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LOCOMOTION IN THE EXTINCT NOTOUNGULATE *PROTYPOTHERIUM*

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ABSTRACT

This study characterizes the primary locomotor habit of *Protypotherium*, an interatheriid notoungulate from the early Miocene of Santa Cruz, Argentina. Locomotor habit was assessed both qualitatively (i.e., by noting osteological features correlated with specific locomotor habits in extant mammals) and quantitatively (i.e., by using multivariate analyses to compare limb element lengths, widths, and ratios to those of extant mammals). Because the body mass of *Protypotherium* has been estimated at 5-10 kg, its locomotor habit was evaluated relative to mammals of similar size and known locomotor habit; the comparative dataset included 39 genera of artiodactyls, carnivorans, caviomorph rodents, hyraxes, and lagomorphs. For each genus, 11 limb bone variables and eight indices (ratios) were measured; these were analyzed using principal components analysis and discriminant function analysis. Qualitative and quantitative analyses indicate that *Protypotherium* was most likely a generalized terrestrial mammal tending toward cursoriality. Proximal and distal limb elements of *Protypotherium* mostly resemble those of cursorial mammals in qualitative characters, but intermediate elements are more similar to those of arboreal and semifossorial mammals. Multivariate analyses generally group *Protypotherium* with arboreal and/or semifossorial mammals, but this is likely a phylogenetic effect, possibly attributable to fossorial habits in ancestral interatheriids and/or notoungulates. The postcranial adaptations of *Protypotherium* are intermediate between those of more basal interatheriids and the middle Miocene interatheriid *Miocochilius*. In conjunction with this study, investigations of other interatheriids would permit a detailed analysis of the evolution of locomotor habits within this highly successful clade.

KEY WORDS: locomotion; Mammalia; morphology, functional; Notoungulata; paleoecology; South America

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INTRODUCTION

For most of the Tertiary, South America was geographically and biotically isolated from other major land masses – a period of "splendid isolation" for the mammals of that continent (Simpson 1980). A diversity of endemic clades flourished during this interval and representatives of many of these still characterize South American faunas today (e.g., armadillos, sloths, opossums, marmosets, capybaras, chinchillas; Patterson and Pascual 1968; Flynn and Wyss 1998). Some of these clades left no living representatives, most notably the various groups of hoofed plant eaters that likely filled niches presently occupied in South America by deer, camels, tapirs, peccaries, and other groups (Bond 1986; Bond et al. 1995; Croft 1999). Among these extinct ungulate clades, the notoungulates ('southern ungulates') were the most speciose and morphologically diverse; the group reached its zenith in the Oligo-Miocene and was still represented by several lineages in the Pleistocene (Cifelli 1985; Marshall and Cifelli 1990; Croft 1999).

One of the most successful notoungulate clades in terms of temporal range, geographic range, and abundance was the Interatheriidae (suborder Typotheria). Although this group did not persist past the Pliocene, interatheriids are the longest ranging notoungulate family and are common constituents of most late Eocene to middle Miocene faunas (e.g., Simpson 1967; Tauber 1996; Reguero et al. 2003; Hitz et al. 2006; Croft 2007; see Croft et al. 2004 and Croft and Anaya 2006 for exceptions to this pattern). Like most typotheres, interatheriids were small to medium in size (body mass < 15 kg) and all Miocene species were characterized by ever-growing/rootless (hypselodont) molars. Like nearly all notoungulates, they lacked any form of cranial appendages. They have traditionally been regarded as cursorial (i.e., adapted for running and/or moving efficiently over long distances) and as grazers (i.e., consuming mostly grass and/or other low, open habitat vegetation) (Sinclair 1909; Scott 1932; Bond 1986; Tauber 1996). The idea that interatheriids were grazers has recently been called into question based on new data from enamel microwear (Townsend and Croft 2005, in press). The locomotor adaptations of the group have yet to be rigorously investigated; several studies have included descriptions of interatheriid postcranial elements (e.g., Sinclair 1909; Stirton 1953; Tauber 1996; Shockey and Anaya, in press; Hitz et al., in press), or included interatheriids in investigations of other notoungulates (Elissamburu 2004), but none of these has investigated potential locomotor habits relative to extant mammals.

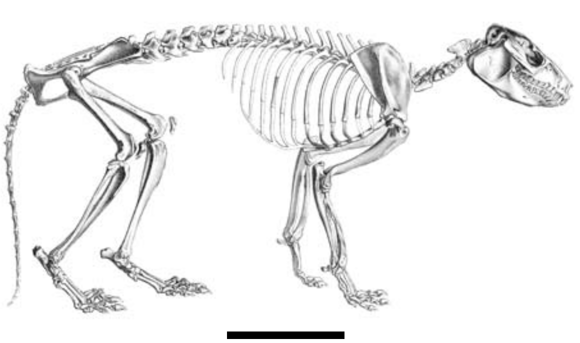

Figure 1. Skeletal reconstruction of the interatheriid notoungulate *Protypotherium* (from Sinclair 1909). Scale bar equals approx. 10 cm.

This study focuses on the postcranial morphology of a common interatheriid, *Protypotherium* (Figure 1). The genus occurs in various Miocene faunas in Argentina (Bordas 1939; Bondesio et al. 1980a, b; Barrio et al. 1989; Kramarz et al. 2005), Chile (Flynn et al. 2002, in press; Wyss et al. 2003), and possibly Venezuela (Linares 2004) but is best known from the coastal deposits of the Santa Cruz Formation of Patagonia, Argentina (approx. 50-51.5° S, Santa Cruz Province). These exceptionally rich deposits are late early Miocene in age (ca. 16-17.5 Ma; Flynn and Swisher 1995) and have produced the largest and best-preserved sample of Tertiary mammals in South America, including many specimens of *Protypotherium* (Simpson 1940; Marshall 1976; Marshall et al. 1986; Tauber 1997). Charles Darwin was among the first to comment on Santa Cruz mammals (based on fossils found by Captain B.J. Sulivan; Brinkman 2003), and important collections of Santa Cruz fossils were later made by Carlos Ameghino, John Bell Hatcher, and Elmer Riggs (Marshall 1976; Simpson 1984). Fossils collected by Hatcher (now curated at Yale Peabody Museum of Natural History) were described by W.B. Scott (e.g., Scott 1903a, 1903b) and J.W. Sinclair (e.g., Sinclair 1909) in the spectacularly illustrated *Reports of the Princeton University Expedition to Patagonia, 1896-1899*. Many of the mammals from the Santa Cruz Formation are represented by skulls and/or partial skeletons (Scott 1932), and many of these are the most completely known representatives of extinct families and/or subfamilies. Owing to these exceptional fossils, Santa Cruz Formation mammals are highly amenable to paleoecological investigations of diet and locomotion, such as those

Table 1. Mensural data (mm) for *Protypotherium* specimens used in this study (all FMNH PM specimens). Specimens 13023, 13026, 13031, and 13071 were also examined, but no measurements were recorded. *Erroneously identified as *Hegetotherium* in collections (DAC pers. obs.)

Specimen Number	FDML	FL	GTH	HDML	HL	HWD	MT3L	OL	TL	UDML
13003	-	-	-	-	63.5	-	-	10.4	-	-
13005	8.1	83.9	8.6	-	-	-	38.2	-	-	-
13029	-	-	-	-	76.2	15.4	-	-	-	2.7
13038	8.4	-	-	6.4	-	22.1	-	13.7	-	3.5
13043	7.9	66.3	-	6.0	-	17.4	-	11.2	-	3.8
13235	-	-	10.4	8.1	91.6	23.9	43.1	17.4	107.3	-
13237	-	-	-	-	91.1	24.7	-	15.7	-	4.6
15333*	12.0	111.3	-	-	-	-	-	-	118.2	-
UC 1329	-	-	-	-	75.7	18.2	-	-	-	-
MEAN	9.1	87.2	9.5	6.8	79.6	20.3	40.7	13.7	112.8	3.7

Table 1 (continued).

Specimen Number	UL	BI	CI	EI	FRI	GI	HRI	IFA	MFI
13003	56.1	88.3	-	-	-	-	-	22.8	-
13005	-	-	-	-	9.7	10.3	-	-	45.5
13029	-	-	-	20.2	-	-	-	-	-
13038	-	-	-	-	-	-	-	-	-
13043	-	-	-	-	11.9	-	-	-	-
13235	-	-	-	26.1	-	-	8.8	-	-
13237	-	-	-	27.1	-	-	-	-	-
15333*	-	-	106.2	-	10.8	-	-	-	-
UC 1329	70.7	93.4	-	24.0	-	-	-	-	-
MEAN	63.4	90.9	106.2	24.4	10.8	10.3	8.8	22.8	45.5

undertaken here (e.g., Tauber 1991; Vizcaíno 1994; Vizcaíno and Fariña 1997; Argot 2003; Vizcaíno et al. 2006).

MATERIALS AND METHODS

Twelve specimens of *Protypotherium* preserving postcranial bones were examined at The Field Museum, Chicago (FMNH) (Table 1). Due to the lack of a complete *Protypotherium* skeleton in the collections, measurements from 10 specimens were combined (averaged) to provide a complete dataset for the multivariate analyses described below. Only one of these specimens had been identified to species (FMNH PM 13235, *P. australe*), but no differences in postcranial morphology have been described among *Protypotherium* species that would be expected to affect these analyses. Functional indices were calculated before averaging and were only recorded for specimens in which all necessary variables could be measured (i.e., indices were not calculated from mean values).

