



Ecomorphological analysis of bovid remains from the Plio-Pleistocene hominin-bearing deposit of Unit P at Kromdraai, South Africa

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ABSTRACT

The site of Kromdraai is known for the first discovery of *Paranthropus robustus* remains. Research conducted at Kromdraai shows its rich fossiliferous deposits, geological complexity and potential to highlight the evolutionary history of Plio-Pleistocene hominin lineages in a dynamic and changing environment. Here, we provide the results of the first application of ecomorphology to bovid postcranial specimens from the newly excavated deposit of Kromdraai Unit P (KW-Unit P). Four anatomical elements of the bovid skeleton were measured and examined as they represent locomotion and substrate interaction: the astragalus and the proximal, intermediate and distal phalanges. Four discriminant function analyses (DFA) were conducted to determine each element's ability to predict habitat affiliation accurately. This was done by comparing the morphologies of the fossil specimens to modern bovids found in broadly defined habitats (open, light cover, heavy cover, and forest). For the modern assemblage, the DFA cross-validation tests correctly returned classifications ranging from 58.8% to 72.0% in a four-habitat system for the four bone elements. Fossil results revealed that bovids from KW-Unit P had varied morphological adaptations to open and light cover habitats (91.7% combined) with few forest (4.7%) and heavy cover (2.3%) adaptations. This indicates that during the deposition of KW-Unit P, the environment was open with savanna grasslands, tall grasses and light bushes. Forest which is a continuous tree canopy and heavy cover environments represented by dense woodlands and bushes were also present to a lesser degree. Overall, KW-Unit P is characterized as a mosaic with more open and light cover habitats indicating open savanna and grasslands, a riparian forest, woodlands and bushes. These reconstructions are consistent with previous palaeoenvironmental interpretations for KW-Unit P and Kromdraai B (KB) as a whole. Since our results are not entirely limited to KW-Unit P, we, therefore, argue that *Paranthropus robustus* found at Kromdraai thrived in mosaic environmental settings around the time when open habitats were dominant.

1. Introduction

Fossil bovids have long been used as proxies for palaeoenvironmental reconstruction because they are abundant in the African fossil record and represent primary consumers that provide crucial information on the surrounding environment (e.g., Gentry 1970; Vrba 1980; Scott 1983; Janis 1984; Solounias & Moelleken 1993; Spencer 1995, 1997; deMenocal 1995, 2004; Reed 1996, 1997, 1998, 2008; Bobe & Eck 2001; Bobe & Behrensmeier 2002, 2004; Alemseged 2003; Bobe

2006; de Ruiter et al. 2008). Ecomorphology has for a long time been employed to reconstruct palaeoenvironments based on bovid bones (Kappelman 1986, 1988, 1991; Plummer & Bishop 1994; Spencer 1997; Kappelman et al. 1997; Sponheimer et al. 1999; Degusta & Vrba 2003, 2005; Kovarovic & Andrews 2007; Plummer et al. 2008; Meachen-Samuels & Van Valkenburgh 2009; Barr 2014; Curran & Haile-Selassie 2016; Forrest et al. 2018; Kovarovic et al. 2021; Gruwier & Kovarovic 2022). This method analyzes the relationship between a species' bone morphology and its behaviour in order to determine habitat preferences

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during life. The basic hypothesis of ecomorphology is that an animal's functional adaptations (related to locomotion, diet, etc.) hold information about the ecological variables (e.g., substrate, vegetation, food availability, etc.) to which they are adapted. Ecomorphology requires broad taxonomic identification of fossils to the Family level (e.g., Bovidae). As a group of terrestrial mammals, bovids have specialized functional anatomy to avoid predators in a wide range of habitats (Kappelman 1986, 1988, 1991; Degusta & Vrba 2003, 2005; Weinand 2007). Hence most of their postcranial elements, including limb bones, e.g., femora, metapodials, radii, and tibiae (Kappelman 1988, 1991; Plummer & Bishop 1994; Kappelman et al. 1997; Kovarovic & Andrews 2007; Curran 2012) and pes and manus bones, e.g., carpals, tarsals and phalanges (Degusta & Vrba 2003, 2005; Weinand 2007; Plummer et al.

2008; Bishop et al. 2011; Barr 2014, 2015) have been used before. This study represents the first ecomorphological analysis of bovid astragali and phalanges from the Kromdraai site. This study aims to determine the palaeoenvironment of Kromdraai Unit P in which the hominins evolved. It also contributes to the ongoing faunal research at Kromdraai to better document its rich faunal assemblage.

2. Site background

Kromdraai is located in a palaeokarst cave system along the southern side of the Bloubaank River, in the Cradle of Humankind, approximately 2 km east of Sterkfontein Gauteng province, South Africa (Fig. 1). The site is an unroofed dolomitic cave truncated by several meters of surface

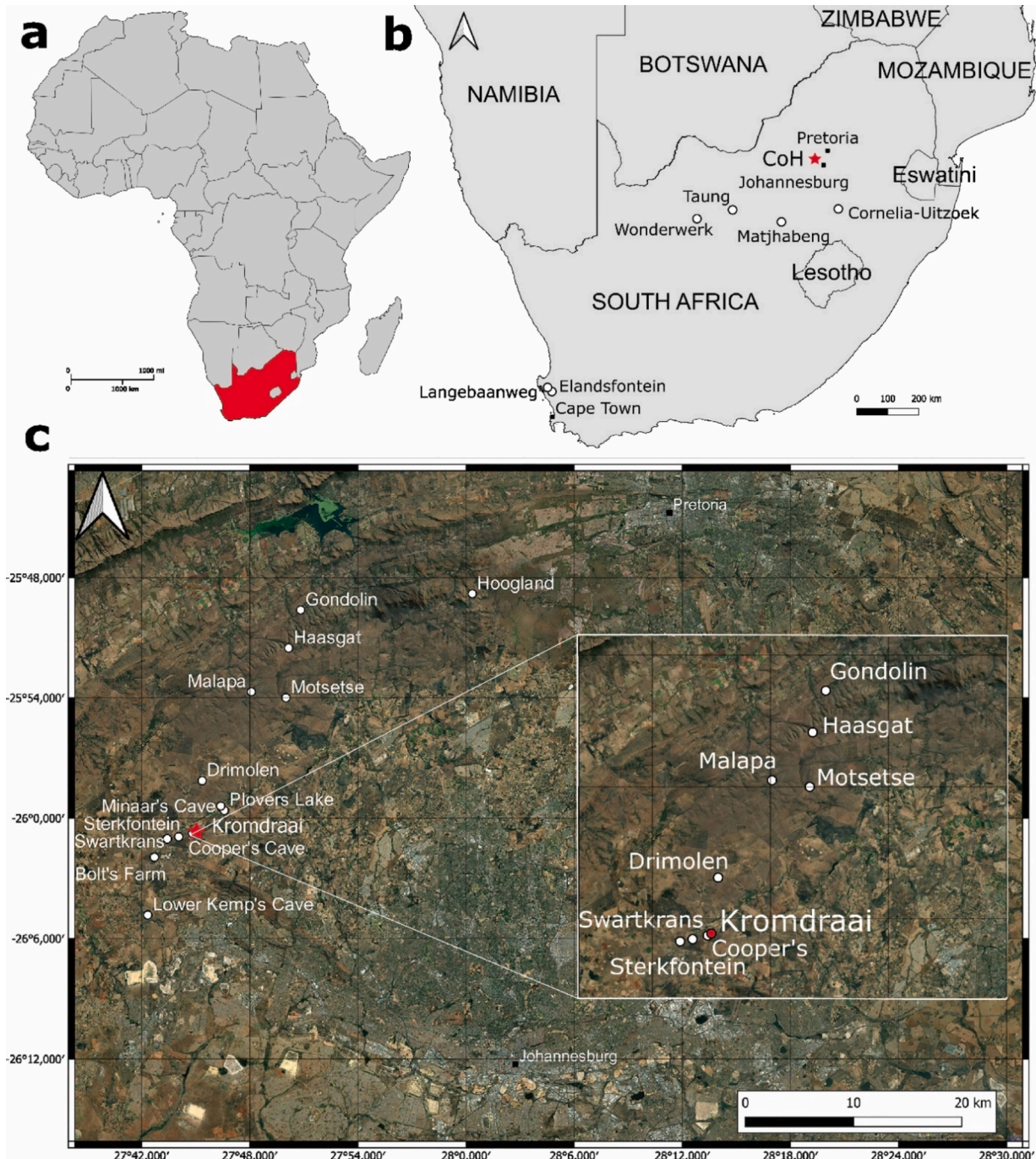


Fig. 1. Map of southern Africa showing the location of the Kromdraai site in the Cradle of Humankind in relation to the other key fossil sites.

