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Authors: Bōgner, Emily, and Samuels, Joshua X.

Source: Journal of Paleontology, 96(6) : 1379-1389

Published By: The Paleontological Society

URL: https://doi.org/10.1017/jpa.2022.46

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Journal of Paleontology, 96(6), 2022, p. 1379–1389

0022-3360/22/1937-2337
doi: 10.1017/jpa.2022.46

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

The first canid from the Gray Fossil Site in Tennessee: new perspective on the distribution and ecology of *Borophagus*

Emily Bōgner[1]* and Joshua X. Samuels[2,3]

[1]Department of Integrative Biology, University of California Berkeley, Berkeley, CA, USA <bogneremilyl@berkeley.edu>
[2]Department of Geosciences, East Tennessee State University, Johnson City, TN, USA <samuelsjx@etsu.edu>
[3]Don Sundquist Center of Excellence in Paleontology, East Tennessee State University, Johnson City, TN, United States of America <samuelsjx@etsu.edu>

Abstract.—*Borophagus* is the terminal genus of the highly diverse and successful subfamily, Borophaginae. Skeletal remains of this bone-crushing canid are most commonly found in transitional or grassland environments across North America between Late Miocene–Middle Pleistocene, but are rare or absent in forested habitats. Here, we describe a humerus from the Gray Fossil Site of Tennessee, which is the first occurrence of this genus in a heavily forested ecosystem. The distinct limb proportions of *Borophagus* suggest the genus may have been well suited for a closed habitat like the Gray Fossil Site, contrary to where a majority of their fossils have been previously found. This discovery documents the first pre-Pleistocene occurrence of a canid in the Appalachian region of the eastern United States.

Introduction

Borophagines were a diverse and successful subfamily of canids that thrived throughout North America for nearly 30 million years. The group lived across the continent, and their fossils have been recovered from as far north as Saskatchewan, south into Mexico and Honduras, the Pacific Coast, and more recently along the Atlantic Coast (Wang et al., 1999; Eshelman and Whitmore, 2008; Wang and Tedford, 2008; Tseng and Geisler, 2016) (Table 1; Fig. 1). The majority of fossil localities where *Borophagus* is represented indicate environments dominated by relatively open habitats (grassland, savannah, and steppe), although some sites do indicate more extensive vegetation along streams and marshes, or more forested areas on their edges (Cook, 1922; Matthew, 1924, 1930; Matthew and Stirton, 1930; Meade, 1945; Dalquest, 1969; Bjork, 1970; Hulbert et al., 2009). Other vertebrates commonly found with *Borophagus* include equine and hipparionine horses (including *Hipparion*, *Dinohippus*, and *Equus*) (Cook, 1922; Matthew, 1924, 1930; Matthew and Stirton, 1930; Meade, 1945; Miller and Carranza-Castañeda, 1998; Hulbert et al., 2009), hornless rhinoceros (*Aphelops* and *Teleoceras*) (Matthew, 1924, 1930; Matthew and Stirton, 1930; Hulbert et al., 2009), camels (including *Megatylopus*, *Hemiauchenia*, and *Camelops*) (Cook, 1922; Matthew, 1924, 1930; Matthew and Stirton, 1930; Meade, 1945; Miller and Carranza-Castañeda, 1998; Hulbert et al., 2009), and mastodons (Matthew, 1930; Matthew and Stirton, 1930; Meade, 1945; Hulbert et al., 2009), which have been interpreted as suggesting grass-dominated habitats (Cook, 1922; Matthew, 1924, 1930; Matthew and Stirton, 1930; Meade, 1945; Hulbert et al., 2009).

Appendicular bones are important to understanding the ecology of carnivorans because their predatory behavior has driven the morphological evolution of their limbs (Van Valkenburgh, 1987; Samuels et al., 2013; Martín-Serra et al., 2016). In general, the anatomy of the forelimbs is very telling of the type of predatory behavior, whereas hind legs give a better indication of speed (Van Valkenburgh, 1987; Andersson and Werdelin, 2003; Andersson, 2005; Meachen-Samuels and Van Valkenburgh, 2009; Figueirido and Janis, 2011; Fabre et al., 2013; Samuels et al., 2013; Janis and Figueirido, 2014; Figueirido et al., 2015; Martín-Serra et al., 2016). Postcranial material of *Borophagus* has been recovered rarely, making their predatory behavior and locomotion controversial, because their appendicular skeleton is extremely different from modern members of Caninae (Dalquest, 1969; Munthe, 1989; Wang et al., 1999; Figueirido et al., 2015; Martín-Serra et al., 2016). *Borophagus* has limb proportions with longer proximal elements and shorter distal elements, leading to the inference that these dogs were not strongly running-adapted (Matthew, 1930; Dalquest, 1969; Munthe, 1989). Munthe (1989) hypothesized that the short and robust limbs of *Borophagus* would have been better adapted for closed habitats where open environments never formed, but with a lack of ecological data at the time, these hypotheses were not able to be assessed. Based on the skeletal and muscular morphology of *Borophagus*, it was interpreted as flexible and opportunistic in hunting strategies and habitats (Munthe, 1989). Figueirido et al. (2015) examined the elbow morphology of a wide range of fossil canids, and inferred secondarily derived ambush hunting predatory behavior in *Borophagus*. The habits of *Borophagus* in the late Neogene were noted to have contrasted with other canids at the time, which show a general trend toward greater cursorial specialization and pursuit-hunting habits, and further suggests a diversity

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*Corresponding author.

Table 1. Previously reported occurrences of *Borophagus* in North America. Data derived from the MIOMAP/FAUNMAP databases (Carrasco et al., 2007; Graham and Lundelius, 2010), NOW database (The NOW Community, 2019), and recent publications (Wang et al., 1999; Tseng and Geisler, 2016; Wang et al., 2018). AZ = Arizona; CA = California; CO = Colorado; FL = Florida; ID = Idaho; IN = Indiana; KS = Kansas; NC = North Carolina; NE = Nebraska; NM = New Mexico; NV = Nevada; OK = Oklahoma; OR = Oregon; SC = South Carolina; TN = Tennessee; TX = Texas; WA = Washington.

