

Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain

Donald R. Prothero and Paul C. Sereno

Abstract.—Barstovian (medial Miocene) mammalian faunas from the Texas Gulf Coastal Plain contained four apparently sympatric species of rhinoceroses: the common forms *Aphelops megalodus* and *Teleoceras medicornutus*, a dwarf *Teleoceras*, and a dwarf *Peraceras*. Previous work has suggested positive allometry in tooth area with respect to body size in several groups of mammals, i.e., larger mammals have relatively more tooth area. However, dwarfing lineages were shown to have relatively more tooth area for their body size. Our data show no significant allometry in post-canine tooth area of either artiodactyls or ceratomorphs. Similarly, dwarf rhinoceroses and hippopotami show no more tooth area than would be predicted for their size. Limbs are proportionately longer and more robust in larger living ceratomorphs (rhinos and tapirs) than predicted by previous authors. Limb proportions of both dwarf rhinoceroses and dwarf hippopotami are even more robust than in their living relatives.

The high rhinoceros diversity reflects the overall high diversity of Barstovian faunas from the Texas Gulf Coastal Plain. The first appearance of several High Plains mammals in these faunas indicates "ecotone"-like conditions as faunal composition changed. Study of living continental dwarfs shows that there is commonly an ecological separation between browsing forest dwarfs and their larger forebears, which are frequently savannah grazers. This suggests that the dwarf rhinoceroses might have been forest browsers which were sympatric with the larger grazing rhinos of the High Plains during the Barstovian invasion. The continental dwarf model also suggests that insular dwarfism may be explained by the browsing food resources that predominate on islands.

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Introduction

The phenomenon of phyletic size increase in the fossil record is regarded as such a common occurrence as to merit special recognition as an evolutionary generalization—Cope's Rule. Its counterpart, phyletic dwarfism, has received comparably little attention, even though significant size decrease in phyletic lineages appears to be common (Boucot 1976). Insular dwarfing of larger mammals is a very common phenomenon (reviewed by Sondaar 1977) with perhaps "fewer exceptions than any other ecotypic rule" (Van Valen 1973). Continental dwarfing, exemplified by the living pygmy hippopotamus, may occur more often than was previously thought (Marshall and Corruccini 1978; Ford 1980).

Recently Heaney (1978), Case (1979), and Wassersug et al. (1979) have presented models for insular body size trends, and Marshall and Corruccini (1978) and Gould (1975a) have considered aspects of allometry in dwarfing lineages. Gould predicted that in dwarfing lineages tooth area should not decrease as rapidly as

body size. We test this hypothesis and examine allometry in the postcranial elements of several dwarf hippopotami and in heretofore undescribed dwarf rhinoceroses from the Miocene of Texas.

From 1936 until 1964, the Frick Laboratory of the American Museum of Natural History made collections of fossil mammals from the Texas Gulf Coastal Plain (Fig. 1). The Barstovian (medial Miocene) faunas contained four apparently sympatric species of rhinoceros (Prothero and Manning, in prep.). Two were the common Barstovian species, *Teleoceras medicornutus* and *Aphelops megalodus*, and two were dwarfed forms of the genera *Teleoceras* and *Peraceras* (a close relative of *Aphelops*) (Fig. 2). The great size disparity was probably not due to sexual dimorphism, since no other ceratomorphs (rhinos and tapirs), living or fossil, show significant dimorphism in size or, for that matter, in structures that are commonly dimorphic, such as horns. The only significant difference between sexes in the Rhinocerotidae occurs in the shape of the lower tusk, and both

Ma	EPOCH	NALMA	NPZ	HIGH PLAINS	TEXAS	GULF COAST		
10	Medial Miocene	Early Clarendonian	N13	Snake Creek Formation	Goliad Formation	Lapara Creek Fauna		
11								
12		Late Barstovian	N9	Valentine Formation	Upper Fleming Formation	Cold Spring Fauna		
13								
14				N8		Olcott Formation	Burkeville L. F.	Trinity River L. F.
15								
16		Early Barstovian	N7	Olcott Formation	Burkeville L. F.	Point Blank L. F.		
15								
16		Late Hemingfordian		Sheep Creek Formation				
17								

FIGURE 1. Stratigraphy of medial Miocene mammal localities in North America. "NALMA" = North American Land Mammal Age. "NPZ" = Neogene Planktonic Zones. After Tedford et al. (in press).

male- and female-shaped incisors are present in the sample. The sympatry of the four rhinoceroses is suggested in several quarries, such as Texas Memorial Museum Locality 31219, in San Jacinto County, Texas, where remains of all four rhinos are found.

The dwarfs were most closely related to *Peraceras* and *Teleoceras* from the late Hemingfordian (late early Miocene, about 16 Myr BP), such as those known from the Sheep Creek Formation of Nebraska (Skinner et al. 1977). The late Hemingfordian *Peraceras* and *Teleoceras* were approximately the same size as their Barstovian counterparts and much larger than the Texas dwarfs. In addition, the sister taxa of *Teleoceras* and *Peraceras* (Prothero and Manning, in prep.) are all larger than the dwarfs. This supports the hypothesis that the small Texas forms were indeed dwarfs, rather than smaller, more primitive members of their respective genera. The dwarfs are the smallest post-Arikareean rhinoceroses in North America.

The dwarfs occurred in the Point Blank, Trinity River, Burkeville, and Cold Spring Local Faunas (Fig. 1), which range in age from early to late Barstovian (about 13–15 Myr BP) (Tedford et al., in press). By the Clarendonian (about 10 Myr BP), the dwarf rhinoceroses disappeared from the record, although a large species of *Teleoceras* is found in the Clarendonian Lapara Creek Fauna. The descriptions and systematics of the dwarf rhinos are presented elsewhere (Prothero and Manning, in prep.). In



FIGURE 2. Comparison of the skulls of the dwarf *Peraceras* (TMM 31219-228, top) and *Peraceras profeetus* (F:AM 108338, bottom). Scale bar is 20 cm long in 2 cm increments.

a preliminary notice (Prothero and Sereno 1980), we mistakenly reported the dwarf *Peraceras* to be a dwarf *Aphelops*, the closest sister-group of *Peraceras*. Better preserved specimens from the collections of the Texas Memorial Museum have since made it clear to us that the dwarf aceratherine rhinoceros is *Peraceras*, not *Aphelops*.

