# A hyaena on stilts: Comparison of the limb morphology of *Ictitherium ebu* (Mammalia: Hyaenidae) from the Late Miocene of Lothagam, Turkana Basin, Kenya with extant Canidae and Hyaenidae (#92989)



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# A hyaena on stilts: Comparison of the limb morphology of *Ictitherium ebu* (Mammalia: Hyaenidae) from the Late Miocene of Lothagam, Turkana Basin, Kenya with extant Canidae and Hyaenidae

**Julien van der Hoek** Corresp., [1] , **Lars Werdelin** [2]

[1] Department of Earth and Environmental Sciences, University of Manchester, Manchester, Greater Manchester, United Kingdom

[2] Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Stockholm County, Sweden

Corresponding Author: Julien van der Hoek
Email address: julien.vanderhoek@manchester.ac.uk

The long, gracile morphology of the limb bones of the Late Miocene hyaenid *Ictitherium ebu* has led to the hypothesis that this animal was cursorial. The forelimb and femur of the holotype were compared with specimens of extant Hyaenidae and Canidae. Two morphometric methods were used. The first used measurements to calculate indices of different morphological characters. The second method involved capturing photographs of the anterior distal humerus of each specimen, mapping six landmarks on them, and calculating truss distances. These distances represent a schematic reproduction of the elbow. Multivariate statistical analysis primarily separated the data based on taxonomy, yet locomotor and habitat categories were also considered. *Ictitherium ebu* has an overall morphology similar to that of the maned wolf and a distal humerus reminiscent of that of the aardwolf. The long, gracile limb bones of *I. ebu* are suggested to be adaptations for pouncing on prey, for locomotor efficiency, and for looking over the tall grass of the open environments the animal lived in, much like the present-day maned wolf.

# A hyaena on stilts: Comparison of the limb morphology of Ictitherium ebu (Mammalia: Hyaenidae) from the Late Miocene of Lothagam, Turkana Basin, Kenya with extant Canidae and Hyaenidae

J. van der Hoek[1], L. Werdelin[2]

[1]Department of Earth and Environmental Sciences, University of Manchester, Manchester, Greater Manchester, United Kingdom.

[2]Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Stockholm County, Sweden

Corresponding Author:
Julien van der Hoek[1]

Dover Street, Manchester, Greater Manchester, M13 9NT, United Kingdom
Email address: julien.vanderhoek@postgrad.manchester.ac.uk

## Abstract

The long, gracile morphology of the limb bones of the Late Miocene hyaenid *Ictitherium ebu* has led to the hypothesis that this animal was cursorial. The forelimb and femur of the holotype were compared with specimens of extant Hyaenidae and Canidae. Two morphometric methods were used. The first used measurements to calculate indices of different morphological characters. The second method involved capturing photographs of the anterior distal humerus of each specimen, mapping six landmarks on them, and calculating truss distances. These distances represent a schematic reproduction of the elbow. Multivariate statistical analysis primarily separated the data based on taxonomy, yet locomotor and habitat categories were also considered. *Ictitherium ebu* has an overall morphology similar to that of the maned wolf and a distal humerus reminiscent of that of the aardwolf. The long, gracile limb bones of *I. ebu* are suggested to be adaptations for pouncing on prey, for locomotor efficiency, and for looking over the tall grass of the open environments the animal lived in, much like the present-day maned wolf.


## Introduction

Hyaenidae is a family of considerable palaeontological interest, due to their occurrence in many Miocene-Pleistocene sites in Eurasia (Kurtén, 1968; Turner, Antón & Werdelin, 2008) and the significance of the three larger species of hyaenids for their respective ecosystems (Rieger, 1981; Mills, 1982; Turner, Antón & Werdelin, 2008; Hayssen & Noonan, 2021).The pattern of their evolution in Eurasia is clear. They started off as viverrid- and herpestid-like forms, which, through canid-like and cursorial forms, over time evolved into the bone crushing animals we know today (Turner, Antón & Werdelin, 2008). During the Miocene-Pliocene mammalian turnover the number of cursorial, canid-like hyaenid species decreased, while the number of Canidae increased. Few bone-crushing hyaenids are known from the latest Miocene, whereas they show up more prominently during the Pliocene. During the Pleistocene Hyaenidae became increasingly adapted to bone-crushing, with the more cursorial morphotypes disappearing.

This clear pattern is contrasted with community patterns in Late Miocene Africa, which are not yet well understood, especially when compared to the evolutionary pattern of Eurasia (Werdelin, 2003). The carnivore material from Lothagam (Kenya) may allow for such an investigation to take place (Werdelin, 2003), in part through better understanding of the ecological roles of the species found in this material.

Lothagam is a Miocene-Pliocene site located near Lake Turkana in Turkana County, Kenya (Fig. 1). It has been dated from 8 to slightly less than 4 Ma (Leakey, 2003). The exceptional preservation of fossils at the site is due to the initial accumulation of sediment from a large meandering river system. Massive faulting led to the formation of a horst, which has kept the fossils from being buried. The resistance of the fine-grained matrix of most of the site has also contributed to the preservation. It is an important site for mammal palaeontology, as it is the type site for seven genera and 21 species of mammal.

The carnivoran fauna of Lothagam includes Amphicyonidae, Mustelidae, Viverridae, Hyaenidae, Felidae and Canidae and resembles Langebaanweg in South Africa in overall structure (Werdelin,

2003). The hyaenid fauna of Lothagam includes *Ictitherium ebu*, *Hyaenictitherium cf. H. parvum*, *cf. Hyaenictis sp*., and *Ikelohyaena cf. I. abronia*. The first two species have been identified as jackal/wolf- like ecomorphotypes, *Hyaenictis* as a genus of cursorial meat eaters, and *I. abronia* as a transitional bone cracker (Coca-Ortega & Pérez-Claros, 2019).

The holotype of *I. ebu*, KNM-LT 23145, was found in the Lower Nawata Member of the Nawata Formation (Werdelin, 2003). This formation represents fluvial facies that show fluctuations in water budget and subsidence rate (Feibel, 2003). The Lower Nawata Member is characterised by conglomerate beds of varying thickness, sandstones, and mudstones, together with volcanic detritus with a large amount of intercalated altered distal tephra. The age of the Lower Nawata is 7.4 ± 0.1 to 6.5 ± 0.1 Ma (McDougall & Feibel, 2003). The palaeosols of the Lower Nawata mainly represent relatively open grassland, gallery woodland and thornbush savanna (Wynn, 2003). Pure grassland has not been recorded in the palaeosols, meaning that it was likely not long-lived if present. The Lower Nawata is characterised by the presence of Bovidae, Hippopotamidae, Suidae and Cercopithecidae, which indicate a well-vegetated habitat (Leakey & Harris, 2003).

Of the four hyaenids found at Lothagam, *I. ebu* is by far the best preserved, as it includes both postcranial and craniodental material (Werdelin, 2003). It has dentition that is seemingly adapted for a more hypercarnivorous lifestyle than other members of *Ictitherium*. This lifestyle seems to be supported by the notably long slender limbs of the species, which could be interpreted as an adaptation for cursoriality. The ecology and behaviour of canid-like hyaenids has been mentioned as needing further investigation (Turner, Antón & Werdelin, 2008).The present study provides insight into the ecology of a canid-like hyaenid, as well as the apparent cursorial adaptations of *I. ebu*.

Extant carnivorans can be classified into different locomotor categories, such as arboreal, scansorial, terrestrial and semi-fossorial, as shown by Van Valkenburgh (1987). By comparing body mass and skeletal measurements using bivariate and multivariate analysis, it was found that skeletal indicators can predict locomotor behaviour in extant carnivorans. This technique was also applied to extinct carnivorans, with partial success. Van Valkenburgh (1987) noted that the characters that define locomotor behaviour in extant carnivorans might differ from those of extinct carnivorans. However, if the biomechanical function of each part of an extinct carnivoran is understood, then it should be possible to reconstruct its locomotor behaviour as well.

Samuels, Meachen and Sakai (2013) and Andersson (2004) expanded upon the methods of Van Valkenburgh (1987). Samuels, Meachen and Sakai (2013) expanded on the skeletal indicators and added cursorial and semi-aquatic categories. Andersson (2004) applied truss analysis (Strauss & Bookstein, 1982) to the distal humerus to separate grappling from non-grappling predators. These two methods are here combined to test the hypothesis that *I. ebu* was adapted for cursoriality.

Determining the ecomorphology of *I. ebu* will not only shed light on the ecological role of this species but can ultimately contribute to a better understanding of the ecology of the Late Miocene communities of Lothagam and eastern Africa as a whole. Furthermore, the comparisons might reveal whether *I. ebu* had an ecomorphology that converges on the Canidae, among which many species are cursorially adapted (Samuels, Meachen & Sakai, 2013). *Ictitherium* was part of the jackal and wolf-like meat eater ecomorph of Werdelin and Solounias (1996) (see also Turner, Antón & Werdelin, 2008; Coca-Ortega & Pérez-Claros, 2019). This ecomorphology would then be in line with hyaenids in Eurasia having a more cursorial, canid-like morphology before being replaced by canids (Werdelin & Turner, 1996; Turner, Antón & Werdelin, 2008).

The objectives of this study are (1) to create models capable of predicting the ecomorphology of *I. ebu*. (2) to test the hypothesis that *I. ebu* was cursorial. (3) to gain a broader understanding of the ecomorphology of *I. ebu*.

## Materials & Methods

To be able to test if *I. ebu* was adapted for cursoriality, the appendicular skeleton of different extant carnivorans, of which the ecomorphology is known, were compared to the holotype of *I. ebu*, KNM-LT 23145 from the Nawata Formation. The method of Samuels, Meachen & Sakai (2013) was adapted to study the appendicular skeleton as a whole, while the method of Andersson (2004) was used to study the distal humerus. Due to these two different sets of methods utilising two different datasets, the results and discussion sections will be presented separately for the two datasets.

Because *I. ebu* is hypothesized to be a cursorial hyaenid, with cursorial adaptations similar to those of Canidae (Coca-Ortega & Pérez-Claros, 2019), only canids and hyaenids were selected. The four extant Hyaenidae were included in the study as they represent the closest living relatives to *I. ebu*. While the spotted hyaena (*Crocuta crocuta*), the striped hyaena (*Hyaena hyaena*), and the brown hyaena (*Parahyaena brunnea*) are cursors, the aardwolf (*Proteles cristatus*) has a more generalist locomotor type (Mills, 1982; Spoor & Badoux, 1988; Koehler & Richardson, 1990; Hayssen & Noonan, 2021). The Canidae in this study include a wide range of sizes from the small red fox (*Vulpes vulpes*) to the medium sized coyote (*Canis latrans*) and side-striped jackal (*Lupullela adusta*) and the large wolf (*Canis lupus*). The maned wolf (*Chrysocyon brachyurus*) was primarily included for its morphology, as its long, slender limbs bear a resemblance to those of *I. ebu*.

### Specimen collection

The remains used for the study of *Ictitherium ebu* include the manus, radius, ulna, humerus and femur of a cast of specimen KNM-LT 23145 from the Late Miocene of Lothagam, Kenya, housed in the National Museums of Kenya (NMK) (Fig. 2). A tibia is present as well, but it is broken at the diaphysis, which limits its relevance to this study. The collections of Naturhistoriska Riksmuseet (NRM), Museum für Naturkunde (ZMB), Senckenberg Naturmuseum (SMF), Alexander Koenig Zoological Research Museum (ZFMK), Royal Museum

for Central Africa (RMCA), Naturalis Biodiversity Center (RMNH) and La Specola (MZUF) were visited to collect photographs and measurements of 79 specimens of extant species for comparison with KNM-LT 23145 (Table 1). Adult specimens of both sexes were chosen, with a preference for wild-caught individuals.

