

24 Hypsodonty and body size in rodent-like notoungulates

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Abstract

Four families of endemic rodent-like notoungulates of the Suborder Typotheria (“Archaeohyracidae,” Interatheriidae, Hegetotheriidae, and Mesotheriidae) show a high degree of hypsodonty. We evaluate the evolutionary pattern expressed by the variability of hypsodonty and body mass in this group, and consider whether the traits are correlated. We used hypsodonty and body mass data for 36 species of Typotheria to test for an association between these features. Major evolutionary changes in hypsodonty and body size in Typotheria occurred during the Eocene-Oligocene transition (EOT) and it is well documented in the Patagonian fossil record at Gran Barranca. At least two evolutionary trends are recognized in two clades of Typotheria: (1) in Mesotheriidae an increasing of the hypsodonty, associated with increasing of the body mass in species with complex occlusal designs, and (2) the Hegetotheriidae are characterized by possessing high crown teeth with simplified occlusal designs and small body sizes (Hegetotheriidae Pachyrukhinae). The Hegetotheriidae Pachyrukhinae show the highest indices of hypsodonty and were the smallest typotheres.

Resumen

Cuatro familias de notoungulados rodentiformes del Suborden Typotheria (“Archaeohyracidae,” Interatheriidae, Hegetotheriidae y Mesotheriidae) muestran un alto grado de hipsodoncia. Nosotros evaluamos el patrón evolutivo expresado por la variabilidad de la hipsodoncia y la masa corporal en ese grupo. Datos de hipsodoncia y masa corporal de 36 especies de Typotheria fueron utilizados para explorar la asociación entre estos caracteres. Los mayores cambios evolutivos en hipsodoncia y tamaño corporal ocurren durante la transición Eoceno-Oligoceno (EOT) y están bien documentados en el registro patagónico de Gran Barranca. Al menos dos tendencias evolutivas fueron reconocidas en dos clados de Typotheria: 1) en los Mesotheriidae hay un incremento de la hipsodoncia, asociado a un incremento de la masa corporal en especies con diseños oclusales complejos, y 2) los Hegetotheriidae se caracterizan por poseer molariformes de coronas muy altas con diseños oclusales muy simplificados y tamaño corporal pequeño (Hegetotheriidae Pachyrukhinae).

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Los Hegetotheriidae Pachyrukhinae muestran los índices de hipsodoncia más altos y fueron los tipoterios más pequeños.

Introduction

Notoungulates are unique in having attained impressive morphologic and taxonomic diversity (13 or so families, at least 140 genera: Croft 1999) without leaving a single living representative. Among them, the Typotheria, so-called “rodent-like” notoungulates, experienced a broad adaptive radiation including small rodent-like (Interatheriidae), rabbit-like (Hegetotheriidae), and sheep-like (Mesotheriidae) forms.

The most noteworthy period of concentrated evolutionary change in morphological enhancements to tooth functional longevity (hypsodonty) and body size in Typotheria occurred during the Eocene–Oligocene transition (EOT) and it is well documented in the Sarmiento Formation at Gran Barranca (Chubut). Gran Barranca contains the most complete sequences of Paleogene continental sediments known in South America. A refined local biostratigraphy has allowed assignment of most mammalian-bearing horizons to specific biostratigraphic zones. Large samples of specimens of Typotheria are available from stratigraphically controlled localities throughout this sequence.

The rodent-like notoungulates were grouped by Simpson (1967) in the suborder Typotheria, and defined by him as notoungulates with “cheek teeth brachydont in earliest and most primitive forms, but with accelerated tendency toward hypsodonty even in the early faunas and by Deseadan time all hypsodont and most rootless” (Simpson 1967, p. 15). His concept of the Typotheria included such primitive and brachydont families as Oldfieldthomasiidae and Archaeopithecidae together with Interatheriidae. The latest systematic and phylogenetic revision of Typotheria (Reguero and Prevosti this book) groups in this suborder only the hypsodont, small to medium-size notoungulates: Campanorciidae, “Archaeohyracidae,” Interatheriidae, Hegetotheriidae, and Mesotheriidae.

During the EOT vertebrate faunas from Gran Barranca show a great radiation of two families of Typotheria, “Archaeohyracidae” and Interatheriidae, possessing high-crowned incisors and cheek teeth that we today associate with life in

“open” habitats (Simpson 1951; Webb 1983; MacFadden 2000a, 2000b; Janis *et al.* 2000). The oldest example of a hypsodont taxon (*Acropithecus* in the Vacan, early Eocene) of Patagonia antedates the first appearance of members of hypsodont clades in the North American fossil record (Oreodontidae, Leporidae, Castoridae, Geomyidae, Heteromyidae).