The simultaneous dwarfing of two closely related ungulates in a continental environment is unusual, to say the least. Even more extraordinary is the apparent sympatry of the dwarf rhinoceroses with their larger relatives. Ecologists have long recognized islands as unique opportunities to study ecological variables too complex to unravel in continental environments. We believe, on the other hand, that living and fossil continental dwarfs may provide key insights toward an explanation of the widespread examples of extinct large-mammal insular dwarfs.

Materials and Methods

Biometrical errors and misinterpretation of the different types of scaling (interspecific, intraspecific, and ontogenetic) are commonplace in the literature on allometry (see Gould 1966, 1975b). Another pitfall of allometric studies is intraspecific variability. Allometric plots using small sample sizes and few or widespread data points are especially susceptible. Gould (1975a), studying scaling in tooth area of suine artiodactyls, remarked that "the slope is determined pri-

TABLE 1. Rhino and hippo allometry data: sample sizes, means and coefficients of variation. ^a Only one humerus is so far known to be associated with *Peraceras profectus*. No skull is available for the dwarf *Teleoceras*. ^b Limb dimensions after Hooijer 1946. ^c Skull length after Boekschoten and Sondaar 1972.

	Dwarf <i>Peraceras</i>	<i>Peraceras</i> <i>profectus</i> ^a	Dwarf <i>Teleoceras</i> ^a	<i>Teleoceras</i> <i>medicor-</i> <i>nutus</i>	<i>Ceratotherium</i> <i>simum</i>	<i>Diceros</i> <i>bicornis</i>	<i>Rhinoceros</i> <i>unicornis</i>	<i>Rhinoceros</i> <i>sondaicus</i> ^b	<i>Dicerorhinus</i> <i>sumatrensis</i>
1. Body weight (kg)	?	?	?	?	2300-3600	1000-1800	2000-4000	1360±	800-1000
2. Log avg. body weight	?	?	?	?	3.45	3.15	3.45	3.13	2.95
3. Number of skulls	4	6	0	13	6	6	7	4	3
4. Log avg. skull length	2.56	2.63	—	2.69	2.80	2.73	2.73	2.66	2.62
5. (coeff. variation)	1.6	4.7	—	6.6	2.7	4.0	0	2.0	2.9
6. Log avg. tooth area	4.28	4.55	—	—	4.64	4.62	4.64	4.50	4.44
7. (coeff. variation)	4.2	7.2	—	7.5	6.1	5.5	3.4	11.7	0.3
8. Number of humeri	1	1	3	14	8	6	6	4	6
9. Log avg. hum. length	2.41	2.42	2.43	2.55	2.59	2.57	2.62	2.59	2.53
10. (coeff. variation)	—	—	4.0	6.3	2.3	4.3	4.7	3.6	3.6
11. Log avg. hum. diam.	1.61	1.70	1.67	1.75	1.93	1.82	1.86	1.80	1.69
12. (coeff. variation)	—	—	4.3	8.8	5.9	10.6	4.2	5.4	8.2
13. Log avg. dist. area	3.75	3.88	3.87	4.08	4.29	4.15	4.26	4.24	4.05
14. Number of femora	1	0	1	7	8	6	6	4	6
15. Log avg. fem. length	2.52	—	2.60	2.66	2.72	2.68	2.73	2.68	2.63
16. (coeff. variation)	—	—	—	5.5	3.5	4.0	5.1	5.0	3.5
17. Log avg. fem. diam.	1.77	—	1.81	1.83	1.91	1.83	1.90	1.86	1.79
18. (coeff. variation)	—	—	—	7.5	4.9	10.4	6.3	3.6	9.8
19. Log avg. dist. area	4.06	—	4.11	4.24	4.42	4.29	4.43	4.42	4.24
20. Number of tibiae	2	0	3	18	8	5	6	4	6
21. Log avg. tib. length	2.40	—	2.38	2.46	2.59	2.56	2.59	2.52	2.49
22. (coeff. variation)	2.8	—	3.4	8.0	3.6	5.5	4.9	1.7	1.6
23. Log avg. tib. diam.	1.60	—	1.63	1.72	1.79	1.73	1.81	1.70	1.68
24. (coeff. variation)	1.3	—	9.3	11.5	6.5	5.5	0.5	6.6	6.3
25. Log avg. dist. area	3.47	—	3.57	3.74	3.91	3.80	3.93	3.84	3.76

marily by the relationship between a cluster of points for smaller suines (pigs, peccaries, and pygmy hippos) and one 'outlying' large animal, *Hippopotamus amphibius*, but then proceeded to measure only one upper tooth row of one skull of *H. amphibius* as an estimate of tooth area. We found hippopotami to be highly variable (see Table 1). For example, in our analysis of allometry in postcranial skeletons, we have yet to find a specimen among nine measured which approaches the size of the single hippo humerus used by McMahon (1975) in his study of ungulate limb proportions. For these reasons, we have taken as large a sample as circumstances allowed. Unfortunately, few museums store more than a few skeletons of hippos or rhinos, particularly those that are extremely rare. Fossil material, especially of the dwarf forms, is also limited.

We measured the skull length in the suine artiodactyls from the tip of the premaxillaries to the occipital condyles, as did Gould (1975a). For the ceratomorphs, however, we measured from the front of the tooth row to the occipital condyles, since many rhinos have small, fragile,

edentulous premaxillaries, often missing in fossils and insignificant when compared to skull length. Maximum transverse and longitudinal dimensions of the bases of the premolars and molars in both upper and lower tooth rows were measured to obtain an approximation of total tooth area. Of course, basal tooth dimensions do not represent the actual surface used to prepare food, as Gould (1975a) recognized. In rhinos, however, basal dimensions are a reasonable approximation of tooth area, since the premolars are fully molarized and quadrate in shape. This area estimate, besides being perhaps the most practical way to measure numerous specimens, also permits direct comparison of our results with those of Gould (1975a).

Body weight data are taken from Walker (1964), von la Chevallerie (1970), Groves (1972), and Groves and Kurt (1972). When the range is very large, it is shown in the plots (Figs. 3c, 4a), and the median for a species is used as the estimate for calculation of the slope.

Maximum limb bone lengths were measured between articular surfaces, ignoring processes such as the deltopectoral crest, which frequently

TABLE 1. Continued.

