# Chapter 7

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# Chapter 7

# Pack Hunting in Miocene Borophagine Dogs: Evidence from Craniodental Morphology and Body Size

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## ABSTRACT

Borophaginae is the largest of the three subfamilies of the dog family Canidae, with some 66 species, spanning approximately 34 m.y. (Orellan to Blancan). Not surprisingly, this extensive radiation of canids includes a diverse array of dietary types, ranging from hypocarnivorous to hypercarnivorous and durophagous. The last 16 m.y. of borophagine history is dominated by hypercarnivorous forms that were the dominant doglike predators within their faunas. Because of their relatively robust skeletons and their resemblance to extant hyenas in craniodental morphology, many or most of these hypercarnivorous species, particularly those of the late Miocene and Pliocene, have been assumed as primarily scavengers rather than hunters. The classification of most hypercarnivorous borophagines as scavengers relegates them to much less important roles in the ecology and evolution of their respective communities than does a classification as hunters. Unlike hunters, scavengers are unlikely to influence the evolution of the animals they eat, and are expected to exist at relatively low densities as do the only extant scavenging carnivorans, brown (*Parahyaena brunnea*) and striped hyenas (*Hyaena hyaena*). Given the substantial fossil record of the Borophaginae, it seems unlikely that all or most of the hypercarnivorous forms were primarily scavengers. Moreover, if some hunted, the larger species might be expected to have done so in groups, as large canids hunt in packs today.

Here we examine possible foraging modes within the Borophaginae using morphometrics and two new approaches to estimating the typical prey size of extinct carnivores. The craniodental morphology of the Borophaginae is compared with that of the living Caninae and Hyaeninae (hyaenids exclusive of *Proteles cristata*, the aardwolf) based on measurements that reflect relative tooth size, jaw muscle leverage, rigidity of the dentary, and grinding versus slicing function of the teeth. The Borophaginae are found to be intermediate in morphology between the Caninae and Hyaeninae. Unlike hyaenids and like canines, they retain substantial postcarnassial molars. However, like hyaenids, the borophagines had significantly stronger jaws and enhanced jaw muscle leverage compared to other canids. Prey size is estimated for borophagines based on correlation between dentary height and typical prey size in living canids. These results are compared with those produced using a recently published energetic model that predicts that all carnivores larger than about 21 kg feed on prey as large or larger than themselves. The methods provide similar predictions, resulting in a list of 11 borophagines (all subtribes Aelurodontina and Borophagina) that probably consumed large prey.

Comparisons with extant hyaenids reveal that the sole hunter of large prey, the spotted hyena (*Crocuta*), differs from the two mainly scavenging species, the brown and striped hyenas, in being significantly larger, more abundant, and widespread. Moreover, morphometric comparisons indicate that spotted hyenas have a more hypercarnivorous dentition. Given this, it is expected that the largest, most common borophagines with the most reduced dental grind-

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ing areas hunted most of their food. Based on their craniodental morphology and abundance in the record, *Epicyon saevus*, *E. haydeni*, *Borophagus secundus*, *Aelurodon ferox*, and *A. taxoides* were hunters. Although it is clear that *Aelurodon* and *Borophagus* were more capable of grasping prey than are extant canids, no borophagine evolved sharp, curved claws as in felids. Consequently, their ability to grapple with prey seems to have been limited, and packs were probably more successful at making a kill than individuals. Previous workers have argued against hunting in borophagines based on heavy dental wear, robust skeletal morphology, and external brain features. None of these precludes either hunting or hunting in packs in our view, and sharp teeth are not required for making a kill. While limb morphology and skeletal proportions of most or all borophagines do not appear adapted for the kind of hunts observed today in the African wild dog *Lycaon pictus*, long-distance, high-speed pursuits over shorter distances would have been possible for borophagines. The association between external brain morphology and social behavior in living carnivorans has not been fully explored, and seems a weak criterion for sociality in extinct species.

## INTRODUCTION

The history of the dog family Canidae has been greatly clarified and illuminated by the work of Richard Tedford and his colleagues, Beryl Taylor and Xiaoming Wang (e.g., Tedford, 1978; Tedford et al., 1997; Wang et al., 1999). We now recognize three successive (but overlapping) radiations over the family's approximately 40 m.y. history, each corresponding to a subfamily (Wang et al., 1999: fig. 143). The initial radiation, the Hesperocyoninae, consisted of small to medium-sized species with diets that varied from mesocarnivory to hypercarnivory. It was succeeded by the Borophaginae, an extensive array of North American species that included hypocarnivores, mesocarnivores, and hypercarnivores, several of which appear to have had hyena-like habits. The borophagines disappeared about 2 Ma, at a time when the current subfamily, the Caninae, was diversifying, primarily in the Old World (Hunt, 1988). Like the Borophaginae, the Caninae include hypo-, meso-, and hypercarnivores, but unlike them, canines have not shown a tendency towards bone cracking.

The Borophaginae was the largest of the three subfamilies of canids, including some 66 species and spanning approximately 34 m.y., all of which were confined to North America. They reached their peak diversity of 16 species in the early Barstovian (16–15 Ma). Relative to extant canids, this is a remarkable level of continental diversity; at present, the maximum number of canid species on any continent is found in South America, where there are 11 (Nowak, 1991). Over the course of their evolutionary history, borophagines tended to become larger and more hypercarnivorous, with the most derived species exhibiting extreme craniodental adaptations for durophagy (Wang et al., 1999). It seems likely that some of the larger, highly carnivorous species hunted in packs as big canids do today, but until recently, there was no way to predict which borophagines were the likely pack hunters. The identification of pack hunting canids in the fossil record could lead to further interesting explorations of predator–prey coevolution.

Van Valkenburgh and Koepfli (1993) argued that canids that regularly hunt prey larger than themselves are very likely to be social. Moreover, among living species, the hunters of large prey can be recognized by a suite of adaptations including deep jaws, broad muzzles, and enlarged incisor and canine teeth, all of which reflect the heavy loads placed on their skulls and teeth by large prey (Van Valkenburgh and Koepfli, 1993). Unlike felids, which retain strong, flexible forelimbs capable of grasping prey, extant canids must capture, hold, and kill with jaws only. Pack hunting canids can work together to down large ungulates, with some individuals holding prey by the throat or muzzle while others wound the prey. Thus, if it can be determined that an extinct canid or canidlike species did not have flexible forelimbs and took prey larger than itself, then it can be assumed that it probably did so in groups.

In this paper, we first make overall comparisons of the craniodental morphology of borophagines, canines, and hyaenids using principal component analysis. We then use two approaches to predicting the probable prey size of extinct borophagines. In the first, we estimate prey size based on the correlation between maximum jaw depth and typical prey size in living canids. In the second, we use a recently established relationship between body mass and diet in carnivorans (Carbone et al., 1999) to predict which borophagines regularly would have taken prey larger than themselves. Carbone et al. (1999) showed that among living carnivores, almost all species larger than about 21 kg take prey as large or larger than themselves, whereas smaller species feed mostly on prey that is 45% or less of their body weight. The exceptions to this pattern were mostly bears, which are mainly omnivorous. Using an energetic model, they argued that it becomes increasingly difficult to subsist on small prey items as predator body mass increases due to limitations on intake rate and foraging time. If their model is correct, then it should be possible to identify hunters of large prey in the fossil record by estimating predator body mass. For the borophagines, we estimated body mass based on previously published regressions of body mass against skull or tooth length in living canids (Van Valkenburgh, 1990).

