Historical Biology
An International Journal of Paleobiology

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713717695

Ecomorphology of the giant bear-dogs **Amphicyon** and **Ischyrocyon**

PLEASE SCROLL DOWN FOR ARTICLE

Ecomorphology of the giant bear-dogs *Amphicyon* and *Ischyrocyon*

B. SORKIN

Department of Biological Sciences, Marshall University, Huntington, WV 25755, USA

Abstract
Giant bear-dogs of the genera *Amphicyon* and *Ischyrocyon* (Carnivora, Amphicyonidae, Amphicyoninae) were the largest carnivorans in North America during middle and late Miocene (17.5–8.8 Mya) with a dental and skeletal morphology that combined features found in living Ursidae, Canidae, and Felidae. This study tests previously proposed models of diet and hunting behaviour of these extinct carnivorans. Relative grinding area (RGA) of lower molars and wear pattern on upper molars suggest that bear-dogs were carnivorous. *Amphicyon* and *Ischyrocyon* possessed skeletal features of both ambush (short distal limb segments) and pursuit (caudally bent olecranon process of ulna) living predators. Therefore, bear-dogs probably pursued their prey (mediportal ungulates) for a longer distance but at a slower speed than do living ambush predators. Upon catching up to its prey a bear-dog probably seized it with powerfully muscled forelimbs and killed it by tearing into its ribcage or neck with canines set in a narrow rostrum.

Keywords: Amphicyonidae, Amphicyon, Ischyrocyon, *diet, hunting behaviour*

Introduction

Giant bear-dogs of the genera *Amphicyon* and *Ischyrocyon* (Carnivora, Amphicyonidae, Amphicyoninae) were the largest carnivorans in North America from the late Hemingfordian to the late Clarendonian (17.5–8.8 millions of years ago (Mya)) (based on qualitative body mass estimates in Munthe (1989), Hunt (1998a,b) and Martin (1998a,b)). The largest individuals of *Amphicyon ingens* (early to mid-Barstovian, 15.8–14.0 Mya), the largest species of *Amphicyon* and of North American Amphicyoninae (Hunt 1998a), attained body mass of 550 kg, placing *A. ingens* among the largest terrestrial predators known (see materials and methods section for body mass estimation). By comparison, the largest male individuals of the Siberian tiger (*Panthera tigris altaica*), the largest extant terrestrial predator, attain body mass of 320 kg (Stroganov 1969). After the extinction of *Amphicyon* in the late Barstovian (14 Mya) (Hunt 1998a), *Ischyrocyon gidleyi* (Clarendonian) also exceeded the Siberian tiger in maximal body mass (see materials and methods section for body mass estimation), although it never attained the body mass of the largest individuals of *A. ingens*.

As the informal name (spelled "beardogs" in Hunt (1998a), "bear dogs" in Viranta (1996)) of their extinct family suggests, the dental and skeletal morphology of *Amphicyon*, *Ischyrocyon* and other members of the subfamily Amphicyoninae was unlike that of any living carnivoran. These bear-dogs possessed short distal limb segments, plantigrade hind feet, and broad molars of the living bears (Ursidae, Ursinae), long narrow rostrum and moderately sectorial carnassials of the living dogs (Canidae, Caninae), and flexible lumbar segment of the vertebral column and long tail of the living cats (Felidae) (Viranta 1996; Hunt 1998a; Ginsburg 1999). This combination of features makes their diet and foraging behaviour difficult to reconstruct.

Viranta (1996) and Ginsburg (1999) reconstructed *Amphicyon* spp. as carnivores with some bone-crushing capability based on the presence of both a nearly vertical (suggesting shearing of flesh) and a horizontal (suggesting crushing of bone) wear facets on the carnassials (P4 and m1) and on the molars (M1–3 and m2–3) of the European species of the genus. However, Hunt (1998a) argued that the enlarged posterior molars (M2–3 and m2–3) of *Amphicyon* spp. indicated that members of the genus

were hypocarnivores that, presumably, included a large amount of plant material in their diet. In contrast, Hunt (1998a) reconstructed *I. gidleyi*, the only species of the genus he recognized, as a hypercarnivore with, presumably, an exclusively carnivorous diet based on its highly sectorial carnassials (P4 and m1) and smaller posterior molars (M2–3 and m2–3). The above reconstruction of the diets of *Amphicyon* and *Ischyrocyon* is implicit in Hunt's (1998a) paper, although he did not explicitly define the terms "hypocarnivore" and "hypercarnivore"; hence the word "presumably" in the two previous sentences.

All of the above authors agreed that the members of *Amphicyon*, *Ischyrocyon* and other amphicyonine genera engaged in active predation. Both Viranta (1996) and Ginsburg (1999) proposed the living Felidae, the big cats (genus *Panthera*) in particular, as a model for the hunting behaviour of *Amphicyon*. However, Viranta (1996) also proposed the living brown bear (*Ursus arctos*) as an alternative model for the hunting behaviour of *Amphicyon*. Given the similarity of its postcranial skeleton to that of *Amphicyon* (Hunt 1998a) these models of hunting behaviour would also apply to *Ischyrocyon*.

This study tests the above models of diet and hunting behaviour of the giant bear-dogs *Amphicyon* and *Ischyrocyon* by comparing their dental and skeletal morphology to those of the living carnivorans representing different ecomorphs (exhibiting suits of dental and skeletal adaptations to different ecological niches): omnivore, ambush predator, and pursuit predator.

Materials and methods

Institutional abbreviations

AMNH, F: AM (Frick American Mammals Collection), American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; LACM HC, Los Angeles County Museum, Hancock Collection, Los Angeles. All institutions are located in the USA.

Specimens

The following specimens of *Amphicyon* and *Ischyrocyon* were examined: *Amphicyon* sp., late Hemingfordian, F: AM 68103—left and right ulnae, F: AM 68108A—right humerus, F: AM 68108a—left humerus; *Amphicyon galushai*, Barstovian, F: AM 25400—skull; *Amphicyon* sp., late Barstovian, F: AM 68212—right humerus and radius; *A. ingens*, Barstovian, F: AM 25470—skull, F: AM 54268—skull, F: AM 68117—right ulna, F: AM 68117—left femur and tibia, F: AM 68118—right humerus, F: AM 68118B—left humerus, F: AM 68120—right ulna, F: AM 68169—right ulna, mounted and displayed skeleton at the AMNH (a composite of several specimens); *Ischyrocyon* sp., Late Barstovian, F: AM 54220—skull, right humerus, left ulna and radius; *Ischyrocyon* sp., Clarendonian, F: AM 49325—skull, F:AM 49327—skull, F: AM 25115—skull, F: AM 68157—left femur and tibia.

The collection names and specimen numbers of the specimens of other carnivoran species examined for this paper are listed next to the measurements or photographs of those specimens.

Body mass estimation

The data used to estimate maximal body masses attained by *A. ingens* and *I. gidleyi* are listed in Table I. If the individual of *A. ingens* represented by the longest femur were isometric to either of the two male Kodiak bears (*U. arctos middendorffi*) it would have weighed either 615 or 490 kg. The assumption of isometry between *A. ingens* and *U. arctos middendorffi* is a reasonable approximation, given the similarity of appendicular skeletal morphologies between Amphicyoninae and Ursinae (Hunt 1998a). The average of the two estimates rounded off to tens of kilograms (550 kg) is used as the best estimate of the maximal body mass attained by *A. ingens*. Based on the basilar skull length (from the posterior margin of the alveoli of the median upper incisors to the anteriormost point on the lower border of the foramen magnum) ranges for *Amphicyon* and *Ischyrocyon* in Hunt (1998a) and the assumption of isometry between the largest species

Table I.   Data for maximal body mass estimation in *A. ingens* and *I. gidleyi*.