Taxon	Locality	Formation	County, State	Age
Borophagus sp.	Gray Fossil Site	—	Gray, TN	Early Blancan
B. diversidens	Black Ranch	Tehama	CA	Early Blancan
B. diversidens	Asphalto	Tulare	CA	Early Blancan
B. diversidens	—	—	Contra Costa, CA	Blancan
B. diversidens	Lisco	Broadwater	NE	Early Blancan
B. diversidens	—	Broadwater	NE	Early Blancan
B. diversidens	Sand Draw	Keim	NE	Early Blancan
B. diversidens	Big Springs	Long Pine	NE	Late Blancan
B. diversidens	Fox Canyon	Rexroad	KS	Early Blancan
B. diversidens	Keef Canyon	Rexroad	KS	Early Blancan
B. diversidens	Rexroad	Rexroad	KS	Early Blancan
B. diversidens	Rexroad	Rexroad	KS	Early Blancan
B. diversidens	Lockwood Meadows	Bone Ivy	Manatee, FL	Hemphillian-2
B. diversidens	Santa Fe River Blancan Sites	Unnamed fissure-fill deposits	Columbia, FL	Late Blancan
B. diversidens	Rigby Shell Pit	Bermont	FL	Irvingtonian-1
B. diversidens	Coso Mountains	Coso	CA	Late Blancan
B. diversidens	Channel Sands Pocket	Panaca	NV	Late Blancan
B. diversidens	Grand View, Nine Foot Rapids	Glenns Ferry	ID	Late Blancan
B. diversidens	Taunton Substation	Ringold	WA	Late Blancan
B. diversidens	Haymaker's Orchard	Ringold	WA	Early Blancan
B. diversidens	Bear Springs, Matthew Wash	Unnamed	AZ	Early Blancan
B. diversidens	Benson	St David	Cochise, AZ	Early Blancan
B. dudleyi	Lee Creek Mine	Yorktown	NC	Hemphillian-4
B. dudleyi	Upper Bone Viy	Bone Viy	Polk, FL	Hemphillian-4
B. hilli	Las Tunas	Unnamed	CA	Early Blancan
B. hilli	Pipe Creek Sinkhole	Pipe Creek Sinkhole	IN	Early Blancan
B. hilli	Upper Bone Viy	Bone Viy	Polk, FL	Hemphillian-4
B. hilli	Hagerman Horse Quarry	Glenns Ferry	ID	Early Blancan
B. hilli	White Bluffs	Ringold	WA	Early Blancan
B. hilli	Truth or Consequences	Palomas	NM	Early Blancan
B. hilli	Rio Cuchillo Nego Creek & Elephant Butte Lake	Palomas	Sierra, NM	Early Blancan
B. hilli	Axtel, Buis Ranch, Currie Ranch	Goodnight Beds	Randall, Armstong, TX	Hemphillian-4
B. hilli	Martin Marietta Oragneburg Quarry	Raysor	Orangeburg, SC	—
B. hilli	Hagerman Fossil Beds	Glens Ferry	Hagerman, ID	Blancan
B. littoralis VanderHoof, 1931	Black Hawk Ranch	Green Ivy	Contra Costa, CA	Clarendonian-3
B. littoralis	Las Trampas Ridge, Ingram Creek	San Pablo	CA	Clarendonian-2, 3
B. littoralis	South Tejon Hills	Chanac	CA	Clarendonian-2
B. littoralis	North Tejon Hills	Chanac	CA	Clarendonian-3
B. littoralis	Warren	Horned Toad	CA	Hemphillian-4
B. littoralis	Brady Pocket	Truckee	Churchill, NV	Clarendonian-3
B. littoralis	Ricardo	Dove Spring	CA	Clarendonian-2, 3
B. littoralis	Lava Mountains	Bedrock Springs	CA	Hemphillian-1
B. littoralis	Crocker Springs Creek	Monterey	CA	Clarendonian-1
B. orc	Withlacoochee River	Hawthorn Group	FL	Hemphillian-2
B. parvus	Turlock Lake & Modesto Reservoir	Merhten	CA	Hemphillian-4
B. parvus	Hemme Hills	Pinole	CA	Hemphillian-4
B. parvus	Old Cabin Quarry	Quiburus	AZ	Hemphillian-3, 4
B. parvus	Wikieup	Big Sandy	Mohave, AZ	Hemphillian-4
B. parvus	Turlock Lake	Mehrten	CA	Late Hemphillian
B. pugnator	Turtle-Carnivore Quarry	Ogallala	NE	Hemphillian-2
B. pugnator	Jack Swayze Quarry	Ogallala	KS	Hemphillian-1
B. pugnator	Wray	Ogallala	Yuma, CO	Hemphillian-2
B. pugnator	Mixons Bone Bed	Alachua	Alachua, FL	Hemphillian-1
B. pugnator	Withlacoochee River	Hawthorn Group	FL	Hemphillian-2
B. pugnator	Upper Bone Viy	Bone Vly	Polk, FL	Hemphillian-4
B. pugnator	Rome	Drewsey	OR	Hemphillian-1
B. pugnator	Reynolds Creek	Poison Creek	Owyhee, ID	Hemphillian-1, 2
B. pugnator	Yakima Canyon	Ellensburg	WA	Hemphillian-3, 4
B. pugnator	Unconsolidated Streem Channel Sand	Hemphill Beds	Lipscomb, TX	Hemphillian-2
B. secundus	Turlock Lake & Modesto Reservoir	Merhten	CA	Hemphillian-4
B. secundus	Mount Eden	—	River Side, CA	Hemphillian-4
B. secundus	Corinto	Unnamed	88,959 & 13,45	Hemphillian-1
B. secundus	Gracias	Gracias	Honduras	Hemphillian-1
B. secundus	Turtle Locality	Ogallala	NE	Hemphillian-3
B. secundus	Aphelops Draw	Snake Creek	NE	Hemphillian-2
B. secundus	Pliohippus Draw	Snake Creek	NE	Hemphillian-3
B. secundus	Edson Quarry	Ogallala	Sherman, KS	Hemphillian-3
B. secundus	San Juan and Rak Camel Quarries	Chamita	Rio Arriba, NM	Hemphillian-2
B. secundus	Ocote	Unnamed	Guanajuato, Mexico	Hemphillian-3, 4
B. secundus	Ocote	Unnamed	Guanajuato, Mexico	Hemphillian-4
B. secundus	San Jos-La Hacienda Beds	Unnamed	Jalisco, Mexico	Hemphillian-4

Table 1. Continued.

Taxon	Locality	Formation	County, State	Age
B. secundus	Teocalitche Fauna	Unnamed	Mexico	Hemphillian-3, 4
B. secundus	Rancho Viejo	Unnamed	Guanajuato, Mexico	Blancan
B. secundus	Ogallala Group	Ogallala	Texas, OK	Hemphillian-3
B. secundus	Coffee Ranch	Hemphill Beds	Hemphill, TX	Hemphillian-2
B. secundus	Goodnight	Goodnight Beds	Armstrong, TX	Hemphillian-3
B. solus VanderHoof, 1936	Coso Mountains	Coso	CA	Hemphillian-3, 4

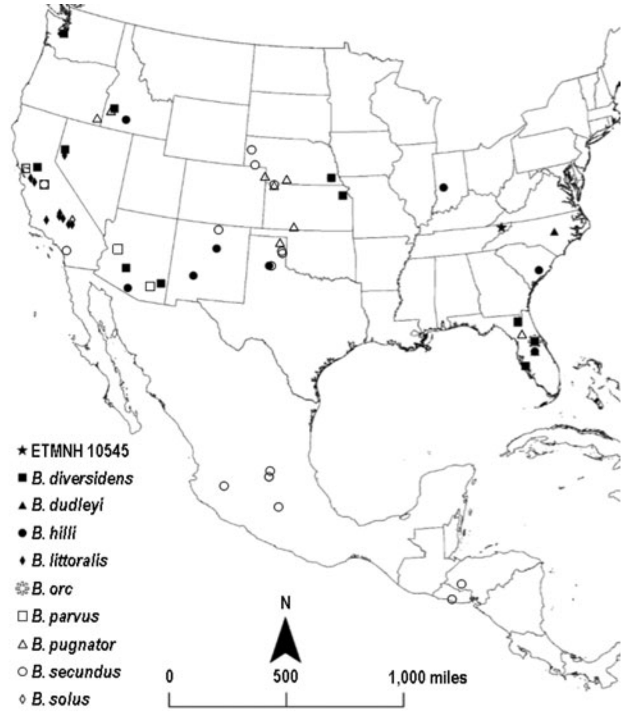

Figure 1. Distribution map of localities for *Borophagus* specimens. Data sources can be found in Table 1.

of (open and closed) habitats were present in North America at the time (Figueirido et al., 2015).

Given the site's age, an Early Pliocene locality located in northeastern Tennessee, the conspicuous absence of *Borophagus* from the Gray Fossil Site (GFS) was previously noted by multiple researchers (Wang and Tedford, 2008; Tseng and Geisler, 2016). A recently discovered canid humerus (Fig. 2) from GFS is described here as *Borophagus*. This new occurrence in the heavily forested Appalachian region can provide new insights on its distribution and ecology of the genus.

Geologic setting

The Gray Fossil Site in Washington County, Tennessee, is an Early Pliocene (late Hemphillian or early Blancan) fossil locality, which dates to ca. 4.9–4.5 Ma (Samuels et al., 2018). The site is located in the Appalachian forests of northeastern Tennessee, making it the only pre-Pleistocene vertebrate fossil locality in the Appalachian region of the eastern United States. Studies suggest that the site was formed when an ancient sinkhole collapsed, became a small lake, and then filled with sediment over several thousand years (Wallace and Wang, 2004; Shunk et al., 2006, 2009). This unique paleontological site records a diverse array of taxa, including a wide variety of flora, invertebrates, fish, amphibians, reptiles, birds, and small and large mammals (Parmalee et al., 2002; Wallace and Wang, 2004; DeSantis and Wallace, 2008; Boardman and Schubert, 2011; Zobaa et al., 2011; Mead et al., 2012; Ochoa et al., 2012, 2016; Worobiec et al., 2013; Bourque and Schubert, 2015; Jasinski and Moscato, 2017; Jasinski, 2018; Short et al., 2019; Siegert and Hermsen, 2020; Quirk and Hermsen, 2021). Flora and fauna at the site have been interpreted to indicate a relatively closed forested ecosystem (Ochoa et al., 2016; Samuels et al., 2018; Quirk and Hermsen, 2021). To date, the only carnivorans described from the site are an ailurid, *Pristinailurus bristoli* Wallace and Wang, 2004, a meline badger, *Arctomeles dimolodontus* Wallace and Wang, 2004, and the earliest record of a wolverine, *Gulo sudorus* Samuels, Bredehoeft, and Wallace, 2018. Wallace and Wang (2004) also noted the presence of *Plionarctos* sp., cf. *Machairodus* sp., and "Canidae" in their faunal list.

Figure 2. *Borophagus* sp. (ETMNH 10545) from the Gray Fossil Site, Tennessee. (**1**) Anterior, (**2**) posterior, (**3**) medial, (**4**) lateral views. Scale bar = 1 cm.

Materials and methods

The GFS fossil canid specimen was qualitatively and quantitatively compared to a broad sample of extant and fossil canids (from Samuels et al., 2013), as well as published descriptions from a variety of sources (Dalquest, 1969; Munthe, 1989; Wang et al., 1999). Measurements followed Samuels et al. (2013) and were taken to the nearest 0.01 mm using digital calipers, these

Table 2. Morphological indices used in the analyses, their definitions, and their inferred functional significance.

Index	Definition & Functional Significance
Shoulder moment index (SMI)	Deltopectoral crest length divided by humerus length (DPCL/HL). Indicates mechanical advantage of the deltoid and pectoral muscles acting across the shoulder joint.
Humeral robustness index (HRI)	Mediolateral diameter of humerus divided by humerus length (HMLD/HL). Indicates robustness of the humerus and its ability to resist bending and shearing stresses.
Humeral epicondylar index (HEI)	Epicondylar breadth of humerus divided by humerus length (HEB/HL). Indicates relative area available for the origins of the forearm flexors, pronators, and supinators.

include: total length of the humerus (HuL), anteriopposterior diameter (HuAPD), mediolateral diameter (HuMLD), length of pectoral crest (HuPCL), epicondylar breadth of the distal humerus (HuEB), and breadth of the distal articular surface (HuHTL). These six measurements were used to compare the humeral proportions among species, and also to calculate three functional indices (Table 2; Fig. 3) used in a variety of studies (Samuels et al., 2013). The overall sample includes 20 extant canid species, from 13 genera, and 20 fossil species, with members of all three canid subfamilies represented (complete data are provided in Table 3). Raw measurements and indices were used in linear regressions to make inferences about the limb proportions, locomotor habits, and body size of the canid from GFS using IBM SPSS Statistics 24. Body mass of the GFS specimen was estimated using published regression equations from Anyonge (1993) and Figuerido et al. (2011).