<i>Tapirus indicus</i>	<i>Tapirus terrestris</i>	<i>Hippopotamus amphibius</i>	<i>Hexaprotodon (=Choeropsis) liberiensis</i>	<i>Hippopotamus lemerlei</i>	<i>Phanourios minor (=H. minutus)</i>	<i>Tayassu pecari</i>	<i>Tayassu tajacu</i>	<i>Catagonus wagneri</i>	<i>Babyrousa babirussa</i>	<i>Hylochoerus meinertzhageni</i>	<i>Phacochoerus aethiopicus</i>	<i>Sus scrofa</i>	<i>Potamochoerus porcus</i>
300	250	1000-2500	160-240	?	?	30	16	?	90	149	60-90	75-200	55-80
2.48	2.40	3.25	1.95	?	?	1.48	1.20	?	1.95	2.17	1.87	2.14	1.88
4	4	12	5	3	3	3	3	2	3	3	3	3	3
2.51	2.45	2.81	2.53	2.65	2.43 ^c	2.37	2.32	2.41	2.45	2.54	2.49	2.53	2.40
2.5	8.2	2.5	4.9	7.9	—								
4.14	4.00	4.53	4.01	4.16	3.87	3.60	3.40	3.66	3.48	3.93	3.58	4.01	3.72
7.5	10.9	6.3	7.8	11.5	3.4								
6	6	9	5	2	2	6	6	0	4	6	4	4	4
2.38	2.34	2.56	2.32	2.41	2.30	2.16	2.07		2.23	2.34	2.27	2.25	2.26
5.0	5.5	12.8	0	2.7	5.6								
1.51	1.40	1.75	1.48	1.57	1.43	1.12	1.09		1.28	1.46	1.33	1.30	1.34
6.1	12.1	10.6	6.7	2.7	11.2								
3.70	3.54												
6	6	8	5	2	2	6	6	0	4	6	4	4	4
2.50	2.47	2.66	2.43	2.49	2.49	2.23	2.16		2.31	2.41	2.32	2.31	2.32
5.1	7.5	14.8	4.0	0	7.3								
1.54	1.50	1.80	1.53	1.61	1.47	1.15	1.12		1.29	1.45	1.32	1.31	1.33
5.8	16.0	9.5	5.8	0	6.8								
3.91	3.74												
6	6	10	5	2	3	6	6	0	4	6	4	4	4
2.41	2.38	2.53	2.31	2.32	2.29	2.19	2.13		2.27	2.32	2.29	2.27	2.26
5.0	6.7	16.3	6.8	1.4	27.1								
1.43	1.37	1.75	1.48	1.54	1.40	1.19	1.12		1.25	1.42	1.34	1.31	1.29
7.5	12.7	17.7	3.3	0	4.0								
3.34	3.20												

projects beyond the head of the humerus in these animals. Prominent but variable bony crests in the sagittal plane, such as the deltopectoral crest of the humerus and the cnemial crest of the tibia, made transverse width, rather than anteroposterior width, a preferable measure of limb diameter. Measurements were taken at midshaft for the femur and tibia and beyond the distal end of the deltopectoral crest for the humerus.

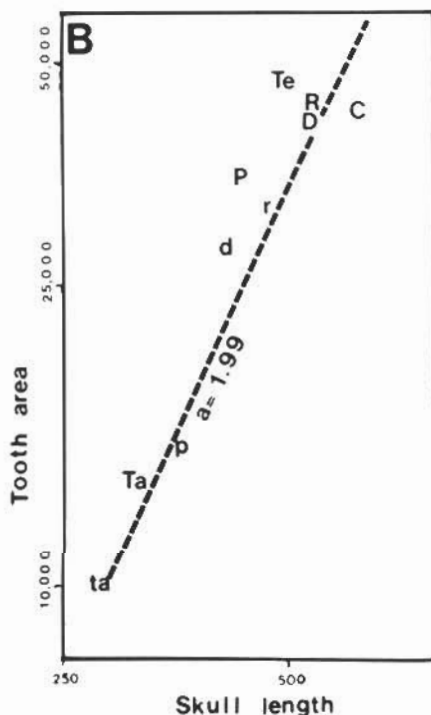
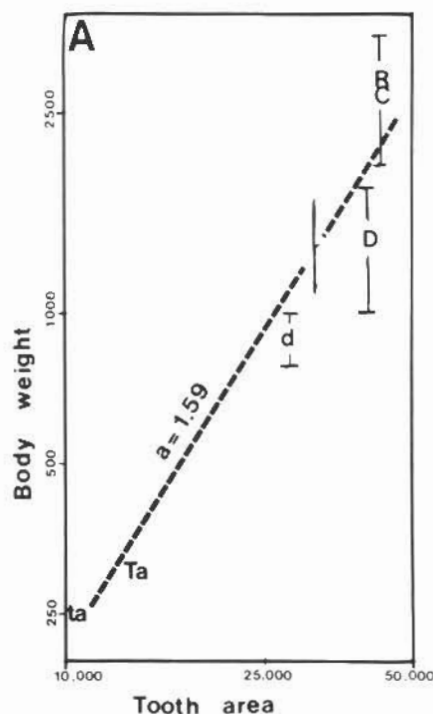
The sample size, mean, and coefficients of variation for each species are listed in Table 1. Means for each species are used in all plots to avoid mixing interspecific and intraspecific variability. These are converted to common logarithms and plotted on log-log scales, allowing calculation of a linear slope for the logarithmic allometric coefficient (Gould 1966). Slopes were calculated by the least squares and reduced major axis methods (Kuhry and Marcus 1977). In nearly all cases, the correlation coefficients (Table 2) were very high (with two exceptions, $r = 0.96$ or higher) and thus the two estimates of slope were very similar.

Fossil specimens are from the Frick Collec-

tion of the American Museum of Natural History (abbreviated F:AM) and the Texas Memorial Museum (abbreviated TMM). Recent specimens were measured in the Department of Mammalogy, American Museum of Natural History, at the Field Museum of Natural History, and at the Museum of Comparative Zoology, Harvard University.

Scaling of Tooth Area

Much of the literature on fossil mammals is devoted to minutiae of form and function in the dental apparatus. Teeth are usually the most diagnostic and best preserved elements of the mammalian skeleton. They also provide paleontologists with an unequalled source of raw material for speculation about adaptation. The primary concern in an assessment of adaptive design is the differentiation of those aspects of form that are due to functional equivalence at differing sizes from those that represent significant adaptations of form or function independent of size. This is particularly important in studies of mammalian dentitions, where primitive forms, often of smaller body size, make the



FIGURES 3-4. Continued.

dental areal requirements of their larger descendants appear to be special adaptations. Until recently (Gould 1975a; Creighton 1980), no interspecific "mouse-to-elephant" data existed on allometry in mammalian teeth.