**Linear morphometrics**

Specimens were measured according to the measurement protocol of Samuels *et al.* (Samuels & Van Valkenburgh, 2008; Samuels, Meachen & Sakai, 2013), with an added measurement for the midshaft mediolateral diameter of the radius (RD) (Fig. 3, Table 2). The measurement for FGT was carried out differently from the one of Samuels *et al.* (Samuels & Van Valkenburgh, 2008; Samuels, Meachen & Sakai, 2013), where the height of the greater trochanter of the femur was measured vertically instead of diagonally.

The measurements were taken with vernier callipers for measurements up to 15 cm. Measuring tape was used for measurements above 15 cm in all museums except for the Museum für Naturkunde in Berlin, where the measurements were carried out with larger callipers. Measurements were recorded to the nearest 0.1 cm (Table S1).

**Index calculations**

The measurements were then converted into indices (Samuels & Van Valkenburgh, 2008; Samuels, Meachen & Sakai, 2013) in Excel 16.0.15330.20260 (Table 3, Dataset S1). The manus proportions index was excluded from further analysis due to a lack of measurements. The radial robustness index, metacarpal radial index, humeral femoral index and metacarpal humeral index were included to be able to take into account the metacarpal III measurements and the relationship between the humerus and the femur.

For initial interpretation, preliminary boxplots of the indices plotted against species were created. These boxplots revealed some outliers in the measurements, among which some are measurement errors. These values were often far too extreme to be viewed as simple extremes in the data. For example, the humeral epicondylar breadth of ZMB MAM 82516 was measured to be half that of the other specimens, while the length is within the range of the other specimens. With the use of ImageJ 1.53n to approximate what measurement would have been obtained on-site, it was determined that 10 outliers needed to be removed from the dataset (Table S2).
Aside from these outliers, there were some missing values in the dataset. For these missing values, means were interpolated in MS Excel 16.0.15330.20260 for species with missing indices by using the mean of the same index for the other specimens of the same species. Boxplots were recreated for the final analysis, with all of these changes incorporated.

**Truss analysis**

The distal humerus of each specimen was photographed in anterior view. The camera was set to have an ISO of 200/250, an aperture of F8-F10, after which the shutter speed was adjusted for brightness. Photographing was carried out with flash. The scale bar was held in place using two

alligator clips on 4-way swivels, at the height of the specimen. Some photographs appeared overexposed after data collection. These images were edited using GIMP 2.10.30 with lowering of highlights and lowering the point at which highlights turn to white. The specimens edited in this manner were SMF 97379, SMF 97380 and ZMB MAM 89495. For a test of the validity of the photographs and removal of invalid photographs, see Article S1, Dataset S1, Table S3, Table S4 and Fig. S1.

**Truss creation**

Using TpsUtil64 1.81 a TPS file was created from the photographs acquired during data collection. The TPS file was imported into TpsDig264 2.32, labelled and scaled according to the scalebar in each image. Six landmarks were assigned to each specimen following Andersson (2004) (Fig. 4). The coordinates of the landmarks for each specimen were exported to Excel 16.0.15330.20260 using MorphoJ 1.07a (Table S4), after which the distances of the truss were calculated (Dataset S1).

**Statistics**

All tests were carried out in RStudio 2022.12.0 (Posit team, 2023) and R version 4.2.2 (R Core Team, 2022). The code and complementary files can be found in Dataset S1. Both the linear morphometric and the Truss dataset were found to be largely non-parametric by using a Shapiro-Wilks normality test (Shapiro & Wilk, 1965) on every index and distance (Table S5, Table S6). Boxplots were created of the 13 indices of the linear morphometrics. Colours for plots were selected using the webpage “Coloring for colorblindness” (Nichols, 2023). Plots were created using ggplot2, ggtext, ggpubr and tidyverse packages (Wickham, 2016; Wickham et al., 2019; Wilke & Wiernik, 2022; Kassambara, 2023). Silhouettes of the different extant species were acquired through PhyloPic (Keesey, 2023).

**Permutational multivariate analysis of variance**

Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used for analysis of the linear morphometrics. It tests if the centroids of a group of objects are the same. The test is a non-parametric alternative to multiple analysis of variance (MANOVA). The assumption for PERMANOVA is that the observations are exchangeable under the null hypothesis. Therefore, objects must be independent and have similar multivariate dispersion.

Assumption tests for similar multivariate dispersion were carried out using the vegan package (Oksanen et al., 2022). A multivariate analogue of Levene's test for homogeneity of variances (betadisper) (Anderson, 2006) was used with Euclidean distances, after which an analysis of variance (ANOVA) (Fisher, 1921), as well as a permutation test of multivariate homogeneity of group dispersions (permutest) (Legendre, Oksanen & ter Braak, 2011) were used to validate the assumption of similar multivariate dispersion.

For species, the ANOVA yielded a p of 0.002, while the permutest yielded a p of 0.011, both of which are significant ($\alpha = 0.05$). For family both results were significant as well, with the

ANOVA and permutest yielding a p of 0.004 and 0.005 respectively. Thus, multivariate dispersion was not similar, which can cause the test to be too conservative when there is large dispersion in groups of large numbers of samples and too liberal when there is large dispersion in groups of small numbers of samples (Anderson & Walsh, 2013). See the discussion for limitations of the statistics.

A two-way PERMANOVA with Euclidean distances and 999 permutations was carried out to compare the indices between family and species, using the function adonis2 from the vegan package (Oksanen et al., 2022). Species is nested in family, therefore the performed PERMANOVA is nested as well. Post-hoc Holm-corrected pairwise PERMANOVAs were carried out to identify differences in variance between pairs of species using the function pairwise.adonis from the wrapper function PairwiseAdonis (Holm, 1979; Martinez Arbizu, 2020). The Holm method of post-hoc correction is a more powerful sequentially rejective Bonferroni correction.

**Non-metric multidimensional scaling**

Non-metric multidimensional scaling (NMDS) (Kruskal, 1964) with a maximum of 999 random restarts, two dimensions and Euclidean distances was carried out using the function metaMDS from the vegan package (Oksanen et al., 2022) for both the indices as well as the Truss distances. Its goal is to plot dissimilar objects far apart from each other and similar objects close together in ordination space (Legendre & Legendre, 1998). First, a distance matrix is constructed using Euclidean distances, as the data are non-ecological. A number of dimensions is chosen, in our case k=2 for ease of interpretability. An initial configuration is chosen; in the case of metaMDS, this is done with metric scaling (Oksanen et al., 2022). This initial configuration is important, as the solution to the algorithm that is used depends partly on this configuration (Legendre & Legendre, 1998).
A matrix of fitted distances is calculated, then compared to the initial distances using monotone regression (which is non-metric) fitted by least-squares (Legendre & Legendre, 1998). Goodness of fit (stress) is used to evaluate the regression, which measures how far the new configuration is from being monotonic to the original distances. It is a relative measure, as it only measures the decrease in lack-of-fit between iterations in this procedure. The configuration is then moved slightly in the direction in which stress decreases the most rapidly (Kruskal, 1964; Legendre & Legendre, 1998). The matrix is then recalculated, and steps are repeated until a minimum lack-of-fit is reached and no more progress can be made or until a tolerated lack-of-fit is reached (Legendre & Legendre, 1998). These then become the coordinates of our two-dimensional ordination. In our case, the programme is allowed to carry out up to 999 random restarts before the process is halted (Oksanen et al., 2022). Data are then centred, as well as rotated so that the first principal component will be on the first axis. The variable scores of the NMDS were used to explain the ordination. The NMDS results were validated using a Shepard diagram and goodness of fit of individual points (Dexter, Rollwagen-Bollens & Bollens, 2018), using the stressplot and goodness functions of the vegan package (Oksanen et al., 2022). These are available in the supplementary material (Fig. S2, Fig. S3, Table S7, Table S8).

### Stepwise flexible discriminant analysis

Stepwise variable selection was carried out for species, family, locomotion and habitat on both datasets. Using a greedy Wilk's lambda F-test (Mardia, Kent & Bibby, 1979) from the klaR package (Weihs et al., 2005) the indices were selected based on an F-test decision of 0.05 (Table S9-Table S12). The variable selection works by defining a start variable that separates the group most, then selects additional variables (Weihs et al., 2005). It makes this selection based on the Wilk's lambda criterion, which means it selects the one which minimises Wilk's lambda of the model, adding more variables if the p-value still shows statistical significance (p = 0.05).
The data were divided into 30% training data and 70% validation data using the caret and tidyverse packages (Wickham et al., 2019; Kuhn, 2022). The training data were then used to carry out flexible discriminant analysis (FDA) (Hastie, Tibshirani & Buja, 1994) for each variable using the function fda from the mda package (Hastie et al., 2022). Flexible discriminant analysis works as an adaptation of linear discriminant analysis (LDA) (Hastie, Tibshirani & Buja, 1994). Linear discriminant analysis finds a reduced number of discriminate coordinate functions to be able to optimally separate groups. This number is always the number of groups minus one.
The non-parametric multiresponse regression technique BRUTO (Hastie, 1989) was used for FDA. It generates a very large base set automatically, then achieves parsimony by shrinking coefficients in a sensible, structured manner (Hastie, Tibshirani & Buja, 1994). The function "bruto" in the mda package functions by fitting a model by adaptive backfitting using smoothing splines (Hastie et al., 2022). The number of adaptive models is equal to the number of response variables in the model, but for each variable the same amount of smoothing is used. The variable can either be omitted, linear, or fitted by a smoothing spline. During each step of the backfitting procedure, model selection is based on an approximation of the generalised cross-validation criterion (Hastie, Tibshirani & Buja, 1994; Hastie et al., 2022). Once selection has finished, the model is backfitted using the chosen amount of smoothing (Hastie et al., 2022).
This model is then validated by testing how accurately the model predicts the validation data using the "predict" function from base-R (R Core Team, 2022). The variable most similar to *I. ebu* was predicted in each model using the same function.

## Results

### Linear morphometrics

#### Analysis of variance

A two-way permutational analysis of variance (PERMANOVA) was carried out on the indices to compare species and family (Table 4). Species were nested in family and 999 permutations were run. Both groupings are significant. The pseudo-F-statistic is much higher for family than for species, indicating more pronounced group separation between the two families than between individual species.

Pairwise one-way PERMANOVAs were carried out with post-hoc Holm corrections, revealing significant differences between some of the species (Table S13, Table S14). Boxplots of the 13

indices were generated to visually compare the different species (Fig. 5, Fig. S4, Fig. S5). The indices show the highest number of significant differences between the maned wolf and the other species (43 significant indices). Aside from *I. ebu*, the brown hyaena, and the coyote, which do not have enough specimens to have significant values for differences, the side striped jackal shows the lowest number of significant differences (17 significant indices). The indices HEI (24), FEI (22), and BI (22) provide the highest number of significant differences (Fig. 5), while URI (12), HFI (10), and HRI (6) provide the lowest number of significant differences.

**Non-metric multidimensional scaling**

A convergent solution was found after 20 tries by the model. Stress for the non-metric multidimensional scaling is 0.13. The Shepards plot shows an $R^2$ of the non-metric fit of 0.98 (Fig. S2). In the goodness of fit table (Table S7), none of the values of goodness of fit are above 0.05. There is a large amount of overlap in the data, particularly in the centre-left of the plot (Fig. 6).

Axis 1 of the NMDS is primarily controlled by SMI and HEI (Table 5). SMI represents the muscles acting across the shoulder joint while HEI represents the relative area for the origins of the forearm flexors, pronators, and supinators. Canids plot more on the left side and hyaenids more on the right side.

Axis 2 is primarily controlled by OLI, URI and RRI. OLI relates to the muscles used in elbow extension, while RRI is the indicator for radial robustness and stress resistance. URI represents the overall robustness and resistance to stress of the ulna. All these indices relate to the robustness of the forearm and extension of the elbow. The maned wolf, aardwolf and striped hyaena plot low on this axis, while the red fox, coyote and spotted hyaena plot high. While the aardwolf overlaps all Canidae except the red fox, the other Hyaenidae do not show overlap with the Canidae. The aardwolf and maned wolf, which are the two non-cursorial species, plot close together. *I. ebu* plots in the polygon formed by the maned wolf as well as the aardwolf.

