

Ecomorphology of the cervid intermediate phalanx and its implications for palaeoenvironmental reconstruction

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Abstract:

This paper reports on newly developed ecomorphological models for the cervid intermediate phalanx. Using a geometric morphometric approach we quantitatively assess the overall gracility of the bone, the depth and concavity of the proximal articulation and the roundness and symmetry of the distal articulation in the intermediate phalanx, to establish relationships between morphology, locomotor behavior and environment. The morphology of the phalanx was found to vary along a gradient from gracile phalanges with shallow proximal articulations in forms adapted to yielding substrate, to robust phalanges with deeper proximal articulations in taxa adapted to firm substrate. Phylogeny and allometry are accounted for using regressions and phylogenetic comparative methods. Although the results indicate phylogeny explains part of the morphological variation, overall the shape of the intermediate phalanx appears mainly

driven by differences in function. Consequently, this element promises to be a useful palaeoenvironmental proxy that can be applied on fossil assemblages with cervid remains.

Keywords: Cervidae, palaeoecology, ecomorphology, morphometrics, locomotion

1. Introduction

Artiodactyls are a common group in Plio-Pleistocene fossil assemblages (Kurten 1968). Because of their high species diversity, which includes many habitat specialists (Putman & Fluek 2011, Barr 2014), they have played an important role in palaeoenvironmental reconstructions of hominin sites (e.g. Vrba 1975, Gentry & Gentry 1978, Plummer & Bishop 1994, Kovarovic & Andrews 2007, Forrest et al. 2018). Traditionally, such studies have examined the presence or absence of certain taxa in the fossil record as an indicator of specific environmental conditions (e.g. Vrba 1975, Gentry & Gentry 1978, Shipman & Harris 1988, White et al. 2009). Although this taxonomically focussed approach has undeniably contributed to our understanding of the ecological context of early human evolution (Andrews & Hixon 2014), it has the potential weakness that it relies on the assumption that the habitat preferences of extinct species were similar to those of their closest living relatives (Andrews 1995).

To circumvent this problem, some researchers have instead focused on the functional morphology of skeletal elements and their relation to ecological variables (e.g. Bishop 1994, Bishop *et al.* 2006, Degusta & Vrba 2003, Scott 2004, Kovarovic & Andrews 2007). In this ecomorphological approach, morphological patterns in extant species are compared with those observed in extinct taxa, which allows for inferences to be made about probable adaptations in fossils (Degusta & Vrba 2003, Andrews & Hixon 2014, Gruwier & Kovarovic 2021). This approach

has the advantage that it directly considers how animals functioned in their ecosystem (Curran 2012), independent of their taxonomic affinity (although see Klein et al. 2010).

Although palaeoecologically focussed ecomorphological analyses have been conducted on multiple artiodactyl families, including bovids (e.g. Kappelman 1988, Kappelman *et al.* 1997, Scott 2004, Plummer *et al.* 2008, Schellhorn 2009, Barr 2018) and suids (e.g. Bishop 1994, Bishop *et al.* 2006), the Cervidae have, so far, received comparatively little attention (e.g. Curran 2012, 2015). Deer fossils are, nevertheless, common in Pleistocene sites throughout Eurasia (Kurten 1968) and their morphology is thought to be constrained by similar selective pressures as the bovids (Geist 1998).

Acknowledging the potential of cervid postcranial elements as a proxy for palaeoenvironmental reconstruction, we present here newly developed ecomorphological models for the intermediate phalanx. Although the focus of our study is on extant cervids, the models we present are intended as a foundation for future palaeontological applications. The selection of this element, with an often fully intact preservation in the fossil record (Aniceti 2020), was also made with an eye on the later inclusion of extinct taxa. In addition, this element of the locomotor apparatus had potential because a correlation between phalangeal morphology and environmental variables was already demonstrated for other mammalian families (Leinders 1979, Köhler 1993, Degusta & Vrba 2005a, Polly 2007). If such a correlation can also be demonstrated for the cervid family, our models can ultimately be applied on fossil specimens and allow for inferences to be made about the characteristics of the palaeoenvironments inhabited by these extinct taxa. As such, cervid fossils can in the future act as a proxy to improve our understanding of past ecological conditions.

2. Theory and functional framework

Artiodactyls have a number of behavioural strategies to cope with predation pressure, but when detected, flight is usually the main predator evasion strategy (Geist 1998). As a consequence, these animals have evolved different modes of locomotion, employed when fleeing from a pursuer. Little concrete data is currently available about the precise relationship between cervid evasion tactics and locomotion. Although other escape behaviours, such as galloping and trotting, exist (Blank 2018), there are generally five main locomotor strategies used by artiodactyls to escape predators: leaping (vertical jump), bounding (long horizontal jump), tacking or zig-zag running (sharp turn that suddenly changes course), stotting (a bouncing gait) and prancing (type of pronounced and exaggerated high step) (Caro, 1986, 1994, Caro et al., 2004). The latter two behaviours are presumably intended to wrongfoot the predator (Caro, 1994, Caro et al. 2004), but tacking is more common when evading predators in dry, open habitat (Caro et al. 2004), while leaping is preferred when animals flee in environments with a dense vegetation and complex terrain (Caro, 1994, Gruwier & Kovarovic 2021).

Researchers have demonstrated that the association between predator evasion strategy, locomotion and the structure of the habitats in which artiodactyls are found, impacts on the morphology of the limb bones (e.g. Kappelman 1988, Degusta and Vrba 2003, 2005a, 2005b, Kovarovic and Andrews 2007, Schellhorn 2009; Barr 2014a, 2018). Animals with a preference for dry, open environments, are thought to have limb bones that accommodate for the forces associated with high speed and quick tacking movements (Leinders 1979, Kappelman 1988, Köhler 1993). Animals of wet or densely vegetated environments, tend to have limb bones that

allow for flexibility and the ability to jump over obstacles, thereby distancing themselves from the pursuing predator (Leinders 1979, Kappelman 1988, Köhler 1993, Curran 2009).

There are a number of ways in which these adaptations are thought to be expressed in the functional morphology of the intermediate phalanx. Although an early model by Leinders (1979) suggested that its shape is primarily driven by differences in the capacity for flexion in the interphalangeal joint, more recent ecomorphological studies (e.g. Curran 2012, Kovarovic et al. 2021) have generally endorsed an alternative functional model by Köhler (1993), which proposes that differences in the capacity for medio-lateral movement explains the main functional difference in the phalanges (Fig. 1). In this model, species found on yielding or wet substrates, allow for more medio-lateral movement along the articulations, for more grip (Köhler 1993, Curran 2012). This is especially seen in the metapodial-phalangeal joint that allows the digits to splay when coping with humid substrate, while species found on high relief terrain tend to splay the terminal phalanx at the interphalangeal joint with the intermediate phalanx (Köhler 1993). On the other hand, animals adapted to locomotion on firm substrate have railed articulations between the interphalangeal joints, preventing disarticulation when running at high speed (Köhler 1993, 2001). In the intermediate phalanx this would be morphologically expressed in deeper, more concave proximal articulations -that reduce medio-lateral movement- in species of dry, open environment (Köhler 1993, 2001). The distal articular surface is predicted to be more rounded in wet environment species, to allow for more medio-lateral movement (Köhler 1993). It is thought to be moreunequally shaped, with a posterior apex, in dry environment forms, (Köhler 1993). A third trait presumed to be functionally correlated, is the general robustness of the phalanx. Köhler (1993) noted that species adapted

to dry, open terrain have more gracile phalanges, but did not discuss the underlying biomechanics. Degusta and Vrba (2005a, 2005b), however, stated that gracile phalanges are actually characteristic of (bovid) species adapted to wet environments.

Using these observations, we have formulated three functional hypotheses related to the intermediate phalanx: phalanges of species adapted to wet or yielding substrate are thought to have a different gracility than those of species adapted to dry, more firm substrate (h1), phalanges of species associated with dry, firm substrate are predicted to have railed, more concave proximal articulations (h2), and phalanges of species associated with dry, firm substrate are predicted to have a more asymmetric distal articular surface with a posterior apex on the medial and lateral side (h3) (Table 1). The validity of these hypotheses and, by extension, whether specific morphological traits can be correlated with locomotor behaviours and environmental conditions, is further explored in this paper.

