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Body mass estimation in amphicyonid carnivoran mammals: A multiple regression approach from the skull and skeleton

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The body masses of sixteen species of amphicyonids (Mammalia, Carnivora, Amphicyonidae) from the New and Old World were estimated on the basis of 86 osteological variables measured from the craniodental ($N = 44$) and postcranial ($N = 42$) skeleton of living species of Canidae and Ursidae. Given the absence of complete and well preserved skeletons of amphicyonids in the fossil record, multiple regression functions were derived separately from measurements taken from the mandible, the cranium and the major limb bones. The accuracy of the regression functions was evaluated using the percentage prediction error and the percentage standard error of the estimates. Mass values were calculated with these equations using measurements taken in adult individuals from a number of daphoenine and amphicyonine species. Results obtained show that three distinct size classes of amphicyonids emerged through the evolutionary history of the "beardog" family and that these size classes correlate with presumably different ecomorphs. Quantitative estimates of body size of amphicyonids are critical for deciphering the paleobiology of this poorly understood family of large fissiped carnivorans and can be used for placing it within a broader ecological context.

Key words: Mammalia, Carnivora, Amphicyonidae, body mass, multiple regression, skull, skeleton.

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Introduction

The extinct family Amphicyonidae Haeckel, 1866, also known as beardogs, comprises a group of mid-Cenozoic carnivorous mammals with Holarctic and Paleotropical distribution. This family is first recorded at the end of the Eocene (Hunt 1998, 2002) and rises in diversity in the Oligocene, playing a pivotal role within the carnivore guild during the Miocene (Viranta 1996). Amphicyonids became extinct in the late Miocene, presumably through competitive replacement by the felids, borophagine canids and dog-like hyaenids (Van Valkenburgh 1999). Throughout their time span, amphicyonids covered a wide body size spectrum (<5 to >200 kg; Hunt 2001, 2003) and were adapted to different ecological roles, ranging from hypercarnivorous to omnivorous (Viranta 1996).

Amphicyonids exhibit a combination of dental and skeletal morphologies unlike any of the living carnivorans (Sorkin 2006), but they also share several common traits with ursids and canids (and hence their informal name of beardogs). For this reason, their systematic position has been under debate since Haeckel (1866) identified them as a taxonomic unit. For example, some authors have considered the amphicyonids as a subfamily of Canidae based on their dog-like dentition and their long and narrow rostrum (Matthew 1924; Helbing 1928; Viret 1951). In contrast, their shortened distal limb segments, their plantigrade hind feet and their broad molars have been used by other researchers for placing them as a subfamily of Ursidae (Hough 1948; Olsen 1960; Ginsburg 1961, 1977; Heizmann 1973; De Beaumont 1984).

The family Amphicyonidae is now considered as monophyletic (Hunt 1974, 1977, 1998), within or allied with the Arctoidea (Hunt 1998), and probably represents the sister group of either bears (Wyss and Flynn 1993) or all extant caniforms (Wesley-Hunt and Flynn 2005). However, their peculiar skeletal morphology, which includes features shared by the living canids combined with others indicative of ursids, as well as the absence of living relatives means that the paleobiology of these carnivores remains elusive. The reason is that there are no close modern analogs for amphicyonids among the living fissiped carnivores. For example, extant canids and ursids are only distantly related to amphicyonids and have

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postcranial skeletons that are highly specialized relative to the earliest caniforms (Wang et al. 2005; Wang and Tedford 2008). Also, the Pleistocene and Recent canine canids and ursine ursids do not cover the entire spectrum of ecological adaptations seen in amphicyonids. In addition, some beardogs more closely parallel living felids in some postcranial features (Hunt 1998) and may even show a combination of skeletal features found in both ambush (e.g., shortened distal limb segments) and pursuit (e.g., elongated forelimbs) carnivores, which suggests that they probably pursued their prey for a longer distance but at a slower speed than do living ambush predators (Sorkin 2006).

An essential step for understanding the adaptations of amphicyonids in a broad ecological and evolutionary context is to obtain reliable size estimates for them. The reason is that body mass in mammals correlates with a plethora of physiological variables (e.g., metabolic rates, heat flux and body temperature, metabolic costs of locomotion, growth and reproduction), with many ecologically relevant characteristics (e.g., life-history traits, diet, population density, home range size and behavioral adaptations) and also with larger-scale patterns in community structure and biogeography (Peters 1983; Calder 1984; Brown and Rosenzweig 1986; LaBarbera 1989; Schmidt-Nielsen 1984). As a result, body mass has implications for resource partitioning and ecological displacement among the members of the same dietary guild, which translates into important ecological and evolutionary consequences (Eisenberg 1990; Maiorana 1990; Simberloff and Dayan 1991; Dayan and Simberloff 2005; Mendoza et al. 2005, 2006; Palmqvist et al. 2008; Meiri et al. 2009).

Body size estimates may be calculated for extinct taxa using the relationship between body mass and the dimensions of the skeletal parts in their closest living relatives. However, it is often difficult to obtain accurate estimates, because the mass of extant species is only approximately reflected in the size of their bones and teeth (for a thorough compilation of appropriate measures and statistical methods for mass estimation in several mammalian groups, see Damuth 1990). For example, skull and tooth measurements correlate with body mass because of the relationships between the size of the animal and the need to process a certain amount of food, but there are important differences among mammals with different diets (e.g., see Fortelius 1990 for all mammals; Van Valkenburgh 1990 for carnivores; Damuth 1990 for archaic ungulates; and Janis 1990a, b for ungulates). In contrast, the dimensions of elements of the appendicular skeleton—and particularly their diaphyseal diameters—are better correlated with body mass, because they bear the animal's weight (Ruff et al. 1989; Fortelius 1990; Scott 1990; Anyonge 1993). It is worth noting that the proximal limb bones are generally more useful for this purpose than the distal ones, as the latter tend to reflect those morphological adaptations related to habitat preferences and mode of locomotion (e.g., Taylor 1989; Anyonge 1996; Egi 2001; Andersson 2004; Polly 2008). Exceptions are presented by a number of fossorial and saltatory species (e.g., some rodents), which can show dramatic modifications of the proximal elements of either the fore- or hind limbs (Biknevicius 1993). Finally, the preservational bias of the fossil record has resulted in the extensive use of dental measurements for predicting the body mass of ancient mammals. The reason is that, because of their denser mineralization, teeth are often better preserved than the bones of the appendicular skeleton and also that teeth tend to be more diagnostic of species identity. In addition, during the early part of the 20th century, paleontologists tended to collect skulls and teeth in preference to skeletal bones, a procedure which biased the museum collections.

In order to obtain reliable inferences on the autecology of the extinct species under study, databases of linear measurements are usually compiled from their closest living relatives, a procedure which minimizes the bias introduced by phylogeny. In addition, the extant species used for comparison should cover the widest spectrum of body masses and morphologies (Gittleman 1985; Figueirido et al. 2009; Figueirido and Soibelzon 2010). However, this is not always possible, because the living relatives may either be phylogenetically distant from the extinct taxa (e.g., canine canids and ursine ursids versus amphicyonids in our case) or may exhibit a low specific diversity and a narrow range of body masses. For example, this would be the case for the living hyenas, which are the best modern analogues for extinct bone-cracking carnivores such as some borophagine canids (Werdelin 1989), although it is worth noting that Van Valkenburgh et al. (2003) have concluded that the most derived borophagines were pack-hunters with bone-cracking abilities.

Conversely, the ancient taxa may show a unique design, not represented among the living forms, which would suggest that they exploited a different ecological niche (e.g., sabertooth machairodonts vs. pantherine cats; Palmqvist et al. 2007; Van Valkenburgh 2007). Thus, the considerable phylogenetic distance and anatomical divergence between canine canids, ursine ursids and amphicyonids introduces a source of bias and uncertainty in the mass estimates based on regression techniques due to the greater bulk and ambulatory life mode of bears and the lean, gracile cursorial limbs of canine canids. In contrast, the Miocene fossil canids and ursids show less morphological distance from early beardogs. However, it is not possible to use these species for calibrating the regression functions, as their actual masses are similarly unknown.

Perhaps due to these limitations, relatively few attempts have been made at estimating the mass of amphicyonids. For example, Van Valkenburgh (1990) estimated the size of *Daphoenus vetus* at ca. 25 kg using equations for mass on head length and head-body length adjusted through least squares regression techniques. Similarly, Viranta (1996) estimated the mass of *Amphicyon major* as ca. 180 kg with the functions derived for limb bones and craniodental measurements by Anyonge (1993) and Van Valkenburgh (1990), respectively. In her seminal study of European Miocene amphicyonids, Viranta (1996) also estimated the masses of other species based on the length of the lower carnassial tooth. Recently, Sorkin (2006) conducted an ecomorpho-

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logical study of the giant beardogs *Amphicyon ingens* and *Ischyrocyon gidleyi*, predicting their body masses as ca. 550 and 410 kg, respectively.

In this paper, we develop a set of equations based on single and multivariate regression techniques and use them to obtain mass estimates for several New World and Old World amphicyonids as a first step for deciphering the paleobiology of this enigmatic family of large fissiped carnivorans. The most accurate of these equations, adjusted with cranial and postcranial measurements taken in a large number of extant canids and ursids, are used for predicting the size of a number of species of the subfamilies Daphoeninae and Amphicyoninae. Unfortunately, the lack of complete preserved skeletons in the fossil record for members of the subfamilies Temnocyoninae and Haplocyoninae or for the East Asian and African amphicyonids precludes testing the accuracy and predictive power of these equations for estimating the mass of such species.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; NHM, Natural History Museum, London, UK; MFN, Museum für Naturkunde, Berlin, Germany; UNSM, University of Nebraska State Museum, Nebraska, USA.

Other abbreviation.—PCA, principal components analysis; PE, prediction error; SEE, standard error of the estimate.

Material and methods

Extant species.—We compiled an extensive database of living carnivores, including 442 specimens belonging to 71 species of the families Felidae, Hyaenidae, Ursidae, and Canidae (see Appendix 2) in order to examine the possible morphological convergences between amphicyonids and the feliform carnivores (Viret 1951; Ginsburg 1961; Viranta 1996; Hunt 1998). Our premise is that those taxa showing the greatest overall similarity to amphicyonids—in terms of morphology—will be the most feasible option for adjusting body mass regression equations that allow estimating their mass values. The results (see below) indicate that the morphology of amphicyonids is closer to canids and ursids than to the living feliforms. Therefore, we have used a sample restricted to the living species of these two families for estimating the mass values of amphicyonids.

This restricted sample of large caniform carnivorans was divided into separate cranial and postcranial databases. The craniodental database comprises 361 individuals belonging to 39 species (31 canids and eight ursids, Table 1). The postcranial database was smaller than the craniodental one, due to the more limited availability of limb bones in the museum collections, and comprises 167 specimens of 25 species (17 canids and eight ursids, Table 1).

Finally, it could be argued that the application of comparative methods (e.g., Smith 2002; Wroe et al. 2003; Garland et al. 2005) could minimize the bias introduced by phylogeny. However, although these approaches are useful tools for exploring morphological or physiological patterns, they are not appropriate for deriving mass estimates in beardogs. The reason is that the phylogenetic relationship of amphicyonids with other caniform taxa is not fully resolved and, as a result, they could be closer to Ursidae, to Canidae, to all arctoids or, perhaps, even to all extant caniforms (see above). In addition, body mass is strongly influenced by phylogeny in caniforms (e.g., living ursine ursids are all mid- to large sized while most mustelids are comparatively small), which discourages removing the phylogenetic effects prior to estimating the body mass of extinct taxa.

Average body masses for the living species (i.e., mean adult mass values combining males and females from different populations) were taken from the literature (see Table 1),

Table 1. Living species used in the statistical analyses, with indication of the total number of skeletal remains (craniodental/postcranial) analyzed per species and their body masses estimated from the literature (see references).