Species	Specimen	Basilar skull length (mm)	Total femur length (mm)[*]	Body mass (kg)
Amphicyon ingens, Barstovian	F: AM 68121B[†]	–	503	–
Ursus arctos middendorffi male	Single individual	–	520[‡]	680[‡]
Ursus arctos middendorffi male	Single individual	–	505[¶]	496[¶]
Amphicyon ingens, Barstovian	Largest known	520[§]	–	–
Ischyrocyon gidleyi, Clarendonian	Largest known (N = 6)	470[§]	–	–

[*]Measured from the femoral head to the medial femoral condyle parallel to the shaft of the bone. [†]Longest femur assigned to the species (N = 7) in the American Museum of Natural History fossil mammals collection; measured by the author. [‡]Viranta (1996), p. 43. [¶]Christiansen (1999), Table 2. [§]Hunt 1998b.

or chronospecies of the two genera, the largest known individual of *Ischyrocyon* (Clarendonian *I. gidleyi*) had a body mass 26% lower than that of the largest known individual of *Amphicyon* (*A. ingens*). Assuming that the individuals of *A. ingens* represented by the longest skull measured by Hunt (1998a) and the longest femur measured by the author had similar body masses, the individual of Clarendonian *I. gidleyi* represented by the longest known skull of the chronospecies would have had a body mass of 410 kg (rounded off to tens of kilograms).

Cranial dimensions

The data on the cranial dimensions of *Amphicyon* and *Ischyrocyon* and the extant species of Carnivora used in the analysis are listed in Table II. All measurements were taken by the author, except those for *Panthera leo atrox*. All individuals measured had a fully erupted permanent dentition. Basal skull length was measured with a metal rule and rostral width at the canines— with a 300 mm digital caliper from ABS Import Tools Inc.

Rostral width was plotted as a function of basal length (Figure 8 of the results section) on the $\log_{10}/\log_{10}$ axes, with each specimen representing a single data point. Linear regression line and 95% confidence (for the regression line) and prediction (for a single data point) intervals were fitted to the data set

for *P. leo*, which included data for the extinct American lion (*P. atrox*), probably a subspecies of *P. leo* (Kurtén 1985), taken from Merriam and Stock (1932).

Limb bone dimensions

The data on the limb segment lengths and the leverage of the forelimb muscles (triceps, deltoids, and pectoralis) in *Amphicyon* and *Ischyrocyon* and other Carnivora used in the analyses are listed in Tables III–V. The mean and the range for the radius/humerus and the tibia/femur ratios are listed in Table VIII of the results section. All individuals measured were adults, as indicated by the fusion of the long bone epiphyses to the diaphysis. The lengths of the humerus, radius, femur and tibia were measured as in Bertram and Biewener (1990) using a 300 mm digital caliper from ABS Import Tools Inc. and a metal rule (for lengths over 310 mm). These interarticular lengths (measured between the proximal and distal joint surfaces of a long bone) are more representative of the functional length of the limb segments than the total lengths of these bones commonly reported in the literature.

The lengths of the ulna (from the distal articular surface to the middle of the semilunar notch) and the olecranon process (from the middle of the semilunar notch to the proximal end of the olecranon process) (Munthe 1989; Figure 2) were measured by applying a metal rule to the medial side of the bone. The values

Table II.   Basal length and rostral width at the canines of the skulls of *Amphicyon* and *Ischyrocyon* and lion, tiger, spotted hyena and grey wolf.

Species	Specimen number	Basal length (mm)	Rostral width (mm)
Amphicyon galushai, Barstovian	F: AM 25400	308.0	68.4
Amphicyon ingens, Barstovian	F: AM 25470	452.0	91.0
Ischyrocyon sp., late Barstovian	F: AM 54220	345.0	83.5
Ischyrocyon sp., Clarendonian	F: AM 25115	353.5	96.4
Ischyrocyon sp., Clarendonian	F: AM 49325	388.0	106.8
Panthera leo atrox★	University of California 14001	404.7	135.9
Panthera leo atrox	2900-3	388.0	141.4
Panthera leo atrox	University of California 20049	375.2	127.3
Panthera leo atrox	2900-9	359.4	122.8
Panthera leo, male	FMNH 35741	323.0	102.9
Panthera leo	FMNH 89926	319.0	105.2
Panthera leo	FMNH 75609	311.5	94.5
Panthera leo, male	FMNH 163109	309.9	94.1
Panthera leo, female	FMNH 35132	257.1	79.1
Panthera leo, female	FMNH 121667	248.0	83.9
Panthera leo, female	FMNH 20756	246.1	78.6
Panthera leo, female	FMNH 20758	236.3	77.0
Panthera tigris, male	FMNH 142009	291.1	106.5
Panthera tigris, male	FMNH 31153	290.4	98.7
Panthera tigris, female	FMNH 159999	273.8	95.3
Crocuta crocuta, male	FMNH 34582	239.7	63.5
Crocuta crocuta, male	FMNH 34583	234.4	65.9
Crocuta crocuta, female	FMNH 98952	229.7	60.6
Crocuta crocuta, female	FMNH 127826	218.9	62.2
Canis lupus, male	FMNH 138797	233.0	49.7
Canis lupus, male	FMNH 138794	229.6	49.0
Canis lupus, female	FMNH 138795	223.8	45.2
Canis lupus, female	FMNH 138774	224.6	46.2

★ Data on the extinct subspecies of *P. leo* from Merriam and Stock (1932, Table 89).

Table III.   Limb segment lengths in *Amphicyon* and *Ischyrocyon* and living Carnivora.

Species	Specimen number	Humerus (mm)	Radius (mm)	Femur (mm)	Tibia (mm)
Amphicyon sp., late Barstovian	F: AM 68212	318.3	257.8	–	–
Amphicyon ingens, Barstovian	F: AM 68117	–	–	491.5	366.0
Ischyrocyon sp., late Barstovian	F: AM 54220	283.1	238.8	–	–
Ischyrocyon sp., Clarendonian	F: AM 68157	–	–	317.5	238.9
Ursus arctos gyas, male	FMNH 63802	444.0	348.5	509.3	353.5
Ursus arctos horribilis, male	FMNH 98919	336.0	280.3	408.5	281.3
Panthera tigris tigris	AMNH 113744	343.0	290.6	396.5	326.8
Panthera tigris tigris, male	AMNH 54460	327.5	274.8	388.0	303.3
Panthera tigris altaica, male	AMNH 85404	323.3	272.0	388.5	313.8
Panthera tigris, female	FMNH 57172	303.4	251.5	358.5	290.4
Panthera tigris, female	FMNH 134497	303.2	255.7	357.3	293.9
Panthera tigris tigris	FMNH 60760	293.1	236.0	336.5	275.8
Panthera leo, male	AMNH 52078	347.0	310.5	390.5	311.4
Panthera leo, male	FMNH 173259	315.6	274.1	350.3	288.9
Panthera leo, female	FMNH 135278	278.4	253.4	319.0	267.0
Panthera leo, female	FMNH 49340	264.8	251.0	304.6	262.6
Canis lupus, male	AMNH 98231	229.9	234.0	253.7	252.0
Canis lupus, male	AMNH 98226	228.9	230.5	253.8	252.2
Canis lupus, male	AMNH 98230	228.4	233.0	251.6	250.5
Canis lupus, female	AMNH 98227	220.8	219.2	240.1	242.0
Canis lupus, female	AMNH 98225	218.3	226.2	238.1	246.3
Crocuta crocuta	FMNH 18855	200.8	215.0	245.8	185.0
Crocuta crocuta, male	FMNH 127825	193.6	208.6	233.5	181.9
Crocuta crocuta, female	FMNH 127826	192.4	212.4	232.2	180.2

Table IV.   Triceps leverage in *Amphicyon* and *Ischyrocyon* and other Carnivora.

