

BODY MASS ESTIMATES IN EXTINCT MAMMALS FROM LIMB BONE DIMENSIONS: THE CASE OF NORTH AMERICAN HYAENODONTIDS

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ABSTRACT. The body mass estimation of several limb bone dimensions (shaft cross-sectional properties, articular sizes, and bone lengths) were examined using bivariate linear regression analyses. The sample included taxonomically and behaviourally diverse small to medium-sized Recent carnivorans and carnivorous marsupials. All examined limb bone dimensions indicated low errors (percentage standard error of estimate, 8–13) for the body mass estimations. Among them, humeral and femoral shaft properties correlated best with body weight, while limb bone lengths gave larger errors. Both humeral and femoral head dimensions have relatively large individual variations, and distal humeral articular dimensions seem to be influenced more by phylogenetic differences. The regressions based on each locomotor group gave slightly lower errors than those based on the total pooled sample. The results were then applied to hyaenodontid creodonts from the Eocene–Oligocene of North America. The estimated body masses (kg) are: *Arfia*, 5.4–9.5; *Prototomus*, <6.0; *Pyrocyon*, 2.6; *Sinopa*, 1.3–1.4; *Tritemnodon*, 7.6–13; *Prolimnocyon*, 1.6; *Thinocyon*, 0.7–2.5; *Machaeroides*, 12; *Limnocyon*, 7.8–16; *Hyaenodon*, 9.1–43. The various limb bone dimensions give different body mass values, but the variation in estimates is smaller compared to those derived from dental or cranial measurements.

KEY WORDS: Hyaenodontidae, carnivorous mammals, body mass estimates, limb bone dimensions.

THE body size of an animal is one of the most important ecological factors influencing dietary preferences, predatory behaviour, and niche partitioning, and is related to biomechanical and physiological demands. To reflect those aspects in evolutionary biology, precise estimation of an animal's body mass is critical. Regressions of dental and cranial dimensions, in addition to postcranial dimensions, relative to body mass have been used for estimating body size in many fossil mammals (for primates, Gingerich 1977; Gingerich *et al.* 1982; Conroy 1987; for carnivores, Legendre and Roth 1988; Van Valkenburgh 1988, 1989, 1990; for ungulates, Damuth 1990; Janis 1990; Scott 1990). Although dental or cranial measurements, which are more intensively studied and are easily available, have been more frequently used, it has been suggested that dimensions of limb bones provide more reliable estimates of body mass in fossils (particularly carnivores) than dental or cranial characters (e.g. Legendre and Roth 1988). Since structure of limb bones can be modified to the stresses that relate to body weight support, limb bone structure should be highly correlated with body size.

Some geometrical properties of various limb bone dimensions, such as long bone shaft cross-sectional shapes and articular dimensions, are influenced by the forces on the bone, which are related to the body size of an animal (Alexander *et al.* 1979; Schmidt-Nielsen 1984; Biewener 1982, 1989; Alexander 1985; Demes and Günther 1989; Swartz and Biewener 1992), and these properties have been suggested to be the best body mass estimators. For example, body mass estimates for large carnivorans based on humeral and femoral cross-sectional properties by Anyonge (1993) showed much smaller errors (about 30 per cent) than body mass estimates based on cranial measurements (skull length and occiput-orbit length) and dental measurements (lower first-molar length) by Van Valkenburgh (1990). Rafferty *et al.* (1995) estimated body mass of three species of *Proconsul*, and suggested that body estimates derived from measurements of postcranial skeletons are consistent with each other, but tooth size in *Proconsul* does not scale like that in modern anthropoids, resulting in overestimation of body mass in the smallest *Proconsul* species and

TABLE 1. Recent carnivore sample.

Abbreviations: N, number of specimens per species; wt., body weight range in kg; loc., locomotory groups; A, arboreal; S, scansorial; Tg, terrestrial (generalized); Tf, terrestrial (semi-fossorial); Ta, terrestrial (semi-aquatic); C, cursorial; assoc., number of specimens with an associated body weight. References for body weights and behavioural information: 1, Abe *et al.* (1994); 2, Anyonge (1993); 3, Bekoff (1982); 4, Bekoff (1987); 5, Berta (1982); 6, Burt and Grossenheider (1976); 7, Clarke *et al.* (1987); 8, Eisenberg (1989); 9, Emmons and Feer (1990); 10, Fish (1993); 11, Ford and Hoffmann (1988); 12, Fox (1982); 13, Fritzell and Haroldson (1982); 14, Gittleman (1986); 15, Gittleman (1989); 16, Godin (1982); 17, Heinrich (1995); 18, Heinrich and Rose (1995); 19, Howard and Marsh (1982); 20, Jenkins and Camazine (1977); 21, Jenkins and McClearn (1984); 22, Kaufmann (1982); 23, Kaufmann and Kaufmann (1965); 24, Kingdon (1977); 25, Kingdon (1997); 26, Krott (1962); 27, Lee *et al.* (1982); 28, Lindzey (1982); 29, Linscombe *et al.* (1982); 30, Long (1973); 31, Lotze and Anderson (1979); 32, MacDonald (1984); 33, McClearn (1992); 34, McCord and Cardoza (1982); 35, McNab (1989); 36, Nowak (1991); 37, Paglayan-Neuwel and Twell (1988); 38, Powell (1981); 39, Redford and Eisenberg (1992); 40, Roberts and Gittleman (1984); 41, Samuel and Nelson (1982); 42, Silva and Dawning (1995); 43, Smith (1982); 44, Strahan (1995); 45, Strickland *et al.* (1982a); 46, Strickland *et al.* (1982b); 47, Taylor (1970); 48, Terres (1939); 49, Towell and Tabor (1982); 50, Trapp (1972); 51, Underwood and Mosher (1982); 52, VanValkenburgh (1987); 53, Wade-Smith and Verts (1982); 54, Williams (1983a); 55, Williams (1983b); 56, Wilson (1982).

Taxa	Common names	N	wt.	Loc.	References
Canidae (Carnivora)					
<i>Alopex lagopus</i>	Arctic fox	6	1.4–9.4	C	6, 15, 17, 36, 51
<i>Canis latrans</i>	coyote	10	7.0–20	C	3, 4, 6, 17, 36, 42
<i>Cerdocyon thous</i>	crab-eating fox	10	5.0–8.9	C	5, 17, 32, 39
<i>Pseudoalopex griseus</i>	Argentine grey fox	5	2.5–5.5	C	32, 36, 39
<i>Urocyon cinereoargenteus</i>	grey fox	9	2.5–7.0	S	6, 13, 14, 17, 36, 41, 48
<i>Vulpes velox</i>	swift fox	3	1.8–3.0	C	6, 32, 36, 41, 42
<i>Vulpes vulpes</i>	red fox	11	2.5–14	C	17, 20, 36, 41, 42 (assoc. 9)
<i>Vulpes zerda</i>	Fennec fox	6	0.8–1.6	C	17, 25, 32, 36, 42
Felidae (Carnivora)					
<i>Herpailurus yaguarondi</i>	jaguarundi	4	4.5–10	S	9, 32, 36, 42 (assoc. 1)
<i>Lynx rufus</i>	bobcat	8	3.8–26	S	34, 36
<i>Neofelis nebulosa</i>	clouded leopard	3	12–23	A	2, 36, 42
<i>Prionailurus bengalensis</i>	leopard cat	6	1.8–7.0	S	1, 32, 36, 42
Herpestidae (Carnivora)					
<i>Atilax paludinosus</i>	marsh mongoose	6	1.8–5.1	Ta	24, 42, 47
<i>Herpestes edwardsii</i>	Indian grey mongoose	5	0.9–1.8	Tg	14, 36, 42
<i>Ichneumia albicauda</i>	white-tailed mongoose	8	1.8–5.2	Tg	24, 36, 42, 47
Mustelidae (Carnivora)					
<i>Conepatus mesoleucus</i>	hog-nosed skunk	9	1.5–4.5	Tf	17, 32, 36, 42 (assoc. 9)
<i>Eira barbara</i>	tayra	9	2.0–7.0	S	9, 14, 17, 23, 39
<i>Galictis vittata</i>	greater grison	5	1.4–3.3	Tg	8, 17, 23, 36, 42, 50
<i>Gulo gulo</i>	wolverine	10	7.0–32	S	6, 17, 26, 36, 56 (assoc. 9)
<i>Ichonyx striatus</i>	zorilla	4	0.4–1.5	Tf	17, 24, 36, 42
<i>Lontra canadensis</i>	Canadian otter	10	3.0–14	Ta	6, 36, 42, 49
<i>Martes americana</i>	American marten	11	0.3–1.5	S	6, 7, 32, 36, 46 (assoc. 11)
<i>Martes pennanti</i>	fisher	11	1.1–5.5	S	6, 17, 36, 38, 42, 45 (assoc. 11)
<i>Meles meles</i>	Eurasian badger	3	6.6–18	Tf	14, 15, 36, 42 (assoc. 1)
<i>Melogale personata</i>	ferret badger	5	1.0–3.0	Tf	17, 36, 42
<i>Mephitis mephitis</i>	striped skunk	10	0.5–5.4	Tf	6, 16, 17, 42, 53
<i>Mustela vison</i>	American mink	9	0.5–2.3	Ta	18, 29, 36, 42, 54, 55
<i>Spilogale putorius</i>	spotted skunk	8	0.2–1.3	Tg	6, 17, 19, 36, 42 (assoc. 2)
<i>Taxidea taxus</i>	American badger	7	3.2–12	Tf	17, 28, 30, 36, 42
Procyonidae (Carnivora)					
<i>Bassaricyon gabbii</i>	olingo	4	1–1.5	A	8, 9, 14, 17, 37

TABLE 1 (continued)

<i>Bassariscus astutus</i>	ringtail	10	0.7–1.3	S	6, 18, 22, 36, 37, 42, 50
<i>Potos flavus</i>	kinkajou	5	1.4–4.6	A	8, 9, 11, 17, 21, 33, 36
<i>Procyon lotor</i>	common raccoon	8	2.0–16	S	6, 14, 17, 20, 22, 31, 33
Ursidae (Carnovora)					
<i>Ailurus fulgens</i>	lesser panda	5	3.0–6.2	S	14, 18, 32, 36, 40, 42
Viverridae (Carnivora)					
<i>Arcitictis binturong</i>	binturong	3	7.6–20	A	18, 35, 36, 42
<i>Genetta genetta</i>	common genet	7	1.0–3.0	S	18, 24, 32, 36, 42, 47
<i>Nandinia binotata</i>	African palm civet	5	1.4–5.0	A	18, 24, 36, 42, 47
<i>Paguma larvata</i>	masked palm civet	6	2.7–5.7	A	1, 36, 42, 52
<i>Paradoxurus hermaphroditus</i>	common palm civet	7	1.5–4.5	A	14, 18, 36
<i>Viverra zibetha</i>	large Indian civet	3	5.0–11	Tg	17, 32, 36
Dasyuridae (Marsupialia)					
<i>Dasyurus viverrinus</i>	eastern quoll	5	0.6–1.8	S	12, 27, 36, 44 (assoc. 1)
<i>Sarcophilus lanianus</i>	Tasmanian devil	5	4.1–12	Tg	12, 36, 44
Didelphidae (Marsupialia)					
<i>Chironectes minimus</i>	yapok	5	0.5–0.8	Ta	8, 9, 10, 36 (assoc. 1)
<i>Didelphis marsupialis</i>	southern opossum	5	0.6–2.8	A	8, 9, 42 (assoc. 2)
<i>Didelphis virginiana</i>	Virginian opossum	9	0.3–5.9	A	6, 9, 21, 42
<i>Philander opossum</i>	grey four-eyed opossum	8	0.2–0.7	S	8, 36, 39, 42 (assoc. 1)
Thylacinidae (Marsupialia)					
<i>Thylacinus cynocephalus</i>	Tasmanian wolf	7	15–35	C	43, 44

underestimation of body mass in the larger *Proconsul* species based on dental measurements. Ruff (1990) also found small errors (9–22 per cent) for body mass estimates based on femoral and tibial cross-sectional properties and articular dimensions for non-human anthropoids.

In this study, body mass estimation equations are derived from long bone dimensions, such as diaphyseal cross-sectional geometries, articular sizes, and bone lengths. Estimation regressions are obtained from a sample consisting of phylogenetically and behaviourally diverse Recent carnivorous mammals. The accuracy of the body mass estimation regressions derived from these long bone dimensions based on a Recent sample are compared, and their applicability to body mass estimation in fossil forms are discussed. The body mass estimate regressions obtained from the Recent sample are then applied to hyaenodontid creodonts from Eocene–Oligocene deposits in North America, for which body masses have not been reliably estimated (see below).

MATERIAL

Recent comparative sample

To estimate body size in extinct forms, the correlation between body size and bone form needs to be tested in living forms. The Recent comparative sample includes seven families of small to medium-sized Carnivora and one American and two Australian carnivorous marsupial families. These groups were chosen because of their predatory habit, which should be ecologically analogous to those in hyaenodontids, and the variability of locomotor behaviour among them.

The sample for obtaining body mass estimate regressions consists of a total of 47 species and 318 individual specimens of known locomotor behaviour and body weight, taken from the literature. The Recent comparative sample is summarised in Table 1. The taxonomy follows Wilson and Reeder (1992). Because confinement of zoo animals may affect bone morphology, wild-caught animals were used, except for some marsupials for which adequate wild-caught samples were not available. Each species includes at least three and usually more than five individuals wherever possible.