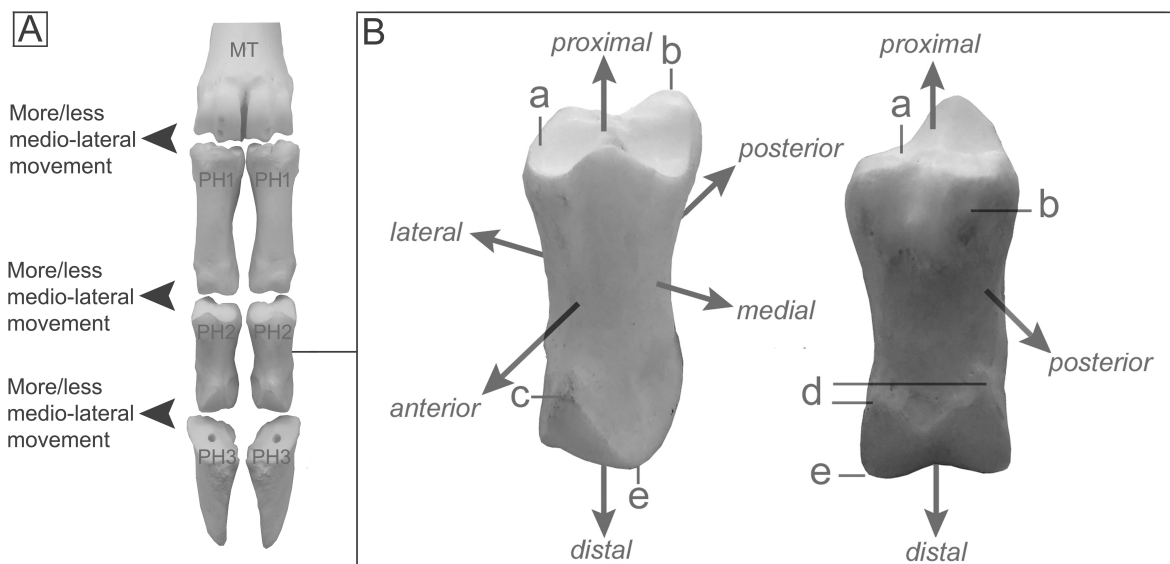


Figure 1: Anatomy of the cervid hindfoot with (A) different elements (MT=metatarsus, PH1=proximal phalanx, PH2=intermediate phalanx, PH3=terminal phalanx) and joints that show variation in medio-lateral movement and (B) parts of the intermediate phalanx (a=proximal

a=articular surface, *b*=plateau postarticulaire, *c*=anterior extensor process, *d*=palmar extensions, *e*=distal articular surface).

Hypothesis 1:	The general shape of the intermediate phalanx is predicted to be more gracile/robust in species adapted to either wet or dry substrates.
Hypothesis 2:	The proximal articulation of the intermediate phalanx is predicted to be deeper or more concave in species adapted to drier substrate, and shallower in species of wet, yielding substrate.
Hypothesis 3:	The shape of the distal articular surface of the phalanx is predicted to be round and symmetric on the medial and lateral side in species adapted to wet substrate and asymmetric with a more posterior apex on the medial and lateral side in forms adapted to dry substrate.

Table 1: Functional hypotheses for the intermediate phalanx.

3. Materials

The validity of our hypotheses was primarily explored using data collected on cervid skeletons at several American and European institutions (see supplementary data). In addition, 3D scans of a limited number of specimens were shared by the Virtual Zooarchaeology of the Arctic project (n=4) (Maschner et al., 2011; Betts et al., 2011) and the Max Planck Institute of Evolutionary Anthropology (n=4) (Niven et al., 2009). In total, our dataset was made up of 131 intermediate phalanges, belonging to 25 species and 6 tribes (Table 2). This sample size was in the same range as many similar studies (e.g. Weinand 2005, Curran 2009, Schellhorn 2009). Data was collected on a maximum of 16 specimens per species in order to prevent the sample from becoming skewed towards more common taxa.

When possible, the medial phalanx of the left hindleg was selected for data collection. In cases where this was impossible, the medial phalanx of the opposite leg was taken instead.

Pathological specimens and non-adults were excluded. We considered an animal as adult if all the epiphyses were fused and the third molar was erupted. Even though it is known that captivity can affect the morphology of the skeleton in certain mammals (O'Regan and Kitchener, 2005), earlier studies on cervids have demonstrated that in the elements of the locomotor apparatus morphology is probably more genetically determined, and that captivity does not substantially confound functional and taxonomic patterns in morphometric studies (Gruwier & Kovarovic 2021). Hence, a number (n=20) of captive specimens were included in this study to maximize taxonomic diversity and sample size (see supplementary data).

Tribe	Species	N	s.	\bar{x} kg	References
Cervini	<i>Axis axis</i>	10	D	86	(Eisenberg and Seidensticker, 1976; Geist, 1998)
	<i>Axis (Hyelaphus) kuhlii</i>	3	I	43	(Blouch and Atmosoedirdjo, 1987; Kurt, 1990; Geist, 1998)
	<i>Axis (Hyelaphus) porcinus</i>	5	W	68	(Blandford, 1888; Geist, 1998; Bhowmik et al., 1999)
	<i>Cervus (Elaphurus) davidianus</i>	3	W	214.5	(Geist, 1998; Hu and Jiang, 2002)
	<i>Cervus (Panolia) eldii</i>	4	W	105	(Geist, 1998; Tordoff et al., 2005)
	<i>Cervus (Rusa) timorensis</i>	5	D	155	(Geist, 1998; Nur Alizati, 2020)
	<i>Cervus (Rusa) alfredi</i>	2	I	-	(Rabor, 1977)
	<i>Cervus (Rusa) marianna</i>	1	I	50	(Taylor, 1934; Geist, 1998; Nur Alizati, 2020)
	<i>Cervus (Rusa) unicolor</i>	6	I	276	(Blandford, 1888; Schaller, 1967)
	<i>Cervus canadensis</i>	5	D	230	(Geist, 1998)
	<i>Cervus elaphus</i>	9	I	230	(Geist, 1998; Koubek and Zima, 1999)
	<i>Cervus nippon</i>	2	I	128.5	(Geist, 1998; Smith and Xie, 2008)
<i>Dama dama</i>	10	D	75.1	(Janis and Wilhelm, 1993; Apollonio et al., 1998; Geist, 1998)	
Muntiacini	<i>Muntiacus reevesi</i>	3	W	14	(Geist, 1998; Chiang, 2007)
	<i>Muntiacus muntjak</i>	6	W	16	(Geist, 1998; Ekwai et al., 2012)
Capreolini	<i>Capreolus capreolus</i>	16	I	23	(Geist, 1998; Stubbe, 1999)
	<i>Hydropotes inermis</i>	8	W	12.5	(Geist, 1998; Zhang et al., 2006)
Rangiferini	<i>Rangifer tarandus</i>	13	T	153.5	(Baskin, 1986; Geist, 1998)
Odocoileini	<i>Mazama Americana</i>	5	W	20	(Bodmer, 1997; Geist, 1998)
	<i>Mazama gouazoubira</i>	1	W	-	(Cartes, 1998; Geist 1998)
	<i>Odocoileus virginianus</i>	3	I	85	(Geist, 1998; Potapov et al., 2014)
	<i>Ozotoceros bezoarticus</i>	1	D	40	(Geist, 1998; Merino and Semeniuk, 2011)

	<i>Hippocamelus antisensis</i>	1	I	68.5	(Geist, 1998; Gazzolo and Barrio 2016)
	<i>Pudu puda</i>	3	W	10	(Herskovitz, 1982 ; Geist, 1998)
Alceini	<i>Alces alces</i>	6	D	557	(Geist, 1998 ; Bauer and Nygrén, 1999)

Table 2: Species used in this study, with total sample of included phalanges (N), assigned substrate type (s., see section 4), average species body mass (\bar{x} kg) and references.

4. Methods and statistical analysis

Based on sources from the literature, we assigned the intermediate phalanges to four different habitat groups (see Table 2). Although the use of a limited number of categories inevitably oversimplifies actual habitat variation, this was a necessary trade off to allow for robust statistical analyses (Curran 2009). Substrate properties are connected to vegetation structure (Boregard 1990), but as earlier studies have correlated the functional morphology of the phalanges directly to substrate type (Köhler 1993, Curran 2009), our habitat groups were primarily based on the latter parameter.