Living species	BM (kg)	References
Alopex lagopus (10/9)	3.66	Angerbjörn et al. 2004
Atelocynus microtis (3/–)	9.5	Renata et al. 2004
Canis adustus (11/5)	8.85	Atkinson and Loveridge 2004
Cuon alpinus (10/3)	14.5	Cohen 1978
Canis aureus (9/3)	8.05	Yadvendradev et al. 2004, Jhala and Moehlman 2004
Chrysocyon brachyurus (4/2)	25	Roddenet et al. 2004
Canis latrans (10/11)	19.65	Gese and Bekoff 2004
Canis lupus (10/10)	43.75	Mech 1974
Canis mesomelas (10/9)	7.75	Loveridge and Nel 2004
Canis simensis (8/1)	14.51	Sillero-Zubiri and Marino 2004
Cerdocyon thous (6/10)	5.7	Courtenay and Mafei 2004
Pseudalopex culpaeus (8/–)	7.28	Jiménez and Novaro 2004
Pseudalopex griseus (10/–)	3.65	González and Rau 2004
Pseudalopex gymnocerus (7/–)	4.87	Lucherini et al. 2004
Pseudalopex vetulus (7/–)	3.35	Dalponte and Courtenay 2004
Fennecus zerda (8/7)	1.45	Asa et al. 2004
Lycaon pictus (7/10)	22.75	Woodroffer et al. 2004
Pseudalopex sechurae (5/–)	3.6	Asa and Cossíos 2004
Nyctereutes procyonoides (6/–)	5.33	Kauhala and Saeki 2004
Otocyon megalotis (11/4)	4.05	Nel and Mass 2004; Clark 2005
Spheotos venaticus (7/–)	6.5	Zuercher et al. 2004
Urocyon cinereoargenteus (10/10)	3.65	Fuller and Cypher 2004
Urocyon littoralis (10/–)	1.9	Roemer et al. 2004
Vulpes bengalensis (7/–)	2.47	Gompper and Vanak 2006
Vulpes chama (10/–)	2.65	Stuart and Stuart 2004
Vulpes corsac (3/–)	2.43	Poyarkov and Ovsyanikov 2004
Vulpes ferrilata (3/–)	3.8	Schaller and Ginsberg 2004
Vulpes macrotis (10/1)	2.1	List and Cypher 2004
Vulpes pallida (10/–)	2.8	Sillero-Zubiri 2004
Vulpes ruepelli (10/–)	1.61	Cuzin and Lenain 2004
Vulpes vulpes (10/12)	5.79	MacDonald and Reynolds 2004
Ursus maritimus (14/11)	290	Andersson 2004
Ursus malayanus (10/3)	45	Fitzgerald and Kraussman 2002
Ursus ursinus (12/6)	100	Nowak 1999; Joshi et al. 1997
Ursus arctos (36/11)	202	Pasitschniak-Arts 1993
Ursus thibetanus (13/7)	125	Christiansen 2007
Ursus americanus (12/10)	125	Andersson 2004; Christiansen 2007
Tremarctos ornatus (2/1)	110	Nowak 1999
Ailuropoda melanoleuca (12/9)	117.5	Chorn and Hoffmann 1978

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following the procedure most commonly employed for dealing with extinct taxa (e.g., Scott 1985, 1990; Janis 1990b; Palmqvist et al. 1999, 2002; Mendoza and Palmqvist 2006; Mendoza et al. 2006). However, it is worth noting that the use of average values may entail some problems, especially in the highly dimorphic species or in those with a wide geographical range (see discussion in Mendoza and Palmqvist 2006). For this reason, an alternative approach would be the use of separate mean mass values for each sex in the living species instead of species averages. This procedure multiplies by two the data used for adjusting the regression functions, which would a priori translate in more predictive equations. However, one major limitation of this approach is the relatively low number of sexed specimens in our database of extant carnivores. This is probably the reason that we obtained mass regression equations with lower predictive power than in those derived from species averages. In addition, it is worth noting that separating extant species into sexed groups for regression analysis is impractical when the sex of many individuals is unknown, and that discriminating among sexes is not possible for most fossil specimens (which is the case in this study). Another possibility would be to split the taxa with pronounced geographic variation (e.g., brown bear and gray wolf) in those populations that show marked size differences. However, information on the localities and actual masses of the measured specimens was not always available in the museum collections. For this reason, we used species means for the osteometric data of the living species sampled and estimates of their average body masses from the literature. It is worth noting, however, that these mass values come from different individuals from those measured in our study, which may represent an additional source of error in the regression adjustments (Turner and O'Regan 2002). In spite of this, the predictive power of the adjusted functions (see below) ensures that the lack of information on the mass, sex and population provenance of many specimens in the database does not represent a considerable source of bias.

Extinct species.—The beardogs studied (see Appendix 1) include *Adilophontes brachykolos* Hunt, 2002, *Amphicyon frendens* Matthew, 1924, *Amphicyon galushai* Hunt, 2003, *Amphicyon ingens* Matthew, 1924, *Amphicyon major* De Blainville, 1841, *Daphoenodon falkenbachi* Hunt, 2002, *Daphoenodon neomexicanus* Hunt, 2009, *Daphoenodon superbus* Peterson, 1907, *Daphoenus hartshornianus* Cope, 1873, *Daphoenus vetus* Leidy, 1853, *Ischyrocyon gidleyi* Matthew, 1902, *Paradaphoenus cuspigerus* Cope, 1878, *Pliocyon medius* Matthew, 1918, *Pseudocyon sansaniensis* Lartet, 1851, *Pseudocyon* sp., and *Ysengrinia americana* Wortman, 1901. Although some European beardogs have been included in this study (e.g., *Pseudocyon sansaniensis* and *Amphicyon major*), the majority of the extinct taxa analyzed comes from North America. We have restricted the analysis to the European and North American amphicyonids because the fossil record of this family in Africa and Asia is extremely sparse. Similarly, the species studied from Europe and North America include only members of Daphoeninae and Amphicyoninae, because complete specimens from other amphicyonid subfamilies (e.g., European Haplocyoninae and North American Temnocyoninae) are uncommon. Consequently, this study does not include all amphicyonid subfamilies. However, the species studied nearly cover the entire range of body size exhibited by the family throughout its evolutionary history. Unfortunately, this was not the case for the range of ecological adaptations displayed by amphicyonids, because some members of Temnocyoninae or Haplocyoninae were presumably adapted for gaits typical of large living cursorial carnivores (Hunt 1998).

Measurements.—All measurements were taken with digital calipers (Sylvac PAT 150 mm and 300 mm) to the nearest 0.1 mm. For those specimens measuring >300 mm a metal rule was used. Prior to the statistical analyses, both databases (i.e., cranial and postcranial) were inspected regressing all the measurements one by one on the total length of each skeletal element. The bivariate plots obtained allowed us to identify errors (i.e., individual outliers within a species) during data gathering. Erroneous data were re-measured, now from digital images (with an appropriate scale bar and in standard orientation) using the software UTHSCSA Image Tool (available on the web at: http://ddsdx.uthscsa.edu/dig/itdesc.html). The accuracy of this software was evaluated measuring some specimens without erroneous variables. Although the differences between these two modes of data gathering were negligible, all the measurements taken from digital images were repeated five times and an arithmetic mean was computed for each variable.

Principal components analysis.—The skeletal morphology of amphicyonids is one of the most enigmatic among the large fissiped carnivorans. For example, previous authors have recognized a number of morphological—and presumably ecological—convergences of amphicyonids with canids (Viret 1951), ursids (Ginsburg 1961), felids (Sorkin 2006) or even hyaenids (Viranta 1996). To explore the morphological convergences between these groups and amphicyonids, a principal components analysis (PCA) was performed on a dataset taken from these carnivoran families (i.e., Canidae, Ursidae, Felidae, Hyaenidae; see Appendix 2). In fact, those families which are morphologically closer to the amphicyonids will be crucial for deriving the most predictive regression equations for obtaining accurate mass values in beardogs.

Regression equations.—In accord with PCA results (see below), Canidae and Ursidae are the families that are morphologically closest to amphicyonids. Therefore, equations for predicting body mass in the living species of canids and ursids were applied separately to the craniodental (Fig. 1, Table 2) and postcranial measurements (Fig. 2, Table 3) taken from amphicyonids. As noted above, the dimensions of the limb bones are the best correlated with the body mass of terrestrial mammals because they bear the animal's weight and the strains produced during locomotion (e.g., Ruff et al. 1989; Jungers 1990; Christiansen 1999a, b, 2002, 2004; Egi 2001;

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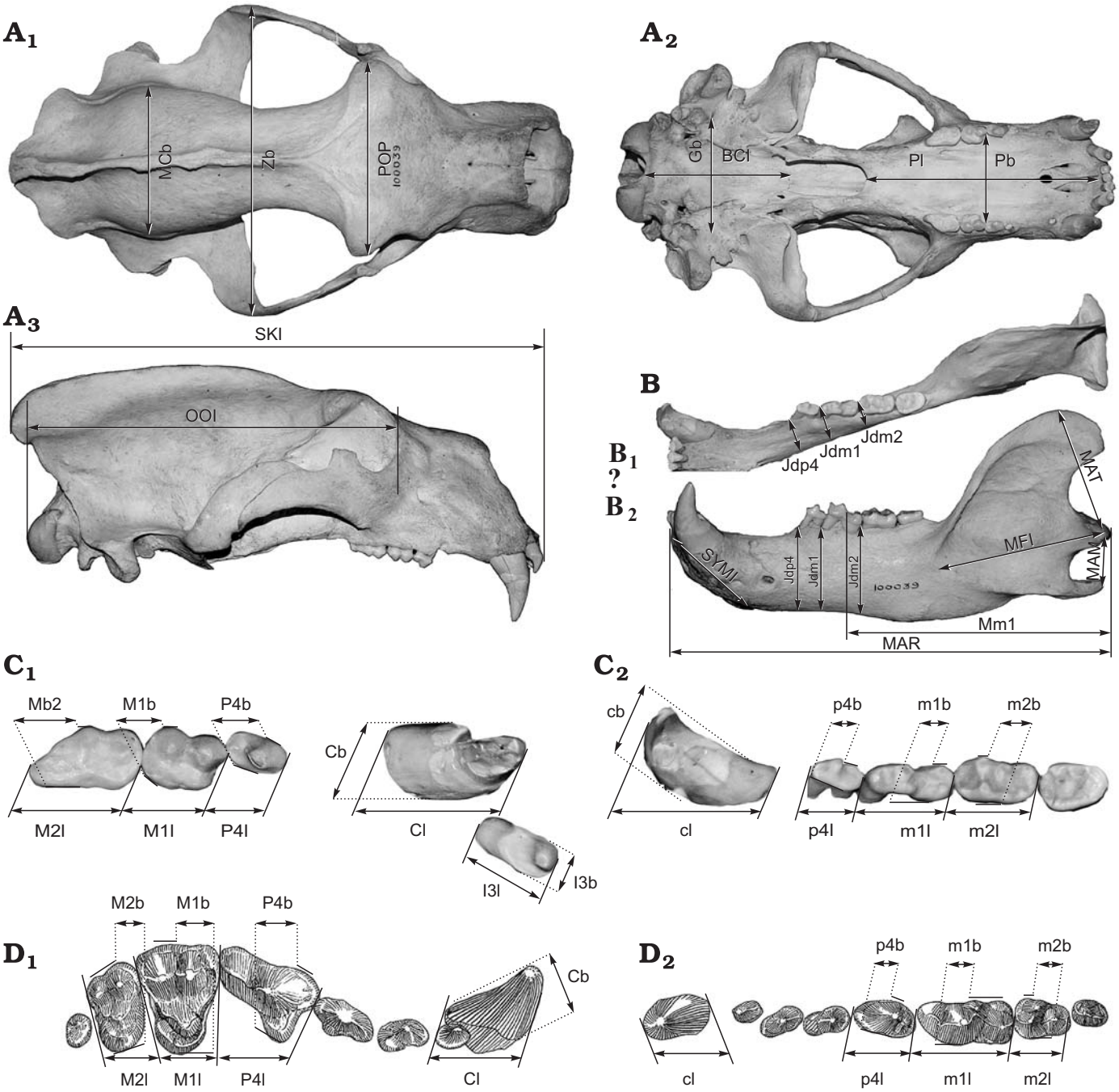

Fig. 1. Osteological measurements used in the regression analyses for the craniodental skeleton, illustrated on a skull of *Ursus maritimus*. **A**. Cranium in dorsal (A_1), ventral (A_2) and lateral (A_3) views. **B**. Mandible in occlusal (B_1) and lateral (B_2) views. **C**. Upper (C_1) and lower (C_2) dentition. **D**. *Daphoenodon falkenbachi*, upper (D_1) and lower (D_2) dentition (modified from Hunt 2002; upper teeth reversed). For abbreviations and definitions of measurements, see Table 2.