The body mass of *Protypotherium* has been estimated at 5-10 kg based on limb bone scaling relationships (Elissamburu 2004; Anderson and Croft 2006; Anderson 2007). Owing to the lack of extant notoungulates, *Protypotherium* was compared to a variety of mammals of similar size from FMNH and Cleveland Museum of Natural History (CMNH) zoology collections including: artiodactyls (10 genera), carnivorans (11 genera), caviomorph rodents (12 genera), hyraxes (3 genera), and lagomorphs (3 genera) (Appendix). One to three adults of each genus were measured, depending on the

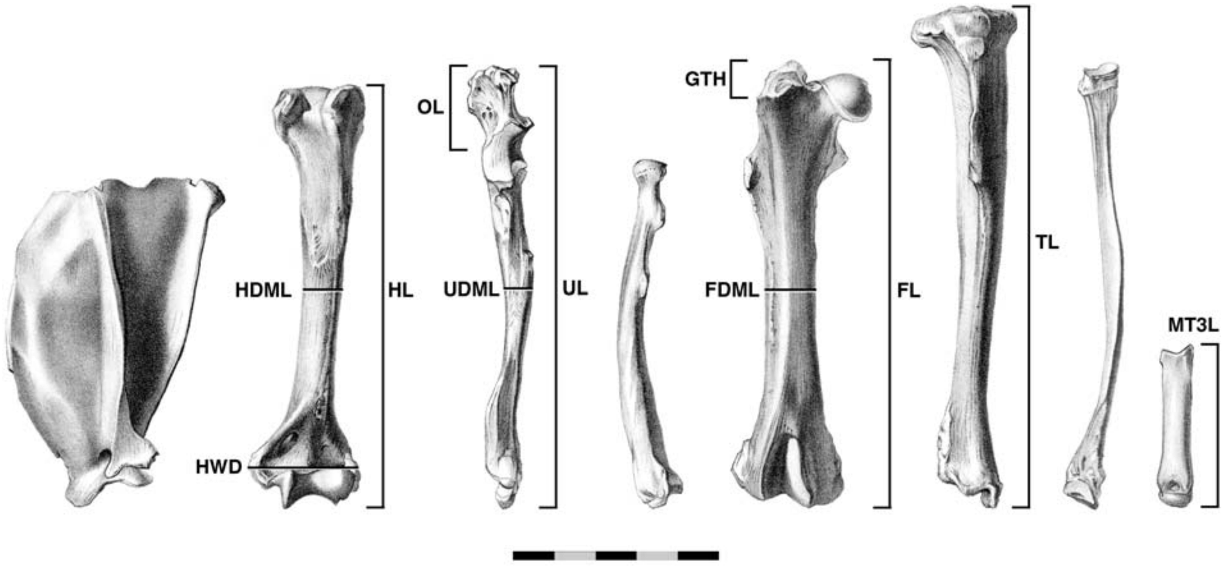

Figure 2. Representative limb bones of *Protypotherium* (from Sinclair 1909) and schematics of the 11 postcranial measurements used in this study (see Table 2 for descriptions). From left to right: left scapula in lateral view (YPM-PU 15828); left humerus in anterior view (YPM-PU 15828); left ulna in anterior view (YPM-PU 15828); left radius in lateral view (YPM-PU 15828); right femur in anterior view (YPM-PU 15340); right tibia in anterior view (YPM-PU 15340); left fibula in internal view (AMNH 9149); and left third metatarsal in dorsal view (AMNH 9149). Scale bar equals 5 cm.

number of available skeletons; in total, 80 individuals were studied. For most genera (28/29), all individuals were of a single species. Each genus was placed into one of five locomotor categories based on its primary mode of locomotion (Appendix): (1) arboreal (climbers plus scansorial mammals); (2) semifossorial (non-subterranean diggers); (3) generalized (terrestrial, non-cursorial non-diggers); (4) bounding (quadrupedal jumpers, leapers, bounders, and hoppers); and (5) cursorial (quadrupedal runners).

For fossil and modern specimens, 11 measurements were taken to the nearest tenth of a millimeter using digital calipers (Figure 2; Table 2). These particular measurements were chosen because they encompass the chief lever arms and muscle insertion areas important for locomotor performance. The data were not log transformed because the species under examination span a relatively small range of body sizes (one order of magnitude). From these measurements, eight indices were calculated that describe characteristics of bones (and muscles) related to limb function (cf. Hildebrand 1985; Carrano 1997, 1999; Vizcaíno et al. 1999; Vizcaíno and Milne 2002; Elissamburu and Vizcaíno 2004; Shockey et al. 2007) (Table 3). Such indices are useful for minimizing the effects of body size and for grouping species into broad locomotor categories, but care must be taken when comparing such indices among phylogenetically disparate species; distantly related mammals of similar locomotor habit do not necessarily have equivalent index values (Garland and Janis 1993). As described by Carrano (1999), because these indices (ratios) express unique mechanical relationships and do not have a common denominator, they likely do not suffer from the statistical shortcomings that affect ratio data in other types of analyses. All indices in this study are expressed as percents (i.e., * 100).

The locomotor habit of *Protypotherium* was assessed using qualitative attributes of the postcranial skeleton and quantitative multivariate analyses of: (1) linear postcranial measurements; and (2) functional indices computed from those measurements. Multivariate analyses included principal components analysis (PCA) and discriminant function analysis (DFA), both executed using SPSS 11.0 statistical software.

PCA reduces a large number of variables into a smaller number of factors (principal components; PCs) that retain most of the variance observed in the original dataset; the smaller number of factors (relative to variables) facilitates comparisons of similarity among species. PCA is generally employed as an exploratory technique in ecomorphological studies, permitting extinct species to be compared with extant ones using only two or three

Table 2. Variables used in this study. Measurements are illustrated in Figure 2. For further discussions of functional indices, see Garland and Janis (1993) and Elissamburu and Vizcaíno (2004).

Code	Variable	Notes
FDML	Femur Diameter (Mediolateral)	Midshaft
FL	Femur Length	Greatest length
GTH	Greater Trochanter Height	From proximalmost point to distalmost area of muscle insertion
HDML	Humerus Diameter (Mediolateral)	Midshaft
HL	Humerus Length	Greatest length
HWD	Humerus Width (Distal)	Across widest portions of epicondyles
MT3L	Metatarsal III Length	Greatest length
OL	Olecranon Length	From the proximalmost point to midpoint of semilunar notch
TL	Tibia Length	Greatest length
UDML	Ulna Diameter (Mediolateral)	Midshaft
UL	Ulna Length	Greatest length
BI	Brachial Index (UL/HL*100)	Outlever/inlever ratio of forelimb; correlated with outvelocity
CI	Crural Index (TL/FL*100)	Outlever/inlever ratio of hind limb; correlated with outvelocity
EI	Epicondyle Index (HWD/HL*100)	Area of origin for muscles acting primarily on the elbow; correlated with outforce
FRI	Femur Robustness Index (FDML/FL*100)	Relative thickness of femoral shaft and area of origin for knee extensors; correlated with outforce
GI	Gluteal Index (GTH/FL*100)	Inlever/outlever ratio of femur; correlated with outvelocity
HRI	Humerus Robustness Index (HDML/HL*100)	Relative thickness of humeral shaft and area of origin for eblow flexors and extensors; correlated with outforce
IFA	Index of Fossorial Ability (OL/(UL-OL)*100)	Outlever/inlever ratio of antebrachium; correlated with outforce
MFI	Metatarsal/Femur Index (MT3L/FL*100)	Relative length of pes; correlated with outvelocity

axes (e.g., Spencer 1995; Woodman 1995; Gingerich 2003, 2005; Van Valkenburgh et al. 2003; Andersson 2005; Woodman and Croft 2005; Weisbecker and Warton 2006; Shockey et al. 2007). Interpreting PCs (axes) requires examining loadings (i.e., relative contribution) of variables. Because all variables usually load highly on PC1, it is often interpreted as summarizing variation due to body size. Subsequent PCs may summarize mostly taxonomic or ecomorphological variation, depending on which variables load highly and how species are distributed along the PC axis.

DFA attempts to sort cases into pre-determined groups using variables believed to be correlated with group membership. In ecomorphological studies, variables are generally osteological (i.e., tooth or bone measurements) and groups are generally behavioral (e.g., locomotor habit, diet). DFA differs from PCA in that the discriminant functions (DFs, analogous to PCs) preferentially weight variables based on how well they discriminate among groups; such discriminatory power is assessed using variable means and variances for each group. Variables with low variances may therefore be important in DFA and relatively unimportant in PCA, if they are good at discriminating between groups. As in PCA, a score for each species can be calculated for each DF. If discrimination among groups is good, the scores of species in one group will differ significantly from those in other groups on at least one DF axis. This is usually evident in discriminant plots; with good discrimination, little overlap exists between groups, and group centroids are clearly separated from one another. In reality, a DFA is rarely able to separate all cases; the percentage of cases classified correctly is a general measure of its effectiveness.

Once DFs have been generated using a 'training' sample (e.g., extant mammals), scores can be calculated for unknowns (e.g., extinct mammals)

Table 3. PCA factor loadings and DFA structure martrix for analyses of linear postcranial measurements (Figures 5-6).

Variable	PC1	PC2	DF1	DF2
FDML	0.852	0.143	0.033	0.330
FL	0.971	-0.083	0.178	0.387
GTH	0.840	0.018	0.073	0.332
HDML	0.966	0.165	0.046	0.354
HL	0.935	0.133	0.115	0.308
HWD	0.790	0.540	-0.154	0.421
MT3L	0.709	-0.661	0.431	0.403
OL	0.904	-0.164	0.160	0.280
TL	0.896	-0.358	0.300	0.328
UDML	0.274	0.915	-0.206	0.123
UL	0.943	-0.083	0.191	0.346
% Variance	71.8%	16.4%	65.9%	23.1%

and used to infer group membership. The probability that an unknown belongs to a particular group (the ‘posterior probability’) is inversely proportional to the distance in discriminant space between the unknown and the group’s centroid. The unknown therefore has the greatest probability of pertaining to the group with the closest centroid (at least when prior probabilities – the a priori probabilities of group membership – are equal). Based on the dispersion of group members around the centroid in discriminant space, a ‘conditional probability’ is also calculated; this is the probability that an unknown pertains to the group, given the characteristics of other group members. If the unknown falls well within the cloud of other group members in discriminant space, the conditional probability is high; if the unknown falls well outside the cloud, the conditional probability is low. In a general sense, the conditional probability describes the degree to which the unknown resembles other members of that group. It is only computed for the group to which the unknown most likely pertains. In contrast, posterior probabilities are computed for all groups. The position of the unknown relative to other cases (and groups) can be assessed visually using DF plots, which are analogous to PC plots.