A first group (type W) consisted of species with a preference for environments with wet, yielding substrate. This included closed habitats, such as tropical rainforest, as well as open wetlands or marshland. The animals in this group are thought to be characterized by less railed phalanges that are not specifically adapted to restrict medio-lateral movement at the interphalangeal joints. A second group (type D) included animals found in environments with dry, firm substrate. This group lumped together species of arid savannah-like environments with dry woodland species and is thought to be characterized by railed phalanges with a more limited capacity for medio-lateral movement. The type I group was composed of intermediate species that were neither true specialists of wet environment, nor strongly associated with dry substrate. They are generalists, not expected to have strongly railed phalanges, but are also

lacking in capacity for medio-lateral movement. A final group (type T) was solely composed of *Rangifer tarandus*, a species of (sub)arctic tundra environments (Geist 1998) that merited its own habitat designation. Its phalanges are thought to be adapted to the particular conditions of the tundra: alternating episodes of frozen soil and melting snow that require additional grip (Hildebrand 1985, Nieminen 1990).

Many earlier ecomorphological studies have made use of linear measurements to quantitatively analyse skeletal morphology (e.g. Kappelman, 1988; Bishop et al., 2006; Kovarovic and Andrews, 2007), but more recent studies have embraced the advantages of geometric morphometrics (GMM) as an effective set of methods to quantify artiodactyl morphology (e.g. Cucchi et al., 2009, 2011; Curran 2009, Brophy et al., 2014; Forrest et al., 2018, Gruwier & Kovarovic 2021). Consequently, our study made use of a landmark based three-dimensional GMM approach to quantify shape. This had the advantage that object geometry was optimally preserved in the measurements (Rohlf and Marcus, 1993; Slice, 2005; Baab et al., 2012) and that size and shape could be separately analysed (Zelditch et al 2004, Viscosi & Cardini 2011). Furthermore, the use of thin plate spline deformation grids allowed us to optimally visualize morphological variation as distortions in a grid (Bookstein 1991, Zelditch et al. 2004).

Data were collected in the form of 3D-surface scans generated with a NextEngine 2020i laser scanner. After cleaning and fusing individual scan divisions in the associated Scanstudio HD package (1.2.3), landmarks were placed on the 3D-objects in Landmark editor 3.0 (Wiley et al. 2005). Eight landmarks were placed at discrete anatomical loci on the phalanges (Fig. 2 and Table 3), capturing variation in standard measures of the phalanx and consistent with previous

ecomorphological models developed for bovid intermediate phalanges (Degusta & Vrba 2005a, 2005b, Kovarovic and Andrews 2007). All landmarks were of type I or type II and are homologous at the level of intersections between different anatomical structures or at the extreme ends of certain structures (Zelditch *et al.* 2004). After exporting the coordinate data, we used Morphologika 2.5 (O'Higgins and Jones 2006) to conduct a generalized Procrustes analysis (GPA) on the data matrix to remove all information irrelevant to differences in shape (Walker 2000, Zelditch *et al.* 2004). Procrustes residuals and ln centroid size were then exported from Morphologika for further statistical analysis in PAST 2.17 (Hammer *et al.*, 2001). The quality of the resulting graphs was enhanced using Photoshop 6.0.

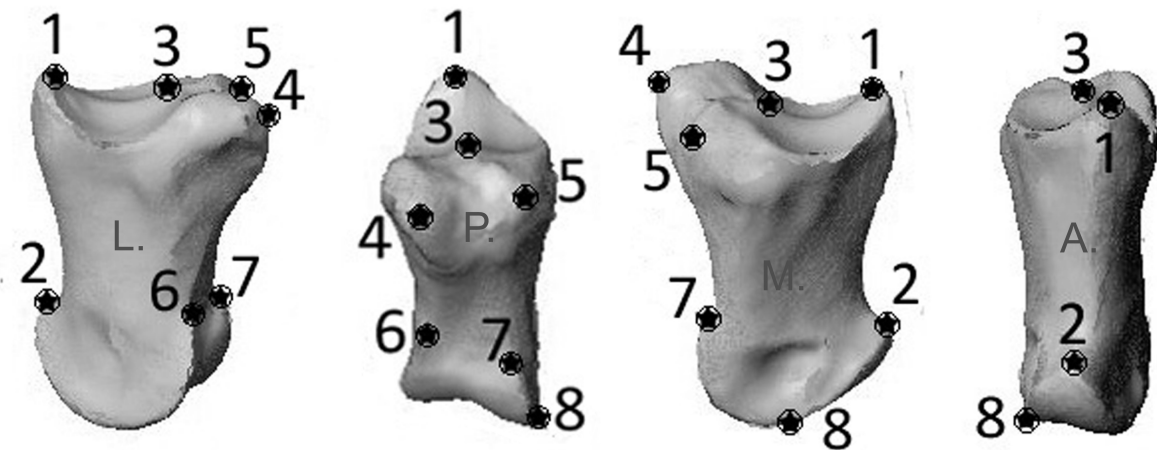


Figure 2: Illustration of landmarks recorded on the lateral (L.), medial (M.), posterior (P.) and anterior (A.) sides of the intermediate phalanx.

Number	Type	Description
1	II	Most anterior point of the proximal articular surface.
2	II	Most proximal point of the anterior extensor process.
3	I	Apex of the proximal articular surface at the junction between the left and the right facet.
4	II	Most posterior point of the lateral extension on the posterior side of the plateau postarticulaire.
5	II	Most posterior point of the medial extension on the posterior side of the plateau postarticulaire.
6	I	Proximal apex of the lateral palmar extension on the posterior shaft.
7	I	Proximal apex of the medial palmar extension on the posterior shaft.

Table 3: Description of the location and type of landmarks (following Bookstein, 1991) recorded on the intermediate phalanx. See Figure 2 for placement of the landmarks on the phalanx.

Principal Component Analysis was used as a dimensionality reduction method and as the primary method to explore morphological variation in the dataset (Dryden and Mardia, 1998; Zelditch et al., 2004). We opted for between groups PCA (bgPCA), as this method is more robust to over-fitting the model than e.g. Linear Discriminant Analysis, when applied on small datasets or those with unequally balanced samples (Kovarovic et al., 2011, Seetah et al. 2012). On the other hand, with eigenvectors derived from the variance-covariance matrix of the group means, bgPCA maintains an emphasis on between group differences (Seetah et al. 2012).

To assess the repeatability of the digitization and landmarking procedures we used an adjusted version of Adriaens (2007) protocol, that involved the scanning of five randomly selected specimens and repeating the landmarking procedure on each specimen five separate times (Gruwier & Kovarovic 2021). If the replicates clustered closely together on the first two axes of a PCA, the digitization error was low (Adriaens 2007).

Statistical significance of group separations in the PCA's was tested using a non-parametric MANOVA (npMANOVA) on the relevant principal components (Schutz et al., 2009; Polly et al., 2013; Marramà and Kriwet, 2017; Hou et al., 2021). We used a permutational test because the assumptions required for parametric testing –including normal distribution and across-group homogeneity of variance-covariance matrices- are not necessarily met by the data resulting from GMM analysis (Cardini et al., 2015; Lopez-Lazaro et al., 2018, Gruwier & Kovarovic 2021).

The results of the overall npMANOVA were followed by post-hoc tests in the form of pairwise

npMANOVAs between all pairs of groups, were used to assess which groups differed significantly (Gruwier & Kovarovic 2021). Bonferroni corrections were used as a multiple comparison correction procedure (Dunn 1961) and the adjusted p -values reported in our results. Those principal components with eigenvalues cumulatively explaining at least 70% of the total variance were retained for further analysis, a commonly used cutoff point in PCA (Jolliffe & Cadima 2016).

A number of tests were conducted to account for factors that could potentially confound the ecomorphological signal. To test for allometric effects in our dataset we first regressed natural log centroid size per species against the natural log of average body mass for each species, to establish the relationship between phalanx size and total body size (Gruwier & Kovarovic 2021). Average body masses were taken from the literature (see Table 2). Consequently, we conducted a regression of the relevant PC-scores against ln centroid size for each specimen (e.g. Cucchi et al., 2011; Owen, 2013, Gruwier & Kovarovic 2021). In cases where the correlation between size and shape was significant, this was considered indicative of an allometric effect (Zelditch et al., 2004).