One complication that was not dealt with in either Van Valkenburgh and Koepfli (1993) or Carbone et al. (1999) is the problem of distinguishing hunters from scavengers. Strong jaws and teeth might be required for both activities, and the foraging energetics might be similar as well. This is especially relevant to the study of borophagines, as they are well known for their similarity to hyenas in craniodental morphology (Werdelin, 1989; Munthe, 1998). Scavenging behavior is not associated with group foraging in living carnivorans. There are no canid species that scavenge frequently at present, but there are two hyena species that do so, the brown hyena (*Parahyaena brunnea*) and the striped hyena (*Hyaena hyaena*) and they usually forage alone. Brown hyenas have diets that include fruits as well as small vertebrates that they kill, but most of their prey is scavenged (90–95%; Mills, 1990). The striped hyena is also omnivorous, scavenging most of its food, but catching insects and small vertebrates (Kruuk, 1976; Macdonald, 1988). Spotted hyenas (*Crocuta crocuta*) are the largest and most carnivorous species of the family, often hunting in groups for prey much larger than themselves (Kruuk, 1972). In an attempt to more confidently infer pack hunting in borophagines, we examine craniodental features associated with hunting as opposed to scavenging within extant Hyaenidae (exclusive of *Proteles cristata*, the aardwolf, a termite specialist). The observed differences are used to interpret foraging behavior (scavenging vs. hunting) within the group of borophagines predicted to have subsisted on large prey.

### INSTITUTIONAL ABBREVIATIONS:

| | |
|---|---|
| AMNH | American Museum of Natural History, New York |
| F:AM | Frick Collection, Division of Paleontology, AMNH |
| UNSM | Nebraska State Museum, University of Nebraska, Lincoln |
| USNM | United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. |

## MATERIALS AND METHODS

SAMPLE: Twenty-six of 66 recognized species in subfamily Borophaginae (Carnivora: Canidae), 27 of 33 extant species in subfamily Caninae (Carnivora: Canidae), and the 3 extant species in subfamily Hyaeninae (Carnivora: Hyaenidae) are included in the sample. The borophagine sample (see appendix) includes representatives of the two major tribes, Phlaocyonini and Borophagini, as well as the subtribes within the latter, and covers the full range of adaptive types seen in the subfamily (table 7.1). Borophagine specimens used in this study are listed in the appendix. The number of specimens measured for each borophagine species varies (table 7.1); skulls and mandibles often are not complete and it is necessary to compute species average values for some measurements. Data for the extant Caninae sample were taken from Van Valkenburgh and Koepfli (1993) and are usually based on four females and four males of each species. For each of the three hyena species, two females and two males are measured (appendix).

TABLE 7.1

**Borophagine and Hyaenid Species Included in the Analysis**

Listed are samples size (*N*) and mean value for morphometric ratios for each species. Ratio abbreviations are defined in table 7.2 and specimens measured are listed in appendix I.

| Taxon | *N* | RBL | RLGA | RUGA | M1BS | M2S | IXP4 | IXM2 | MAT | MAM | I2 | I3 | C1 | C1C1 | P4P | UM2/1 | DIA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BOROPHAGINAE | | | | | | | | | | | | | | | | | |
| *Archaeocyon pavidus* | 1 | 0.627 | 0.939 | 1.205 | 0.096 | 0.068 | 0.057 | 0.066 | 0.316 | 0.210 | 0.017 | 0.021 | 0.038 | 0.138 | 0.606 | 0.702 | 0.793 |
| *Rhizocyon oregonensis* | 1 | 0.624 | 0.943 | 1.087 | 0.099 | 0.070 | 0.055 | 0.063 | 0.285 | 0.205 | 0.018 | 0.023 | 0.039 | 0.179 | 0.575 | 0.616 | 0.789 |
| *Cormocyon haydeni* | 1 | 0.691 | 0.996 | 1.121 | 0.100 | 0.078 | 0.072 | 0.076 | 0.338 | 0.192 | 0.025 | 0.033 | 0.053 | 0.233 | 0.804 | 0.649 | 0.864 |
| *Cormocyon copei* | 1 | 0.685 | 0.867 | 1.154 | 0.111 | 0.076 | 0.052 | 0.059 | 0.306 | 0.146 | 0.021 | 0.026 | 0.039 | 0.168 | 0.590 | 0.716 | 0.831 |
| *Phlaocyon leucosteus* | 1 | 0.617 | 0.995 | 1.249 | 0.095 | 0.070 | 0.054 | 0.061 | 0.333 | 0.173 | 0.019 | 0.022 | 0.039 | 0.178 | 0.622 | 0.710 | 0.779 |
| *Desmocyon thomsoni* | 2 | 0.667 | 0.928 | 1.125 | 0.098 | 0.071 | 0.064 | 0.069 | 0.302 | 0.193 | 0.021 | 0.030 | 0.046 | 0.179 | 0.631 | 0.649 | 0.859 |
| *Desmocyon matthewi* | 1 | 0.637 | 0.894 | 1.106 | 0.111 | 0.074 | 0.071 | 0.072 | 0.275 | 0.215 | 0.026 | 0.032 | 0.049 | 0.221 | 0.606 | 0.650 | 0.876 |
| *Microtomarctus conferta* | 1 | 0.689 | 0.865 | 1.132 | 0.100 | 0.069 | 0.057 | 0.063 | 0.255 | 0.196 | 0.023 | 0.032 | 0.043 | 0.177 | 0.594 | 0.732 | 0.749 |
| *Tephrocyon optatus* | 1 | 0.688 | 0.812 | 1.088 | 0.111 | 0.071 | 0.072 | 0.075 | 0.314 | 0.184 | 0.032 | 0.036 | 0.048 | 0.191 | 0.541 | 0.715 | 0.953 |
| *Cynarctus galushai* | 1 | 0.660 | 0.889 | 1.050 | 0.115 | 0.077 | 0.056 | 0.063 | 0.260 | 0.160 | 0.020 | 0.027 | 0.035 | 0.165 | 0.515 | 0.664 | 0.833 |
| *Psalidocyon marianae* | 1 | 0.667 | 0.901 | 1.016 | 0.103 | 0.072 | 0.065 | 0.067 | 0.297 | 0.188 | 0.022 | 0.027 | 0.045 | 0.195 | 0.524 | 0.625 | 0.858 |
| *Tomarctus hippophaga* | 1 | 0.675 | 0.851 | 1.018 | 0.107 | 0.070 | 0.060 | 0.066 | 0.261 | 0.188 | 0.028 | 0.031 | 0.049 | 0.200 | 0.610 | 0.615 | 0.933 |
| *Tomarctus brevirostris* | 2 | 0.660 | 0.836 | 1.021 | 0.118 | 0.073 | 0.060 | 0.069 | 0.295 | 0.207 | 0.028 | 0.037 | 0.046 | 0.226 | 0.561 | 0.642 | 0.880 |
| *Aelurodon asthenostylus* | 4 | 0.709 | 0.690 | 0.835 | 0.120 | 0.062 | 0.071 | 0.074 | 0.292 | 0.199 | 0.031 | 0.041 | 0.054 | 0.256 | 0.580 | 0.560 | 0.929 |
| *Aelurodon mcgrewi* | 1 | 0.746 | 0.590 | 0.762 | 0.128 | 0.056 | 0.077 | 0.084 | 0.307 | 0.211 | 0.029 | 0.042 | 0.056 | 0.233 | 0.485 | 0.513 | 0.927 |
| *Aelurodon stirtoni* | 2 | 0.750 | 0.562 | 0.724 | 0.139 | 0.057 | 0.076 | 0.076 | 0.277 | 0.214 | 0.032 | 0.046 | 0.057 | 0.244 | 0.535 | 0.461 | 0.953 |
| *Aelurodon ferox* | 4 | 0.752 | 0.610 | 0.846 | 0.126 | 0.058 | 0.075 | 0.081 | 0.298 | 0.201 | 0.030 | 0.040 | 0.055 | 0.251 | 0.535 | 0.582 | 0.874 |
| *Paratomarctus temerarius* | 3 | 0.750 | 0.610 | 0.790 | 0.119 | 0.057 | 0.070 | 0.078 | 0.291 | 0.216 | 0.030 | 0.043 | 0.054 | 0.268 | 0.577 | 0.574 | 0.941 |
| *Carpocyon compressus* | 1 | 0.672 | 0.831 | 1.038 | 0.121 | 0.075 | 0.069 | 0.076 | 0.304 | 0.220 | 0.025 | 0.031 | 0.046 | 0.211 | 0.542 | 0.649 | 0.819 |
| *Carpocyon webbi* | 2 | 0.762 | 0.693 | 0.881 | 0.107 | 0.058 | 0.077 | 0.082 | 0.333 | 0.211 | 0.032 | 0.043 | 0.051 | 0.247 | 0.529 | 0.641 | 0.842 |
| *Protepicyon raki* | 1 | 0.667 | 0.846 | 1.014 | 0.111 | 0.071 | 0.062 | 0.073 | 0.316 | 0.194 | 0.024 | 0.031 | 0.047 | 0.198 | 0.588 | 0.634 | 0.833 |
| *Aelurodon taxoides* | 2 | 0.741 | 0.741 | 1.014 | 0.117 | 0.069 | 0.064 | 0.072 | 0.293 | 0.204 | 0.023 | 0.032 | 0.048 | 0.200 | 0.537 | 0.674 | 0.836 |
| *Paratomarctus euthos* | 1 | 0.733 | 0.682 | 0.840 | 0.133 | 0.070 | 0.069 | 0.079 | 0.326 | 0.206 | 0.029 | 0.035 | 0.047 | 0.222 | 0.492 | 0.549 | 0.926 |
| *Epicyon saevus* | 4 | 0.740 | 0.676 | 0.901 | 0.128 | 0.067 | 0.070 | 0.079 | 0.280 | 0.193 | 0.023 | 0.028 | 0.053 | 0.208 | 0.534 | 0.587 | 0.886 |
| *Epicyon haydeni* | 1 | 0.727 | 0.592 | 0.787 | 0.136 | 0.057 | 0.078 | 0.081 | 0.271 | 0.225 | 0.028 | 0.042 | 0.053 | 0.234 | 0.501 | 0.590 | 0.840 |
| *Borophagus secundus* | 4 | 0.743 | 0.662 | 0.850 | 0.143 | 0.072 | 0.086 | 0.080 | 0.324 | 0.219 | 0.028 | 0.047 | 0.061 | 0.263 | 0.498 | 0.604 | 0.993 |
| HYAENINAE | | | | | | | | | | | | | | | | | |
| *Hyaena hyaena* | 4 | 0.766 | 0.389 | 0.316 | 0.099 | 0.000 | 0.077 | 0.081 | 0.271 | 0.165 | 0.027 | 0.040 | 0.055 | 0.227 | 0.609 | — | 0.892 |
| *Parahyaena bruunea* | 4 | 0.793 | 0.346 | 0.243 | 0.110 | 0.000 | 0.082 | 0.086 | 0.296 | 0.183 | 0.028 | 0.044 | 0.059 | 0.242 | 0.607 | — | 0.920 |
| *Crocuta crocuta* | 4 | 0.878 | 0.194 | 0.000 | 0.142 | 0.000 | 0.074 | 0.090 | 0.324 | 0.172 | 0.032 | 0.047 | 0.057 | 0.249 | 0.566 | — | 0.894 |

