact of the deficient data, but more likely a true reflection of morphologic differences. The overlap between the two groups, with some monomorphic hadrosaurines clustering with some dimorphic lambeosaurines, could be more a function of holes in the data than of real morphologic similarity. Finally, the statistically questionable variables inducing the multivariate separation, especially relative muzzle width and relative distal hindlimb length, may very well have the same relationships and hence the same functional-ecological roles, as reflected in the complete ungulate (with woodland taxa) dataset. We suggest, therefore, that the monomorphic versus dimorphic condition seen in hadrosaurine versus lambeosaurine dinosaurs reflects the same ecological differentiation seen in open-habitat versus closed-habitat ungulates, but seen through the shaded perception of deficient data.

Discussion

The analysis of dinosaur data and the experiments with degraded ungulate data suggest that the monomorphic hadrosaurines were likely open-habitat animals, exhibiting the same wider muzzles and longer distal limbs of open-habitat, less selective-feeding extant ungulates. The dimorphic lambeosaurines were their closed-habitat counterparts, with the narrower muzzles and shorter distal limbs characteristic of more selective feeders. The small absolute value of differences in distal limb length is understandable in light of the overall large size of these animals (see above).

From the comparative analyses, we infer that hadrosaurines were more open--habitat animals and would perhaps have been more gregarious animals, as indicated by the lack of pronounced sexual dimorphism. Similarly, we infer that lambeosaurines inhabited the closed environments and were likely more territorial (and hence displayed marked dimorphism) than their open-habitat counterparts. Our results further indicate that general habitat type was a strong constraint on herbivore morphology and behavior. Nonetheless, the world of the Late Cretaceous, particularly with respect to the Mesozoic flora, was in many ways very different from that of the Cenozoic. For example, grazing *per se* was not possible in the Mesozoic because there were no grasses or grasslands. Still, herbivory on high-fiber, open-habitat plants was certainly a viable (and probably oft-exploited) option.

As emphasized in this study, dinosaur specimens (like those of many fossil taxa) are often incomplete; this incompleteness ranges from missing skeletal elements within an individual to 'missing' information in the form of inadequate population samples. The NMDS technique utilized here is one multivariate method that accommodates such missing data and thus permits more rigorous quantitative analyses of data from fossil taxa. The experiments performed with artificially degraded ungulate datasets produced results and significances similar to those from the complete data. Clearly missing data affect the significance level, but equally clearly they do not necessarily render the results either invalid or statistically useless. Data experiments of this nature are critical if we are to accept the validity of any results derived from paleontological data. With appropriate statistical techniques, the amount of permissible missing data can be increased without marked sacrifice of significance or confidence.

Conclusions

The results of our analyses show that hadrosaur dinosaurs resemble ungulate mammals in the clustering of patterns of sexual dimorphism in different taxa and with morphological features indicative of feeding and habitat preference. The implication of these clusterings is that the monomorphic hadrosaurines were open-habitat, gregarious animals (like monomorphic ungulates), whereas the dimorphic lambeosaurines were more closed-habitat, solitary animals, perhaps exhibiting male territoriality. Late Cretaceous hadrosaurs certainly paralleled late Cenozoic and Recent ungulates in being large, common, and diverse terrestrial herbivores. Our results here suggest that they also paralleled ungulates in aspects of behavioral ecology related to habitat preference. Although late Mesozoic and late Cenozoic terrestrial ecosystems were profoundly different in terms of both animal and plant taxa, there may be universal constraints on the ecological roles played by large herbivores, resulting in convergence in morphology (and, by implication, behavioral ecology) between groups as taxonomically distinct as dinosaurs and mammals.

Incomplete data are certainly an issue for statistical analyses and must be confronted appropriately, but this problem should be dealt with as an obstacle and not an obstruction. Appropriate statistical methodology (here, NMDS) allows deficient data to be examined in a meaningful fashion. Experiments with fully known data allow evaluation of the results with greater confidence. This has the benefit of allowing statistical results for fossil taxa, otherwise rendered uninformative by incompleteness due to preservational, sampling, or other paleontological biases, to be more informative and reliably interpreted.

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Dinozaury kaczodziobe jako ekologiczne odpowiedniki ssaków kopytnych: wygasłe tryby życia a niepełne dane

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Streszczenie

Dinozaury kaczodziobe (Ornithischia: Hadrosauridae) były w późnej kredzie pospolite w Ameryce Północnej i Azji. Wyspecjalizowane przystosowania uzębienia i szkieletu pozaczaszkowego pozwoliły wysunąć przypuszczenie, że trybem życia przypominały dzisiejsze ssaki kopytne. Kopytne przejawiają zespół cech morfologicznych skorelowanych z rodzajem pokarmu, preferencjami siedliskowymi i dymorfizmem płciowym. W niniejszej pracy poddano analizie wieloczynnikowej odnośne cechy hadrozaurów, by sprawdzić, czy i u nich występują podobne prawidłowości. Wstępne wyniki potwierdziły podobieństwa między hadrozaurami a kopytnymi, ale wynik analizy statystycznej mógł zostać znacząco zniekształcony przez niekompletność danych dotyczących dinozaurów. Dlatego zestawy danych dotyczące ssaków kopytnych (pierwotnie kompletne) zostały sztucznie zubożone na wzór danych kopalnych i poddane powtórnej analizie. Uzyskane wyniki okazały się zbieżne z rezultatami wstępnymi i pozwoliły oszacować wpływ brakujących danych na pierwotną strukturę wieloczynnikową. Nasza analiza wspiera hipotezę, że hadrozaury były podobne pod względem ekomorfologicznym do ssaków kopytnych.