Species	Specimen	N	Ulna length (mm)	Olecranon length (mm)
Amphicyon sp., late Hemingfordian	F: AM 68103	2	288.0	49.5
Amphicyon ingens, Barstovian	F: AM 68120, 68169, 68117	3	337.0	78.0
Ischyrocyon sp., late Barstovian	F: AM 54220	1	242.0	51.0
Ursus arctos gyas, male	FMNH 63802	1	358.0	62.0
Ursus arctos horribilis, male	FMNH 98919	1	281.5	46.5
Panthera atrox	FMNH P 27071	1	322.0	70.0
Panthera tigris altaica, female	FMNH 159999	1	269.5	69.0
Panthera tigris ssp., male	FMNH 165401	1	214.0	55.5
Panthera leo, both sexes	FMNH 49340, 173259	2	261.8	52.0
Panthera onca, both sexes	FMNH 57177, 150781	2	192.6	45.0
Panthera pardus, both sexes	FMNH 54247, 153777	2	188.0	40.8
Canis lupus, male	FMNH 60049, 60378	2	229.8	34.1

Table V.   Deltoid and pectoralis leverage in *Amphicyon* and *Ischyrocyon* and Felidae.

Taxon	Humerus length (mm)	Deltoid and pectoral ridges/deltopectoral crest length (mm)	N	Collection
Felidae				
Nimravides sp., Hemphillian	297.8	188.0	3	F: AM
Nimravides sp., late Clarendonian	326.0	209.0	1	F: AM
Panthera atrox	373.3	236.3	4	LACM HC, 2 casts*
Panthera leo	290.2	188.3	2	FMNH
Panthera pardus	194.4	121.6	4	FMNH
Panthera spelaea, Alaska	286.7	167.8	4	F: AM
Panthera tigris altaica	308.3	191.1	5	AMNH
Panthera tigris ssp.	253.6	160.0	1	FMNH
Amphicyoninae				
Amphicyon ingens, Barstovian	388.5	267.0	2	F: AM
Amphicyon sp., late Hemingfordian	292.4	192.5	2	F: AM
Ischyrocyon sp., late Barstovian	283.1	186.0	1	F: AM

* Two of the four humeri measured were casts of display specimens.

Table VI. Regression statistics.

Regression	N	Least squares (Model I)			Reduced major axis (Model II)			r
		Slope	Intercept	95% CI	Slope	Intercept	95% CI	
Log$_{10}$(rostral width) vs. Log$_{10}$(basal skull length) in *Panthera leo*	12	1.137	−0.827	±0.180	1.165	−0.897	±0.180	0.976
Olecranon length vs. ulna length in *Panthera*	6	0.203	6.402	±0.154	0.231	−0.460	±0.154	0.877
Deltoid and pectoral ridge length vs. humerus length in Felidae	8	0.645	−5.204	±0.105	0.654	−7.675	±0.105	0.987

listed for each individual are averages for the bones from both sides of the skeleton, unless bones from only one side were available, as was the case for all bear-dogs and *Panthera atrox*. Olecranon length was plotted as a function of ulna length (without logarithmic transformation) with each species or subspecies represented by a single data point (Figure 3 of the results section). Data points for *P. leo*, *Panthera onca* and *P. pardus* represent averages of one male and one female individuals of each species and the data point for *Canis lupus*—an average of two male individuals. Data points for all other species represent single individuals. Linear regression line and 95% confidence (for the regression line) and prediction (for a single data point) intervals were fitted to the data set for the big cats (genus *Panthera*).

The length of the deltoid and pectoral ridges (including the deltoid tuberosity sensu Crouch and Lackey (1969, Plate 16, Figure 2))/deltopectoral crest of the humerus was measured as shown in Figure 6 of the results section. The values of the humerus length and the deltoid and pectoral ridges/deltopectoral crest length listed for the extinct species are arithmetic means of the measurements of each dimension in up to four humeri assigned to a particular species. Each bone was assumed to represent a separate individual. The values listed for the living species are arithmetic means of the averaged measurements of each humeral dimension from both sides of the skeleton (when available) in up to five individuals. The deltoid and pectoral ridges/deltopectoral crest length was plotted as a function of the interarticular length of the humerus (without logarithmic transformation) with each species or subspecies represented by a single data point (Figure 7 of the results section). Linear regression line and 95% confidence (for the regression line) and prediction (for a single data point) intervals were fitted to the data set for the Felidae.

Statistical analysis

The above regression analyses were performed in SigmaPlot 2000 for Windows, version 6.00. Slopes and intercepts were calculated using both the Least Squares (Model I) and the Reduced Major Axis (Model II) analyses in Microsoft Excel 2000, and are listed in Table VI.

Relative grinding area of the lower molars (RGA)

RGA of the lower molars represents the relative proportion of the molar area devoted to grinding, as opposed to slicing, and is calculated as:

$$\frac{(\text{total grinding area of the lower molars})^{1/2}}{\text{total blade length of the lower carnassial(m1)}}$$

The total grinding area of the lower molars includes the talonid of m1 and the entire occlusal area of m2

Table VII.   Relative grinding area of the lower molars (RGA) and diet in Carnivora.

Species	RGA	Source	Diet (based on Nowak (1999))
Amphicyon longiramus, early Hemingfordian	0.58	Van Valkenburgh (1991)	
Ischyrocyon sp., Clarendonian	0.83	Van Valkenburgh (1991)	
Speothos venaticus	0.55	Van Valkenburgh (1989)	Carnivorous
Lycaon pictus	0.57	Van Valkenburgh (1989)	Carnivorous
Canis lupus	0.66	Van Valkenburgh (1989)	Carnivorous
Cuon alpinus	0.66	Van Valkenburgh (1989)	Carnivorous
Canis mesomelas	0.75	Van Valkenburgh (1989)	Primarily carnivorous
Canis latrans	0.76	Van Valkenburgh (1989)	Primarily carnivorous
Canis aureus	0.90	Van Valkenburgh (1989)	Primarily carnivorous
Ursus arctos	2.23	Van Valkenburgh (1989)	Omnivorous

and m3 (if present) (Van Valkenburgh 1988). The RGA values of *Amphicyon* and *Ischyrocyon* and those of a number of extant carnivorans taken from Van Valkenburgh (1988, 1989, 1991), as well as the diets of the extant species based on the descriptions in Nowak (1999), are listed in Table VII of the results section. A species' diet is described as carnivorous if it does not include any plant material, primarily carnivorous if it includes ≤10% (by volume) of plant material and omnivorous if it includes >10%, but <90% of plant material.

Photographs

All photographs used in the figures were taken by the author using an HP Photosmart 318 digital camera.