Patterson and Pascual (1968) highlighted “the precocity shown by certain ungulates in the acquisition of high-crowned, or hypsodont, and rootless, or hypselodont, teeth. Notohippids by mid-Eocene time were considered as advanced in this respect as equines were in the early Pliocene, about 30 million years later.”

The South American continental biotic record was temporally calibrated against the record of climatic change by Kay *et al.* (1999) in Gran Barranca (for a revision, see Ré *et al.* Chapter 4, this book).

Although the dentitions of these notoungulates are well represented in the fossil record, and many other aspects of the typotheres evolutionary history are well studied, their dietary habitats have been described only in the broadest terms.

In ungulates hypsodonty is widely considered an adaptation for coping with the high rate of dental wear caused by abrasive diets, such as grazing, due to high amounts of fiber, silica, or exogenous grit (dust, sand, ash) on the surface of ingested food (Simpson 1944; Fortelius 1985; Janis 1988; Pérez Barbería and Gordon 2001; Williams and Kay 2001). This evolutionary hypothesis is supported by an apparent correlation of crown height with ecological factors (e.g. diets, habitats) among modern ungulates. Janis (1988) found that crown height was associated with open habitats, but not directly related to the plants ingested. Recently, Williams and Kay (2001) examined several factors, i.e. coevolution of climate, diet, and feeding behavior, with crown height after removing phylogenetic effects; they did not find a relationship between crown height and climate. Williams and Kay (2001) found that tooth crown height was positively correlated with the proportion of monocots (primarily grass) in the diet and was negatively correlated with foraging height preferences.

The evolutionary trend of hypsodonty seen in different early and middle Miocene North American ungulate lineages is often considered as an indication of coevolution with a savanna grassland vegetation (Simpson 1944; Webb 1977; Fortelius 1985; Janis 1988, 1993; Pérez-Barbería and Gordon 1998a, 1998b). However, Muhlbachler and Solounias (2006) in a mesowear study of the North American Artiodactyla Merycoidodontidae found no clear indication that the overall trend of increasing dietary abrasion imposed sufficient selection to drive crown height evolution. In another recent report (Strömberg 2005) demonstrates that habitats dominated by C₃ grasses in the Central Great Plains were established at least 4 m.y. prior to the emergence of hypsodonty among Holarctic equids (Strömberg 2005). This

retardation in the evolution of full hypsodonty was suggested as a result of a weak or fluctuating selection pressures and/or of the phylogenetic inertia (Strömberg 2005).

The hypsodonty exhibited in several lineages of South American ungulates, especially during the EOT, has been considered as associated to environmental changes (Pascual *et al.* 1996), but there is yet no precise analysis of the time of the first appearance and history of change of selective forces that might have acted on hypsodonty. In this chapter we examine the timing of the appearance of hypsodonty. Additionally, we explore the potential relationships between the evolutionary acquisition of hypsodonty and other morphological features, such as body size and occlusal designs, currently considered as very important to understand the biology of organisms.

Materials and methods

Taxa

“Archaeohyracids” are small, somewhat gliriform typotheres, defined by Simpson (1967, p. 104) as “Early notoungulates with accelerated hypsodonty (not reaching continuous growth)” (Fig. 24.1A).

Interatheriids are small, somewhat gliriform typotheres, most of which approximated the size of a house cat (*Felis sylvestris*). They are often very common in the faunas in which they occur but are rare or absent in some mid-latitude faunas (i.e. those between 10° and 23° S latitude) of Chile and Bolivia (Croft *et al.* 2004) (Fig. 24.1B).

Mesotheriids are small to medium typotheres (mostly between 5 kg and 50 kg; Croft *et al.* 2004) that were likely adapted for a fossorial lifestyle (*sensu* Hildebrand 1985; Shockey *et al.* 2004). They are very common in some Oligocene and early Miocene faunas and are moderately abundant in most middle Miocene to Pleistocene faunas, but have not been recorded in any low-latitude faunas (i.e. those north of 10° S; Croft *et al.* 2003, 2004; Reguero and Castro 2004) (Fig. 24.1C).