To estimate the effect of phylogeny in the dataset, we conducted a phylogenetic generalized least squares (PGLS) regression (Martins & Hansen, 1997) in Caper 1.0 in R (Orme et al., 2018). This approach consisted of regressing the mean shape coordinates for each species on the habitat groups transformed into dummy variables (Meloro, 2007, 2008; Walmsley et al., 2012; Barr, 2014a, 2014b; Curran, 2015, Gruwier & Kovarovic 2021). In this weighed regression, phylogeny was included as an error term as part of the regression of shape on the habitat variables (Martins & Hansen, 1997; Walmsley et al., 2012, Gruwier & Kovarovic 2021). Using

phylogenetic tree branch lengths to estimate phylogenetic covariance, the covariance for two species was proportional to the sum of the branch lengths from the root to the last common ancestor (Monteiro, 2013, Gruwier & Kovarovic 2021). Tree branch lengths for the cervid family were taken from the 10KTrees website (Arnold et al., 2010) and their accuracy checked against a recently published cervid phylogenetic framework by Heckeberg (2020). In this context, we assumed that cervid traits evolved according to a Brownian motion model (see Felsenstein, 1985; Monteiro, 2013; Barr and Scott, 2014). As *Cervus mariannus* and *Cervus alfredi* were not part of the phylogenetic tree, we excluded those species from the PGLS regressions.

We used Pagel's λ as a measure of phylogenetic dependence (Pagel, 1999), an approach that uses a maximum likelihood estimate to find the value that best summarizes the variation between taxa at the tips of the phylogenetic tree (Edwards and Cavalli-Sforza, 1964; Kamilar and Cooper, 2013, Gruwier & Kovarovic 2021). This measure is calculated by multiplying the off-diagonal elements (the covariances between species pairs in the phylogenetic variance-covariance matrix) by λ (Pagel, 1999; Harmon, 2019). If Pagel's λ is close to 0, this indicates a weak phylogenetic signal. If the value is close to 1, a strong phylogenetic signal can be inferred (Molina-Venegas and Rodriguez 2017, Gruwier & Kovarovic 2021).

5. Results

Our repeatability test showed that the replicates clustered closely together in a PCA scatterplot of the tested subsample (Fig. 3). The error due to variation in the digitization and acquisition protocol could therefore be considered limited. The results of a PCA on all phalanges provided visual between-group separation along the axes of the first two components (Fig. 4). Because

visual separations were only clear for the first two axes and due to their cumulative variance totaling 96.7 %, only PC1 and PC2 were retained for further analysis.

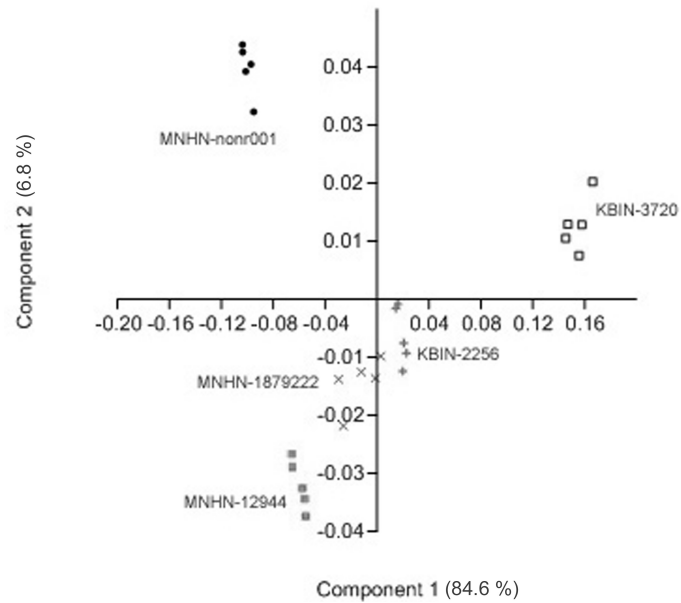


Figure 3: Results of repeatability test (scatterplot of a PCA conducted on five re-scanned and landmarked replicates of five phalanges, with eigenvalues given in parenthesis).

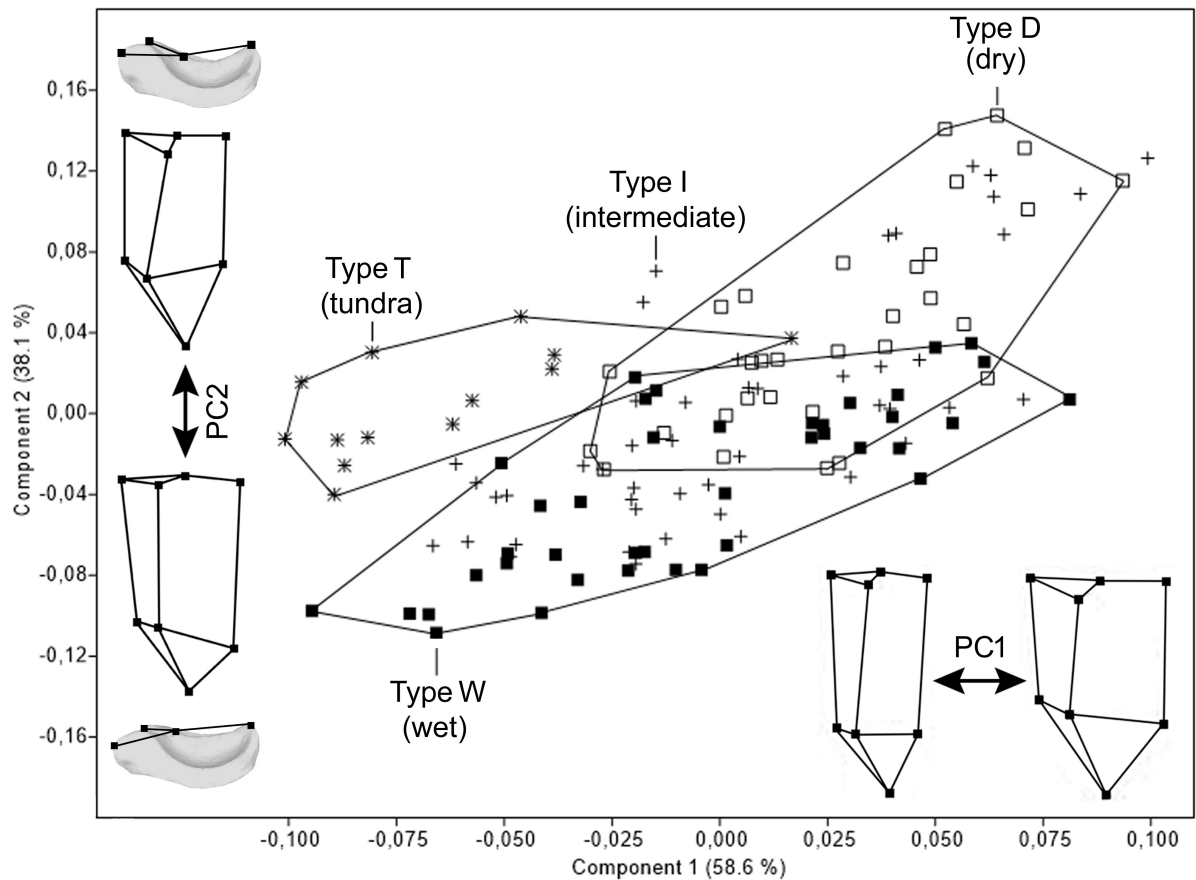


Figure 4: PCA scatterplot of a bgPCA of all phalanges (eigenvalues in parenthesis), with thin plate spline deformation grids and interpretation of the observed shape changes in the proximal articulation in the form of two warped, hypothetical phalanges at both ends of the y-axis.

The results of an npMANOVA on the scores of the first two principal components gave significant overall between-group differences ($F=15.47$, $p<0.001$). Pairwise comparisons showed significant differences between all individual groups (Table 4). This indicated that all habitat groups had an idiosyncratic average shape, as far as the morphological differences described by the first two axes were concerned. Visual assessment of the thin plate spline transformations associated with PC1 revealed that the primary shape difference summarized by this axis was a difference in general robustness of the phalanx (Fig. 4). Specimens with a lower score on PC1

had a more gracile shape than specimens with a high score on this axis. Along the second axis, several shape differences were observed: a difference in the relative proportion of the distal articulation, a variation in the height of the extensor process on the anterior side of the distal articulation, and a difference in depth of the proximal articular surface (Fig. 4). As specimens gave a higher score on PC2, they had a relatively larger distal articulation, an extensor process positioned higher on the anterior side, and a flatter, shallower proximal articular surface.