Results

Diet of Amphicyon *and* Ischyrocyon

Despite having smaller posterior lower molars (m2–3) (Hunt 1998a), *Ischyrocyon* actually had a higher RGA of the lower molars than *Amphicyon* (Table VII). The RGA values of both genera fall within the range of the primarily or exclusively carnivorous living canids. In contrast, the omnivorous brown bear has an RGA that is three to four times higher than those of the bear-dogs. Further evidence for a primarily or exclusively carnivorous diet in both *Amphicyon* and *Ischyrocyon* is provided by the wear pattern on their upper molars. Wear facets developed primarily on the buccal cusps (the paracone and the metacone) of the M1–2, indicating that, despite the large occlusal surface area of these teeth, they were used for shearing (presumably, meat and/or bone) rather than crushing and grinding (Figure 1A,B). A similar wear pattern develops on the M1 of the exclusively carnivorous (Nowak 1999) grey wolf (*C. lupus*) (Figure 1C). In contrast, both the buccal (the paracone and the metacone) and the lingual (the paraconule and the metaconule) cusps of the M1–2 become heavily worn in old individuals of the largely herbivorous (Nowak 1999) Alaskan brown bear (*U. arctos gyas*) (Figure 1D), consistent with the use of these teeth for crushing and grinding plant material. Therefore, the diet of the bear-dogs was, probably, primarily or exclusively carnivorous and included little, if any, plant material. Given their size (adult body mass >25 kg), *Amphicyon* and *Ischyrocyon* probably
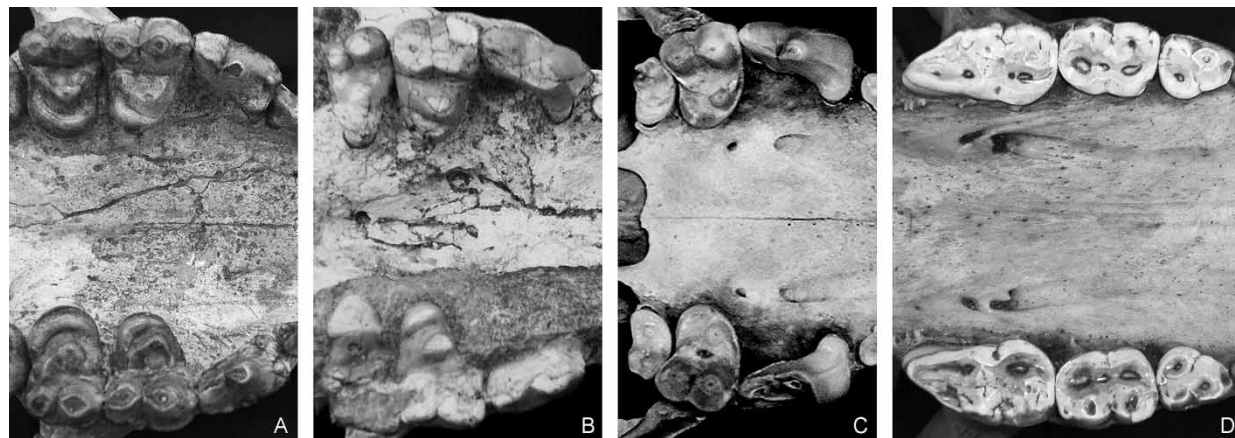

Figure 1.   Wear facets on the upper molars (M1–2) in *Amphicyon*, *Ischyrocyon*, *C. lupus* and *U. arctos*, occlusal view. Upper carnassial (P4) is on the right: (A) *A. ingens*, Barstovian, F: AM 54268; (B) *Ischyrocyon* sp., Clarendonian, F: AM 49327; (C) *C. lupus*, FMNH 138800; (D) *U. arctos gyas* male, FMNH 63802.

obtained most of the animal material in their diet by preying on herbivores of body mass as great as or greater than their own (Carbone et al. 1999).

If the above reconstruction of the diet of *Amphicyon* and *Ischyrocyon* is accurate, then the brown bear appears to be a poor model for the hunting behaviour of these bear-dogs. Although *U. arctos* preys on large ungulates more frequently than does any other living ursid, even the most predacious individuals of the species kill no more than four adult moose (*Alces alces*) with an average body mass of 450 kg per year (Derocher and Stirling 1993). In contrast, an average Siberian tiger kills thirty prey animals (cervids, suids and occasionally, ursids) with an average body mass of 100 kg per year (Stroganov 1969). The cervids (*A. alces, Cervus elaphus, Rangifer tarandus*) and the bovid (*Bison bison*) that the brown bear has been reported to prey upon (Derocher and Stirling 1993) are faster than their predator (based on the maximal running speed data from Garland (1983)). The caribou (*R. tarandus*) and the American bison (*B. bison*) live in an open habitat (tundra and prairie, respectively, Nowak (1999)) with virtually no cover for stalking or ambushing. Therefore, the brown bear can only capture its potential prey either in very uneven terrain, such as a river crossing, in which the prey animal cannot attain its maximal running speed (Derocher and Stirling 1993), or when the prey animal is injured or in poor condition (McNamee 1984). This makes it unlikely that a primarily or exclusively carnivorous animal with the limb morphology of the brown bear could have survived by preying on ungulates with the cursorial limb morphology (sensu Coombs (1978)) and, presumably, the running performance of the living cervids and bovids.

Amphicyon *and* Ischyrocyon *as ambush predators*

The distal segment of the forelimb (the radius) was as long relative to the proximal one (the humerus) in *Amphicyon* and *Ischyrocyon* as it is in the living tiger (*P. tigris*) (Table VIII). The distal segment of the hind limb (the tibia) in the bear-dogs was shorter relative to the proximal one (the femur) than in the tiger, but longer than in the brown bear. The lion (*P. leo*) is the only living big cat and carnivorous terrestrial carnivoran, other than the tiger, to overlap broadly with the species of *Amphicyon* and *Ischyrocyon* in body mass. The lion has relatively longer distal limb segments than either the tiger or the bear-dogs (Table VIII). Although both the lion and the tiger are ambush predators, the lion stalks or ambushes its prey in a more open habitat and chases it for longer distances than does the tiger (Stroganov 1969; Schaller 1972). The grey wolf (*C. lupus*), which is a pursuit predator that chases its prey for much longer distances than any cat (Mech 1970; Schaller 1972), has even more elongated distal limb segments (Table VIII). The spotted hyena (*Crocuta crocuta*), which is also a long distance pursuit predator (Kruuk 1972), does have a tibia that is as short relative to the femur as that of the bear-dogs, but its radius is even longer relative to the humerus than that of the grey wolf (Table VIII). Thus, the relative length of the distal limb segments in *Amphicyon* and *Ischyrocyon* would suggest that, like the living tiger, the bear-dogs were specialized ambush predators. They would have depended on the cover of dense vegetation for closely approaching their intended victim undetected and would have then chased it for a very short distance (shorter, on average, than the distance the living lion chases its prey) before either capturing it or abandoning the chase.

However, the morphology of the ulna in *Amphicyon* and *Ischyrocyon* contradicts the above reconstruction of their hunting behaviour. In the smaller species or chronospecies of the two genera, the late Hemingfordian *Amphicyon* sp. and the late Barstovian *Ischyrocyon* sp., the olecranon process of the ulna was more caudally bent than it is in the tiger, resembling the condition in the lion, while in the early Barstovian *A. ingens* the olecranon was even more caudally bent (Figure 2). In the late Hemingfordian *Amphicyon* sp. the olecranon was also significantly shorter relative to the rest of the ulna than in an average big cat (Figure 3). This would have reduced the leverage

Table VIII.   Relative limb segment lengths in *Amphicyon* and *Ischyrocyon* and living Carnivora.