TABLE 2. Definition of locomotor groups. Terrestrial and cursorial groups are also called terrestrial non-cursors and terrestrial cursors, respectively. The terrestrial group is further divided into three subcategories.

Arboreal:	Rarely on the ground, forages and shelters in trees
Scansorial:	Capable of, or good at climbing, but forages mainly on the ground
Terrestrial:	Rarely or never climbs, little running
	semi-aquatic: some swimming adaptation, mainly to obtain fish or other aquatic organisms as a food component
	semi-fossorial: digs regularly for both food and shelter
	generalized: lacks either of these specializations
Cursorial:	Rarely or never climbs, adaptation for running, often hunts by chasing prey

The size range of the Recent comparative samples is about 500 g to 25 kg. Body weights for each Recent species were obtained from the literature unless an associated body weight was available for individual specimens. Associated body weights were available for 58 individuals in 12 species. For other individuals, species mean, sex-specific mean, or subspecies mean body weight, whichever was available from the literature, was used.

Each sample species is assigned to one of the locomotor groups based on the literature. 'Locomotor behaviour' includes several aspects, such as substrate use, posture, gait, speed, and so on. To use locomotor behavioural information in statistical comparisons among multiple samples, each extant species was assigned to one of four locomotor categories. Although this categorisation is in some ways an oversimplification, it has proved to be efficient in several previous works (e.g. Taylor 1974, 1976; Eisenberg 1981; Van Valkenburgh 1985, 1987; Heinrich 1995). I followed the locomotor categories defined by Van Valkenburgh (1985) mostly, but some modifications were needed to adjust the categories to my sample species, of which body sizes are smaller than hers. The categories used in this study are summarised in Table 2.

Each locomotor category includes species from multiple families and two different supraordinal taxa, and the distribution of sample species over taxonomic groups is summarised in Table 3. Some techniques to control phylogenetic effects on morphological data have been proposed (e.g. phylogenetic autocorrelation: Cheverud *et al.* 1985; Gittleman and Kot 1990; nested analysis of degree of freedom: Harvey and Pagel 1991; Smith 1994a). However, these techniques require large sample sizes throughout many taxonomic hierarchies, and are not applicable to this study, which uses mean values of each species; thus, quantitative removal of phylogenetic effects from morphology was not attempted in this study.

The majority of the specimens for the Recent mammalian sample were examined at the Department of Mammalogy, United States National Museum of Natural History (Washington, DC) and Museum Support Center of the Smithsonian Institution (Suitland, MD), and the Department of Mammalogy, the American Museum of Natural History (New York, NY). Certain additional carnivoran skeletons with associated body masses were provided by Dr R. E. Heinrich (Department of Biological Sciences, Ohio University, Athens, OH).

Fossil sample

Hyaenodontidae is a family in the Order Creodonta. It is a group of archaic carnivorous mammals, which is phylogenetically separated from true carnivorans and was the dominant mammalian predator component in terrestrial faunas for most of the Tertiary. The fossil record of the family begins in the Lower Eocene of North America and Europe; they spread to Asia and Africa before they became extinct in the Miocene. Although postcranial skeletons of hyaenodontids are much rarer than their dental materials, a total of 94 hyaenodontid specimens from the Eocene–Lower Oligocene of North America were available for this study. All of these specimens have at least one structure (shaft or articulation) that is useful for the quantitative analyses in this study; however, the completeness of the skeletal elements for each individual varies considerably among the specimens. Developmental age of the individuals was defined by the fusion of epiphyses at joints: no obvious epiphyseal line found at any joints (adult), joints firmly attached to shaft, but some epiphyseal line observed (subadult), or epiphyses not fused (juvenile).

TABLE 3. Distribution of Recent comparative sample species with regard to locomotor groups and taxonomic groups at family level. Abbreviations for locomotory groups: A, arboreal; S, scansorial; T, terrestrial (pooled); Tg, terrestrial (generalized); Tf, terrestrial (semi-fossorial); Ta, terrestrial (semi-aquatic); C, cursorial.

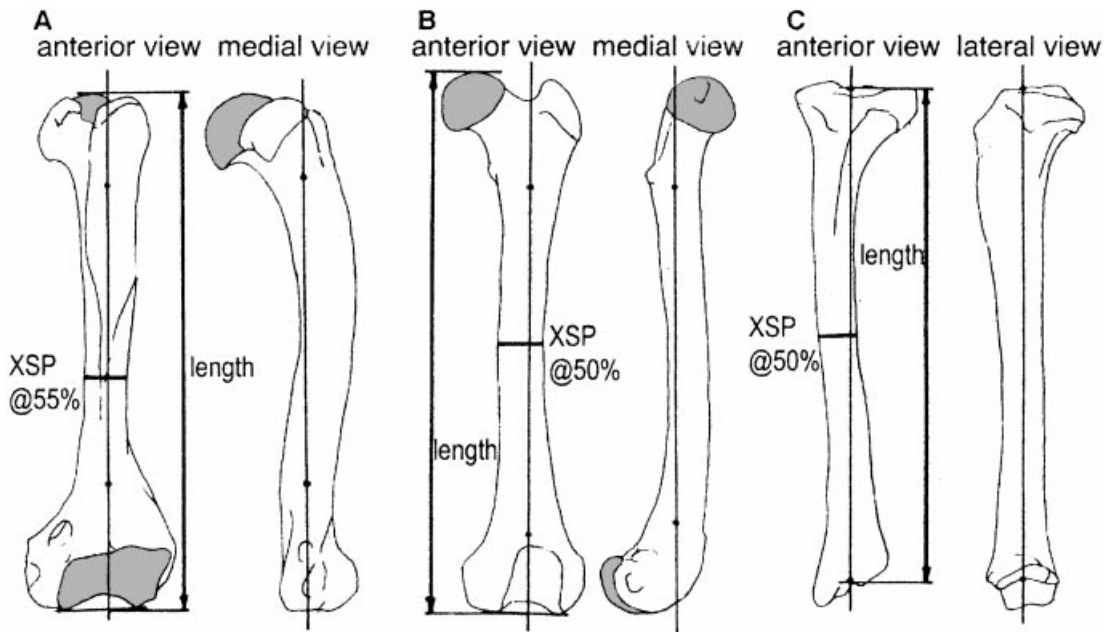
Taxa	Superfamily or Suborder	Family	Locomotor groups							Total
			A	S	T	Tg	Ta	Tf	C	
Eutheria–Carnivora	Caniformia	Canidae		1					7	8
		Mustelidae		4	10	2	2	6		14
		Procyonidae	2	2						4
		Ursidae		1						1
	Feliformia	Felidae	1	3						4
		Herpestidae			3	2	1			3
Marsupialia	Dasyuroidea	Viverridae	4	1	1	1				6
		Dasyuridae		1	1	1				2
		Thylacinidae							1	1
	Didelphoidea	Didelphidae	2	1	1		1			4
Total number of species			9	14	16	6	4	6	8	47

Most of the postcranial materials are associated with dental materials, and about three-quarters of the specimens were taxonomically identified to genus level. Among the specimens identified to genus, two-thirds were also identified to species. Taxonomic attributions of many other specimens can be identified based on their similarity to other specimens of known taxonomy, their bone size, and geologic age. Use of taxonomic names for the ten hyaenodontid genera and a list of specimens on which this study is based are provided in the Appendix.

The Eocene Epoch is divided into five North American Land Mammal Ages (NALMA): Wasatchian (55.5–50.3 Ma), Bridgerian (50.3–46 Ma), Uintan (46–40.5 Ma), Duchesnean (40.5–37 Ma), and Chadronian (37–33.7 Ma) (Woodburne 1987; Prothero and Berggren 1992; Berggren *et al.* 1995). The land mammal ages have been further subdivided based on lithology and/or faunal composition (e.g. Sandcouleean, Graybullian, Lysitean, and Lostcabinian subages, and Wa₀–Wa₇ biostratigraphic levels for Wasatchian and Gardnerbuttean, Blackforkian, and Twinbuttean subages, and Br_{0–3} biostratigraphic levels for Bridgerian; Gingerich 1980, 1983, 1989; Schankler 1980; Krishtalka *et al.* 1987; Gunnell, 1989). Wasatchian and Bridgerian localities have been well-studied stratigraphically (e.g. Gingerich 1989; Bown *et al.* 1994; Stucky 1984), and stratigraphic levels have been identified for many of the specimens.

The fossil hyaenodontid sample of this study includes the following nine genera from the Eocene of North America: *Arfia*, *Pyrocyon*, *Prolimnocyon*, *Prototomus* (Wasatchian), *Tritemnodon* (Wasatchian and Bridgerian), *Thinocyon*, *Machaeroides*, *Sinopa* (Bridgerian), and *Limnocyon* (Bridgerian and Uintan). Because taxonomic diversity within the family in North America decreases after the Bridgerian Land Mammal Age, postcranial specimens suitable for the analysis in this study were not available for hyaenodontids of later Eocene age (except for Uintan *Limnocyon*). Additionally, *Gazinocyon vulpeculus* from the late Wasatchian (Polly 1996) was examined based on data from the literature. Among these genera, *Prolimnocyon*, *Thinocyon*, and *Limnocyon* are classified in the subfamily Limnocyoninae, and *Arfia*, *Pyrocyon*, *Prototomus*, *Sinopa*, and *Tritemnodon* belong to the subfamily Proviverrinae. Machaeroidine *Machaeroides* is also included in the hyaenodontid sample in this paper, although the systematic position of this subfamily has been controversial (see Appendix). Most of the Wasatchian and Bridgerian hyaenodontid specimens have come from various localities in Wyoming, except for a few Wasatchian specimens from New Mexico (San Juan Basin). The *Limnocyon potens* specimen, the only sample for the Uintan Land Mammal Age in this study, comes from Wyoming (Washakie Basin).

Ten specimens of *Hyaenodon* (Hyaenodontinae) from the Orellan (early Oligocene; 34–32 Ma; Van Valkenburgh 1994) were also examined. All come from the Oredon beds of the White River Formation in



TEXT-FIG. 1. Orientation and data acquisition points of the long bones. A, humerus, B, femur, and C, tibia. Sagittal and coronal planes are indicated for each long bone, and dots indicate the position where the centroids of shafts were determined. Data collected are bone length (bold line with arrows), diaphyseal cross-sectional geometry (XSP: bold line), and articular dimension measurements (grey parts).

South Dakota, Nebraska and Wyoming. *Hyaenodon* *Neohyaenodon horridus* and *H. Protohyaenodon crucians* are also known from the middle Chadronian (36–35 Ma) and late Chadronian (35–34 Ma), respectively, as well as from the Orellan (Mellett 1977; Van Valkenburgh 1994).

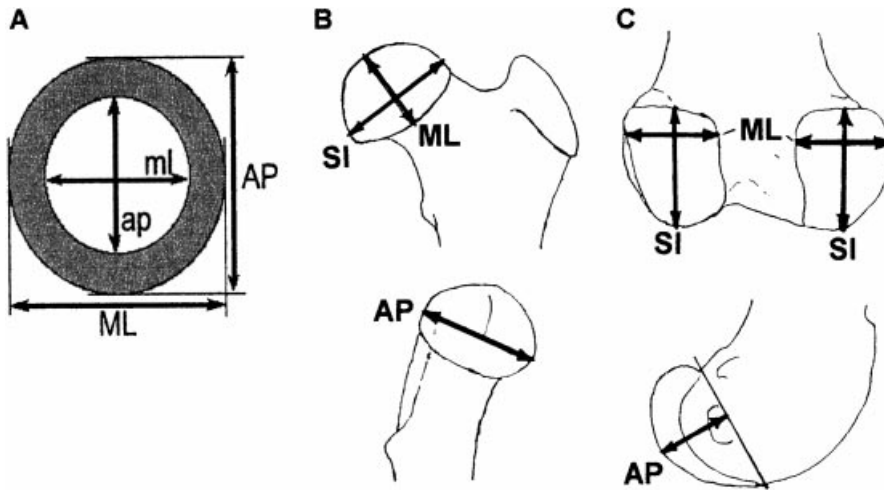
The hyaenodontid specimens examined belong to the following institutions: Department of Vertebrate Paleontology, the American Museum of Natural History, New York, NY (AMNH); Denver Museum of Natural History, Denver, CO (DMNH); Duke University Primate Center, Durham, NC (DPC); Museum of Geology, South Dakota School of Mines and Technology, Rapid City, SD (SDSM); University of Michigan Museum of Paleontology, Ann Arbor, MI (UM); Department of Paleobiology, the United States National Museum of Natural History, Washington, DC (USNM). The collection of the United States Geological Survey, Denver, CO (USGS), is now housed at the USNM.

METHODS

Measurements

The bone characters used here as body mass estimators were as follows: humeral, femoral, and tibial lengths, humeral, femoral, and tibial cross-sectional properties, and total proximal and distal articular dimensions of humeri and femora. These are the skeletal measurements which have been shown to correlate highly with body weight (and give smaller errors for body mass estimation), and they have been applied to body mass estimation of various fossil mammals (see above).

To obtain repeatable and comparable data for the analyses, orientation axes are pre-defined for humerus, femur and tibia (Text-fig. 1). Concerning the bone length measurements, humeral length was taken here from the most proximal point of the humeral head to the mid-point between the most distal points of the trochlea and capitulum (Text-fig. 1A). Femoral length is measured as the size of the vector parallel to the longitudinal axis from the proximal point of the femoral head to the midpoint between the distal points of the two condyles (Text-fig. 1B). Proximal and distal points of tibial length are set as the anterior edge of the condyles and the mid-point of the talar articular surface, respectively (Text-fig. 1C).