erosion (Vrba 1981; Braga et al. 2017, 2022b; Braga & Thackeray 2016). Kromdraai is known to have yielded the type specimen of *Paranthropus robustus* (Broom 1938, 1942, 1943). Broom's initial fieldwork lasted until 1944, which was subsequently followed by a series of four-phase excavations led by Brain (1955–56), Vrba (1977–80), Thackeray (1993–2002), and the Kromdraai Research Project since 2002 (see Braga & Thackeray 2016; Braga et al. 2017, 2022b). The faunal remains recovered during the first three phases (1938–2002) (Broom 1938; Brain 1975, 1981; Vrba 1981; Thackeray et al. 2001) mostly derived from *ex-situ* breccia blocks or sediments with no detailed stratigraphic context (Braga & Thackeray 2016; Braga et al. 2013, 2016, 2017, 2022b). Therefore, the former biochronological and palaeoenvironmental interpretations of the faunal assemblage should be considered cautiously. Unit O which dates to 1.95 Ma (Thackeray et al. 2002) represents the oldest fossiliferous sedimentary unit from Kromdraai yet known and is older than the immediately overlying KW-Unit P (Braga et al. 2022b), previously referred to as Member 2 (e.g., Vrba 1981; Braga & Thackeray 2016). Since 2014, KW-Unit P has provided a large and taxonomically diverse sample of bird and mammal species (Fourvel et al. 2016, 2018; Pavia 2020), including hominins (Braga et al. 2016, 2017, 2021, 2022a, 2022b; 2023; Harper et al. 2022; Braga & Grine 2024). The age of the Kromdraai deposits remains contentious due to the lack of good stratigraphic resolution. However, Kromdraai B (KB) as a whole has been considered as “nearly contemporaneous” (Mckee et al. 1995:244) with the Member 5 deposits at Sterkfontein that are associated with the appearance of earliest Oldowan tools in South Africa currently dated at 2.18 ± 0.21 Ma (Granger et al. 2015). Although there are uncertainties associated with faunal age estimates, biochronology of the KB fauna suggests dates between 2.0–1.5 Ma (Delson 1988; McKee 1995; Vrba & Panagos 1982). The assessment of suids fauna from Kromdraai suggest that KB is older than Kromdraai A (KA) (1.8–1.6 Ma) due to the presence of *Potamochoeroides hypsodon* (Pickford 2013). The most recent biochronological study of the KW-Unit P indicates that the bovid assemblage is dominated by a marked diversity of extinct Pliocene species (i.e. *Gazella gracilior*, *Makapania broomi*, *Numidocapra cf. porrocornutus*) and younger Quaternary taxa (*Tragelaphus strepsiceros*, *Oreotragus oreotragus*, *Raphicerus campestris*, *Damaliscus lunatus*), all of which suggest that Unit P accumulated between 2.9 and 1.8 Ma (Hanon et al. 2024). This date is supported by the carnivore association, which indicates an older age than 2.0 Ma (Fourvel et al. 2016; Fourvel & Thackeray 2022).

The partial taphonomic analysis of its faunal assemblage indicates that at least part of KW-Unit P accumulated by carnivores – particularly felids (small and medium feline, large pantherine, and dirk-tooth cat), hyenids (*Parahyaena brunnea*, *Hyanea hyaena*, *Proteles cf. amplidentus*) and the wild dog cf. *Lycaon*, with bovids as the main prey species (Fourvel et al. 2016, 2018). However, the age-at-death distribution of the *P. robustus* assemblage from KW-Unit P mirrors the natural mortality profiles observed in wild chimpanzees and human hunter-gatherers, which differs from Swartkrans Member 1, whose composition reflects carnivore consumption (Braga & Grine 2024). Generally, *Paranthropus*-bearing deposits in southern Africa, including Swartkrans Member 1 and 3, Sterkfontein Member 5, Kromdraai Members 2 (Unit P) and 3 are known to be largely accumulated by leopards (*Panthera pardus*) (Brain 1981; De Ruiter & Berger 2000, 2002; Fourvel et al. 2018). The composition of the bovid and bird assemblages, the presence of the Cape clawless otter *Aonyx capensis* and the African *Civettictis cf. civetta* – both known to live near a water source (Lariviere 2001; Stuart & Stuart 2008), as well as the functional interpretations of the Cercopithecoidea occupying wooded and moist environments (Fourvel & Thackeray 2022). The remains suggest that the older deposit ‘KW-Unit P’ is a mosaic of habitats with elements of open savanna woodlands, nearby wetlands or a riverine and rocky outcrops (Fourvel et al. 2016, 2018; Pavia 2020; Fourvel & Thackeray 2022).

3. Materials

3.1. Study specimens

A sample of 43 well-preserved fossil specimens were analyzed in this study. The material comes from the 2016–2018 excavations within KW-Unit P at Kromdraai. These include eight astragali, seven proximal, 16 intermediate, and 12 distal phalanges. A total of 493 comparative specimens of 18 modern African bovid species used here are curated at the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg. The taxonomic composition of the modern sample and habitat classifications are given in Table 1, and a summary of the number of specimens in each habitat is given in Table 2. The fossil and modern comparative specimens range between bovid size class 1 and 3. Bovid size classes were derived from Brain (1974) and Klein (1976). Phalanges were sampled randomly with respect to the forelimb and hindlimb, but there was no method used to determine their placement.

4. Methods

4.1. Measurements

Measurements were taken using a digital caliper and recorded to the tenth of a millimeter (see SOM Table 1 for the fossil measurements). We used the measurements defined by Degusta & Vrba (2003, 2005; see Figs. 2–5). Measurements of the modern sample are given in SOM Tables 2. Abbreviations are given in Table 3, and the descriptions of each metric and measurement are detailed in SOM Table 3. Seven measurements were taken for the astragalus, the proximal and intermediate phalanx, and five for the distal phalanx. To avoid intra-observer error, all measurements were taken twice by one individual (RS) with a week's separation between measurements.

4.2. Exploring morphometric variability among modern South African bovids

We first explored the morphometric variability captured by our measurements on modern bovids and quantified the relative contributions of phylogeny, allometry, and habitat preference on each bone. Following Kappelman et al. (1997) and Degusta & Vrba (2003, 2005), each modern bovid species was assigned to one of four habitat groups (see Table 1):

- Open: grassland, arid country, ecotone bordering open country
- Light cover: light bush, tall grass, hilly areas
- Heavy cover: heavy bush, woodland, densely vegetated swamp
- Forest: continuous tree canopy

African bovids have a wide range of body sizes and could be a complicating factor that must be given attention. The body size differences of these individuals may account for the majority of the difference between the clusters of specimens, obscuring other relationships (Kovarovic & Andrews 2007:666). To address the influence of size, we followed the approach of Curran & Haile-Selassie (2016) by dividing the raw measurements by the geometric mean, thus generating Mosimann Shape Variables (MSV) as described by Mosimann (1970). We then calculated the mean of these MSV for each species in order to estimate interspecific morphometric variation. In order to reduce data dimensionality, principal component analyses (PCA) were performed on the mean MSV. The importance and proportion of variance of each PC are given in SOM Table 4. For all the analyses exploring morphometric variability that follow, the two first components (PC1 and PC2), which together account for more than 98% of the total variance, are used as the morphometrical variables. The last components were considered neglectable (Baylac & Frieß 2005).

Table 1
Taxonomic composition and habitat assignments of the modern African bovid sample.

Subfamily	Tribe	Species	Common Name	Size Class	Habitat Group	n Astragalus	n Prox. phalanx	n Int. phalanx	n Dist. phalanx
Alcelaphinae	Aepycerotini	<i>Aepyceros melampus</i>	Impala	2	Light cover	5	21	17	17
	Alcelaphini	<i>Damaliscus lunatus</i>	Common Tsetsebe	3	Open	2	8	7	8
		<i>Connochaetes taurinus</i>	Blue Wildebeest	2	Open	2	7	7	6
		<i>Connochaetes gnou</i>	Black Wildebeest	3	Open	1	7	6	6
		<i>Alcelaphus buselaphus</i>	Hartebeest	3	Open	2	8	8	8
		<i>Damaliscus pygargus phillipsi</i>	Blesbok	3	Open	5	20	18	17
		Antilopinae	Cephalophini	<i>Sylvicapra grimmia</i>	Grey Duiker	1	Light cover	3	8
<i>Philantomba monticola</i>	Blue Duiker			1	Forest	3	0	0	0
Oreotragini	<i>Oreotragus oreotragus</i>		Klipspringer	1	Heavy Cover	0	2	2	2
Antilopini	<i>Antidorcas marsupialis</i>		Springbok	2	Open	8	9	10	7
	<i>Raphicerus campestris</i>		Steenbok	1	Light cover	6	10	5	3
	<i>Madoqua kirki</i>		Dik-dik	1	Forest	2	0	0	0
Bovinae	Tragelaphini		<i>Tragelaphus scriptus</i>	Bushbuck	2	Forest	3	16	15
		<i>Tragelaphus angasii</i>	Nyala	3	Forest	2	8	8	8
		<i>Tragelaphus strepsiceros</i>	Greater Kudu	3	Heavy Cover	4	8	8	8
Reduncinae	Reduncini	<i>Redunca fulvorufula</i>	Mountain Reedbuck	2	Light cover	4	16	16	16
		<i>Kobus ellipsiprymnus</i>	Waterbuck	3	Heavy Cover	6	10	6	7
Caprinae	Caprini	<i>Ovis canadensis</i>	Mountain Sheep	2	Light cover	0	2	1	0
Total						58	160	142	133

Abbreviations: Prox = proximal, Int = intermediate, Dist = distal.