Hegetotheriids are similar in size to interatheriids, and some of the later representatives were very similar in overall morphology to modern rabbits (leporids) or certain caviomorph rodents (e.g. *Dolichotis*) (Elissamburu 2004; Reguero *et al.* 2007). Two hegetotheriid subfamilies are generally recognized: Hegetotheriinae and Pachyrukhinae. Hegetotheriinae is likely paraphyletic, though it may include a monophyletic subset of Miocene taxa (Cifelli 1993; Croft 2000; Croft and Anaya 2004; Croft *et al.* 2004; Reguero and Prevosti this book). Pachyrukhinae is universally considered monophyletic (Cerdeño and Bond 1998; Reguero and Prevosti this book) and the clade is certainly recognizable as early as the Deseadan (Dozo *et al.* 2000) and potentially as early as the Tinguirirican (Reguero 1993) (Fig. 24.1D).

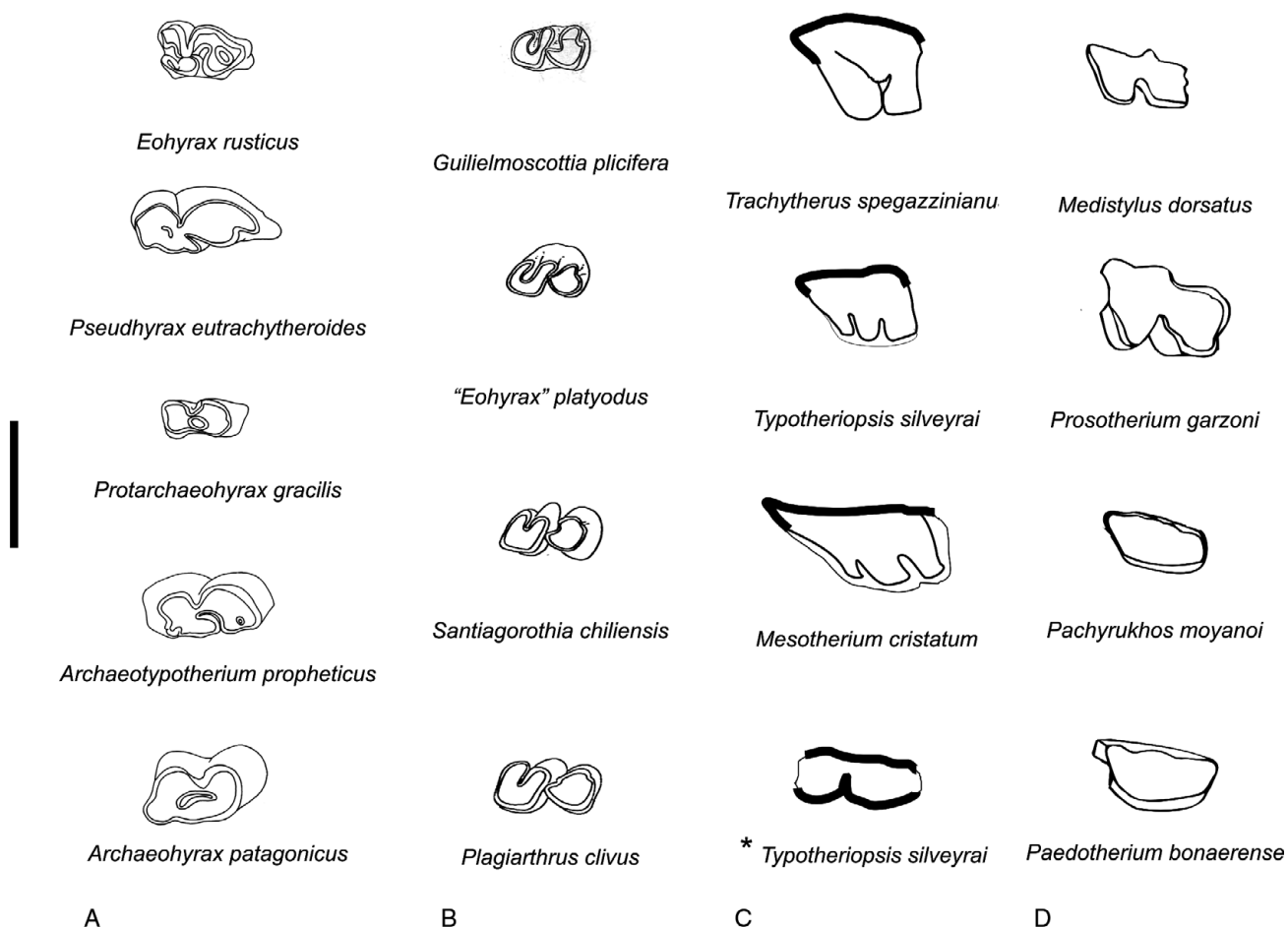


Fig. 24.1. Occlusal schematic views of left m1 (A–B) and left M1 (C–D, except tagged * left m1). (A) “Archaeohyracidae”; (B) Interatheriidae; (C) Mesotheriidae; (D) Pachyrukhinae. Scale bar 1 cm.