In a stimulating paper, Gould (1975a) demonstrated that postcanine tooth area of herbivorous mammals (hystricomorph rodents, suine artiodactyls, cervoid artiodactyls, and primates) increased with positive allometry to body size, presumably in response to metabolic or ecologic demands. But he also found that phyletic dwarfs (dwarf hippopotami) retained a larger postcanine tooth area than predicted by interspecific trends. In other words, during phyletic size decrease, postcanine area decreased relatively slower than did body size.

Gould suggested that if trends toward relatively greater tooth area in dwarfs are confirmed as general, dental proportions might serve as a criterion for recognizing dwarfs in the fossil record. The dwarf rhinoceroses from Texas provide a rare opportunity to test this hypothesis. In the following analysis, we reexamine scaling of tooth area in Pleistocene dwarf hippopotami and determine comparable allometric trends for the undescribed Miocene dwarf rhinoceroses.

To establish trends in the scaling of tooth area of suine artiodactyls more rigorously, we measured the total tooth area (premolars and molars of both upper and lower tooth rows) of as large a sample of living suine artiodactyls as possible (9 taxa, minimum of 3 complete skulls per taxon) and of every dwarf hippo to which we had access. In an interspecific plot of total tooth area vs. skull length in the living suines (except the pygmy hippo), the slope of 2.41 (Fig. 3a) is greater than Gould's slope of 2.31 (Gould 1975a, Fig. 2) and significantly greater than the isometric slope of 2.0. Although the data for the suines is strongly influenced by one conspicuous 'outlier' (*Hippopotamus amphibius*), our measurements support Gould's hypothesis of positive allometry of tooth area with respect to skull length for suine artiodactyls.

But just how well does skull length approximate body weight? Gould (1975a, p. 313) used skull length as a surrogate measure for body weight because of the inadequacy of published weight data and because skull length was tied directly to the specimens on which he measured

tooth area. He abandoned skull length only when it "had demonstrable allometric relationships with body size." He tested for allometry in skull length in suines by comparing skull length to femur length and found an isometric slope of 0.99. However, he never compared skull length directly to available weight data, which has recently been summarized by von la Chevallerie (1970). We plotted the body weight data of Walker (1964) and von la Chevallerie (1970) against our own measurements of skull length for suines and found a slope of 3.92, which is significantly greater than the isometric slope of 3.0 (Fig. 3b). Similarly, a comparison of body weight to skull length in ceratomorphs (Fig. 3c) showed significant positive allometry ($a = 3.26$). Could Gould's "positive allometry of tooth area" simply be an artifact of the negative allometry of skull length to body weight?

Our results suggest that this is indeed the case. Direct comparison of body weight to tooth area in suines (Fig. 3d) shows no significant allometry of tooth area ($a = 1.52$; isometry = 1.5). In similar plots for ceratomorphs (Fig. 4a), tooth area scales with significant negative allometry ($a = 1.59$; isometry = 1.5). But given the large scatter of ceratomorph body weight data, the slope is a reasonable approximation of isometry. Rather than corroborating Gould's prediction of positive allometry of tooth area with increasing body size, we find no allometry in either case. Larger suines and rhinos have tooth area proportional to their body weight.

What does this imply for scaling in the teeth of dwarfs? Because most of the dwarfs are extinct, we cannot use body weight for comparison with tooth area. Instead, we use skull length (bearing in mind its inherent allometric bias) and look to see if the dwarfs follow the general trends of their group. In dwarf hippos (Fig. 3a), the slope of 1.74 agrees with Gould's (1975a, Fig. 5) slope of 1.75 and shows that dwarf hippos have relatively larger tooth area compared to their suine relatives. The difference, however, is not statistically significant ($t = 3.17$, 2 degrees of freedom).

The dwarf *Peraceras* (Fig. 4b) plots on the negative side of the line for the living ceratomorphs, contrary to the expectation of higher tooth area in dwarfs. However, the dwarf *Peraceras* is not a statistically-significant outlier

($t = 0.27$, 7 d.f.) using the method of Snedecor and Cochran (1967, p. 157). No complete skull is available for the dwarf *Teleoceras*.

In conclusion, relatively larger tooth area in dwarfs, as a general rule, remains to be quantitatively documented. Ford (1980, p. 35) was misled in claiming that Marshall and Corruccini (1978) had shown negative allometry in tooth area vs. body size in dwarfed Pleistocene marsupials. They made no such claim. They only studied allometry *within* dentitions and never compared molar area to body size. Suggestions of relatively larger tooth area in callithricid monkeys (Ford 1980) and in Pleistocene dwarf elephants (Maglio 1972, 1973) remain undocumented by quantitative data. Our analysis has shown that tooth dimensions do not depart significantly from isometry in the dwarfing lineages we examined. Therefore, in groups of animals that do not exhibit positive allometry of tooth area to body size, dwarfs should not be expected to retain relatively greater tooth area than non-dwarfs of comparable size.

Allometry in Limbs

McMahon (1973, 1975) and Alexander and his colleagues (Alexander 1977; Maloij et al. 1979; Alexander et al. 1979) have tried to establish allometric regularities in the limb proportions of mammals. McMahon's (1973) model of elastic similarity predicts an allometric distortion of shape as animals increase in size. Preservation of elastic similarity over size increase, he suggested, requires bone lengths proportional to $(\text{body mass})^{0.25}$ and corresponding bone diameters proportional to $(\text{body mass})^{0.375}$. Bone length would then be proportional to $(\text{bone diameter})^{0.67}$. This model predicts that large bones would be relatively thick and short, since for isometric scaling, length and width scale as $(\text{body mass})^{0.33}$. McMahon (1975) found support for his model in the limb bone proportions of bovids but was less successful with other groups of ungulates. Cervids plotted consistently above predicted slopes, while suids and perissodactyls fell well below. However, McMahon measured more than one individual in several common species and thus mixed intraspecific and interspecific scaling in his plots. In considering a much wider range of mammals (from seven taxonomic orders and five orders of magnitude

in size), Alexander and others (1979) showed that limb bone lengths were proportional to (body mass)^{0.35} and that limb diameters were proportional to (body mass)^{0.36}. The Bovidae proved to be atypical among mammals, with elongate limbs whose length scaled at a significantly lower exponent of body mass ($a = 0.26$).