Andersson 2004; Christiansen and Harris 2005; Mendoza and Palmqvist 2006; Mendoza et al. 2006; Figueirido et al. 2010). However, variables measured from the skull and teeth have been used to predict the body mass of extinct mammals in those cases in which the postcranial material was scarce or absent (e.g., Legendre and Roth 1988; Van Valkenburgh 1990; Palmqvist et al. 1999, 2002). Consequently, we have derived predictive equations from postcranial measurements when the measurements incorporated by these functions were available in the fossil specimens. In those cases in which the postcranial remains were fragmentary or missing, we have based our estimations exclusively on craniodental measurements. However, it is worth noting that the skulls of some amphicyonids are disproportionately large relative to their postcranial bones (Hunt 1998), which could introduce a source of bias in their estimated body masses.

Predictive equations for body mass were adjusted using simple and multiple regression approaches with log-trans-

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Table 2. Osteological measurements used in the regression analyses (see also Fig. 1 for their locations on the corresponding skeletal part).

Craniodental measurements		
Mandible	cl	anteroposterior diameter of the canine
	cb	mediolateral diameter of the canine
	p4l	anteroposterior diameter of the fourth premolar
	p4b	mediolateral diameter of the fourth premolar
	m1l	anteroposterior diameter of the carnassial
	m1b	mediolateral diameter of the carnassial
	m2l	anteroposterior diameter of the second molar
	m2b	mediolateral diameter of the second molar
	MAT	moment arm of the temporalis muscle
	MAM	moment arm of the masseter muscle
	MAR	mandible length
	Mm1	distance between the condyle and the trigonid/talonid notch
	MFl	length of the masseter fossa
	Jdp4	jaw depth at the p3/p4 interdental gap
	Jdm1	jaw depth at the p4/m1 interdental gap
	Jdm2	jaw depth at the m1/m2 interdental gap
	Jbp4	jaw breadth at the p3/p4 interdental gap
	Jbm1	jaw breadth at the p4/m1 interdental gap
	Jbm2	jaw breadth at the m1/m2 interdental gap
	SYMl	length of the mandibular symphysis
Cranium	I3l	anteroposterior diameter of the third incisor
	I3b	mediolateral diameter of the third incisor
	Cl	anteroposterior diameter of the canine
	Cb	mediolateral diameter of the canine
	P4l	anteroposterior diameter of the carnassial
	P4b	mediolateral diameter of the carnassial at the level of protocone
	M1l	anteroposterior diameter of the first molar
	M1b	mediolateral diameter of the first molar
	M2l	anteroposterior diameter of the second molar
	M2b	mediolateral diameter of the second molar
	SKl	skull length
	BCl	basicranial length
	Ool	occiput to orbit length
	Pl	palatal length
	Pb	palatal breadth
	Gb	skull breadth at the auditory bullar
	Zb	zygomatic breadth
	POP	skull breadth at the postorbital process
	MCb	skull breadth at the braincase

formed data from the sample of extant species. In order to avoid the over-representation of canids (31 species sampled in our database) with respect to ursids (eight living species) due to their differences in species diversity, it is advisable to weight the cases according to the number of species of their respective families prior to analyzing the data. This procedure ensures an equal contribution of both carnivoran families to the regression models and improves their predictive power (Mendoza and Palmqvist 2006; Mendoza et al. 2006).

A set of functions was computed through least squares bivariate regressions of body mass on each single measurement. These equations were used with those amphicyonids for which no complete skeleton was available, with the realization that amphicyonid cranial and postcranial proportions differ among species. Multiple regression analyses were also conducted with the forward stepwise method (Norusis 1988) for selection of variables, following Mendoza et al. (2006). There are two main procedures for adjusting predictive equations using multiple regression techniques. One is the direct method, which incorporates all the variables together in the analysis. However, this procedure includes redundant information in the predictor variables and, in addition, the high number of variables in the functions usually results in their low statistical rigor, particularly when sample size is small (see details in Palmqvist et al. 2002). Other multiple regression techniques consider only the most relevant variables for the models, as in the forward and backward stepwise methods (Norusis 1988; Mendoza et al. 2006). The forward procedure, which is the one used here, selects the independent variable best correlated with body mass and, after incorporating it within the regression function, searches among the other morphological variables for the one that accounts for more variance of the independent variable not explained by those previously included in the function (the backward method, which produces fairly similar results, begins by incorporating all the variables in the regression function and then excludes at each step the one that correlates less with body mass; see details in Mendoza et al. 2006).

The equations obtained may be used with those amphicyonids better preserved in the record and have the advantage of incorporating the complementary information contained in the variables. Multiple regressions of body mass of variables measured on the mandible (including the lower dentition), cranium and each major limb bone (i.e., radius, ulna, tibia, femur, and humerus) were also computed separately, which helps to bypass the scarcity or absence of complete skeletons for most amphicyonids. The statistical significance of the differences in the regression slopes adjusted separately for canids and ursids was tested by a multivariate analysis of covariance (MANCOVA) using the body mass as the covariable, the family as the factor and the measurements taken in the craniodental and postcranial skeleton as the dependent variables.

Comparing the accuracy of the functions.—The *F*-statistic and the correlation coefficient were used for evaluating the accuracy of the functions adjusted through simple and multiple regressions. However, the correlation coefficient is a poor indicator of the predictive power of these equations, because it can take high values even with large residuals. Consequently, we calculated the following two indices that measure the average deviation between the predicted and observed values, the percentage of prediction error (%PE) and the percentage standard error of the estimate (%SEE) (Smith 1981, 1984; Van Valkenburgh 1990; Egi 2001; Andersson 2004), which were computed as follows:

$$\%PE = [(O_{BM} - P_{BM})/ P_{BM} \cdot 100] \text{ and } \%SEE = 10^{2+SEE} - 100,$$

where P_{BM} and O_{BM} are the predicted and observed body mass (respectively) for each species used in the adjustment after

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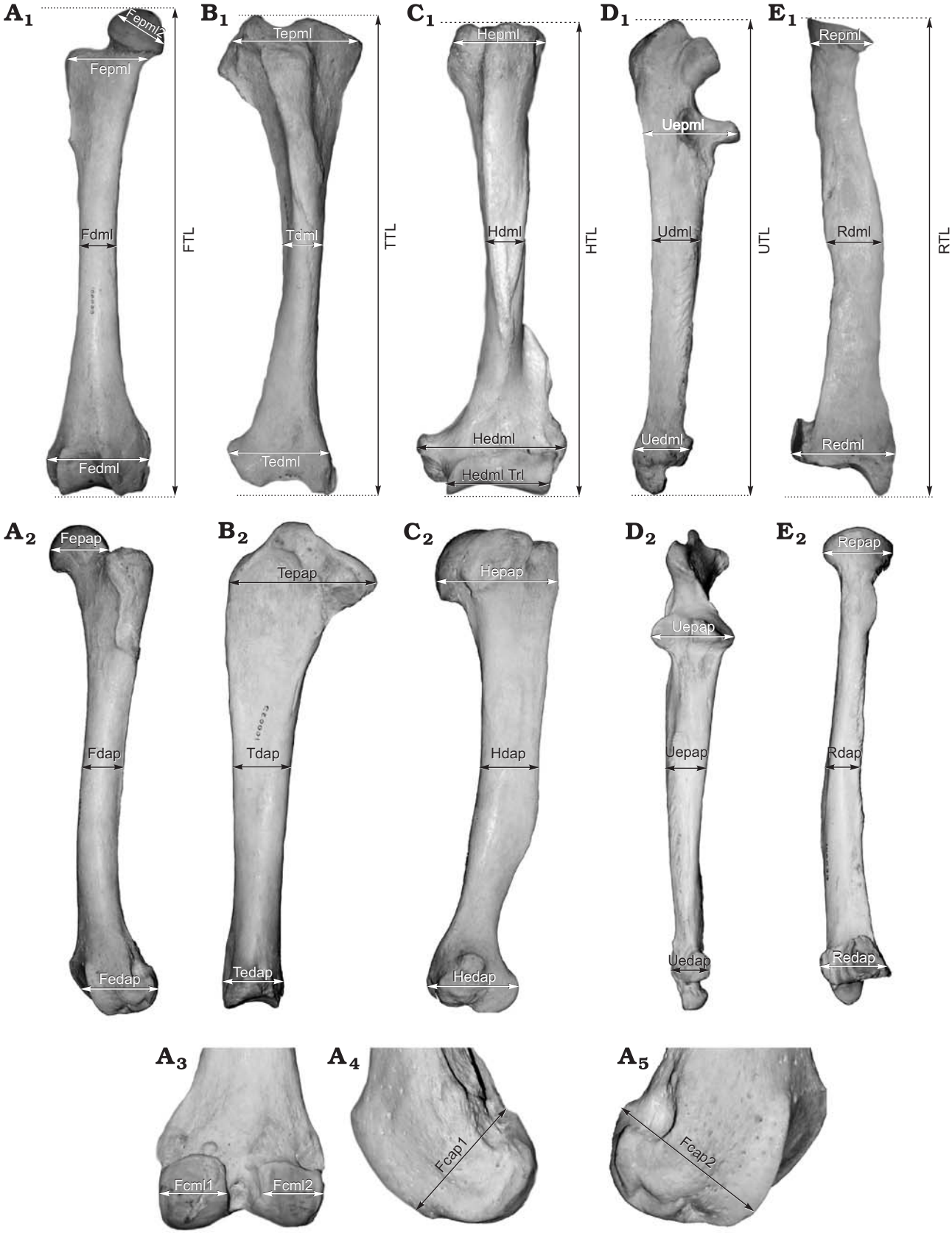

Fig. 2. Osteological measurements used in the regression analyses, illustrated on the bones of a postcranial skeleton of *Ursus maritimus*. **A**. Femur in anterior (A_1) and lateral (A_2) views, and in the posterior (A_3), medial (A_4), and lateral (A_5) views of the distal epiphysis. **B**. Tibia in anterior (B_1) and lateral (B_2) views. **C**. Humerus in anterior (C_1) and lateral (C_2) views. **D**. Ulna in anterior (D_1) and lateral (D_2) views. **E**. Radius in anterior (E_1) and lateral (E_2) views. For abbreviations and definitions of measurements, see Table 3.

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Table 3. Postcranial measurements used in the regression analyses (see also Fig. 2 for their locations on the corresponding skeletal part).