*Kappelman et al. (1997) and Degusta & Vrba (2003, 2005).

Table 2
Taxonomic composition of the modern sample: Number of specimens in each habitat.

Element	Open	Light cover	Heavy cover	Forest	Total
Astragalus	20	18	10	10	58
Proximal phalanx	59	57	20	24	160
Intermediate phalanx	56	47	16	23	142
Distal phalanx	52	44	17	20	133

Phylogenetic relationships and distances between different species may explain a significant portion of the morphological variability captured by our measurements. We evaluated the strength of the phylogenetic signal associated with morphometric variation by using

Adams's *Kmult* (function *physignal* in the R package *geomorph*, Adams & Otárola-Castillo 2013), which is the extension of the K-statistic method (Blomberg et al. 2013) for multivariate traits. This method compares trait variations observed in a dataset with their expected variations under a Brownian motion evolutionary model, assuming that Bovidae traits evolved according to this model (Blomberg et al. 2003). With this method, a K-value of 1 indicates that the considered trait evolved according to Brownian motion. K-value $\gg 1$ indicates a greater similarity among clades than anticipated by Brownian motion, i.e. a strong phylogenetic signal. In contrast, a K-value close to 0 points to a weak or absent phylogenetic signal. Phylogenetic consensus trees for Bovidae were downloaded from 10Ktrees.nunn-lab.org (Arnold & Nunn 2010). To visualize and explore patterns of morphometric variability in a

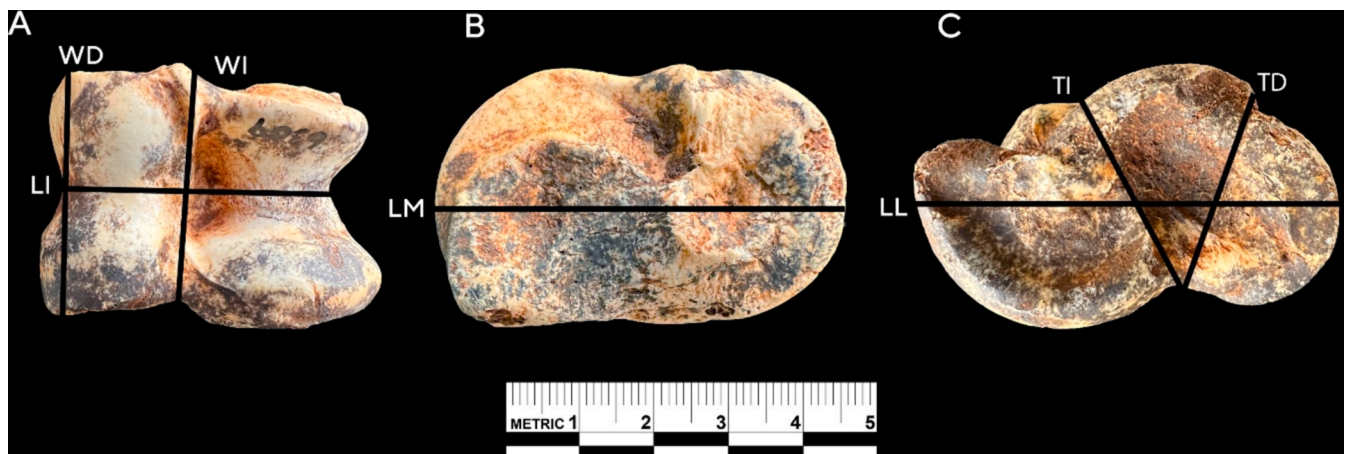


Fig. 2. Caliper measurements were used in this study on an astragalus. Metric abbreviations and descriptions obtained from (Degusta & Vrba 2003): Seven measurements marked on the (A) Anterior view of bovid right astragalus; (B) Medial view of bovid astragalus; (C) Lateral view of bovid right astragalus. (Photographs by R. Sambo).

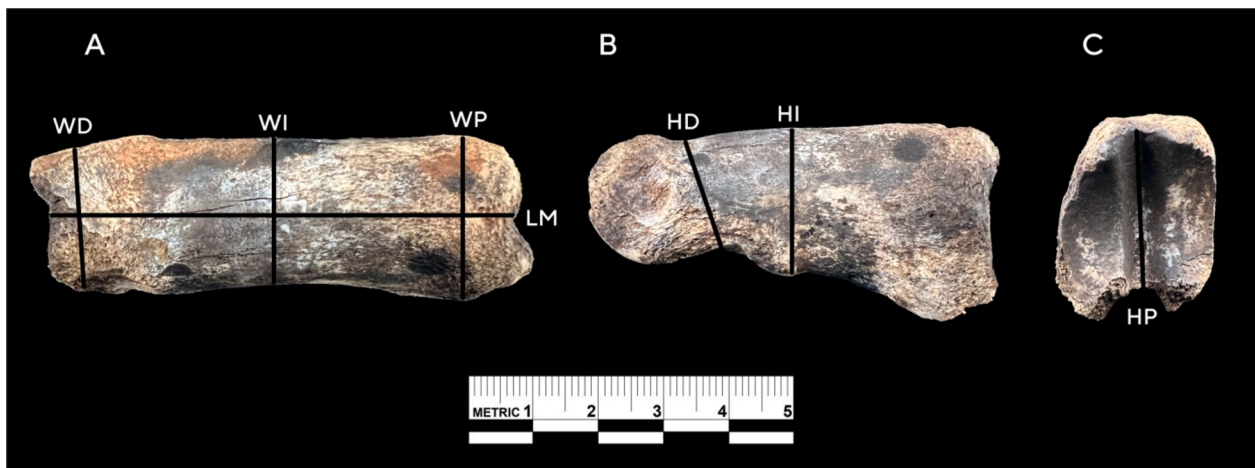


Fig. 3. Caliper measurements on the proximal phalanx were used in this study. Metric abbreviations and descriptions obtained from (Degusta & Vrba 2005): Seven measurements marked on the (A) Dorsal view of the proximal phalanx; (B) Side view of the proximal phalanx; (C) Proximal view of the proximal phalanx. (Photographs by R. Sambo).

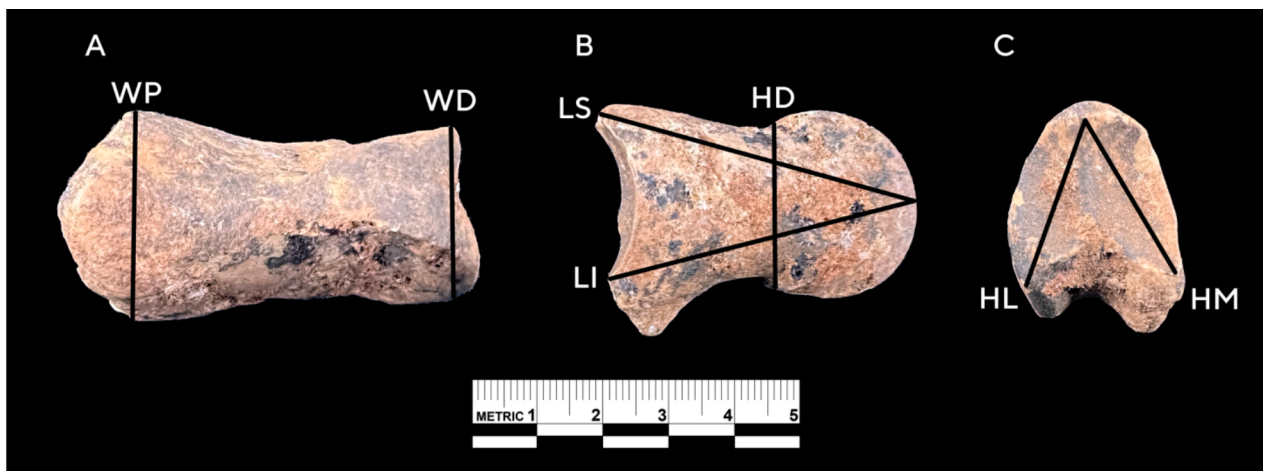


Fig. 4. Caliper measurements on intermediate phalanx were used in this study. Metric abbreviations and descriptions obtained from (Degusta & Vrba 2005): Seven measurements marked on the (A) Dorsal view of intermediate; (B) Side view of intermediate phalanx; (C) Proximal view of intermediate phalanx. (Photographs by R. Sambo).