TEXT-FIG. 2. Modelling for data acquisition. A, diaphyseal cross-sectional geometries using biplanar symmetric model (ap, internal anteroposterior diameter; ml, internal mediolateral diameter; AP, external anteroposterior diameter; ML, external mediolateral diameter). B, articular sizes of proximal articulations using partial sphere model (AP, anteroposterior diameter; SI, superoinferior diameter; ML, depth). C, articular sizes of distal articulations using partial cylinder model (AP, anteroposterior diameter or depth; SI, superoposterior diameter or height; ML, mediolateral width).

Concerning cross-sectional geometry data, each bone segment was set in a defined orientation, and measurements were taken at the mid-shaft for the femur and tibia (Text-fig. 1B–C). For the humerus, to avoid the deltopectoral crest, which extends to about the mid-shaft in some of the sample species, cross-sectional geometry data were taken at the point 55 per cent from the proximal end (Text-fig. 1A). For most specimens, cross-sectional geometric data were obtained from biplanar x-ray images (i.e. images from anteroposterior and mediolateral aspects) using the methods described by Heinrich (1995; see also Runestad *et al.* 1993). This method models the cross-sections of long bones as two concentric ovals, the contour of the subperiosteal surface externally and the contour of the medullary cavity internally (Runestad *et al.* 1993; present study: Text-fig. 2A). As suggested in Runestad *et al.* (1993; also in Heinrich 1995, and Appendix here), the estimates from the concentric oval model are similar to the directly measured cross-sectional geometric values obtained from mid-diaphyseal sections of humeri, femora, and tibiae of many mammals. Consequently, this method dramatically increases sample sizes, because most museum specimens cannot be sectioned.

Cross-sectional properties obtained were cortical area (CA) and polar second moment of area (J). These are measures of rigidity against pure axial loadings (compression and tension) and torsional and overall bending loadings, respectively (Ruff and Hayes 1983; Biewener 1992; Swartz 1993). Total subperiosteal area (TA) was also calculated to allow comparison with fossil specimens that may have radiographically opaque material in the medullary cavity and do not allow calculation of any other cross-sectional properties. For some fossil specimens where a naturally broken section near mid-shaft was available, the section was photographed and digitised using a 2D digitiser, and the cross-sectional geometric data were calculated using the SLICE program (Nagurka and Hayes 1980). Otherwise, these properties were calculated using the biplanar x-ray technique, and the formulae are as follows:

$$CA = (\pi/4) \times ((AP \times ML) - (ap \times ml))$$

$$J = (\pi/64) \times ((AP^3 \times ML) - (ap^3 \times ml) + (AP \times ML^3) - (ap \times ml^3))$$

$$TA = (\pi/4) \times AP \times ML$$

where AP and ML indicate anteroposterior and mediolateral external diameters that were directly measured from the bones (Text-fig. 2A). Anteroposterior and mediolateral internal diameters (ap and ml) were measured from x-rays using needle-nosed callipers. It is common that x-ray images of bones are enlarged. Magnification factors (μ) of x-ray images for each bone in anteroposterior and mediolateral views were calculated as:

$$\mu = \text{ext. diameter from x-ray} / \text{ext. diameter from bone}$$

If the magnification due to x-ray was larger than 1.01, the internal diameters were corrected using the following formula:

$$\text{correct int. diameter} = \text{int. diameter from x-ray} / \mu$$

Many cross-sectional properties for the humerus and femur of Caniforms and some viverrids in this study include those used in Heinrich (1995) and Heinrich and Rose (1995). These raw data were available courtesy of Dr Heinrich.

Articular dimensions collected from the proximal and distal humeral and femoral articulations in this study are volume and surface area (Text-fig. 1A–B). Both properties are considered to be related to the degree of loadings transmitted through the joints. Articular volume affects the amount of bone that can exist in the joint, while surface area influences the distribution of the stress during the load transmission and mobility of the joint (Curry 1984). These articular dimensions were calculated from measurements (diameters, depths, and widths) taken directly from specimens using digital callipers by modelling the joints as partial spheres, partial cylinders, or partial cones (Text-fig. 2B–C). A high correlation between direct measurement of the articular size and model estimation has been demonstrated for humeral and femoral heads of primates and other mammals including Carnivora (Swartz 1989; Godfrey *et al.* 1991; Rafferty and Ruff 1994; Godfrey *et al.* 1995; Rafferty 1996). Formulae used to estimate the articular size are from Rafferty (1996) for humeral and femoral heads, from Runestad (1994) for femoral condylar volumes, and from Beyer (1991) for others.

Humeral and femoral heads were calculated as partial spheres (Rafferty 1996; Text-fig. 2B).

$$\text{Volume} = (\pi / 3) \times d^2 \times ((3 \times r) - d)$$

$$\text{Surface area} = 2 \times \pi \times r \times d$$

where depths (d) are superoinferior (proximodistal) and mediolateral lengths of the humeral and femoral heads, respectively. The radius (r) for the femoral head is one-half of the average of anteroposterior (AP) and superoinferior (SI) diameters.

$$r = (AP + SI)/4$$

The real radius (r) for the humeral head, of which depth is less than one-half of the diameters, was calculated from the following equation:

$$r = (SI/2) + (((AP + ML)/2)^2 / (8 \times SI))$$

AP and ML are anteroposterior and mediolateral diameters of the humeral head, respectively, and SI is superoinferior depth of the humeral head.

Volume and surface area of distal humeral and femoral parts are calculated as the sum of capitulum and trochlea and the sum of medial and lateral condyles, respectively. The humeral capitulum, the posterior portion of the humeral trochlea, and the femoral condyles were calculated as half of elliptical cylinders (Text-fig. 2C).

$$\text{Volume} = (\pi/2) \times a \times b \times w$$

$$\text{Surface area} = \pi \times ((a^2 + b^2)/2)^{1/2} \times w$$

where a and b are one-half of the anteroposterior and superoinferior lengths, respectively, and width (w) is the mediolateral dimension for humeral capitulum and femoral condyles. For the posterior portion of the

humeral trochlea, both a and b are one-half of the anteroposterior length at the median point in the humeral distal articulation, and w is the capitulum length measured at the anterior surface. The anterior portion of the humeral trochlea was calculated as a partial cone:

$$\text{Volume} = (\pi / 6) \times w \times (t^2 + ts + s^2)$$

$$\text{Surface area} = (\pi / 2) \times (s + t) \times (w^2 + (t - s)^2)^{1/2}$$

where t is half of the longest or medial diameter and s is half of the smallest or median diameter for the humeral distal articulation, and w is mediolateral length of the trochlea.

Statistical procedures

Body mass estimation regression equations (dependent variable = log-transformed body mass, and independent variables = various log-transformed limb bone measurements) were calculated from the Recent comparative sample using the reduced major axis (RMA) model. Although there have been arguments that the least squares model is more appropriate for predicting body mass from independent variables than the RMA model, the RMA model was used here because it is known that the least squares model underestimates the body mass of larger species (*Hyaenodon* species in this study) (Smith 1994b; Aykroyd *et al.* 1997).

The regression equations were calculated for the total pooled sample and each locomotor group. The data for these regressions were natural log-transformed species mean values. Differences in limb bone dimensions relative to body size among locomotor categories are often found in carnivores and other mammals (e.g. in primates: Schaffler *et al.* 1985; Ruff 1990; Rafferty 1996; in carnivorans: Heinrich 1995). Consequently, estimation of locomotor behaviour should be determined prior to body mass estimation. If differences exist in limb bone dimensions relative to body mass among locomotor groups, body mass estimation regressions within an appropriate locomotor group should provide better body mass estimates for each fossil form.

Additionally, the regression equations based on a set of 31 scansorial mustelid individuals with associated body mass were obtained in order to assess the errors owing to (intrasubfamilial) individual variation. The sample consists of 11 *Martes americana*, 11 *Martes pennanti*, and 9 *Gulo gulo*, weighing from 0.46 to 19.6 kg (Heinrich, pers. comm. 1996). These two mustelid genera are phylogenetically closely related (Bryant *et al.* 1993; Dragoo and Honeycutt 1997) and have similar gaits. For some other genera in the sample, each few individuals have associated body weights. However, these taxa were not included in this analysis because their phylogenetic and/or behavioural differences from *Martes* and *Gulo* would make evaluation of individual variation in the regressions difficult.

The ability of regression equations to predict dependent variables from independent variables (e.g. body mass from cross-sectional properties) can be measured by the percentage standard error of the estimate (per cent SEE; Smith 1981, 1984; Van Valkenburgh 1990). Per cent SEE can be calculated as:

$$\%SEE = \text{EXP}(2 + \text{SEE}) - 100$$

where SEE is standard error of estimation derived from the regression between variables in natural log space.

Body masses of fossil forms were first predicted using the body mass estimation regression equations in log-scale; the values were then anti-log-transformed into an arithmetic scale. As discussed by Smith (1993), this procedure causes a detransformation bias (i.e. difference between the predicted body mass value in the arithmetic scale and actual body mass value). The detransformation bias was corrected by multiplying the detransformed predicted value in the arithmetic scale by a ratio estimator (the ratio estimate technique; Smith 1993).

ACCURACY OF BODY MASS ESTIMATE REGRESSIONS IN EXTANT SAMPLE

Regressions for body mass estimation from limb bone measurements (lengths, cross-sectional properties, and articular dimensions) were calculated based on the Recent carnivore sample. Examples are given in

Text-fig. 3. Percentage standard errors of the estimate (per cent SEE) were used to compare the degree of error among the body mass estimation regressions derived from different limb bone measurements (Table 4). It was expected that elements of limb bone structure that are more plastic in response to loading would have a better correlation with body size. A good body mass estimator should have a small error for the predicted value (and usually a high correlation between the bone measurement and body mass). Body mass estimators should also have minimal phylogenetic influence. Phylogenetic influence on the limb bone measurements is assessed by comparing a sample with wide taxonomic diversity (e.g. the scansorial group, consisting of eight families) to one with smaller taxonomic diversity (e.g. scansorial mustelids).

Interspecific errors

In the regression of some bone measurements on body mass, elevational and/or slope differences were found between carnivorans and marsupials, suggesting some phylogenetic influence on the limb bone structure. These measurements are: humeral and tibial lengths, femoral cortical area, tibial cross-sectional properties, and distal humeral and femoral articular dimensions (volumes and surface areas). Differences in the reduced major axis (RMA) slope between the two taxonomic groups were tested using the method described by Clarke (1980), and differences in elevation were tested using the nonparametric quick test (Tsutakawa and Hewett 1977) with statistical significance 0.05. When statistically significant differences are found, marsupials were excluded for the calculation of regression statistics, because the uneven distribution of marsupials over the body size range of the total sample would bias the regressions.

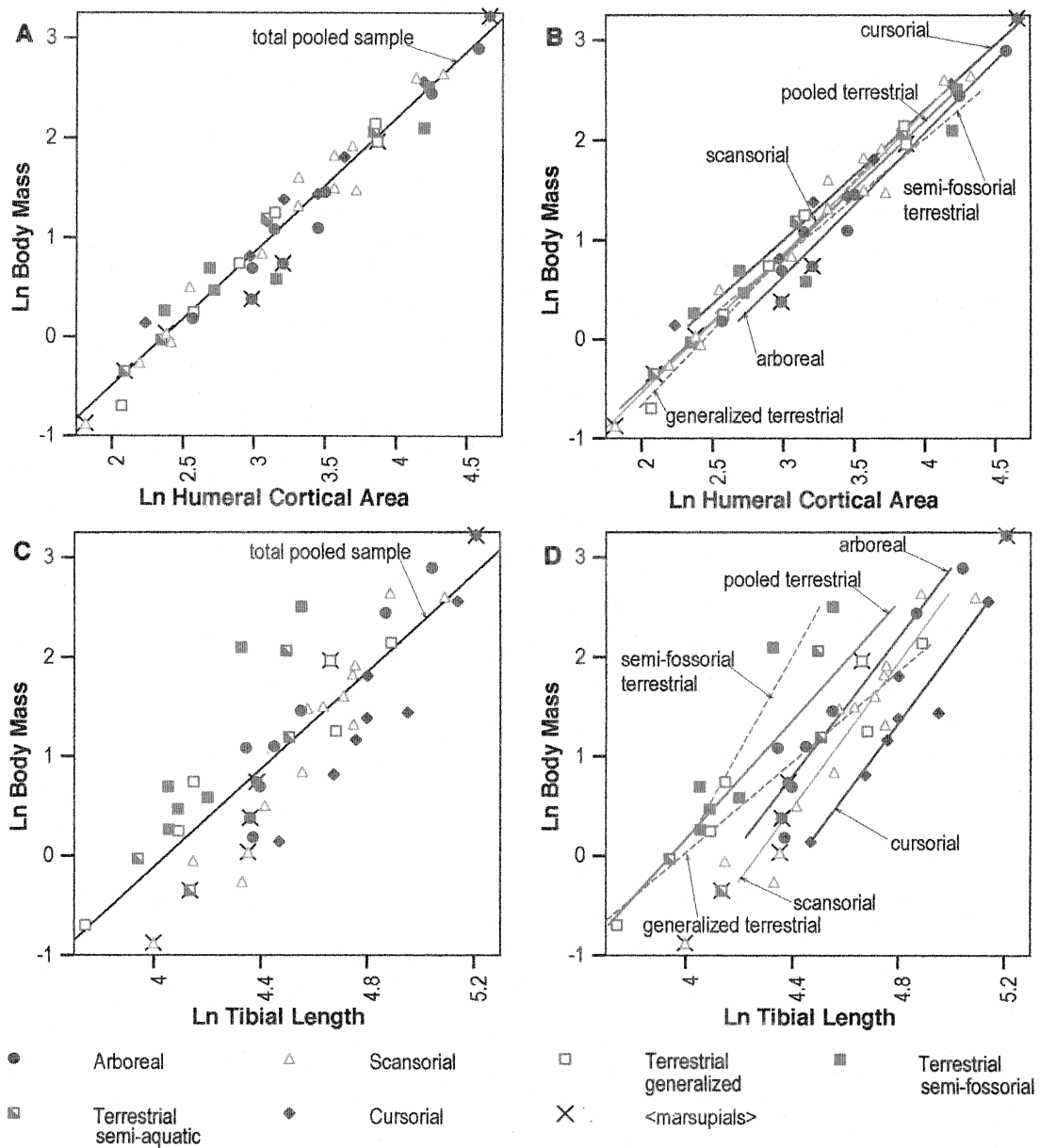
Body mass estimation regressions were calculated for the total pooled sample and for each locomotor group (arboreal, scansorial, pooled terrestrial, generalised terrestrial, semi-fossorial, and cursorial). The regression equations for the semi-aquatic group, one of the three non-cursorial terrestrial groups, were not calculated because the number of points in the samples for this group is too small and no strong evidence of semi-aquatic adaptation was found among hyaenodontids (Matthew 1915; Denison 1938). The species categorised as semi-aquatic were still included in the pooled terrestrial group.