Repositories and institutional abbreviations.—The figured specimen examined in this study is deposited in the East Tennessee State University Museum of Natural History (ETMNH), Tennessee, USA. Additional specimens measured in this study are reposited in the American Museum of Natural History (F:AM), National Museum of Natural History (USNM), Midwestern University (MU), and University of California Museum of Paleontology (UCMP).

Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Suborder Caniformia Kretzoi, 1943
Family Canidae Fischer de Waldheim, 1817
Subfamily Borophaginae Simpson, 1945
Genus *Borophagus* Cope, 1892

Type species.—*Borophagus diversidens* Cope, 1892 (TMM 40287-10), from Mt. Blanco, Blanco Formation, Crosby County, Texas, U.S.A, by original designation.

Borophagus sp.
Figure 2, Table 3

Occurrence.—Gray Fossil Site, Washington County, Tennessee, Early Pliocene (late Hemphillian or early Blancan age).

Diagnosis.—Supratrochlear foramen present, entepicondylar foramen absent, medial condyle enlarged, distal articular surface with mediolaterally broad and proximodistally shallow trochlea, strongly curved diaphysis, and proportions of the element all support assignment to *Borophagus*.

Description.—The GFS humerus (ETMNH 10545) is relatively complete, missing a portion of the greater tubercle and bearing some erosion of the lesser tubercle and posterior surface of the trochlea (Fig. 2). The humeral diaphysis is robust and fairly strongly curved, convex along its anteroposterior axis and minimally convex along the mediolateral axis, and broader anteroposteriorly than mediolaterally. Proximally, the diaphysis is rounded in cross section, but transitions to triangular distally. The proximal epiphysis is not completely fused, suggesting the individual was not fully mature. Due to the incomplete proximal end, we are unable to determine if the greater tubercle projects above the humeral head. The intertubercular groove is relatively broad and shallow. The deltopectoral crest is prominent and elongate, extending more than half-way down the diaphysis. Distally, the humerus is extremely wide compared to its length, in part, due to the enlarged and flanged medial epicondyle. The articular surface is relatively broad and the trochlea is strongly keeled, but the capitulum lacks a spline and the groove between the trochlea and capitulum is shallow. Below the medial epicondyle are four clear facets for muscle attachment, interpreted as the origins of the carpal and digital flexor muscles. The supracondylar ridge is clear, but not particularly expanded. No entepicondylar foramen is present. The radial fossa is relatively small and round, lying directly above the lateral portion of the capitulum. A round and deep coronoid fossa is medial to the radial fossa. The olecranon fossa is roughly triangular in outline, and though the edges are broken, the fossa merges with the coronoid fossa to form a supratrochlear foramen.

Material.—ETMNH 10545, right humerus.

Remarks.—A number of morphological characteristics of the GFS humerus (ETMNH 10545) facilitate its comparison to previously described humeri of various carnivoran taxa. In canids, the olecranon, coronoid, and radial fossae often fuse to form a supratrochlear foramen; while not observed in all extinct species (Wang and Tedford, 2008), this feature is characteristic of nearly all canids. In contrast to canids, the supratrochlear foramen is absent in previously described and studied felids, hyaenids, mustelids, procyonids, mephitids, ailurids, ursids, and amphicyonids (Montavon et al., 2009). Similarly, ETMNH 10545 does not have an entepicondylar foramen, which is present in many carnivorans, including felids, mustelids, procyonids, mephitids, ailurids, and amphicyonids. The entepicondylar foramen is variably present in ursids (Merriam and Stock, 1925; Bjork, 1970). Among canids, the entepicondylar foramen is present ancestrally, in taxa from all three canid subfamilies: Hesperocyoninae (*Hesperocyon*, *Mesocyon*, and *Paraenhydrocyon*), Borophaginae (*Archaeocyon* and *Cormocyon*), and Caninae (*Leptocyon*) (Wang, 1993; Wang et al., 1999; Tedford et al., 2009; Figueirido et al., 2015). The foramen was lost several times among canids, both within the genus *Borophagus* and in derived members of

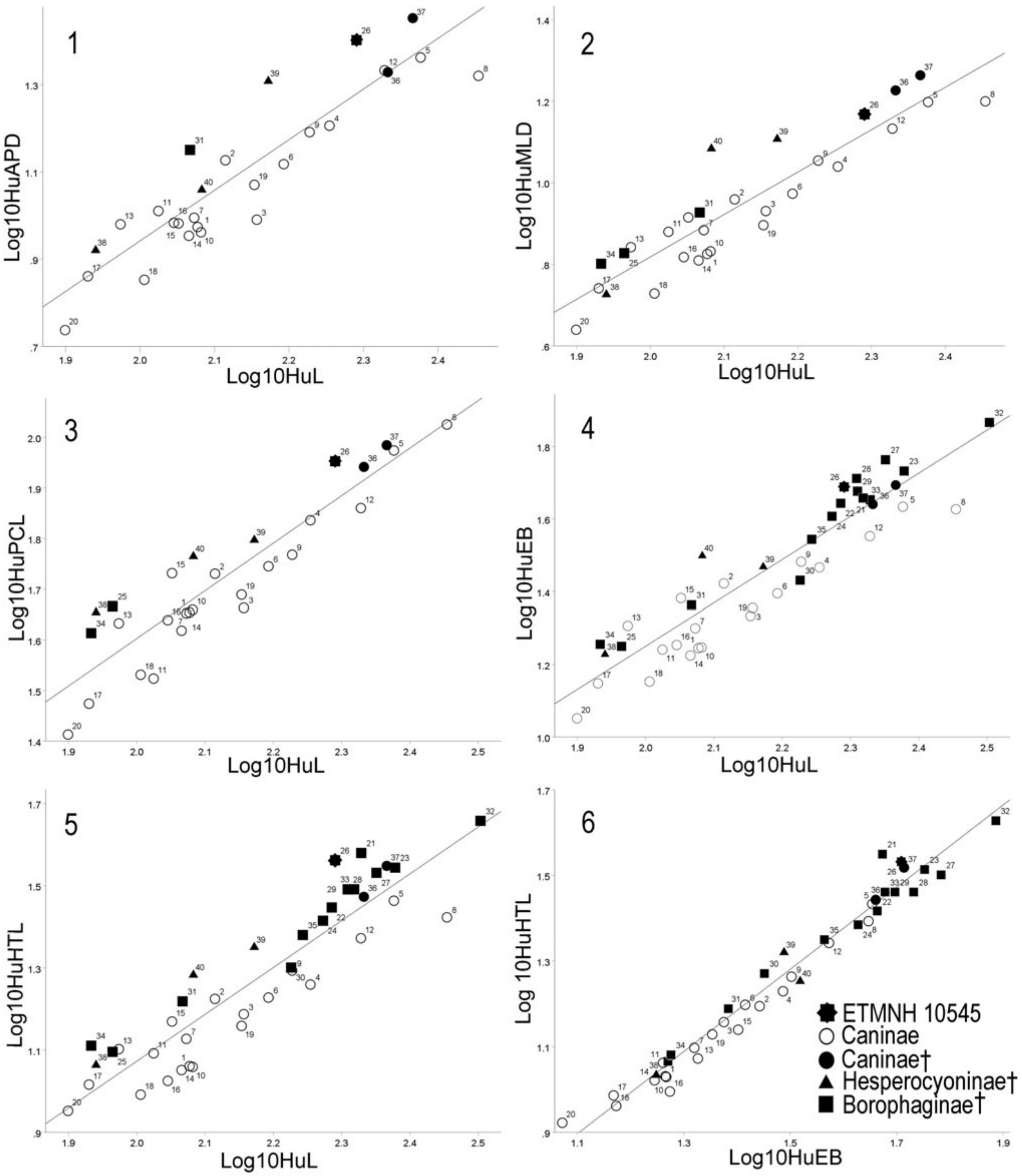

Figure 3. Linear regression comparisons of humeral proportions among canid species. See Table 3 for species list. (**1**) Log/ log plot of humerus length against anteroposterior diameter, (**2**) log/log plot of humerus length against mediolateral diameter, (**3**) log/log plot of humerus length against deltopectoral crest length, (**4**) log/log plot of humerus length against epicondylar breadth, (**5**) log/log plot of humerus length against trochanter length, (**6**) log/log plot of epicondylar breadth against trochanter length. Extinct taxa are denoted by † symbol.

the Caninae (both Canini and Vulpini) (Wang et al., 1999; Tedford et al., 2009; Figueirido et al., 2015). The combined presence of a supratrochlear foramen and lack of an entepiconylar foramen indicate the GFS humerus is that of a canid.