We calculated limb proportions in the living Ceratomorpha, which range in size from about 250 kg (*Tapirus terrestris*) to 3600 kg (*Ceratotherium simum*), more than an order of magnitude. In all plots of limb length vs. diameter (Table 2, Fig. 5a–5c), our slopes ($a = 0.47$ – 0.61) were consistently below McMahon's (1975) prediction of $a = 0.67$ and closer to his slopes for the Suidae. McMahon's slopes for the Suidae are questionable since they are based on three species and a total of five specimens with little range in body weight. If he had correctly averaged the measurements within species, his plot would consist of three points.

In plots of limb diameter vs. body size (Table 2, Fig. 6a–6c), our slopes of 0.39–0.45 are significantly greater than those predicted by Alexander et al. ($a = 0.36$) and McMahon ($a = 0.375$). Limb lengths scaled with coefficients ranging from 0.20–0.25, significantly less than the coefficients of 0.35 and 0.26 predicted by Alexander et al. and McMahon respectively. Scaling in the limbs of ceratomorphs entails sizeable increases in diameter and moderate decreases in length, relative to body size.

We suspect that the difference between predicted and observed slopes is due, in part, to the lack of large, graviportal ungulates in the sample of Alexander et al. (1979). They included only three ungulates larger than 300 kg: an African buffalo, a dromedary camel, and an African elephant. The elephant occasionally plotted far off the line drawn from the smaller animals. Perhaps if hippos and rhinos were added to their sample, a noticeable deviation from their slope in larger mammals would be apparent.

We compared the limbs of the dwarf rhinos to those of both their ancestors and the living ceratomorphs. In plots of limb length vs. limb diameter, the limbs of the dwarf rhinoceroses show a marked trend toward robustness (Fig. 5). The dwarf limb bones consistently fall on the robust side of the line for living cerato-

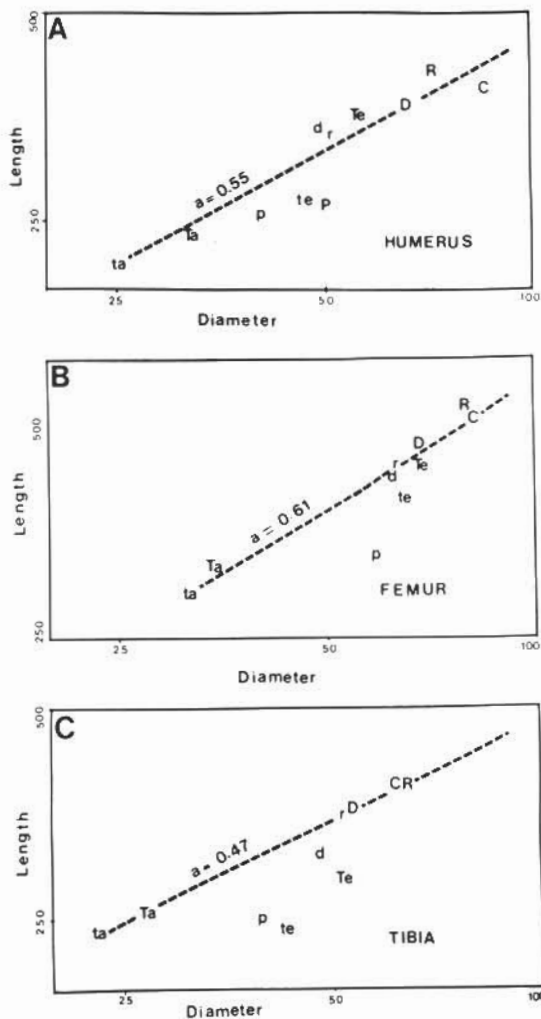


FIGURE 5. Comparison of limb lengths and diameters in ceratomorphs. Abbreviations as in Fig. 3.

morphs. Some crushing of the bones is apparent and may have affected our measure of shaft diameter. To test for this, we measured the transverse and anteroposterior diameters of the distal end of each bone since the total area of the distal end should be preserved, even after crushing. Using distal area as an estimate of fossil limb diameter, we find that scaling in the majority of the dwarf rhino limbs is now consistent with the allometric trends of the living ceratomorphs (Fig. 7). The apparent robustness of most of the dwarf rhinoceros limbs, calculated from shaft diameter, seems to be an artifact of postmortem crushing. The dwarf *Peraceras* femur (Fig. 7b;

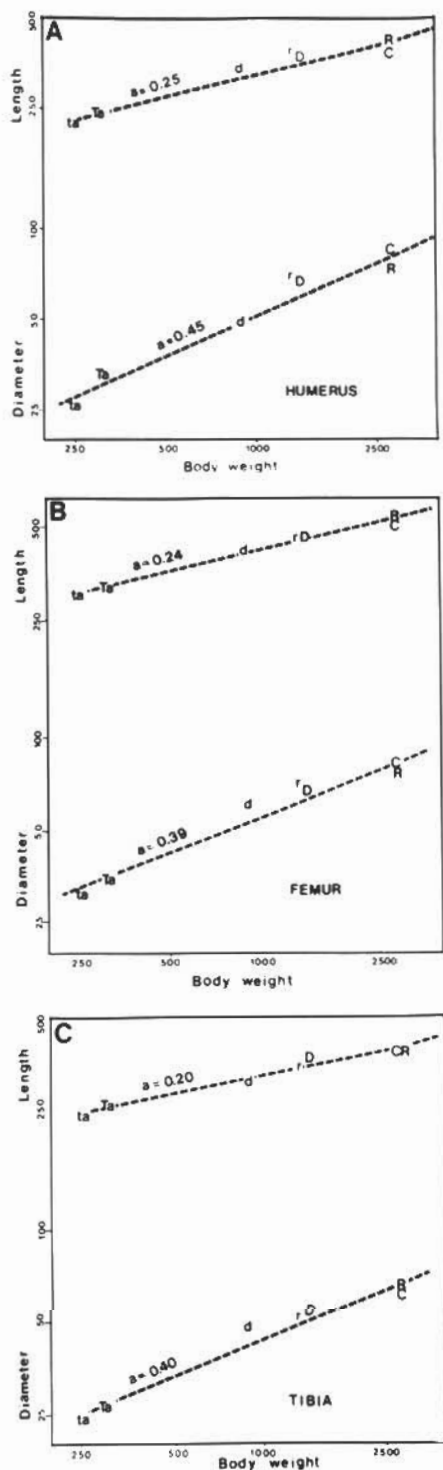


FIGURE 6. Comparison of limb dimensions with body weight in ceratomorphs. Abbreviations as in Fig. 3.