**Flexible discriminant analysis**

Stepwise flexible discriminant analysis was performed on the 13 morphometric indices, of which 9 were selected using a greedy Wilk's lambda F-test. The indices FEI, BI, HFI, MCRI, HEI, GI, OLI, URI and MCHUM were selected based on an F-test decision of 0.05 (Table S9). The resulting plot of the first two axes has some overlap in the centre, with the coyote, wolf and aardwolf overlapping each other.

Together, the first two dimensions account for 69.96% of the data. The first dimension accounts for 46.72% of the data, while the second dimension accounts for 23.24% of the variance. The test data were predicted by the model with an accuracy of 0.8.

The red fox is separated from the rest of the data and clusters to the left (Fig. 7). The more cursorial Hyaenidae plot together on the right. In the centre are the other Canidae and the aardwolf, with the maned wolf plotted lower on CV2. When *I. ebu* is added to the model, it is predicted to be a maned wolf specimen.

Three other models were generated based on family, locomotion and habitat. As FDA reduces the dimensions of the tested groups by one, these were one-dimensional models (Fig. 8). The family model predicted the test data with an accuracy of 0.86. *I. ebu* scores a low value on CV1 and was predicted as Canidae, which is incorrect. The locomotion model predicted the test data with an accuracy of 0.77. *I. ebu* was predicted as cursorial and has an intermediate value on CV1. Finally, the habitat model predicted the test data with an accuracy of 1 and *I. ebu* was predicted as an open habitat species and has a value slightly above intermediate for the plot.

**Truss analysis**

**Non-metric multidimensional scaling**

A repeat of the best solution was reached after 26 tries. Stress is 0.03. The Shepards plot shows an $R^2$ of the non-metric fit of 0.99 (Fig. S3) and no goodness of fit value is higher than 0.01 for the individual points (Table S8). There is a lot of overlap between species, mainly on the left side of the plot (Fig. 9).

The first axis is mostly controlled by 5-6, the distal width of the trochlea, and 4-5, the distal width of the capitulum (Table 6). It reflects overall size. The second axis is primarily controlled by 5-6 and 2-5 and relates to the distal extension of the trochlea. It separates species like the wolf, with a less extended trochlea and squarer anterior distal humerus, from species like the striped hyaena, with a more extended trochlea. *I. ebu* is separated from the other species, indicating an intermediate size and trochlear extension.

**Flexible discriminant analysis**

The model accounts for 89.81 % of the variance in its first two dimensions. CV1 accounts for 52.46% of the variance. It reflects the shape of the capitulum and with it, the overall anterior distal humerus from a squarer (wolf) to a more rectangular (brown hyaena) shape. CV2 accounts for 37.35% of the variance. It reflects the overall size of the specimens (Fig. 10). Model accuracy is 0.72. It separates species in a manner similar to the NMDS. When *I. ebu* is added to the model, it is predicted as being a specimen of the aardwolf.

Three other models were generated based on family, locomotion and habitat. As FDA reduces dimensions of the tested groups by one, these were one-dimensional models (Fig. 11). The family model predicted the test data with an accuracy of 0.95. *I. ebu* was predicted as Hyaenidae and has a relatively high value on the plot. The locomotion model predicted the test data with an accuracy of 0.71. *I. ebu* had a high value and was predicted as having a generalist locomotor mode. Finally, the habitat model predicted the test data with an accuracy of 0.81 and *I. ebu* was predicted as an open habitat species with a relatively high value.

# Discussion

## Implications of the linear morphometrics

### Variance

The permutational analysis of variance demonstrates that there are significant differences between the morphometric indices of families, as well as between species (Table 4). Indices HEI, FEI and BI have the most significant differences in the pairwise PERMANOVAs, showing that forelimb length and epicondylar breadth are important characteristics when separating species (Fig. 5, Table S13). These are also important characteristics for separating cursorial carnivores from other groups (Samuels, Meachen & Sakai, 2013), indicating that these indices detect similar differences in morphology in this smaller dataset.

While *Ictitherium ebu* has no significant pairwise comparisons due to only being a single individual, it can be visually separated from other species in the boxplots (Fig. 5, Fig. S4, Fig. S5). The animal has lower than average values of OLI, GI, RRI, HEI, FEI, HFI and a high BI. Except for GI and HFI, these indices are in the range of those of the maned wolf. The maned wolf and *I. ebu* also show overlap in SMI, OLI, URI, MCHUM and MCRI, meaning that they overlap in 10 of the 13 different indices, suggesting similar overall proportions and thus adaptations.

### Non-metric multidimensional scaling

The first axis of the NMDS mainly discriminates between the two families. As SMI and HEI correlate quite well with these variables, it seems that relative deltopectoral crest size and epicondylar size have a phylogenetic signal. However, these differences are also due to size, as most hyaenids are larger than most canids.

Forearm robustness and the relative size of the olecranon are important explanatory variables for NMDS2. The maned wolf, aardwolf and striped hyaena all plot lower on NMDS2. They all have a shorter olecranon, which reflects the fact that these predators do not need to apply much strength with their forelimbs during hunting and handling prey (Martín-Serra, Figueirido & Palmqvist, 2016). Furthermore, they have less robust forearms. The striped hyaena is predominantly a scavenger (Rieger, 1981) and thus plots lower than the spotted hyaena, which more commonly hunts large prey (Hayssen & Noonan, 2021). The maned wolf and aardwolf are generalist species. *I. ebu* plots within the range of the maned wolf, not far from the aardwolf, indicating some overlap with these species in forearm function. Overall, it appears that NMDS2 reflects shape that is impacted by hunting strategy and cursoriality.

### Flexible discriminant analysis

The flexible discriminant analyses predict *I. ebu* to be a maned wolf, Canidae, cursorial and open habitat. These findings contradict each other. In large part these contradictions exist due to the different indices used for the different models, making comparisons more difficult.

The species FDA somewhat resembles the NMDS, with *I. ebu* predicted as a maned wolf. This is not surprising, because in the NMDS *I. ebu* is plotted within the point cloud of the maned wolf and has quite similar morphology to this gracile-limbed animal.
*I. ebu* is predicted as Canidae in the family model, indicating a more canid-like morphology. Of course, effects of size must be accounted for, but the animal is quite similar in overall morphology to the maned wolf, a canid. As a hyaenid from the Miocene, *I. ebu* also falls in a group of less robust, more canid-like, primitive hyaenids, which would be replaced by the more robust Hyaenidae of the post-Miocene (Coca-Ortega & Pérez-Claros, 2019).

A model with just three indices, OLI, MCRI and HFI, predicts *I. ebu* to be cursorial, which contradicts the NMDS, where *I. ebu* is plotted in the point clouds of the two generalist species. It also contradicts the similarity of *I. ebu* and the maned wolf. *I. ebu* plots in the area where the locomotor groups overlap, and there are more cursorial species in the dataset.
Finally, *I. ebu* is predicted to be an open habitat species, which is in agreement with the NMDS and overall similarity to the maned wolf. The validation test here gives a value of 1, which is very high. This result is likely due to random chance, as both test and training datasets were acquired randomly.

**Implications of the Truss analysis**

**Non-metric multidimensional scaling**

The first axis of the NMDS reflects overall size, whereas NMDS2 reflects the extension of the trochlea. A size pattern was observed by Andersson (2004), where species <10kg are quite uniform in the main principal component that reflects shape. At 10-80 kg, the differences increase with size.

This pattern can be observed in the NMDS as well, even with the different loadings of NMDS1 and NMDS2. The smaller extant species (red fox, side-striped jackal, coyote and aardwolf) all plot around the 0-value of NMDS2. The larger extant Hyaenidae and Canidae are split into the low-scoring brown hyaena, striped hyaena and spotted hyaena and the higher scoring maned wolf and wolf. The Hyaenidae have lower values on NMDS2 due to more extended medial trochlear flanges. This extension reflects an increase in lateral stability during humeral articulation, which is an indicator of an animal that grapples with its prey (Andersson, 2004). Andersson (2004) placed both Hyaenidae and Canidae in a group with the cheetah (*Acinonyx jubatus*) to indicate non-grapplers. Only the maned wolf is interpreted as a grappler but has the elbow joint morphology of a non-grappler (Andersson, 2004). However, of note is that if figure 6 from Andersson (2004) is compared to the NMDS, the figures show the same difference between the larger canids and hyaenids.

**Flexible discriminant analysis**

*I. ebu* is predicted to be an aardwolf, Hyaenidae, generalist and open habitat by the different models of the discriminant function analysis. These models use the same truss distances and can

thus also be more easily compared with each other. None of the models contradict each other, as the aardwolf is a generalist, open habitat hyaenid. The NMDS would predict similar results, because *I. ebu* plots closest to the aardwolf in the NMDS. The species model even resembles the NMDS, although shape is more important than size. Furthermore, *I. ebu* does not plot in areas of overlap in any of the one-dimensional analyses.

**Implications of the combined morphometric methods**

Size explains a large amount of dissimilarity in all of the species plots. However, on the first axis of the linear morphometrics results family seems to be the main distinguishing factor. For the species FDA of the truss analysis, size even appears to be secondary to shape, as the main axis of variance represents the shape of the capitulum.

The presence of a phylogenetic signal within the shape variables cannot be eliminated because extant canids have a cursorial ancestry (Andersson, 2004). This can be seen in the maned wolf, a generalist species that has traits of a more cursorial animal (Andersson, 2004; Samuels, Meachen & Sakai, 2013).

A pattern emerges when the morphometric methods are analysed together. While a quick look at the variance showed a closer similarity of *I. ebu* to the maned wolf in the overall morphology of the limb bones, both the maned wolf and aardwolf showed similar values in the NMDS. The species FDA predicted *I. ebu* to be similar to the maned wolf, far from the other species data. The truss analysis of the distal humerus showed a closer affinity to the aardwolf in both the NMDS and species FDA.

While family was predicted as Canidae in the linear analysis, the truss analysis interpreted the family as Hyaenidae. It may be that the morphology of *I. ebu* is overall more similar to Canidae, but the elbow is more similar to Hyaenidae. While the locomotor model predicts cursorial locomotion for the overall morphology, the elbow predicts generalist locomotion. However, both species predictions would suggest a generalist animal. The models interpret *I. ebu* as an open habitat animal, in agreement with Werdelin (2003). The Lower Nawata represents a relatively mixed habitat, as pure grassland was likely not long-lived but could have been present (Wynn, 2003). Therefore, *I. ebu* could have been present during a short time when there were pure grasslands. Other explanations for the presence of an open-habitat species in mixed habitat are that species do not always live in their ideal habitat, or that the animal was drawn to the location to drink and died there.

Overall, the long, gracile limbs of *I. ebu* were not an adaptation for cursoriality, but for being able to look over the tall grasses of its environment and pounce on prey, similar to the maned wolf (Hildebrand, 1954; Janis & Wilhelm, 1993) and possibly the serval (*Leptailurus serval*), a felid not analysed here that removes prey from crevices (Janis & Wilhelm, 1993; Ewer, 1998). The longer legs of *I. ebu* also contribute to its walking efficiency, as locomotion efficiency increases with longer legs at all gaits (Pennycuick, 1975; Janis & Wilhelm, 1993).