Humerus	HTL	humerus total length
	Hepml	mediolateral diameter of the humeral proximal epiphysis
	Hepap	anteroposterior diameter of the humeral proximal epiphysis
	Hedml	mediolateral diameter of the humeral distal epiphysis
	Hedml.TrL	mediolateral diameter of the humeral trochlea
	Hedap	anteroposterior diameter of the humeral distal epiphysis
	Hdml	mediolateral diameter of the humeral diaphysis at the midshaft
	Hdap	anteroposterior diameter of the humeral diaphysis at the midshaft
	Hdml35%	mediolateral diameter of humeral diaphysis at 35% from the distal end
	Hdap35%	anteroposterior diameter of humeral diaphysis at 35% from the distal end
Radius	RTL	radius total length
	Repml	mediolateral diameter of the radius proximal epiphysis
	Repap	anteroposterior diameter of the radius proximal epiphysis
	Redml	mediolateral diameter of the radius distal epiphysis
	Redap	anteroposterior diameter of the radius distal epiphysis
	Rdml	mediolateral diameter of the radius diaphysis at the midshaft
	Rdap	anteroposterior diameter of the radius diaphysis at the midshaft
Ulna	UTL	ulna total length
	Uedml	mediolateral diameter of the ulna distal epiphysis
	Uedap	anteroposterior diameter of the ulna distal epiphysis
	Uepml	mediolateral diameter of the ulna proximal epiphysis
	Uepap	anteroposterior diameter of the ulna proximal epiphysis
	Udml	mediolateral diameter of the ulna diaphysis at the midshaft
	Udap	anteroposterior diameter of the ulna diaphysis at the midshaft
Femur	FTL	femur total length
	Fepml	mediolateral diameter of the femoral proximal epiphysis
	Fepap	anteroposterior diameter of the femoral proximal epiphysis (femoral head)
	Fedml	mediolateral diameter of the femoral distal epiphysis
	Fedap	anteroposterior diameter of the femoral distal epiphysis
	Fcml1	mediolateral diameter of the lateral femoral cotyle
	Fcap1	anteroposterior diameter of the lateral femoral cotyle
	Fcml2	mediolateral diameter of the medial femoral cotyle
	Fcap2	anteroposterior diameter of the medial femoral cotyle
	Fdml	mediolateral diameter of the femoral diaphysis at the midshaft
	Fdap	anteroposterior diameter of the femoral diaphysis at the midshaft
Tibia	TTL	tibia total length
	Tepml	mediolateral diameter of the tibia proximal epiphysis
	Tepap	anteroposterior diameter of the tibia proximal epiphysis
	Tedml	mediolateral diameter of the tibia distal epiphysis
	Tedap	anteroposterior diameter of the tibia distal epiphysis
	Tdml	mediolateral diameter of the tibia diaphysis at the midshaft
	Tdap	anteroposterior diameter of the tibia diaphysis at the midshaft

transformation to non-logarithmic data and SEE is the standard error of the estimate. Also, we calculated mass values for amphicyonids using the body mass regression equations of Van Valkenburgh (1990) using craniodental measurements and those of Anyonge (1993) using the postcranial skeleton, derived from all extant carnivoran families used here. All the statistical procedures (PCA, simple and multiple regression functions, and MANCOVA) were computed with the software SPSS v. 14.

Results

Principal components analysis: the craniodental morphology of beardogs.—PCA of logarithmically transformed craniodental measurements for the entire dataset of large fissiped carnivorans yielded three significant principal components, which jointly explain >95% of the original variance. The first component (~84% of the variance explained) can be interpreted in an ad hoc manner as a size vector (Reyment 1991) because all the log-transformed variables take positive loadings, which in most cases are close to one (Table 4). In contrast, the morphological variables take positive and negative factor loadings on the second component (~8% of the variance accounted), which indicates that this axis is a shape vector.

Table 4. Factor loadings, eigenvalues and percentages of variance explained by the first three principal components of the entire sample of craniodental measurements.

Variables	PC I	PC II	PC III
cap	0.976	0.085	-0.075
cml	0.980	-0.014	-0.078
p4l	0.807	-0.508	0.252
P4b	0.899	-0.369	0.111
m1l	0.887	-0.006	0.388
m1b	0.940	-0.097	0.248
MAT	0.984	0.076	-0.044
MAM	0.935	0.207	0.051
MAR	0.961	0.226	0.068
MFL	0.974	-0.083	-0.080
JdP4	0.976	0.072	-0.110
JdM1	0.986	0.037	-0.036
JdM2	0.987	0.011	-0.039
JbP4	0.974	-0.094	-0.027
JbM1	0.976	-0.090	0.018
JbM2	0.976	0.035	-0.043
I3ap	0.972	0.053	0.050
I3ml	0.969	0.012	0.024
Cap	0.977	0.059	-0.113
Cml	0.972	-0.058	-0.151
P4l	0.698	-0.593	0.369
P4pb	0.883	-0.344	0.245
M1l	0.403	0.872	0.242
M1b	0.487	0.648	0.545
SKl	0.981	0.129	-0.020
BCl	0.956	0.220	0.025
Ool	0.950	0.117	-0.136
Fl	0.922	0.311	0.059
Pb	0.863	-0.448	0.112
Gb	0.879	0.168	-0.205
Zb	0.986	0.006	-0.109
POP	0.937	-0.017	-0.254
POC	0.874	0.151	-0.321
MCb	0.937	0.131	-0.232
Cb	0.875	-0.416	-0.167
eigenvalues	29.369	2.820	1.262
% var. explained	83.911	8.057	3.606

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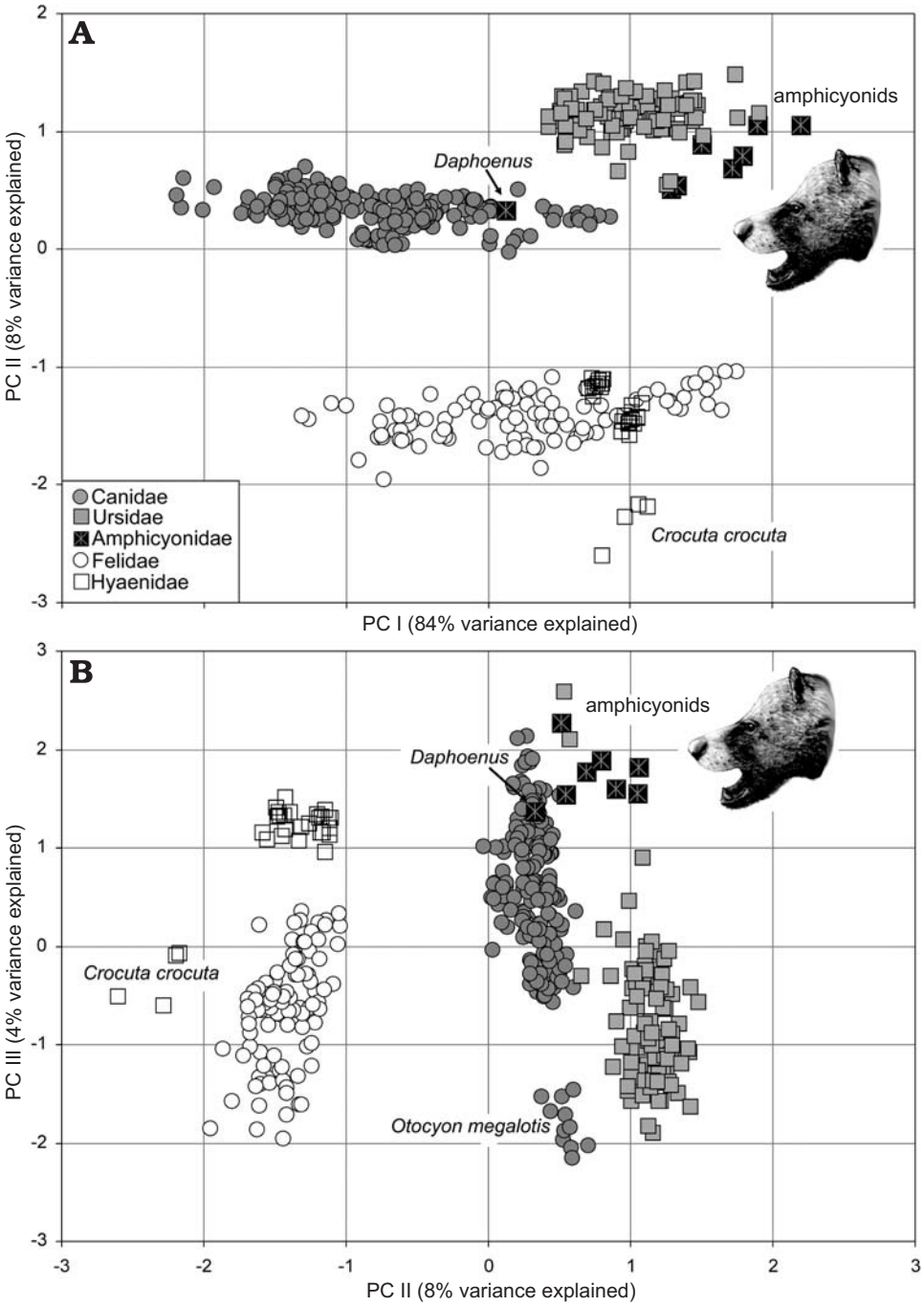

Fig. 3. Bivariate plots with the scores of 442 specimens on the bivariate craniodental morphospaces depicted by the first three principal components. **A**. Morphospace depicted from first (*x*-axis) and second (*y*-axis) principal components. **B**. Morphospace depicted from second (*x*-axis) and third (*y*-axis) principal components.

Figure 3A shows the scores of the specimens on a bivariate plot defined by the first two principal components. According to their distribution on the morphospace, all felids and hyaenids take negative scores on principal component II while ursids, amphicyonids and canids score positively on this component in accord with different osteometric variables (see Table 4). Interestingly, amphicyonids are not close to the feliforms in the morphospace. In contrast, all beardogs plot between the two living caniform families included in the sample.

Figure 3B shows the scores of the specimens on the morphospace depicted by the second and third principal components (~4% of the variance explained). Both axes are clearly interpreted as shape vectors (which is indicated by the positive and negative factor loadings of the metric variables; Table 4). All amphicyonids and the hypercarnivorous pack-hunting canids plot with high positive scores on the third principal component, while the hypocarnivores *Otocyon megalotis*, *Ursus* (*Melursus*) *ursinus*, and *Ursus* (*Helarctos*)

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malayanus score with the lowest negative values in accord with different skeletal variables.

Therefore, the results obtained from this analysis of patterns of craniodental morphology in this carnivoran dataset suggest that these amphicyonids are closest in morphology to the living canids and the ursids. However, we should bear in mind that the phylogenetic legacy could be masking some minor convergences between amphicyonids and the feliform taxa. In fact, some variables not used here are the ones in which amphicyonids resemble felids. In any case, it is clear that canids and ursids are the living carnivorans that are closer—at least in terms of craniodental measurements—to amphicyonids. Within the limits of the method applied here, this provides a rationale for the use of canids and ursids in the adjustment of mass regression equations that allow estimating the body size of amphicyonids.

Body mass regressions in living taxa.—Different mass regression equations were derived from a metric sample restricted to the families Canidae and Ursidae. Table 5 and Appendices 3, 4 show the predictive equations for body mass and their associated statistics. As a general rule, multiple regressions predict the body mass more accurately than bivariate ones. However, it is worth noting that the single regression adjusted for the mediolateral diameter of the femur measured at the midshaft provides the best mass predictions.

The next most predictive equation is derived from the humerus, which incorporates the mediolateral diameter of the diaphyseal shaft measured at 35% from the distal end and the mediolateral diameter of the humeral trochlea. The accuracy of these two functions was tested separately with the species of canids and ursids (Table 5). The equation derived from the femur is more precise for bears than that from canids, while the function that incorporates the humeral measurements is slightly more accurate for canids.