In contrast to ETMNH 10545, most members of Caninae (e.g., *Canis* and *Vulpes*) have (1) a small medial epicondyle, (2) proximodistally deep and mediolaterally narrow capitulum and trochlea, (3) a deep groove between the capitulum and

Table 3. Humerus measurements (in mm) of *Borophagus* sp. from the Gray Fossil Site, and species mean values for a comparative sample of extant and fossil canids. Measurements for other canids derived from Samuels et al. (2013): *Alopex lagopus* Linnaeus, 1758; *Atelocynus microtis* (Sclater, 1882); *Canis adustus* Sundevall, 1846; *Canis latrans* Say, 1823a; *Canis mesomelas* Hilzheimer, 1906; *Cerdocyon thous* (Linnaeus, 1766); *Cuon alpinus* (Pallas, 1811); *Lycalopex gymnocerus* Fischer de Waldheim, 1814; *Otocyon megalotis* (Desmarest, 1822); *Urocyon cinereoargenteus* (Schreber, 1775); *Urocyon littoralis* (Baird, 1857); *Vulpes macrotis* Merriam, 1888; *Vulpes vulpes* Linnaeus, 1758; *Vulpes zerda* (Zimmerman, 1780); *Aelurdon asthenostylus* (Henshaw, 1942); *Aelurdon ferox* Leidy, 1858; *Aelurdon taxoides* (Hatcher, 1893); *Archaeocyon stirtoni* (Webb, 1969b); *Archaeocyon leptodus* Schlaikjer, 1935; *Cynarctus crucidens* Barbour and Cook, 1914; *Desmocyon thomsoni* (Matthew, 1907); *Epicyon saevus* (Leidy, 1858); *Tomarctus robustus* (Green, 1948); *Mesocyon coryphaeus* (Cope, 1884). Extinct species are denoted by a † symbol.

	Taxon	Subfamily	HuL	HuAPD	HuMLD	HuPCL	HuHTL	HuEB	SMI	HRI	HEI	HartI
1	*Alopex lagopus*	Caninae	106.47	8.39	6.69	44.08	11.51	17.59	0.414	0.063	0.165	0.063
2	*Atelocynus microtis*	Caninae	116.01	11.93	9.1	52.55	16.78	26.45	0.453	0.078	0.228	0.078
3	*Canis adustus*	Caninae	127.84	8.72	8.52	45.03	15.4	22.66	0.352	0.067	0.177	0.067
4	*Canis latrans*	Caninae	160.06	14.32	10.95	67.03	18.18	29.27	0.419	0.068	0.183	0.068
5	*Canis lupus*	Caninae	212.12	20.52	15.77	92.11	29.08	43.05	0.434	0.075	0.203	0.075
6	*Canis mesomelas*	Caninae	138.95	11.69	9.4	54.35	16.9	24.85	0.391	0.068	0.179	0.068
7	*Cerdocyon thous*	Caninae	105.34	8.81	7.65	43.91	13.41	19.94	0.417	0.073	0.19	0.073
8	*Chrysocyon brachyurus*	Caninae	253.65	18.63	15.83	103.67	26.5	42.35	0.409	0.062	0.167	0.062
9	*Cuon alpinus*	Caninae	150.52	13.84	11.33	57.29	19.66	30.36	0.381	0.075	0.202	0.075
10	*Lycalopex gymnocerus*	Caninae	107.59	8.16	6.79	44.62	11.46	17.66	0.415	0.063	0.164	0.063
11	*Lycalopex* sp.	Caninae	94.33	9.13	7.58	32.65	12.37	17.42	0.346	0.08	0.185	0.08
12	*Lycaon pictus*	Caninae	189.77	19.18	13.57	70.85	23.57	35.71	0.373	0.071	0.188	0.071
13	*Nyctereutes procyonoides*	Caninae	83.9	8.51	6.95	41.98	12.66	20.25	0.5	0.083	0.241	0.083
14	*Otocyon megalotis*	Caninae	103.64	8.01	6.45	40.6	11.26	16.79	0.392	0.062	0.162	0.062
15	*Speothos venaticus*	Caninae	100.37	8.55	8.22	52.67	14.78	24.11	0.525	0.082	0.241	0.082
16	*Urocyon cinereoargenteus*	Caninae	98.95	8.58	6.57	42.58	10.6	17.94	0.43	0.066	0.181	0.066
17	*Urocyon littoralis*	Caninae	75.87	6.47	5.51	29.12	10.38	14.06	0.384	0.073	0.186	0.073
18	*Vulpes macrotis*	Caninae	90.3	6.35	5.35	33.22	9.81	14.22	0.368	0.058	0.157	0.058
19	*Vulpes vulpes*	Caninae	126.89	10.48	7.87	47.79	14.42	21.55	0.377	0.062	0.17	0.062
20	*Vulpes zerda*	Caninae	70.7	4.87	4.36	25.3	8.96	11.26	0.358	0.062	0.159	0.062
21	*Aelurdon asthenostylus*† F:AM 28356	Borophaginae	190	—	—	—	38	45	—	—	0.237	—
22	*Aelurdon ferox*† F:AM 27479	Borophaginae	172	—	—	—	28	44	—	—	0.256	—
23	*Aelurdon taxoides*† F:AM 30902	Borophaginae	213	—	—	—	35	54	—	—	0.254	—
24	*Archaeocyon stirtoni*† USNM 215320	Borophaginae	167	—	—	—	26	40.5	—	—	0.243	—
25	*Archaeocyon leptodus*†	Borophaginae	82.15	—	6.72	45.35	12.47	17.79	0.552	0.082	0.217	0.082
26	*Borophagus* sp.† ETMNH 10545	Borophaginae	174	22.49	14.71	87.71	36.48	48.81	0.504	0.085	0.281	0.085
27	*Borophagus dudleyi*† MU 8034	Borophaginae	200	—	—	—	34	58	—	—	0.29	—
28	*Borophagus parvus*† UCMP 30490	Borophaginae	181.5	—	—	—	31	51.5	—	—	0.284	—
29	*Borophagus pugnator*† F:AM 67633	Borophaginae	182	—	—	—	31	47	—	—	0.261	—
30	*Cynarctus crucidens*† F:AM 49172	Borophaginae	150	—	—	—	20	27	—	—	0.18	—
31	*Desmocyon thomsoni*†	Borophaginae	104	12.6	8.45	—	16.55	23.1	—	0.081	0.222	0.081
32	*Epicyon haydeni*† F:AM 67665	Borophaginae	284	—	—	—	45.5	73.5	—	—	0.259	—
33	*Epicyon saevus*† F:AM 67489	Borophaginae	185.5	—	—	—	31	45.5	—	—	0.245	—
34	*Phlaocyon leucosteus*†	Borophaginae	76.44	—	6.33	40.15	12.91	18.02	0.525	0.083	0.236	0.083
35	*Tomarctus robustus*† UCMP 33569	Borophaginae	156	—	—	—	24	35	—	—	0.224	—
36	*Canis armbrusteri*†	Caninae	191.69	18.99	16.84	85.48	29.73	43.7	0.428	0.084	0.219	0.084
37	*Canis dirus*†	Caninae	207.04	25.26	18.34	94.35	35.35	49.4	0.456	0.089	0.239	0.089
38	*Hesperocyon gregarius*†	Hesperocyoninae	77.7	7.42	5.32	44.09	11.58	16.91	0.567	0.069	0.218	0.069
39	*Mesocyon coryphaeus*†	Hesperocyoninae	132.47	18.12	12.8	61.27	22.41	29.4	0.463	0.106	0.245	0.106
40	*Paraenhydrocyon josephi*†	Hesperocyoninae	107.87	10.21	12.12	56.86	19.19	31.52	0.527	0.112	0.292	0.112

trochlea, (4) less-curved diaphysis, and (5) proximodistally oriented trochlea (not mediolaterally deflected). Two extant canids studied, *Nyctereutes* and *Speothos*, are distinct from other members of the Caninae in a number of ways; both have enlarged medial epicondyles and relatively elongate deltopectoral crest, which reflect their relatively non-cursorial locomotor habits (Samuels et al., 2013). While *Canis* (*C. ferox* Miller and Carranza-Castañeda, 1998, and *C. lepophagus* Johnston, 1938), *Vulpes* (*V. stenognathus* Savage, 1941, and *V. velox* [Say, 1823b]), *Urocyon* (*U. galushai* Tedford, Wang, and Taylor, 2009), and *Eucyon* (*E. davisi* [Merriam, 1911]) are all known from the time period recorded by GFS (Tedford et al., 2009), those taxa do not have humerus morphology or proportions comparable to the GFS canid.