## Limitations of the research

### Data collection

Only three of the nine spotted hyaena specimens used in this study had completely fused epiphyses (ZMB MAM 7784, ZMB MAM 13295 and ZMB MAM 47515), which is normally the main indicator of an adult animal. However, according to Egeland, Egeland & Bunn (2008), sub-adulthood is characterised by unfused or partially fused epiphyses with solid bone surfaces. Sponginess only occurs at near-epiphyses. Adults have epiphyses that are mostly or completely fused, with the entire surface of the bone being solid. Specimens ZMB MAM 14818, ZMB MAM 16575, and ZMB MAM 82415 have fused epiphyses with entirely solid bone surfaces; only thin grooves show the epiphyses to not be entirely fused. They could thus be interpreted as adult specimens. ZMB MAM 82413, ZMB MAM 82471 and ZMB MAM 82516 do not have fused epiphyses, but do not show much spongy bone around the epiphyses. These specimens can then be interpreted as older sub-adults. The striped hyaena ZMB MAM 82363 also had a humerus that was not fully fused, which would indicate a subadult if interpreted in the same way as the spotted hyaena specimens (Egeland, Egeland & Bunn, 2008). However, it does not have any measurements that are below the range of the other specimens. Only the radial diameter is smaller than the others, but three specimens have equally small radial diameters. Truss distances all fall within the range of other specimens.

MZUF 13354 (wolf) illustrates the difference between zoo animals and wild animals quite accurately. In the species dataset, MZUF 13354 has the most extreme value for every single index, with 8 outliers. The short bones of this animal are the likely cause of these values.

### Statistics

Sample sizes differed for the species, with the brown hyaena and coyote having merely represented by two and one specimens, respectively. The permutational analysis of variance could have been affected as a consequence of this unbalanced design. While PERMANOVA can handle unbalanced designs, it can be affected by heterogeneous dispersions (Anderson & Walsh, 2013; Anderson et al., 2017). Use of the betadisper test for homogeneity of variances, followed by ANOVA and permutest found heterogeneous dispersions in the data. The NMDS shows a pattern that clearly separates species by size and morphology. The pairwise PERMANOVAs serve to identify significant differences between species more specifically.

## Conclusions

*Ictitherium ebu* was hypothesised to be cursorial, based on its long, gracile limbs. Through a combination of two and three dimensional morphometric techniques it was found that *I. ebu* resembled the maned wolf in the overall morphology of the limbs, while it resembled the aardwolf in the morphology of the knee joint. As neither of these animals is cursorial, *I. ebu* would not have been cursorial either. Similar to the maned wolf, the long slender limbs of *I. ebu* would have been an adaptation for looking over the tall grasses of its environment, pouncing on prey and walking efficiency. Further research on the ecomorphology of the hyaenids of Lothagam and other Late Miocene African sites will help to categorise the as yet understudied African community patterns of Hyaenidae.

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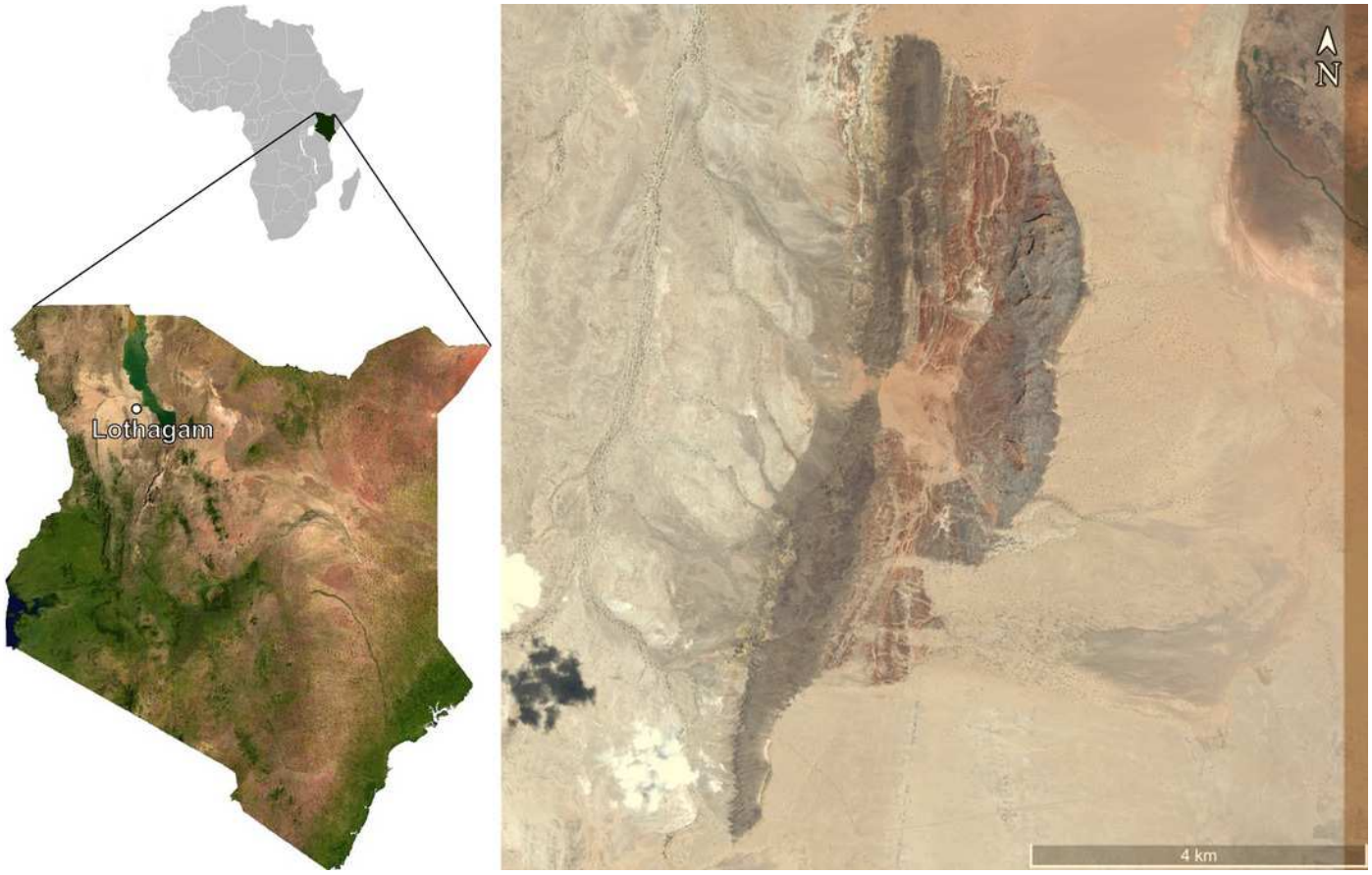
# Figure 1

Map of Kenya showing the location of Lothagam, with the fossil site on the right.

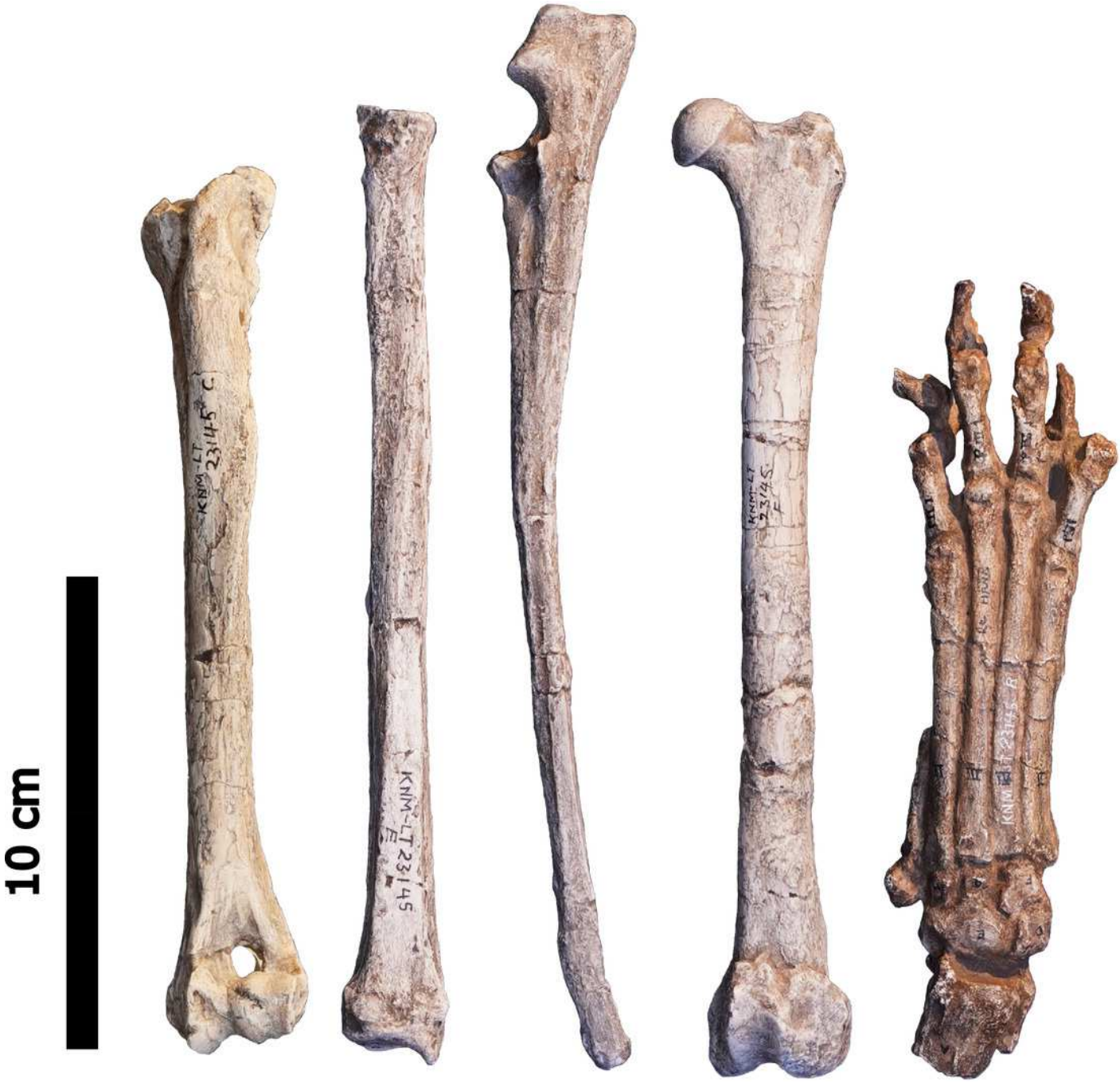
Maps of Africa and Kenya were obtained from Wikimedia Commons (2023a; 2023b). The map of Lothagam was obtained from Google Earth Pro (Maxar Technologies and Airbus).



# Figure 2

The left anterior humerus, left anterior radius, left lateral ulna, left anterior femur and dorsal right manus of specimen KNM-LT 23145 (*Ictitherium ebu)*.