	Type D	Type I	Type T
Type I	0.0144	-	-
Type T	0.0006	0.0036	-
Type W	0.0006	0.0378	0.0006

Table 4: Bonferroni corrected p-values ($\alpha=0.05$) of pairwise comparisons of an npMANOVA on the first two principal components of a between groups PCA on the phalanx dataset.

An evaluation of specimen distribution in the scatterplots associated with the first two principal components confirmed the trends seen in the results of the npMANOVA (Fig. 4). When PC1 was plotted against PC2, type D specimens generally gave a higher score on both axes. Type W species gave a more negative scores, while type I species were intermediate, overlapping with types W and D. This pattern indicated a gradient from dry adapted, robust type D species with a larger distal articulation, an extensor process positioned higher on the anterior side, and a deeper proximal articular surface, over intermediate type I forms, to the wet adapted type W species with a more gracile morphology, smaller distal articulation, shallower proximal articular surface and lower extensor process. The type T specimens (tundra substrate) formed a group that was well separated from the three other groups. Its position implied that the phalanx in reindeer had a gracile shape similar to the wet adapted species, but articulations that were more like those of the dry adapted type D forms.

To test if the size of the intermediate phalanx was a good proxy for total body size, we first regressed average \ln centroid size per species against average total body masses from the literature. The results gave a significant correlation ($R^2=0.315$, $p=0.0035$) between phalanx size and total body mass, suggesting that individual element size was an acceptable approximation for total body mass. The results of the regressions of the shape variables against \ln centroid size suggested a limited allometric effect (Fig. 5). A regression of PC1 against \ln centroid size indicated a significant, but weak correlation ($R^2=0.062$, $p=0.002$), implying that only a small portion of the shape variance summarised by PC1 could be attributed to allometry. A larger effect was suggested by the regression of PC2 against \ln centroid size ($R^2=0.257$, $p<0.001$), but this was still relatively limited and only partially explained the measured variation in shape.

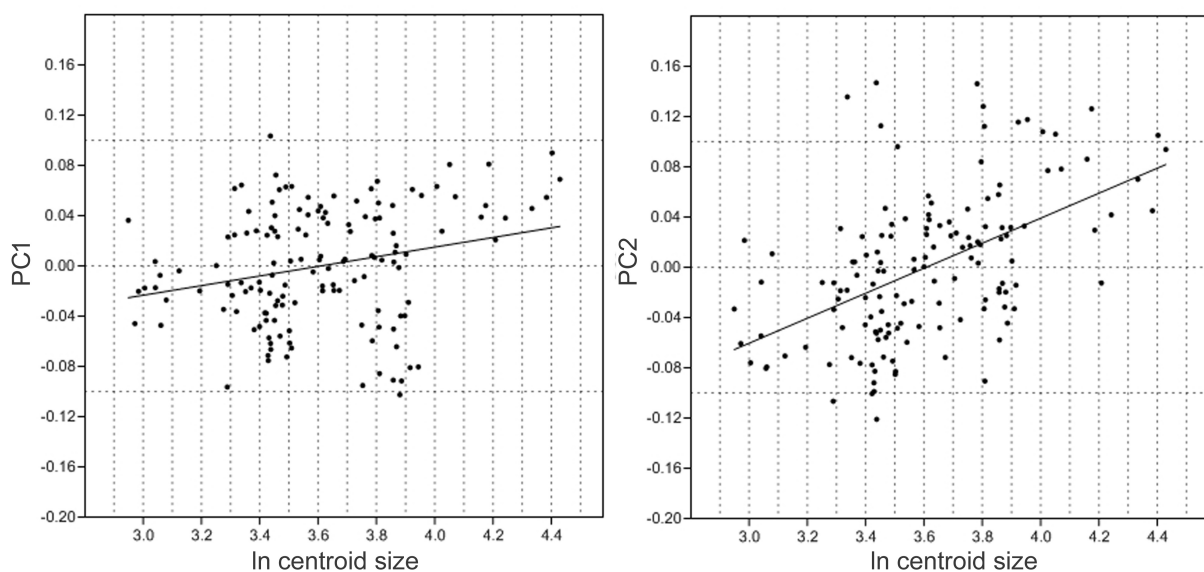


Figure 5: Results of regressions of PC1 ($R^2=0.062$, $p=0.002$), and PC2 ($R^2=0.257$, $p<0.001$) against \ln centroid size for all extant phalanges.

Our PGLS regression of the relevant principal components (PC1 and PC2, $R^2=0.127$, $p=0.309$) against the habitat variable resulted in a relatively high Pagel's λ (0.711) that was significantly

different from 1 ($p(H_0:\lambda=1)=0.011$), but not significantly different from 0 ($p(H_0:\lambda=0)=0.097$). This indicated that the phylogenetic signal was relatively limited in the overall dataset. When considering the effects for the first component separately ($R^2=0.228$, $p=0.38$), Pagel's λ was high (0.86) and significantly different from the lower bound ($p(H_0:\lambda=0)=0.021$), but not from the upper bound ($p(H_0:\lambda=1)=0.106$). For the second component the PGLS regression ($R^2=0.43$, $p=0.038$) resulted in a low Pagel's λ (0.333), significantly different from the upper bound ($p(H_0:\lambda=1)<0.01$), but not from the lower bound (bound ($p(H_0:\lambda=0)=0.347$). The results therefore indicated that a phylogenetic signal was primarily present in PC1, while the effects in PC2 were limited.

6. Discussion

The variation summarized by the first axis of the PCA (see Fig. 4) confirmed the premise of our first functional hypothesis: specimens were distributed along a gradient from species of dry, firm substrate (type D) with robust phalanges, over intermediate species (type I), to species of wet, yielding substrate (type D) with gracile phalanges. This was in line with Degusta and Vrba's (2005b) observation that species of wet environments have more gracile phalanges, but at odds with Köhler's (1993) hypothesis, which proposed that gracile phalanges were typically found in animals of dry, open environment. Nevertheless, Degusta and Vrba (2005b) did not provide specific functional explanations for the gracility in the phalanx. Interpreting variation in this trait was therefore not straight forward. Considering the fact that longer, more gracile phalanges are connected with wet substrate, it is not unlikely that this trait is also an accommodation to allow for better grip or stability on yielding substrate types. The position of

the type T group (only reindeer) did not contradict this interpretation: specimens within this group were similar in gracility to the wet adapted species (see Fig. 4). The characteristic nature of tundra substrate, with alternating episodes of frozen soil and melting snow (Hildebrand 1985, Nieminen 1990), probably also requires a phalangeal morphology adapted to negotiating complex, difficult terrain.

It should, however, be kept in mind that PC1 displayed a relatively strong phylogenetic signal. In other words, species with phalanges of similar gracility were often also more closely related. Although not explicitly tested in other studies of the intermediate phalanx (e.g. Kovarovic & Andrews 2007, Degusta & Vrba 2005b), Kovarovic (2004) acknowledged that phylogeny could also partially explain the shape variation in this element in bovids. The presence of a phylogenetic signal need not necessarily obscure all functional patterns. Morphological traits are often not driven by either functional aspects *or* phylogenetic relatedness, but rather by a combination both (Elton et al. 2016). This is not surprising, as taxonomically related groups can share a preference for similar habitats (Scott & Barr 2014). While caution is warranted when interpreting specific traits (such as the gracility of the phalanx) in isolation, the best way to assess the ecological significance of morphological similarities between species, is to look at how they behave in a model, despite their taxonomic affinities (Gruwier & Kovarovic 2021).

Furthermore, functional hypothesis 2 (Table 1) appeared to be confirmed by the shape variation summarized by the second axis. Although our set of landmarks only partially captured this trait, the variation along this axis apparently reflected a gradient from species of dry, firm substrate (type D), with deeper proximal articulations, to saltatorial species of wet,

environments (type W), with shallow proximal articulations. Although no clear confirmation was found of hypothesis 3 (the distal articulation was predicted to have a more posterior apex in dry adapted species), variation in some aspects of the distal articulation was clearly summarized by PC2. The relative size of the distal articulation (larger in type D) and the placement of the extensor process on the anterior side (placed higher in type D) may also be functionally driven aspects, related to differences in splaying capacity. Although no significant phylogenetic signal was measured for the second axis, PC2 showed a limited allometric effect. Nevertheless, only a small portion of the morphological variation (25.7%) was explained by size differences, indicating its effects were not substantial. This was in line with the results of other studies. Even though the effects of allometry in the cervid intermediate phalanx have not been explicitly studied before, a number of workers have considered the problem in bovids. Most of these studies (Kovarovic & Andrews 2007, Degusta and Vrba 2005b) have made use of linear size corrections to eliminate the effects of body size differences from morphometric variables. While such an approach is probably less efficient in excluding size differences than the GMM methods used in our study, no significant confounding effects were reported after size corrections (Kovarovic 2004, Kovarovic & Andrews 2007, Degusta and Vrba 2005b). Similar studies on the terminal phalanx in cervids found a similarly limited allometric effect for this element (Curran 2009, 2012, 2015).