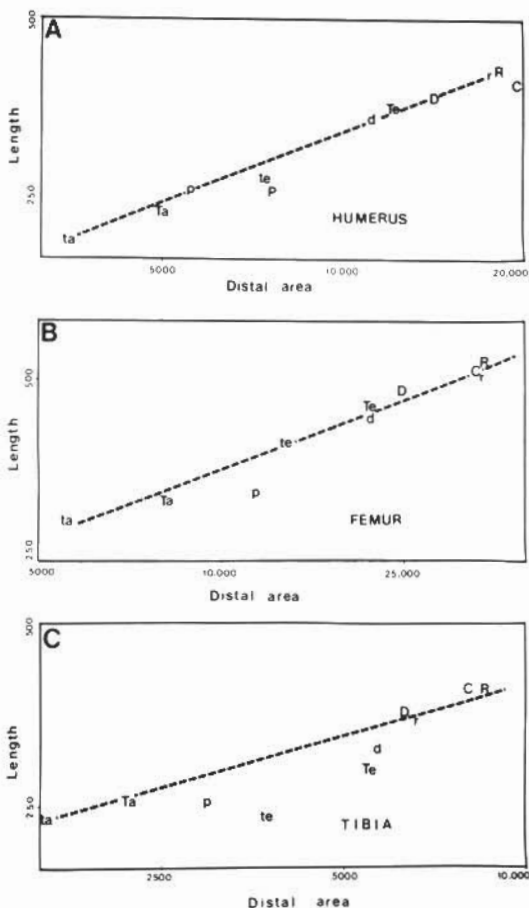


FIGURE 7. Comparison of limb lengths and distal areas in ceratomorphs. Abbreviations as in Fig. 3.

$t = 2.6$, 5 d.f.) and the dwarf *Teleoceras* tibia (Fig. 7c; $t = 3.5$, 5 d.f.), however, are significantly more robust than would be predicted from scaling in living ceratomorphs.

The limbs of dwarf hippopotami, on the other hand, are consistently more robust (Table 2, $a = 0.75$ – 0.84) than would be predicted from scaling in living suine artiodactyls ($a = 0.58$ – 0.68). The sketchy data on scaling in the limb proportions of living and fossil dwarfs suggest a general trend toward increased robustness in the proportions of dwarf limbs.

Paleoecology

Early Miocene faunas from the Gulf Coast of Texas and Florida were characterized by a high degree of endemism. These unusual faunas, labeled the Miocene Gulf Coast Chronofauna

TABLE 2. Statistics of plots in Figs. 3-7.

Fig.	Group	x axis	y axis	N	r	Least squares	Y intercept	Reduced major axis	Isometry	t (* if significant) $\alpha = 0.05$ n - 2 d.f.
3a.	Hippopotami	Log skull length	Log tooth area	4	0.988	1.71	-0.3	1.74	2	0.1
	Suines	Log skull length	Log tooth area	9	0.926	2.24	-1.8	2.41	2	12.8*
3b.	Suines	Log skull length	Log body weight	8	0.979	3.92	-7.8	4.00	3	35.7*
3c.	Ceratormorphs	Log skull length	Log body weight	7	0.970	3.26	-5.6	3.36	3	16.2*
3d.	Suines	Log tooth area	Log body weight	8	0.926	1.52	-3.7	1.64	1.5	0.9
4a.	Ceratormorphs	Log tooth area	Log body weight	7	0.969	1.59	-4.1	1.64	1.5	9.2*
4b.	Ceratormorphs	Log skull length	Log tooth area	7	0.976	1.99	-0.8	2.04	—	—
5a.	Ceratormorphs	Log humerus diameter	Log humerus length	7	0.968	0.55	1.6	0.57	0.67	19*
5b.	Ceratormorphs	Log femur diameter	Log femur length	7	0.994	0.61	1.6	0.61	0.67	19*
5c.	Ceratormorphs	Log tibia diameter	Log tibia length	7	0.980	0.47	1.7	0.48	0.67	47*
6a.	Ceratormorphs	Log body weight	Log humerus diameter	7	0.981	0.45	0.4	0.46	0.36	18*
	Ceratormorphs	Log body weight	Log humerus length	7	0.966	0.25	1.8	0.26	0.35	25*
6b.	Ceratormorphs	Log body weight	Log femur diameter	7	0.977	0.39	0.6	0.40	0.36	4*
	Ceratormorphs	Log body weight	Log femur length	7	0.990	0.24	1.9	0.25	0.35	40*
6c.	Ceratormorphs	Log body weight	Log tibia diameter	7	0.982	0.40	0.4	0.41	0.36	10*
	Ceratormorphs	Log body weight	Log tibia length	7	0.989	0.20	1.9	0.20	0.35	91*
7a.	Ceratormorphs	Log humerus distal area	Log humerus length	7	0.992	0.37	1.0	0.38		
7b.	Ceratormorphs	Log femur distal area	Log femur length	7	0.982	0.37	1.0	0.38		
7c.	Ceratormorphs	Log tibia distal area	Log tibia length	7	0.958	0.28	1.5	0.29		
	Hippopotami	Log humerus diameter	Log humerus length	4	0.997	0.84	1.1	0.84	0.54	95*
	Hippopotami	Log femur diameter	Log femur length	4	0.998	0.82	1.2	0.83	0.58	81*
	Hippopotami	Log tibia diameter	Log tibia length	4	0.960	0.72	1.3	0.75	0.41	27*

(Webb 1977; Tedford et al., in press), lived in a nearshore forested environment that surrounded brackish lagoons and estuaries (Stenzel et al. 1944). The Gulf Coast faunas contemporaneous with the Texas dwarf rhinoceroses

showed an unusually high diversity of forms. This was apparently due to mixing of the endemic Miocene Gulf Coast Chronofauna with a number of High Plains immigrants (Webb 1977; Tedford et al., in press). The Trinity Riv-

er Local Fauna (Fig. 1), for example, contained five species of horses: the first known *Cormohipparion* (then an endemic), the High Plains *Hypohippus*, *Desmatippus*, *Merychippus*, and an undescribed pliohippine (Skinner and Macfadden 1977; Tedford et al., in press). The artiodactyl fauna was dominated by High Plains immigrants but also contained several endemics: the bizarre protoceratid *Paratoceras wardi* (Patton and Taylor 1973), the endemic syntheoceratid *Prosynthetoceras trinitiensis* (Patton and Taylor 1971), and two undescribed endemic camels (B. Taylor, pers. comm.). The endemic floridatragulids and *Prosynthetoceras francisi* were not present in the Trinity River Local Fauna but occurred later in the Cold Spring Fauna. The remarkable feature of these faunas was the scarcity of such common High Plains forms as oreodonts and chalicotheres.