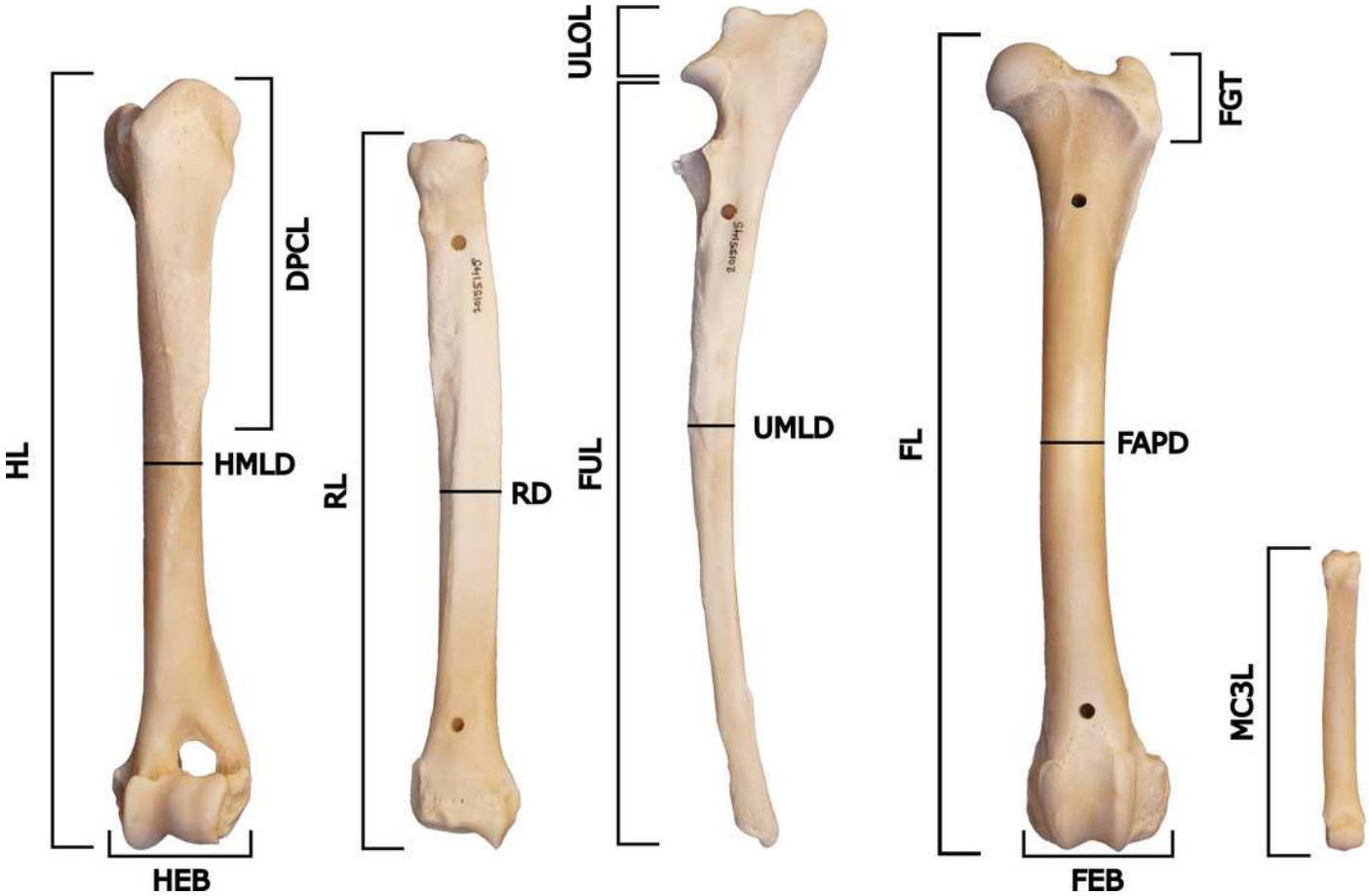
Scalebar is 10 cm.



# Figure 3

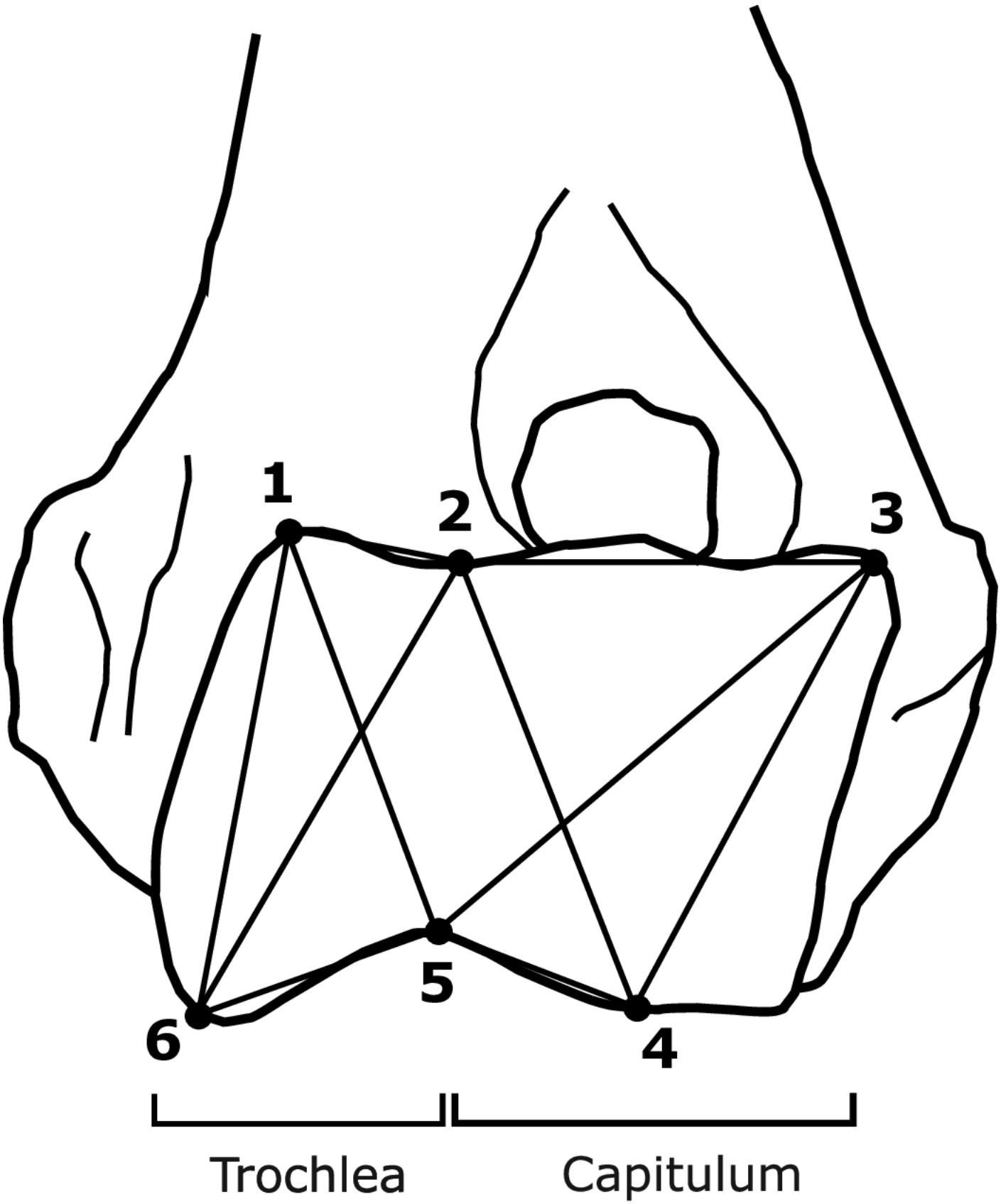
Measurements of the postcrania used in the project, based on Samuels & Van Valkenburgh (2008) and Samuels, Meachen and Sakai (2013).

The specimen figured is NRM 20155145 (*Canis lupus*) and shows the left anterior humerus, left anterior radius, left lateral ulna, left anterior femur and dorsal right manus (not to scale).



# Figure 4

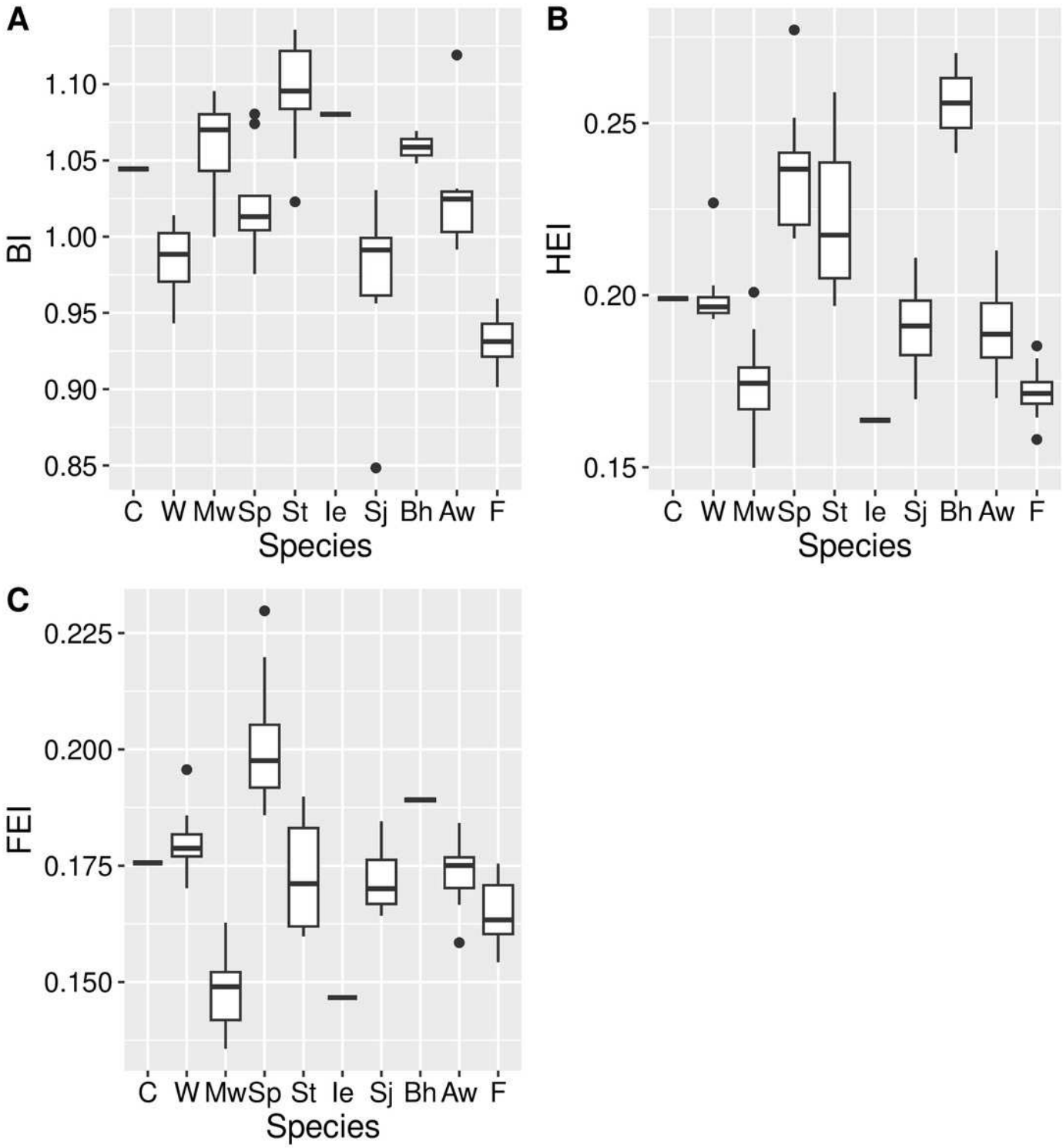
Schematic representation of the elbow joint with truss coordinates and distances marked out as dots and lines respectively. Figure adapted from Andersson (2004).


1
2
3
5
6
4
Trochlea
Capitulum

# Figure 5

Boxplots of the species for the three most discriminant limb ratios.