The separately treated type T group (reindeer) gave relatively high scores on the second axis in our study. This meant that the morphology of the type T phalanges was similarly gracile as that of wet adapted species, but as far as the landmarks could capture this part of the bone, seemingly with deeper proximal articulations and with large, anteriorly extended distal

articulations as in dry adapted species. These observations did not necessarily contradict functional hypothesis 1 (variation in gracility). Reindeer may well require gracile phalanges that are accommodated for the variable structure of tundra substrate, but at the same time retain some characteristics (deeper proximal articulations) that are optimized for cursorial locomotion in dry, open environment. The results certainly showed that reindeer have phalanges with a unique morphology.

Overall, the PCA and the regressions suggested that the morphological variation of the phalanx was driven by a combination of function and, to an extent, phylogeny. Allometry played a more limited role. This showed that, despite the presence of confounding factors, the intermediate phalanx is a useful predictor of substrate type. The meaningful separations in the scatterplot, and the confirmation of two of our three functional hypotheses, suggest that specimens giving correspondingly high or low scores on both axes, probably do so because of functional reasons. This was in line with the results of earlier ecomorphological work on the intermediate phalanx in artiodactyls. Previous studies on bovids (Kovarovic & Andrews 2007, Degusta & Vrba 2005a, 2005b) overall gave high reclassification rates for this element as well as for the proximal phalanx, and agreed that both are fairly good predictors of habitat. Although no other studies exist that focus explicitly on the cervid intermediate phalanx, Curran's (2012, 2015) analysis of the third phalanx in cervids also found clear correlations between morphology and substrate type for the latter element.

7. Conclusions

The results presented in this paper have shown that the morphology of the intermediate phalanx correlates with habitat type. This suggests that the element has potential as a proxy for palaeoenvironmental reconstruction. More specifically, the shape of the proximal articular surface and the overall gracility of the phalanx were found to be a good predictor of substrate type. As such, our study expanded ecomorphological methods for this element in cervids. It also improved the way such studies have usually been conducted on ruminant bones, by making use of geometric morphometrics and by relying more strongly on the underlying functional aspects of the element.

When ultimately applied on fossil specimens of unknown taxonomic and ecological affinity, our models will probably be informative about the environments to which extinct cervids were adapted. They promise to be of particular use to palaeontologists and archaeozoologists working on Pleistocene faunal assemblages from Europe and Asia, where cervid fossils are commonly found. Its application on hominin sites from the region would be especially interesting, as this will potentially contribute to a better understanding of the ecological context of human evolution.

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9. Bibliography

Adriaens, P. (2007). Protocol for Error Testing in Landmark Based Geometric Morphometrics. Unpublished document consulted on 19/12/13 at: <http://www.funmorph.ugent.be/Miscel/Methodology/Morphometrics.pdf>.

Andrews, P. (1995). Mammals as palaeoecological indicators. *Acta Zoologica Cracoviensia* 38, 59-72.

Andrews, P. and Hixson, S. (2014). Taxon-free methods of palaeoecology. *Ann. Zool. Fennici* 51, 269-284.

Aniceti, V. (2020). The zooarchaeological analyses from Vetricella (Scarlinto, Grosseto): An overview of animal exploitation at the site, In: Bianchi, G. & Hodges, R. (eds.), *The NEU-Med project: Vetricella, an early medieval royal property on Tuscany's Mediterranean*, *Bibliotheca di Archeologia Medievale*, 121-129.

Apollonio, M., Focardi S., Toso S. and Nacci L. (1998). Habitat selection and group formation patterns of fallow deer *Dama dama* in a submediterranean environment. *Ecography* 21, 225-234.

Arnold, C., Matthews, L.J. & Nunn, C.L. (2010). The 10kTrees website: a new online resource for primate phylogeny. *Evolutionary Anthropology* 19, 114-118.

Baab, K.L., McNulty, K.P. & Rohlf, F.J. (2012). The shape of human evolution: A Geometric Morphometrics perspective. *Evolutionary Anthropology* 21, 151-165.

Barr, W.A. (2014a). *The paleoenvironments of early hominins in the Omo Shungura Formation (Plio-Pleistocene Ethiopia): Synthesizing multiple lines of evidence using phylogenetic ecomorphology*. PhD dissertation University of Texas at Austin.

Barr, W.A. (2014b). Functional morphology of the bovid astragalus in relation to habitat: controlling phylogenetic signal in ecomorphology. *Journal of Morphology* 275 (11), 1201-1216.

Barr, W.A. (2018). The morphology of the bovid calcaneus: Function, phylogenetic signal and allometric scaling. *Journal of Mammalian Evolution* 27 (1), 1-11.

Barr, W.A. and Scott, R.S. (2014). Phylogenetic comparative methods complement discriminant function analysis in ecomorphology. *American Journal of Physical Anthropology* 153, 663-674.

Baskin, L.M. (1986). Differences in the ecology and behaviour of reindeer populations in the USSR. *Rangifer* 6, 333-340.

Bauer, K. and Nygrén, K. (1999). *Alces alces*, In: Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralík, V. and Zima, J., editors. The Atlas of European Mammals. London: T. & A.D. Poyser.

Betts, M.W., Maschner, H.D.G., Schou, C.D., Schlader, R., Holmes, J., Clement, M. and Smuin, M. (2011). Virtual zooarchaeology: building a web-based reference collection of northern vertebrates for archaeofaunal research and education. *Journal of Archaeological Science* 38 (4), 755-762.

Bhowmik, M. K., Chakraborty, T. and Raha, A. K. (1999). The habitat and food habits of hog deer (*Axis porcinus*) in protected areas of sub-Himalayan West Bengal. *Tiger Paper* 26 (2), 25-27.

Bishop, L. (1994). *Pigs and the ancestors: Hominids, suids and environments during the Plio-Pleistocene of East Africa*. PhD dissertation Yale University.

Bishop, L., King, T., Hill, A. and Wood, B. (2006). Palaeoecology of *Kolpochoerus heseloni* (= *K. limnetes*): a multiproxy approach. *Transactions of the Royal Society of South Africa* 61, 81-88.

Blanford, W.T. (1888). *The fauna of British India, including Ceylon and Burma*. London: Taylor and Francis.

Blank, D.A. (2018). Escaping behavior in goitered gazelle. *Behavioural Processes* 147, 38-47.

Blouch, R. A., & Atmosoedirdjo, S. (1987). *Biology of the Bawean deer and prospects for its management*. In: C. M. Wemmer (Ed.), *Biology and management of the Cervidae*. Smithsonian Institution Press. 320-327.

Bodmer, R. (1997) *Ecologia e conservação dos veados mateiro e catingueiro na Amazônia*, In: Duarte, J.M.B., (ed.), *Biologia e conservação de cervídeos sul-americanos: Blastocerus, Ozotoceros e Mazama*. Jaboticabal: FUNEP. 69-77.

Bookstein, F.L. (1991). *Morphometric tools for landmark data*. Cambridge: Cambridge University Press.

Boregard, S.O. (1990). Vegetation development in abandoned gravel pits: effects of surrounding vegetation, substrate and regionality, *Journal of Vegetation Science* 1 (5), pp. 675-682.