Species	N	Radius/humerus × 100 (%)		Tibia/femur × 100 (%)	
		Mean	Range	Mean	Range
Amphicyon sp., late Barstovian	1	81.0	–	–	–
Amphicyon ingens, Barstovian	1	–	–	74.5	–
Ischyrocyon sp., late Barstovian	1	84.4	–	–	–
Ischyrocyon sp., Clarendonian	1	–	–	75.2	–
Ursus arctos gyas, male	1	78.5	–	69.4	–
Ursus arctos horribilis, male	1	83.4	–	68.9	–
Panthera tigris, both sexes	6	83.4	80.5–84.7	81.1	78.2–82.4
Panthera leo, both sexes	4	90.5	86.9–94.8	83.0	79.7–86.2
Canis lupus, both sexes	5	101.5	99.3–103.6	100.5	99.3–103.4
Crocuta crocuta, both sexes	3	108.4	107.1–110.4	76.9	75.3–77.9

Figure 2.   Ulnae of the bear-dogs and the big cats in lateral view; (B) is right, all others are left: (A) *Amphicyon* sp., late Hemingfordian, F: AM 68103H; (B) *Amphicyon ingens*, Barstovian, F: AM 68117; (C) *Ischyrocyon* sp., late Barstovian, F: AM 54220; (D) *P. tigris* female, FMNH 57172; (E) *P. leo* male, FMNH 173259.

of the triceps muscle in a crouched posture (in which the ulna is held at an angle of 90° or less to the humerus) and, therefore, the ability to accelerate from this posture in the bear-dogs (based on Van Valkenburgh (1987, p. 172)). The triceps inserts on the olecranon process and is the main extensor of the forearm in both bears and cats (Davis 1964; Crouch and Lackey 1969). Although both the orientation and the relative length of the olecranon process in *Ischyrocyon* were similar to those of the lion, the relative length of the distal segment of its forelimb falls below the ranges for *P. leo* and the relative length of the distal segment of the hindlimb falls below the ranges for both *P. leo* and *P. tigris* (Table VIII). Thus, *Ischyrocyon* resembled *Amphicyon* in being less able to accelerate from a crouched posture and, therefore, in being less adapted for ambush predation than a living

big cat with distal limb segments of the same relative length.

The morphology of its lumbar vertebrae provides further indication that *A. ingens* was less adapted for ambush predation than the living big cats. The lumbar vertebrae of the bear-dog had cranially angled spines with ample space between them like those of a big cat (the tiger), allowing for extensive flexion and extension (Figure 4, interpretation based on Currey (2002)). The elongation of the spines suggests the presence of powerfully developed extensors of the vertebral column (longissimus dorsi and multifidus dorsi muscles), which insert on the spines of thoracic and lumbar vertebrae in living Canidae (Olsen 1960), as well as in living Felidae (Crouch and Lackey 1969). However, the transverse processes of the lumbar vertebrae of *A. ingens* were nearly horizontal, unlike
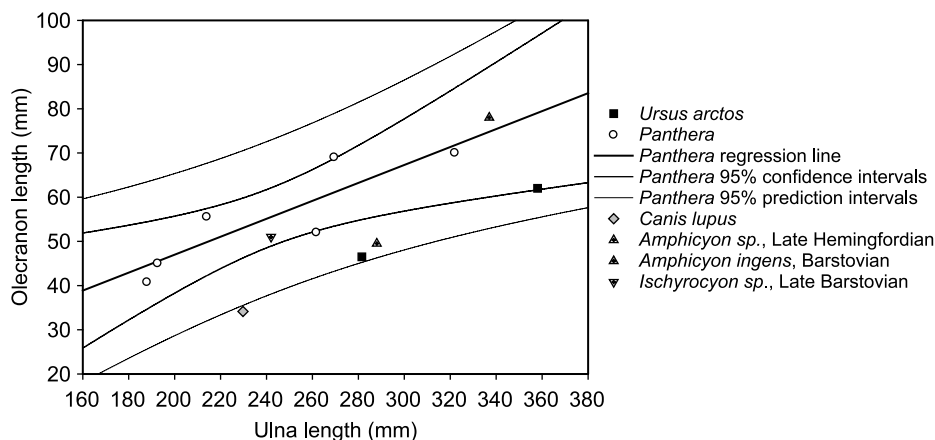

Figure 3.   Leverage of the triceps muscle in *Amphicyon* and *Ischyrocyon* and living Carnivora.
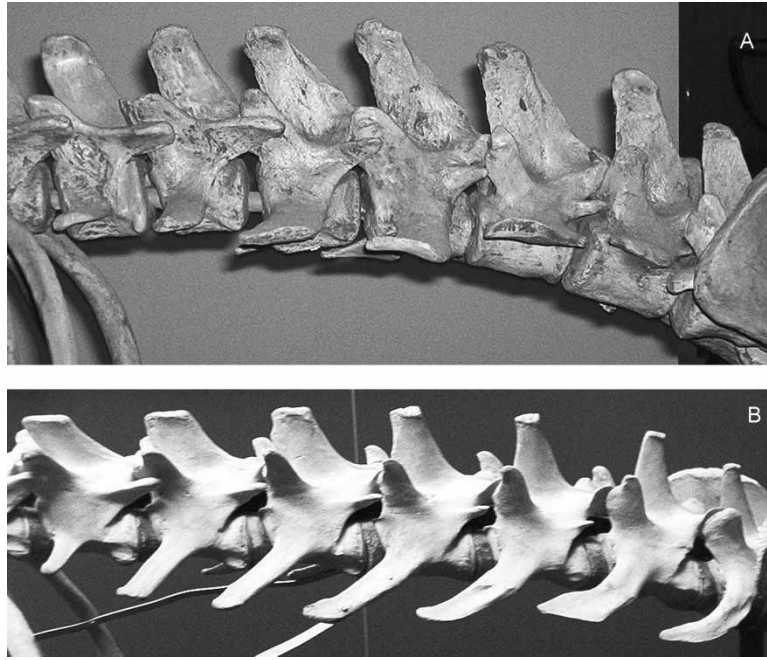
Figure 4.   Lumbar vertebrae of the mounted skeletons of *A. ingens* (A) and *P. tigris* (B) in left lateral view. The skeletons are on display at the AMNH and the FMNH, respectively.

the ventrally projecting ones in the tiger, providing little leverage for the intertransversarial muscles to flex the vertebral column (Figure 4, interpretation based on Currey (2002)). Therefore, while flexion and extension of the vertebral column in *A. ingens* probably contributed as much to the bear-dog's maximal running speed by increasing the effective length of the stride as it does in the big cats, it probably contributed less to the bear-dog's acceleration. Combined with the short tibia and the short plantigrade hind foot (Table VIII, Hunt 1998a) of the hind limb, the morphology of its lumbar vertebrae suggests that *A. ingens* was inferior to the big cats in its ability to accelerate rapidly. Rapid initial acceleration is crucial to the hunting success of the African lion (Alexander 1993) and other big cats (Turner and Antón 1997).