DATA AND DATA ANALYSIS: The morphometric analyses were based on 29 linear measurements of the cranium, mandibles, and teeth. These measurements were used by themselves or to produce a set of ratios that reflect three aspects of craniodental function: relative tooth size or shape, jaw muscle leverage, and relative rigidity of the dentary (table 7.2). Craniodental linear measurements were taken on the borophagines (by XW) and the hyaenids (by BVV) following the methods used in Van Valkenburgh and Koepfli (1993); the measurements are described in table 7.2 in the ratio definitions. In addition to the morphometric data, typical prey sizes and body mass for the extant canids were taken from the literature (sources are listed in Van Valkenburgh and Koepfli, 1993).

OVERALL MORPHOLOGY: The craniodental morphology of the borophagines was compared with that of extant canines and hyaenids using principal component analysis and analysis of variance (ANOVA) in Statview (version 4.51). The principal component analysis was performed on the ratio data as well as on residuals from regressions of each variable on skull length. Because the results were similar for both, we present the results for the ratio data set alone.

PREDICTION OF PREY SIZE: Least squares regression was used to model the relationship between typical prey size and body mass, as well as typical prey size and maximum jaw depth in extant Caninae. The regression equation for jaw depth was then used to predict typical prey size for all sampled borophagines. These results were then compared with those produced by utilizing body mass and the Carbone et al. (1999) model. Body mass of borophagines was estimated from condylobasal skull length and m1 length, separately, using equations published in Van Valkenburgh (1990) for extant Caninae. The mean of the two body mass estimates for each borophagine species was used to estimate prey size according to the energetic model of Carbone et al. (1999). That is, all those borophagine species estimated to have been at least 21.5 kg are predicted to have taken prey as large or larger than themselves.

HUNTING VERSUS SCAVENGING: To highlight the possible differences between hunters and scavengers, the three hyena species were compared using ANOVA and Bonferroni–Dunn post hoc significance tests. Significant differences in craniodental ratio values between the spotted hyena (a habitual hunter) and the other two species that scavenge more than hunt were assumed to reflect feeding behavior.

## RESULTS

OVERALL MORPHOLOGY: The three clades, Borophaginae, Caninae, and Hyaeninae, occupy separate areas within a plot of the first two principal components (fig. 7.1). However all three overlap to varying degrees on the first axis (66% of the total variance). The hyaenids exhibit low, negative values on the first axis along with several of the borophagines. The remainder of the borophagines overlap with canines on this axis. The most important variables on the first component are those that describe relative jaw rigidity (IXP4, IXM2), relative incisor and canine tooth size (I3, C1), and crowding of the teeth (DIA; table 7.3). The extant canids tend to have relatively weaker jaws and smaller teeth than those of hyaenids and some Borophaginae. The second axis accounts for another 14% of the variance and separates the hyaenids from the borophagines and most of the Caninae. The most significant variables on this axis were relative grinding area (RLGA, RUGA) and moment arm of the masseter (MAM). Hyaenids have very reduced postcarnassial molars relative to the other two subfamilies, and the Borophaginae tend to have relatively large jaw angles.

Analysis of variance of the ratio values by subfamily reveals that the Borophaginae are almost always intermediate in morphology between the Caninae and Hyaenidae (table 7.4). For example, all three subfamilies differ significantly in the size of the trigonid relative to the talonid (RBL), with hyaenids displaying the largest trigonid and canids the smallest. The Borophaginae are most similar to the hyaenids in having good temporalis muscle leverage (MAT), large lower carnassial blades (M1BS), and crowded cheek teeth (DIA). They differ little from extant canines in relative grinding area (RUGA, RLGA).

PREDICTION OF PREY SIZE FROM JAW DEPTH:

TABLE 7.2

**Variables (Ratios) Used in the Analysis and Their Definitions**

All measurements made with digital calipers to the nearest 0.01 mm. For illustrations of some of the measures, see Van Valkenburgh and Koepfli (1993).