For the body mass estimation regressions based on the total pooled sample of Recent carnivores, per cent SEE ranges from 8.9 to 12.6 (the first column in Table 4), suggesting that limb bone dimensions in general give smaller errors for body mass estimates than the body mass estimates derived from dental or cranial measurements (e.g. per cent SEE for body mass estimate regressions derived from M_1 length, occiput-orbital length, skull length, and head-body length of large carnivorans are 138 per cent, 61 per cent, 66 per cent, and 53 per cent, respectively; Van Valkenburgh 1990).

Cross-sectional properties give better estimates (lower per cent SEE) among the skeletal measurements used in this study. Body mass estimates from bone lengths have more error than estimates based on cross-sectional properties or articular dimensions. Concerning body mass estimates derived from cross-sectional properties and bone length measurements, humeral and femoral properties are better estimators (lower per cent SEE) of body mass than tibial measurements. Among articular measurements, the total distal femoral articulations have the lowest per cent SEE value, and the per cent SEE value is similar to those of humeral and femoral cross-sectional properties. There is not much difference in per cent SEE values between polar second moments of area (J) and cortical area (CA) of the same shaft, and between volume and surface area measurements of the same articulation. This may result because these pairs of measurements were calculated from the same skeletal dimensions and are not independent of one another.

If the magnitude of loading that acts on bones is influenced by an animal's locomotion, and if bones are remodelled to resist those loadings, it is expected that a sample consisting of a variety of animals would be more variable in bone structure in relation to body mass than a sample consisting of animals of similar locomotor behaviour. Consequently, it is expected that per cent SEE of body mass estimation regressions in each locomotor group will decrease compared with those of the total pooled sample. Per cent SEE of the body mass estimate regressions for the locomotor categories are listed in the second to seventh columns in Table 4. As shown in the table, the errors are slightly improved for most cases compared with those of the total pooled sample. The lowest per cent SEEs, on average, are found in the arboreal and cursorial groups.

Contrary to expectations, however, per cent SEE for body mass estimation regressions based on cross-sectional properties increased for the pooled terrestrial and semi-fossorial groups, and per cent SEE for the



TEXT-FIG. 3. Examples of body mass estimate regressions and data scatters. Vertical and horizontal axes are natural log-transformed body mass and limb bone dimensions as bone mass estimators, respectively. Regressions were calculated for the total pooled sample (A and C) and the locomotor groups (B and D). Statistics relating to these regressions are listed in Tables 4–5. For limb bone dimensions, humeral cortical area (A–B) and tibial length (C–D) are shown as examples. Humeral cortical area gave relatively better per cent SEE among the body mass estimators, while tibial length gave higher per cent SEE.

TABLE 4. Per cent SEE of body mass estimation regressions derived from Recent carnivores. Abbreviations: N, number of species per group (number of carnivorous species); n, number of *Martes* and *Gulo* individuals with an associated body weight; *, marsupial data are excluded; CA, cortical area; J, polar second moment of area; TA, total subperiosteal area; V, articular volume; SA, articular surface area.

x variable	All pooled sample N = 47 (40)	Arboreal N = 9 (7)	Scansorial N = 14 (12)	Terrestrial pooled N = 16 (14)	Terrestrial generalized N = 6 (5)	Terrestrial semi-fossorial N = 6 (6)	Cursorial N = 8 (7)	Scansorial mustelids n = 31
humeral length*	11.2	9.4	9.3	10.1	8.5	8.4	9.5	8.7
femoral length	11.3	9.4	9.2	11.2	9.6	8.9	9.2	8.8
tibial length*	12.6	10.3	10.3	12.3	10.0	10.8	9.8	9.3
humerus -CA	9.1	8.9	8.9	9.2	8.6	9.9	8.3	8.7
J	8.9	8.5	8.8	9.3	8.4	9.7	8.6	8.8
TA	8.9	8.4	8.8	9.2	8.3	9.4	8.7	9.0
femur -CA*	9.1	8.8	8.8	9.2	8.1	10.1	8.2	8.7
J	9.0	8.6	8.7	9.4	8.7	9.8	8.3	9.1
TA	9.2	8.7	8.8	9.6	9.1	9.6	8.4	9.3
tibia -CA*	9.5	9.4	9.4	10.1	9.9	9.9	8.4	9.2
J*	9.6	9.2	9.5	10.0	10.0	9.8	8.4	8.8
TA*	9.7	9.1	9.7	10.1	10.0	9.7	8.4	8.9
humeral head -V	9.4	8.2	9.8	9.4	10.1	9.6	9.6	9.1
SA	9.4	8.2	9.8	9.6	10.4	9.8	9.5	9.2
distal humerus -V*	9.9	8.9	11.1	9.2	8.6	9.3	8.7	8.5
SA*	9.8	8.8	11.3	9.2	8.7	9.5	8.5	8.5
femoral head -V	9.8	9.4	10.0	10.4	9.6	12.1	9.3	8.9
SA	9.8	9.5	10.0	10.4	9.5	12.1	9.4	9.0
distal femur -V*	9.2	8.6	8.8	9.6	9.3	9.4	8.7	8.7
SA*	9.0	8.5	9.1	9.3	9.0	9.4	8.6	8.6

regressions based on tibial cross-sectional properties increased for the generalised terrestrial group compared with the total pooled sample regressions. The per cent SEE of body mass estimation from femoral head measurements also increased in pooled terrestrialists and semi-fossorial terrestrialists, and that from distal femoral measurements increased in pooled terrestrialists, semi-fossorial terrestrialists and terrestrial generalists compared with the total pooled sample. All per cent SEEs for body mass estimates derived from articular dimensions, except total distal femoral articular volume, are larger in the scansorial group than in the total pooled sample. Per cent SEE of body mass estimation from humeral head dimensions is larger in all locomotor groups, except the arboreal group, than in the total pooled sample.

In general, as for the total pooled sample, body mass estimate regressions derived from bone lengths show a higher error than those from cross-sectional properties or articular dimensions, and regressions derived from humeral and femoral cross-sectional properties have a lower per cent SEE compared to those derived from tibial cross-sectional properties and articular dimensions in each locomotor group. The exception is the arboreal group, which has a lower per cent SEE of body mass estimate regression based on humeral head dimensions than either those of other locomotor groups or arboreal regressions derived from other measurements.

Errors owing to variations among individual specimens

In addition to the body mass estimation regressions based on species mean values, per cent SEE of body mass estimation regressions from limb bone measurements were obtained from a set of 31 scansorial mustelid individuals with associated body mass in order to assess the errors because of (intrasubfamilial) individual variation (last column in Table 4). The regressions based on scansorial mustelid individuals (last column in Table 4) were compared with the regressions based on species mean values of scansorial taxa (third column in Table 4), which includes six carnivoran and two marsupial families.

Compared with the body mass estimation regressions for the scansorial group using species mean values, the per cent SEE of most of the regressions using the scansorial mustelid individuals is slightly smaller, especially for the regression derived from distal humeral articular measurements. The per cent SEE of the regressions based on humeral cross-sectional properties and distal femoral articular volumes, where the per cent SEE in the scansorial group is low (less than 9 per cent), is very similar between the scansorial group using species mean values and the scansorial mustelid individuals. In body mass estimates based on humeral total subperiosteal area (TA) and femoral polar second moment of area (J) and total periosteal area (TA), per cent SEE is higher for the regressions based on scansorial mustelid individuals than those based on scansorial species mean values. The similarities between body mass estimate regressions derived from scansorial mustelid individuals and those derived from scansorial species indicate that the low per cent SEE for body mass estimate regressions derived from species mean data are not artificial, and can be applied to body mass estimates in individual specimens.

Smaller per cent SEE among the regressions using the scansorial mustelid individuals were found in the regressions based on distal humeral articular volumes and surface area (8.5 per cent), and distal femoral articular volume (8.7 per cent) and surface area (8.6 per cent). There is not much difference in per cent SEE values among the regressions based on bone lengths, cross-sectional properties, and articular measurements (8.5–9.3 per cent.). Bone length measurements provide less accurate body mass estimates compared with diaphyseal cross-sectional properties and articular measurements in the scansorial group based on species mean data; however, in the scansorial mustelid individual sample, the regressions based on bone lengths (especially humeral and femoral lengths) indicate errors as small as those of shaft and articular properties. This suggests that bone lengths can be reliable body mass estimators if the locomotor and phylogenetic diversity of a sample is small and if proportions of limb length relative to body mass remain constant. This conclusion is consistent with that suggested for body mass estimates in primates (Ruff 1989). Humeral and femoral cortical area (8.7 per cent) are better body estimators than other cross-sectional properties among the scansorial mustelid individuals.

Body mass estimations from tibial length, femoral total subperiosteal area, humeral head dimensions, and femoral head dimensions indicated relatively high per cent SEE among scansorial mustelid individuals

with associated body weights. This suggests relatively large individual random error among these properties in relation to body weight.

Discussion

Shaft cross-sectional properties and articular sizes turned out to be better body mass estimators than bone lengths in this study, and this is consistent with the cases of anthropoid primates (Ruff 1990) and large-sized carnivorans (Anyonge 1993). It has been suggested that long bone shaft diaphyseal structure is more sensitive to loading than articular dimensions and bone lengths, while articular structure is heavily influenced by relative mobility of joints (Ruff 1988; Swartz 1989; Godfrey *et al.* 1991; Rafferty and Ruff 1994). This suggestion accords with the results of this study, which show that humeral and femoral cross-sectional properties give smaller errors than articular dimensions. The higher error in body mass estimation based on tibial cross-sectional properties compared with those based on humeral and femoral cross-sectional properties seems to be related to the load transmitted through the fibula relative to the tibia in the lower leg. Similar observations (i.e. higher error in body mass estimation based on tibial dimensions compared with those based on femoral dimensions) have been found in primates (Ruff 1989). Cursors, which have a reduced fibula, have higher accuracy of body estimates based on tibial cross-sectional properties, comparable to those of humeral and femoral properties.

The increased per cent SEEs in terrestrial groups and scansorial groups compared with those in the total pooled sample may result because these groups consist of animals of different gaits (e.g. bouncing, galloping, and jumping for the scansorial group), animals of different behaviour specialisations (e.g. swimming versus digging within the terrestrial group; different degree of fossoriality within the semi-fossorial group), or animals of different phylogeny. Phylogenetic influence on distal humeral articular morphology was found in scansors and terrestrial generalists (Egi 1999; pers. obs. based on morphometric analysis of articular outlines). This explains the large error in the body mass estimate in regressions derived from distal humeral articular dimensions compared to regressions derived from any other measurements in the scansorial group.

The differences in per cent SEE between the scansorial regressions based on species mean values and the scansorial mustelid regressions based on individual specimen values probably result from the difference in phylogenetic diversity. However, the differences in phylogenetic diversity may also reflect different ranges of locomotor behaviour between these two sample sets. It is expected that per cent SEE of the body mass estimation from articular dimensions, which are more influenced phylogenetically, would decrease in a phylogenetically narrow sample. This expectation proved particularly true in the distal humeral articulation, and also in humeral and femoral head dimensions. Consequently, the suggestion that articular structure is more phylogenetically constrained than shaft diaphyseal structure, which is more plastic in relation to an animal's current activity (Ruff and Runestad 1992), is corroborated for distal humeral morphology, as well as for humeral and femoral head dimensions.

BODY MASS ESTIMATES FOR HYAENODONTIDS

Reconstruction of body sizes for hyaenodontids have been problematic. The taxon has been somewhat neglected. For many species, their body sizes have been suggested qualitatively, by indicating Recent carnivores whose skeletons are similar in size to those of hyaenodontids. Recently, Morlo (1999) provided body sizes of many hyaenodontids from the North American and European Eocene, by assigning them to six body mass classes. Particular body mass values have been estimated for only three genera, *Megistotherium osteothlastes* from the Miocene of East Africa (Savage 1973), *Hyaenodon horridus* and *H. crucians* from the lower Oligocene of North America (Van Valkenburgh 1987), and *Prolimmocyon atavus* from lower Eocene of North America (Gebo and Rose 1993). These quantitative body mass estimates are based on regression analyses of bone measurements or dental/cranial measurements relative to body mass. However, as mentioned by Van Valkenburgh (1987), it is probable that dentally or cranially-derived body size estimates give unreasonably large values in hyaenodontid creodonts because of their disproportionately large heads.