The GFS is an Early Pliocene fossil site and only two species of *Borophagus* are currently known to have survived into the Pliocene, with both *B. diversidens* and *B. hilli* (Johnston, 1939), present in the early Blancan. Given the fact both taxa have broad geographic distributions ranging from the Pacific Northwest to Florida, these are the most likely contenders for the identity of the GFS canid. To date, only two species of *Borophagus* are actually known to lack an entepicondylar foramen, in all known specimens of *B. diversidens* (Wang et al., 1999) and some specimens of the late Hemphillian *B. secundus* (Matthew and Cook, 1909) (Figueirido et al., 2015), making those species likely candidates for the identity of the GFS canid. However, it is important to note that while *B. diversidens* and *B. secundus* have known postcranial material, humeri of *B. orc* Webb, 1969a, *B. hilli*, and *B. dudleyi* White, 1941, have not been recovered, and thus those taxa cannot be ruled out. *Borophagus dudleyi* is also known from the latest Hemphillian of Florida, but is only represented by a single skull, thus it cannot be directly compared to the GFS canid. *Borophagus parvus* Tedford, Wang, and Taylor, 2009, and *B. pugnator* (Cook, 1922), are also known from the late Hemphillian and were widely distributed, but reported specimens of those taxa possess an entepicondylar foramen (Wang et al., 1999), suggesting they are not the same taxon as the GFS canid.

Results

Age and body size.—A study by von Pfeil et al. (2009) examined the epiphyseal plates in modern canids and found that most domestic dogs reach 90% of their adult size by 10 months, with the majority of growth plates fusing between 4–12 months. The proximal humeral epiphysis fully fuses between 10–12 months of age, while the distal humeral epiphysis fuses earlier, between 5–8 months (von Pfeil et al., 2009). The distal epiphysis of the humerus from the GFS specimen is fully fused, but the proximal epiphysis is partially fused, suggesting the GFS specimen is most likely between the ages of 8–12 months. A body mass estimate was calculated using published equations; the formula provided by Anyonge (1993) yielded a body mass estimate of 74.13kg, while that of Figuerido et al. (2011) produced a body mass estimate of 52.48kg.

Morphometric comparison.—The length of the GFS humerus (ETMNH 10545) is greater than most other canids studied, with the exception of the gray wolf (*Canis lupus* Linnaeus, 1758), African hunting dog (*Lycaon pictus* Griffith, Smith, and Pidgeon, 1827), dire wolf (*Canis dirus* Leidy, 1858), and Armbruster's wolf (*Canis armbrusteri*) (Table 3). The GFS canid has a very robust shaft (Table 3) and only one other canid studied has a larger diaphyseal diameter; *C. dirus*. Three other species, *C. lupus*, *C. armbrusteri* Gidley, 1913, and the maned wolf (*Chrysocyon brachyurus* [Illiger, 1815]), have greater mediolateral diameter. The deltopectoral crest length of ETMNH 10545 is relatively large (Table 3), only *C. lupus*, *C. dirus*, and *C. brachyurus* have greater lengths, and each of those taxa has a much longer overall humerus length, meaning the GFS canid has a proportionately longer pectoral crest and thus shoulder moment index (SMI) (Fig. 3). The epicondylar breadth of ETMNH 10545 is the second largest of the canids studied, only behind the much larger *C. dirus*, but the relative size of the epicondyles (HEB) is much greater than *C. dirus* and all other canids studied, with exception of the early hesperocyonine *Paraenhydrocyon josephi* (Cope, 1881) (Table 3; Fig. 3). The distal articular surface, including the capitulum and trochlea, is very broad in specimens of *Borophagus*, greater than all other studied taxa, with exception of the borophagine *Epicyon haydeni* Leidy, 1858, which is also much larger and relatively broader (compared to humerus length) than in any other canid (Table 3). The shoulder moment index is >0.5 in ETMNH 10545 (Table 3) and in the early canids *Hesperocyon gregarius* Wortman and Matthew, 1899, *Paraenhydrocyon josephi*, and *Phlaocyon leucosteus* Matthew, 1899, and the extant *Nyctereutes procyonoides* (Gray, 1834) and *Speothos venaticus* (Lund, 1842). The humeral robustness (HRI) of *C. dirus*, *H. gregarius*, and *P. josephi* is greater than the GFS specimen (Table 3).

Discussion

Recovered postcranial elements of *Borophagus* are rare, with only 16 specimens having been reported from the fossil record (Dalquest, 1969; Munthe, 1989; Wang et al., 1999). The addition of the GFS humerus aides in understanding the ecology of the genus, both in terms of locomotion and habitat preference. While the humerus is attributable to the genus *Borophagus*, there was not enough evidence to assign a species; however, based on the age and morphology of the humerus, the most likely contender is *B. diversidens*.

The two body mass estimates for *Borophagus* produced here, 52.48 kg and 74.13 kg, are larger than the average mass of the modern gray wolf (*Canis lupus*). Figueirido et al. (2015) provided estimated body mass for several species of *Borophagus* based on the humerus, with estimated masses of *B. parvus* = 34.5 kg, *B. pugnator* = 58.5 kg, and *B. secundus* = 33.1 kg and 39.1 kg. These estimates are fairly similar, indicating relatively large body mass in *Borophagus* and supporting inference of predatory specialization for larger taxa (Carbone et al., 1999, 2007). Cursorial carnivorans have generally gracile limbs characterized by low HRI and have smaller humeral epicondyles, while semifossorial and semiaquatic carnivorans have enlarged humeral epicondyles to allow for larger area for forearm flexor, pronator, and supinator muscles (Samuels et al., 2013). Humeri in non-cursorial canid taxa are relatively robust, likely as a consequence of ambush predatory behavior, which demands short bursts of speed and extra strength to take down prey (Van Valkenburgh, 1985; Munthe, 1989; Anyonge, 1996; Figueirido et al., 2015; Martín-Serra et al., 2016). Extant ambush predators have a humeral head that is posteriorly oriented and an anteroposteriorly convex shaft; attributes that suggest the humerus is flexed when taking down prey (Martín-Serra et al., 2016). Additionally, ambush predators have a large medial epicondyle where the flexor muscles would attach and increase the ability to grasp prey (Martín-Serra et al., 2016). A shallow trochlea allows supination of the forearm (Andersson, 2005; Figueirido and Janis, 2011; Janis and Figueirido, 2014; Figueirido et al., 2015; Martín-Serra et al., 2016), but also indicates long-distance running is not a specialty; instead, animals possessing such features have the ability to perform a variety of tasks (Munthe, 1989; Fabre et al., 2013; Figueirido et al., 2015; Martín-Serra et al., 2016). The presence of a shallow trochlea with a circular-shaped diaphysis cross section allows movement of the forearm to occur outside the parasagittal plane (Figueirido and Janis, 2011; Janis and Figueirido, 2014; Figueirido et al., 2015; Martín-Serra et al., 2016).

The GFS specimen possesses all features of those seen in ambush predator humeri, and given the presence of a heavily forested habitat, for which rapid locomotion was not well suited, *Borophagus* most likely would have been an ambush predator. Additionally, the presence of *Borophagus* in Honduras (and now eastern Tennessee), which are parts of North America that never transitioned to open grassland or steppe environments, could suggest *Borophagus* was adapted to live in both open- and closed-habitat environments (Munthe, 1989).

The shoulder moment index (SMI) of ETMNH 10545 is similar to *Hesperocyon gregarious*, *Paraenhydrocyon josephi*, and *Phlaocyon leucosteus*, indicating a high mechanical advantage across the shoulder joint (Fig. 3). *Paraenhydrocyon josephi*, an early member of the hesperocyonine subfamily, was adapted for a semi-arboreal lifestyle, while *H. gregarious* evolved in a forested environment. The humeral robustness indices (HRIs) of *C. dirus*, *H. gregarious*, and *P. josephi* are similar to the GFS specimen (Fig. 3). The relative size of the humeral epicondyles (HEB) in ETMNH 10545 is much greater than all other canids studied, other than *P. josephi*, and quite distinct from the relatively narrow epicondyles of cursorially adapted pursuit predators (Fig. 3). The large medial epicondyle would have provided for large areas of origin for the wrist and digital flexors, which would have facilitated grasping movements that are typical of ambush hunting predators. Due to the somewhat similar dimensions with the four taxa listed above, it can be concluded the GFS *Borophagus* was not well adapted for running long distances and most likely was not a pursuit predator. *Borophagus* may have spent some of its time digging, possibly for refuge from larger competitors (given its size, it needed to feed on prey 50% of its size) (Carbone et al., 1999, 2007).

Borophagus has been found to inhabit grasslands, transitional, coastal, and now forested habitats. Skeletal and muscular morphology indicate the genus was not adapted for a cursorial lifestyle, which would have been problematic because of their highly cursorial prey. It is thought *Borophagus* may have been a social animal, and in packs could have hunted larger prey (Wang et al., 2018). This method may have suited *Borophagus* in open environments, but specimens found in forested environments, where their skeletal morphology may have been more functionally adapted, may not have needed these pack hunting skills because the forests would have provided sufficient cover for an ambush attack.

Conclusions

The GFS humerus identified as belonging to *Borophagus* sp. is the first occurrence of the genus in Tennessee and in a heavily forested ecosystem. Weighing between 52–74 kg, the GFS *Borophagus* is interpreted as adapted to an ambush predatory lifestyle in a closed forested habitat, distinct from the cursorial locomotion other canids living in open habitats. *Borophagus* would have been one of the largest predators in the GFS forest, alongside saber-toothed cats, and with an abundance of tapirs (*Tapirus polkensis* Olsen, 1960) and other large herbivores at the site, there certainly would have been enough food resources to support both apex predators.