| Abbreviations and Definitions | |
|---|---|
| RBL | Relative blade length of the lower first molar (carnassial) measured as the ratio of trigonid length to total anteroposterior length of the m1. |
| RLGA | Relative lower molar grinding area measured as the square root of the summed areas of the m1 talonid and m2 divided by the length of the m1 trigonid. Tooth area was estimated as the product of maximum breadth and maximum length of the talonid and m2, respectively. |
| RUGA | Relative upper molar grinding area measured as the square root of the summed areas of the M1 and M2 divided by the maximum anteroposterior length of the P4 (carnassial). Tooth area was estimated as the product of maximum breadth and maximum length of the M1 and M2, respectively. |
| M1BS | Size of the cutting blade (trigonid) of the m1 relative to dentary length, estimated by dividing the maximum anteroposterior length of the trigonid by dentary length. Dentary length was measured as the distance between the posterior margin of the mandibular condyle and the anterior margin of the canine tooth. |
| M2S | Relative size of the m2 estimated by the square root of m2 area divided by dentary length. Tooth area was measured as in RLGA and dentary length as in M1BS. |
| IXP4 | Relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area of the dentary relative to dentary length at the interdental gap between the third and fourth premolars. The second moment of area was calculated using the formula $I_x = (\pi * D_x * D_y^3/64$ where $D_x$ is maximum dentary width and $D_y$ is maximum dentary height at the p3-p4 interdental gap. $I_x$ relative to dentary length was then estimated as the fourth root of $I_x$ divided by dentary length. Dentary length was measured as in M1BS. |
| IXM2 | Relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area of the dentary relative to dentary length at the interdental gap between the m1 and m2. Estimated as in IXP4 except that maximum breadth and height were taken at the m1-m2 interdental gap. |
| MAT | Mechanical advantage of the temporalis measured as the distance from the approximate midpoint of the mandibular condyle to the apex of the coronoid process of the ascending ramus divided by dentary length (measured as in M1BS) |
| MAM | Mechanical advantage of the masseter, measured as the distance from the approximate midpoint of the mandibular condyle to the ventral border of the mandibular angle, divided by dentary length (measured as in M1BS). |
| I2 | Relative size of the upper second incisor estimated by the square root of the basal area of I2 divided by skull (condylobasal) length. I2 area was calculated as the product of maximum anteroposterior length and mediolateral breadth measured at the alveolar margin. |
| I3 | Relative size of the upper third incisor estimated by the square root of the basal area of I3 divided by skull (condylobasal) length. I3 area was calculated as the product of maximum anteroposterior length and mediolateral breadth measured at the alveolar margin. |
| C1 | Relative size of the upper canine estimated by the square root of the basal area of C1 divided by skull (condylobasal) length. C1 area was calculated as the product of maximum anteroposterior length and mediolateral breadth measured at the alveolar margin. |
| C1C1 | Relative rostral breadth measured as the maximum mediolateral breadth between lateral margins of the upper canines, divided by skull (condylobasal) length. |
| P4P | Relative size of the protocone of the P4 (carnassial) estimated by maximum mediolateral breadth of the P4 across the protocone, divided by maximum anteroposterior length of the P4. |
| UM2/1 | Square root of M2 area divided by the square root of M1 area. Areas estimated as in RUGA. |
| DIA | Relative spacing of the upper premolars estimated by the ratio of the sum of the anteroposterior lengths of C1, P2-4 divided by the distance between the posterior margin of P4 and the anterior margin of C1. |

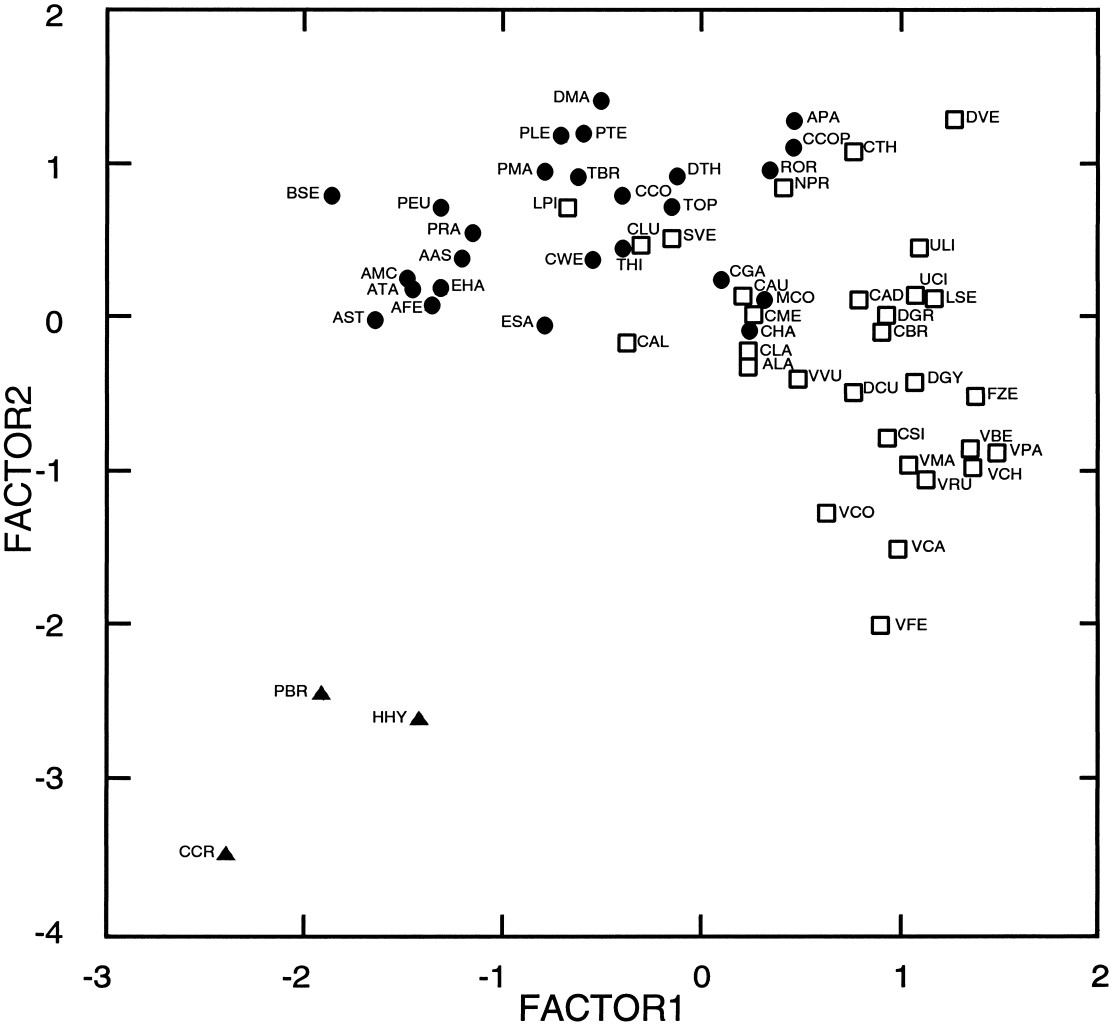

Fig. 7.1. Plot of the first two principal components from a PCA performed on the ratio data set for the Borophaginae (circles), Caninae (squares), and Hyaenidae (triangles). The axes were not transformed. Variable loadings are listed in table 7.3. Species codes as follows: **Borophaginae:** *Aelurodon asthenostylus,* AAS; *A. ferox,* AFE; *A. mcgrewi* AMC; *A. stirtoni,* AST; *A. taxoides,* ATA; *Archaeocyon pavidus,* APA; *Borophagus secundus,* BSE; *Carpocyon compressus,* CCO; *C. webbi,* CWE; *Cormocyon copei,* CCOP; *C. haydeni,* CHA; *Cynarctus galushai,* CGA; *Desmocyon matthewi,* DMA; *D. thomsoni,* DTH; *Epicyon haydeni,* EHA; *E. saevus,* ESA; *Microtomarctus conferta,* MCO; *Paratomartcus euthos,* PEU; *P. themerarius,* PTH; *Phlaocyon leucosteus,* PLE; *Protepicyon raki,* PRA; *Psalidocyon marianae,* PMA; *Rhizocyon oregonensis,* ROR; *Tephrocyon optatus,* TOP; *Tomarctus brevisrostris,* TBR; *T. hippophaga,* THI. **Caninae:** *Alopex lagopus,* ALA; *Canis adustus,* CAD; *C. aureus,* CAU; *C. latrans,* CLA; *C. lupus,* CLU; *C. mesomelas,* CME; *C. simensis,* CSI; *Cuon alpinus,* CAL; *Disucyon culpaeus,* DCU; *D. griseus,* DGR; *Lycaon pictus,* LPI; *Vulpes chama,* VCH; *V. corsac,* VCO; *V. macrotis,* VMA; *V. vulpes,* VVU. **Hyaeninae:** *Crocuta crocuta,* CCR; *Hyaena hyaena,* HHY; *Parahyaena brunnea,* PBR.