In this study, significance levels of DFA variables and functions were assessed using Wilks’ Lambda ($p < 0.05$). Prior probabilities for group membership were considered equal (i.e., it was assumed equally likely that *Protypotherium* could pertain to any locomotor group).

APPENDICULAR MORPHOLOGY

As is the case for most Santa Cruz Formation mammals, descriptions and detailed illustrations of the postcrania of *Protypotherium* were published in the *Reports of the Princeton University Expedition to Patagonia, 1896-1899* (see Sinclair 1909). We include relevant illustrations here and add functional interpretations to Sinclair’s physical descriptions. Some of the volumes of this series are available free on the Internet at http://www.archive.org/.

Scapula (Figure 1, Figure 2)

The scapula is roughly quadrangular in overall shape; the spine runs nearly parallel to the caudal border, and intersects the superior (vertebral) border at an angle close to 90°. The supraspinous fossa is larger than the infraspinous fossa. Although a small extension for the attachment of teres major is present, it is less developed than in fossorial taxa (Shockey et al. 2007). The scapula contrasts markedly with the triangular scapulae of artiodactyls and some rodents, more closely resembling those of canids and the generalized mammal *Didelphis*.

The unbroken length of the metacromion process in *Protypotherium* is unknown. The presence of a long, slender metacromion has been correlated with quadrupedal bounding in modern mammals such as lagomorphs (Janis and Seckel 2005), but the shape of this structure in *Protypotherium* does not closely resemble that seen in modern lagomorphs. Metacromia of other shapes and sizes are present in many mammals including some larger notoungulates (e.g., the toxodontid *Nesodon*; Scott 1912). The relative importance of function (versus phylogeny) in the presence of this structure in *Protypotherium* cannot be inferred with confidence.

Humerus (Figure 2, Figure 3)

The overall form of the humerus of *Protypotherium* suggests a generalized terrestrial mammal tending toward cursoriality: the greater tubercle projects slightly above the humeral head and may have partially limited mobility of the shoulder joint; neither the supinator crest nor the deltopectoral crest are prominent (the latter extends approximately half the length of the humerus), suggesting muscles attaching in these areas were not particularly well developed; the medial trochlear ridge is pronounced, providing support for the ulna and restricting movements to the parasagittal plane; and the capitulum is flattened and confluent with

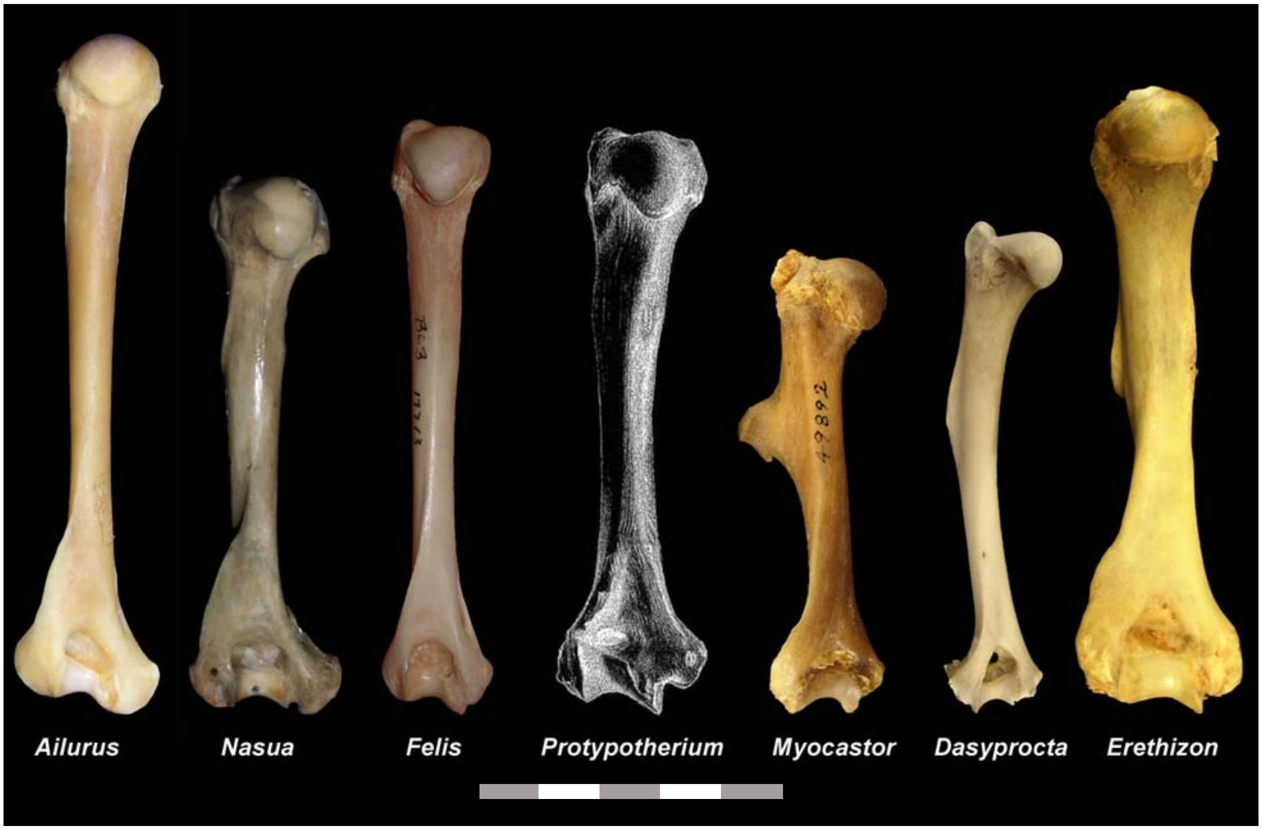

Figure 3. Left humeri in posterior view: *Ailurus* (arboreal; CMNH 19723); *Nasua* (arboreal; CMNH 17611); *Felis* (generalized; CMNH 17713); *Protypotherium* (YPM-PU 15828; from Sinclair 1909); *Myocastor* (semifossorial; FMNH 49892); *Dasyprocta* (cursorial; FMNH 60408); and *Erethizon* (arboreal; FMNH 47173). Scale bar equals 5 cm.

the trochlea rather than rounded and distinct, indicating little supinatory movement at the radial head. The prominence of the medial epicondyle suggests *Protypotherium* may have had large forearm muscles and some digging tendencies; fossoriality has been suggested for other notoungulates and may be an ancestral attribute of this clade (Shockey et al. 2007). A pronounced circular depression is present on the lateral surface of the greater tubercle, possibly marking the attachment of a well-developed supraspinatus muscle (Figure 1). This accords with the size of the supraspinous fossa of the scapula (Figure 2).

In overall form the humerus is most similar to that of *Felis* (Figure 3), here considered a generalist. The most significant differences between the two include: slightly more prominent greater tubercle in *Felis*; more proximally extended (and laterally arched) lesser tubercle in *Protypotherium*; longer supinator crest in *Felis*; and larger medial epicondyle in *Protypotherium*. The humerus of *Protypotherium* lacks the extreme extension of the greater tubercle seen in artiodactyls. It also lacks the large, distally positioned deltoid tuberosity and broad supinator ridge commonly seen in arboreal and semifossorial mammals.

Radius and Ulna (Figure 2)

In contrast to the humerus, the ulna and radius of *Protypotherium* are more similar to those of a semifossorial mammal such as *Myocastor* than to a generalized mammal like *Felis*. Both elements are proportionately shorter and more robust than those of *Felis*, and the ulna bears a large, medially curved olecranon with an anterosuperiorly oriented fossa for muscle attachment present along its medial surface. As in *Felis* and more cursorial mammals, however, the radial notch of the ulna is pronounced, suggesting relatively little movement of the radial head.

Manus (Figure 1, Figure 4)

The structure of the manus is notable in that digit I is absent and digit IV is greatly reduced (and therefore would likely have been non-functional in life). Such lateral digit reduction is typical of cursorial mammals (Hildebrand and Goslow 2001); this, in combination with the absence of trenchant or

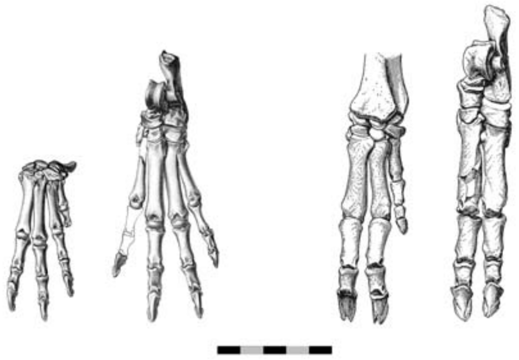

Figure 4. Interatheriid manus and pedes in anterior view. From left to right: left manus and left pes (both AMNH 9149) of *Protypotherium* (from Sinclair 1909); left manus and left pes (both UCMP 38091) of *Miocochilius* (from Stirton 1953). Scale bar equals 5 cm.

enlarged claws, suggests that *Protypotherium* was not a committed semifossorial mammal nor particularly adept at climbing or manual manipulation.

Femur (Figure 2, Figure 5)

Several features of the femur suggest cursorial adaptations in the hind limb. The greater trochanter, which extends proximally above the level of the head, would have reduced the mobility of the hip joint and created a greater lever arm for the gluteal hip extensors. The short, robust femoral neck also would have reduced hip mobility. The lesser trochanter, in addition to being sharply pointed and quite enlarged, is primarily directed posteriorly (rather than medially), better positioned for parasagittal flexion than abduction.