Acknowledgments

Collection of specimens at the Gray Fossil Site in Tennessee was partially funded through a National Science Foundation Grant (NSF Grant #0958985) to S.C. Wallace and B.W. Schubert. We would like to thank the ETMNH collections managers, A. Nye and B. Compton, who kindly allowed access to specimens in their care. Review and helpful suggestions by X. Wang and A. Atwater improved the quality of this manuscript.

References

Andersson, K., 2005, Were there pack-hunting canids in the Tertiary, and how can we know? Paleobiology, v. 31, p. 56–72.

Andersson, K., and Werdelin, L., 2003, The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology: Proceedings of the Royal Society of London. Series B: Biological Sciences, v. 270, p. 163–165.

Anyonge, W., 1993, Body mass in large extant and extinct carnivores: Journal of Zoology, v. 231, p. 339–350.

Anyonge, W., 1996, Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis: Journal of Zoology, v. 238, p. 395–413.

Baird, S.F., 1857, Mammals—Canidae—*Vulpes littoralis*, *in* United States War Department and United States Army Corps of Engineers, Reports of Explorations and Surveys for a Railroad Route from the Mississippi River to the Pacific Ocean: Washington, D.C., Beverly Tucker, Printer, v. 8, p. 143–145.

Barbour, E.H., and Cook, H., 1914, Two new fossil dogs of the genus Cynarctus from Nebraska: Nebraska Geological Survey, v. 4, p. 225–227.

Bjork, P.R., 1970, The Carnivora of the Hagerman local fauna (Late Pliocene) of southwestern Idaho: Transactions of the American Philosophical Society, v. 60, p. 3–54.

Boardman, G.S., and Schubert, B.W., 2011, First Mio-Pliocene salamander fossil assemblage from the southern Appalachians: Palaeontologia Electronica, v. 14, 16A. https://palaeo-electronica.org/2011_2/257/index.html.

Bourque, J.R., and Schubert, B.W., 2015, Fossil musk turtles (Kinosternidae, *Sternotherus*) from the Late Miocene–Early Pliocene (Hemphillian) of Tennessee and Florida: Journal of Vertebrate Paleontology, v. 35. e885441. https://doi.org/10.1080/02724634.2014.885441.

Bowdich, T.E., 1821, An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers: Paris, J. Smith, v. 115, p. 16.

Carbone, C., Mace, G.M., Roberts, S.C., and Macdonald, D.W., 1999, Energetic constraints on the diet of terrestrial carnivores: Nature, v. 402, p. 286–288.

Carbone, C., Teacher, A., and Rowcliffe, J.M., 2007, The costs of carnivory: PLoS Biology, v. 5, p. 363–368.

Carrasco, M.A., Barnosky, A.D., Kraatz, B.P., and Davis, E.B., 2007, The Miocene mammal mapping project (MIOMAP): an online database of Arikareean through Hemphillian fossil mammals: Bulletin of Carnegie Museum of Natural History, v. 39, p. 183–188.

Cook, H.J., 1922, A Pliocene fauna from Yuma County, California, with notes on the clearly related Snake Creek beds from Nebraska: Proceedings of the Colorado Museum of Natural History, v. 4, p. 3–29.

Cope, E.D., 1881, On the Nimravidae and Canidae of the Miocene Period: Bulletin of the United States Geological and Geographical Survey, v. 6, p.165–181.

Cope, E.D., 1884, The vertebra of the Tertiary formations of the west: Reports of the United States Geological Survey of the Territories, v. 3, p. 1–1009.

Cope, E.D., 1892. On a new genus of Mammalia from the Laramie Formation. American Naturalist, v. 26, p. 758–762.

Dalquest, W.W., 1969, Pliocene carnivores of the Coffee Ranch (type Hemphill) local fauna: Bulletin of the Texas Memorial Museum, v. 15, p. 1–44.

DeSantis, L.R.G., and Wallace, S.C., 2008, Neogene forests from the Appalachians of Tennessee, USA: geochemical evidence from fossil mammal teeth: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 266, p. 59–68.

Desmarest, A.G., 1822, Mammalogie ou description des especes de mammiferes. Seconde partie, contenant les ordres de Rongeurs des Edentes, des Pachydermes, des ruminans et des Cetaces. En encyclopedie methodique: Paris, Veuve Agasse, v. 196, 277 p.

Eschelman, R.E., and Whitmore, F.C., 2008, Early Pliocene (late Hemphillian) land mammals from the Lee Creek Mine, Aurora, North Carolina: Virginia Museum of Natural History Special Publication, v. 14, p. 17–38.

Fabre, A.C., Cornette, R., Slater, G., Argot, C., Peigné, S., Goswami, A., and Pouydebat, E., 2013, Getting a grip on the evolution of grasping in musteloid carnivorans: a three-dimensional analysis of forelimb shape: Journal of Evolutionary Biology, v. 26, p. 1521–1535.

Figueirido, B., and Janis, J.M., 2011, The predatory behavior of the thylacine: Tasmanian tiger or marsupial wolf?: Biology Letters, v. 7, p. 937–940.

Figueirido, B., Pérez-Claros, J.A., Hunt, R.M., Jr., and Palmqvist, P., 2011, Body mass estimation in amphicyonid carnivoran mammals: a multiple regression approach from the skull and skeleton: Acta Palaeontologica Polonica, v. 56, p. 225–246.

Figueirido, B., Martín-Serra, A., Tseng, Z.J., and Janis, C.M., 2015, Habitat changes and changing predatory habits in North American fossil canids: Nature Communications, v. 6, 7976. https://doi.org/10.1038/ncomms8976.

Fischer de Waldheim, G., 1814, Zoognosia tabulis synopticis illustrata. Volumen Tertium: Mosquae, Nicolas Sergeidis Vsevolozsky, v. 24, p. 1–732.

Fischer de Waldheim, G., 1817, Adversaria zoologica: Mémoires de la Société Impériale des Naturalistes de Moscou, v. 5, p. 357–428.

Gidley, J.W., 1913, Preliminary report on a recently discovered Pleistocene cave deposit near Cumberland, Maryland: Proceedings of the United States National Museum, v. 46, p. 93–102.

Graham, R.W., and Lundelius, E.L., Jr., 2010, FAUNMAP II: new data for North America with a temporal extension for the Blancan, Irvingtonian and early Rancholabrean: FAUNMAP II Database, version 1.0. https://ucmp.berkeley.edu/faunmap/index.html.

Gray, J., 1834, Illustrations of Indian zoology, consisting of coloured plates of new or hitherto unfigured Indian animals chiefly selected from the collection of Major-General Hardwicke, F.R.S.: London, Adolph Richter & Co., v. 2.

Green, M., 1948, A new species of dog from the lower Pliocene of California: University of California Publications, Bulletin of the Department of Geological Sciences, v. 24, p. 81–90.

Griffith, E.C., Smith, A.N, and Pidgeon, E., 1827, The animal kingdom arranged in conformity with its organization by the Baron Cuvier, with additional descriptions of all the species hitherto named, and of many not before noticed: London, William, Clowes, 353 p.

Hatcher, J.B., 1893, On a small collection of vertebrate fossils from the Loup Fork beds of northwestern Nebraska, with note on the geology of the region: American Naturalist, v. 28, p. 236–248.

Henshaw, P.C., 1942, A Tertiary mammalian fauna from the San Antonio Mountains near Tonopah, Nevada: Carnegie Institute Washington Publications, v. 530, p. 77–168.

Hilzheimer, M., 1906, Die geographische Verbreitung der afrikanischen Grauschakale: Zoologischer Beobachter, v. 47, p. 363–373.

Hulbert, R.C., Jr., Wallace, S.C., Klippel, W.E., and Parmalee, P.W., 2009, Cranial morphology and systematics of an extraordinary sample of the late Neogene dwarf tapir, *Tapirus polkensis* (Olsen): Journal of Paleontology, v. 83, p. 238–262.

Illiger, K., 1815, Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile: Abhandlungen der physikalishe Klasse der Koeniglich-Preussischen (Berlin: Akademie der Wissenschaften), v. 1811, p. 39–159.

Janis, C.M., and Figueirido, B., 2014, Forelimb anatomy and the discrimination of the predatory behavior of carnivorous mammals: the thylacine as a case study: Journal of Morphology, v. 275, p. 1321–1338.

Jasinski, S.E., 2018, A new slider turtle (Testudines: Emydidae: Deirochelyinae: *Trachemys*) from the late Hemphillian (Late Miocene/Early Pliocene) of eastern Tennessee and the evolution of the deirochelyines: PeerJ, v. 6, e4338. https://doi.org/10.7717/peerj.4338.

Jasinski, S.E., and Moscato, D.A., 2017, Late Hemphillian colubrid snakes (Serpentes, Colubridae) from the Gray Fossil Site of northeastern Tennessee: Journal of Herpetology, v. 51, p. 245–257.

Johnston, C.S., 1938, Preliminary report on the vertebrate type locality of Cita Canyon, and the description of an ancestral coyote: American Journal of Science, v. 35, p. 383–390.

Johnston, C.S., 1939, Preliminary report on the late Middle Pliocene Axtel locality, and the description of a new member of the genus *Osteoborus*: American Journal of Science, v. 237, p. 895–898.

Kretzoi, M., 1943, *Kochitis centenii* n.g. n.sp., ein alterümlicher Creodonte aus dem Oberoligozän Siebenbürgens: Földtany Közlony, v. 73, p. 268–271.