As might be expected, maximum prey size tends to increase with predator size in the extant Caninae ($r^2 = 0.643$, $p < 0.01$; fig. 7.2A; table 7.5). Almost the same relationship can be found based on maximum jaw depth ($r^2 = 0.667$, $p < 0.01$; fig. 7.2B; table 7.5). The slope of the log/log regression of prey size on jaw depth is positively allome-

TABLE 7.3

**Factor Scores on the First Two Unrotated Principal Components of a PCA Analysis on the Ratio Data set for Borophagines, Canines, and Hyaenids**

See figure 7.1 for a plot of the first two components.

| Ratio | PCA 1 | PCA 2 |
|---|---|---|
| RBL | 0.762 | −0.502 |
| RLGA | −0.679 | 0.666 |
| RUGA | −0.665 | 0.673 |
| M1BS | 0.827 | −0.034 |
| IXP4 | 0.955 | 0.157 |
| IXM2 | 0.959 | 0.143 |
| MAT | 0.757 | 0.366 |
| MAM | 0.656 | 0.608 |
| I2 | 0.847 | 0.119 |
| I3 | 0.939 | 20.001 |
| C1 | 0.949 | 0.080 |
| C1C1 | 0.923 | 0.100 |
| P4P | 0.360 | 20.34 |
| DIA | 0.901 | 0.223 |

tric (>3), with prey size (in kilograms) increasing much more rapidly than jaw depth (in millimeters). The scatter is greater among canids that take smaller prey (<10 kg), with some species falling below the regression line and thus taking relatively small prey given their jaw depth. However, the three species that regularly take prey larger than themselves (wolf, dhole, wild dog) all fall above the line and thus have slightly shallow mandibles given their prey sizes (C, K, F in fig. 7.2B). Moreover, these are the only species shown in the figure that regularly hunt in packs.

For extinct species, jaw depth is preferred over estimated body mass as a predictor of prey size because jaw depth can be measured directly. Based on the regression of canid jaw depth against typical prey size, 11 of the 26 borophagines are predicted to have consumed prey larger than themselves (table 7.6). Interestingly, the borophagines predicted to hunt or scavenge prey larger than themselves are confined to the subtribes Aelurodontina and Borophagina. None of the primitive borophagines or Cynarctini appears to have taken large prey. However, not all members of the Aelurodontina and Borophagina are predicted to have relied on prey larger than themselves.

PREDICTION OF PREY SIZE USING THE MODEL OF CARBONE ET AL.: Within the Carnivora, Carbone et al. (1999) found a shift from feeding primarily on small prey (defined by

TABLE 7.4

**Mean Values of the Ratios for the Sampled Borophagines, Canines, and Hyaenids**

Ratios are defined in table 7.2. Superscripts indicate that the species mean is significantly different from that of the listed species at the 0.05 level or better (ANOVA on ratio data). Superscripts are defined as follows: B = Borophaginae, C = Caninae, H = hyaenids. Ratios M2S and UM2/1 could not be computed for hyaenids because they lack M2.

| Ratio | Borophaginae | Caninae | Hyaenidae |
|---|---|---|---|
| RBL | $0.695^{C, H}$ | $0.641^{B, H}$ | $0.812^{B, C}$ |
| RLGA | $0.788^{H}$ | $0.839^{H}$ | $0.309^{B, C}$ |
| RUGA | $0.987^{H}$ | $1.0^{H}$ | $0.186^{B, C}$ |
| M1BS | $0.115^{C}$ | $0.092^{B, H}$ | $0.117^{C}$ |
| M2S | $0.068^{C}$ | 0.058 B | |
| IXP4 | $0.067^{C, H}$ | $0.047^{B, H}$ | $0.077^{B, C}$ |
| IXM2 | $0.073^{C, H}$ | $0.054^{B, H}$ | $0.086^{B, C}$ |
| MAT | $0.298^{C}$ | $0.234^{B, H}$ | $0.297^{C}$ |
| MAM | $0.199^{C}$ | $0.171^{B}$ | 0.173 |
| I2 | $0.025^{C}$ | $0.021^{B H}$ | $0.029^{C}$ |
| I3 | $0.034^{C, H}$ | $0.025^{B, H}$ | $0.044^{B, C}$ |
| C1 | $0.048^{C, H}$ | $0.035^{B, H}$ | $0.057^{B, C}$ |
| C1C1 | $0.211^{C}$ | $0.171^{B, H}$ | $0.239^{C}$ |
| P4P | $0.566^{C}$ | $0.516^{B, H}$ | $0.594^{C}$ |
| UM2/1 | $0.627^{C}$ | $0.674^{B}$ | |
| DIA | $0.869^{C}$ | $0.717^{B, H}$ | $0.902^{C}$ |

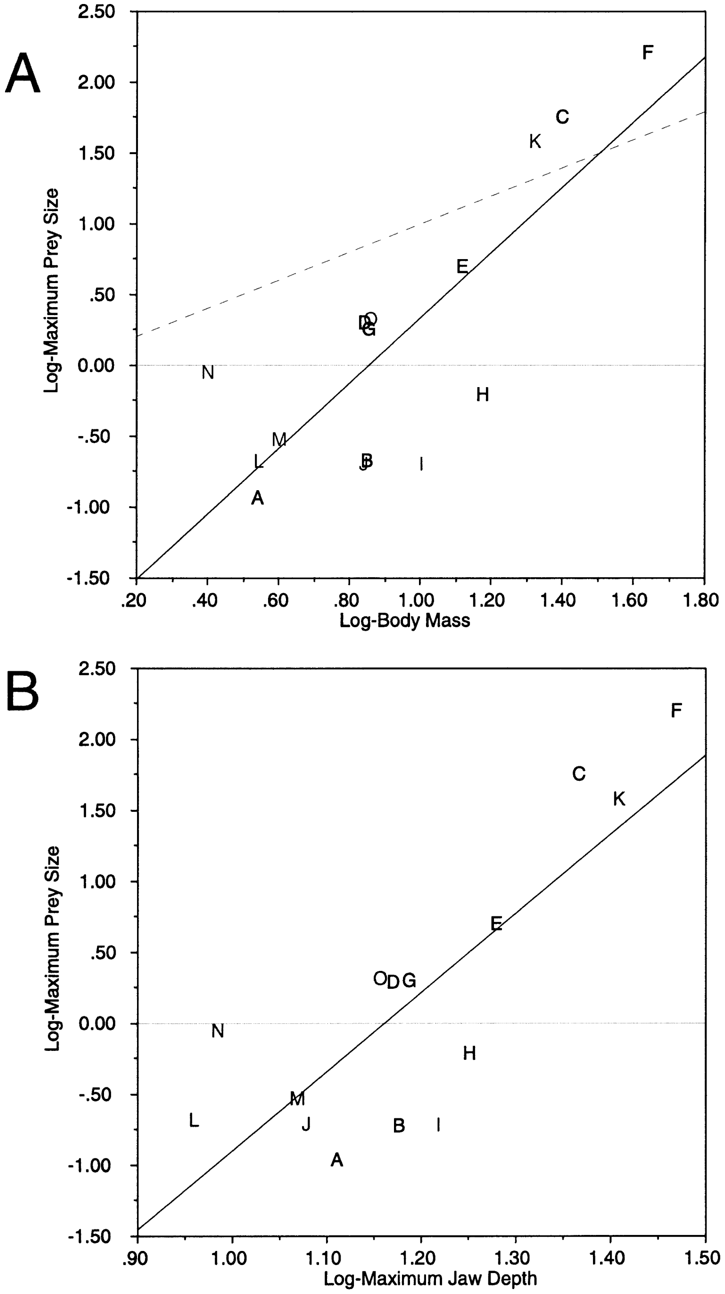

Fig. 7.2. **A,** $\mathrm{Log}_{10}/\mathrm{log}_{10}$ plot of typical prey mass in kilograms against body mass in kilograms for 15 species of canids. Solid line represents results of least squares regression. Regression equation as follows: $y = 2.306x - 1.972$, $r^2 = 0.643$. **B,** $\mathrm{Log}_{10}/\mathrm{log}_{10}$ plot of typical prey weight against jaw depth (measured in millimeters at the m1/m2 interdental gap) for 15 species of canids. Solid line represents results of least squares regression. Regression equation as follows: $y = 5.583x - 6.482$, $r^2 = 0.667$. Species: A, *Alopex lagopus*; B, *Canis adustus*; C, *Cuon alpinus*; D, *C. aureus*; E, *C. latrans*; F, *C. lupus*; G, *C. mesomelas*; H, *C. simensis*; I, *Dusicyon culpaeus*; J, *D. griseus*; K, *Lycaon pictus*; L, *Vulpes chama*; M, *V. corsac*; N, *V. macrotis*; O, *V. vulpes*.