Data

Specimens analyzed are housed at Museo Provincial “Egidio Feruglio,” Trelew, Argentina, Museo de La Plata, La Plata, Argentina, and Museo de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina.

Estimation of body size is a controversial issue (Fortelius 1990; Smith 2002). We use specific body masses (g) for a total of 36 species of Typotheria. Although estimating body mass using only dental remains is more error-prone than if the estimates were based on skeletons, most of the species in Typotheria are known by dental remains, so we used dental measurements for estimating body mass.

The masses were predicted using regression equation of Damuth (1990) of body mass, based on first molar length calculated from recent non-selenodont ungulates:

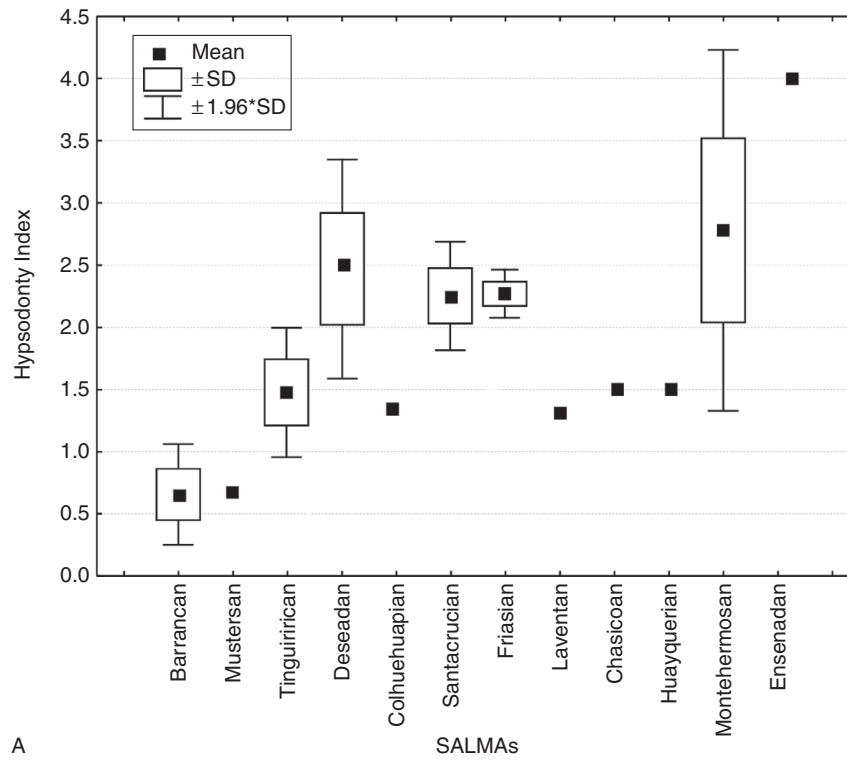
$$\log_{10} \text{ body mass} = 3.17 * \log_{10} \text{ m1 length} + 1.04.$$

Molar length was used instead of area because length values tend to be more highly correlated with body mass in living