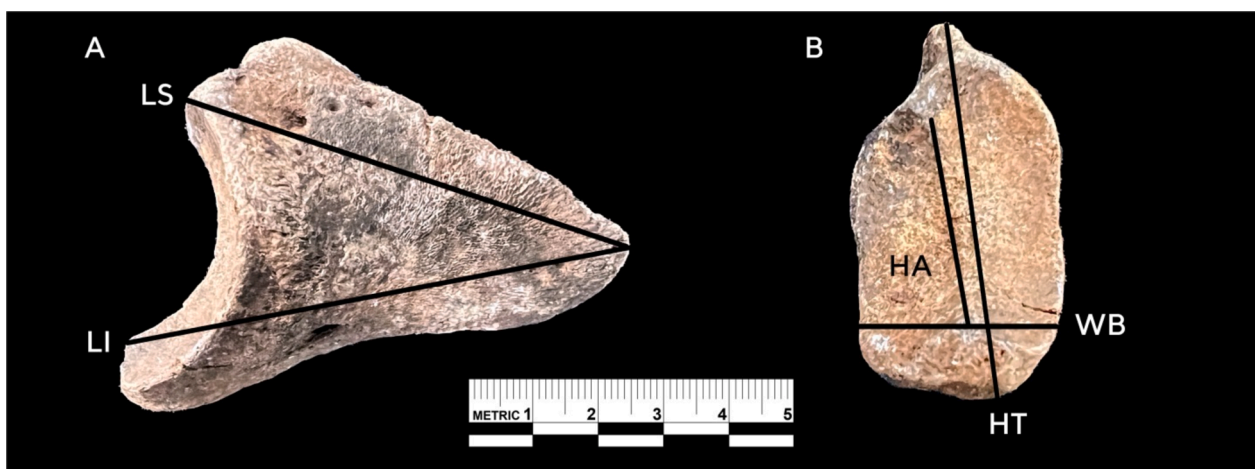


Fig. 5. Caliper measurements on distal phalanx were used in this study. Metric abbreviations and descriptions obtained from (Degusta & Vrba 2005): Five measurements marked on the (A) Side view of distal phalanx (B) Proximal view of distal phalanx. (Photographs by R. Sambo).

Table 3
Measurements used in the analyses (illustrated in Figs. 2-5).

Caliper measurements and abbreviations			
Astragalus	Proximal phalanx	Intermediate phalanx	Distal phalanx
LM – Medial length	LM – Midline length	LS – Superior length	LS – Superior length
LL – Lateral length	WP – Proximal width	LI – Inferior length	LI – Inferior length
TI – Intermediate thickness	WI – Intermediate width	WP – Proximal width	WB – Basal width
TD – Distal thickness	WD – Distal width	WD – Distal width	HA – Articular facet height
LI – Intermediate length	HP – Proximal height	HM – Medial height	HT – Total height
WI – Intermediate width	HI – Intermediate height	HL – Lateral height	
WD – Distal width	HD – Distal height		

Table 4
Results of Phylogenetic Generalized Least Squares (PGLS) regression of PC1 + PC2 against the habitat variable for each extant anatomical element.

Element	λ	F-statistic	Adjusted R ²	p-value
Astragalus	0	3.034	0.29	0.07
Proximal phalanx	0.769	3.208	0.31	0.06
Intermediate phalanx	1	2.746	0.26	0.08
Distal phalanx	0	2.407	0.23	0.12

phylogenetic context, we performed a phylogenetic principal component analysis (pPCA) on the mean MSVs per species, using the *phylobase* (Hackathon 2020) and *adephylo* (Jombart et al. 2017) R packages.

We tested the effect of habitat category on morphometric variation by conducting a Phylogenetic Generalized Least Squares (PGLS) regression (Martins & Hansen 1997) between the morphometrical variables (PC1 and PC2) and the habitat categories. This approach allowed us to assess whether morphometric variation was influenced by different habitat categories while accounting for phylogenetic relationships among the species. The analysis was performed using the R package *capser* (Orme et al. 2013). PGLS analysis returns a lambda value, also known as Pagel's λ , which is a measure of phylogenetic independence (Pagel 1999). This approach finds the value that best summarises the variation between the species at the tips of the phylogenetic tree using a maximum likelihood estimate under a Brownian motion model (Edwards & Cavalli-Sforza 1964; Kamilar & Cooper 2013; Gruwier & Kovarovic 2021, 2022). Under this model, lambda values close to 1 indicate a strong phylogenetic signal, while those close to 0 indicate a weak phylogenetic signal (Freckleton et al. 2002; Molina-Venegas & Rodriguez 2017).

To account for allometry (i.e., size-related changes of morphometric traits), we regressed the morphometric variables (PC1 + PC2) against the natural log of average body mass for each species. Information on weight for each bovid species was obtained from scientific literature (Brain 1974,1981; Klein 1976).

4.3. Inferring paleohabitats with ecomorphology

Discriminant Function Analysis (DFA) was used to test whether morphology could distinguish bovids from different habitats and to predict habitat categories for the fossil samples. DFA is a statistical technique used to classify a set of observations into previously determined, hypothesized habitat groups based on predictor variables (James 1985; Kappelman 1986, 1988, 1991; Plummer et al. 2008, 2015; Bishop et al. 2011). For each element, a Principal Component Analysis (PCA) was performed on the whole MSV dataset (including extant and fossil specimens) to regularize the problem and avoid over-fitting. The scores

of the first two components, which retained more than 95% of the geometric variability, were used as explanatory variables (i.e. predictors) in the DFA. DFA assumes that the predictor variables are normally distributed; this was tested using a Shapiro-Wilk's test (Shapiro & Wilk 1965; Razali & Wah 2011), which detects departures from normality due to either skewness or kurtosis, or both (Althouse et al. 1998). Predictors with non-normal distributions were transformed by applying the Inverse Normal Distribution Function (IDF-normal) (Brophy 1985; Shore 1988; Abernathy & Smith 1993) to satisfy the assumptions about normality, using the R package *bestNormalize* (Peterson 2021). IDF-normal is the distribution of functions inverted and the distribution of the reciprocal of a random variable. With the given mean and standard deviation, it returns the value derived from the normal distribution. According to Abernathy & Smith (1993), this tool can be used to evaluate the equality of variances, perform an analysis of variance, ascertain the value of the normal distribution, and provide the value corresponding to a particular cumulative probability. Box's M (Box 1949) and Bartlett (Bartlett 1937) tests were used to assess the across-group homogeneity, using the *biotools* (da Silva & da Silva 2017) and built-in *stats* packages in R. Quadratic Discriminant Analysis (QDA) was preferred over Linear Discriminant Analysis (LDA) because it relaxes the assumption of homogeneity in variance-covariance matrices across the groups. QDA evaluated the performance of *a priori* classifications and categorized fossil specimens into most likely habitat affiliations. It was performed with 5-fold cross-validation. Cross-validation is based on the leave-one-out procedure or elimination of one specimen from the training set and re-running the analysis. Here, 5-fold cross-validation means that the dataset is divided into five subsets, with each subset used once as a test set while the remaining four serve as the training set, ensuring that the model is validated on different data portions. The performance of each model was evaluated using two main metrics: accuracy and Kappa. Accuracy measures the overall correctness of the model's predictions, and Kappa (or Cohen's Kappa – Cohen 2008) measures inter-rater agreement for categorical items. QDA was carried out using the R package *caret* (Kuhn 2015).

5. Results

5.1. Extant bovid morphometric variability

Results of K-statistics indicate that morphometric variation has no statistically phylogenetic signal for the astragalus ($K = 0.5063$, $p = 0.39$) and the distal phalanx ($K = 0.7438$, $p = 0.075$). However, a weak phylogenetic signal is detected for the proximal phalanx ($K = 0.8492$, $p = 0.037$) and the intermediate phalanx ($K = 0.8892$, $p = 0.03$). Fig. 6 displays a scatterplot of the first two principal component scores of the pPCA.

The visual exploration of morphometric variability within phylo-morphospace reveals distinct clustering patterns for each anatomical element, alongside marked differences in morphometric divergence among tribes. In the Reduncini tribe, the two species *Kobus ellipsiprymnus* and *Redunca fulvorufula* exhibit significant morphometric differentiation across all anatomical elements. In contrast, members of the Alcelaphini tribe display a relatively uniform morphology across each skeletal element. Among the Tragelaphini, the morphometric landscape is more complex, and varies according to the bone: while the astragalus retains a strongly conserved morphometry, the three phalanges cluster far from one another. Consequently, the overall distribution of species within morphological space only partially reflects their phylogenetic relationships, consistent with the previously observed weak or statistically non-significant phylogenetic signal.