It is also worth noting that the equations obtained from variables measured in the distal limb segments (i.e., radius and ulna, tibia and fibula) are worse mass predictors than those computed using the variables taken in the proximal ones (i.e., femur and humerus), which probably reflects the fact that the dimensions of the distal bones correlate more with locomotor adaptations and/or hunting techniques (Anyonge 1993, 1996; Palmqvist et al. 2003): for example, carnivores that pursue their prey in open habitat have relatively longer radii and tibiae than those that ambush from dense vegetation, because their elongated distal limb segments increase stride length, while concentrating muscle mass in the proximal limb, to achieve a more energy-efficient gait. For this reason, the lower accuracy of the functions derived from the distal limb segments, particularly the tibia, could be reflecting the existence of different modes of locomotion in the sample used for deriving these equations (i.e., canine canids and ursine ursids). However, Meachen-Samuels and Van Valkenburgh (2009) have demonstrated recently that the whole forelimb apparatus (i.e., both the proximal and distal limb segments) is well adapted for hunting in cats and the same applies to the hindlimb (Egi 2001). Thus, the distal limb segments are probably more poorly correlated with body mass than the proximal ones because they are composed of two different bones (i.e., radius and ulna for the forelimb, tibia and fibula for the hindlimb) while the proximal segments (i.e., humerus and femur, respectively) incorporate only a single element for supporting the animal's weight (Egi 2001). This is in agreement with our results, because the %PE and %SEE values of the regressions derived separately from the distal limb segments are higher than those estimated from the proximal ones. This may relate to the loads transmitted through the radius and ulna in the forelimb, which share the weight of the anterior part of the body, and the tibia and fibula in the hindlimb, which bear the weight of the posterior part. It is worth noting that the tibia provides lower estimates of body mass for primates than those based on femoral dimensions (Ruff 1989).

As expected, except for the regression function derived from the tibia, the equations adjusted with the variables of the appendicular skeleton have more predictive power than

Table 5. Multiple regression functions and associated statistics for the craniodental and postcranial measurements (see text for details). Abbreviations: BM, body mass, in kg; metric variables, in mm (for abbreviations of the measurements incorporated within the functions, see Tables 2 and 3); N, sample size; r, coefficient of correlation; F, variance explained by the model; p, significance level; %SEE: percentage standard error of the estimate; %PE: percentage prediction error (%PEc and %PEu are the percentage prediction errors for canids and ursids, respectively).

Element	Functions	N	r	F	p	%SEE	%PE	$\%PE_c$	$\%PE_u$
Radius	Log_{10} (BM) = -1.972 (±0.120) +1.674 (±0.255)Log_{10}(Redml) + 0.825 (±0.239)Log_{10}(Redap)	25	0.992	624.716	<0.001	23.78	14.79	19.00	12. 36
Ulna	Log_{10} (BM) = -1.649 (±0.204) +1.631 (±0.254)Log_{10}(Uepap) + 0.718 (±0.192)Log_{10}(Uedml)	25	0.984	613.621	<0.001	23.91	15.55	33.45	16.24
Tibia	Log_{10} (BM) = -2.284 (±0.165) + 1.922 (±0.566)Log_{10}(Tdml) + 1.229 (±0.536)Log_{10}(Tedap)	25	0.983	298.614	<0.001	35.77	26.45	30.80	16.52
Humerus	Log_{10} (BM) = -1.874 (±0.096) + 1.400 (±0.337)Log_{10} (HedmlTrcl) + 1.061(±0.402) Log_{10}(Hdml35%)	25	0.993	730.747	<0.001	21.83	14.20	13.38	15.68
Femur	Log_{10} (BM) = -1.742 (±0.310) + 2.659(±0.249)Log_{10} (Fdml)	25	0.994	1956.815	<0.001	18.64	14.06	15.48	11.22
Mandible	Log_{10} (BM) = -5.044 (±0.300) + 3.132 (±0.564) Log_{10} (Mm1) -1.373 (±0.317) Log_{10} (SYMl) +1.801 (0.482) Log_{10} (MAT)	38	0.989	517.868	<0.001	30.31	22.05	19.72	22.57
Cranium	Log_{10} (BM) = -6.641 (±.469) + 0.692 (±0.477) Log_{10} (POP) +6.7209 (±1.242) Log_{10} (SKl) - 3.790 (±0.868) Log_{10} (BSCl)	38	0.990	548.513	<0.001	29.35	20.52	21.15	17.74

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those derived from skull measurements (Table 5; Appendices 3, 4). In particular, the function that incorporates cranial variables is slightly more accurate than the one derived from the mandible. However, apart from their lower predictive power, it is important to be cautious in the use of craniodental variables for estimating the mass of amphicyonids. The reason is that some beardogs have relatively large heads and strong jaws compared to any living terrestrial caniform. In fact, there is probably a different allometric pattern of head length on body mass in amphicyonids and in the creodont *Hyaenodon horridus* Leidy, 1853, relative to other carnivores (Van Valkenburgh 1990; Hunt 1998). For this reason, mass values calculated for the largest amphicyonids using craniodental measurements could lead to an overestimation of their actual masses.

The MANCOVA test indicates that canids and ursids show different slopes for the scaling of body mass on the measurements taken in the craniodental and postcranial skeleton (Wilk's lambda < 0.5; $p < 0.001$). This result was expected in part given the greater bulk and ambulatory mode of locomotion of bears compared to the lean, gracile cursorial limbs of canine canids (see also Bertram and Biewener 1990; Anyonge 1996). However, amphicyonids show a similar spectrum of body sizes and ecomorphological adaptations to that displayed by the living canids and ursids considered together. For this reason, the difference in allometric scaling between both families does not invalidate combining the data for deriving mass regression equations. In addition, box plots of the regression residuals for the living species of both families (Fig. 4) clearly show the absence of a systematic bias in the estimates of body mass obtained with these equations.

Body mass estimates for amphicyonids.—Multiple regression functions (Table 5) were applied to the extinct taxa whenever the corresponding measurements were available. In those cases where more than one specimen of the same skeletal element was available, mass values were estimated from each and the arithmetic and geometric means were calculated (Mosimann and James 1979). This provides an integrated estimate of mass for each amphicyonid species (Table 6). In addition, the use of an average mass estimate for each skeletal element avoids potential biases introduced by intraspecific variation in the data (e.g., sexual dimorphism, ecogeographic differences among populations). However, for those species in which the limited availability of specimens in the fossil record resulted in a single mass estimate, intraspecific variation could introduce a source of bias and error (i.e., to consider as representative of the species the mass derived from a very large or very small specimen). However, this bias is in large part unavoidable: although sexual dimorphism has been documented in amphicyonids (Hunt 2003: 82, fig. 4.13), in most cases it is not possible to determine the gender of single specimens.

The mass estimates obtained with the functions computed by Van Valkenburgh (1990) and Anyonge (1993) fall in most cases within the range of mass values calculated with

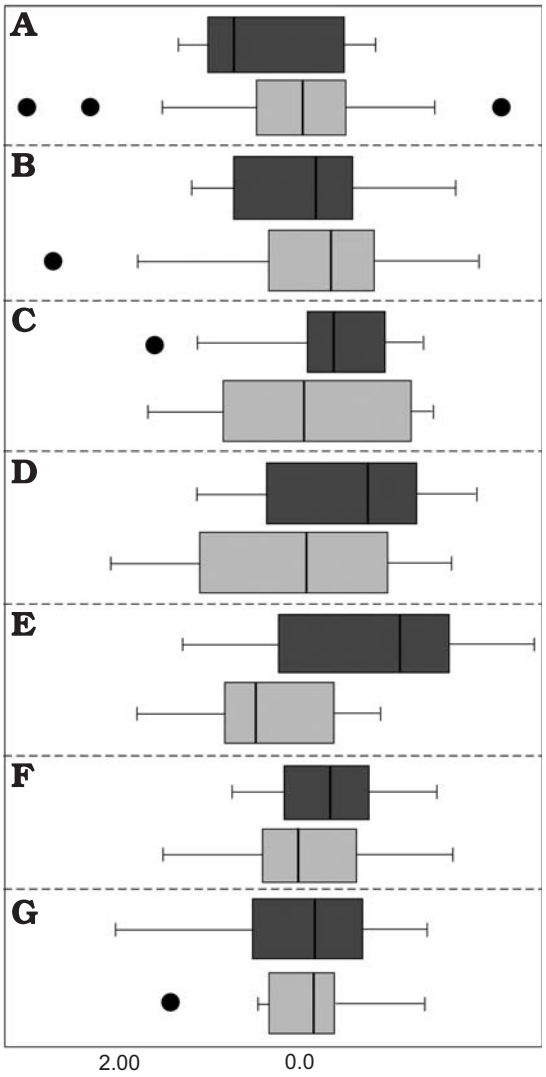

Fig. 4. Box plots of the residuals (log-scale) derived from multiple regression functions. **A**. Residuals derived from the cranium regression. **B**. Residuals derived from the mandible regression. **C**. Residuals derived from the radius regression. **D**. Residuals derived from the ulna regression. **E**. Residuals derived from the tibia regression **F**. Residuals derived from the humerus regression. **G**. Residuals derived from the femur regression. Vertical lines inside the boxes are the medians. Box length is the interquartile range (IQR) and shows the difference between the 75th and 25th percentiles. Horizontal bars include the largest and smallest values (5–95% confidence limits). Black dots are outliers. Dark grey tones represent the family Ursidae and light grey tones the family Canidae.

the equations adjusted in this study (Table 6). This supports the interpretation that the unreliable estimates of size obtained for the larger amphicyonids using those equations derived from craniodental measurements result from their peculiar allometric scaling of head length on body mass (Hunt 1998). However, it is worth noting that the mass values obtained with the functions derived by Anyonge (1993) using postcranial measurements tend to underestimate slightly our mass estimates and those obtained using the equation of Van Valkenburgh (1990: table 6). This most probably reflects the fact that the sample of Anyonge (1993) was strongly biased

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Table 6. Body mass estimates for each amphicyonid species (in kg) obtained from each skeletal part. BMR, BMF, BMH, BMT, BMJ, and BMC, estimates derived from the regression functions adjusted for the radius, femur, humerus, ulna, tibia, mandible and cranium, respectively (Tables 2, 3); RANGE, minimum and maximum mass estimates for each extinct species; BIFE, best individual function estimate (i.e., those derived from femoral dimensions); GM, AM, geometric and arithmetic means computed with the estimates based on different skeletal elements, respectively; F1, F2, body mass estimations based on the functions of Van Valkenburgh (1990) and Anyonge (1993) respectively.

Taxa	BMR	BMF	BMH	BMU	BMT	BMJ	BMC	RANGE	BIFE	AM	GM	F1	F2
Adilophontes brachykolos	83	154	88	–	–	191	143	83–191	154	132	125	184	108
Daphoenodon falkenbachi	–	–	–	–	–	–	137	–	137		137	115	–
Daphoenodon skinneri	–	–	–	–	–	–	40	–	40		40	–	–
Daphoenodon neomexicanus	70	135	70	–	100	76	79	–	135	88	86	97	–
Ysengrinia americana	154	231	115	105	293	–	214	105–293	231	185	173	211	145
Pliocyon medius	107	145	100	–	136	160	130	100–160	145	130	128	144	–
Ischyrocyon gidleyi (Barstovian)	156	194	194	–	219	394	336	194–394	194	250	235	339	132
Ischyrocyon gidleyi (Claredonian)	–	–	–	–	–	–	546	–	546		546	539	–
Pseudocyon sp. (Nebraska)	–	–	–	–	–	396	–	–	310		350	331	–
Pseudocyon sp. (New Mexico)	–	–	–	–	–	773	760	–	773	767	773	–	–
Pseudocyon sansaniensis	–	–	–	245	–	–	–	–	245		245	–	–
Amphicyon ingens	372	579	300	350	786	1170	860	300–1170	579	631	547	706	378
Amphicyon frendens	–	–	–	–	–	432	–	–	432		432	–	–
Amphicyon galushai	–	191	130	–	–	241	204	130–241	191	192	187	191	152
Amphicyon major	195	183	312	–	–	–	–	–	183	230	223	–	–
Daphoenus vetus	–	27	32	36	–	–	19	19–36	27	29	25	32	27
Daphoenus hartshornianus	–	–	10	–	–	–	12	–	10	11	11	15	–
Paradaphoenus cuspigerus	–	–	–	–	–	4	–	–	4		4	6	–

towards cats with body masses ranging between 5 and 181 kg, as noted by Andersson (2004).