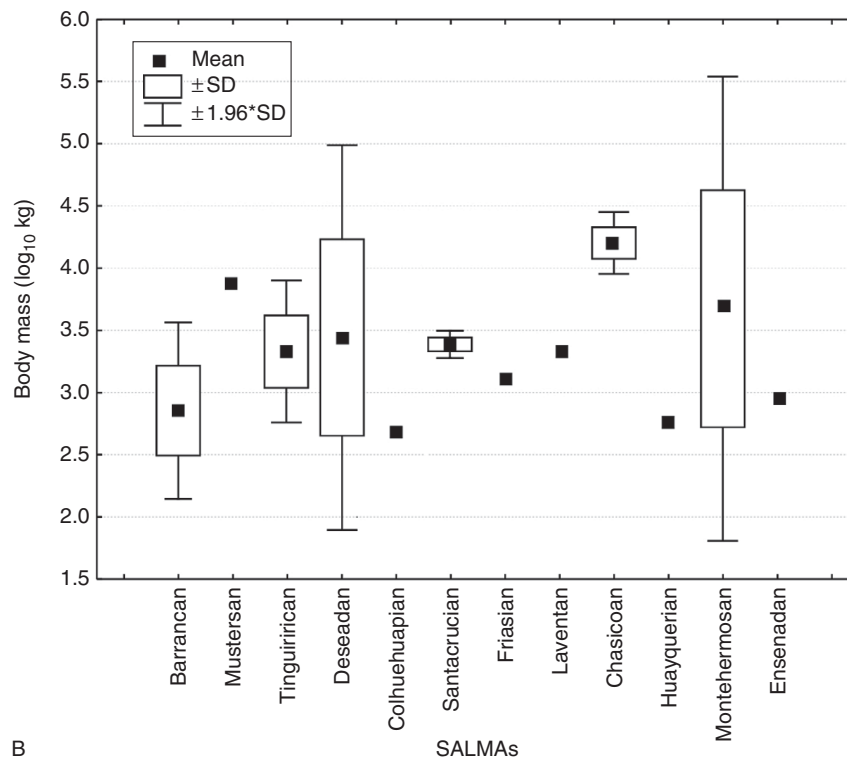
ungulates (Janis 1990). Accurate molar crown height data are very difficult to obtain, particularly among hypsodont ungulates, because it is difficult to find specimens at the precise age where a tooth crown is fully formed yet unworn. Among the material examined, m1 was generally unmeasurable, so we used m2, the only tooth for which we were able consistently to find examples with a measurable unworn tooth for each species. Samples used for the study are listed in Appendix 24.1. We followed Janis (1988) by calculating a crown height ratio (m2 ratio) as the crown height divided by the labiolingual width of the tooth. Crown height was measured on the labial side of the tooth at the hypoflexid.

Statistical analyses

The comparison of body size with hypsodonty using a reduced major axis regression analysis was performed using PAST software version 1.86d Hammer *et al.* (2001). Because the body mass variable departs from normality,



A



B

Fig. 24.2. Box plot of hypsodonty index (A) and body mass, \log_{10} transformed (B) in *Tytopheria* through time (represented by SALMAS).

Table 24.1. Results of simple linear regression for each group

Taxon	Range of W (g)	n	R^2	Intercept at $W = 1$ g	Standard error	Slope	Standard error	Significance p value ($d.f.$)
Tytopheria	224–73435	36	$1.6E^{-04}$	–1.501	0.6261	1.045	0.1792	0.941 ($I, 34$)
Mesotheriidae	2358–73435	11	0.337	–0.0919	0.5822	0.5366	0.1456	0.0611 ($I, 9$)
Hegetotheriidae	224–13681	11	0.543	6.748	0.8349	–1.289	0.2904	<0.01* ($I, 9$)
Interatheriidae	283–2817	7	0.182	–3.426	1.8726	1.797	0.7268	0.340 ($I, 5$)
Tytopheria (-H)	224–73435	25	0.255	–1.416	0.5913	0.911	0.1639	<0.01* ($I, 23$)

Note: The regressions were not significant in all groups at p level of 0.05 except for Hegetotheriidae and Tytopheria (without Hegetotheriidae) tagged by an asterisk ($p = 0.01$).

this variable was \log_{10} transformed. The hypsonty index (HI) and \log_{10} -transformed body mass are normally distributed (Shapiro-Wilk: W : 0.968, p 0.375; and Shapiro-Wilk: W : 0.944, p 0.066, respectively). When the regression was significant, outliers and residual distribution were examined.

Results

Species of Tytopheria increase in hypsodonty through time (Fig. 24.2A), whereas the body mass shows no identifiable pattern (Fig. 24.2B). This may be the result of processes of change of body mass and hypsodonty operating differently among the diverse lineages of Tytopheria.

The initiation and increase of hypsodonty among tytopheres is detected in Gran Barranca in the Tinguirirican and Deseadan SALMAs (Fig. 24.2A). However, Kohn *et al.* (2004) considered that this phenomenon had begun previously, between 39.3 and 38.0 Ma, ~ 5 m.y. prior to the EOT. The increase in grass abundance (Mazzoni 1979) and possible small increase in $\delta^{18}\text{O}$ values in teeth at that time suggest that a small decrease in relative humidity ($\sim 5\%$) could have driven hypsodonty (Kohn *et al.* 2004). Thus, the rise of hypsodonty in South American could reflect climate change and its impact on floras, but probably started prior to the EOT, which seems insignificant climatically. As is depicted in Fig. 24.2A the increase of the hypsodonty is continuous through the Oligocene in Patagonia when the highest diversity at the family level was recorded. Outside Patagonia, high values of hypsodonty are recorded in the Montehermosan when Tytopheria show a decline in its diversity, and one of the clades, Hegetotheriidae, experienced a radiation of the smallest representatives (Pachyrhinae).