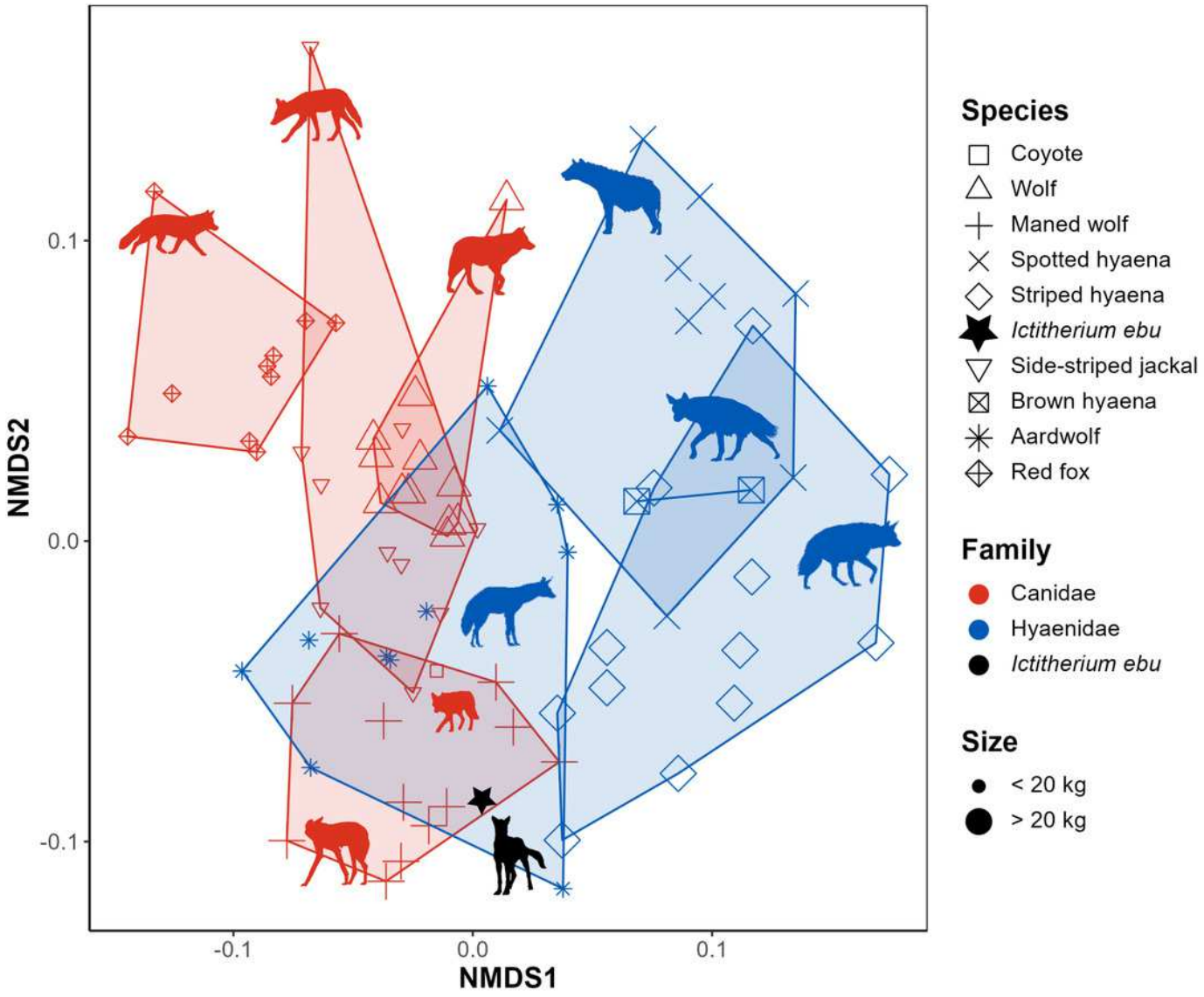
(A). Branchial index. (B). Humeral epicondylar index. (C). Femoral epicondylar index. C = Coyote, W = Wolf, Mw = Maned wolf, Sp = Spotted Hyaena, St = Striped hyaena, Ie = *Ictitherium ebu*, Sj = Side-striped jackal, Bh = Brown hyaena, Aw = Aardwolf, F = Fox.


A
BI
1.10
1.05
1.00
0.95
0.90
0.85
C W Mw Sp St Ie Sj Bh Aw F
Species
B
HEI
0.25
0.20
0.15
C W Mw Sp St Ie Sj Bh Aw F
Species
C
FEI
0.225
0.200
0.175
0.150
C W Mw Sp St Ie Sj Bh Aw F
Species

# Figure 6

NMDS plot of the morphometric indices.

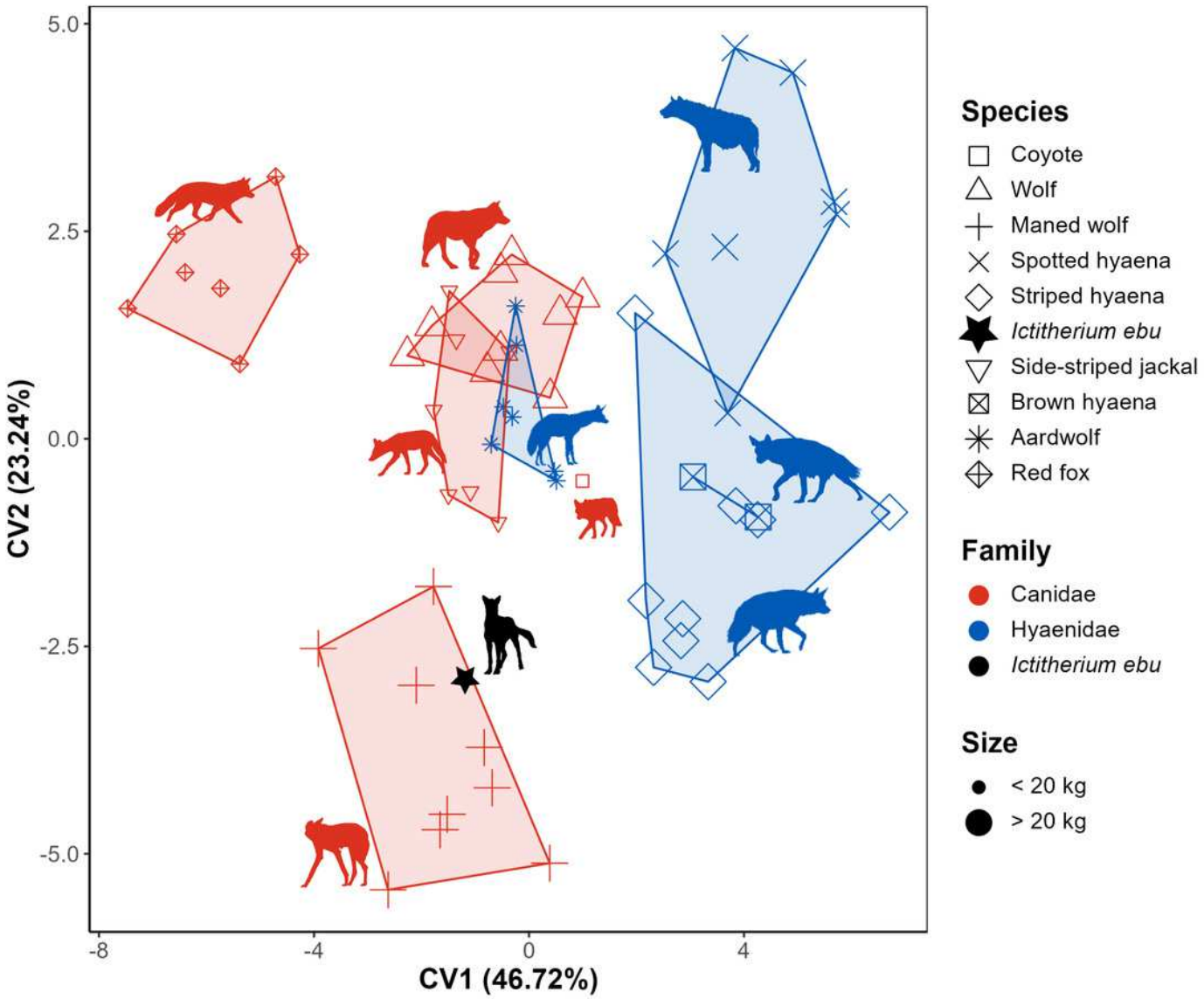
Species are labelled by shape, family by colour and size by largeness of the dots. Minimum convex polygons for each species are shown in the colour of their family. *I. ebu* is plotted as a black star. NMDS1 is inverted to plot smaller species on the left and larger species on the right. Species silhouettes except for *Ictitherium ebu* from Phylopic (Keesey 2023). Silhouette of *Ictitherium ebu* traced from the reconstruction by Javier Herbozo.



# Figure 7

Flexible discriminant analysis of the morphometric indices.

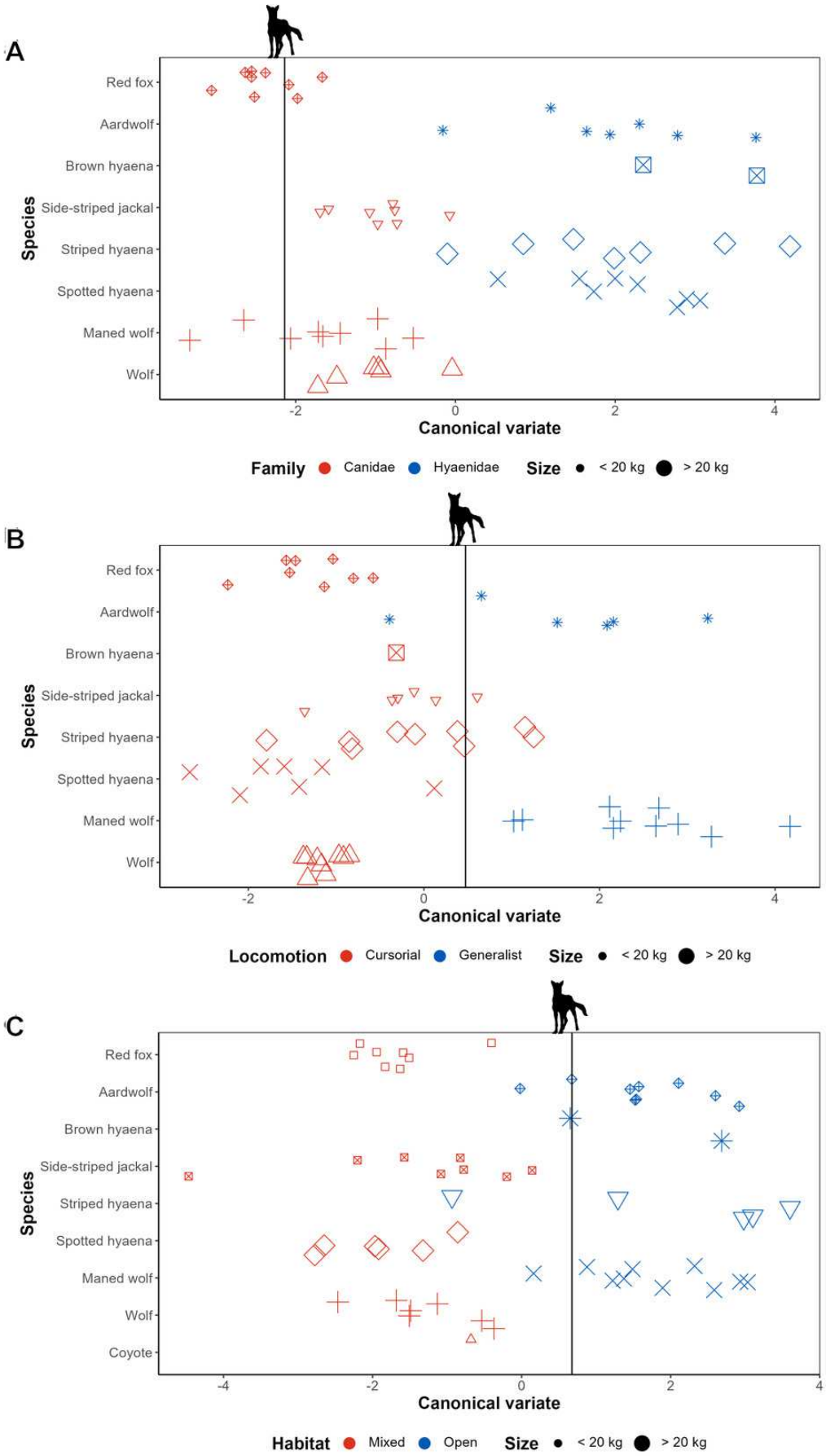
Species are labelled by shape, family by colour and size by largeness of the dots. Minimum convex polygons for each species are shown in the colour of their family. The predicted value of *I. ebu* is plotted as a black star. CV1 is inverted to plot smaller species on the left and larger species on the right. Species silhouettes except for *Ictitherium ebu* from Phylopic (Keesey 2023). Silhouette of *Ictitherium ebu* traced from the reconstruction by Javier Herbozo.