TABLE 7.5

**Maximum Jaw Depths (at the interdental gap between m1 and m2), Mean Body Mass, and Typical Prey Sizes of Extant Canids**

Estimates of typical prey size are shown for a solitary individual in all cases except those denoted by an asterisk; the latter are typical prey size estimates for canids hunting in groups of two or more (data unavailable for solitary hunters). Jaw depth data are from Van Valkenburgh and Koepfli (1993; see references therein for data on typical prey size and body mass).

| Species | Max. jaw depth (mm) | Body mass (kg) | Typical prey size (kg) |
|---|---|---|---|
| *Alopex lagopus* | 13.00 | 3.5 | 0.11 |
| *Canis adustus* | 14.99 | 7 | 0.20 |
| *Cuon alpinus* | 23.25 | 25 | 58.00* |
| *Canis aureus* | 14.81 | 7 | 2.00 |
| *Canis latrans* | 18.98 | 13 | 5.00 |
| *Canis lupus* | 29.45 | 43 | 162.00* |
| *Canis mesomelas* | 15.26 | 7 | 2.00 |
| *Canis simensis* | 17.85 | 15 | 0.60 |
| *Dusicyon culpaeus* | 16.56 | 10 | 0.20 |
| *Dusicyon griseus* | 11.98 | 7 | 0.20 |
| *Lycaon pictus* | 25.52 | 21 | 38.00* |
| *Vulpes chama* | 9.09 | 3.5 | <0.20 |
| *Vulpes corsac* | 11.73 | 4 | 0.30 |
| *Vulpes macrotis* | 9.61 | 2.5 | 0.90 |
| *Vulpes vulpes* | 14.44 | 7 | 2.00 |

them as less than half of predator mass) to exclusively on large prey (near predator mass) at predator body masses of 21.5 to 25 kg. Furthermore, their model of energetic requirements and invertebrate intake rates predicts a maximum sustainable mass of 21.5 kg for a predator feeding on small prey (Carbone et al., 1999). The estimated body masses of the 26 species of Borophaginae sampled here range from 2 kg for the earliest species, *Archaeocyon pavidus*, to 75 kg for one of the youngest species, *Epicyon haydeni* (table 7.6). Based on these estimates and the Carbone et al. (1999) model, nine species are likely to have taken large prey (in bold, table 7.6). These same species are predicted to have taken large prey using the alternative predictor, jaw depth, but two additional species are added, *Aelurodon stirtoni* (body mass = 20 kg), and *Paratomarctus euthos* (body mass = 12 kg).

HUNTERS VERSUS SCAVENGERS: Analysis of variance indicates that there are significant differences among the three hyaenids in 11 of the 14 ratios calculated (table 7.7). The highly predatory spotted hyena was significantly different from both of its more omnivorous and scavenging relatives in six ratios, I2, RBL, M1BS, RLGA, RUGA, and MAT. Spotted hyenas have larger upper second incisors, greater jaw muscle leverage, longer carnassial cutting blades, and reduced dental grinding areas relative to either brown or striped hyenas. Interestingly, a similar suite of characteristics has been shown to differentiate highly carnivorous from more omnivorous canids (Van Valkenburgh and Koepfli, 1993). The less predatory brown and striped hyenas differed from one another in seven ratios: I3, RUGA, M1BS, IXP4, C1C1, DIA, and MAT (table 7.7). Compared with the brown hyena, the striped hyena appeared less carnivorous with smaller upper lateral incisors, larger upper dental grinding surfaces, smaller cutting blades, reduced mandibular rigidity, narrower snout, and decreased jaw muscle leverage.

## DISCUSSION

The Borophaginae were intermediate in morphology between extant canids and hyaenids. Like the extant subfamily Caninae, the borophagines included hypo-, meso-, and hypercarnivorous species (Wang et al., 1999), but borophagines tend to exhibit

TABLE 7.6

**Estimates of Body Size of Borophagines and Their Typical Prey (rounded to the nearest kilogram) and First Appearance Datum (FAD, from Wang et al., 1999) for Each Species**

Species in bold are predicted to take relatively large prey based on jaw depth.

| Species | Body size (kg) | Typical prey size (kg) | FAD (ma) |
|---|---|---|---|
| *Archaeocyon pavidus* | 2 | <1 | 32 |
| *Rhizocyon oregonensis* | 3 | <1 | 30 |
| *Cormocyon haydeni* | 4 | <1 | 29 |
| *Cormocyon copei* | 5 | <1 | 30 |
| *Phlaocyon leucosteus* | 3 | <1 | 22 |
| *Desmocyon thomsoni* | 7 | 2 | 24 |
| *Desmocyon matthewi* | 8 | 2 | 19 |
| *Microtomarctus conferta* | 7 | 1 | 17 |
| *Tephrocyon optatus* | 13 | 6 | 16 |
| *Cynarctus galushai* | 12 | 4 | 15 |
| *Psalidocyon marianae* | 9 | 5 | 16 |
| *Tomarctus hippophaga* | 14 | 9 | 16 |
| *Tomarctus brevirostris* | 18 | 14 | 16 |
| ***Aelurodon asthenostylus*** | 23 | 53 | 16 |
| ***Aelurodon mcgrewi*** | 29 | 127 | 15 |
| ***Aelurodon stirtoni*** | 20 | 40 | 13 |
| ***Aelurodon ferox*** | 31 | 153 | 15 |
| *Paratomarctus themerarius* | 11 | 6 | 16 |
| *Carpocyon compressus* | 16 | 15 | 16 |
| ***Carpocyon webbi*** | 26 | 57 | 16 |
| ***Protepicyon raki*** | 23 | 42 | 16 |
| ***Aelurodon taxoides*** | 41 | 284 | 12 |
| ***Paratomarctus euthos*** | 12 | 22 | 13 |
| ***Epicyon saevus*** | 28 | 97 | 12 |
| ***Epicyon haydeni*** | 75 | 1148 | 10 |
| ***Borophagus secundus*** | 23 | 67 | 9 |

deeper jaws, larger teeth, and smaller dental grinding areas than their putative ecological equivalents among canids. In these features, they resemble hyenas. However, although a few species equal extant bone-cracking hyenas in features such as jaw muscle leverage and relative carnassial blade size, they differ markedly from hyenas in retaining postcarnassial molars and not enlarging their anterior premolars (Werdelin, 1989). Unlike hyenas, they must have used their rearmost lower premolar (p4) and upper carnassial (P4) to crack large bones (ibid.). Smaller bones and bone fragments were likely crushed with the carnassials and postcarnassial molars just as in extant canids (Van Valkenburgh, 1996). Because gape diminishes as the jaw joint is approached, the more rearward position of the bone cracking teeth results in limitations on the size of bones that can be broken easily and consumed. Moreover, as Werdelin (1989) pointed out, the proximity of the bone-cracking teeth to the cutting blades of the carnassials results in heavy apical wear on the cutting teeth, compromising their slicing function.