Figure 24.2B shows no clear tendency of change in body mass from the late Eocene to middle Miocene in Patagonia, a period when the hypsodonty increases and the highest

diversity of Tytopheria is recorded. A possible increase of body mass seems to appear from the Colhuehuapian to the Chasicoan, but the few available individuals make this possible tendency uncertain.

Regression analyses for Tytopheria indicate that there was not a significant relation between hypsodonty and body mass (see Table 24.1, Fig. 24.3A), so the body mass would have no influence on variation of hypsodonty. However, it is possible that this result, obtained through all the species of Tytopheria (which pertain in turn to more than one clade; see Reguero and Prevosti this book), express variation due to both within and among taxa (Harvey and Page 1991). Therefore, the relationships between both characters were also analyzed separately at different taxonomic groups. The regression of hypsodonty on \log_{10} body mass considering only Hegetotheriidae is significant, showing a negative slope (Table 24.1, Fig. 24.3C), whereas for Mesotheriidae and Interatheriidae the regressions were not significant (Table 24.1, Fig. 24.3B). However, when the analysis was performed without Hegetotheriidae the regression resulted as significant with a positive slope (Table 24.1, Fig. 24.3D). This suggests the existence of different relationships between these characters within different clades.

Discussion

As interpreted for all ungulates, hypsodonty is thought to arise as a consequence of various dietary and environmental factors: (1) high silica phytolith abundance in especially coarse grasses, (2) prevalence of grass life forms with areas of exposed soil around them, (3) high levels of soil disturbance or soil mineral mobility, (4) large areas of continuously available accumulations of volcanic ash (and other potential sources of mineral dust) subject to erosion–entrainment–transport–deposition cycles extending over evolutionary timescales. The advantage of hypsodonty is to increase the useful life of the dental battery and allow