The body mass estimate regressions based on the Recent carnivore sample are applied to hyaenodontids to delimit the body size range for the hyaenodontid species more accurately, and the differences among the estimated body masses are discussed in the following section.

Procedure

Body mass estimation regressions (i.e. slope, intercept, and ratio estimator values) derived from the 20 bone measurements for the total pooled Recent sample and six locomotor groups (arboreal, scansorial, pooled terrestrial, generalised terrestrial, semi-fossorial, and cursorial) are listed in Table 5. Although they are listed here for completeness, the regressions based on the total pooled sample were not used here because they tend to have higher per cent SEE and relationships between bone measurements and body mass seem to be influenced by the uneven distribution of locomotor groups over the body size range.

Locomotor behaviours for the hyaenodontid genera were estimated categorically in another study (Egi 1999) by comparing them with Recent carnivores based on bivariate linear regression analyses and canonical variate analyses of limb bone dimensions and morphometric analyses of distal humeral and femoral articulations. Based on the locomotor behaviour estimates for hyaenodontid taxa, regressions based on one (or two) of the six locomotor groups were applied to calculate body mass for each hyaenodontid individual. If two locomotor groups were suggested for a hyaenodontid taxon (e.g. it fell between two modern groups in morphometric analyses), a mean of predicted body mass values from regressions based on the two locomotor groups was used. For the body mass estimates of *Gazinocyon vulpeculus*, of which locomotor estimates were not attempted in the above-mentioned study because of the incompleteness of the specimen, the generalised terrestrial group was chosen based on the locomotor interpretation by Polly (1996). If the relationships among bone measurements for hyaenodontid individuals were similar to those of one of the Recent carnivore locomotor groups on which the regressions are based, the range of body mass estimations derived from various bone measurements for each hyaenodontid individual should be small. In other words, if the appropriate locomotor category is chosen for hyaenodontid species, the body mass estimates based on different bone measurements should be similar.

As discussed in the previous section, the body mass estimations from different bone measurements have different accuracy and give different predictions for the same individual. A body mass estimate for each hyaenodontid individual was calculated in the following manner:

1. Assign each hyaenodontid taxon to one (or two) locomotor group(s).
2. Calculate body mass estimates from each bone measurement.
3. For each bone element (shaft or articulation), obtain a mean value of the estimates derived from different bone dimensions (e.g. cortical area and polar second moment of area, and articular volume and surface area), because it is redundant to use different properties of the same structure and these pairs are not independent measures.
4. If both proximal and distal articular dimensions are available for humeri or femora, obtain a mean of the estimates derived from the two articulations so that articular structure does not influence the body mass estimates more than shaft properties, which are better body mass estimators.
5. Calculate a body mass estimate for each individual by taking a mean of estimates from all the bone structures (humeral shaft, humeral articulation, femoral shaft, femoral articulation, and tibial shaft) available for the specimen.

Body mass estimates derived from total subperiosteal area (TA) of shaft cross-sections were used only when neither cortical area nor polar second moment of area was available. Although the estimation regressions were listed earlier, bone lengths were not used for estimating body mass due to the higher per cent SEE of the regressions.

Mean and range of estimated body masses among adult individuals within each species are listed in Table 6. The body mass estimate for each hyaenodontid individual as well as species means of adult individuals are presented in Text-fig. 4.

TABLE 5. Slope and intercept of body mass estimate regressions. Abbreviations: N, number of species per group (number of carnivoran species); RE = ratio estimators; *, marsupial data are excluded; CA, cortical area; J, polar second moment of area; TA, total subperiosteal area; V, articular volume; SA, articular surface area.

		All sample N = 47 (40)		Arboreal N = 9 (7)		Scansorial N = 14 (12)		Terrestrial pooled N = 16 (14)		Terrestrial generalized N = 6 (5)		Terrestrial semi-fossorial N = 6 (6)		Cursorial N = 8 (7)	
x variable		slope	intercept	slope	intercept	slope	intercept	slope	intercept	slope	intercept	slope	intercept	slope	intercept
humeral length*		2.642	-10.52	3.068	-12.54	3.400	-14.11	2.892	-11.16	2.526	-9.88	3.085	-11.81	3.255	-13.84
femoral length		2.774	-11.43	3.262	-13.75	3.206	-13.61	2.936	-11.72	2.546	-10.25	3.206	-12.70	3.280	-14.22
tibial length*		2.694	-10.97	3.499	-14.60	3.658	-15.62	2.982	-11.76	2.280	-9.09	4.812	-19.17	3.616	-16.02
humerus -	CA	1.372	-3.274	1.432	-3.661	1.412	-3.363	1.341	-3.175	1.510	-3.693	1.181	-2.712	1.295	-2.879
	J	0.685	-2.505	0.722	-2.846	0.696	-2.541	0.662	-2.350	0.764	-2.806	0.600	-2.142	0.701	-2.554
	TA	1.366	-3.789	1.452	-4.228	1.391	-3.873	1.316	-3.549	1.521	-4.200	1.197	-3.254	1.450	-4.143
femur-	CA*	1.408	-3.299	1.497	-3.856	1.494	-3.565	1.416	-3.261	1.375	-3.262	1.392	-3.085	1.330	-2.964
	J	0.725	-2.732	0.749	-3.020	0.763	-2.967	0.720	-2.594	0.672	-2.445	0.725	-2.471	0.700	-2.575
tibia -	TA	1.454	-4.172	1.526	-4.570	1.540	-4.537	1.430	-3.957	1.323	-3.682	1.484	-3.987	1.438	-4.139
	CA*	1.345	-3.133	1.376	-3.200	1.458	-3.566	1.302	-2.929	1.232	-2.965	1.332	-2.802	1.352	-3.249
	H*	0.660	-2.207	0.687	-2.291	0.726	-2.629	0.636	-1.986	0.600	-2.050	0.645	-1.833	0.695	-2.568
	TA*	1.312	-3.417	1.394	-3.648	1.454	-4.002	1.261	-3.122	1.182	-3.106	1.283	-2.993	1.409	-3.990
humeral head -	V	0.987	-4.816	1.010	-5.004	0.965	-4.733	1.002	-4.817	1.070	-5.251	0.929	-4.409	1.061	-5.331
	SA	1.476	-6.989	1.521	-7.302	1.433	-6.794	1.495	-7.016	1.599	-7.591	1.399	-6.538	1.577	-7.583
distal humerus -	V*	0.913	-4.049	0.960	-4.178	0.958	-4.322	0.914	-3.991	1.008	-4.539	0.798	-3.375	0.874	-4.056
	SA*	1.376	-6.196	1.452	-6.525	1.448	-6.593	1.361	-6.065	1.496	-6.776	1.209	-5.312	1.293	-5.906
femoral head -	V	1.010	-4.748	0.996	-4.698	1.016	-4.777	1.036	-4.856	1.143	-5.546	0.974	-4.565	1.005	-4.764
	SA	1.522	-6.848	1.480	-6.658	1.531	-6.886	1.563	-7.027	1.739	-8.015	1.458	-6.542	1.523	-6.893
distal femur -	V*	0.991	-4.264	1.019	-4.364	1.053	-4.714	1.012	-4.260	0.910	-3.895	1.115	-4.615	0.941	-4.089
	SA*	1.483	-6.295	1.525	-6.466	1.585	-6.918	1.473	-6.160	1.343	-5.678	1.580	-6.545	1.437	-6.122

TABLE 6. Species means and ranges of estimated body mass for hyaenodontids. Abbreviations: N, number of adult or subadult individuals per species; sub., subadult; body masses are in kg. (See Appendix for the classification of *Sinopa*.)

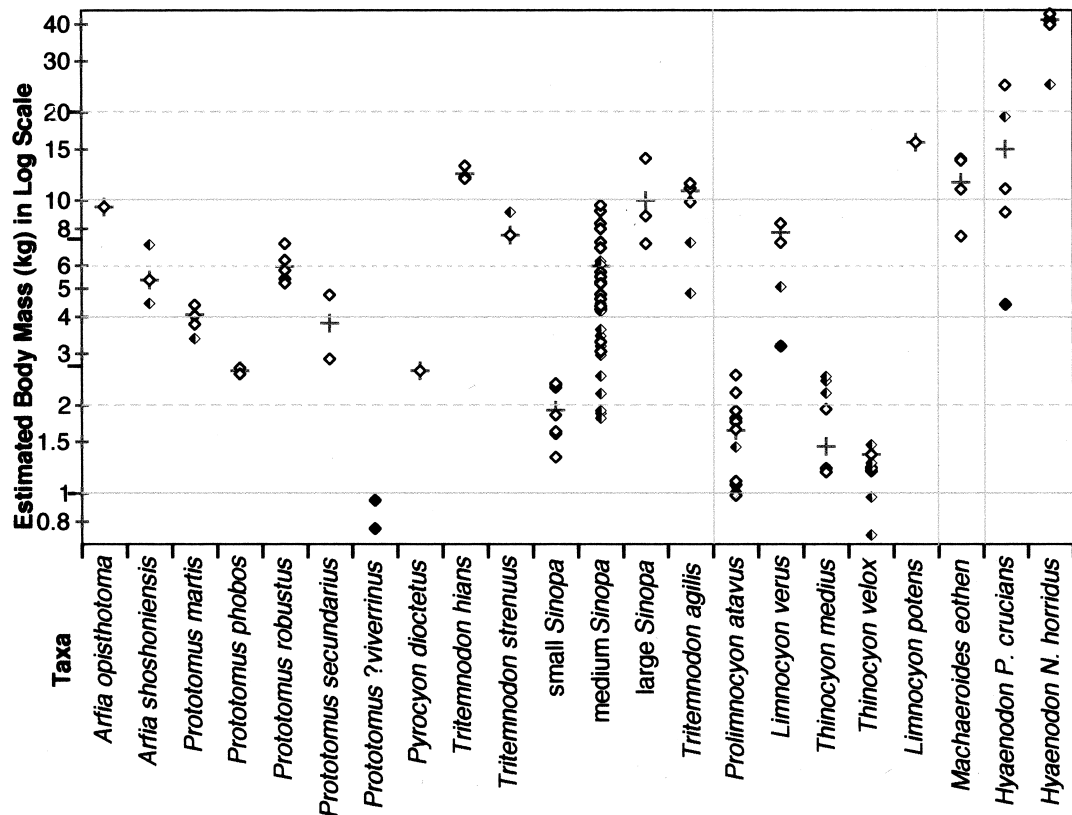
		N		mean		range (adult + sub.)	
Taxa	age	adult	(sub.)	adult	(adult + sub.)	smallest	largest
Proviverrines							
<i>Arfia opisthotoma</i>	Wasatchian	1	0	9.52			
<i>Arfia shoshoniensis</i>	Wasatchian	1	2	5.36	5.63	4.45	7.08
<i>Prototomus martis</i>	Wasatchian	3	1	4.07	3.90	3.38	4.39
<i>Prototomus phobos</i>	Wasatchian	2	0	2.62		2.56	2.68
<i>Prototomus robustus</i>	Wasatchian	5	1	5.95	5.83	5.22	7.13
<i>Prototomus secundarius</i>	Wasatchian	2	0	3.81		2.87	4.76
<i>Pyrocyon dioctetus</i>	Wasatchian	1	0	2.62			
<i>Tritemnodon hians</i>	Wasatchian	3	0	12.37		11.90	13.15
<i>Tritemnodon strenuus</i>	Wasatchian	1	1	7.62	8.38	7.62	9.14
small <i>Sinopa</i>	Bridgerian	7	0	1.92		1.33	2.37
medium <i>Sinopa</i>	Bridgerian	17	13	5.97	4.86	1.80	9.64
large <i>Sinopa</i>	Bridgerian	3	0	9.99		7.14	13.97
<i>Tritemnodon agilis</i>	Bridgerian	3	2	10.78	8.87	4.82	11.44
Limnocyonines							
<i>Prolimnocyon atavus</i>	Wasatchian	12	1	1.64	1.63	0.98	2.54
<i>Limnocyon versus</i>	Bridgerian	2	1	7.78	6.87	5.07	8.36
<i>Thinocyon medius</i>	Bridgerian	3	3	1.45	1.91	1.18	2.50
<i>Thinocyon velox</i>	Bridgerian	1	6	1.36	1.10	0.72	1.46
<i>Limnocyon potens</i>	Uintan	1	0	15.84			
Machaeroidines							
<i>Machaeroides eothen</i>	Bridgerian	4	0	11.54		7.56	13.92
Hyaenodontines							
<i>Hyaenodon P. crucians</i>	Orellan	3	1	14.97	16.08	9.14	24.80
<i>Hyaenodon N. horridus</i>	Orellan	3	2	41.42	38.22	24.93	43.31

Comparison among estimated body masses

Although small per cent SEE values in the Recent sample were suggested for body mass estimators in the previous section, some bone measurements consistently seem to either underestimate or overestimate body masses for hyaenodontids, presumably because of differences in skeletal proportions between Recent carnivores and hyaenodontids, as discussed in earlier sections. To illustrate this, body mass estimates derived from dimensions of various bone elements were compared with one another for 49 adult and subadult individuals which have more than two bone elements available (selected individuals are shown in Text-fig. 5). The body mass estimates derived from dimensions of each bone element were divided by average of body mass estimates for the individual, so that the values were normalised and could be compared among individuals.