We calculated the mass of the giant beardog *Amphicyon ingens* as ca. 547 kg, which is in accordance with previous estimates obtained by Sorkin (2006), who provided a figure of ca. 550 kg based on the proportions of the femur. It is worth noting that this value is intermediate between those obtained with the functions derived by Van Valkenburgh (1990) and Anyonge (1993) for the craniodental and postcranial skeleton (706 and 378 kg, respectively; see Table 6). This result indicates that, along with the Pleistocene lion *Panthera atrox*, the Kodiak Island *Ursus arctos*, the Mio-Pliocene *Agriotherium* and the Pleistocene *Arctodus simus* (a species that is hypothesized to have behaved more as an omnivore than as an active predator, Figueirido et al. 2010), *A. ingens* was one of the largest mammalian carnivores ever known. In fact, the body masses of these three species are probably close to the upper limit for a mammalian terrestrial predator (Carbone et al. 2007).

The other North American species of *Amphicyon* included in the analysis are clearly smaller than *A. ingens*. Specifically, the mass of *A. galushai* was calculated at ca. 187 kg, a value which clearly agrees with the ones obtained with the functions of Van Valkenburgh (1990) and Anyonge (1993), and the estimate for *A. frendens* was ca. 432 kg. These values reach the size of a grizzly bear and a polar bear, respectively. The few remains of the European *A. major* analyzed in this study provide lower mass estimates (ca. 223 kg) than those obtained from the New World specimens.

Concerning North American *Pseudocyon* sp., the only material included in this paper consists of two mandibles and a cranium from different individuals collected from different sites. The mass estimate derived from a mandible collected from the Santa Fe Group (New Mexico) was ca. 773 kg. This mandible (F:AM 49247) is of medial Barstovian age and clearly represents a very large individual of *Pseudocyon*. However, the mass estimate for another mandible (F:AM 54209) is ca. 370 kg, a figure in agreement with the one provided by a skull of ca. 396 kg (F:AM 25144), both remains collected from the early Clarendonian of Nebraska. It is also worth noting that the mass estimate obtained with the function of Van Valkenburgh (1990) for the specimen F:AM 25144 is 331 kg, a value in agreement with our results. Also, the mass of *Pseudocyon sansaniensis* from Europe (ca. 245 kg) is close to the estimate derived from the North American specimens.

These different body mass estimations of *Pseudocyon* could be attributed to a marked sexual dimorphism in this extinct species, because the fossils most probably represent a single lineage.

We calculated the mass of the beardog *Ysengrinia americana* as ca. 173 kg, but the mass obtained from the best individual function estimate (BIFE, derived from the diameter of the femur at the midshaft) yields a higher estimate (ca. 231 kg). In fact, a broad range in the estimates derived from postcranial bones occurs for this species (Table 6). The variability in the masses obtained for *Y. americana* may result from several biases which are difficult to avoid in those extinct species with no living analogues (e.g., amphicyonids). Such biases may arise from anatomical differences related to inter- or intrapopulational variation (e.g., sexual dimorphism and ecogeographic variations). The postcranial bones of *Y. ameri-*

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cana included in the database belong to a number of individuals of early Miocene age (late Arikareean, North American Land Mammal Ages) that were preserved together in a waterhole at Harper Quarry, Sioux County, Nebraska (USA). However, it is clear that the geometric mean of the mass estimates for *Y. americana* lies within the range of values (145–211 kg) obtained with the functions of Van Valkenburgh (1990) and Anyonge (1993). A similarly-sized beardog was *Pliocyon medius,* with a mean mass estimated at ca. 128 kg (ca. 145 kg with the function of Van Valkenburgh 1990).

The mass of *Ischyrocyon gidleyi* was estimated at ca. 235 kg for the Barstovian specimens and ca. 546 kg for the individuals from the Clarendonian. Despite this divergence in body size, *I. gidleyi* apparently represents a single lineage during its time span (14–9 Ma) and could be split into two species, one comprising the smaller forms of the Barstow (California) and Valentine Formations (Nebraska), and the other the huge individuals from the Clarendon Beds (Texas). In any case, a systematic revision of the genus is necessary for corroborating such a possibility.

Our results show that *Daphoenodon* contains mid-sized to large amphicyonids, represented in this work by three North American species: *D. skinneri*, *D. falkenbachi*, and *D. neomexicanus*. Among them, *D. skinneri* was estimated to be the smallest, with a mass of ca. 40 kg (derived from the regression function adjusted with the variables of the mandible), whereas *D. neomexicanus* and *D. falkenbachi* were considerably larger, with estimates of 79 kg and 137 kg, respectively. *D. neomexicanus* is represented in our database by only the skull of a single individual and is the size of a large male wolf. It is worth noting that mass estimate obtained for *D. neomexicanus* with the function of Van Valkenburgh (1990), adjusted for the craniodental skeleton using a much wider sample of carnivorans, was ca. 79 kg (see table 6). Concerning *Adilophontes brachykolos*, its body mass was estimated to be ca. 125 kg.

The genus *Daphoenus* includes small-sized amphicyonids with a generalized postcranial skeleton (Hunt 1998). The mass estimate for *D. vetus* is ca. 25 kg and the one for *D. hartshornianus* ca. 11 kg. However, these species are not the smallest amphicyonids, as the estimate for *Paradaphoenus cuspigerus* is only ca. 4 kg. This result agrees with the suggestion that *Paradaphoenus* includes some of the smallest New World amphicyonids, never exceeding 3–4 kg (Hunt 2001).

Discussion

According to the range of body masses estimated for amphicyonids, the beardogs analyzed in this study distribute among three size groups (Fig. 5): (i) the small daphoenines (e.g., *Daphoenus* and *Paradaphoenus*); (ii) the mid-sized daphoenines (e.g., *Daphoenodon* and *Adilophontes*); and (iii) the largest amphicyonines (e.g., *Amphicyon*, *Ischyrocyon*, *Ysengrinia*, and *Pseudocyon*). The mass estimates reported in this paper are in agreement with the different ecomorphs exhibited by the family Amphicyonidae throughout its evolutionary history, ecomorphs established using independent anatomical criteria (e.g., Hunt 1998).

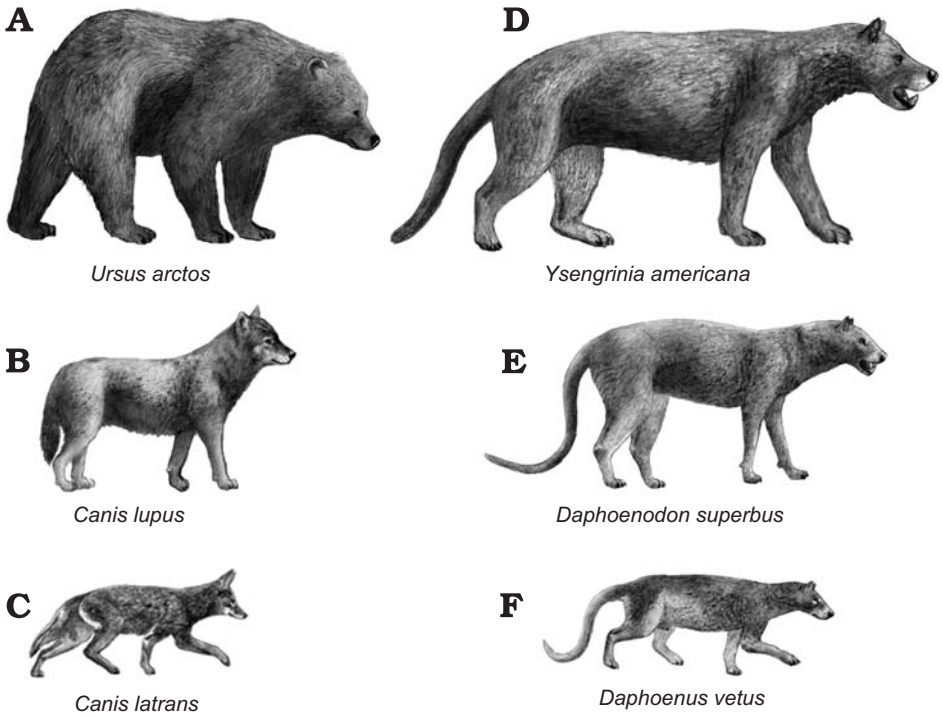

Fig. 5. Reconstruction of three extinct beardogs (right column) compared with their presumed analogues or ecomorphs among the living caniforms (left column). **A.** *Ursus arctos*. **B**. *Canis lupus*. **C**. *Canis latrans*. **D**. *Ysengrinia americana*. **E**. *Daphoenodon superbus*. **F**. *Daphoenus vetus*. Note the three different size classes among these caniforms, and the three types of ecomorphs mentioned in the text. Drawings by Óscar San-Isidro.

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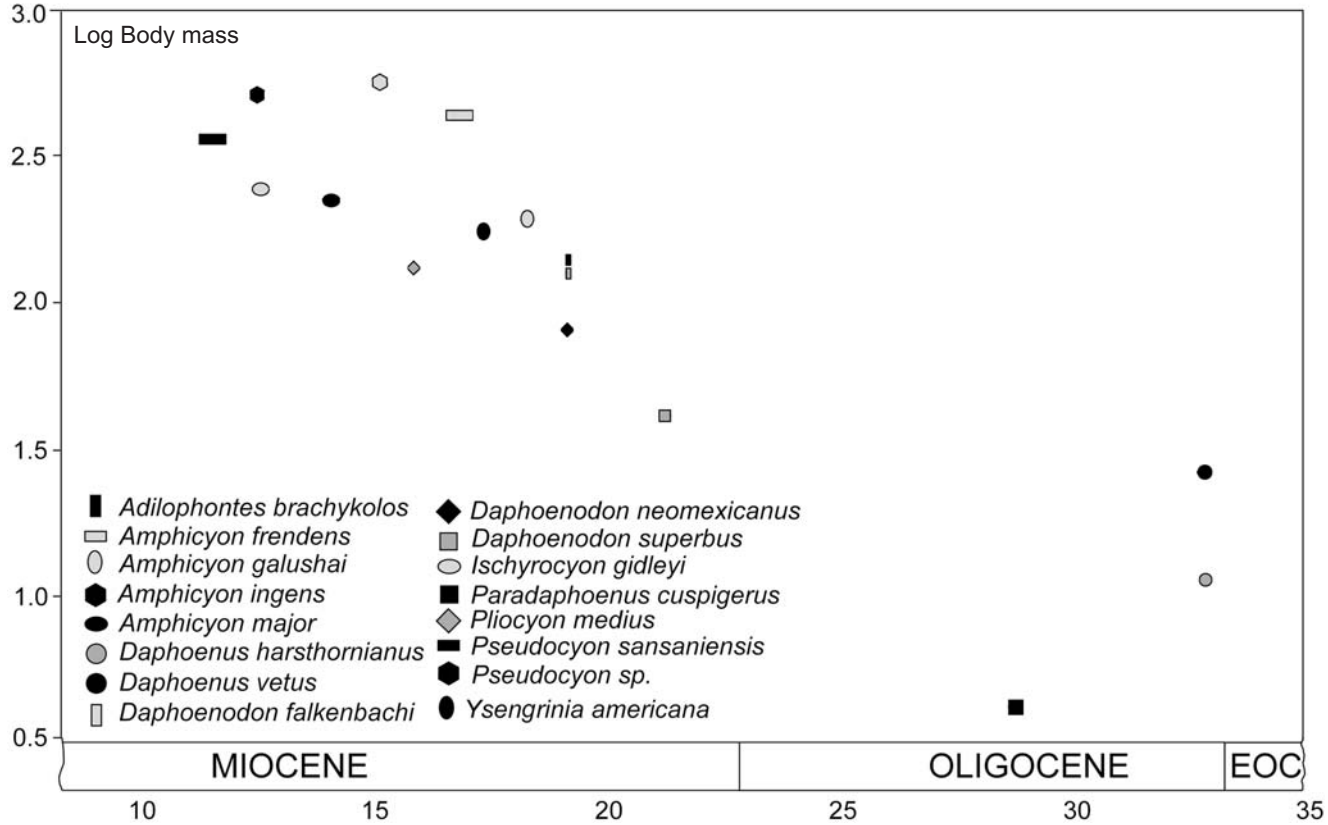

Fig. 6. Mean values of body mass (*y*-axis, $\log_{10}$-scale) estimated for all amphicyonids included in this study. Each amphicyonid species is represented by a symbol positioned at the midpoint of its stratigraphic range (*x*-axis; data from Hunt 1998, 2001, 2002, 2003, 2009; Peigné et al. 2006). Timescale (in Ma) from Prothero (1998).