Despite the cursorial features of the femur, it is relatively short and robust compared to those of small artiodactyls and carnivorans such as *Felis* and *Canis*. In this regard, it is more similar to semifossorial rodents (e.g., *Myocastor*, *Cuniculus*). The third trochanter is more distinct in *Protypotherium* than in extant cursorial mammals of similar size, but is much more proximally positioned than in some arboreal mammals (e.g., *Erethizon*); in other arboreal mammals (e.g., *Ailurus*) the third trochanter is essentially absent. Given the presence of a prominent third trochanter in most perissodactyls (regardless of size or locomotor habit), this trait could be a phylogenetic correlate rather than a functional one in *Protypotherium* and other notoungulates. The patellar groove is intermediate in breadth between cursorial mammals and arboreal/semifossorial ones.

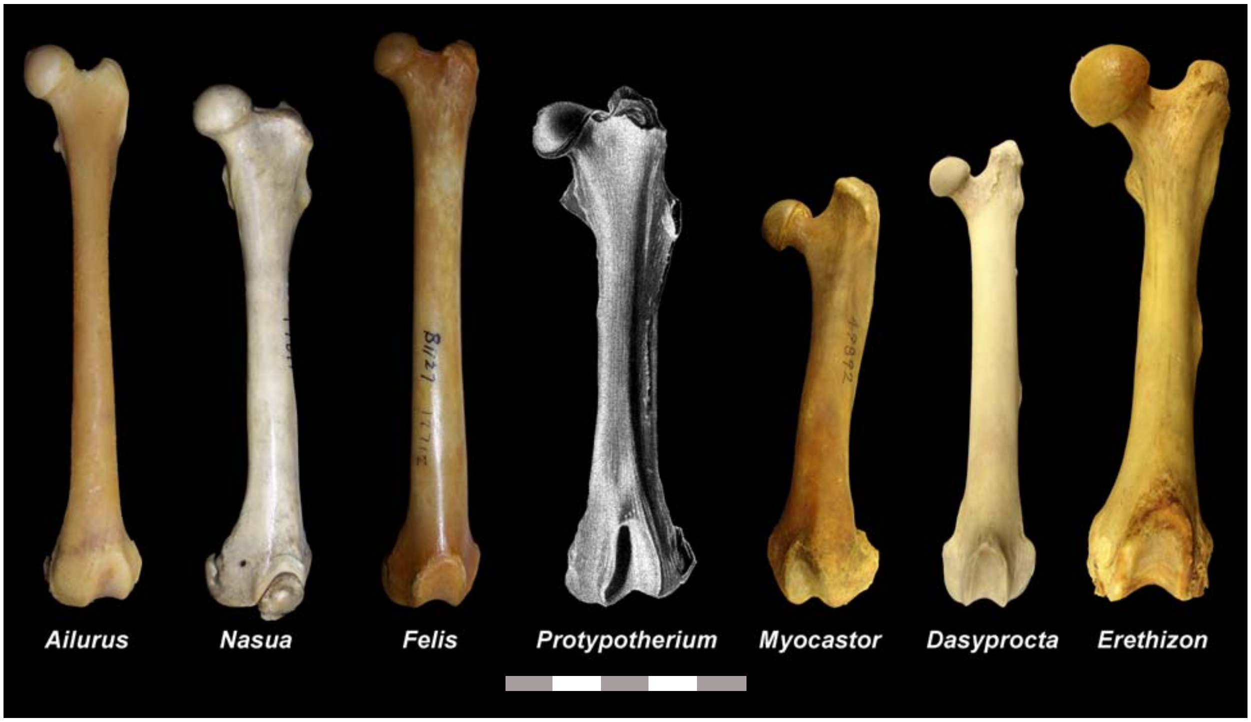

Figure 5. Left femora in anterior view: *Ailurus* (arboreal; CMNH 19723); *Nasua* (arboreal; CMNH 17611); *Felis* (generalized; CMNH 17713); *Protypotherium* (YPM-PU 15340, shown as left; from Sinclair 1909); *Myocastor* (semifossorial; FMNH 49892); *Dasyprocta* (cursorial; FMNH 60408); and *Erethizon* (arboreal; FMNH 47173). Scale bar equals 5 cm.

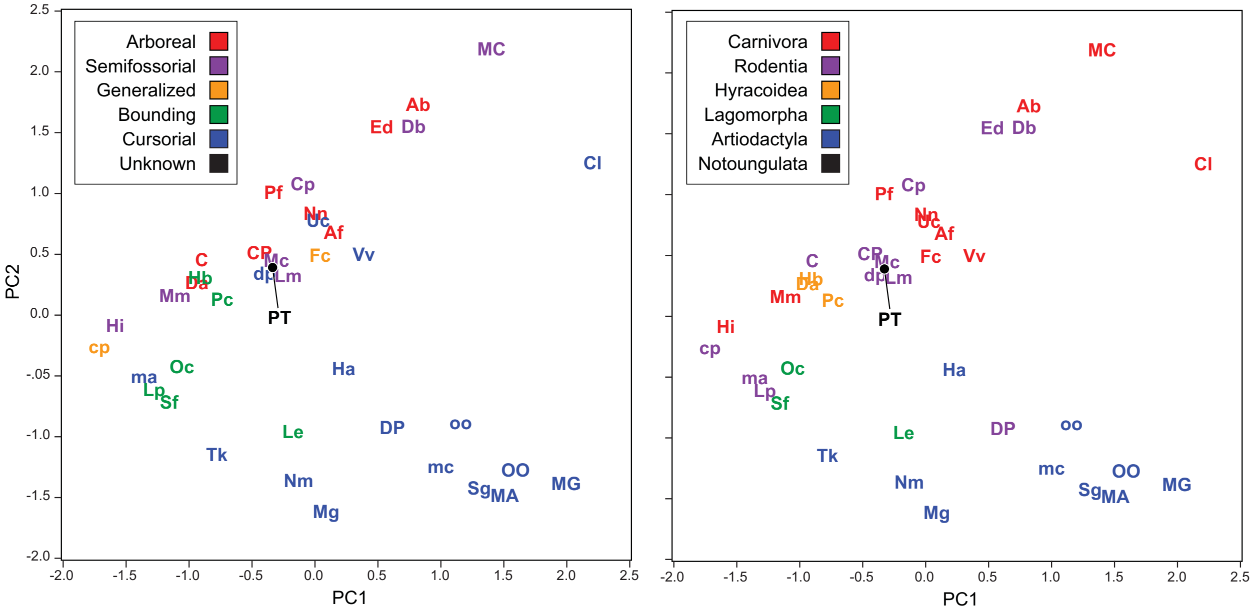

Figure 6. PCA of 11 postcranial variables for 39 extant mammals and *Protypotherium*; genera are color-coded by locomotor habit (left) and taxonomic order (right). See Appendix for taxon codes.

Tibia and Fibula (Figure 2)

The prominence of the cnemial crest in *Protypotherium* is more similar to the condition in semifossorial rodents such as *Myocastor* and *Cuniculus* than cursorial carnivorans and ungulates. The relative size of the fibula is also similar, as is the presence of a variable degree of distal fusion (either syndesmosis or synostosis) between the tibia and fibula (though the proximal fusion in rodents is opposite the distal fusion of *Protypotherium*). Both proximal and distal tibiofibular fusion also occurs in bounding/cursorial mammals (e.g., lagomorphs), as well as hegetotheriids, a group of typothere notoungulates generally regarded as cursorial (Cifelli 1985; Elissamburu 2004; Croft and Anaya 2006). Proximal tibiofibular fusion in *Protypotherium* therefore could be functionally related either to strengthening the hind limbs to brace the animal during digging or to limiting movement between these elements during bounding locomotion.

Pes (Figure 4)

Like the manus, the pes suggests *Protypotherium* was not a particularly proficient digger or climber. The astragalar trochlea is high and narrow, indicating movements limited to the parasagittal plane at the crurotarsal joint. Arboreal and semifossorial mammals typically have a lower, broader astragalar trochlea permitting greater mobility. Similarly, both the neck of the astragalus and the calcaneal tuber are elongate, more typical of the distal limb elongation seen in cursorial mammals. The absence of the first digit is compatible with many locomotor habits.

MULTIVARIATE ANALYSES

Linear Postcranial Measurements

A PCA of linear postcranial measurements resulted in two factors with eigenvalues > 1.0, together accounting for 88.2% of the variance. PC1 described postcranial variation primarily attributable body size; all variables except Ulna Diameter (UDML; see Table 2 for abbreviations) had very high positive loadings on PC1 (> 0.700, most > 0.850; Table 3). PC2 described postcranial variation primarily attributable to locomotor habit; UDML and HWD had high positive loadings (arboreal and semifossorial mammals typically have robust forelimb bones) whereas Metatarsal III Length (MT3L) had a high negative loading (distal limb elongation is typical of cursorial and some bounding mammals).

A plot of these first two PCs generally supports the interpretations above (Figure 6). On PC1, some of the smallest genera plot furthest to the left (e.g., *Cavia*, *Herpestes*, *Myoprocta*) and some of the largest plot furthest to the right (e.g., *Canis*, *Mazama*, *Ourebia*, *Muntiacus*). Most cursorial mammals have low values on PC2 (e.g., most artiodactyls, *Lepus*, *Dolichotis*) and semifossorial and arboreal mammals have high values on this axis (e.g., *Mellivora*, *Arctictis*, *Dinomys*, *Erethizon*).