Results of the PGLS analyses (Table 4) show that the habitat category has a limited impact on the overall morphometric dataset. The proximal phalanx exhibits the most significant relationship with habitat variables, with an F-statistic of 3.208 and an adjusted-R² of 0.31, suggesting that approximately 31% of the morphometric variability can potentially be

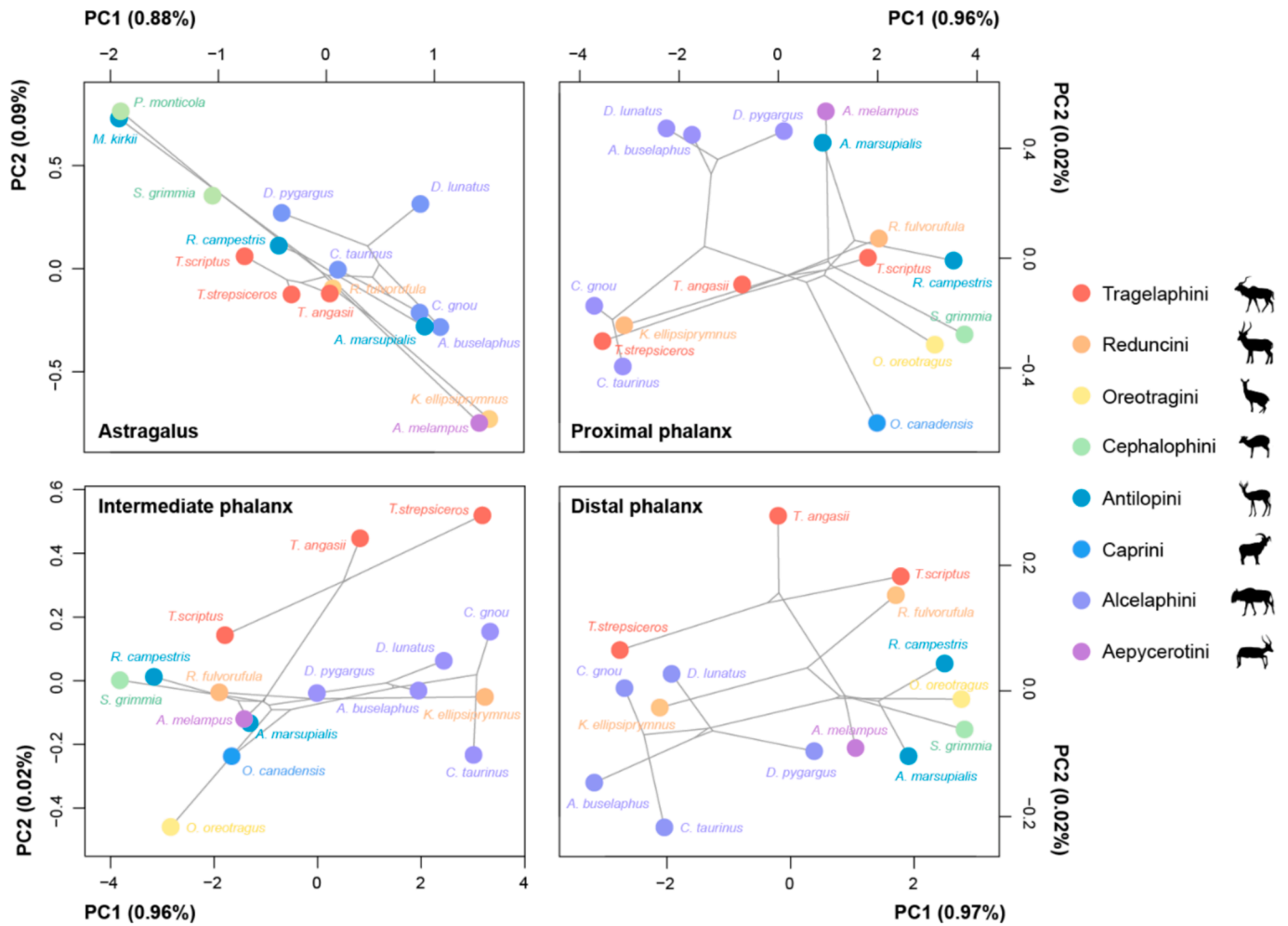


Fig. 6. Phylomorphospace of the two principal components identified by pPCA, showing morphometric variation in several African extant bovid species. Colours are used to differentiate among each tribe. Phylogenetic relationships among species are visualized by grey lines.

explained by habitat variables. Pagel’s $\lambda = 0.769$ indicates that the model assumes a moderate phylogenetic signal in the data, implying that evolutionary history has a fair influence on the observed relationship. However, the p -value is slightly above the 0.05 threshold, indicating that the relationship is not statistically significant at the conventional level, though it is close to significance. The intermediate phalanx exhibits a strong phylogenetic signal ($\lambda = 1$) and a moderate association with habitat variables (F -statistic = 2.746), but the statistical significance of $p = 0.08$ warrants further investigation or consideration of larger sample sizes. In contrast, the astragalus and the distal phalanges exhibit no phylogenetic signal ($\lambda = 0$). The distal phalanx appears to be the least informative bone regarding adaptations to habitat, as expressed by a lower F -statistic (2.407) and a p -value of 0.12.

A significant part of morphometric variability is explained by the influence of size on the morphology of each anatomical element, as shown in Table 5.

The allometric effect is strong for the phalanges ($R^2 = 0.58, 0.69$, and

Table 5
Results of regressions of PC1 + PC2 against log(body mass) for each extant anatomical element.

Element	R ²	p-value
Astragalus	0.36	0.014
Proximal phalanx	0.58	< 0.001
Intermediate phalanx	0.69	< 0.001
Distal phalanx	0.72	< 0.001

0.72 for the proximal, intermediate, and distal phalanx, respectively, with $p < 0.001$ for each element) and moderate for the astragalus ($R^2 = 0.36, p = 0.007$). These values are similar to those observed in other studies using a limited number of measurements in a classical morphometric context (e.g., Degusta & Vrba 2003, 2005; also see Curran & Haile-Selassie 2016; Gruwier & Kovarovic 2021, 2022).

Those results may affect the performances of our predictive models used in subsequent analyses, since factors such as allometry or phylogeny contribute more to morphometric variation than habitat.

5.2. Discriminant function analyses – modern bovid sample

Four scatterplots showing morphometric variation summarized by the two QDA predictors are presented in Fig. 7.

Cross-validated performances and results are given in Table 6 and Table 7. They indicate varying levels of classification performance across the different bones studied. In particular, the intermediate phalanx shows the highest accuracy, with 72.0% of the samples correctly predicted, followed closely by the intermediate phalanx with an overall accuracy of 67.5%. The corresponding Kappa values of 0.581 and 0.527, respectively, indicate a moderately fair agreement between the model’s predictions and the actual habitats. The astragalus and distal phalanx performed less in predicting habitat. Their overall accuracy was 58.8% and 58.9%, respectively.

The classification success rates of all four models used in this study are mostly similar to some of those derived in previously published