Prey-killing behaviour of Amphicyon *and* Ischyrocyon

While inferior to the big cats in their ability to sneak up on and then catch up to a prey animal, the bear-dogs appear to have been well adapted to hold onto the victim once they did catch up to it. *Amphicyon spp.* shared with the brown and black bears (*U. arctos* and *Ursus americanus*) and the giant anteater (*Myrmecophaga tridactyla*) the presence of a large postscapular fossa on the scapula (Davis 1949, Olsen 1960, Figure 5). The postscapular fossa was also present in the amphicyonine *Cynelos lemanensis* (Ginsburg 1977) and in the daphoenine *Daphoenodon superbus* (Peterson 1910), suggesting that this feature of scapular morphology was plesiomorphic in Amphicyonidae and, therefore, was probably present in *Ischyrocyon*
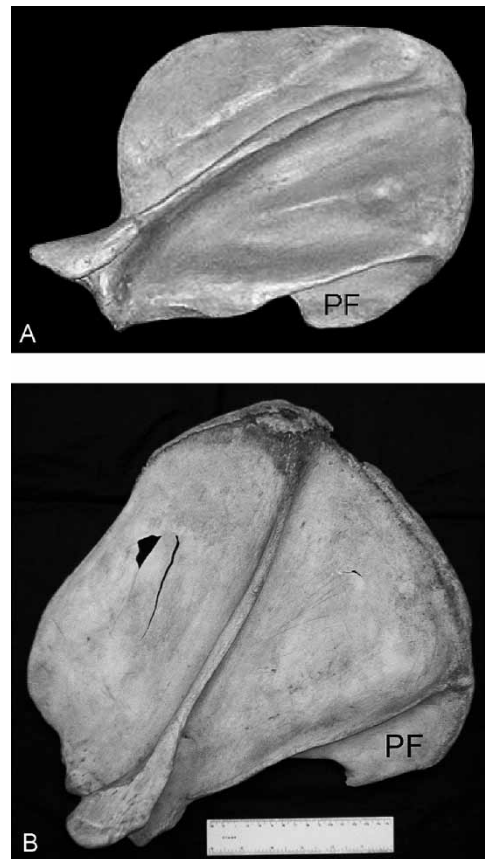

Figure 5.   Left scapulae of *A. ingens* (part of the mounted and displayed skeleton at the AMNH) (A) and *U. arctos gyas* male, FMNH 63802, (B) in lateral view. PF: postscapular fossa.
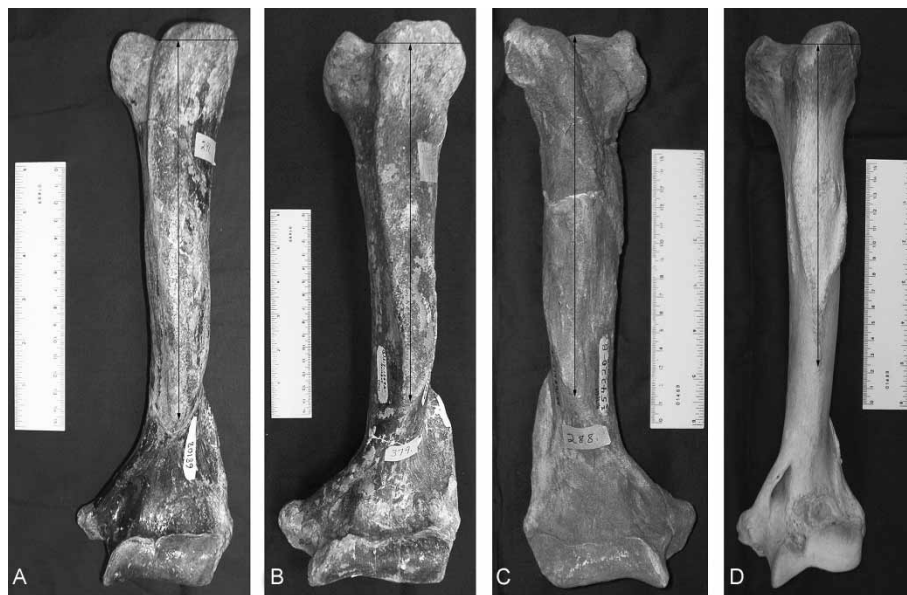
Figure 6.   Humeri of *Amphicyon*, *Ischyrocyon* and *Panthera* in anterior view. (C) is right, all others are left: (A) *Amphicyon* sp., late Hemingfordian, F: AM 68108a; (B) *A. ingens*, Barstovian, F: AM 68118B; (C) *Ischyrocyon* sp., late Barstovian, F: AM 54220; (D) *P. tigris* female, FMNH 57172. The line with arrowheads at both ends represents the length of the deltopectoral crest or the deltoid and pectoral ridges in each specimen. This length was measured by placing one external measuring face of the caliper on the distal end of the crest or on the distal end of the confluence of the two ridges (the deltoid tuberosity sensu Crouch and Lackey (1969)) and aligning the other with the most proximal point on the proximal articular surface of the humerus, indicated by the horizontal line, while holding the caliper parallel to the shaft of the bone.

as well. The presence of the postscapular fossa strongly suggests that the subscapularis minor muscle, which originates in that fossa in both *U. americanus* and *M. tridactyla* (Davis 1949), was powerfully developed in the bear-dogs. Its primary action is to fix the shoulder joint, preventing dislocation of the head of the humerus from the glenoid cavity of the scapula by a pull along the longitudinal axis of the forelimb (Davis 1949), such as the pull that would have been exerted by a prey animal being held by the forepaws of a bear-dog as it struggled to break free.

The morphology of the humerus in *Amphicyon* and *Ischyrocyon* was also well adapted for holding onto a struggling prey animal with the forepaws. Instead of separate deltoid and pectoral ridges, Amphicyoninae,

including *Amphicyon* and *Ischyrocyon*, possessed a deltopectoral crest on the humerus (Hunt 1998a, Figure 6), which was significantly longer relative to the length of the bone than the deltoid and pectoral ridges (including the deltoid tuberosity sensu Crouch and Lackey (1969, Plate 16, Figure 2)) of an average felid (Figure 7). This suggests more distal insertions and, therefore, greater leverage of the deltoid and pectoralis muscles, which insert on the deltoid and pectoral ridges in felids (Crouch and Lackey 1969) and are crucial to the big cats' ability to subdue large prey (Turner and Antón 1997).

Amphicyon and *Ischyrocyon* shared with the big cats a prominent medial epicondyle of the humerus (Figure 6), suggesting powerful development of the
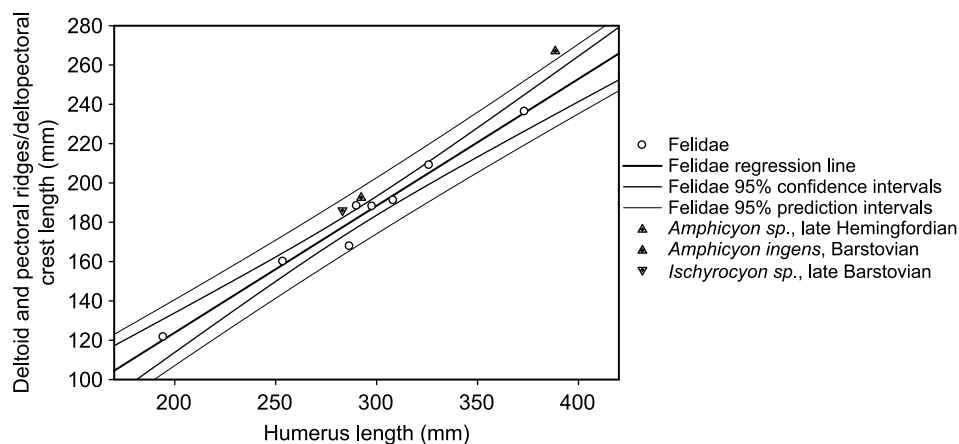