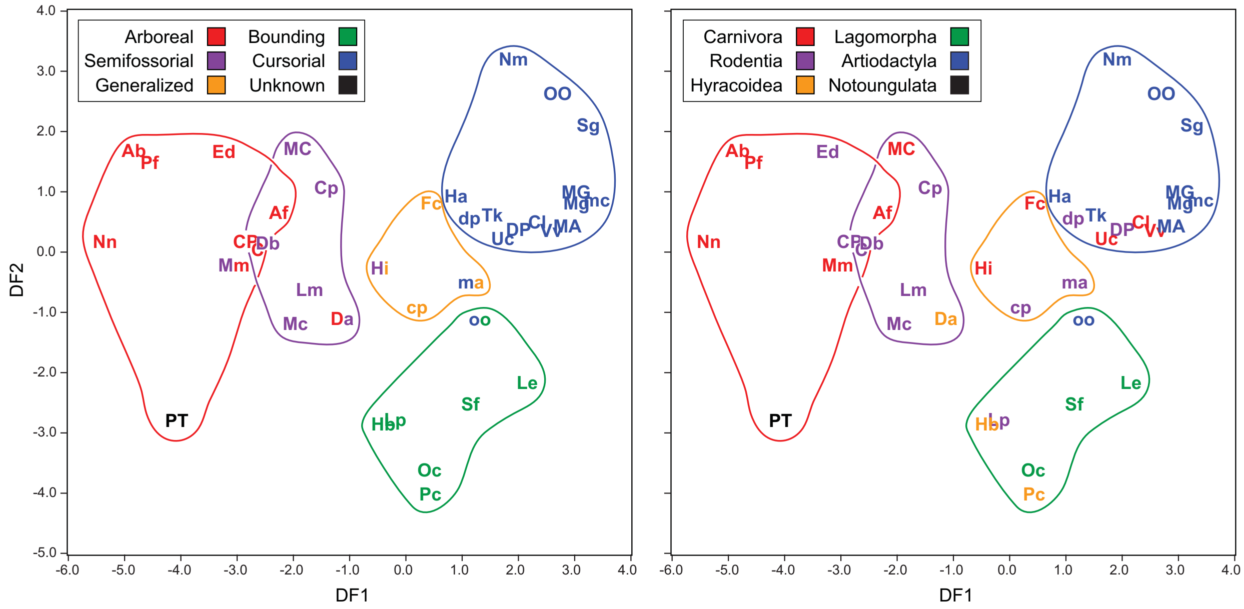

Figure 7. DFA of 11 postcranial variables for 39 extant mammals and *Protypotherium*; genera are color-coded by locomotor habit (left) and taxonomic order (right) but are grouped by locomotor category in both. For misclassified genera, the first letter reflects the true locomotor habit, and the second reflects the predicted locomotor habit. See Appendix for taxon codes.

Significant variation exists in both of these patterns, however. Conspicuous exceptions include the cursorial canids, which plot high on PC2 instead of low, and some small semifossorial carnivorans (i.e., *Mephitis*, *Herpestes*), which have values close to zero on PC2. In the case of canids, their position on PC2 may reflect their more generalized morphology (relative to artiodactyls) and/or their tendency to dig on occasion. For the small carnivorans, this apparently reflects an overall trend for smaller-bodied mammals (i.e., those with low PC1values) to approach zero on PC2. In functional terms, this suggests that smaller mammals tend to have less specialized postcrania for a given locomotor habit than larger bodied ones; in other words, postcranial morphologies correlated with force production (i.e., diggers and climbers) and speed (i.e., runners and bounders) tend to be more pronounced in the larger mammals included in this dataset. Phylogenetic factors also influence the positions of taxa in the PC morphospace; all three hyraxes plot very close on PC2, despite the more arboreal habits of *Dendrohyrax*. This is no doubt partly attributable to the less specialized morphology of *Dendrohyrax* relative to most other arboreal taxa (e.g., *Arctictis*, *Erethizon*).

Protypotherium plots near the center of both PC axes, extremely close to the cursorial rodent *Dasyprocta*. Other nearby taxa include two semifossorial rodents (*Myocastor* and *Lagostomus*) and an arboreal one (*Capromys*). All of these except *Dasyprocta* have body masses of 6-9 kg, within the range inferred for *Protypotherium*. The position of *Protypotherium* in PC morphospace suggests that it is postcranially more similar to medium-sized caviomorph rodents than to comparably-sized carnivorans, lagomorphs, hyracoids, or artiodactyls; it says little about its locomotor habit other than that its postcrania are not as modified for force production as *Erethizon* or *Dinomys* nor as modified for speed as *Dolichotis*.

A DFA of postcranial measurements classified 87.2% (34/39) of extant mammals correctly by locomotor habit; all variables were significantly different among groups except Femur Diameter (FDML), and the first two functions demonstrated significant differences among groups. DF1 primarily separated cursorial and bounding mammals from arboreal and semifossorial ones (Figure 7); MT3L and Tibia Length (TL) had the greatest positive correlations with DF1 and UDML and Distal Humerus Width (HWD) had the only negative correlations (Table 3). DF2 separated bounding mammals from all others; HWD and MT3L had the highest correlations (> 0.400), but nearly all other variables had correlations between 0.300 and 0.400, with the exception of UDML (0.123).

Misclassified mammals included: *Dendrohyrax* (semifossorial instead of arboreal), *Herpestes* (generalized instead of semifossorial),

Table 4. PCA factor loadings and DFA structure matrix for analyses of functional indices (Figures 7-8).

Variable	PC1	PC2	DF1	DF2
BI	-0.589	0.642	-0.121	0.330
CI	-0.804	0.384	-0.254	0.159
EI	0.762	0.393	0.769	0.007
FRI	0.666	0.149	0.204	-0.114
GI	0.300	0.602	0.153	0.113
HRI	0.458	0.795	0.206	0.133
IFA	0.467	0.198	-0.001	-0.174
MFI	-0.752	0.466	-0.345	0.638
% Variance	38.8%	24.8%	76.0%	20.1%

Mephitis (arboreal instead of semifossorial), *Myoprocta* (generalized instead of cursorial), and *Oreotragus* (bounding instead of cursorial). Except for *Dendrohyrax*, the true locomotor group of each of these mammals had the next highest posterior probability; in *Dendrohyrax*, it had the second lowest posterior probability (higher only than cursorial). It is notable that in no case was an arboreal or semifossorial mammal misclassified as bounding or cursorial (or vice versa).

Protypotherium was classified as arboreal with a high posterior probability (0.984) but an extremely low conditional probability (0.000). In other words, based on these data, *Protypotherium* resembles arboreal mammals more than those in other locomotor groups, but it is quite different from the arboreal mammals considered here. This is apparent in Figure 7; *Protypotherium* plots closest to the arboreal group centroid but is much farther from that centroid than any member of that group. Semifossorial was the second most probable classification for *Protypotherium*. Based strictly on the DFA of linear postcranial measurements, it is unlikely that *Protypotherium* was a highly cursorial or bounding mammal.

Functional Indices

A PCA of functional indices resulted in two factors with eigenvalues > 1; the first two accounted for 63.6% of the variance (Table 4). PC1 primarily described variation due to locomotor habit and therefore resembled PC2 of the linear postcranial measurements analysis; arboreal and semifossorial mammals generally had high values on this axis whereas cursorial and bounding mammals generally had low values. Epicondylar Index (EI) and Femur Robustness Index (FRI) had the highest positive loadings (Index of Fossorial Ability, IFA, and Humeral Robustness Index, HRI, are slightly lower) and Crural Index (CI), Metatarsal/Femur Index (MFI), and Brachial Index (BI) all had high negative loadings; the former are expected to be greater in arboreal and semifossorial mammals whereas the latter are expected to be greater in cursorial and bounding mammals. Only a few exceptions to the locomotor distributions on PC1 are evident (Figure 8). *Ailurus*, an arboreal carnivoran, is positioned close to the cursorial side of PC1; it has the lowest EI of any arboreal or semifossorial mammal and the lowest FRI of any mammal (along with *Canis* and *Vulpes*). *Hyemoschus*, a cursorial artiodactyl, is positioned on the edge of the semifossorial/arboreal region; among cursorial mammals, it has the lowest CI and relatively low MFI and BI. Given that *Hyemoschus* inhabits dense woods and is a member of a more basal family of artiodactyls, this is not particularly surprising; more notable is its distance from the other tragulid in this analysis (*Tragulus*), which plots among other cursorial artiodactyls. All three hyraxes plot close together in the semifossorial/arboreal region, despite two of these (*Procavia* and *Heterohyrax*) being classified as bounding mammals. Hyraxes are somewhat generalized in their morphology, and one might therefore have expected them to plot closer to the center of PC1 (if not with other bounding mammals). The two mammals classified as generalists in this analysis, *Felis* and *Cavia*, are split between the two regions; *Felis* (which is relatively long-legged) plots on the left side of PC2, and *Cavia* (which has relatively shorter limbs) falls to the right.

PC2 was primarily a phylogenetic axis, with mammals more or less distributed based on their ordinal affiliation, irrespective of locomotor habit; these groupings had much overlap, however. HRI,

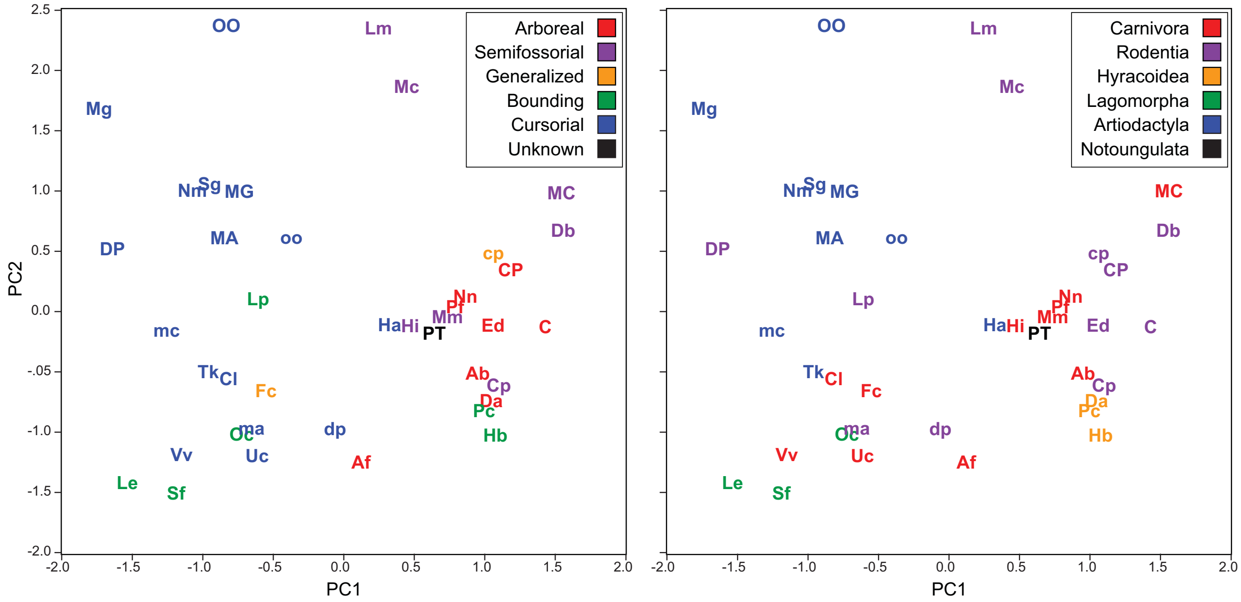

Figure 8. PCA of eight functional indices for 39 extant mammals and *Protypotherium*; genera are color-coded by locomotor habit (left) and taxonomic order (right). See Appendix for taxon codes.