Leidy, J., 1858, Notice of remains of extinct Vertebrata, from the valley of the Niobrara River, collected during the exploring expedition of 1857, in Nebraska, under the command of Liet. G. K. Warren, U. S. Topographical Engineer, by Dr. F. V. Hayden, Geologist to the expedition: Proceedings of Academy of Natural Sciences of Philadelphia, v. 10, p. 20–29.

Linnaeus, C., 1758, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata: Stockholm, Laurentii Salvii, v. 1, 824 p.

Linnaeus, C., 1766–1768, Systema Naturae. 12th edition: Holmiae, Laurentii Salvii, 1327 p.

Lund, P.W., 1842, Blik paa Brasiliens Dyreverden for Sidste Jordomvaeltning: Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger, v. 9, p. 137–208.

Martín-Serra, A., Figueirido, B., and Palmqvist, P., 2016, In the pursuit of the predatory behavior of Borophagines (Mammalia, Carnivora, Canidae): inferences from forelimb morphology: Journal of Mammalian Evolution, v. 23, p. 237–249.

Matthew, W.D., 1899, A provisional classification of the freshwater Tertiary: Western Bulletin of the American Museum of Natural History, v. 12, p. 19–75.

Matthew, W.D., 1907, A lower Miocene fauna from South Dakota: Bulletin of the American Museum of Natural History, v. 23, p. 169–219.

Matthew, W.D., 1924, Third contribution to the Snake Creek fauna: Bulletin of the American Museum of Natural History, v. 50, p. 59–210.

Matthew, W.D., 1930, The phylogeny of dogs: Journal of Mammalogy: v. 11, p. 117–138.

Matthew, W.D., and Cook, H.J., 1909, A Pliocene fauna from western Nebraska: American Museum of Natural History Bulletin, v. 26, p. 361–414.

Matthew, W.D., and Stirton, R.A., 1930, Osteology and affinities of *Borophagus*: University of California Publications, Bulletin of the Department of Geological Sciences, v. 19, p. 171–216.

Meachen-Samuels, J., and Van Valkenburgh, B., 2009, Forelimb indicators of prey-size preference in the Felidae: Journal of Morphology, v. 270, p. 729–744.

Mead, J.I., Schubert, B.W., Wallace, S.C., and Swift, S.L., 2012, Helodermatid lizard from the Mio-Pliocene oak-hickory forest of Tennessee, Eastern USA, and a review of monstersaurian osteoderms: Acta Palaeontologica Polonica, v. 57, p. 111–121.

Meade, G.E., 1945, The Blanco fauna: University of Texas Publications, v. 4401, p. 509–557.

Merriam, C.H., 1888, Description of a new fox from southern California: Proceedings of the Biological Society Washington, v. 4, p.135–138.

Merriam, J.C., 1911, Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada. Part 2. Vertebrate faunas: Bulletin of the Department of Geology of the University of California, v. 11, p. 199–304.

Merriam, J.C., and Stock, C., 1925, Relationships and structure of the short-faced bear, *Arctotherium*, from the Pleistocene of California: Carnegie Institution of Washington Publication, v. 347, p. 1–35.

Miller, W.E., and Carranza-Castañeda, O., 1998, Late Tertiary canids from central Mexico: Journal of Paleontology, v. 72, p. 546–556.

Montavon, P.M., Voss, K., and Langley-Hobbs, S.J., eds., 2009, Feline Orthopedic Surgery and Musculoskeletal Disease: Philadelphia, Saunders Elsevier Health Sciences, 515 p.

Munthe, K., 1989, The skeleton of the Borophaginae (Carnivora, Canidae): morphology and function: University of California Publications in Geological Sciences, v. 133, p. 24–47.

Ochoa, D., Whitelaw, M., Liu, Y.S.C., and Zavada, M., 2012, Palynology of Neogene sediments at the Gray Fossil Site, Tennessee, USA: floristic implications: Review of Palaeobotany and Palynology, v. 184, p. 36–48.

Ochoa, D., Zavada, M.S., Liu, Y., and Farlow, J.O., 2016, Floristic implications of two contemporaneous inland upper Neogene sites in the eastern US: Pipe Creek Sinkhole, Indiana, and the Gray Fossil Site, Tennessee (USA): Palaeobiodiversity and Palaeoenvironments, v. 96, p. 239–254.

Olsen, S.J., 1960, Age and faunal relationships of *Tapiravus* remains from Florida: Journal of Paleontology, v. 34, p. 164–167.

Pallas, P.S., 1811, Zoographia Rosso-Asiatica: sistens omnium animalium in extenso Imperio Rossico, et adjacentibus maribus observatorum recensionem, domicilia, mores et descriptiones, anatomen atque icones plurimorum: Petrópolis, Nova Acta Academiae Scientiarum Imperialis, 568 p.

Parmalee, P.W., Klippel, W.E., Meylan, P.A., and Holman, J.A., 2002, A Late Miocene–Early Pliocene population of *Trachemys* (Testudines: Emydidae) from east Tennessee: Annals of Carnegie Museum, v. 71, p. 233–239.

Quirk, Z.J., and Hermsen, E.J., 2021, Neogene *Corylopsis* seeds from eastern Tennessee: Journal of Systematics and Evolution, v. 59, p. 611–621.

Samuels, J.X., Meachen, J.A., and Sakai, S.A., 2013, Postcranial morphology and the locomotor habits of living and extinct carnivorans: Journal of Morphology, v. 274, p. 121–146.

Samuels, J.X., Bredehoeft, K.E., and Wallace, S.C., 2018, A new species of *Gulo* from the Early Pliocene Gray Fossil Site (Eastern United States); rethinking the evolution of wolverines: PeerJ, v. 6, e4648. https://doi.org/10.7717/peerj.4648.

Savage, D.E., 1941, Two new Middle Pliocene carnivores from Oklahoma with notes on the Optima Fauna: American Midland Naturalist, v. 25, p. 692–710.

Say, T., 1823a, *Canis latrans*, *in* James, E., compiler, Account of an Expedition from Pittsburgh to the Rocky Mountains, Performed in the Years 1819 and '20: Philadelphia, H.C. Garey and I. Lea, v. 1, p. 168.

Say, T., 1823b, *Canis velox*, *in* James, E., compiler, Account of an Expedition from Pittsburgh to the Rocky Mountains, Performed in the Years 1819 and '20: Philadelphia, H.C. Garey and I. Lea, v. 2, p. 356.

Schlaikjer, E.M., 1935, Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. IV: new vertebrates and the stratigraphy of the Oligocene and Early Miocene: Bulletin of the Museum of Comparative Zoology, v. 76, p. 97–189.

Schreber, J.C.D., 1775, Die Saugethiere in Abbildungen nach der Nature mit Beschreibungen: Leipzig, W. Walther, v. 3, p. 281–590.

Sclater, P.L., 1882, Reports on the additions to the society's menagerie in June, July, August, September, and October: Proceedings of the Zoological Society of London, p. 630–631

Short R.A., Wallace, S.C., and Emmert L.G., 2019, A new species of *Teleoceras* (Mammalia, Rhinocerotidae) from the late Hemphillian of Tennessee: Bulletin of the Florida Museum of Natural History, v. 56, p. 183–260.

Shunk, A.J., Driese, S.G., and Clark, G.M., 2006, Latest Miocene to earliest Pliocene sedimentation and climate record derived from paleosinkhole fill deposits, Gray Fossil Site, northeastern Tennessee, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 231, p. 265–278.

Shunk, A.J., Driese, S.G., and Dunbar, J.A., 2009, Late Tertiary paleoclimatic interpretation from lacustrine rhythmites in the Gray Fossil Site, northeastern Tennessee, USA: Journal of Paleolimnology, v. 42, p. 11–24.

Siegert, C., and Hermsen, E.J., 2020, *Cavilignum pratchettii* gen. et sp. nov., a novel type of fossil endocarp with open locules from the Neogene Gray Fossil Site, Tennessee, USA: Review of Palaeobotany and Palynology, v. 275, 104174. https://doi.org/10.1016/j.revpalbo.2020.104174.

Simpson, G.G., 1945, The principles of classification and a classification of mammals: Bulletin of the American Museum of Natural History, v. 8, p. 1–350.

Sundevall, C.J., 1846, Nya Mammalia fran Sydafrica: Õfversigt af kongl. Vetenskaps-Akademiens Förhandlingar, v. 3, p. 118–121.

Tedford, R.H., Wang, X., and Taylor, B.E., 2009, Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae): Bulletin of the American Museum of Natural History, v. 2009, p. 1–218.

The NOW Community, 2019, New and Old Worlds Database of Fossil Mammals (NOW): Licensed under CC BY 4.0. Retrieved January 15, 2013. https://nowdatabase.org/now/database/.

Tseng, Z.J., and Geisler, J.H., 2016, The first fossil record of borophagine dogs (Mammalia, Carnivora) from South Carolina, U.S.A.: Journal of Vertebrate Paleontology, v. 36, p.e1062022. https://doi.org/10.1080/02724634.2015.1062022.

VanderHoof, V.L., 1931, *Borophagus littoralis* from the marine Tertiary of California: University of California Publications, Department of Geology Bulletin, v. 21, p. 15–24.