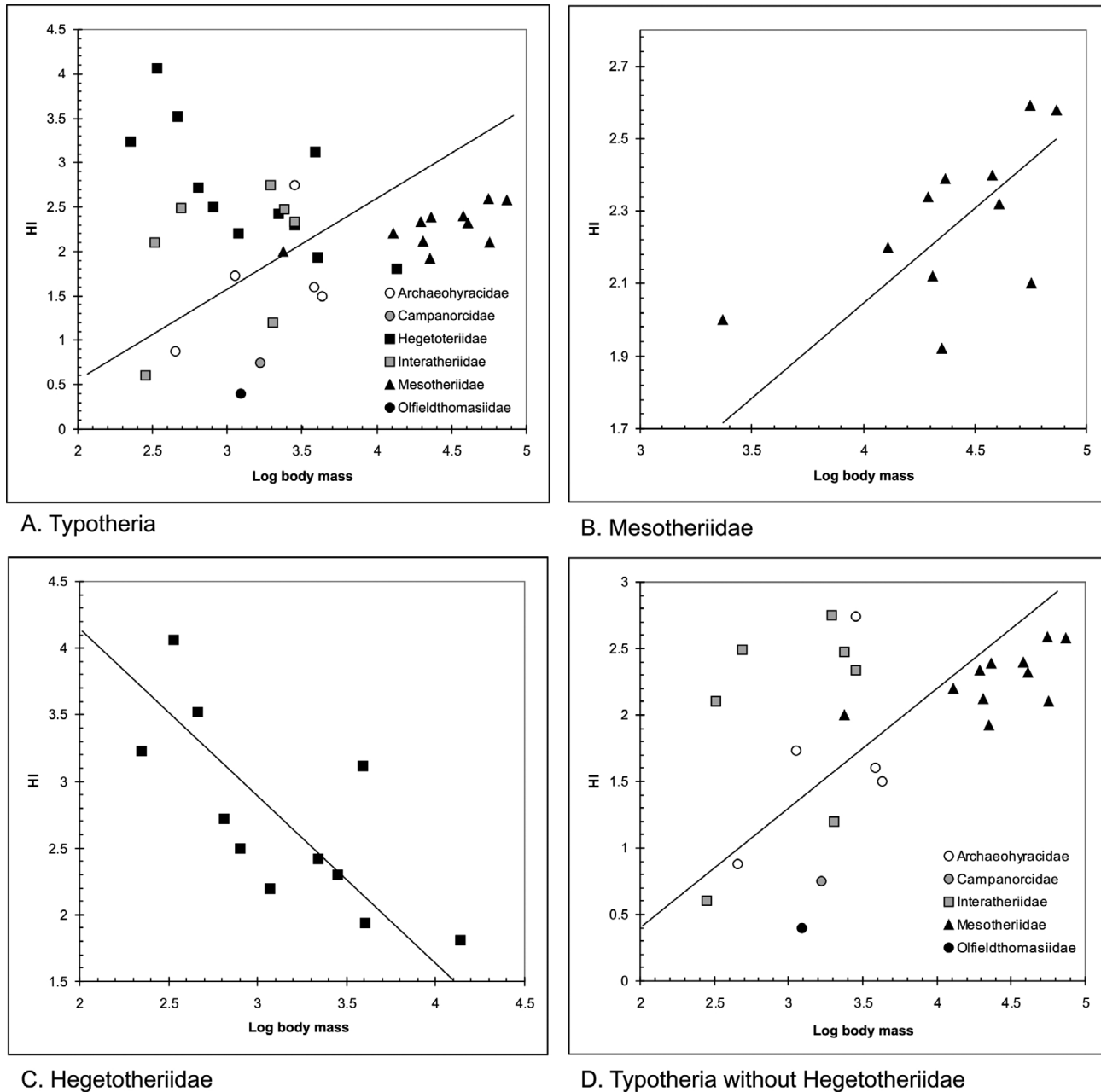


Fig. 24.3. Relationship between hypsodonty index (HI) and body mass (log10 transformed).

more abrasive material to be processed without shortening the functional life of the teeth (Radinsky 1984). McNaughton *et al.* (1985) observed that herbivores that feed close to the ground ingest significant quantities of gritty dust along with their plant food. In extant ungulates there is correlation between hypsodonty and exogenous grit incorporation, when feeding close to the ground in open habitats (Williams and Kay 2001; Mendoza and Palmqvist 2008). Abrasive materials

(whether from phytoliths in grass or from exogenous grit) associated with open areas may have been important selective factors acting on hypsodonty in typotherian notoungulates. At Gran Barranca, the specimens of Typotheria recorded before and near the time of the EOT document increasing hypsodonty (Fig. 24.2A). The initiation of an evolutionary response to increased tooth abrasion seems to be related to local change in vegetation and eolian deposition.

For some hypsodont mammals, body size has been proposed to be correlated with increased hypsodony, a result that would be manifested by a positive allometric scaling to accommodate the metabolic requirements of mammals with larger body size or to permit extend tooth use in mammals with longer lifespans (Simpson 1944; Radinsky 1984). But studies of extant and fossil Holarctic ungulates have rejected these hypotheses (Fortelius 1985; Janis 1988; Solounias *et al.* 1994).

In at least some clades of Typotheria the variation of hypsodony may be reflecting correlated changes due to changes in body size plus a variation due to directional selection, independent of body size. Our observations indicate that at least two evolutionary trends can be identified in Typotheria: (1) one characterized by increasing hypsodony, associated with increasing body size in species with complex occlusal designs (*Mesotherium cristatum*: Figs. 24.1C, 24.3B), and (2) another characterized by increasing hypsodony associated with decreasing body mass in species with simplified occlusal designs (*Paedotherium bonaerense*: Figs. 24.1D, 24.3C). The highest indexes of hypsodony are seen in species with the most simple designs (Hegetotheriidae).

Occlusal designs seem to play an important role in the relationship between hypsodony and body size, and these three factors would form a complex of characters, all being targets selection. In the case of larger species, complex occlusal designs would increase the effectiveness of chewing (Strömberg 2005).

This understanding of selective factors and adaptive response of hypsodony in association with other morphological features, such as body mass and occlusal designs, in Typotheria, can only be tested with a higher-resolution phytolith record at Gran Barranca, or by other plant fossil material allowing a detailed reconstruction of vegetation changes during Eocene to Miocene in southern South America. Whether hypsodony arose coincidentally with or just after the spread of open grass-dominated habitats in South America remains to be tested.

We hope that the understanding of the variation of these features may be useful to test hypothesis regarding the adaptive nature of hypsodony in South American ungulates, and its value as an indicative feature of environmental changes during South American Paleogene.