BI, and Gluteal Index (GI) had the highest positive loadings on this axis and no variable loaded negatively.

Protypotherium plots closest in the PCA to *Herpestes* and *Mephitis*, two small (2-3 kg), semifossorial carnivorans. Other closely positioned mammals include *Hyemoschus* (discussed above) and *Potos* (an arboreal carnivoran similar in size to *Herpestes* and *Mephitis*). Given that *Hyemoschus* plots distant from other cursorial artiodactyls, *Protypotherium* can best be described as plotting in the generalized end of the semifossorial/arboreal region of PC1 and among rodents and carnivorans on PC2. It is quite distant from most cursorial and bounding mammals.

A DFA of functional indices classified 87.2% (34/39) of known cases correctly; all variables were significantly different among groups except IFA, and the first two functions were significant. DF1 primarily separated cursorial and bounding mammals from arboreal and semifossorial ones (Figure 9); EI had the greatest positive correlation with DF1 whereas MFI and CI had the greatest negative correlations (Table 4). DF2 primarily separated bounding mammals from all others; MFI had a high positive correlation whereas FRI and IFA had smaller negative correlations.

Two of the mammals misclassified by the DFA of functional indices were also misclassified by the DFA of linear postcranial measurements: *Mephitis* was classified as arboreal instead of semifossorial (as in the DFA of linear measurements), and *Dendrohyrax* was classified as generalized instead of arboreal (it was classified as semifossorial in the DFA of linear measurements). The three other misclassified mammals included *Hyemoschus* (generalized instead of cursorial), *Cuniculus* (arboreal instead of semifossorial), and *Dasyprocta* (generalized instead of cursorial). As in the other DFA, except for *Dendrohyrax*, the true locomotor group of each of these mammals was second most probable. In no case was an arboreal or semifossorial mammal misclassified as bounding or cursorial (or vice versa).

Protypotherium was classified as semifossorial with a moderately low posterior probability (0.493) and a higher conditional probability (0.654). The second most likely classification for *Protypotherium* was arboreal, with a posterior probability of 0.441. In contrast to its position in the DFA of postcranial measurements, *Protypotherium* falls well within the morphospace occupied by extant mammals, close to *Myocastor* (Figure 9). Concordant with the DFA of postcranial measurements, the DFA of functional indices suggests it is unlikely that *Protypotherium* was a highly cursorial or bounding mammal.

DISCUSSION

The analyses above do not paint a clear picture of the locomotor habit of *Protypotherium*, but they do suggest it was not highly specialized for any particular mode of locomotion. In neither PCA does *Protypotherium* plot near the edge of the

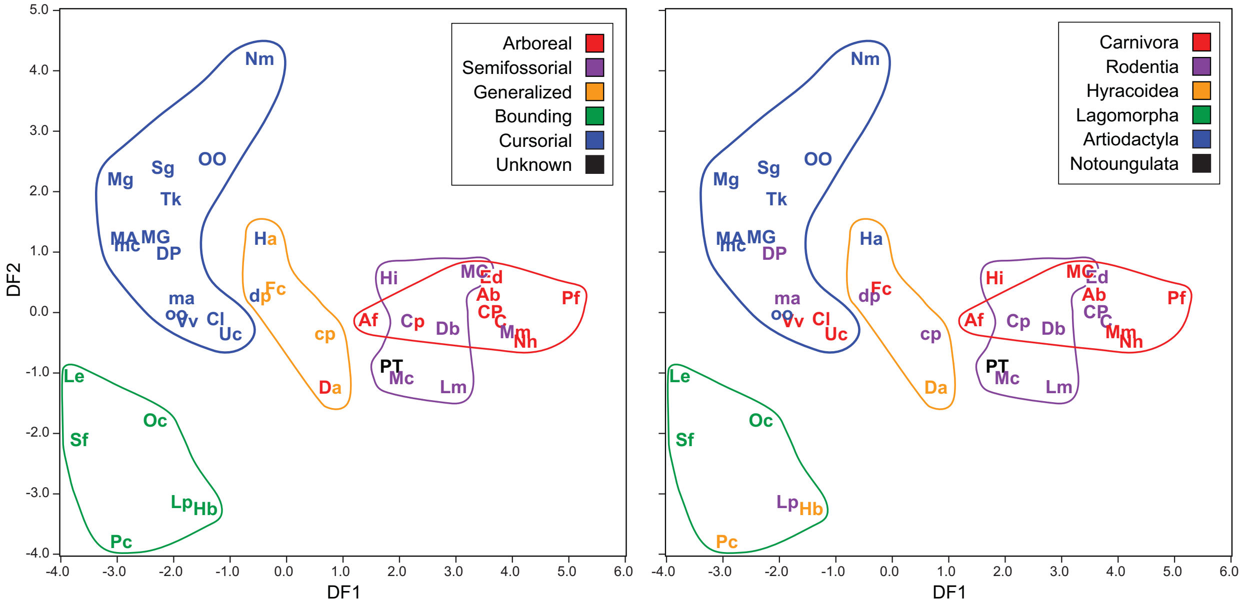

Figure 9. DFA of eight functional indices for 39 extant mammals and *Protypotherium*; genera are color-coded by locomotor habit (left) and taxonomic order (right) but are grouped by locomotor category in both. For misclassified genera, the first letter reflects the true locomotor habit and the second reflects the predicted locomotor habit. See Appendix for taxon codes.

modern mammal morphospace. Instead, it is close to the center with mammals of varying locomotor habits, implying a generalized morphology. The DFA of linear measurements indicates some aspects of *Protypotherium* skeletal morphology are unusual relative to the modern mammals considered, but the DFA of functional indices does not show a similar pattern. Both DFAs suggest an arboreal or semifossorial lifestyle for *Protypotherium*, with the latter having a higher conditional probability. The functional indices themselves do not suggest a single locomotor style. BI of *Protypotherium* is < 100, similar to hyraxes and some arboreal and semifossorial mammals; CI of *Protypotherium* is > 100, close to values seen in cursorial canids (Appendix). Few mammals show as great a discrepancy between the relative lengths of fore- and hind limbs and this could be a phylogenetic characteristic of notoungulates. The relatively high EI of *Protypotherium* resembles that of semifossorial and arboreal mammals, but MFI is higher than one would expect for an arboreal mammal (thus favoring semifossoriality). Qualitatively, the limb bones of *Protypotherium* also show a mix of characters; the proximal and distal elements share features with generalized and cursorial mammals, whereas the intermediate elements more closely resemble semifossorial ones.

So was *Protypotherium* a generalist, or did it have a more specialized locomotor habit? Because all notoungulates are extinct, it is impossible to unequivocally 'calibrate' morphology and behavior to determine the locomotor habit of a notoungulate with a generalized skeleton. As an analogy, even though *Dasyprocta* is a cursorial rodent, one might not make such an inference based solely on comparisons with non-rodents. DFAs of our dataset bear this out; *Dasyprocta* was sometimes classified as generalized when other rodents were excluded. Clearly inferences about extinct taxa are biased to some degree by the extant animals available for comparison. This holds true for all extinct species, but the problem is exacerbated in mammals like notoungulates (and litopterns, uintatheres, palaeanodonts, etc.) in which the entire order is extinct (as opposed to just the suborder or family).

That being said, it is unlikely that the skeleton of a committed runner (or digger or climber) would lack any characteristics suggestive of such habits. It is therefore unlikely that *Protypotherium* spent all of its time either running, digging, or climbing. On the other hand, it is just as unlikely that it spent an equal proportion of its time in each of those pursuits; interpreting it merely as a 'generalist' is neither very enlightening nor very satisfying. The overall attributes of the *Protypotherium* postcranial skeleton suggest a locomotor habit tending toward cursoriality; moment arms for muscles mostly favor speed over force and articulations tend more to restrict movement than to increase mobility. The

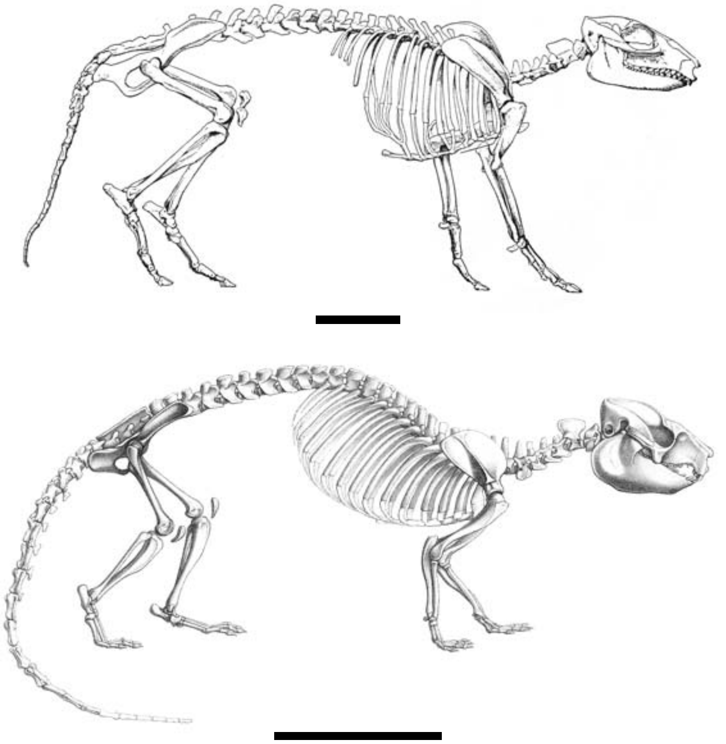

Figure 10. Skeletal reconstructions of *Miocochilius* (above, from Stirton 1953) and *Interatherium* (below, from Sinclair 1909), two early to middle Miocene interatheriid notoungulates. Scale bars equal approx. 10 cm.

digits are reduced – most compatible with a terrestrial/cursorial habit – and the unguals show no specializations for excavation or climbing. Qualitatively, *Protypotherium* is better designed for cursoriality than anything else, though it certainly is not proportioned like a cursor nor highly designed for that mode of locomotion.