5.0
2.5
0.0
-2.5
-5.0
CV2 (23.24%)
-8
-4
0
4
CV1 (46.72%)
Species
Coyote
Wolf
Maned wolf
Spotted hyaena
Striped hyaena
Ictitherium ebu
Side-striped jackal
Brown hyaena
Aardwolf
Red fox
Family
Canidae
Hyaenidae
Ictitherium ebu
Size
< 20 kg
> 20 kg

# Figure 8

(A) Family, (B) locomotion and (C) habitat model strip charts.

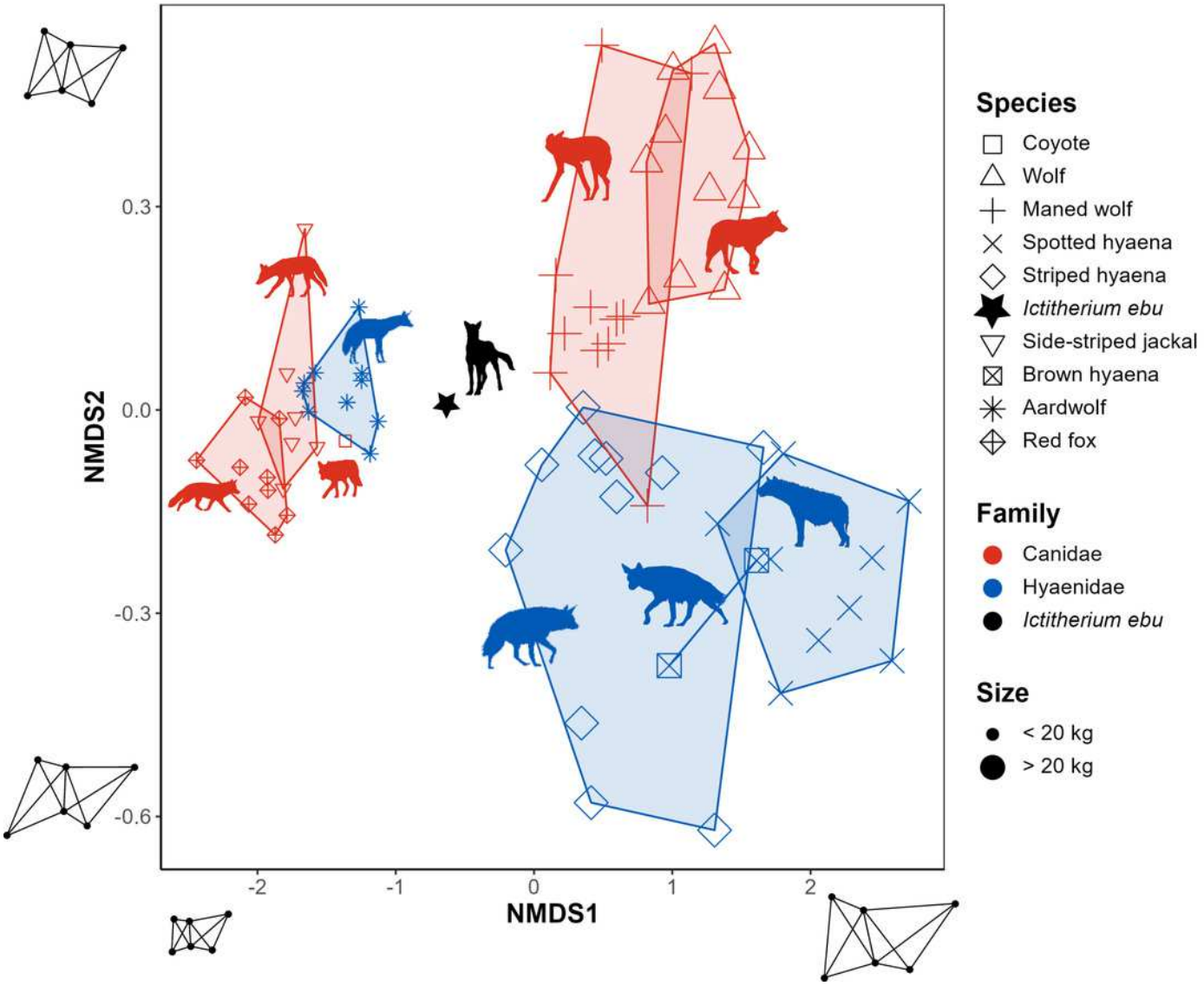
Points are jittered to allow for a clearer view of the data. Groups are labelled by colour, species by shape. The prediction of *I. ebu* is plotted as a line. Silhouettes of *Ictitherium ebu* traced from the reconstruction by Javier Herbozo.


A
Red fox
Aardwolf
Brown hyaena
Side-striped jackal
Striped hyaena
Spotted hyaena
Maned wolf
Wolf
Species
-2
0
2
4
Canonical variate
Family Canidae Hyaenidae Size < 20 kg > 20 kg
B
Red fox
Aardwolf
Brown hyaena
Side-striped jackal
Striped hyaena
Spotted hyaena
Maned wolf
Wolf
Species
-2
0
2
4
Canonical variate
Locomotion Cursorial Generalist Size < 20 kg > 20 kg
C
Red fox
Aardwolf
Brown hyaena
Side-striped jackal
Striped hyaena
Spotted hyaena
Maned wolf
Wolf
Coyote
Species
-4
-2
0
2
4
Canonical variate
Habitat Mixed Open Size < 20 kg > 20 kg

# Figure 9

NMDS plot of the truss analysis.

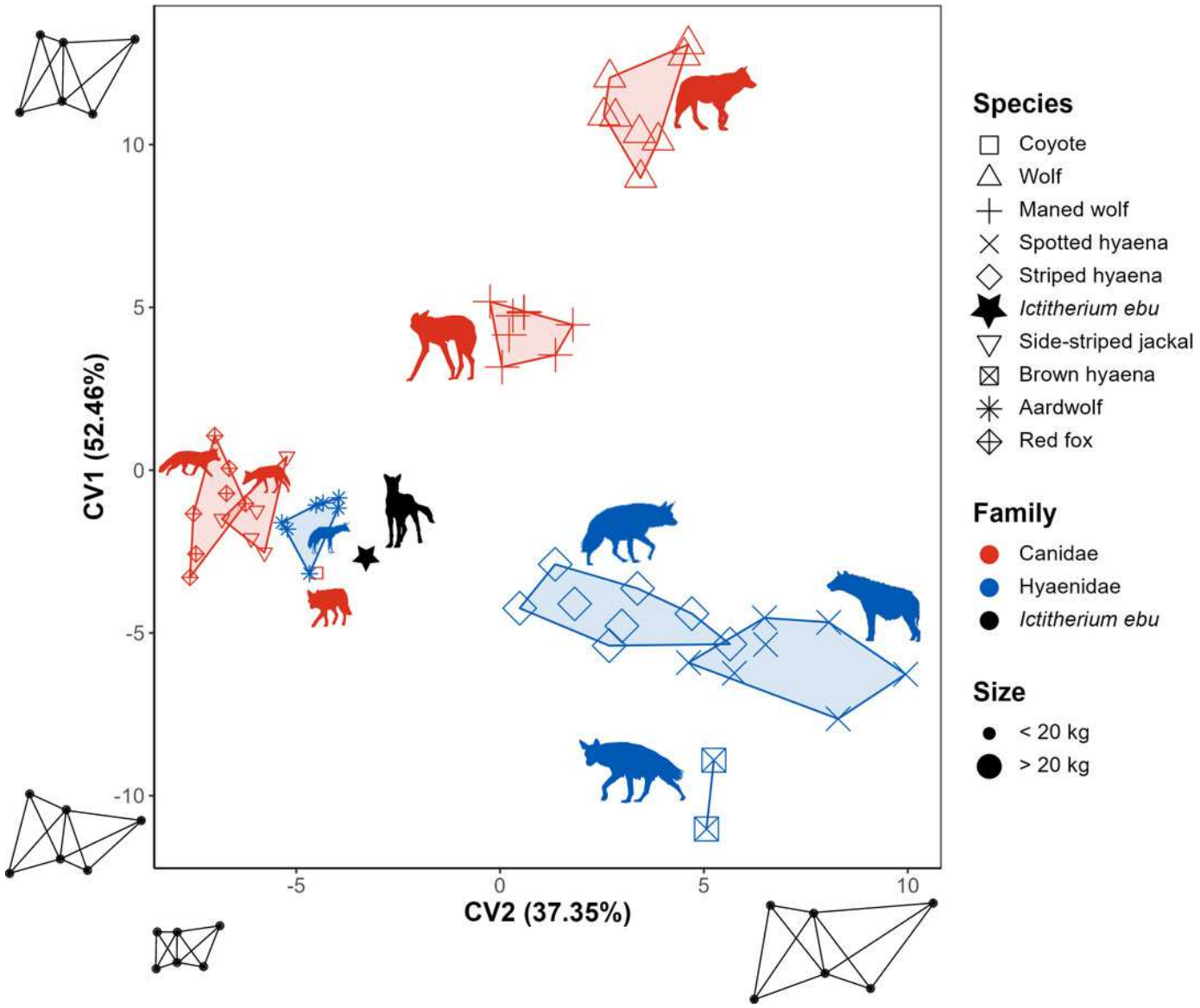
Species are labelled by shape and family by colour. Minimum convex polygons for each species are shown in the colour of their family. The predicted value of *I. ebu* is plotted as a black star. NMDS2 is plotted in reverse to be able to more easily compare it to the linear NMDS. Species silhouettes except for *Ictitherium ebu* from Phylopic (Keesey 2023). Silhouette of *Ictitherium ebu* traced from the reconstruction by Javier Herbozo.



# Figure 10

Flexible discriminant analysis of the truss distances.

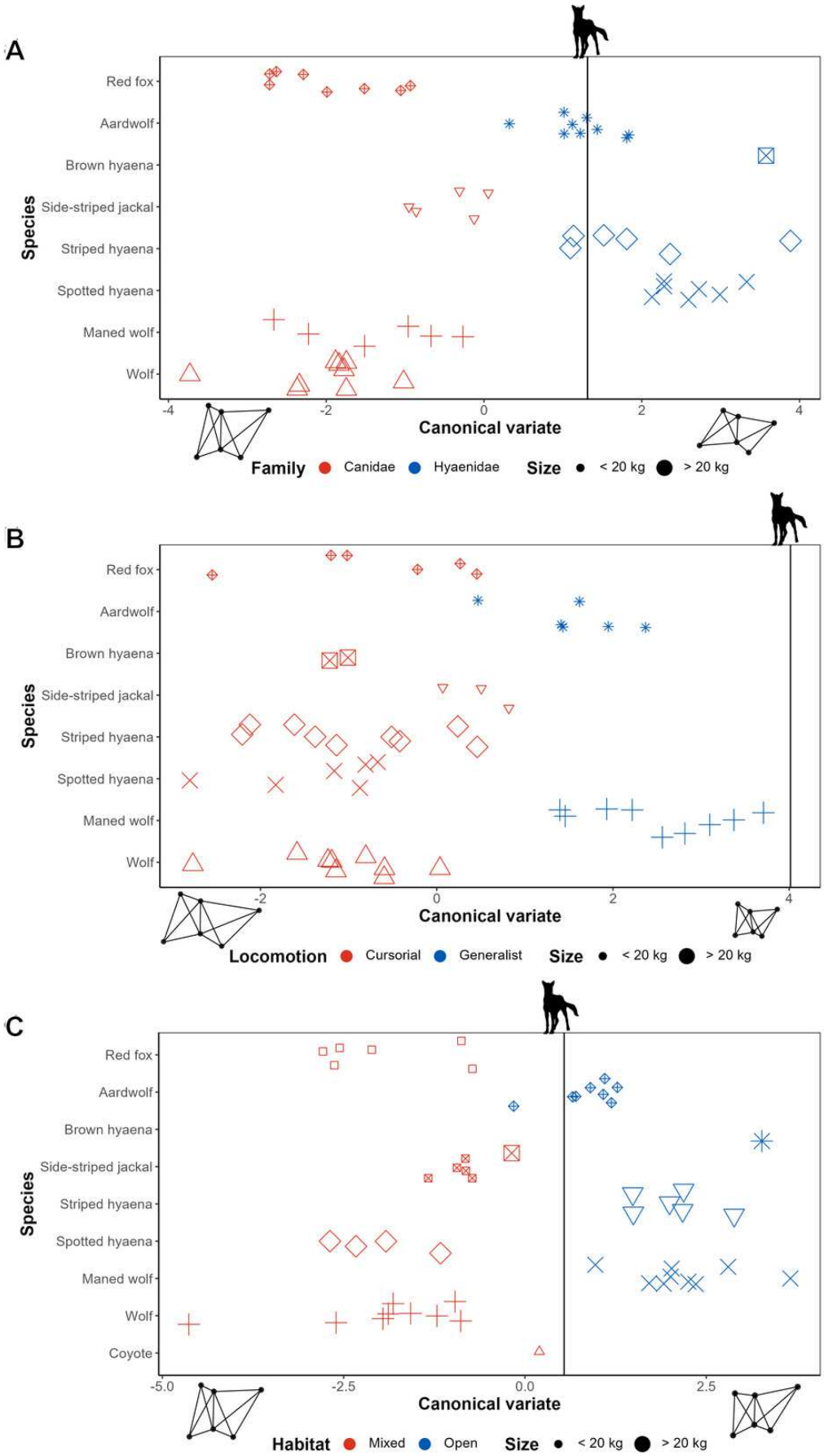
Species are labelled by shape and family by colour. Minimum convex polygons for each species are shown in the colour of their family. The predicted value of *I. ebu* is plotted as a black dot. Axis 2 was plotted horizontally and axis 1 vertically, with axis 2 reversed for ease of comparison to the other plots. Species silhouettes except for *Ictitherium ebu* from Phylopic (Keesey 2023). Silhouette of *Ictitherium ebu* traced from the reconstruction by Javier Herbozo.