- Brophy, J.K., de Ruiter, D.J., Athreya, S. and DeWitt, T.J. (2014). Quantitative morphological analysis of bovid teeth and implications for paleoenvironmental reconstruction of Plovers Lake, Gauteng Province, South Africa. *Journal of Archaeological Science* 41, 376-388.
- Cardini, A., Seetah, K. and Barker, G. (2015). How many specimens do I need? Sampling error in geometric morphometrics. Testing the sensitivity of means and variances in simple randomized selection experiments. *Zoomorphology* 134 (2), 149-163.
- Cartes, J. L. (1998). *Distribución y uso de hábitat de la corzuela parda en los Llanos de La Rioja, Argentina*, Masters dissertation National University of Cordoba.
- Caro, T.M. (1986). The functions of stotting in Thomson's gazelles: some tests of the prediction. *Animal Behaviour* 34, 663-684.
- Caro, T. M. (1994). Ungulate antipredator behaviour: preliminary and comparative data from African bovids. *Behaviour* 128, 189-228.
- Caro, T. M., Graham, C. M., Stoner, C. J. and Vargas, J. K. (2004). Adaptive significance of antipredator behaviour in artiodactyls. *Animal Behaviour* 67, 205-228.
- Chiang, P. J. (2007). *Ecology and conservation of Formosan clouded leopard, its prey, and other sympatric carnivores in southern Taiwan*. PhD dissertation Virginia Polytechnic Institute and State University.
- Cucchi, T., Fujita, M. and Dobney, K. (2009). New insights into pig taxonomy, domestication and human dispersal in Island South East Asia: molar shape analysis of *Sus* remains from Niah caves, Sarawak. *International Journal of Osteoarchaeology* 19, 508-530.
- Cucchi, T., Hulme-Beaman, A., Yuan, J. and Dobney, K. (2011). Early Neolithic pig domestication at Jiahu, Henan Province, China: clues from molar shape analysis using geometric morphometric approaches. *Journal of Archaeological Science* 38, 11-22.
- Curran, S. (2009). *Hominin Paleoecology and Cervid Ecomorphology*. PhD dissertation University of Minnesota.
- Curran, S. (2012). Expanding ecomorphological methods: geometric morphometric analysis of Cervidae post-crania. *Journal of Archaeological Science* 39, 1172-1182.
- Curran, S. (2015). Exploring *Eucladoceros* ecomorphology using geometric morphometrics. *The Anatomical Record* 298, 291-313.
- DeGusta, D. and Vrba, E. (2003). A method for inferring paleohabitats from the functional morphology of bovid astragali. *Journal of Archaeological Science* 30, 1009-1022.

DeGusta, D. and Vrba, E. (2005a). Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science* 32, 1099-1113.

Degusta, D. and Vrba, E. (2005b). Methods for inferring paleohabitats from discrete traits of the bovid postcranial skeleton. *Journal of Archaeological Science* 32, 1115-1123.

Dryden, I.L. and Mardia, K.V. (1998). *Statistical shape analysis*. Chichester: Wiley.

Dunn, O.J. (1961). Multiple comparisons among means, *Journal of the American Statistical Association* 56 (293), 52-64.

Edwards, A.W.F. and Cavalli-Sforza, L.L. (1964). Reconstruction of evolutionary trees: phenetic and phylogenetic classification. *Syst. Assoc. Publ.* 6, 67-76.

Eisenberg, J. F. and Seidensticker, J. (1976). Ungulates in Southern Asia: a consideration of biomass estimates for selected habitats. *Biological Conservation* 10 (4), 293-308.

Ekwal, I., Tahir, H. and Tahir, M. (2012). Modelling of Habitat Suitability Index for Muntjac (*Muntiacus muntjak*) Using Remote Sensing, GIS and Multiple Logistic Regression. *Journal of Settlements and Spatial Planning* 3 (2), 93-102.

Elton, S., Jansson, A.U., Meloro, C., Louys, J., Plummer, T. and Bishop, L. (2016). Exploring morphological generality in the Old World monkey postcranium using an ecomorphological framework. *Journal of Anatomy* 8 (4), 534-560.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist* 125 (1), 1-15.

Forrest, F.L., Plummer, T.W. and Raaum, F.L. (2018). Ecomorphological analysis of bovid mandibles from Laetoli Tanzania using 3D geometric morphometrics: implications for hominin palaeoenvironmental reconstruction. *Journal of Human evolution* 114, 20-34.

Gazzolo, G. and Barrio, B. (2016). Feeding Ecology of Taruca (*Hippocamelus antisensis*) populations during the rainy and dry seasons in Central Peru, *International Journal of Zoology* 2, 1-6.

Geist, V. (1998). *Deer of the World*. Mechanicsburg: Stackpole Books.

Gentry, A.W. and Gentry, A. (1978). Fossil Bovidae (Mammalia) from Olduvai Gorge, Tanzania: parts I & II, *Bul. Br. Mus.(Nat. Hist.) Geol. Series* 30, 1-83.

Gruwier, B. and K. Kovarovic (2021). Ecomorphology of the cervid calcaneus as a proxy for paleoenvironmental reconstruction. *The Anatomical Record* 305 (9), 2207-2226. <https://doi.org/10.1002/ar.24845>

Hammer, Ø., Harper, D.A.T. and Ryan, P.D. 2001, PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1), 1-9.

Harmon, L.J. (2019). *Phylogenetic comparative methods*. South Carolina: Luke J. Harmon.

Heckeberg, N.S. (2020). The systematics of the Cervidae: a total evidence approach. *PeerJ* 8, 1-76.

Hershkovitz, P. (1982). Neotropical deer (Cervidae) part I: Pudu, Genus *Pudu* Gray. *Fieldiana: Zoology* 11, 1-86.

Hildebrand, M. (1985). *Walking and running*, In: Hildebrand, M., Bramble, D.M., Liem, K.F. & Wake, D.B. (eds), *Functional vertebrate morphology*, Cambridge, MA, 38-57.

Hou, S.Y., Zhou, W., Hongwei, D., Hai, M.W., Wen, Y.F. and Zhou, J. (2021). Soft tissue facial changes among adult females during alignment stage of orthodontic treatment: a geometric morphometric study. *Oral Health* 21 (57), 1-9.

Hu, H. and Jiang, Z. (2002). Experimental release of Père David's deer in Dafeng Reserve, China. *Oryx* 36, 196-199.

Janis, C.M. and Wilhelm, P.B. (1993). Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *Journal of Mammalian Evolution* 1 (2), 102-125.

Jolliffe, I.T. and Cadima, J. (2016). Principal component analysis: a review and recent developments. *Philosophical Transactions of the Royal Society A*. 374, 1-16.

Kamilar, J.M. and Cooper, N. (2013). Phylogenetic signal in primate behavior, ecology and life history. *Philosophical Transactions of the Royal Society B*. 368, 1-10.

Kappelman, J. (1988). Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* 198, 119-130.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A. and Appelton, S. (1997). Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *Journal of Human Evolution* 32, 229-256.

Klein, R. G., Franciscus, R. G. and Steele, T. E. (2010). Morphometric identification of bovid metapodials to genus and implications for taxon-free habitat reconstruction. *Journal of Archaeological Science* 37, 389-401.

Köhler, M. (1993). Skeleton and habitat of recent and fossil ruminants. *Münchner Geowissenschaftlichen abhandlungen* 25, 1-88.

Köhler, M. & Moya-Sola, S. (2001). Phalangeal adaptations in the fossil insular goat *Myotragus*. *Journal of Vertebrate Paleontology* 21 (3), 621-624.

Koubek, P. and Zima, J. (1999). *Cervus elaphus*, In: Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralík, V. and Zima, J., editors. The Atlas of European Mammals, London: T. & A.D. Poyser.

Kovarovic, K. (2004). *Bovids as palaeoenvironmental indicators: an ecomorphological analysis of bovid post-cranial remains from Laetoli, Tanzania*. PhD dissertation University College London.

Kovarovic, K., Aiello, L.C., Cardini, A. and Lockwood, C.A. (2011). Discriminant function analyses in archaeology: are classification rates too good to be true?. *Journal of Archaeological Science* 38, 3006-3018.

Kovarovic, K. and Andrews, P. (2007). Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *Journal of Human Evolution* 52, 663-680.

Kovarovic, K., Tyler Faith, J., Jenkins, K.E., Tryon, A.C. and Peppe, D. (2021). Ecomorphology and ecology of the grassland specialist, *Rusingoryx atopocranion* (Artiodactyla: Bovidae), from the late Pleistocene of western Kenya. *Quaternary Research* 101, 187-204.

Kurt, F. (1990). *Axis deer (Genus Axis)*. In: Parker, S.P., editor. Grzimek encyclopedia of mammals, vol. 5. New York: McGraw-Hill.

Kurten, B. (1968). *The Pleistocene mammals of Europe*. New Jersey: Routledge.

Leinders, J. J. (1979). On the osteology and function of the digits of some ruminants and their bearing on taxonomy. *Zeitschrift für Saugetierkunde* 44, 305-318.

Lopez-Lazaro, S., Aleman, I., Viciano, J., Irurita, J. and Botella, M.C. (2018). Sexual dimorphism of the first deciduous molar: a geometric morphometric approach. *Forensic Science International* 290, 94-102.