A skeleton more adapted for force than speed is suggested by the DFAs, but this may be a phylogenetic effect rather than evidence for a particular mode of locomotion. As noted above, *Protypotherium* is being judged against other clades of mammals; such comparisons may not discriminate a slightly more arboreal (scansorial) notoungulate from a slightly more cursorial one, especially if the ancestral locomotor habit is fossoriality (see discussion in Shockey et al. 2007). A notoungulate tending toward cursoriality may look like a generalized or semifossorial carnivoran (or rodent) merely because it started out further away from that end of the locomotor spectrum and still bears features characteristic of its ancestry.

Moreover, although most of the important moment arms of the appendicular skeleton were used as variables in the quantitative analyses, these only describe a small proportion of overall skeletal morphology. For example, the relative lengths of the ulna and olecranon are functionally important and vary predictably with locomotor habit (e.g., Vizcaíno and Milne 2002), but neither of these metrics describes the shape of the olecranon, the morphology of the semilunar notch, or how the radial head articulates with the ulna – additional attributes of functional importance (e.g., Rose 1990, 2001). The subset of postcranial measurements used might not be providing the same picture of locomotor habit as that of a larger, more comprehensive dataset.

Indirect support for cursorial tendencies in *Protypotherium* comes from two other Miocene interatheriids: *Miocochilius* and *Interatherium*. *Miocochilius* is best known from the middle Miocene of Colombia (Stirton 1953; Kay et al. 1997). It is likely the sister-taxon to *Protypotherium* (Reguero et al. 2003) and although the two genera are similar craniodentally (Hitz et al. 2000; Reguero et al. 2003; Croft 2007) they differ postcranially; most conspicuously, *Miocochilius* bears only two functional digits on the fore- and hind limbs (Stirton 1953; Figures 4 and 10). *Interatherium* is best known from the Santa Cruz Formation and is more distantly related to *Protypotherium* (Hitz et al.

2000, 2006; Reguero et al. 2003); it has an elongate body and short limbs (Sinclair 1909; Figure 10). *Miocochilius* and *Interatherium* clearly represent divergent postcranial specializations within Interatheriidae: the former closely resembles some artiodactyls and was presumably cursorial (Stirton 1953; Cifelli 1985; Kay and Madden 1997a, b), whereas the latter is more similar to a mustelid and was probably more fossorial (certainly not cursorial; Cifelli 1985; Elissamburu 2004). If these interpretations of locomotor habit are correct, then these two taxa can provide rough 'calibration' points for interatheriid morphology and locomotor habit. In this context, *Protypotherium* looks more cursorial than not, a parsimonious interpretation given its more recent common ancestry with *Miocochilius*. A recently described late Oligocene interatheriid from Salla, Bolivia, further supports a trend of increasing cursoriality within Interatheriidae; the skeleton of this older species resembles that of *Protypotherium* but is generally characterized by shorter and more robust limb elements typical of semifossorial mammals (Hitz et al., in press). This new species is presumably closer to the ancestral condition of the clade.

CONCLUSIONS

Almost nothing was known of the locomotor habits of notoungulates (or other endemic South American ungulates) prior to about 10 years ago, despite the presence of many excellent specimens. Since then, several studies have begun to explore the locomotor diversity in the group and the paleobiology of certain species/clades. Shockey (1997) described notohippid postcrania from Salla, Bolivia, and suggested that some of these animals may have had significant forelimb mobility; the locomotor habits were not discussed in detail, however. Later, Shockey (2001) suggested that a knee lock mechanism similar to those of horses might have been present in *Toxodon* (a toxodontid notoungulate), casting doubt on the supposed semiaquatic habits of these Pleistocene mammals. Elissamburu (2004) studied the late Cenozoic hegetotheriid notoungulate *Paedotherium* and inferred that it had both cursorial and fossorial (burrowing) characteristics, similar to some caviomorph rodents. Most recently, Shockey et al. (2007) studied mesotheriid notoungulates and inferred highly fossorial habits for all members of the family for which adequate postcranial material is known. Other recent observations on late Oligocene notoungulates from Salla (Shockey and Anaya, in press) and Eocene notoungulates from Argentina (Shockey and Flynn, 2007) are forthcoming and should provide insights into the habits of more basal notoungulates.

The locomotor habits of most notoungulates remain uninvestigated, and much more information is needed to adequately characterize the roles of notoungulates in Cenozoic ecosystems. Studies of other interatheriids in particular would permit a more detailed analysis of the evolution of locomotor habits within this highly successful clade, perhaps providing insights into the group's diversity and distribution.Thanks to the studies noted above, a basic picture of notoungulate locomotor habits is emerging. The present study adds to this picture by inferring the habits of one of the most common interatheriid notoungulates, *Protypotherium*. Based on the analyses presented here, *Protypotherium* was most likely a generalized terrestrial mammal tending toward cursoriality. Its appendicular skeleton does not closely resemble that of any modern mammal, but is most similar to those of some medium-sized caviomorph rodents. Proximal and distal limb elements of *Protypotherium* mostly resemble those of cursorial mammals in qualitative characters, but intermediate elements are more similar to those of arboreal and semifossorial mammals. PCA and DFA indicate that appendicular bones statistically ally with those of some arboreal and semifossorial mammals. This may be a phylogenetic effect attributable to fossorial habits in ancestral interatheriids and/or notoungulates. In a phylogenetic context, the postcranial adaptations of *Protypotherium* are intermediate between those of more basal interatheriids and the middle Miocene *Miocochilius*; *Interatherium* appears to represent a divergent locomotor strategy within the family.

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Summary postcranial data for species included in this study. See Table 2 for explanations of variables.

Classification follows Wilson and Reeder (2005).