Figure 7.   Leverage of the deltoid and pectoralis muscles in *Amphicyon* and *Ischyrocyon* and Felidae.
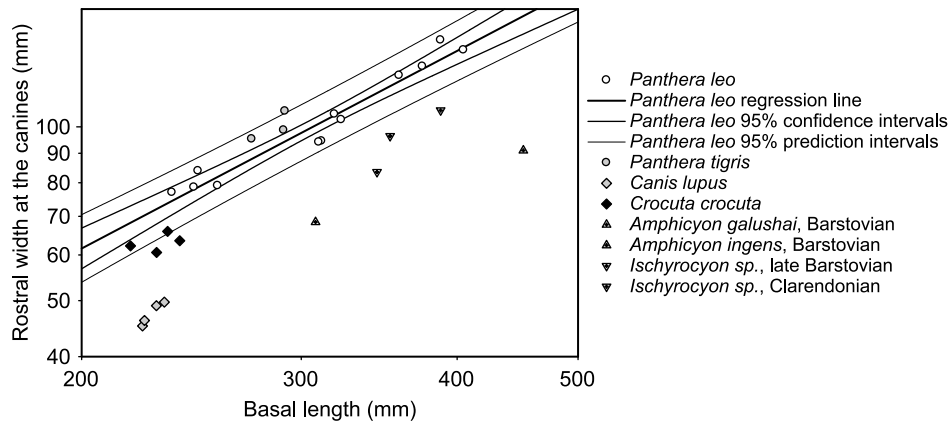
Figure 8.   Rostral width at the canines as a function of basal skull length in *Amphicyon* and *Ischyrocyon* and living Carnivora.

pronator teres muscle as well as the flexors of the wrist and digits (palmaris longus, flexor carpi radialis, flexor carpi ulnaris and flexor digitorum profundus muscles), which originate on that epicondyle in both bears and cats (Davis 1964; Crouch and Lackey 1969). Therefore, pronation of the forearm and flexion of the wrist and digits, all of which are crucial to grasping a large prey animal with the forelimbs (based on Turner and Antón (1997)), were probably, as powerful in the bear-dogs as they are in the living big cats.

The trochlea of the humeral condyle in *Amphicyon* and *Ischyrocyon* was shallower than that of a big cat (the tiger) (Figure 6), suggesting greater freedom of movement at the humeroulnar joint than is present in the big cats. This mobility, combined with the highly mobile radioulnar joints (Hunt 1998a), probably allowed as great or greater pronation-supination of the forearm in the bear-dogs than is possible in the big cats.

Ungual phalanx morphology in *Amphicyon* suggests that it and, probably, *Ischyrocyon* and other amphicyonines lacked the felids' ability to retract their claws to keep them sharp (Olsen 1960). However, the brown bear is able to hold onto a large cervid with its forepaws despite having non-retractile claws (McNamee (1984, p. 240), Derocher and Stirling (1993), 3rd shot in the sequence of four showing a female brown bear bringing down a caribou).

Even though *Amphicyon* and *Ischyrocyon* may have resembled the living big cats in the use of their forelimbs to immobilize a prey animal, they must have differed greatly from *Panthera* in the way they killed it. Living big cats kill prey of body mass equal to or greater than their own with a carefully directed bite that clamps either the trachea or the nose and mouth of the prey animal shut, causing death by suffocation. Smaller prey is killed by a bite directed with equal care either through the nape of the neck, which severs the spinal cord, or, in the case of the jaguar (*P. onca*)—through the ears into the brain (Turner and Antón 1997). This prey-killing behaviour is reflected in the

shape of their skulls, which have broad rostra (Figure 8). In contrast, the skull shape of the bear-dogs resembled that of the living pursuit predators, such as the grey wolf and the spotted hyena, which have narrow rostra relative to the basal lengths of their skulls (Figure 8). These predators hunt in social groups and kill their prey, which is usually much larger than an individual predator, by eating it to death (Mech 1970; Kruuk 1972; Turner and Antón 1997). The skulls of *Amphicyon* and *Ischyrocyon* also resembled those of the grey wolf and the spotted hyena in having small infraorbital foramina (Figure 9), suggesting less developed vibrissae (based on Turner and Antón (1997)). The tactile sensory information provided by these modified hairs contributes to a big cat's ability to deliver a carefully directed bite to its prey (Turner and Antón 1997). Thus, cranial morphology suggests that the bear-dogs did not kill their prey with a carefully directed bite.

Discussion

The morphology of the ulna and of the lumbar vertebrae in *Amphicyon* and *Ischyrocyon* suggests that their hunting success was not as dependent on closely approaching their prey undetected and then rapidly overtaking it, as is the hunting success of the living big cats. However, *Amphicyon* and *Ischyrocyon* probably did stalk and ambush their prey, since even the grey wolf, a specialized pursuit predator, does so (Mech 1970). Given their short distal limb segments, it is unlikely that the bear-dogs pursued their prey for a long distance (up to 5 km) at a high speed (50–60 km/h), as do the living grey wolf and the spotted hyena (Mech 1970; Kruuk 1972). The skeletal morphology of *Amphicyon* and *Ischyrocyon* is consistent with pursuing prey for a longer distance (more than 200 m (Schaller 1972)) but at a slower speed (< 50 km/h (Elliott et al. 1977, Figure 5)) than do the living big cats. Such pursuit capability would appear inadequate for capturing ungulates with cursorial limb morphology (sensu Coombs 1978) on a regular basis,

Figure 9.   Skulls of *Amphicyon* and *Ischyrocyon* and living Carnivora in right fronto-lateral view. The arrow is pointing to the infraorbital foramen. (A) *A. galushai*, Barstovian, F: AM 25400; (B) *Ischyrocyon* sp., late Barstovian, F: AM 54220; (C) *P. leo* male, FMNH 89926; (D) *C. crocuta* male, FMNH 34583; (E) *C. lupus* male, FMNH 138797.

because extant bovids, cervids, and equids, all of which possess such limb morphology, can attain running speeds of more than 50 km/h (Garland 1983). However, the inferred pursuit capability of the bear-dogs does appears well-matched with the locomotor performance of mediportal ungulates (sensu Coombs (1978)), which in the case of the living tapir (*Tapirus americanus*), are reported to have a maximal running speed of only 40 km/h (Garland 1983). Such ungulates, particularly the Ticholeptinae (Artiodactyla, Tylopoda, Oreodontoidea, Merycoidodontidae) and the Rhinocerotidae (Perissodactyla, Ceratomorpha), were diverse and abundant in North America from the late Hemingfordian to the late Clarendonian, the time when *Amphicyon* and then *Ischyrocyon* were the largest terrestrial predators on that continent (Lander 1998; Prothero 1998) and probably formed the prey base for these predators.

The discovery of the dental and skeletal remains of at least five adult individuals (one of them in association with a juvenile) of *D. superbus* (Carnivora, Amphicyonidae, Daphoeninae) in three adjacent burrows (Hunt et al. 1983) suggests that at least some bear-dogs were social predators. However, *D. superbus* had digitigrade hind feet and more elongated distal segments of both the fore and the hind limbs than the amphicyonine bear-dogs, including *Amphicyon* and *Ischyrocyon* (Hunt 1998a). Among the living big cats the social lion (Schaller 1972) has more elongated distal limb segments than the similar-sized solitary tiger (Stroganov 1969) (Table VIII). Therefore, *Amphicyon* and *Ischyrocyon* were, probably, solitary predators. The lack of assistance from other members of a social group in prey capture would have been partially compensated by a bear-dog's ability to immobilize the prey animal by holding onto it with the forepaws, an ability absent in the living pursuit social predators (Turner and Antón 1997). Therefore, the grey wolf and the spotted hyena appear to be poor models for the prey-killing behaviour of the bear-dogs, despite the similarities in skull shape and development of the vibrissae, the latter suggested by the similar sizes of the infraorbital foramina.