Marramà, G., and Kriwet, J. (2017). Principal component and discriminant analyses as powerful tools to support taxonomic identification and their use for functional and phylogenetic signal detection of isolated fossil shark teeth. *PLoS One* 12 (11), 1–22.

Martins, E. P., and Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist* 149, 646–667.

- Maschner, H.D.G., Betts, M.W. and Schou, C.D. (2011). Virtual zooarchaeology of the Arctic project. *The SAA Archaeological Record* 11, 41-43.
- Meloro, C. (2007). *Plio-Pleistocene large carnivores from the Italian Peninsula: Functional morphology and macroecology*. PhD dissertation University Federico II Naples.
- Meloro, C. (2008). The shape of the mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. *Zoological Journal of the Linnean Society* 154, 832-845.
- Merino, M.L. and Semeniuk, M.B. (2011). Effect of cattle breeding on habitat use of Pampas deer *Ozotoceros bezoarticus celer* in semiarid grasslands of San Luis, Argentina. *Journal of Arid Environments* 75 (8), 752-756.
- Molina-Venegas, R. and Rodriguez, M.A. (2017). Revisiting phylogenetic signal: strong or negligible impacts of polytomies and branch length information?. *BMC Evol. Biol.* 17 (53), 1-10.
- Monteiro, L.R. (2013). Morphometrics and the comparative method: studying the evolution of biological shape. *Hystrix* 24 (1), 25-32.
- Nieminen, M. (1990). Hoof and foot loads for reindeer (*Rangifer tarandus*), *Rangifer* (special issue) 3, 249-254.
- Niven, L., Steele, T.T., Finke, H., Gernat, T. and Hublin, J.J. (2009). Virtual skeletons: using a structured light scanner to create a 3D faunal comparative collection. *Journal of Archaeological Science* 36, 2018-2013.
- Nur Alizati, N. G. A., Mohd Lutfi, A., Siti Azizah Mohd, N., Tan Min, P., Noor Azleen Mohd, K., & Darlina Md, N. (2020). A review of the genus *Rusa* in the Indo-Malayan archipelago and conservation efforts. *Saudi Journal of Biological Sciences* 28(1), 10–26.
- O’Higgins, P. and Jones, N. (2006). *Tools for statistical shape analysis*. Hull York Medical School. Consulted at: <http://hyms.fme.googlepages.com/resources>.
- O’Regan, H. and Kitchener, A.C. (2005). The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review* 35 (3-4), 215-230.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. and Pearse, W. (2018). *Package ‘caper’: comparative analysis of phylogenetics and evolution in R*. Consulted at: <http://caper.r-forge.r-project.org/>.
- Owen, J.T.D. (2013). *Morphological variation in wild and domestic suids*. PhD dissertation University of Durham.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* 401, 877-884.

Plummer, T. W. and Bishop, L.C. (1994). Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution* 27, 47-75.

Plummer, T. W., Bishop, L.C. and Hertel, F. (2008). Habitat preference of extant African bovids based on astragalus morphology: operationalizing ecomorphology for paleoenvironmental reconstructions. *Journal of Archaeological Science* 35, 3016-3027.

Polly, P.D. (2007). *Limbs in Mammalian Evolution*, In: Hall, B. K., (eds.), *Fins into Limbs: Evolution, Development and Transformation*. Chicago: The University of Chicago Press, 245-268.

Polly, P.D., Polyakov, A.V., Ilyashenko, V.B., Onischenko, S.S., White, T.A., Shchipanov, N.A., Bulatova, N.S., Pavlova, S.V., Borodin, P.M. and Searle, J.B. (2013). Phenotypic variation across chromosomal hybrid zones of the common shrew (*Sorex araneus*) indicates reduced gene flow. *PLOS one* 8 (7), 1-12.

Potapov E., Bedford, A., Bryntesson, F., Cooper, S., Nyholm, B. and Robertson, D. (2014). White-tailed deer (*Odocoileus virginianus*) suburban habitat use along disturbance gradients. *American Midland Naturalist* 171, 128-138.

Putman, R. and Flueck, W.T. (2011). Intraspecific variation in biology and ecology of deer: magnitude and causation. *Animal production science* 51 (4), 277-291.

Rabor, D. S. (1977). *Philippine birds and mammals*. Quezon City: University of the Philippines Press.

Rohlf, F.J. and Marcus, L.F. (1993). A revolution in morphometrics. *Trends in Ecology and Evolution* 8, 129-132.

Schaller, G.B. (1967). *The deer and the tiger: A study of wildlife in India*. Chicago: University of Chicago Press.

Schellhorn, R. (2009). *Eine Methode zur Bestimmung fossiler Habitate mittels Huftierlangknochen*. PhD dissertation University Tübingen.

Schutz, H., Polly, P.D., Krieger, J.D. and Guralnick, R.P. (2009). Differential sexual dimorphism: size and shape in the cranium and pelvis of grey foxes (*Urocyon*). *Biological Journal of the Linnean Society* 96 (2), 339-353.

Scott, R.S. (2004). *The Comparative Paleoecology of Late Miocene Eurasian Hominoids*. PhD dissertation University of Texas at Austin.

Scott, R.S. & Barr, A. (2014). Ecomorphology and phylogenetic risk: Implications for habitat reconstruction using fossil bovids. *Journal of Human Evolution* 73, 47-57.

Seetah, T.K., Cardini, A. and Miracle, P.T. (2012). Can morphospace shed light on cave bear spatial-temporal variation? Population dynamics of *Ursus spelaeus* from Romualdova Pécina and Vindija (Croatia). *Journal of Archaeological Science* 39, 500-510.

Shipman, P. and Harris, J.M. (1988). *Habitat preference and paleoecology of Australopithecus bosei in Eastern Africa*. In: Grine, F.E. (ed.), *Evolutionary history of the "robust" Australopithecines*. New York: Routledge. 343-382.

Slice, D.E. (2005). *Modern morphometrics*, In: Slice, D.E. (ed.), *Modern morphometrics in physical anthropology*. New York: Springer. 1-45.

Smith, A. and Xie, Y. (2008). *A Guide to the Mammals of China*. New Jersey: Princeton University Press.

Stubbe, C. (1999). *Capreolus capreolus*, In: Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralík, V. and Zima, J. (eds.), *The Atlas of European Mammals*. London: T. & A.D. Poyser.

Taylor, E.H. (1934). *Philippine land mammals*. Manila: Manila Bureau of Printing.

Tordoff, A. W., Timmins, R. J., Maxwell, A., Keavuth, H., Lic Vuthy and Khou Eang Hourt (2005). *Biological assessment of the Lower Mekong Dry Forests Ecoregion*. Phnom Penh: WWF Cambodia Publication.

Viscosi, V. and Cardini, A. (2011). Leaf morphology, taxonomy and geometric morphometrics: a simplified protocol for beginners. *Plos ONE* 6, 1-20.

Vrba, E.S. (1975). Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* 254, 301-304.

Walker, J.A. (2000). The ability of geometric morphometric methods to estimate a known covariance matrix. *Syst. Biol.* 49, 686-696.

Walmsley, A., Elton, S., Louys, J., Bishop, L.C. and Meloro, C. (2012). Humeral epiphyseal shape in the Felidae: the influence of phylogeny, allometry and locomotion. *Journal of Morphology* 273, 1424-1438.

Weinand, D. (2005). *A Reevaluation of the paleoenvironmental reconstructions associated with Homo erectus from Java, Indonesia, Based on the functional morphology of fossil bovid astragali*. PhD dissertation University of Tennessee.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Owen Lovejoy, C., Gen Suwa, Woldegabriel, G. (2009). *Ardipithecus ramidus* and the Paleobiology of Early Hominids. *Science* 326 (5949), 64-86.

Wiley, D.F., Amenta, N., Alcantara, D.A., Deboshmita, G., Kil, Y.J., Delson, E., Harcourt-Smith, W., Rohlf, J., St. John, K. and Hamann, B. (2005). *Evolutionary Morphing*. Proceedings of IEEE Visualization 2005. Washington.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D. and Fink, W.L. (2004). *Geometric Morphometrics for Biologists: a Primer*. Berlin: Academic Press Inc.

Zhang, E. D., Teng, L. W. and Wu, Y. B. (2006). Habitat selection of the Chinese water deer (*Hydropotes inermis*) in Yancheng Nature Reserve, Jiangsu Province. *Acta Theriologica Sinica* 26, 368-372.