Genus	Species	Code	Common Name	Order	Family	Prefix	Nos.	Mass (kg)	Locomotor Group
Ailurus	*fulgens*	Af	Red panda	Carnivora	Ailuridae	CMNH	19723	9.6	Arboreal
Arctictis	*binturong*	Ab	Binturong	Carnivora	Viverridae	CMNH	17660	4.9	Arboreal
Canis	*latrans*	Cl	Coyote	Carnivora	Canidae	CMNH	166, 21951	11.5	Cursorial
Capromys	*pilorides*	CP	Desmarest's hutia	Rodentia	Capromyidae	FMNH	47769, 47770, 72803	7.0	Arboreal
Cavia	*porcellus*	cp	Guinea Pig	Rodentia	Caviidae	FMNH	54246, 122151, 122239	1.0	Generalized
Coendou	spp.	C	Prehensile-tailed porcupine	Rodentia	Erethizontidae	FMNH	15611, 43289, 122987	1.0	Arboreal
Cuniculus	*paca*	Cp	Lowland paca	Rodentia	Cuniculidae	FMNH	48177, 52438, 152058	5.2	Semifossorial
Dasyprocta	*punctata*	dp	Central American agouti	Rodentia	Dasyproctidae	FMNH	60408, 60569, 152059	2.5	Cursorial
Dendrohyrax	*arboreus*	Da	Southern tree hyrax	Hyracoidea	Procaviidae	FMNH	163770, 17508	3.1	Arboreal
Dinomys	*branickii*	Db	Pacarana	Rodentia	Dinomyidae	FMNH	57186, 166523	12.5	Semifossorial
Dolichotis	*patagonum*	DP	Patagonian mara	Rodentia	Caviidae	FMNH	12178, 49213, 49231	11.0	Cursorial
Erethizon	*dorsatum*	Ed	North American porcupine	Rodentia	Erethizontidae	FMNH	47173	12.3	Arboreal
Felis	*catus*	Fc	Domestic Cat	Carnivora	Felidae	CMNH	17710, 17712, 17713	4.0	Generalized
Herpestes	*ichneumon*	Hi	Egyptian mongoose	Carnivora	Herpestidae	CMNH	17672	2.5	Semifossorial
Heterohyrax	*brucei*	Hb	Yellow-spotted hyrax	Hyracoidea	Procaviidae	FMNH	165385	2.4	Bounding
Hyemoschus	*aquaticus*	Ha	Water chevrotain	Artiodactyla	Tragulidae	FMNH	57210	10.8	Cursorial
Lagidium	*peruanum*	Lp	Northern viscacha	Rodentia	Chinchillidae	FMNH	49757, 49758, 49759	2.8	Bounding
Lagostomus	*maximus*	Lm	Plains viscacha	Rodentia	Chinchillidae	FMNH	53704, 53737	6.9	Semifossorial
Lepus	*europaeus*	Le	European hare	Lagomorpha	Leporidae	FMNH	84478, 84479	3.7	Bounding
Madoqua	*guentheri*	Mg	Günther's dik-dik	Artiodactyla	Bovidae	FMNH	32922	5.0	Cursorial
Mazama	*gouazoupira*	MG	Brown brocket deer	Artiodactyla	Cervidae	FMNH	28305	16.8	Cursorial
Mellivora	*capensis*	MC	Honey badger	Carnivora	Mustelidae	CMNH	14112	10.0	Semifossorial
Mephitis	*mephitis*	Mm	Striped Skunk	Carnivora	Mephitidae	CMNH	18423, 18533	2.7	Semifossorial
Moschus	*chrysogaster*	mc	Alpine musk deer	Artiodactyla	Moschidae	FMNH	36759	13.0	Cursorial
Muntiacus	*atherodes*	MA	Bornean yellow muntjac	Artiodactyla	Cervidae	FMNH	68763	19.5	Cursorial
Myocastor	*coypus*	Mc	Coypu	Rodentia	Myocastoridae	FMNH	15617, 49892	8.3	Semifossorial
Myoprocta	*acouchy*	ma	Green acouchi	Rodentia	Dasyproctidae	FMNH	125383, 140915	1.0	Cursorial
Nasua	*nasua*	Nn	South American coati	Carnivora	Procyonidae	CMNH	17611	4.2	Arboreal
Neotragus	*moschatus*	Nm	Suni	Artiodactyla	Bovidae	FMNH	129363, 129364	4.8	Cursorial
Oreotragus	*oreotragus*	oo	Klipspringer	Artiodactyla	Bovidae	FMNH	19580, 160010	12.8	Cursorial
Oryctolagus	*cuniculus*	Oc	European rabbit	Lagomorpha	Leporidae	FMNH	54314, 54320, 129384	2.0	Bounding
Ourebia	*ourebi*	OO	Ouribi	Artiodactyla	Bovidae	FMNH	60546, 127970, 127975	17.5	Cursorial
Potos	*flavus*	Pf	Kinkajou	Carnivora	Procyonidae	CMNH	17612	3.0	Arboreal
Procavia	*capensis*	Pc	Rock hyrax	Hyracoidea	Procaviidae	FMNH	147999, 160006	3.1	Bounding
Sylvicapra	*grimmia*	Sg	Bush duiker	Artiodactyla	Bovidae	FMNH	127998, 127999, 12800	13.8	Cursorial
Sylvilagus	*floridanus*	Sf	Eastern cottontail rabbit	Lagomorpha	Leporidae	FMNH	36728, 154664, 156862	1.4	Bounding
Tragulus	*kanchil*	Tk	Lesser Mouse-deer	Artiodactyla	Tragulidae	FMNH	36725, 68767, 68778	4.0	Cursorial
Urocyon	*cinereoargenteu*	Uc	Gray fox	Carnivora	Canidae	CMNH	172, 12467, 19346	5.0	Cursorial
Vulpes	*vulpes*	Vv	Red fox	Carnivora	Canidae	CMNH	18524, 17522, 21824	6.3	Cursorial
†*Protypotherium*	sp.	PT	n/a	†Notoungulata	†Interatheriidae	FMNH	(see Table 1)	n/a	Unknown

GTH	HDML	HL	HWD	MT3L	OL	TL	UDML	UL	BI	CI	EI	FRI	GI	HRI	IFA	MFI
17.0	7.3	112.8	24.6	33.5	14.0	111.6	3.9	103.1	91.4	95.2	21.8	7.0	14.5	6.4	15.7	28.5
13.9	10.1	123.1	32.9	32.5	21.4	113.0	6.0	124.9	101.5	90.0	26.7	9.7	11.1	8.2	20.6	25.9
19.6	12.5	169.3	31.5	83.8	27.2	200.3	7.8	209.6	123.9	105.1	18.6	7.0	10.3	7.4	14.9	44.0
10.2	6.2	70.6	19.5	24.9	16.2	85.6	3.6	78.3	110.9	99.1	27.7	12.1	11.8	8.8	26.3	29.2
6.2	3.1	36.3	7.6	15.0	8.1	44.7	2.1	38.5	105.8	106.4	20.9	14.6	14.8	8.5	28.1	35.8
8.4	5.9	63.1	16.3	16.1	8.9	66.7	3.0	60.2	96.4	92.1	25.8	13.2	11.4	9.4	17.3	21.9
9.3	6.6	84.1	20.9	33.3	19.0	96.7	5.8	81.8	97.3	94.3	24.9	11.7	9.1	7.9	30.3	32.5
8.2	5.9	80.6	15.1	44.8	13.7	100.2	4.5	82.0	101.7	103.6	18.7	10.7	8.5	7.3	20.1	46.3
8.1	5.1	66.2	14.6	19.7	14.2	65.8	3.2	60.7	91.8	93.3	22.1	10.9	11.5	7.7	30.6	27.9
15.7	10.9	104.2	26.5	34.2	20.8	110.3	5.9	109.9	104.8	94.0	25.3	13.7	13.1	10.2	23.2	29.3
13.2	7.0	106.3	18.1	66.3	22.0	159.0	1.5	169.0	159.0	132.2	17.0	10.3	11.0	6.6	15.0	55.1
11.3	9.0	103.5	26.9	20.9	19.2	107.9	5.7	123.5	119.3	92.7	26.0	12.9	9.7	8.7	18.4	18.0
9.9	7.6	99.3	19.6	51.9	13.5	117.2	4.8	115.4	116.2	104.7	19.7	8.4	8.9	7.7	13.2	46.3
6.4	3.7	44.5	10.5	23.1	7.7	50.6	2.7	43.9	98.6	101.2	23.6	10.0	12.9	8.2	21.4	46.2
7.6	5.3	70.2	13.9	18.0	17.0	64.8	3.5	60.1	85.6	93.0	19.8	9.9	10.9	7.5	39.4	25.8
18.1	7.3	93.0	17.6	59.2	18.3	116.2	1.9	97.0	104.3	96.8	18.9	10.2	15.1	7.8	23.3	49.3
8.3	3.5	46.9	9.0	31.6	10.3	86.3	2.1	52.5	112.1	128.7	19.3	8.9	12.4	7.5	24.3	47.1
17.8	6.2	63.2	17.9	42.3	13.1	118.8	4.3	82.2	130.0	131.3	28.2	10.7	19.4	9.7	20.3	46.7
10.0	5.7	96.3	12.0	52.1	12.3	138.3	1.4	116.1	120.6	116.9	12.5	7.9	8.4	5.9	11.8	44.0
15.1	7.0	81.1	14.0	108.6	18.2	143.0	0.9	112.6	138.8	135.7	17.3	8.3	14.3	8.6	19.3	103.0
23.4	11.9	134.0	24.7	147.3	32.3	203.0	1.8	163.0	121.6	116.0	18.4	8.3	13.4	8.9	24.7	84.2
29.9	11.8	126.9	33.6	35.3	25.3	112.6	7.5	132.7	104.5	83.4	26.4	9.2	22.1	9.3	23.6	26.1
8.6	4.6	57.8	16.5	19.1	10.6	65.7	2.6	60.0	103.9	101.1	28.6	8.8	13.2	8.0	21.5	29.4
18.2	9.1	125.6	20.0	125.3	21.7	176.0	1.9	130.2	103.7	120.5	15.9	7.3	12.5	7.2	20.0	85.8
15.2	10.9	122.1	22.0	139.7	32.8	184.0	1.7	153.2	125.5	112.2	18.0	8.1	9.3	8.9	27.2	85.2
11.2	7.1	68.4	19.0	40.6	18.3	97.4	4.3	89.2	130.4	117.5	27.7	10.6	13.5	10.4	25.8	49.1
5.3	3.7	54.0	8.5	36.3	8.2	72.4	2.1	54.4	100.7	117.0	15.6	11.3	8.5	6.8	17.8	58.6
12.1	8.3	88.9	25.8	30.2	13.8	103.4	3.9	95.2	107.1	95.3	29.0	9.0	11.1	9.4	17.0	27.9
14.7	5.9	76.3	15.6	97.6	17.3	120.0	0.9	96.0	125.5	119.3	20.5	8.1	14.5	7.7	21.8	97.2
21.8	9.8	115.3	21.5	96.5	26.8	164.7	1.9	133.4	115.7	110.6	18.7	8.1	14.6	8.5	25.2	64.8
7.3	4.7	65.7	10.6	37.1	10.5	96.6	2.3	70.0	106.9	114.7	16.2	9.1	8.5	7.1	17.5	44.1
17.3	11.6	105.4	22.9	150.8	30.3	187.7	2.5	161.0	152.8	118.8	21.8	9.3	10.9	11.0	23.1	95.4
12.5	7.2	83.7	24.7	31.9	10.6	91.6	4.6	78.6	93.9	101.3	29.5	9.0	13.9	8.6	15.5	35.3
8.9	5.9	74.3	12.9	19.1	19.2	71.1	3.2	67.8	91.3	92.4	17.3	10.0	11.6	7.9	39.6	24.8
17.8	9.9	112.2	21.0	134.0	29.1	173.0	1.6	148.8	132.5	114.5	18.7	8.2	11.9	8.8	24.3	88.7
6.2	4.1	63.0	8.1	35.6	7.7	93.5	1.8	66.5	105.5	116.0	12.9	8.4	7.7	6.6	13.2	44.2
9.3	4.8	69.8	11.4	65.4	12.3	95.7	0.8	73.9	105.9	113.3	16.4	8.5	11.0	6.9	20.0	77.3
10.8	7.1	103.2	18.5	47.8	13.6	119.4	6.0	110.5	107.0	104.1	17.9	7.8	9.4	6.9	14.1	41.6
12.3	7.7	121.1	20.1	61.2	15.1	139.7	5.5	135.2	111.6	111.6	16.6	7.0	9.9	6.3	12.5	48.8
9.5	6.8	79.6	20.3	40.7	13.7	112.8	3.7	63.4	90.9	106.2	24.4	10.8	10.3	8.8	22.8	45.5