The common species of *Daphoenus* (*D. vetus*, *D. hartshornianus*), which show a canid-like craniodental morphology (Hunt 1998), were small amphicyonids (ca. 11–25 kg), and the smallest species of the genus were probably scansorial (Van Valkenburgh 1987). Compared to the amphicyonines, their skulls are not so enlarged in relation to their body length and they also retain canid-like premolars, which has been previously interpreted as indicative of a mesocarnivorous diet (Hunt 1998). The genus *Paradaphoenus* includes some of the smallest amphicyonids (ca. 4 kg), with a lack of cursorial specializations and probably facultative climbing abilities (Hunt 2001).

The daphoenine species of *Daphoenodon* and *Adilophontes* have intermediate mass values (60–150 kg), which along with their morphology suggest that they probably belong to a different ecomorph. *Daphoenodon* shows shearing carnassials as well as highly prominent canines and premolars, features that both indicate a carnivorous diet. Their postcranial skeleton reveals a subdigitigrade stance, which is in accordance with an ambush predator of ungulate prey in open grasslands and riparian streams (Hunt 2002).

The scenario depicted above changes completely in the more derived species of amphicyonines (e.g., *Amphicyon ingens*, *Pseudocyon sansaniensis*, and *Ischyrocyon gidleyi*), as they were animals with large heads, powerful jaws, a stoutly built appendicular skeleton and a body mass often above 150 kg. Thus, some authors have envisaged a "bear-like" mode of life for some of these species (Fig. 5). However, in contrast to the living ursine bears, the evidence available on their craniodental and postcranial anatomy suggests that many amphicyonines had a more mobile attack behavior, rushing from ambush to capture prey, much as seen in the big cats (Hunt 1998; Sorkin 2006). Furthermore, compared with the extant canids, amphicyonines (e.g., *Amphicyon major*, *A. ingens*, and *A. frendens*) have a highly developed molar grinding area and strongly reduced premolars, characters which they share with the living bears (Ginsburg 1961) and are probably indicative of omnivory (Goillot et al. 2009). Also, their powerful and stoutly built skull allows speculation on their bone-cracking abilities (Viranta 1996; Bergounioux and Crouzel 1973). However, although their massive skeletons may hint at an ambulatory, "bear-like" mode of locomotion, some species within this subfamily show functional morphologies that probably indicate different ecological strategies (e.g., hypercarnivory, omnivory, and bone-cracking). This is especially the case for *Amphicyon ingens*, which exhibits the largest conical canines among the amphicyonines, a robust skeleton and an extremely developed sagittal crest that indicates the presence of massive jaw muscles (BF, personal observation). These features together with specializations of the limbs and feet suggest a large ambush predator.

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Several authors have reported on a marked trend of body size increase through the evolutionary history of amphicyonids (e.g., Hunt 1998; Finarelli and Flynn 2006, 2007). At first sight, the average mass values estimated for the members of this family seem to corroborate the increase in size through time (Fig. 6), thus following Cope's rule (Stanley 1973; Alroy 1988). However, this hypothesis deserves to be studied in further depth, in order to evaluate if there is a true trend toward greater body size or these data may be explained by a passive trend (or even by a random walk). In addition, Finarelli and Flynn (2007) described a negative allometry for braincase size on body mass in amphicyonids, a trend which in part reverses that shown by other caniform taxa. However, it is worth noting that Meachen-Samuels and Van Valkenburgh (2009) reported on a similar negative allometry for felids. The mass values obtained here corroborate the conclusion of Finarelli and Flynn (2007) that the relatively anomalous relationship between brain size and body mass in amphicyonids did not result from biased size estimates but the consequence of an allometric pattern of this extinct family.

Conclusions

As revealed by principal components analysis, based on the linear dimensions employed in this study, the craniodental morphology of beardogs appears to be "intermediate" between the morphologies of the living canids and ursids. Amphicyonids displayed very different skull proportions from living felids and hyaenids, the two feliform families included in this analysis. Whereas some morphologic convergences between the extinct amphicyonids and living felids and hyaenids have been reported (Bergounioux and Crouzel 1973; Viranta 1996; Hunt 1998; Sorkin 2006), the results of this study suggest that living canids and ursids, which were employed here, are the best available comparators.

The principal goal of our study was the estimation of the body masses of amphicyonids, particularly those belonging to the Daphoeninae and Amphicyoninae. Therefore, given the well-recognized morphological resemblances between the living caniforms and amphicyonids, we have used the extant species of Canidae and Ursidae for adjusting regression functions that allow estimation of amphicyonid body mass. In addition, we have also estimated their mass values with the equations published by Van Valkenburgh (1990) and Anyonge (1993), adjusted using all large-bodied extant carnivoran families, in order to check the biases in our estimates. In fact, the estimates calculated from these functions fall within the range of mass estimates obtained in this study for each species.

As a general rule, multiple regressions tend to predict body mass more accurately than single ones, although the best mass predictor is the one derived from femoral dimensions, an equation which incorporates only one variable, the mediolateral diameter of the femur at midshaft. As expected, the regression equations derived from the distal limb segments are worse predictors of body mass than those adjusted with the proximal ones. This may suggest that the dimensions of the distal limb segments are more correlated with the carnivoran locomotor adaptations and/or hunting techniques (Anyonge 1993, 1996). However, it may also reflect the fact that the distal limb segments are composed of two bones that jointly bear the weight of the animal, while the proximal segments are made up of only a single bone (Meachen-Samuels and Van Valkenburgh 2009).

The craniodental equations are worse mass predictors than those adjusted with the major limb bones. Also, body mass estimates derived for amphicyonids from skull measurements should be taken with caution, not only because these functions have lower predictive power than those adjusted with the postcranial skeleton, but also because amphicyonids have disproportionately large heads in relation to body mass (Finarelli 2006). For this reason, although we present here the mass values of amphicyonids derived from the craniodental skeleton, these values merit some skepticism, particularly for the larger species.

A set of multiple regression functions was applied to amphicyonids according to the availability of measurements. The values of body mass estimated for beardogs seem to show a relationship between the increase in body size and the appearance of different ecomorphs during the evolution of this carnivoran family. Specifically, the species of amphicyonids cluster in three size groups: (i) the small daphoenines, which converge on the living foxes, jackals and coyote; (ii) the mid-sized daphoenines, whose anatomy resembles in some aspects that of pack-hunting canids (e.g., *Canis lupus* or *Lycaon pictus*); and (iii) the largest amphicyonines, which most probably should be envisaged as bear-like foragers.

This study suggests that body size increased in amphicyonids through their evolutionary history, which agrees with previous studies (Hunt 1998; Finarelli and Flynn 2006, 2007), and that the appearance of new ecomorphs in the family (e.g., canid-like or bear-like) is probably expressed as a progressive alteration in skeletal form and body size (i.e., allometry) as influenced by natural selection. Future studies on the relationship among size and shape in amphicyonids are crucial for understanding the morphological evolution of beardogs.

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Appendix 1

Extinct species and catalogue numbers of fossil specimens used in this study.

Extinct species	Catalogue numbers
Adilophontes brachykolos	F:AM-54148, F:AM-27568, F:AM-54140
Daphoenodon falkenbachi	F:AM-54144
Daphoenodon skinneri	F: AM-70801
Daphoenodon neomexicanus	F:AM-49239, F-AM-49240, JEM 7-105, JEM 7-106, JEM 6-86, JEM 5-72, JEM 5-74
Ysengrinia americana	F:AM- 54147, UNSM-44600, UNSM-44606, UNSM-44604, UNSM-44690, UNSM-44623
Pliocyon medius	F:AM-54319, F:AM-54342, F:AM-54322, F:AM-68201, F:AM-68128A, F:AM-68128, F:AM-68129A, F:AM-68123, F:AM-68123C, F:AM-68123A, F:AM-68130
Ischyrocyon gidleyi	F:AM-54220, F:AM-49325, F:AM-49327, F:AM-25115, F:AM-68222, F:AM-68227, F:AM-96638, F:AM-68217, F:AM-25139, F:AM-68176A, F:AM-68157, F:AM-68153, F:AM-68152A, F:AM-68158, F:AM-68152B, F:AM-68158A, F:AM-68158B, F:AM-68158C, F:AM-68181A, F:AM-68162A, F:AM-68162, 68159
Pseudocyon sp.	F:AM-49247, F:AM-96627, F:AM-54209, F:AM-25144
Pseudocyon sansaniensis	MNHN-215
Amphicyon ingens	F:AM-54262, F:AM-54270, F:AM-25470B, F:AM-54268, F:AM-25470, F:AM-28307, F:AM-68117, F:AM-68147A, F:AM-28306, F:AM-28307, F:AM-28343, F:AM-25480, F:AM-68121A, F:AM-68121B, F:AM-68122A, F:AM-68122B, F:AM-68122C, F:AM-68145, F:AM-23788
Amphicyon frendens	F: AM-54423, F:AM-54391, F:AM-54226
Amphicyon galushai	F:AM-25400
Amphicyon major	MNHN-95, MNHN-150, MNHN-105
Daphoenus vetus	AMNH-9759, AMNH-39098, AMNH-39099, AMNH-11857, F:AM-63343, F:AM-63921
Daphoenus harsthornianus	F:AM-63351, AMNH-1387
Paradaphoenus cuspigerus	AMNH-6852

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Appendix 2

Species of large fissiped carnivorans included in the principal components analysis (sample size in parentheses).