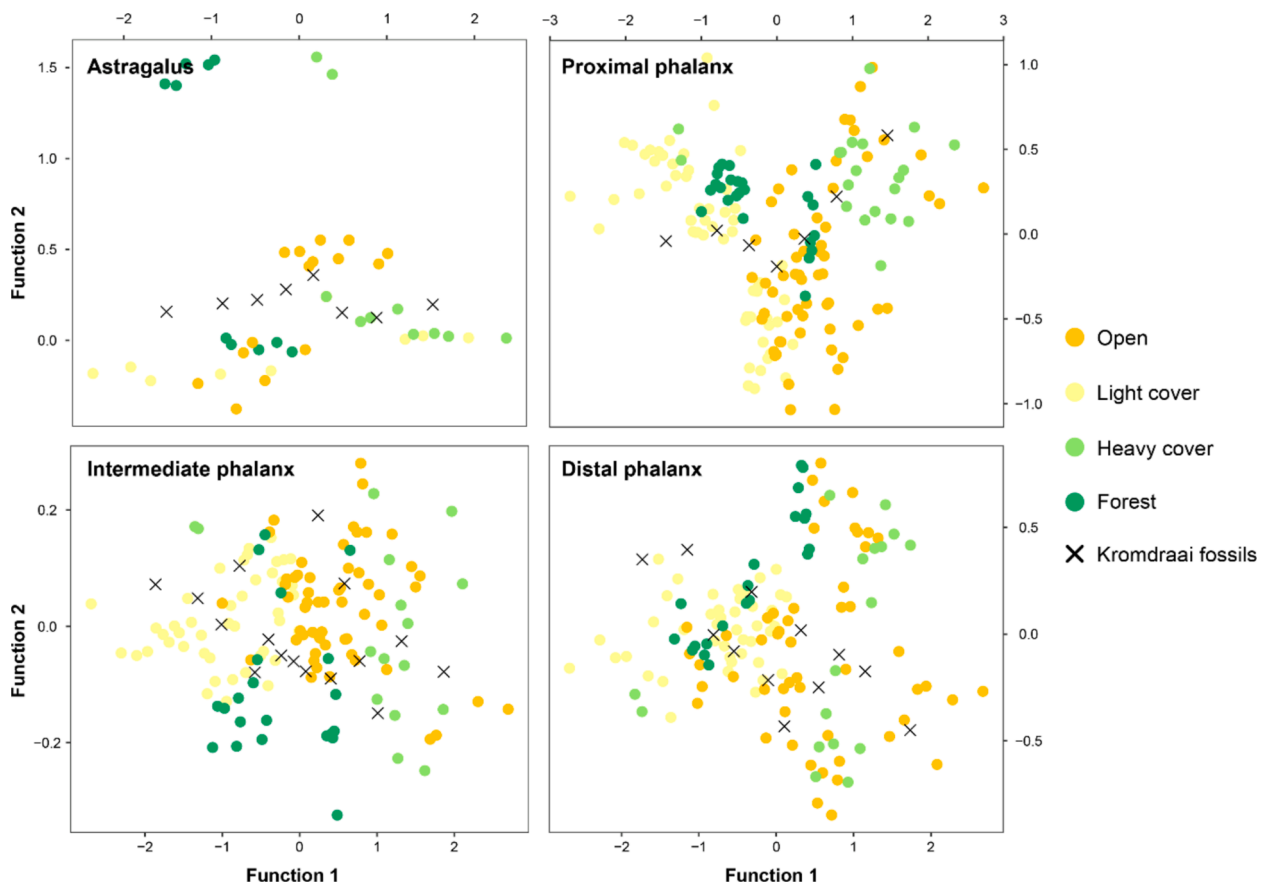


Fig. 7. Scatterplots of discriminant Function 1 versus Function 2 for the modern bovid sample. The actual habitat group for the specimens are denoted by colored circles. The fossil bovids from Kromdraai, whose habitat will be determined via DFA, are indicated by a black cross.

Table 6
Cross-validation classification rates for QDA analyses.

Performance metric	Astragalus	Proximal phalanx	Intermediate phalanx	Distal phalanx
Accuracy	0.588	0.675	0.720	0.589
Kappa	0.408	0.527	0.581	0.389

studies (DeGusta & Vrba 2003, 2005; Weinand 2007; Kovarovic & Andrews 2007; Plummer et al. 2008; Bishop et al. 2011; Barr 2015; Dumouchel et al. 2021), while some are comparably lower than those in other previously published studies (see Table 8 for success rate comparisons). Table 9 shows specific misclassifications made by DFA that are relevant to taxa. For all four models, misclassified specimens are classified into the next habitat group. For example, the astragalus model misclassified all forest-adapted *T. scriptus* and *T. angasii* species to open and light cover. The proximal phalanx model misclassified all heavy cover-adapted *O. oreotragus* into light cover and all *T. angasii* were misclassified into the open category. The intermediate phalanx model misclassified all the heavy cover-adapted *O. oreotragus* species into light cover. Lastly, the distal phalanx model misclassified all the heavy cover species into the next closest group. For example, *O. oreotragus* was misclassified into light cover and forest, *T. strepsiceros* into open and forest, and *K. ellipsiprymnus* into open category.

5.3. Discriminant function analyses – Combined fossil results

The Kromdraai fossil bovid classification to habitat group is provided in Fig. 8. Based on the discriminant function results, all four habitats are represented in the KW-Unit P fossil sample, with the majority of

Table 7
Confusion matrix giving cross-validated QDA classifications of modern samples by habitat group (four-habitat model).

Actual habitat	Predicted habitat			
	Forest	Heavy cover	Light cover	Open
Astragalus				
Forest	5	0	0	0
Heavy cover	0	4	2	0
Light cover	3	5	11	4
Open	2	1	5	16
Proximal phalanx				
Forest	14	0	3	3
Heavy cover	0	6	0	6
Light cover	2	2	43	5
Open	8	12	11	45
Intermediate phalanx				
Forest	15	0	3	0
Heavy cover	0	5	0	5
Light cover	3	2	33	2
Open	4	10	9	51
Distal phalanx				
Forest	8	2	5	4
Heavy cover	0	0	0	0
Light cover	10	1	36	14
Open	2	14	3	34

specimens (48.7%) indicating adaptations to open habitats. For the astragali, the highest habitat classification is light cover at 50% and open at 37.5% as the second highest, followed by forest at 12.5%. The

Table 8
Accuracies of habitat prediction methods from bovid astragali and phalanges.

Habitat scheme	Element	Accuracy (%) ^a	Method ^b	Reference
Four habitats	Astragalus	67	LDA	DeGusta & Vrba (2003)
Four habitats	Proximal phalanx	71	LDA	DeGusta & Vrba (2005)
Four habitats	Intermediate phalanx	71	LDA	DeGusta & Vrba (2005)
Four habitats	Distal phalanx	71	LDA	DeGusta & Vrba (2005)
Four habitats	Astragalus	79	Comb.	Weinand (2007)
Four habitats	Astragalus	78	LDA	Weinand (2007)
Four habitats	Astragalus	74	rpart	Weinand (2007)
Seven habitats	Proximal phalanx	57	LDA	Kovarovic & Andrews (2007)
Seven habitats	Intermediate phalanx	55	LDA	Kovarovic & Andrews (2007)
Seven habitats	Distal phalanx	51	LDA	Kovarovic & Andrews (2007)
Four habitats	Astragalus	87	LDA	Plummer et al. (2008)
Four habitats	Astragalus	87	LDA	Bishop et al. (2011)
Four habitats	Proximal phalanx	90	LDA	Bishop et al. (2011)
Four habitats	Intermediate phalanx	88	LDA	Bishop et al. (2011)
Four habitats	Distal phalanx	87	LDA	Bishop et al. (2011)
Four habitats	Astragalus	66	LDA, QDA	Barr (2015)
Four habitats	Astragalus	60	LDA	Dumouchel et al. (2021)
Four habitats	Astragalus	59	QDA	This study
Four habitats	Proximal phalanx	68	QDA	This study
Four habitats	Intermediate phalanx	72	QDA	This study
Four habitats	Distal phalanx	59	QDA	This study

^a Accuracies are presented as the percentage of those individuals correctly assigned to habitat class and as the value of the percentage relative to chance.

^b QDA, quadratic discriminant analysis; LDA, linear discriminant analysis; rpart, recursive partitioning and Comb., the combination of the LDA and recursive partitioning methods.

proximal phalanx classified both open and light cover at 42.9% equally, followed by heavy cover at 14.2%. The intermediate phalanx classified habitat groups for the fossil specimens from highest to lowest in the following order: 56.2% open, 37.5% light cover, 6.3% forest. Similarly, the discriminant function for the distal phalanx produced the highest classification rate for open habitat at 58.3%, and light cover at 41.7%, with no forest and heavy cover.

6. Discussion

6.1. The influence of size and phylogeny

The significant positive allometric correlation between the data for the phalanges (MSVs) and body mass ($R^2 = 0.64, 0.65, \text{ and } 0.72$) suggests that each element size was an acceptable approximation for total body mass. Similarly, a strong correlation between measurements of the three sets of phalanx and body mass was demonstrated ($R^2 = 0.89\text{--}0.91$) in [Degusta & Vrba's \(2005\)](#) study of bovid phalanges. This can be explained at least in part by the fact that our measurements are limited in number and primarily reflect the general proportions of each skeletal element (such as its length, width, etc.) rather than the specific details of

its anatomy. More refined methods for describing morphology, such as geometric morphometrics (GMM), should be less affected by the influence of allometry on morphometric variables. For instance, [Gruwier & Kovarovic \(2022:12\)](#) used GMM to study the phalanx of cervids and found a significant but weak correlation ($R^2 = 0.062, p = 0.002$), implying that “only a small portion of the morphology is explained by allometry”. Among the four skeletal elements in our study, the astragalus has the most limited allometric effect ($R^2 = 0.041, p = 0.007$). The morphology of the bone in relation to the habitat group is not well explained by the influence of the phylogeny; on the astragalus scatterplot, we can see that some tribes cluster well together (for instance, Alcelaphini are almost plotted together for each bone, while the two species of Reduncini have a distinctive morphology). This probably suggests that the astragalus morphology is tightly linked to locomotor adaptations (see [Curran 2015; Curran & Haile-Selassie 2016; Dunn & Avery 2021](#)). Hence its morphology is a good proxy for locomotion in different habitats, while the proximal, intermediate and distal phalanx are more phylogenetically conservative.

6.2. Palaeoenvironmental implications of the Kromdraai Unit P fauna

The QDA predicted the average habitat classifications for the fossil samples. The high concentration of open-adapted bovids (48.7%) across all samples suggests that most of these bovids frequented environmental settings with grasslands, arid country, and a category ecotone bordering open country. Relatively, light cover-adapted bovids (43.0%) suggest the presence of light bushes, tall grasses, and hilly areas, which would allow for less complex manoeuvrability. The environment was also suitable for forest (4.7%) and heavy cover-adapted bovids (2.3%) inhabiting a continuous tree canopy and heavy bushes, woodlands, and densely vegetated swamps. The tall grasses (edaphic grasslands for fresh grazers), bushland, woodland, vegetated swamps and forest at KW-Unit P are indicative of a riparian environment that supports the rich vegetation. This points to the presence of a water source in the vicinity, which in this case is the known existing nearby ancient spring feed of the Bloubank River. The presence of these different arrays of habitats suggests that during the deposition of KW-Unit P, the site could have been a transitional zone of vegetation or an ecotone bordering light cover, open and heavy cover habitats. Morphologically, bovids from KW-Unit P display varied morphological adaptations best suited for mosaic habitats.