Among the three bone lengths, three shaft rigidities, and four articular sizes used for body mass estimations, humeral shaft rigidities, tibial shaft rigidities, and distal femoral articular dimensions provide the closest estimates to the result calculated from the combination of dimensions of bone elements.

Although femoral cross-sectional properties were suggested to be one of the best body mass estimators among the bone measurements in the above analysis and other previous studies, femoral cross-sectional properties frequently give much larger body mass values for hyaenodontids than other body mass estimators. This is consistent with the conclusion reached from the locomotor assessment (Egi 1999)

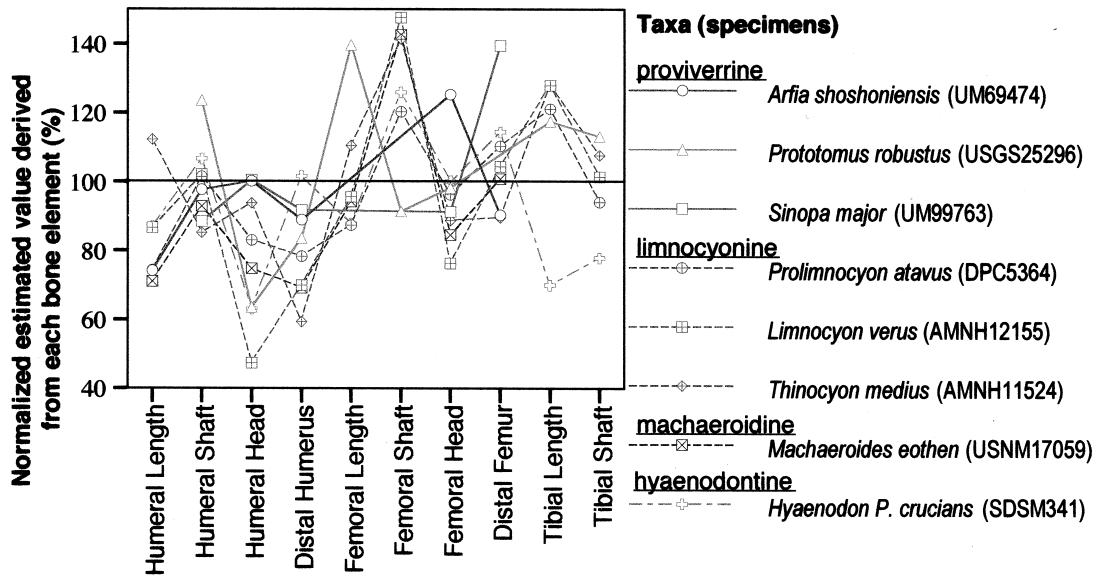


TEXT-FIG. 4. Summary of estimated body masses for hyaenodontids. The cross represents the species mean based on adult individuals. Other symbols indicate the developmental age of each specimen: open, adult; half-closed, sub-adult; closed, juvenile (see Appendix for the classification of *Sinopa*).

that femoral shaft rigidities are larger relative to humeral and tibial shaft rigidities and femoral articular dimensions in hyaenodontids than in Recent carnivorans. Body mass estimates derived from femoral shaft dimensions are larger than the body mass estimates derived from combinations of all bone elements in 25 of the 26 individuals, suggesting a possible overestimate.

On the contrary, tendencies for smaller body mass values were found in the estimates derived from distal humeral articular dimensions (in 25 out of 30 individuals) and femoral head dimensions (29 out of 35 individuals). Humeral head dimensions also tend to give smaller body mass estimate values, and in about one-half of the individuals, body mass estimates derived from humeral head dimensions are less than 90 per cent of the body mass estimates derived from the combined bone elements. The underestimation of body mass derived from distal humeral articulation relates to the distal humeral articular morphology of hyaenodontids, which is anteroposteriorly and proximodistally small. It is not clear why humeral and femoral head dimensions give relatively smaller body mass estimates for hyaenodontids based on modern carnivore regressions. The relatively large individual variation for humeral and femoral head dimensions, which was suggested in the comparisons of per cent SEE of regressions, may have affected the results, or other limb bone dimensions may overestimate body masses, rather than humeral and femoral head dimensions underestimating body mass.

Although not used for body mass estimates in North American hyaenodontids, estimates derived from bone lengths seem to be influenced by the choice of locomotor groups for the taxa. For example, the regressions of the pooled terrestrial group, which has short limbs, were applied to *Thinocyon*. Limbs of



TEXT-FIG. 5. Comparison of estimated body masses from different bone elements. Eight selected specimens are shown here. Symbols indicate the presence of the bone element for the specimen.

Thinocyon seem not to be shortened relative to other bone dimensions as much as those of modern terrestrialists of similar size, resulting in larger body mass estimates derived from bone lengths. It is suggested that a locomotor group needs to be chosen very carefully when a body mass is estimated from bone lengths.

Estimated body mass in this study vs. previous suggestions

Body masses of 24 species in 10 genera of North American hyaenodontids are estimated based on measurements of limb bones in this study. This section summarises the body masses obtained, and compares them with body sizes for hyaenodontid species suggested in previous studies.

For some of the species, considerable intraspecific variation in estimated body masses was observed. Large variation in estimated body mass was observed in *Sinopa* and *Prolimnocyon*. These taxa include many individuals for which body mass was estimated from one bone element, and the large variation probably resulted in part from the differences in body mass estimates between bone elements rather than true intraspecific variation in body size. In addition, medium-sized *Sinopa*, and possibly small *Sinopa*, contains two species (*S. rapax* and *S. grangeri* for the medium form and *S. minor* and *S. pungens* for the small form), which probably increases the variation.

The other possible cause of large intraspecific variation is dimorphism in size because of sexual differences, which is common among modern carnivorans. It is most obvious in some *Martes* and *Mustela* species among the fissipeds, but differences in body size between males and females are known in a variety of living species, such as large felids, wolves, bears, procyonids and badgers (Burt and Grossenheider 1976; MacDonald 1984), and intraspecific dimorphism was reported in a fossil carnivoran species, *Miacis petilus* (Heinrich and Rose 1995). Sex-dependent size differences are also known in some Recent carnivorous marsupials (e.g. *Dasyurus*; Strahan 1995). Dimorphic body size in fossil species has been argued, for primates particularly, with regard to both taxonomy [i.e. females and males of one species or co-occurrence of more than one species (Josephson *et al.* 1996 and references cited therein), e.g. in *Australopithecus afarensis*, Kimbel *et al.* 1994] and evolution of sexual dimorphism in association with socioecology (Krishtalka *et al.* 1990; Kelley 1995).

Intraspecific dimorphism has been suggested for two species of North American hyaenodontids, *Thinocyon velox* (Matthew 1909) and *Hyaenodon horridus* (Matthew 1901; Scott and Jepsen 1936; Mellett 1977). It is difficult to compare the estimated body sizes for hyaenodontid fossils because the values fluctuate a lot depending on which elements are available for body mass estimation of each hyaenodontid individual; however, the result in this study seems to support the suggestion. The small sample size of skeletal materials for many taxa limits the ability to estimate intraspecific variation, so it is not clear how common dimorphism was among hyaenodontid creodonts at this point. A study involving dental measurements would provide size-frequency distributions within species more accurately, and may resolve this question.

For Wasatchian genera, the *Arfia* sample includes two species, *A. shoshoniensis* and *A. opisthotoma*. The body mass for the former is estimated to have been about 7 kg for an adult, and the latter is estimated at about 9.5 kg. This estimated body mass for *Arfia shoshoniensis* is similar to that suggested by Gingerich and Deutsch (1989; 5–7 kg). *Pyrocyon dioctetus* is estimated to have weighed about 2.6 kg. Body mass for *Prolimnocyon* (*P. atavus*) is estimated at about 1–2.5 kg in this study. One quantitative estimate was attempted for *Prolimnocyon atavus* by Gebo and Rose (1993) using Gingerich's regressions (1990) of limb lengths and diameters against body mass among Recent mammals, which provides an estimate of 1.8–1.9 kg, with a range from 1.5–3 kg. The *Prolimnocyon* individual examined by Gebo and Rose (1993; DPC 5364) is larger than other individuals examined in this study. For this particular individual, the body mass value estimated in this study is similar to that suggested by Gebo and Rose (1993). The reason why DPC 5364 is larger than others is not clear. It may be the result of intraspecific variation. Five species of *Prototomus* are included in this study, and their body masses are estimated as: about 0.76 and 0.95 kg for juveniles of *P. ?viverrinus*; 2.6 kg for *P. phobos*; 2.9–4.8 kg for *P. secundarius*; 3.4–4.4 kg for *P. martis*; and 5.2–7.1 kg for *P. robustus*. Gingerich and Deutsch (1989) estimated *P. martis* to be 1–2 kg, much smaller than the value estimated here, but they provided no justification for their estimate. Wasatchian *Tritemnodon* species are larger than *Prototomus*, and *T. strenuus* and *T. hians* are estimated to have weighed about 8 and 12 kg, respectively. *Gazinocyon vulpeculus* from the late Wasatchian seems to have weighed about 8 kg. Of the 12 species mentioned above, ten (*Arfia shoshoniensis*, *A. opisthotoma*, *Prolimnocyon atavus*, *Prototomus phobos*, *P. martis*, *P. secundarius*, *P. robustus*, *Pyrocyon dioctetus*, *Tritemnodon strenuus*, and *Gazinocyon vulpeculus*) are also included in Morlo (1999). For eight species, body mass estimates in this study are consistent with his assignment of body sizes to six body mass classes (less than 1 kg, 1–3 kg, 3–10 kg, 10–30 kg, 30–100 kg, and more than 100 kg; Morlo 1999). For *Prolimnocyon atavus* and *Prototomus martis*, the results in this study is slightly greater than those in Morlo (1999). Because these studies were carried out using different specimens, the differences are probably a reflection of individual variation.

Among the Bridgerian hyaenodontids, *Sinopa* has the largest number of species. Although the species identifications are not clear for some specimens, the estimates made in this study suggest that smaller species (*S. minor* and possibly *S. pungens*) weighed 1.3–2.4 kg, medium-sized species (*S. rapax* and *S. grangeri*) weighed up to about 10 kg, and the largest species (*S. major*) weighed up to 14 kg. Morlo (1999) assigned *Sinopa minor* to the 1–3 kg body mass class and *S. grangeri* and *S. rapax* to the 3–10 kg body mass class, and these are consistent with my results. Matthew (1909) suggested that the Bridger *Tritemnodon*, *T. agilis*, was the size of a wolverine (7–32 kg; Nowak 1991). My results suggest that this species weighed about 10 kg, which is within the lower range of wolverine body size. The bones of *T. agilis* are intermediate in size between those of the two Wasatchian *Tritemnodon* species, and body mass estimates for *T. agilis* are accordingly between those estimated for the two Wasatchian *Tritemnodon* species.

Matthew (1909) suggested that *Thinocyon velox* was about the size of a mink (0.5–2.3 kg; see Table 1 for references). A body mass range of 0.7 to 1.5 kg was estimated from my analyses. The body masses of *T. medius* range from 1.2 to 2.5 kg. Matthew (1909) pointed out that *Thinocyon velox* has large intraspecific variation in size cranially and postcranially, and suggested the existence of sexual dimorphism in this species similar to that in Recent mustelids. Fortunately, both of the *Thinocyon* species are known from individuals that have relatively complete skeletons, and the sample I examined seems to support the existence of dimorphism in *Thinocyon velox* and *T. medius* (Text-fig. 4). Among *Thinocyon*

medius, the three subadult individuals are larger than the three adult individuals. Two of the adults are much smaller than the three subadult individuals. Smaller *Thinocyron medius* is estimated to have weighed around 1.2 kg based on an adult individual with complete humeri and femora (AMNH 12154), whereas larger individuals weighed nearly 2.5 kg (AMNH 11529 and USNM 361373). For *Thinocyron velox*, one adult, six subadults and one juvenile were available for study. Two subadults (AMNH 13081 and DMNH 21764) seem to be smaller individuals, and their body masses were estimated at around 0.7 kg. Other individuals, including the juvenile (AMNH 13082), are larger than these two subadults, and larger *Thinocyron velox* probably weighed around 1.4 kg (based on AMNH 12630 and USNM 22480). One of the other possible explanations for the intraspecific variation could be geographical variation, which is found in some modern carnivores (e.g. *Prionailurus bengalensis*, *Lontra canadensis* and *Taxidea taxus* in this study). However, two of the *Thinocyron velox* individuals, one smaller and the other larger forms (AMNH 13081 and 13082), came from the same fossil site; therefore, this explanation does not fit with this case.

In Recent carnivorans such as *Mustela* and *Martes*, males are 30–100 per cent larger than female (MacDonald 1984). For example, in *Martes pennanti*, mean body masses are 2.40 kg in females (s.d. = 0.06, N = 32) and 4.85 kg in males (s.d. = 0.13, N = 36) (Coulter 1966, cited in Strickland *et al.* 1982a). Though the sample is small, the difference in body size between smaller and larger forms in each *Thinocyron* species compares well with data from the Recent species. It has been suggested that the sexual dimorphism in body size in *Mustela* and *Martes* species is associated with their smaller body size, relating to different constraints on reproductive strategies and on hunting methods between sexes (King 1989). The dimorphism in *Thinocyron* might have had an ecological significance similar to that in the smaller mustelids.