We identified 9 of the 26 borophagine species in our sample as probable consumers of prey larger than themselves based on estimated body mass and the energetic model of Carbone et al. (1999). According to this model, all carnivorous species estimated to have a body mass of at least 21.5 kg are assumed to take large prey because of energetic constraints on foraging time and efficiency. The jaw depth approach identified two additional species, *Aelurodon stirtoni* (body mass = 20 kg, prey size = 40 kg), and *Paratomarctus euthos* (body mass = 12 kg, prey size = 22 kg) as probable consumers of large prey. Given that our body mass figures are estimates, it would not be surprising to find

TABLE 7.7

**Mean Values of Ratios for the Three Hyaenid Species**

Ratios are defined in table 7.2. Superscripts indicate that the species mean is significantly different from that of the listed species at the 0.05 level or better (ANOVA on $\log_{10}$-transformed data). Superscripts are defined as follows: C = *Crocuta crocuta,* H = *Hyaena, hyaena,* P = *Parahyaena brunnea.* Ratios M2S and UM2/1 could not be computed because hyaenids lack M2.

| Ratio | *Crocuta crocuta* | *Hyaena hyaena* | *Parahyaena brunnea* |
|---|---|---|---|
| RBL | 0.879$^{\mathrm{H,P}}$ | 0.766$^{\mathrm{C}}$ | 0.793$^{\mathrm{C}}$ |
| RLGA | 0.192$^{\mathrm{H,P}}$ | 0.39$^{\mathrm{C}}$ | 0.347$^{\mathrm{C}}$ |
| RUGA | 0.00$^{\mathrm{H,P}}$ | 0.316$^{\mathrm{C,P}}$ | 0.243$^{\mathrm{C,H}}$ |
| M1BS | 0.142$^{\mathrm{H,P}}$ | 0.099$^{\mathrm{C,P}}$ | 0.110$^{\mathrm{C,H}}$ |
| M2S | — | — | — |
| IXP4 | 0.074$^{\mathrm{P}}$ | 0.074$^{\mathrm{P}}$ | 0.082$^{\mathrm{C,H}}$ |
| IXM2 | 0.090$^{\mathrm{H}}$ | 0.081$^{\mathrm{C}}$ | 0.086 |
| MAT | 0.324$^{\mathrm{H,P}}$ | 0.271$^{\mathrm{C,P}}$ | 0.296$^{\mathrm{C,H}}$ |
| MAM | 0.169 | 0.165 | 0.183 |
| I2 | 0.032$^{\mathrm{H,P}}$ | 0.027$^{\mathrm{C}}$ | 0.028$^{\mathrm{C}}$ |
| I3 | 0.047$^{\mathrm{H}}$ | 0.041$^{\mathrm{C,P}}$ | 0.044$^{\mathrm{H}}$ |
| C1 | 0.057 | 0.055 | 0.059 |
| C1C1 | 0.249$^{\mathrm{H}}$ | 0.227$^{\mathrm{C,P}}$ | 0.243$^{\mathrm{H}}$ |
| P4P | 0.566 | 0.608 | 0.608 |
| UM2/1 | — | — | — |
| DIA | 0.894 | 0.892$^{\mathrm{P}}$ | 0.920$^{\mathrm{H}}$ |

that *A. stirtoni* was somewhat larger, above the 21.5 kg boundary. However, the assignment of *P. euthos* as a hunter of large prey is notable. It reflects the fact that *P. euthos* has both a deeper jaw and smaller m1 relative to other borophagines of similar skull length. The deep jaw suggests large prey and the small m1 results in a lowered body mass estimate.

The notion that a 12-kg predator would have regularly hunted prey larger than itself is not inconsistent with the Carbone et al. model. The authors did not argue that species smaller than 21.5 kg cannot take large prey; rather they made the point that species above this weight are "forced" to take large prey to meet their nutritional needs. Because jaw depth is expected to reflect typical loads placed on jaws during killing and feeding, we retain the full list of 11 species as likely to have relied on prey as large or larger than themselves. This should be considered a minimum number for the subfamily because, due to incomplete material, our sample excluded a number of large borophagines that were close relatives of several of the 11 species.

Of the 11 species, which were primarily hunters and which were primarily scavengers? This is a difficult question to answer. Based on the comparison of the three extant hyena species, there is no single morphological feature that clearly distinguishes hunters from scavengers. They do not differ in jaw strength despite the fact that one struggles with large, live prey while the others simply consume already dead prey. Dentally, spotted hyenas have less grinding area and longer cutting blades in their dentition than the other two, reflecting their commitment to a purely carnivorous diet. Notably, the spotted hyena is much heavier than either of the other two species, averaging 50–70 kg as opposed to 35–50 kg for the brown hyena and 25–40 kg for the striped hyena (Richardson and Bearder, 1984). Moreover, it is much more abundant and has a greater geographic range than any other living hyaenid. Undoubtedly, this reflects their ability to acquire food by hunting as well as scavenging. Given this, it is expected that the largest, most common borophagines with the most reduced dental grinding areas should be assumed to have hunted most of their food. Based on their craniodental morphology and abundance in the record, this would certainly include at least 5 of the 11 species predicted to have taken large prey: *Epicyon saevus, E. haydeni, Borophagus secundus, Aelurodon ferox,* and

*A. taxoides*. It should not be concluded that these species never scavenged; they almost certainly did so opportunistically, just as spotted hyenas and lions do today. However, their size and abundance are more consistent with group hunters than solitary scavengers. Searching for food to scavenge is best done alone, as the returns are not usually large enough to share. In support of this, both brown and striped hyenas forage alone although they may aggregate at clumped resources (e.g., striped hyenas at dumps; Macdonald, 1988) and for raising young (brown hyena dens; Mills, 1990).

The remaining six species should not be assumed to have scavenged most of their food. They range in estimated size from 12 kg (*Paratomarctus euthos*) to 29 kg (*A. mcgrewi*), and all have relatively large grinding areas and blade sizes that are comparable to those of extant Caninae that take large prey (e.g., *Cuon alpinus*, *Lycaon pictus*, *Canis lupus*). The fact that they do not appear to have been as abundant as the five borophagine species listed above does not preclude their being hunters. After all, the African wild dog, *L. pictus*, is a pack hunter that exists today at low densities relative to the two other social hunters, lion and spotted hyena (Creel and Creel, 1998). The wild dog would be expected to have (and does have) a much more limited fossil record than the two more abundant species (Turner, 1990). Thus rarity in the record should not be assumed to indicate habitual scavenging in hypercarnivorous borophagines. On the other hand, a large, hypercarnivorous borophagine that is common in the record probably existed at fairly high densities and therefore is more likely to have sustained itself by hunting than scavenging.

Van Valkenburgh and Koepfli (1993) argued that unlike felids, canids that kill prey much larger than themselves must do so in groups because they do not have the forelimb flexibility to grapple with and hold prey. Instead canids work together, with some individuals holding the prey while others wound the prey with repeated bites. This association between group hunting and relative prey size holds for living canids because their ability to rotate their paws inwards (supinate) is constrained by the morphology of the radioulnar joint. However, many of the Borophaginae displayed more mobility in this joint and were capable of moderate supination of the forepaws (Munthe, 1989). This suggests that they may have had some ability to grapple with their prey. Nevertheless, they did not have sharp, curved, retractile claws as do felids; instead the nails are blunt and relatively straight as in living Caninae (Munthe, 1989). Thus, it may have been difficult for borophagines to hold large prey, but their moderate supinating abilities could have been used to hit prey and knock them down during a chase, as brown bears have been observed to do when hunting ungulates (Cole, 1972; Boertje et al., 1988).