Appendix 24.1 Chronological distribution, number of specimens (*n*), body mass (in g and log₁₀ transformed), and hypsodonty index (HI) for the species of *Typotheria* studied

Taxa	Family	SALMA ^a	<i>n</i>	Body mass (g)		HI
				Mean	Log ₁₀	Mean
<i>Oldfieldthomasia debilitata</i>	Oldfieldthomasiidae	BAR	3	1 238	3.093	0.40
<i>Punahyrax bondesioi</i>	“Archaeohyracidae”	BAR	2	453	2.656	0.88
<i>Notopithecus adapinus</i>	Interatheriidae	BAR	3	283	2.452	0.60
<i>Typotheriopsis silveyrai</i>	Mesotheriidae	CHA	2	23 244	4.366	1.93
<i>Cochilius volvens</i>	Interatheriidae	COL	2	490	2.691	2.49
<i>Archaeohyrax patagonicus</i>	“Archaeohyracidae”	DES	3	2 817	3.450	2.74
<i>Sallatherium altiplanense</i>	Hegetotheriidae	DES	2	2 817	3.450	2.30
<i>Propachyrucos smithwoodwardii</i>	Hegetotheriidae	DES	1	798	2.902	2.50
<i>Prosotherium garzoni</i>	Hegetotheriidae	DES	2	644	2.809	2.72
<i>Pachyrukhos moyanoi</i>	Hegetotheriidae	DES	3	461	2.664	3.52
<i>Prohegetotherium schiaffinoi</i>	Hegetotheriidae	DES	3	1 178	3.071	2.20
<i>Anatrachytherus soriai</i>	Mesotheriidae	DES	1	25 025	4.398	1.92
<i>Trachytherus spegazzinianus</i>	Mesotheriidae	DES	3	40 752	4.610	2.32
<i>Trachytherus curuzucuatense</i>	Mesotheriidae	DES	1	56 694	4.754	1.85
<i>Plagarthrus clivus</i>	Interatheriidae	DES	3	2 063	3.314	2.75
<i>Archaeophylus patrius</i>	Interatheriidae	DES	2	333	2.522	2.10
<i>Mesotherium cristatum</i>	Mesotheriidae	ENS	3	73 436	4.866	2.02
<i>Microtypotherium choquecotense</i>	Mesotheriidae	FRI	1	12 927	4.112	2.20
<i>Eutypotherium lehmannitschei</i>	Mesotheriidae	FRI	2	19 551	4.291	2.03
<i>Hemihegetotherium achataleptum</i>	Hegetotheriidae	HUA	2	13 681	4.136	1.81
<i>Miocochilius anomopodus</i>	Interatheriidae	LAV	2	2 393	3.379	2.47
<i>Tremacyllus impressus</i>	Hegetotheriidae	MAR	3	224	2.351	3.23
<i>Paedotherium bonaerense</i>	Hegetotheriidae	MAR	3	340	2.531	4.06
<i>Hemihegetotherium sp. nov.</i>	Hegetotheriidae	MON	1	3 909	3.592	3.12
<i>Hemihegetotherium torresi</i>	Hegetotheriidae	MON	2	4 032	3.606	3.61
<i>Plesiotypotherium achirensense</i>	Mesotheriidae	MON	1	20 359	4.309	2.12
<i>Pseudotypotherium hystatum</i>	Mesotheriidae	MON	2	38 014	4.580	2.10
<i>Mesotherium maendrum</i>	Mesotheriidae	MON	2	55 656	4.746	2.00
<i>Pseudhyrax eutrachytheroides</i>	“Archaeohyracidae”	MUS	2	3 825	3.583	1.60
<i>Hegetotherium mirabile</i>	Hegetotheriidae	SAN	2	2 190	3.340	2.42
<i>Eotypotherium chico</i>	Mesotheriidae	SAN	1	2 358	3.373	2.00
<i>Protypotherium australe</i>	Interatheriidae	SAN	4	2 817	3.450	2.34
<i>Archaeotypotherium propheticus</i>	“Archaeohyracidae”	TIN	3	4 285	3.632	1.50
<i>Protarchaeohyra × gracilis</i>	“Archaeohyracidae”	TIN	3	1 125	3.051	1.73
<i>Santiagorothia chiliensis</i>	Interatheriidae	TIN	2	2 030	3.307	1.20
<i>Campanorco inauguralis</i>	Campanorcidae	VAC	1	1 665	3.221	0.75

Note: ^aSALMA abbreviations (ordered temporally): VAC, Vacan; BAR, Barrancan; MUS, Mustersan; TIN, Tinguirirican; DES, Deseadan; COL, Colhuehuapian; SAN, Santacrucian; FRI, Friasian; LAV, Laventan; CHAS, Chasicosan; HUA, Huayquerian; MON, Montehermosan; MAR, Marplatan; ENS, Ensenadan.

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