As noted earlier, Kromdraai is situated on the southern side of the Bloubank River, 2 km east of Sterkfontein Caves. In the past, the river was larger and wider ([Kuman 1996; Kuman & Clarke 2000; Martini et al. 2003; Kuman et al. 2018](#)) but now it is 500 m away from Sterkfontein (measurements courtesy of L. [Bruxelles pers. comm. 2017](#) to [Kuman et al. 2018](#)). If we rely on the mapping estimates of the terrace gravel provided by T.C. Patridge, then it is possible that Kromdraai was approximately 300–450 m away from the river. This proximity would have supported the riparian vegetation, such as tall grasses, bushland, woodland, vegetated swamps and forest. However, our results do not show high proportions of water-dependent, heavy cover and forest-adapted bovids. It is important to mention here that freshwater birds such as Anatidae ([Pavia 2020](#)) and the Cape clawless otter *Aonyx capensis* ([Fourvel et al. 2016, 2018](#)) are abundant within the KW-Unit P faunal assemblage and these species have narrow habitat tolerance and highly dependent on water environments.

The palaeoenvironmental reconstruction revealed by the current study is in general agreement with previous reconstructions for both ‘Kromdraai B’ (KB) as a whole and KW-Unit P. [Vrba's \(1975\)](#) ‘alcelaphini + antilopini criterion’ (AAC) study of bovid assemblages from key South African Plio-Pleistocene sites, suggested that the high proportion of Alcelaphini and Antilopini species identified at KB and KW-Unit P indicates the predominance of open grassland environments ([Hanon et al. 2024](#)). The result of KB should be treated with caution since the stratigraphic provenience of most faunal remains recovered before 2014

Table 9
Modern taxa – Discriminant function habitat classifications by taxa.

Species	Habitat Group	Astragalus		Proximal phalanx		Intermediate phalanx		Distal phalanx	
		#Classified	#Misclassified ^a	#Classified	#Misclassified ^a	#Classified	#Misclassified ^a	#Classified	#Misclassified ^a
<i>Aepyceros melampus</i>	Light cover	4	1HC	20	11O	8	9O	12	3O, 2F
<i>Damaliscus lunatus</i>	Open	1	1LC	8		7		4	4F
<i>Connochaetes taurinus</i>	Open	1	1O, 1LC	6	1HC	6	1HC	6	
<i>Connochaetes gnou</i>	Open	1		2	4HC	2	4HC	6	
<i>Alcelaphus buselaphus</i>	Open	2		9		8		8	
<i>Damaliscus pygargus</i>	Open	3	2LC	15	3F, 1HC, 1LC	20		10	7LC
<i>Sylvicapra grimmia</i>	Light cover	3		8		8		7	1F
<i>Cephalophus monticola</i>	Forest	3							
<i>Antidorcas marsupialis</i>	Open	8		5	4LC	8	2LC	7	
<i>Raphicerus campestris</i>	Light cover	3	3O	10		5		3	
<i>Madoqua kirki</i>	Forest	2							
<i>Oreotragus oreotragus</i>	Heavy cover			0	2LC	0	2LC	0	1LC, 1F
<i>Tragelaphus scriptus</i>	Forest	0	1O, 2LC	14	2LC	1	1O, 3LC	2	10LC
<i>Tragelaphus angasii</i>	Forest	0	1O, 1LC	0	8O	6	2O	6	2O
<i>Tragelaphus strepsiceros</i>	Heavy cover	2	1O, 1LC	4	4O	3	5O	0	7O, 1F
<i>Redunca fulvorufula</i>	Light cover	2	2O	13	3F	11	3F	14	2F
<i>Kobus ellipsiprymnus</i>	Heavy cover	2	4LC	2	8O	2	5HC	0	7O
<i>Ovis canadensis</i>	Light cover			2		1			

^a This column lists the specimens of those taxon that were misclassified, broken down by habitat group (abbreviated using the initial letter of the group) that they were mistakenly assigned to by the discriminant function. Abbreviations: O = open; L.C. = light cover; H.C. = heavy cover; F = forest.

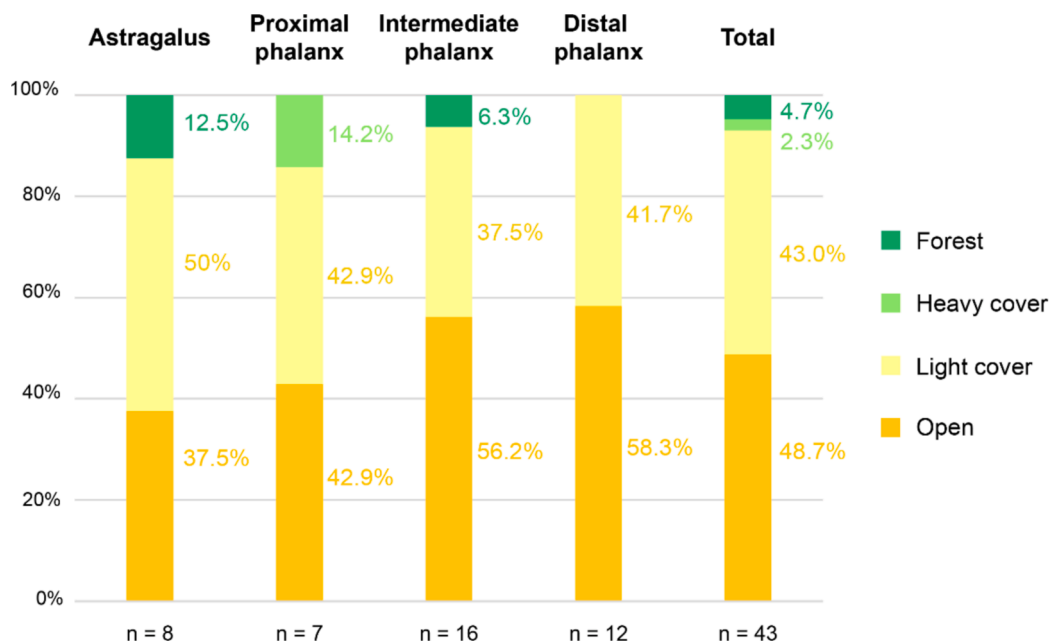


Fig. 8. Habitat classification of KW-Unit P fossils by anatomical part for each anatomical element, and for the total number of elements.

is unknown (Braga et al. 2017). A more comprehensive study by Reed (1997) argued that KB was open grassland due to the high percentages of terrestrially adapted animals. Elton’s (2001) functional morphology analysis of the large Papionini monkey (*Papio robinson*) also supports the presence of open habitats at KB. Taxonomic attributions of bovids and carnivores from KB indicate open and savanna grassland environments (Vrba 1981; Brain 1981; Fourvel & Thackeray 2022). In addition, isotopic evidence extracted from enamel of one fossil rodent (*Aethomys [Micaelamys] namaquensis*) at KB supports the presence of predominant C₄ grassland environments (Thackeray 1999). Likewise, the diverse faunal assemblage at KW-Unit P corresponds with the reconstruction of the current study, indicating light cover and open environments. For example, the bovid assemblage is dominated by a marked diversity (i.e. *Gazella gracilis*, *Makapania broomi*, *Numidocapra cf. porrocornutus*, *Tragelaphus strepsiceros*, *Oreotragus oreotragus*, *Raphicerus campestris*, *Damaliscus lunatus*) all of which characterizes Unit P as a grassland-

dominated environment (Hanon et al. 2024).

Although carnivores are not the best palaeoenvironmental indicators, the presence of the Cape fox (*Vulpes chama*), the wild dog (cf *Lycaon*) and the jackal (*Canis* sp.) at KW-Unit P suggests open, semi-arid environments (Kingdom & Hoffman 2003; Fourvel et al. 2018). The taxonomic analysis of the KW-Unit P faunal assemblage indicates the presence of a leopard (*Panthera pardus*) (Hanon et al. 2024). This ambush predator is known to be adapted to wide geographic and habitat-type ranges (Brain 1981) but prefers tree covers near year-round standing water (Pickering et al. 2004). The presence of the bird *Geronticus thackerayi*, sp. nov. strongly indicates rocky outcrops or cliffs in the area with a nearby water supply for breeding and open dry savanna for feeding (Pavia 2020). The comparison of the bird assemblages from the older Kromdraai Unit P and the younger deposits from Coopers’ D suggests a transition from woody habitats to more open habitats during the Plio-Pleistocene transition (Pavia et al. 2022).