In her study of borophagine postcranial morphology, Munthe (1989) identified *Epicyon saevus* and *E. haydeni* as having limbs that come closest in morphology to those of extant large Caninae. They are relatively long, slender, and restricted in flexibility. On that basis she identified these species as probable pursuit hunters, and we would agree, adding that they probably usually hunted in groups. Because of their somewhat more flexible and robust forelimbs, Munthe (1989) felt that most or all *Aelurodon* species were solitary, ambush hunters of large prey. Although we agree that aelurodonts probably were not the extreme sort of endurance runner that we see today among canids, their running abilities are difficult to determine. After all, spotted hyenas are very capable pursuit hunters and yet their limb proportions and ankle morphology would suggest something much slower (Van Valkenburgh, 1987; Janis and Wilhelm, 1993). It is possible that groups of *Aelurodon* pursued large prey over limited distances, perhaps swatting them down with their forepaws and then killing them with multiple bites.

The youngest species in our sample, *Borophagus secundus*, is also the most robust in craniodental morphology and postcranial skeleton. According to Munthe (1989), it had the most flexible forelimbs of the large Borophaginae, as well as heavily blunted teeth, suggesting to her that it was much more of a scavenger than a hunter. Werdelin (1989) also classified *Borophagus* as a scavenger rather than a hunter, based on tooth wear. Arguing against a scavenger hypothesis is the abundance of this species in the record, and its tendency to occur in sizable numbers at single localities (e.g., Coffee Ranch, Optima; see Wang et al., 1999). Were this species similar to the brown hyena in its habits, it would be expected to have existed at low densities over a fairly limited range. Instead, it ranged from Central America to California and Nebraska and dominates the preserved carnivore fauna at several sites. The heavy apical tooth wear certainly suggests it consumed bones regularly, as do wolves today, but its abundance implies it hunted much of the time. Sharp teeth are probably not essential for killing prey; museum collections include numerous lions, leopards, hyenas, and other carnivores that survived for considerable lengths of time with broken and blunted canine and cheek teeth (Van Valkenburgh, 1988).

In conclusion, we believe that at a minimum, 11 species of Borophaginae regularly ate prey larger than themselves. Moreover, many or most of these probably hunted much of their prey, and did so in groups. In particular, both species of *Epicyon*, *Aelurodon ferox*, *A. taxoides*, and *Borophagus secundus* are predicted to have been social hunters based on their hypercarnivory and relative abundance in the fossil record. As noted above, previous workers have favored a predominantly scavenging lifestyle for most large borophagines, with the possible exception of *Epicyon* (Werdelin, 1989; Munthe, 1998). Their conclusions are based largely on the heavily blunted teeth and lack of gracile limb proportions that characterize pursuit-hunting canids today. However, as expressed above, we do not find these reasons sufficient to conclude that most hypercarnivorous borophagines rarely hunted. The only living carnivoran that can be described as a hypercarnivorous scavenger is the brown hyena. This species has a geographic range limited to southern Africa, and is only abundant where spotted hyenas are relatively rare (Mills, 1990). The low diversity and geographic restriction of this ecomorph undoubtedly reflects the difficulty of its lifestyle, and argues against such ecomorphs ever having been common within communities.

One further reason for believing that borophagines could not have been pack hunters was proposed by Radinsky (1969, 1973). According to Radinsky (1969), canid brains have a larger prorean gyrus than those of felids, and pack hunting canids exhibit still further expansion of this region. Because borophagines do not have an expanded prorean gyrus, Radinsky (1973) inferred that they could not have displayed packlike social organization. Although the difference in brain morphology is intriguing, it does not seem to be sufficient to exclude social behavior in the borophagines. The functional relationship between external brain morphology and complex behavior such as sociality is not well established. On the other hand, the association of group hunting with hypercarnivorous dentition, strong jaws, reduced forelimb flexibity, and body mass in excess of 21 kg follows from both energetic and functional considerations.

All 11 species predicted to consume large prey appear in the Barstovian (16 Ma) or later. Although we were unable to include all species within the subfamily in our study, it seems clear that the subfamily shifted in its ecological emphasis around 16 Ma. Prior to that time, the subfamily was dominated by consumers of smaller prey and more omnivorous species (Wang et al., 1999). In the future, it would be useful to examine the 11 borophagine species proposed here to have consumed large prey in an ecological context. Notably, the initial diversification of the highly carnivorous borophagines occurs at a time when the species richness of other North American hypercarnivores is either low (felids, nimravids) or declining (amphicyonids and hemicyonine bears; Van Valkenburgh, 1999). The subsequent decline to extinction of the hypercarnivorous borophagines occurs steadily from about 14 Ma to 2 Ma, alongside an increase in large felid diversity. By examining suites of sympatric borophagines and other carnivorans (i.e., paleoguilds), it might be possible to more confidently assign various taxa to scavenging and hunting roles given that purely scavenging species are likely to have existed at low diversity as they do today. Typical prey sizes for all extinct carnivores can now be more confidently estimated using the jaw depth and body size models, allowing us to better track the evolution of predator–prey relationships as well as ecological separation among predators. Of course, such paleoecological analyses are greatly enhanced by having a solid and well-delineated phylogeny in hand, and few groups have received as thorough a treatment as the Borophaginae. It is to be hoped that more such monographs appear on extinct North American felids, amphicyonids, and ursids in the not-too-distant future.

## ACKNOWLEDGMENTS

In honoring Richard Tedford in this volume, we take pleasure to acknowledge his great contributions to the evolutionary history of Carnivora in general and Canidae in particular. This study has benefited from recent systematic revisions of the borophagines, a project initiated by Dick and Beryl Taylor. We also thank the curatorial staff of the United States National Museum for allowing us access to the mammalogy collections.

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## APPENDIX

### List of Borophagine and Hyaenid Specimens Measured for This Study

FAMILY CANIDAE, SUBFAMILY BOROPHAGINAE
- *Archaeocyon pavidus*: F:AM 63222
- *Rhizocyon oregonensis*: AMNH 6879
- TRIBE PHLAOCYONINI
  - *Phlaocyon leucosteus*: AMNH 8768
- TRIBE BOROPHAGINI
  - *Cormocyon haydeni*: F:AM 49448
  - *Cormocyon copei*: AMNH 6885
  - *Desmocyon thomsoni*: AMNH 12874; F:AM 49096A
  - *Desmocyon matthewi*: F:AM 49177
  - SUBTRIBE CYNARCTINA
    - *Cynarctus galushai*: F:AM 27543
    - *Psalidocyon marianae*: F:AM 27397
    - *Microtomarctus conferta*: F:AM 27548
  - SUBTRIBE AELURODONTINA
    - *Tephrocyon optatus*: F:AM 61278, 61267
    - *Tomarctus hippophaga*: F:AM 61156, 61315
    - *Tomarctus brevirostris*: F:AM 61158, 61122
    - *Aelurodon asthenostylus*: F:AM 27156, 28351, 28356
    - *Aelurodon mcgrewi*: F:AM 22410
    - *Aelurodon stirtoni*: UNSM 25789; F:AM 27492
    - *Aelurodon ferox*: F:AM 25230, 61746, 61753, 61771, 27346
    - *Aelurodon taxoides*: F:AM 67036, 67040, 70755, 70757
  - SUBTRIBE BOROPHAGINA
    - *Paratomarctus temerarius*: F:AM 27255, 67121, 61071
    - *Paratomarctus euthos*: F:AM 61101
    - *Carpocyon compressus*: UNSM 2256-90
    - *Carpocyon webbi*: F:AM 61328, 105334
    - *Protepicyon raki*: F:AM 61738
    - *Epicyon saevus*: AMNH 8305; F:AM 61381, 61387, 61367
    - *Epicyon haydeni*: F:AM 61501
    - *Borophagus secundus*: F:AM 61640, 61641, 31004, 23357A

FAMILY HYAENIDAE, SUBFAMILY HYAENINAE
- *Crocuta crocuta*: USNM 163101, 163102, 162921, 163100
- *Parahyaena brunnea*: USNM 296134, 296135, 429177, 429178
- *Hyaena hyaena*: USNM 182034, 182045, 182047, 182079