Canidae	Felidae	Ursidae	Amphicyonidae
Alopex lagopus (10)	*Acinony jubatus* (13)	*Ursus maritimus* (16)	*Adilophontes brachykolos* (1)
Atelocynus microtis (1)	*Felis aurata* (2)	*Helarctos malayanus* (9)	*Pliocyon medius* (1)
Canis adustus (6)	*Felis caracal* (9)	*Ursus ursinus* (12)	*Pseudocyon sansaniensis* (1)
Cuon alpinus (6)	*Felis lynx* (7)	*Ailuropoda melanoleuca* (2)	*Ischyrocyon gidleyi* (1)
Canis aureus (11)	*Felis maniculara* (1)	*Ursus arctos* (34)	*Amphicyon ingens* (1)
Chrysocyon brachyurus (1)	*Felis rufus* (1)	*Ursus tibethanus* (13)	*Amphicyon galushai* (1)
Canis latrans (10)	*Felis serval* (2)	Ursus americanus (12)	*Amphicyon frendens* (1)
Canis lupus (9)	*Felis temmnicki* (1)	*Tremarctos ornatus* (2)	*Daphoenus vetus* (1)
Canis mesomelas (8)	*Felis viverrina* (2)		*Daphoenus* sp. I (1)
Canis simensis (5)	*Felis widdei* (1)		*Daphoenus* sp. II (1)
Cerdocyon thous (5)	*Felis yagourondi* (1)		
Dusicyon culpaeus (5)	*Neofelis nebulosa* (10)		
Duscicyon griseus (10)	*Puma concolor* (8)		
Dusicyon gymnocerus (5)	*Panthera leo* (8)		
Dusicyon vetulus (5)	*Panterhaonca* (8)		
Fennecus zerda (4)	*Panthera pardus* (11)		
Lycaon pictus (4)	*Panthera tigris* (8)		
Licalopex sechurae (5)	*Panthera uncia* (7)		
Nyctereutes procyonoides (5)	*Crocuta crocuta* (4)		
Otocyon megalotis (11)	*Hyaena hyaena* (12)		
Speothos venaticus (6)	*Hyaena brunea* (13)		
Urocyon cineroargenteus (10)			
Urocyon litorales (8)			
Vulpes bengalensis (4)			
Vulpes cana (1)			
Vulpes chama (7)			
Vulpes corsac (1)			
Vulpes ferrilata (1)			
Vulpes macrotes (11)			
Vulpes pallida (8)			
Vulpes ruepelli (10)			
Vulpes vulpes (10)			

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Appendix 3

Single regression statistics for the craniodental measurements; the regression equations are expressed as: Log(body mass) = a + bLog(X), where body mass is in kg and X's are measured in mm.

Variables	r	F	a ± 95% CI		b ± 95% CI		P	%PE	%SEE
Cl	0.944	291.864	-1.142	± 0.630	2.443	± 0.579	< 0.001	34.24	79.06
Cb	0.936	256.488	-0.558	± 0.531	2.298	± 0.592	< 0.001	39.63	85.30
P4l	0.630	23.622	- 2.643	± 3.410	4.273	± 3.537	< 0.001	108.96	292.14
P4b	0.867	109.130	-1.057	± 0.992	3.788	± 1.471	< 0.001	71.25	140.05
m1l	0.777	54.676	-4.021	± 2.999	4.508	± 2.473	< 0.001	106.26	202.80
m1b	0.753	109.612	-2.136	± 1.399	4.330	± 1.677	< 0.001	69.38	139.70
m2l	0.963	452.923	-1.765	± 0.621	3.013	± 0.575	< 0.001	46.94	61.13
m2b	0.904	338.902	-1.331	± 0.625	3.177	± 0.700	< 0.001	47.04	72.42
MAT	0.978	773.104	-3.603	± 0.740	3.209	± 0.468	< 0.001	29.01	44.87
MAM	0.957	387.103	-3.706	± 1.066	3.702	± 0.763	< 0.001	41.01	66.72
MAR	0.961	438.695	-7.503	± 1.733	4.178	± 0.809	< 0.001	38.18	62.28
Mm1	0.981	913.621	-5.326	± 0.910	3.622	± 0.486	< 0.001	26.13	40.81
MFl	0.949	325.66	-4.360	± 1.308	3.453	± 0.777	< 0.001	37.52	74.14
Jdp4	0.968	535.355	-1.910	± 0.596	2.485	± 0.435	< 0.001	26.97	55.74
Jdm1	0.966	504.890	-2.312	± 0.686	2.783	± 0.502	< 0.001	31.56	57.39
Jdm2	0.967	525.509	-2.405	± 0.688	2.807	± 0.497	< 0.001	31.25	56.07
Jbp4	0.943	286.854	-1.429	± 0.702	2.984	± 0.715	< 0.001	37.34	79.87
Jbm1	0.938	263.618	-1.883	± 0.838	3.404	± 0.850	< 0.001	46.60	83.93
Jbm2	0.952	348.902	-1.655	± 0.684	3.124	± 0.678	< 0.001	41.30	71.20
SYMl	0.921	201.44	-3.327	± 1.371	3.030	± 0.866	< 0.001	42.02	98.39
I3l	0.938	264.207	-0.698	± 0.556	2.687	± 0.671	< 0.001	47.56	83.82
I3b	0.936	253.955	-0.423	± 0.500	2.666	± 0.678	< 0.001	47.25	85.80
Cl	0.953	359.149	-1.060	± 0.553	2.361	± 0.505	< 0.001	32.16	70.01
Cb	0.942	283.412	-0.464	± 0.484	2.224	± 0.536	< 0.001	35.23	79.32
P4l	0.391	6.5100	-1.325	± 4.381	2.531	± 4.024	0.015	132.62	404.52
P4b	0.818	72.840	-2.550	± 1.907	4.520	± 2.147	< 0.001	128.77	174.90
M1l	0.954	362.661	-3.056	± 0.964	4.084	± 0.870	< 0.001	74.31	69.61
M1b	0.701	34.731	-4.175	± 3.865	5.143	± 3.540	< 0.001	48.54	250.61
M2l	0.962	444.241	-0.866	± 0.460	2.127	± 0.409	< 0.001	96.33	61.83
M2b	0.924	211.130	-3.233	± 1.313	4.518	± 1.261	< 0.001	46.74	95.63
SKl	0.976	719.363	-7.767	± 1.393	4.024	± 0.609	< 0.001	58.52	46.79
BCl	0.939	267.419	-7.804	± 2.294	4.117	± 1.021	< 0.001	29.30	83.24
OOl	0.942	281.262	-7.248	± 2.032	4.232	± 1.023	< 0.001	41.40	80.80
Pl	0.955	372.171	-6.370	± 1.644	3.916	± 0.823	< 0.001	38.99	68.56
Pb	0.810	68.592	-7.050	± 4.158	5.115	± 2.505	< 0.001	36.85	180.55
Gb	0.946	308.361	-6.440	± 1.822	4.661	± 1.076	< 0.001	74.72	76.55
Zb	0.948	320.652	-5.707	± 1.621	3.476	± 0.788	< 0.001	46.78	74.82
POP	0.980	874.467	-4.371	± 0.800	3.311	± 0.509	< 0.001	32.93	41.85
MCb	0.969	547.421	-7.038	± 1.473	4.638	±0.804	< 0.001	40.71	54.74

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Appendix 4

Single regression statistics for postcranial measurements; the regression equations are expressed as: Log(body mass) = a + bLog(X), where body mass is in kg and X's are measured in mm.

Variables	r	F	a ± 95% CI		b ± 95% CI		P	%PE	%SEE
RTL	0.943	176.618	-6.392 ±	2.470	3.506 ±	1.094	< 0.001	36.09	71.53
Redml	0.987	826.699	-2.165 ±	0.537	2.518 ±	0.363	< 0.001	19.54	29.83
Redap	0.974	413.674	-1.426 ±	0.611	2.330 ±	0.475	< 0.001	24.72	43.95
Repml	0.977	453.442	-2.172 ±	0.726	2.780 ±	0.541	< 0.001	24.57	41.73
Repap	0.969	342.942	-1.036 ±	0.586	2.032 ±	0.455	< 0.001	25.95	48.89
Rdml	0.964	285.789	-1.768 ±	0.817	2.797 ±	0.686	< 0.001	29.71	54.26
Rdap	0.965	296.489	-1.000 ±	0.622	2.559 ±	0.616	< 0.001	28.83	53.13
FTL	0.979	516.761	-5.901 ±	1.355	3.173 ±	0.579	< 0.001	21.28	38.77
Fedml	0.991	1183.455	-2.788±	0.524	2.678 ±	0.323	< 0.001	16.45	24.49
Fedap	0.984	686.061	-3.457 ±	0.546	3.108 ±	0.492	< 0.001	21.68	33.08
Fepml	0.989	943.198	-3.072 ±	0.623	2.723 ±	0.368	< 0.001	19.06	27.73
Fepml2	0.991	1229.866	-1.963 ±	0.416	2.538 ±	0.301	< 0.001	16.30	23.98
Fepap	0.989	1027.785	-2.012 ±	0.463	2.575 ±	0.334	< 0.001	17.88	26.45
Fdml	0.994	1956.815	-1.749 ±	0.310	2.659 ±	0.249	< 0.001	14.06	18.64
Fdap	0.988	904.258	-1.682 ±	0.448	2.708 ±	0.374	< 0.001	20.66	28.38
Fcml1	0.987	827.947	-1.318 ±	0.417	2.384 ±	0.344	< 0.001	18.28	29.80
Fcap1	0.986	781.250	-2.240 ±	0.563	2.795 ±	0.415	< 0.001	21.56	30.77
Fcml2	0.987	819.871	-1.457 ±	0.429	2.522 ±	0.365	< 0.001	19.70	29.96
Fcap2	0.987	811.535	-2.780 ±	0.631	3.181 ±	0.463	< 0.001	20.33	30.13
HTL	0.978	476.662	-6.215 ±	1.470	3.366 ±	0.639	< 0.001	22.43	40.57
Hedml	0.989	995.741	-2.108 ±	0.482	2.187 ±	0.288	< 0.001	17.96	26.92
Hedml .TrcL	0.991	1144.224	-1.946 ±	0.430	2.276 ±	0.279	< 0.001	14.91	24.94
Hedap	0.984	651.243	-2.232 ±	0.616	2.531 ±	0.412	< 0.001	22.42	34.05
Hepml	0.988	891.997	-2.839 ±	0.609	2.786 ±	0.387	< 0.001	19.84	28.60
Hepap	0.983	649.262	-3.370 ±	0.800	2.938 ±	0.478	< 0.001	22.24	34.11
Hdml	0.987	825.150	-1.430 ±	0.433	2.447 ±	0.353	< 0.001	19.41	29.86
Hdap	0.988	868.789	-1.674 ±	0.456	2.502 ±	0.353	< 0.001	18.13	29.02
Hdml35%	0.987	831.661	-1.696 ±	0.469	2.703 ±	0.388	< 0.001	20.48	29.73
Hdap35%	0.989	943.462	-1.324 ±	0.391	2.271 ±	0.307	< 0.001	17.03	27.73
UTL	0.953	218.922	-6.924 ±	2.368	3.630 ±	1.017	< 0.001	30.37	63.21
Uepml	0.942	173.309	-0.975 ±	0.805	1.833 ±	0.577	< 0.001	46.41	68.39
Uepap	0.984	660.388	-2.239 ±	0.612	2.511 ±	0.405	< 0.001	23.75	33.79
Uedml	0.972	378.212	-0.355 ±	0.420	1.872 ±	0.399	< 0.001	32.11	46.24
Uedap	0.963	284.895	-0.586 ±	0.536	1.530 ±	0.431	< 0.001	32.07	54.35
Udml	0.968	318.667	-1.169 ±	0.642	2.561 ±	0.596	< 0.001	33.67	50.80
Udap	0.975	430.382	-0.380 ±	0.398	1.719 ±	0.344	< 0.001	22.73	42.98
TTL	0.894	87.375	-7.644 ±	4.056	4.003 ±	1.776	< 0.001	52.39	106.91
Tepml	0.976	443.286	-2.767 ±	0.850	2.649 ±	0.522	< 0.001	30.84	42.27
Tepap	0.947	191.440	-3.960 ±	1.647	3.462 ±	1.038	< 0.001	38.78	68.29
Tedml	0.896	89.331	-1.461 ±	1.325	2.020 ±	0.887	< 0.001	100.37	105.58
Tedap	0.973	395.926	-2.377 ±	1.082	3.001 ±	0.386	< 0.001	30.23	71.76
Tdml	0.979	496.156	-2.138 ±	0.688	3.183 ±	0.593	< 0.001	24.74	39.66
Tdap	0.972	381.687	-1.587 ±	0.670	2.603 ±	0.553	< 0.001	32.83	46.01

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