Various Recent animals (e.g. grison, raccoon, otter, and badger; Wortman 1901; Matthew 1909) were suggested to be similar in size to *Limnocyron verus*, which implies a body size anywhere from 1 kg (smaller grison, *Galictis cuja*; Nowak 1991) to 14 kg (large river otter, *Lontra canadensis*; Nowak 1991); hardly a precise estimate. Morlo (1999) provided the smaller body size range of 3–10 kg for this species. Body masses for adult individuals of Bridgerian *Limnocyron*, *L. verus*, are here estimated as 7.2 and 8.4 kg. Although the sample for *Limnocyron verus* consists of only four individuals, the femora in one of the two adults is half the size of that in the other, and it is possible that dimorphism also existed in this species (unless there are two species).

The body size of *Machaeroides eothen* is the largest of the Bridgerian species studied here, and is estimated at 11–14 kg. *Limnocyron potens* from the Uintan is even larger than *M. eothen*, and estimated to have weighed about 16 kg.

Two Orellan *Hyaenodon* species examined here are the smaller *H. crucians* and larger *H. horridus*. The possible existence of sexual dimorphism in *Hyaenodon* species was suggested by Matthew (1901) and Scott and Jepsen (1936), who argued that *H. horridus* and *H. cruentus* are different sexes of the same species. Later, Mellett (1977) also concluded that the differences between these two species are a result of dimorphism based on the frequency distribution of tooth size; hence, he synonymized *H. cruentus* with *H. horridus*. Dimorphism in body size is also supported in *Hyaenodon*, at least for one species (*H. crucians*). Among *Hyaenodon crucians*, two adult individuals (USNM 15936 and an uncatalogued USNM specimen with a field number 102-32) seem to belong to smaller forms, and the other adult (USNM, uncatalogued) and one subadult individual (SDSM 383) seem to belong to larger forms. The two forms weighed around 10 and 20 kg, respectively. Dimorphism in *Hyaenodon horridus* is not clear from the results of my study. Two subadult individuals (AMNH 9809 and SDSM 2610) in a similar stage of development are very different in size, which may support the existence of dimorphism (Text-fig. 4). One individual had been assigned to *Hyaenodon cruentus* (AMNH-F 75692), which has been interpreted as a smaller form of *Hyaenodon horridus* (Mellett 1977). This individual is proportionally smaller (except in humeral head size) than other adult specimens and the larger subadult individual, but the differences between them are not very great.

It is difficult to compare the intraspecific variation in *Hyaenodon* species to that in Recent carnivorans because Recent carnivorans similar in size to *Hyaenodon* in size usually do not show sexual dimorphism (e.g. body sizes are not distinguishable between sexes in some canids such as *Lycaon* and hyaenids; MacDonald 1984). For larger carnivores, differences in body size between sexes are reported to be about

60 per cent (males 60 per cent larger than female) in *Ursus arctos* from Yellowstone National Park (Craighead and Mitchell 1982) and about 50 per cent in *Panthera pardus* (MacDonald 1984). Though the body estimates in this study support Mellett's (1977) observation about intraspecific dimorphism in *Hyaenodon*, its ecological significance is not clear.

In this study, the largest adult individual of *H. crucians* among the sample is estimated to have weighed about 25 kg, while smaller adult individuals only weighed about 10 kg. Adult and larger subadult *Hyaenodon horridus* individuals included here seem to have weighed about 40 kg, and not exceeded 60 kg, and the smaller subadult individual weighed 25 kg. Van Valkenburgh (1987) estimated the body mass for *H. crucians* and *H. horridus* at 28 kg and 153 kg based on skull lengths and 9 kg and 32 kg based on head-body lengths, respectively, using regressions of skull length and head-body length against body weight in a sample of 139 Recent carnivore individuals in 70 species. Because of the large differences in the results between the two body mass estimators, Van Valkenburgh (1987) pointed out that neither skull length nor head-body length is reasonable for *Hyaenodon*. The *H. crucians* individual (PU 13603) of which head-body length was measured in her study, seems to be a smaller adult, while one of the two *H. horridus* individuals of which head-body length were measured (PU 10995; based on Mellett 1977, fig. 35), seems to be a larger adult. The large difference between the estimated body masses from the two measurements in Van Valkenburgh (1987) seems to have been influenced by the sample available for measurement. Although her sample differed from the *Hyaenodon* sample used here, the body mass estimates I obtained seem to be more similar to her estimates based on head-body length than those based on skull length. This is especially true for *H. horridus*. It may be concluded that body mass estimates based on cranial measurements give larger values, whereas estimates based on skeletal measurements give more consistent body masses.

Chronological trends in body size among North American hyaenodontids

Body sizes of the North American hyaenodontids available for study were compared with each other in relation to their chronological distributions in order to clarify the change in range and/or shift in body size among North American hyaenodontids through geological time. From a palaeoecological standpoint, variation and chronological changes in locomotor behaviour and body mass suggest the possible existence of microhabitat partitioning and/or interspecific competition in predator guilds that consisted of hyaenodontids and other carnivorous vertebrates (Van Valkenburgh 1985, 1988, 1992). Because dental and/or cranial morphologies vary among hyaenodontid subfamilies, interspecific comparison of body size among hyaenodontid species had been difficult until body masses with small errors were obtained for these species.

Table 7 summarises the distribution of hyaenodontid species and their body size ranges in each North American Land Mammal Age (Table 7A–B, Wasatchian; C, Bridgerian; D, Uintan; E, Orellan). There is a lot of overlap in body size range among Wasatchian hyaenodontid species when the samples from all the subages are combined. Consequently, the Wasatchian sample was further divided into Wa_{0–2} [the Sandcouleean, or below Shankler's Biohorizon A (1980) in the Bighorn Basin; not shown because only *Arfia shoshoniensis* was available for this period among the hyaenodontids known from this interval: e.g. *Arfia zeke*, *Acarictis ryani*, *Galecyon mordax*, *Prolimmocyon haematus*, and *Prototomus deimos*], Wa_{3–4} [the early and middle Graybullian, or below Shankler's Biohorizon B (1980) in the Bighorn Basin; Table 7A], and Wa_{5–7} [the late Graybullian, Lysitean, and Lostcabinian, or above Shankler's Biohorizon B (1980) in the Bighorn Basin; Table 7B], which presumably reflects the condition of coexistence of hyaenodontid species better. Similarly, Table 7C consists of hyaenodontids from the Br₂ level only (early and late Bridgerian were omitted from the table because of the small sample size).

Among the hyaenodontid sample from Wa_{3–4} (Table 7A), *Arfia* (*A. opisthotoma*) is larger than the three *Prototomus* species. Another hyaenodontid that is known from this period but is not included in the sample is *Prolimmocyon atavus* (Gingerich and Deutsch 1989), which is smaller than the *Prototomus* species. Some other species, such as *Galecyon mordax*, *Prolimmocyon haematus*, and *Prototomus deimos* are known from the earliest Wa₃ stage, and the size of teeth (Gingerich and Deutsch 1989; Morlo 1999) indicates that, apart from *Galecyon*, these taxa were smaller than *Prolimmocyon atavus*.

TABLE 7. Distribution of the hyaenodontid species with regard to body size ranks and North American Land Mammal Age. Intervals of body size ranks were defined using log-scale; P, L, M, and H refer the subfamilies Proviverrinae, Limnocyoninae, Machaeroidinae, and Hyaenodontinae, respectively; x indicates the existence of individual(s) in the rank; (x) denotes that all the individuals in the rank are subadult. Juveniles were not included. Species that are not included in the table are: A, proviverrine *Galecyon mordax* and *Prototomus deimos*, and limnocyonine *Prolimnocyon haematus* (from early Wa₃); B, proviverrine *Prototomus viverrinus* (from Wa₅₋₆), proviverrine *Gazinocyon vulpeculus*, limnocyonine *Prolimnocyon antiquus*, and machaeroidine *Machaeroides simpsoni* (from Wa₇); C, limnocyonine *Thinocyon mustelinus*; and D, limnocyonine *Oxyaenodon dysclerus*, and *O. dysodus*, and machaeroidine *Apataleurus kayi*. See Appendix for the classification of *Sinopa*.

Taxa	(subfamily)	body size ranks (kg)								
		~1.00	~1.65	~2.72	~4.48	~7.39	~12.2	~20.1	~33.1	33.1~
A, Wa3–4: early middle Wasatchian										
<i>Protomus phobos</i>	(P)			x						
<i>Prototomus martis</i>	(P)				x					
<i>Arfia shoshoniensis</i>	(P)				(x)					
<i>Prototomus robustus</i>	(P)					x				
<i>Arfia opisthotoma</i>	(P)						x			
B, Wa5-7: middle–late Wasatchian										
<i>Pyrocyon diocetus</i>	(P)			x						
<i>Prototomus secundarius</i>	(P)				x	x				
<i>Prototomus robustus</i>	(P)					x				
<i>Tritemnodon stenuus</i>	(P)							x		
<i>Tritemnodon hians</i>	(P)							x	x	
<i>Prolimnocyon atavus</i>	(L)	x	x	x						
C, Br2: middle Bridgerian										
small <i>Sinopa</i>	(P)		x	x	x					
small <i>Sinopa</i>	(P)				(x)	x		x		
large <i>Sinopa</i>	(P)					x		x		
<i>Tritemnodon agilis</i>	(P)					(x)		x		
<i>Thinocyon velox</i>	(L)	(x)	x							
<i>Limnocyon verus</i>	(L)					x				
<i>Machaeroides eothen</i>	(M)							x	x	
D, Uintan										
<i>Limnocyon potens</i>	(L)								x	
E. Orellan (34–32 Ma)										
<i>Hyaenodon P. crucians</i>	(H)						x	(x)	x	
<i>Hyaenodon N. horridus</i>	(H)								(x)	x

Both of the *Tritemnodon* species (*T. stenuus* and *T. hians*) are larger than any *Prototomus* from Wa₅₋₇ interval (Table 7B). *Tritemnodon stenuus* is similar to *Arfia opisthotoma* from Wa₃₋₄ in size, and *Tritemnodon hians* is larger than *T. stenuus*, extending the upper limit of the body size range for hyaenodontids from the later part of the Wasatchian. *Gazinocyon vulpeculus* from Wa₇ was probably the same size as *Arfia opisthotoma* and *Tritemnodon* species. For both *Gazinocyon vulpeculus* and *Machaeroides simpsoni* from Wa₇, well-preserved adult or subadult specimens are needed to obtain precise body size estimates and to compare body sizes with other hyaenodontids. Both *Pyrocyon diocetus* and *Prolimnocyon atavus* are smaller than *Prototomus robustus* and *P. secundarius*, and *Prolimnocyon atavus* is smaller than *Pyrocyon*. Another *Prolimnocyon* species, *P. antiquus*, is known from this interval, but its size relative to *P. atavus* is not clear. My sample lacks any good adult or subadult skeletons for *Prototomus viverrinus*. Gingerich and Deutsch (1989) suggested that *P. viverrinus* is slightly smaller than *P. phobos*. It is not clear how *P. viverrinus* would fit relative to *Pyrocyon* and *Prolimnocyon* in the hyaenodontid body size range of this period.

The data on the hyaenodontids from the middle Bridgerian (Br₂; Table 7c) indicate that body size ranges for the two subfamilies, proviverrines (*Sinopa* and *Tritemnodon*) and limnocyonines (*Thinocyon* and *Limnocyon*), overlap with one another. Some scansorial adaptations in addition to terrestrial locomotion have been suggested for Bridgerian proviverrines, while Bridgerian limnocyonines seem to have been more adapted for digging; thus, regardless of their similarity in body size, competition between them may have been avoided. *Sinopa major* and one *S. grangeri* specimen are similar in size to Wasatchian *Tritemnodon* species as well as Bridgerian *Tritemnodon* (*T. agilis*). *Sinopa* extended the upper limit of its body size range slightly compared with Wasatchian *Prototomus*. Concerning the body size range for limnocyonines from Br₂, *Thinocyon velox* is the smallest species in my sample. The small body size in *Thinocyon* species was maintained only during Br₂ times. The *Thinocyon* species known from the late Bridgerian (Br₃), *T. medius*, is about twice as large as *T. velox*. *Machaeroides eothen* (Machaeroidinae) is larger than any of proviverrines and limnocyonines from the Bridgerian as well as from the Wasatchian.

Limnocyon potens was the only specimen available for the Uintan age (Table 7d). It is slightly larger than Bridgerian *Machaeroides* (*M. eothen*). Hyaenodontids which had a scansorial tendency (proviverrines) disappeared by the end of the Bridgerian, and only limnocyonines (*Limnocyon potens* and *Oxyaenodon*) and machaeroidines (*Apataleurus*) are known from the Uintan (Denison 1938). M₁₋₂ lengths (Denison 1938) indicate that *Oxyaenodon* was slightly smaller than *Limnocyon potens* and *Apataleurus* was much larger (about 50 per cent larger in dental dimensions). In contrast to the hyaenodontids from the Wasatchian to Br₂, limnocyonines and machaeroidines seem to have had a strong tendency toward increasing body size from the middle Bridgerian to the Uintan.

My sample lacks data from the later part of the Eocene (Duchesnean and Chadronian). *Hyaenodon* species from the earliest part of the Oligocene epoch (Orellan; Table 7e) are very different from Wasatchian and Bridgerian hyaenodontids in their larger body size, and are distinct from Wasatchian, Bridgerian, and Uintan hyaenodontids in their cursorial adaptations (Matthew 1909). Both of the North American *Hyaenodon* subgenera, *Protohyaenodon* and *Neohyaenodon*, are first known from the Duchesnean (Mellett 1977). Mellett (1977) mentioned that *H. P. venturae* was a small *Protohyaenodon* and *H. N. vetus* was larger than smaller *Protohyaenodon*. It is not clear how the body size range of Duchesnean, Chadronian, or Orellan *Hyaenodon* compares with that of Uintan limnocyonines based on the data in this study.