If they were solitary predators, *Amphicyon* and *Ischyrocyon* probably preyed, primarily, on animals of body mass similar to their own, as do the living solitary predators (Earle 1987). The only recent mammalian predator with a narrow dog-like rostrum reported to have killed prey of such size without the assistance of other members of a social group on a regular basis was the recently extinct *Thylacinus cynocephalus* (Marsupialia, Thylacinidae). Although the thylacine hunted the Eastern grey kangaroo and the red-necked wallaby (*Macropus giganteus* and *M. rufogriseus*) in small family groups consisting of a mated pair and their offspring, the prey animal was killed by a single individual (Paddle 2000). The thylacine stood on the body of its prey (which it had, presumably, knocked down) and

bit into and tore open its ribcage (Paddle 2000). *Amphicyon* and *Ischyrocyon* may have killed their prey in a similar way, once they knocked or pulled it down. A bear-dog could also have torn open the ribcage of a standing prey animal while holding onto it with its forepaws. Alternatively, the bear-dogs may have killed their prey by biting and tearing into its neck to sever major blood vessels, rather than to sever the spinal cord or clamp the trachea, as do the big cats. *Amphicyon* and *Ischyrocyon* would have been less likely to attack the abdomen of their prey because a wound in this area would not kill an animal quickly (Martin 1980). The potential danger for a solitary predator in attacking the abdomen of the prey animal is illustrated by an incident described by McNamee (1984, p. 240). A female brown bear was wounded by an elk (*C. elaphus*), she had already pulled down and disembowelled.

Conclusions

1. Molar morphology and wear pattern suggest that both *Amphicyon* and *Ischyrocyon* were primarily or exclusively carnivorous.
2. The lengths of the distal limb segments relative to the proximal ones and the morphology of the ulna and of the lumbar vertebrae suggest that *Amphicyon* and *Ischyrocyon* were less dependent on closely approaching their prey undetected and then rapidly overtaking it for their hunting success than are the living big cats.
3. The lengths of the distal limb segments relative to the proximal ones suggest that *Amphicyon* and *Ischyrocyon* were solitary predators on contemporary mediportal ungulates of body mass similar to their own, which they pursued for a longer distance but at a slower speed than the living big cats pursue their prey.
4. Morphology of the forelimb bones (including the scapula) and the skull suggests that upon catching up to their prey *Amphicyon* and *Ischyrocyon* seized it with the forepaws and killed it by biting and tearing into either its ribcage or its neck.

Acknowledgements

References

Alexander RMcN. 1993. Legs and locomotion in Carnivora. Symp Zool Soc Lond 65:1–13.

Bertram JEA, Biewener AA. 1990. Differential scaling of the long bones in the terrestrial Carnivora and other mammals. J Morphol 204:157–169.

Carbone C, Mace GM, Roberts SC, Macdonald DW. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Christiansen P. 1999. Long bone scaling and limb posture in non-avian theropods: Evidence for differential allometry. J Vert Paleontol 19:666–680.

Coombs Jr, WP. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. Q Rev Biol 53:393–418.

Crouch JE, Lackey MB. 1969. Text-atlas of cat anatomy. Philadelphia: Lea and Febiger.

Currey JD. 2002. Bones: Structure and mechanics. Princeton: Princeton University Press.

Davis DD. 1949. The shoulder architecture of bears and other carnivores. Fieldiana Zool 31:285–305.

Davis DD. 1964. The giant panda: A morphological study of evolutionary mechanisms. Fieldiana Zool Mem 3:1–339.

Derocher AE, Stirling I. 1993. Bears as predators. In: Stirling I, editor. Bears: Majestic creatures of the wild. Emmaus, Pennsylvania: Rodale Press, Inc.. p 84–85.

Earle M. 1987. A flexible body mass in social carnivores. Am Nat 129:755–760.

Elliott JP, McTaggart Cowan I, Holling CS. 1977. Prey capture by the African lion. Can J Zool 55:1811–1828.

Garland Jr, T. 1983. The relation between maximal running speed and body mass in terrestrial mammals. J Zool London 199:157–170.

Ginsburg L. 1977. *Cynelos lemanensis* (Pomel), carnivore ursidé de l'Aquitanien d'Europe. Ann Paléontol (Vertébrés) 63:57–104.

Ginsburg L. 1999. Order Carnivora. In: Rössner GE, Heissig K, editors. The miocene land mammals of Europe. München: Verlag Dr. Friedrich Pfeil. p 109–148.

Hunt Jr, RM. 1998a. Amphicyonidae. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America, volume 1: Terrestrial carnivores, ungulates and ungulatelike mammals. Cambridge: Cambridge University Press. p 196–227.

Hunt Jr, RM. 1998b. Ursidae. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America, volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge: Cambridge University Press. p 174–195.

Hunt Jr, RM, Xiang-Xu X, Kaufman J. 1983. Miocene burrows of extinct bear dogs: Indication of early denning behavior of large mammalian carnivores. Science 221:364–366.

Kruuk H. 1972. The spotted hyena: A study of predation and social behavior. Chicago: University of Chicago Press.

Kurtén B. 1985. The Pleistocene lion of Beringia. Ann Zool Fenn 22:117–121.

Lander B. 1998. Oreodontoidea. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America, volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge: Cambridge University Press. p 402–425.

Martin LD. 1980. Functional morphology and the evolution of cats. Trans Nebr Acad Sci 8:141–154.

Martin LD. 1998a. Felidae. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America, volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge: Cambridge University Press. p 236–242.

Martin LD. 1998b. Nimravidae. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America, volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge: Cambridge University Press. p 228–235.

McNamee T. 1984. The grizzly bear. New York: Alfred A. Knopf.

Mech LD. 1970. The wolf: The ecology and behavior of an endangered species. Garden City, New York: Natural History Press.

Merriam JC, Stock C. 1932. The felidae of rancho la brea. Carnegie Institution of Washington Publications. 442., p 1–231.

Munthe K. 1989. The skeleton of the Borophaginae (Carnivora, Canidae): Morphology and function University of California publications in geological sciences. 133., p 1–115.

Nowak RM. 1999. Walker's mammals of the world. 2. 6th ed., Baltimore: The Johns Hopkins University Press.

Olsen SJ. 1960. The fossil carnivore *Amphicyon longiramus* from the Thomas Farm Miocene part II. Postcranial skeleton. Bull Mus Comp Zool 123:1–44.

Paddle R. 2000. The last tasmanian tiger: The history and extinction of the thylacine. Cambridge: Cambridge University Press.

Peterson OA. 1910. Description of new carnivores from the Miocene of western Nebraska. Memoirs of the Carnegie Museum 4(5):205–278.

Prothero DR. 1998. Rhinocerotidae. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America, volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge: Cambridge University Press. p 595–605.

Schaller GB. 1972. The Serengeti lion: A study of predator-prey relations. Chicago: University of Chicago Press.

Stroganov SU. 1969. Carnivorous mammals of siberia. (Zveri sibiri: Khishchnye). Izdatel'stvo Akademii Nauk SSSR, Moskva 1962. Translated from Russian. Jerusalem: Israel Program for Scientific Translation.

Turner A, Antón M. 1997. The big cats and their fossil relatives: An illustrated guide to their evolution and natural history. New York: Columbia University Press.

Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. J Vert Paleontol 7(2):162–182.

Van Valkenburgh B. 1988. Trophic diversity in past and present guilds of large predatory mammals. Paleobiology 14(2):155–173.

Van Valkenburgh B. 1989. Carnivore dental adaptations and diet: A study of trophic diversity within guilds. In: Gittleman JL, editor. Carnivore behavior, ecology, and evolution. Ithaca, New York: Comstock Publishing Associates, a division of Cornell University Press. p 411–436.

Van Valkenburgh B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): Evolutionary interactions among sympatric predators. Paleobiology 17(4):340–362.

Viranta S. 1996. European Miocene Amphicyonidae—taxonomy, systematics and ecology. Acta Zool Fenn 204:1–61.