Tedford (pers. comm.) suggests that the mixing of the chronofaunas represents "ecotone" conditions—a period of high diversity due to overlapping of the geographic ranges of the members of two ecological communities. The paleoecological setting suggests that the Texas dwarf rhinoceroses might have been members of the Miocene Gulf Coast Chronofauna. Later the dwarfs became sympatric with their larger relatives after the immigration of High Plains forms. However, the presence of a dwarf *Peraceras* (Prothero and Manning, in prep.) in the Barstovian faunas of New Mexico may cast doubt on this scenario. Except for the rhinoceroses, the New Mexico faunas are more similar to the High Plains and Great Basin faunas than they are to the Gulf Coast faunas (Tedford, pers. comm.). The Santa Fe area had a mild climate and was low in elevation in the Barstovian (Axelrod and Bailey 1976) although there is no direct evidence to indicate whether it was as forested as the coastal plain. Further work on the Santa Fe faunas is needed to resolve this problem.

Most documented cases of phyletic dwarfism in large mammalian herbivores come from Pleistocene deposits on widely scattered islands (for a review, see Sondaar 1977). The exceptional regularity observed in insular body size trends for different animals is poorly understood and only quite recently documented adequately (Foster 1963, 1964; Carlquist 1974; Sondaar

1977; Case 1978). Elephants, hippos, deer, bats, and an assortment of small carnivores show a decrease in body size, almost without exception. On the other hand, rodents, bears, and insectivores increase in body size.

The causes of insular dwarfism have been widely discussed (see Van Valen 1973; Heaney 1978; Marshall and Corruccini 1978; Ford 1980), and Case (1978) has recently proposed a model that predicts body size, given certain ecological variables. Perhaps the most spectacular reduction of body size has occurred in large, insular herbivores—notably elephants, hippos, and deer. Except for the Florida key deer, all of these are now extinct. The paucity of extant examples of large mammal insular dwarfs has only heightened speculation concerning their origin and evolution but, surprisingly, has not generated significant study of living continental dwarfs.

Within many animal groups there is a strong correlation between adult body size and the quality of food that is eaten (Bell 1971; Jarman 1974; Janis 1976; Case 1979). In herbivores, species of larger body size nearly always eat food of lower caloric value. Dietary preferences among African antelopes of various body sizes have been studied in detail (Gwynne and Bell 1968; Bell 1969; Stewart and Stewart 1970; Field 1972). Antelopes of large body size, such as the wildebeest and topi, consume coarse, low-nutrient grass with a high fiber/protein ratio, whereas medium- to small-sized gazelles, such as Grant's and Thompson's gazelles, supplement their diet with leaves and fruit that are much richer in carbohydrates and proteins (Bell 1969). In general, grazing ungulates that consume large quantities of grass attain larger body sizes than browsing ungulates which feed selectively on the leaves and fruit of dicotyledonous plants. These size-related dietary preferences are observed in many other animal groups. Primates of large body size are usually folivores, whereas their smaller relatives are often frugivores or insectivores (Napier and Napier 1967). Capybaras, beavers, and porcupines, the largest living rodents, consume a much higher proportion of fiber in their diet than do smaller rodents (Walker 1964).

The spatial distribution of food quality in natural environments has a profound influence on

body size. It is often noted that poor quality foods are relatively abundant, while foods of higher caloric content are more dispersed. Jarman (1974, p. 220) remarked that "there is a frequent major distinction between grasses and browse plants in a community in their forms of dispersion. Grasses frequently occur in a continuous type of dispersion, in which the next nearest plant to a grass is highly likely to be another grass. . . . By contrast browse plants tend to more discrete dispersion, in which their nearest neighbor is much less likely to be another browse plant."

Naturally, the feeding strategy of a given herbivore will reflect the availability and dispersion of palatable food items. Jarman (1974) describes generalized feeding strategies among African antelopes: species which feed very selectively on particular plant parts of various plant species are either browsers, consuming flowers, twig tips, fruits, and seed pods, or grazers that eat seeds and newly-emerged foliage. This highly selective feeding strategy is practiced predominantly by small-bodied antelope whose food items are typically of high nutritive value. Many antelopes of moderate body size utilize a diverse diet of grasses and browse that varies seasonally. The largest antelopes feed unselectively on a wide variety of grasses that are generally low in nutritive value. Jarman (1974, pp. 226-7) writes: "In simplified terms, those species which feed very selectively on discrete food items tend to be small, while the wide-ranging, relatively unselective feeders tend to be large." Thus, the abundance and distribution of high-quality food appears to limit the body size of animals that eat these foods.

The physical nature of small body size is also advantageous for the utilization of high-quality food. Small-bodied animals are physically better suited for selecting individual plant parts. Jarman (1974, p. 227) remarks: "A typical grass plant, for instance, becomes a heterogeneous assemblage of parts which can be differentiated by the mouth of a small antelope, but remains as one food item which can be only bitten or rejected totally by a large antelope." Other physiological, reproductive, behavioral, and ecologic constraints govern ultimate body size (see Stahl 1962; Rosenzweig 1968; Schoener 1969; Jarman 1974). For example, the consis-

tently higher metabolic rate of smaller-bodied animals may necessitate a more nutritious diet.

The correlation between body size and dietary selectivity observed in many animal groups (Rensberger 1973; Jarman 1974; Case 1979) is generalized in Levin's (1968) concept of environmental "grain." He suggests that as body size decreases, the heterogeneity of the environment increases (i.e., the environment becomes coarse-grained). Possibly under these circumstances small-bodied animals have a greater opportunity to develop dietary specialization that can effectively utilize the patchy distribution of higher-quality foods.

Island environments are ecologically diverse and often more productive because of a more moderate climate (Carlquist 1974, pp. 355-365). Large expanses of low-quality food are rare. Nevertheless, the quality of food resources available to island inhabitants rarely enters into discussions of insular dwarfing. One common explanation for insular dwarfing calls upon the need for adequate population levels under conditions of severely limited space and resources (Kurtén 1965, 1968; Hooijer 1967; Sondaar and Boekschoten 1967). As observed by Heaney (1978), and Marshall and Corruccini (1978), this argument is group-selectionist—large herbivores get small for the good of the island population. Wassersug et al. (1979) used a computer model that generated phylogenetic trees by a stochastic branching process. In the evolving lineages, body size exhibited stochastic change, but a predetermined "carrying capacity" regulated the total size, or "biomass," of a lineage. As one would expect, a few large-bodied lineages would be more susceptible to extinction than several small-bodied lineages under these simplified conditions.