Species
Coyote
Wolf
Maned wolf
Spotted hyaena
Striped hyaena
Ictitherium ebu
Side-striped jackal
Brown hyaena
Aardwolf
Red fox
Family
Canidae
Hyaenidae
Ictitherium ebu
Size
< 20 kg
> 20 kg
CV1 (52.46%)
CV2 (37.35%)
10
5
0
-5
-10
-5
0
5
10

# Figure 11

Family (A), locomotion (B) and habitat (C) model strip charts.

Points are jittered to allow for a clearer view of the data. Groups are labeled by colour, species by shape. The prediction of *I. ebu* is plotted as a line. Silhouettes of *Ictitherium ebu* traced from the reconstruction by Javier Herbozo.


A
Red fox
Aardwolf
Brown hyaena
Side-striped jackal
Striped hyaena
Spotted hyaena
Maned wolf
Wolf
Species
-4
-2
0
2
4
Canonical variate
Family Canidae Hyaenidae Size < 20 kg > 20 kg
B
Red fox
Aardwolf
Brown hyaena
Side-striped jackal
Striped hyaena
Spotted hyaena
Maned wolf
Wolf
Species
-2
0
2
4
Canonical variate
Locomotion Cursorial Generalist Size < 20 kg > 20 kg
C
Red fox
Aardwolf
Brown hyaena
Side-striped jackal
Striped hyaena
Spotted hyaena
Maned wolf
Wolf
Coyote
Species
-5.0
-2.5
0.0
2.5
Canonical variate
Habitat Mixed Open Size < 20 kg > 20 kg

## Table 1 (on next page)

The species used in this study including number of specimens, their locomotor type, habitat and body mass.

**I. ebu* was hypothesised to be cursorial by Werdelin (2003). **The Lower Nawata where *I. ebu* was found represents a mixed habitat (Wynn 2003). *** Body mass estimated by Werdelin (2003). 1. Koehler & Richardson (1990). 2. Spoor & Badoux (1988). 3. Rieger (1981). 4. Mills (1982). 5. Hayssen & Noonan (2021). 6. Matthews (1939). 7. Sillero-Zubiri *et al.* (2004). 8. Mech (1974). 9. Hildebrand (1954). 10. Janis & Wilhelm (1993). 11. Coelho *et al.* (2018). 12. Bekoff (1977). 13. Bingham & Purchase (2002). 14. Nowak & Paradiso (1983). 15. Dietz (1985).

1

| Family | Genus | Species | Common name | Locomotor type | Habitat | Body mass (kg) | n |
|---|---|---|---|---|---|---|---|
| Hyaenidae | *Ictitherium*[†] | *ebu*[†] | n.a. | Cursorial[*] | Mixed[**] | 10-15[***] | 1 |
| Hyaenidae | *Proteles* | *cristatus* | Aardwolf | Generalist[1] | Open[1] | 47-79[1] | 10 |
| Hyaenidae | *Hyaena* | *hyaena* | Striped hyaena | Cursorial[2] | Open[3] | 22-55[3] | 12 |
| Hyaenidae | *Parahyaena* | *brunnea* | Brown hyaena | Cursorial[4] | Open[4] | 28-47.5[4] | 2 |
| Hyaenidae | *Crocuta* | *crocuta* | Spotted hyaena | Cursorial[5] | Mixed[6] | 47-79[5] | 9 |
| Canidae | *Lupulella* | *adusta* | Side-striped jackal | Cursorial[7] | Mixed[7] | 8-10[13] | 10 |
| Canidae | *Vulpes* | *vulpes* | Red fox | Cursorial[7] | Mixed[7] | 3-14[14] | 10 |
| Canidae | *Canis* | *lupus* | Wolf | Cursorial[8] | Mixed[8] | 18-80[8] | 12 |
| Canidae | *Chrysocyon* | *brachyurus* | Maned wolf | Generalist[9,10] | Open[11] | 23[15] | 12 |
| Canidae | *Canis* | *latrans* | Coyote | Cursorial[12] | Mixed[12] | 7-20[12] | 1 |

2

## Table 2 (on next page)

Measurements according to Samuels & Van Valkenburgh (2008) and Samuels, Meachen and Sakai (2013), with RD added.

1
2

| Measurement | Description |
|---|---|
| HL | Greatest length of the humerus |
| HMLD | Midshaft mediolateral diameter of the humerus |
| DPCL | Length of the deltopectoral crest |
| HEB | Epicondylar breadth of the distal humerus |
| RL | Greatest length of the radius |
| RD | Midshaft mediolateral diameter of the radius |
| FUL | Functional length of the ulna |
| UMLD | Midshaft mediolateral diameter of the ulna |
| ULOL | Length of the olecranon process of the ulna |
| MC3L | Greatest length of metacarpal 3 |
| FL | Greatest length of the femur |
| FAPD | Midshaft anteroposterior diameter of the femur |
| FGT | Height of the greater trochanter of the femur |
| FEB | Epicondylar breadth of the distal femur |

## Table 3 (on next page)

Indices following Samuels & Van Valkenburgh (2008) and Samuels, Meachen and Sakai (2013), with RRI, MCRI, MCHUM and HFI added and MANUS removed.

1

| Index | Description |
|---|---|
| Shoulder moment index (SMI) | Deltopectoral crest length divided by functional length of the humerus (DPCL/HL). Indicates mechanical advantage of the deltoid and pectoral muscles acting across the shoulder joint. |
| Brachial index (BI) | Functional length of the radius divided by functional length of the humerus (RL/HL). Indicates relative proportions of proximal and distal elements of the forelimb. |
| Humeral robustness index (HRI) | Mediolateral diameter of humerus divided by functional length of the humerus (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 functional length of the humerus (HEB/HL). Indicates relative area available for the origins of the forearm flexors, pronators, and supinators. |
| Olecranon length index (OLI) | Olecranon process length divided by functional length of the ulna (ULOL/FUL). Indicates relative mechanical advantage of the triceps brachii and dorsoepitrochlearis muscles used in elbow extension. This is identical to the index of fossorial ability used by Hildebrand (1985). |
| Ulnar robustness index (URI) | Mediolateral diameter of ulna divided by functional length of the ulna (UMLD/FUL). Indicates robustness of the ulna and its ability to resist bending and shearing stresses, and relative area available for the origin and insertion of forearm and manus flexors, pronators, and supinators. |
| Femoral robustness index (FRI) | Anteroposterior diameter of femur divided by functional length of the femur (FAPD/FL). Indicates robustness of the femur and its ability to resist bending and shearing stresses (AP diameter is used due to transverse expansion of the femora in semiaquatic rodents). |
| Gluteal index (GI) | Length of distal extension of the greater trochanter of the femur divided by functional length of the femur (FGT/FL). Indicates relative mechanical advantage of the gluteal muscles used in retraction of the femur. |
| Femoral epicondylar index (FEI) | Epicondylar breadth of femur divided by the functional |

| | |
|---|---|
| | length of the femur (FEB/FL). Indicates relative area available for the origins of the gastrocnemius and soleus muscles used in extension of the knee and plantar-flexion of the pes. |
| Radial robustness index (RRI) | Greatest length of the radius divided by the midshaft mediolateral diameter of the radius (RD/RL). Indicates robustness of the radius and its ability to resist bending and shearing stresses. |
| Metacarpal radial index (MCRI) | Greatest length of metacarpal 3 divided by the functional length of the radius (MC3L/RL). Indicates relative proportions of the third metacarpal compared to the radius. |
| Metacarpal humeral index (MCHUM) | Greatest length of metacarpal 3 divided by the functional length of the humerus (MC3L/HL). Indicates relative proportions of the third metacarpal compared to the length of the humerus. |
| Humeral femoral index (HFI) | Functional length of the radius divided by the functional length of the femur(HL/FL). Indicates relative proportions of the humerus compared to the femur. |

2

## Table 4(on next page)

Results of the two-way permutational analysis of variance (PERMANOVA) of indices compared to species and family.

Df = Degrees of freedom. SumofSqs = Sum of Squares. R2 = R-squared F = F-statistic.

Pr(>F) = Significance.

1

| | Df | SumOfSqs | R2 | F | Pr(>F) |
|---|---|---|---|---|---|
| Family | 2 | 0.23 | 0.24 | 24.08 | 0.001 |
| Family:Species | 7 | 0.40 | 0.42 | 12.07 | 0.001 |
| Residual | 69 | 0.33 | 0.34 | | |
| Total | 78 | 0.95 | 1 | | |

2

## Table 5 (on next page)

NMDS1 and NMDS2 loadings of the non-metric multidimensional scaling of the morphometric indices.

1

| | NMDS1 | NMDS2 |
|---|---|---|
| SMI | -0.16 | 0.08 |
| BI | -0.01 | -0.06 |
| HRI | -0.05 | 0.03 |
| OLI | 0.03 | 0.17 |
| URI | -0.02 | 0.17 |
| FRI | -0.03 | 0.04 |
| GI | -0.03 | 0.05 |
| FEI | -0.02 | 0.06 |
| HEI | -0.12 | 0.04 |
| RRI | 0.01 | 0.12 |
| MCRI | 0.06 | -0.0004 |
| HFI | 0.08 | -0.01 |
| MCHUM | -0.01 | -0.05 |

2

## Table 6 (on next page)

NMDS1 and NMDS2 loadings of the non-metric multidimensional scaling for the truss analysis.

| | NMDS1 | NMDS2 |
|---|---|---|
| 2-6 | 0.10 | 0.01 |
| 2-5 | -1.53 | -0.45 |
| 3-5 | -0.03 | -0.02 |
| 1-5 | -0.02 | -0.18 |
| 2-4 | 0.36 | -0.18 |
| 5-6 | 3.43 | 0.71 |
| 4-5 | 3.12 | 0.07 |
| 3-4 | -1.04 | -0.11 |
| 2-3 | 2.15 | 0.37 |
| 1-2 | -0.65 | -0.02 |
| 1-6 | 0.44 | -0.06 |