Furthermore, the representation of forest and heavy cover-adapted bovids as revealed by this study agrees with Hanon's et al. (2024) study of bovids, which indicates that the overall taxonomic distribution of KW-Unit P has low proportions of forest and heavy cover taxa. The heavy cover element, as seen in this study, was also observed at KB as a whole with the predominance of cercopithecoids whose presence indicates relatively wooded and moist environmental settings (Fourvel & Thackeray 2022). One *Ourebia ourebi* specimen identified at KW-Unit P by Fourvel et al. (2018) supports the presence of heavy cover or closed environments. The presence of the Bloubaan River in the area and the evidence of a riparian environment, as suggested by the current study also corresponds with Reed's (1997) habitat reconstruction at KB. Although she did not specify the species, she argues that a high proportion of frugivorous mammals whose habitat preference is riparian woodland is present. However, Reed (1997) does not also specify or allude to the dominance of the riparian woodland component. The Cape clawless otter *Aonyx capensis* and the African *Civettictis* cf. *civetta* were also identified at KB and KW-Unit P. Both species are known to live in the vicinity of water or a riverine area (Lariviere 2001; Stuart & Stuart 2008).

6.3. Comparison with other Cradle sites

Palaeoenvironmental interpretations presented here for KW-Unit P are similar to those presented at Sterkfontein Member 4 (STK-M4) ~ 3.4 Ma (Granger et al. 2022) and Member 5 East, Oldowan (STK-M5E, Oldowan) ~ 2.18 Ma (Granger et al. 2015), Swartkrans Member 1 Lower Bank (SKX-M1 LB) ~ 2.2 Ma (Kuman et al. 2021) and Member 2 (SKX-M2) ~ 1.5 Ma (Vrba 1985; Brain 1993). Sambo's (2020) ecomorphological study reports that bovids from these four deposits had varied morphological adaptations to mosaic habitats. The general observation was that there was a substantial decrease in the proportions of heavy cover and forest-adapted bovids over time at each site compared to those in open and light cover habitats, signalling a significant period of environmental change. These observations are further supported by previous palaeoenvironmental research based on various methods (e.g.,

bovid and micromammal taxonomy, isotopic analysis, functional morphology, and palaeobotany) for the deposits at Sterkfontein (see Reed 1997; Bamford 1999; Bishop et al. 1999; Kuman & Clarke 2000; Avery 2001; Luyt & Lee-Thorp 2003; Reynolds & Kibii 2011; Leichliter et al. 2017), and Swartkrans (see Vrba 1975; Brain 1981; Watson 1993; Avery 2001; Lee-Thorp et al. 2007; Reed & Rector 2007; Leichliter et al. 2017). Table 10 compares the site's palaeoecological assessments. The Kromdraai Unit P is assumed to record a period between Sterkfontein Member 4 and the younger Sterkfontein Member 5 and Swartkrans Member 1 (Braga et al. 2017, 2022b). Therefore, KW-Unit P most likely corresponds to a phase of significant environmental shift.

6.4. Palaeoenvironmental implications for *Paranthropus robustus*

Investigating palaeoenvironments using faunal assemblages from KW-Unit P offers us an opportunity to indirectly infer the selective environments associated with *Paranthropus robustus* (*P. robustus*). Our results are not entirely limited to KW-Unit P but also address 'Kromdraai B' (KB) as a whole. Based on our reconstructions, *P. robustus* (specializes in tough fallback foods – Grine 1981) has found at KB seems to have thrived in mosaic environmental settings dominated by open habitats (grasslands, arid country and ecotone), light cover (edaphic grasses, light bushes, and hilly areas) and a considerable element of forest for tree cover and heavy cover constituting heavy bushes, woodlands and densely vegetated swamps. This result is supported by Reed's (1997) claims that *Paranthropus robustus* frequented both wooded and more open environments but consistently foraged edaphic grasslands and wetlands. As mentioned above, KW-Unit P straddles a period recorded for some Plio-Pleistocene deposits at Sterkfontein and Swartkrans. According to Vrba's (1975) AAC study, this period saw major events of African faunal turnover, linking faunal changes to the aridity and the expansion of grasslands between 2.7–1.7 Ma. These events coincided with significant environmental shifts and hominin evolution in both East and South Africa and led to the extinction of australopithecines and the endurance of *P. robustus*. Therefore, *P. robustus* at Kromdraai existed around the time when the environment was gradually becoming drier

Table 10

Comparison sites with dates and palaeoecological assessments.

Site	Members	Published dates	Palaeoecological assessments	Method for palaeoecological reconstruction	References
Sterkfontein	Member 4 (<i>Australopithecus africanus</i>)	3.4 Ma, Simple and isochron cosmogenic nuclides (Granger et al. 2022).	Mosaic habitat: forest, open woodland/ bushland, and grassland with riparian forest in the vicinity.	Bovid taxonomy, palaeobotany, bovid carbon isotope analysis of micromammals, bovid ecomorphology.	Vrba (1975,1980); Reed (1997); Bamford (1999); Kuman & Clarke (2000); Luyt & Lee-Thorp (2003); Leichliter et al. (2017); Sambo (2020)
	Member 5 East, Oldowan infill (<i>Paranthropus</i> and <i>Homo habilis</i>)	2.18 ± 0.21 Ma, Cosmogenic Nuclides (Granger et al. 2015).	Drier and more open habitat and tree cover with riparian forest in the vicinity.	Bovid taxonomy, taxon-free analysis of bovids, carbon isotopes, and bovid ecomorphology.	Vrba (1975); Reed(1997); Bishop et al. (1999); Kuman& Clarke (2000); Luyt & Lee-Thorp (2003); Reynolds & Kibii (2011); Sambo (2020)
Swartkrans	Member 1,Lower Bank (LB) (<i>Paranthropus robustus</i> , <i>Homo ergaster</i> , <i>Homo</i> sp.)	~2.2 Ma, Cosmogenic Nuclides (Kuman et al. 2018).	Moderately open savanna, grassland with tree cover, savanna woodland near a river with reed beds.	Alcelaphini- Antilopini Index (ACC), bovid taxonomy, functional morphology, carbon isotopes of micromammals, and bovid ecomorphology.	Vrba (1975,1980); Watson (1993); Reed (1997); Avery (1998); Lee-Thorp et al. (2007); Reed &Rector (2007); de Ruiter et al.(2008); Leichliter et al. (2017); Sambo (2020)
	Member 2, (<i>Paranthropus robustus</i> , <i>Homo</i> sp.)	1.5 Ma, Bovid and equid data (Vrba 1985; Churcher & Watson 1993; Brain 1993).	Wooded grassland with wetlands, open savanna, and riparian forest in the vicinity.	Bovid functional morphology taxonomy and bovid ecomorphology.	Vrba (1975); Watson (1993); Reed (1997); Lee-Thorp et al. (2007); Sambo (2020)
Kromdraai	Unit-P	2.9 and 1.8 Ma, Bovid biochronology data (Hanon et al. 2024).	Mosaic habitat: dominated by open and light cover habitats indicating open savanna and grasslands, with moderate riparian forest, woodlands and bushes.	Bovid ecomorphology.	This study

and more open. It is important to note that in analyses where a limited number of habitat categories (e.g., a four-habitat system) are being used, actual habitat variation will inevitably be oversimplified, but this is a necessary trade-off to allow for robust statistical analyses (Curran 2009; Gruwier & Kovarovic 2022). Ecomorphology is a reliable method because it visualizes differences between habitat categories to improve our ability to interpret results. In this case, ecomorphology has demonstrated that Kromdraai Unit-P had mostly open and light cover-adapted bovids.

7. Summary and conclusion

The application of bovid ecomorphology has provided insights into the palaeoenvironmental conditions at KW-Unit P. All four elements used produced reliable predictive results for bovids at KW-Unit P. This deposit is characterized as ‘mosaic’ with different types of habitats (represented in varying degrees) ranging from open, light cover, forest and heavy cover suitable for bovids with varied morphological adaptations in less complex and dense environmental settings. These environmental settings dominated by open habitats, would have been conducive for *P. robustus* that frequented both open and closed habitats. The nearby palaeo-Bloubank River was a great source of support for the riparian vegetation (e.g., tall grasses, bushland, vegetated swamps, forest and woodland). In conclusion, the availability of large samples in future for the astragali and phalanges can potentially produce more reliable estimates of past environments. We hope to expand the current sample size and include more specimens recovered from the ongoing excavations at Kromdraai.

CRedit authorship contribution statement

Recognise Sambo: Writing – review & editing, Writing – original draft, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Raphaël Hanon:** Writing – review & editing, Supervision, Conceptualization. **Nompumelelo Maringa:** Writing – review & editing. **Christine Steininger:** Writing – review & editing, Supervision, Funding acquisition. **Bernhard Zipfel:** Writing – review & editing, Supervision. **José Braga:** Writing – review & editing, Validation, Supervision, Conceptualization. **Pierre Linchamps:** Writing – review & editing, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2024.104871>.

Data availability

Data will be made available on request.

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