Fortunately, body masses have been estimated for several North American *Hyaenodon* from the Chadronian and later periods by Van Valkenburgh (1994). The body mass estimates for *Hyaenodon* species (especially for subgenus *Neohyaenodon*) by Van Valkenburgh (1994) seem to be larger than the estimates in this study in general, but they can be used to compare the body size of *Hyaenodon* species unavailable for this study to *H. P. crucians* and *H. N. horridus*.

From the Chadronian North American Land Mammal Age, five species of *Hyaenodon* (hyaenodontine) and two species of *Hemipsalodon* (*H. grandis* and *H. viejaensis*; pterodontine, *sensu* Polly 1996) are known. The skull length of *Hemipsalodon* (37–45 cm; Gustafson 1986) indicates that the genus was a rather large animal. Tentative body mass estimates based on femoral mid-shaft circumference and femoral distal articular area of *Hemipsalodon grandis* (AMNH 10637; from the Chadronian of Saskatchewan), calculated using Anyonge's (1993) equation, were about 760 and 430 kg, respectively. Although there is a considerable difference between the two estimates, *Hemipsalodon* was clearly the largest hyaenodontid in North America.

Both of the Chadronian *Protohyaenodon* (*H. P. mustelinus* and *H. P. microdon*) were smaller than Orellan *H. P. crucians*, and body mass in the smaller *H. P. mustelinus* was suggested to be about 5 kg (Van Valkenburgh 1994), which is the size of medium-sized *Sinopa*. In addition to *Hyaenodon N. horridus*, two other *Neohyaenodon* are known from the Chadronian: one, *H. N. montanus*, is about three-quarters of the size of *H. N. horridus*, and the other, *H. N. megaloides*, is three times heavier (based on data from Van Valkenburgh 1994; if proportions between limb dimensions and craniodental measurements scale isometrically in *Hyaenodon*, body masses of about 30 kg and about 120 kg can be suggested). As estimates by Van Valkenburgh (1994) showed, the body size range of *Hyaenodon* was greatest in the Chadronian, but it quickly lost the wide body size range and species diversity before the beginning of the Orellan.

To summarise, body size range of North American hyaenodontids changed gradually from the

Wasatchian to the Bridgerian. Smaller hyaenodontids disappeared at the end of the Bridgerian with the extinction of many genera, and hyaenodontids from the Uintan were larger than Wasatchian and Bridgerian species. Smaller hyaenodontids reappeared from the Duchesnean. After this age, the body size range of North American hyaenodontids fluctuated a lot owing to the existence of some very large forms.

Some reasons might be suggested for the change in body size range: e.g. environmental change, change in composition of prey, or appearances and disappearances of other predators. Beginning in the middle Eocene, the climate of North America began to cool down and became dry, and the tropical forests changed to less dense vegetation, such as a subtropical woodland with open grass lands (Prothero 1994). This change in vegetation triggered declines in diversity of taxa living in dense forests (Prothero 1994), and the disappearance of proviverrines at the end of the Bridgerian may be associated with it. In addition, medium-sized mammals became rare from about the beginning of the Uintan (Alroy 1998). The change in prey community may have resulted in the disappearances of smaller hyaenodontids in the Uintan.

In the late Eocene (Duchesnean and Chadronian), many new carnivoran families (e.g. amphicyonids, nimravids, and small primitive members of modern caniform families such as canids, ursids, and mustelids; Van Valkenburgh 1994) appeared. As suggested by previous studies (Mellett 1977; Van Valkenburgh 1985, 1987, 1994), *Hyaenodon* was the most cursorial terrestrial predator of its time (Van Valkenburgh 1987), and the species diversity of *Hyaenodon* was largest in the Chadronian. The decrease in smaller species of *Hyaenodon* (*Protohyaenodon*) seems to have been associated with an increase in species diversity of canids (Van Valkenburgh 1994), which were more scansorial at first and transformed into more cursorial (Wang 1993). The decrease in larger species of *Hyaenodon* (*Neohyaenodon*) was suggested to be related to competition with nimravids (Mellett 1977).

CONCLUSION

To summarise, the first objective of this project was to obtain body mass estimate regressions based on limb bone dimensions among Recent carnivores, and to discuss their accuracy. It is suggested that body mass estimates derived from limb bone dimensions in general give small errors (8.2–12.6 per cent). Among the measurements, humeral and femoral cross-sectional properties and distal femoral articular dimensions showed smaller errors, while bone lengths generated relatively larger errors. The error of estimates decreased when locomotor diversity was limited, suggested that choosing animals with an appropriate locomotor behaviour as reference taxa is important to get good body mass estimates. Differences in the body mass estimators (except dimensions of distal humeral articulation) among phylogenetic groups were small, indicating that they can be applied not only to close affinities but also to phylogenetically distant groups.

The second objective was to obtain body mass estimates for hyaenodontids, which have not been well studied in the past. Some skeletal measurements tend to give consistently larger or smaller estimate values (e.g. femoral mid-shaft, distal humeral articulations). However, compared with dental or cranial measurements, limb bone dimensions give rather consistent body mass estimate values. The intraspecific variations in estimated body masses may relate to (1) dimorphism in size, (2) unsolved systematics at species level for some taxa, and (3) preservation condition of each specimen (i.e. availability of bone elements to be used in body mass estimations). A large sample with better skeletons may in future clarify the degree of intraspecific variations of body mass in hyaenodontids. Comparison of body sizes among hyaenodontids from different chronologic intervals indicated that body size range expanded gradually from the Wasatchian to the Bridgerian and shifted upwards from the Bridgerian to the Uintan. The largest North American hyaenodontid appeared in the Chadronian, and the body size range of North American hyaenodontids was greatest at this time; however, this diversity rapidly decreased subsequently.

Estimation of body mass has become increasingly important since body mass is strongly correlated with a wide range of biological factors. Because of its small error, estimating the body size of extinct forms from the regressions of body mass on limb bone dimensions can predict a relatively narrow size range. Accumulation of data on the dimensions of limb bones and body mass for Recent taxa would help the determination of body mass estimates in many other extinct taxa. Quantitatively estimated body masses

can be easily compared among extinct species, and applications of body mass estimations have much potential for analysing the ecological structure of extinct animals and historical change in their lives more clearly.

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APPENDIX

Use of taxonomic names for the hyaenodontid species considered in this study

Several recent revisions (Lange-Badré 1979; Barry 1988; Gingerich and Deutsch 1989; Ivy 1993; Polly 1993, 1996; de Muison and Lange-Badré 1997; Gunnell 1998) have contributed to our understanding of hyaenodontid systematics. However, phylogenetic relationships among hyaenodontid genera are far from resolved.

For Wasatchian materials, I mostly follow taxonomic names used by Gingerich and Deutsch (1989), with the few exceptions mentioned below. It should be noted, however, that use of these names is tentative, especially at the species level, since it is not clear whether Gingerich and Deutsch's (1989) classification based on materials from the Clarks Fork Basin can be applied to hyaenodontids from other places (e.g. southern Bighorn Basin and San Juan Basin). Postcrania of five of the seven genera (*Prototomus*, *Tritemnodon*, *Prolimnocyon*, *Arfia*, and *Pyrocyon*) recognised by Gingerich and Deutsch were available for study. The postcranium of *Pyrocyon dioctetus*, one of the taxa named by Gingerich and Deutsch, is known only from the type specimen. Gingerich and Deutsch suggested the gradual evolution

of *Tritemnodon* from the *Prototomus* lineage, and questioned the usage of *Tritemnodon* in the Wasatchian as a downward extension of typical Bridgerian *Tritemnodon*, and they recognized only one Wasatchian *Tritemnodon* species, synonymising *T. hians* with *T. strenuus*. Ivy (1993) suggested that Wasatchian *Tritemnodon* species could be included in *Pyrocyon*, and later Gunnell (1998) and Morlo (1999) followed this view. Following Gingerich and Deutsch's classification (1989), the generic name *Tritemnodon* was used in this study. However, differing from their observation, two species of Wasatchian *Tritemnodon* are recognised here: *T. strenuus* appeared earlier, and *T. hians* occurred rather later (Cope 1875, 1877; Matthew 1915). *T. hians* is larger than *T. strenuus*, and it seems that specimens attributed to this species were not included in Gingerich and Deutsch's study (1989). Further study is needed to determine if two species are justified and in which genera they should be classified. Gingerich and Deutsch suggested that one species of *Prototomus* (*P. vulpeculus*) should be separated from the genus. It was subsequently placed in the new genus, *Gazinocyon*, by Polly (1996). Information on the postcrania of this species is taken from Polly (1996).

Concerning hyaenodontids from the Bridgerian, identification of genera is much easier and less controversial than for Wasatchian taxa. Postcrania of *Sinopa*, *Tritemnodon* (*T. agilis*), *Thinocyon* (*T. velox* and *T. medius*), and *Limnocyon* (*L. verus*) were available. Use of *Sinopa* is limited here to eight Bridgerian specimens listed in Ivy (1993). The *Sinopa* sample includes specimens that had been identified to species, such as *S. minor*, *S. rapax*, and *S. grangeri*. Other *Sinopa* specimens were classified by their size (e.g. small *Sinopa* = *S. minor*, *S. pungens*, or *S. eganensis*; medium *Sinopa* = *S. rapax*, *S. lania*, or *S. grangeri*; large *Sinopa* = *S. major* or *S. magnus*) relative to the specimens with species identification. For *Limnocyon*, the type specimen of *L. potens* of Uintan age was also available.

The subfamily Machaeroidinae (*Machaeroides* from the Wasatchian and the Bridgerian and *Apataelurus* from the Uintan) has been included in Hyaenodontidae traditionally (McKenna and Bell 1997), but some recent authors (Ivy 1993; de Muison and Lange-Badré 1997) suggested that it should be classified in Oxyaenidae, another creodont family. The classification still remains controversial, and *Machaeroides* is included in the hyaenodontid sample in this study.

Hyaenodon was studied intensively by Mellett (1977). He recognised two subgenera, *Neohyaenodon* and *Protohyaenodon*, among ten North American *Hyaenodon* species. Following his taxonomy, *H. P. crucians* and *H. N. horridus* (including *H. cruentus*) from the Orellan were included in my study.

The following specimens were examined (* and ** indicate that the individuals are subadults and juveniles, respectively; † indicates that the specimen consists of multiple individuals): Proviverrinae, *Arfia opisthotoma*, AMNH 15244; *A. shoshoniensis*, UM 69474*, 76554, YPM 36932*; *Gazinocyon vulpeculus*, UCMP 137216**; *Prototomus martis*, UM 63906, 87356*, 93598, USGS 25021; *P. phobos*, UM 98550, USGS 25275; *P. robustus*, DMNH 6080, UM 64500†, USGS 4272, 21837, 25296; *P. secundarius*, AMNH 55476, USGS 27236; *P. ? viverrinus*, AMNH 48700**, USGS 25128**; *Pyrocyon dioctetus*, UM 94757; *Sinopa grangeri*, AMNH 11537; *S. minor*, AMNH 11532, 11540, 11546; *S. rapax*, AMNH 11531, 13142**, USNM 173513†; small *Sinopa*, DMNH 25046, 26080, 28843, 32224; medium *Sinopa*, AMNH 11533, 92768, DMNH 6136, 17702*, 26008, UM 99832*; large *Sinopa*, DMNH 17104, UM88763, USNM 173514; *Tritemnodon agilis*, AMNH 11536, 11545, USNM 5917, 361351*, 361354*; *T. hians*, AMNH 16821, USGS 1824, 6111; *T. strenuus*, USGS 7157, 16475; Limnocyoninae; *Prolimnocyon atavus*, DPC 5364, UM 75555, USGS 6088†, 15916*, 25225; *Limnocyon potens*, AMNH 13138; *L. verus*, AMNH 12155, UM 33658*, USNM 299722**, 361359; *Thinocyon medius*, AMNH 11529*, 12154, DMNH 14186, USNM 361373*, 361392, 361400*; *Thinocyon velox*, AMNH 11524*, 12630*, 13081*, 13082**, DMNH 21764*, UM 33479**, USNM 22480, 362783*, 362787*; Machaeroidinae, *Machaeroides eothen*, AMNH 92803, DMNH 17290, USNM 17059, 80-42=103; Hyaenodontinae, *Hyaenodon Neohyaenodon horridus*, AMNH 9809*, AMNH-F 75692, 75701, SDSM 341, 2610*; *H. Protohyaenodon crucians*, SDSM 383*, USNM (uncatalogued), 15936, 16717**, 102-32.

Reliability of the biplanar x-ray method

The reliability of the biplanar x-ray method for humeral and femoral data was tested for carnivorans by Heinrich (1995), who compared radiographic estimates with sectioned specimen data and showed the two to be not significantly different. For tibial cross-sectional geometry, the reliability of the concentric oval model was tested by comparing external polar moments of area estimated from external diameters with external polar moments of area obtained from the contour of moulds around the tibial mid-shaft using 29 carnivoran and 3 carnivorous marsupial species. The enlarged images of shaft cross-sections were digitised using a 2D digitiser connected to an MS-DOS computer. Then the total subperiosteal area was calculated using a modified version of the computer program SLICE (Nagurka and Hayes 1980). The differences between the two methods were insignificant (LS slope = 0.99, intercept 0.01, R = 1.00, per cent SEE = 7.35). The contour of the medullary cavity is usually more circular than the contour of the subperiosteal surface, so the differences between the two methods will be smaller for the cross-sectional properties used in this study, and it is concluded that the biplanar x-ray method can be applied to the tibial mid-shaft.