VanderHoof, V.L., 1936, Notes on the type *Borophagus diversidens*: Journal of Mammalogy, v. 17, p. 415–416.

Van Valkenburgh, B., 1985, Locomotor diversity within past and present guilds of large predatory mammals: Paleobiology, v. 11, p. 406–428.

Van Valkenburgh, B., 1987, Skeletal indicators of locomotor behavior in living and extinct carnivores: Journal of Vertebrate Paleontology, v. 7, p. 162–182.

von Pfeil, D.J.F., and DeCamp, C.E., 2009, The epiphyseal plate: physiology, anatomy, and trauma: Compendium Continuing Education for Veterinarians (Yardley, PA), v. 31, p. 1–12.

Wallace, S.C., and Wang, X., 2004, Two new carnivores from an unusual late Tertiary forest biota in eastern North America: Nature, v. 431, p. 556–559.

Wang, X., 1993, Transformation from plantigrady to digitigrady: functional morphology of locomotion in *Hesperocyon* (Canidae: Carnivora): American Museum Novitates, v. 3069, p. 1–24.

Wang, X., and Tedford, R.H., 2008, Dogs: Their Fossil Relatives and Evolutionary History: New York, Columbia University Press, 219 p.

Wang, X., Tedford, R.H., and Taylor, B.E., 1999, Phylogenetic systematics of the Borophaginae (Carnivora, Canidae): Bulletin of the American Museum of Natural History, v. 243. p. 1–391.

Wang, X., White, S.C., Balisi, M., Biewer, J., Sankey, J., Garber, D., and Tseng, Z.J., 2018, First bone-cracking dog coprolites provide new insight into bone consumption in *Borophagus* and their unique ecological niche: ELife, v. 7, e34773. https://doi.org/10.7554/eLife.34773.001.

Webb, S.D., 1969a, The Pliocene Canidae of Florida: Bulletin of the Florida State Museum Biological Sciences, v. 14, p. 273–308.

Webb, S.D., 1969b, The Burge and Minnechaduza Clarendonian mammalian fauna of north-central Nebraska: University of California Publications in Geological Sciences, v.78, p.1–191.

White, T.E., 1941, Additions to the fauna of the Florida Pliocene: Proceedings of the New England Zoological Club, v. 18, p. 67–70.

Worobiec, E., Liu, Y.-S., and Zavada, M.S., 2013, Palaeoenvironment of late Neogene lacustrine sediments at the Gray Fossil Site, Tennessee, USA: Annales Societatis Geologorum Poloniae, v. 83, p. 51–63.

Wortman, J.L., and Matthew, W.D., 1899, The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae: Bulletin of the American Museum of Natural History, v. 12, p. 109–139.

Zimmerman, E.A.W., 1780, Geographische Geschichte des Menschen, und der vierfussigen Thiere: Weygandschen Buchhandlung, Leipzig, Germany v. 2, 432 p.

Zobaa, M.K., Zavada, M.S., Whitelaw, M.J., Shunk, A.J., and Oboh-Ikuenobe, F.E., 2011, Palynology and palynofacies analyses of the Gray Fossil Site, eastern Tennessee: their role in understanding the basin-fill history: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 308, p. 433–444.

Accepted: 9 May 2022

Appendix

Humoral lengths of extant canid specimens studied. Measurement abbreviations include: total length of the humerus (HuL), anterioposterior diameter (HuAPD), mediolateral diameter (HuMLD), length of pectoral crest (HuPCL), breadth of the distal articular surface (HuHTL), and epicondylar breadth of the distal humerus (HuEB).

Species	HuL	HuAPD	HuMLD	HuPCL	HuHTL	HuEB
Alopex lagopus	107.18	8.28	6.95	44.16	11.47	17.48
Alopex lagopus innuitus	105.75	8.5	6.42	43.99	11.55	17.7
Atelocynus microtis	116.01	11.93	9.1	52.55	16.78	26.45
Canis adustus	127.84	8.72	8.52	45.03	15.4	22.66
Canis latrans	173.78	15.1	11.38	71.89	21.36	30.87
Canis latrans dickeyi	178.14	16.09	12.44	85.75	23.19	32.56
Canis latrans merriam	153.16	14.51	10.43	64.16	14.31	27.56
Canis latrans merriam	149.63	13.39	10.61	56.29	20.87	26.91
Canis latrans ochropus	149.86	12.6	9.37	63.82	14.38	28.94
Canis latrans ochropus	155.78	14.2	11.44	60.24	14.98	28.8
Canis lupus	208.46	18.71	15.47	106.93	26.87	40.65
Canis lupus	199.53	20.97	14.51	89.18	28.15	41.09
Canis lupus	188.18	20.25	14.6	72.87	25.92	37.97
Canis lupus	254.03	23.38	16.24	101.07	34.01	52.94
Canis lupus	228	22.38	17.09	93.27	31.51	45.32
Canis lupus	194.51	17.41	16.7	89.36	28.04	40.31
Canis mesomelas	139.34	10.54	9.56	53.16	16.18	24.08
Canis mesomelas	138.56	12.83	9.24	55.53	17.62	25.62
Cerdocyon thous	103.66	8.2	7.24	42.77	12.35	19.49
Cerdocyon thous	118.05	11.02	8.16	47.75	15.46	21.92
Cerdocyon thous	94.32	7.22	7.56	41.21	12.41	18.41
Chrysocyon brachyurus	263.84	19.8	16.6	101.77	27.4	41.16
Chrysocyon brachyurus	237.41	18.79	14.76	106.27	25.64	40.13
Chrysocyon brachyurus	256.24	18.16	16.96	97.95	28.59	43.66
Chrysocyon brachyurus	243.37	17.04	14.79	96.36	22.49	40.3
Chrysocyon brachyurus	267.38	19.37	16.06	115.99	28.36	46.5
Cuon alpinus	150.52	13.84	11.33	57.29	19.66	30.36
Lycalopex gymnocerus	111.61	8.72	7.02	43.77	11.95	18.29
Lycalopex gymnocerus	103.56	7.6	6.56	45.47	10.96	17.02
Lycalopex sp.	94.33	9.13	7.58	32.65	12.37	17.42
Lycaon pictus	173.83	17.27	12.27	65.84	21.26	32.5
Lycaon pictus	205.71	21.09	14.86	75.85	25.87	38.92
Nyctereutes procyonoides	84.28	8.29	6.85	41.99	13.45	19.43
Nyctereutes procyonoides	83.51	8.72	7.04	41.96	11.87	21.06
Otocyon megalotis	100.86	8.35	7.05	42.17	11.52	17.23
Otocyon megalotis	102.81	7.78	6.27	39.06	12.25	17.14
Otocyon megalotis	101.92	8.55	6.43	40.87	11.29	17.29
Otocyon megalotis	108.97	7.35	6.03	40.29	9.98	15.49
Speothos venaticus	107.97	8.63	8.6	65.89	15.73	24.22
Speothos venaticus	91.79	8.51	7.07	48.41	13.78	23.57
Speothos venaticus	101.16	8.44	8.79	45.12	15.13	24.15
Speothos venaticus	104.63	8.29	8.37	48.09	14.55	24.15
Speothos venaticus	96.31	8.88	8.27	55.86	14.7	24.44
Urocyon cinereoargenteus	92.32	8.13	6.3	34.17	9.28	16.66
Urocyon cinereoargenteus	101.08	8.65	6.67	38.93	9.17	19.38
Urocyon cinereoargenteus	98.03	9.32	6.9	39.49	10.05	18.53
Urocyon cinereoargenteus	94.13	7.47	6.02	38.9	11.26	16.83
Urocyon cinereoargenteus	104.26	8.66	6.55	46.07	12.98	18.65
Urocyon cinereoargenteus	100.77	8.85	6.69	39.79	9.93	18.26
Urocyon cinereoargenteus	102.06	8.98	6.87	60.68	11.54	17.26
Urocyon littoralis dickeyi	83.61	6.31	5.45	31.17	11.04	14.15
Urocyon littoralis santacruzae	71.99	6.52	5.31	26.73	8.54	14.04
Urocyon littoralis santacruzae	76.15	6.42	5.82	28.78	10.88	14.31
Urocyon littoralis santacruzae	71.71	6.63	5.45	29.78	11.04	13.72
Vulpes macrotis	94.72	6.87	5.54	31.81	10.26	14.34
Vulpes macrotis		6.05	5.75	31.92	9.78	14.35
Vulpes macrotis	94.99	6.88	5.72	33.34	9.1	15.02
Vulpes macrotis	82.5	6.03	4.75	37.15	9.86	13.54
Vulpes macrotis arsipus	88.98	5.93	5.01	31.87	10.06	13.85
Vulpes vulpes alascensis	129.67	10.34	8.08	52.8	15.05	21.79
Vulpes vulpes alascensis	122.16	10.38	7.54	47.32	14.28	20.88
Vulpes vulpes alascensis	131.59	12.28	8.57	49.92	14.97	23.12
Vulpes vulpes alascensis	124.13	8.92	7.29	41.12	13.39	20.4
Vulpes zerda	70.66	4.85	4.45	26.66	9.3	10.95
Vulpes zerda	70.73	4.89	4.27	23.93	8.62	11.56