But what if smaller species, by virtue of their habitat preference, are better adapted to an insular environment? Are larger and smaller versions of the same animal ecologically similar, as the argument above assumes? Living continental dwarfs—animals that differ from their larger relatives mainly in body size—provide the best test of these hypotheses. *Syncerus caffer caffer*, the savannah subspecies of the African buffalo, is primarily a grazer and weighs up to 900 kg, while the forest subspecies (*Syncerus caffer nanus*) is a browser and rarely exceeds 330 kg

(Walker 1964; Case 1979). *Hexaprotodon* (formerly *Choeropsis*) *liberiensis* (Coryndon 1977), the pygmy hippo, inhabits swampy forests and river margins, foraging on land for vegetables, roots and grasses. It weighs less than 300 kg. Its relative, *Hippopotamus amphibius*, weighs about 3000 kg with a diet consisting mostly of grasses. Even in the African elephant *Loxodonta*, where the diet is usually more varied, individuals of the forest, or western race, are often smaller (Walker 1964). Although we have no direct evidence of their diet, the dwarf rhinoceroses (as indicated above) may have inhabited a swampy forest environment, in contrast to the dryer habitat that is usually associated with their larger High Plains relatives. There seems to be a consistent relationship between body size and diet in animals that differ only in body size. The animal of smaller proportions tends toward a browsing diet of higher caloric value.

Corroboration of this tendency can be seen in the lophodont aspects of the molars of *Phanourios*, the extinct dwarf hippo of Cyprus (Sondaar 1977, Fig. 6). This lophodonty, not seen to this extent in other members of the Hippopotamidae, increases with age and wear. This led Sondaar (1977) to suggest that "the hippo from Cyprus had a mode of life somewhat like a leaf-eating pig" (p. 689). Perhaps adaptation to a more diverse insular environment can arise by evolutionary decrease in size with very little change in shape. Larger litters and shorter generation times (Bonner 1965; Bourliere 1975), rapid maturation and early reproduction (Gould 1977), as well as greater population densities (Kurtén 1968; Wassersug et al. 1979) are often cited as the best strategies for island inhabitants. Perhaps these tendencies are simply size-related correlates of adaptation by large continental herbivores to a smaller-herbivore diet.

As Gould (1971) has pointed out, dwarfing of various sorts has occurred in historical times in many groups of animals (including man) and has often appeared independently in several populations. Many studies of dwarfism in domestic animals and man demonstrate a simple genetic basis for many of these quantum alterations in body size. Proportional dwarfism—miniature versions of the normal form—has been traced to a simple autosomal recessive in cattle and man (Mead et al. 1942; Johnson et al. 1950; McKusick 1955; McKusick et al. 1965;

see Grüneberg, 1963, for proportional dwarfism in mice). Chondrodystrophic ("achondroplastic") dwarfism—identical or reduced body size with disproportionately shortened limbs—has been traced to a simple recessive in rabbits (Brown and Pearce 1945; Crary and Sawin 1952) and sheep (Landauer and Chang 1949) and to a semidominant gene in cattle (Mead et al. 1946) and chickens (Landauer and Dunn 1930). Chondrodystrophy is a disturbance of the epiphyseal cartilage structure which inhibits the longitudinal growth of bones. Occasionally other skeletal disturbances are also present, such as syndactyly, or limb bone fusion (Grüneberg 1963).

An intriguing comparison can be made between the limb proportions of historical chondrodystrophic animals and those of various island dwarfs. In dwarf hippos (Sondaar 1977) and dwarf elephants (Ambrosetti 1968), the limb bones are noticeably shorter and stockier than their normal-shaped counterparts. Ambrosetti (1968) records a drastic shortening of the limbs relative to the body size in the dwarf *Elephas falconeri*, as well as fusion of the radius and ulna and of the tibia and fibula. A definite trend toward relatively shorter and more robust limbs can be seen in dwarf hippos and in a few of the dwarf rhino limbs. Bone diameters have rarely been measured in chondrodystrophic animals but are usually more robust when recorded (Cock 1966; Stephens 1943). Sondaar (1977) observes progressively greater reductions in the distal limb elements (metapodials and phalanges) in insular hippos, elephants, and ruminants. There is a striking resemblance between the limb bone proportions of the chondrodystrophic Storrs-Norway Ancon sheep (Landauer and Chang 1949) and the extinct *Myotragus balearicus* (dwarf bovid from Mallorca) and *Phanourios minor* (dwarf hippo from Cyprus; see Figs. 4 and 5 in Sondaar 1977). The metapodials are extremely short and the phalanges are reduced to stubs.

Perhaps the most remarkable aspect of Pleistocene dwarfism is the brief time interval in which extreme size reduction has occurred. Rapid dwarfing in geologic time may have transpired over a single generation, as in the Ancon sheep, or over a few thousand generations, in small, isolated populations under stringent selective conditions. In most cases of fossil dwarfs,

precise measurement of the rate of size decrease is beyond the resolution of the stratigraphic record. Nevertheless, the simple genetic basis and frequent occurrence of dwarfing in historical times deserves greater attention as a possible mechanism for rapid evolution of size decrease in the past.

Summary and Conclusions

Medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain offer an unusual opportunity to test hypotheses about dwarfing. Contrary to previous statements about relatively larger tooth area in dwarfs, the dwarf rhinos have tooth area proportional to body size. In addition, the dwarf rhinoceroses have more robust limbs than would be predicted from scaling in living ceratomorphs. Both of these trends are seen in dwarf hippopotami as well.

The dwarf rhinoceroses are part of an unusually diverse fauna that may represent an "ecotone" between Gulf Coast endemics and High Plains immigrants. The presence of dwarf rhinos in a more forested coastal setting (compared to their larger, savannah-dwelling relatives) suggests ecological parallels with the pygmy hippo, the dwarf African buffalo, and other continental dwarfs. Both continental and insular dwarfing may be best explained by models that correlate body size trends with the quality of available food resources. Such a correlation is well-documented in living mammals, and is a simpler and more general explanation for both insular and continental dwarfing than models which attempt to explain insular dwarfing only.

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