



A method for inferring paleohabitats from the functional morphology of bovid astragali

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Abstract

The functional morphology of bovid postcranial fossils can be used to infer paleoenvironments, an approach often labeled ‘ecomorphology’. Such techniques have some advantages over taxon-based methods of inferring paleoenvironments (e.g. they do not assume stasis in a lineage’s habitat preference over evolutionary time). Current methods for predicting habitat preference from bovid postcrania are restricted to femora and metapodials, whose preservation is often limited. We describe here a method for predicting paleohabitats using measurements of bovid astragali. The astragalus method correctly predicted the habitat preference for 146 of 218 modern bovid specimens (67%, 2.7 times better than chance; $p < 0.0001$). This accuracy compares well with that of femur and metapodial methods (1.8–3.4 times better than chance). In addition, analysis of the probabilities associated with the habitat predictions allows a confidence threshold to be established that identifies specific predictions which have <5% chance of being in error. This raises the effective accuracy of the method to 95%. Extensive exploration and manipulation of the underlying data demonstrate that the habitat predictions are generally robust, and are relatively independent of body weight, taxonomy, and sample composition. The accuracy of this method and its broad applicability make it a useful addition to the existing array of techniques for inferring past environments.

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1. Introduction

The environment is a key component of most hypotheses regarding the pattern and process of hominid biological and technological evolution (e.g. [20,21,31,32]). Accurate and precise reconstructions of paleoenvironments play a crucial role in the testing and refinement of such hypotheses. An increasingly popular method of reconstructing paleoenvironments is to use the functional morphology of mammalian postcranial fossils to infer their locomotor adaptations and, by association, their habitat preferences [1,3,4,10–13,16,19,25]. This approach is commonly known as ‘ecological morphology’ or ‘ecomorphology’. While these labels do serve to identify this approach, their use

is generally avoided here as they might imply that the approach involves a web of interactions between a variety of taxonomically diverse organisms, which it does not. Instead, this approach focuses on the mechanical interaction between an organism and the physical substrates it moves across. This is simply functional morphology.

The theoretical basis for using postcranial functional morphology to infer habitat preference is that, in theory, an organism’s locomotor anatomy should have adaptations to the particular substrate(s) and environment(s) it locomotes across [8,22,23]. This is particularly true for animals, like bovids, that are apparently under selection by predation and typically employ locomotion to escape [14,18]. Such selection is likely to result in taxa whose locomotor anatomy is relatively specialized for movement across the substrates they frequent. If this is the case, then it should be possible to predict the habitat

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preference from the functional morphology: an organism adapted for running fast and straight over level terrain likely prefers open country, whereas an organism adapted for lateral dodging over uneven terrain likely prefers a more closed habitat. This approach is analogous to predicting the ‘habitat preference’ of automobiles based on their engineering: a drag racer is adapted for straight movement across level open terrain, while a four-wheel drive jeep is adapted for movement across obstacle-laden uneven terrain. Once the habitat preference(s) have been inferred from the functional morphology, they can be used to reconstruct aspects of the paleoenvironment (though of course attention must be paid to taphonomic factors as well). For example, if the bovid remains from a particular fossil assemblage all evince adaptations for open country habitat, it is likely that the assemblage samples an open environment.

One advantage of this approach to reconstructing past environments is its relative independence from taxonomy and phylogeny. Taxon-based ‘faunal list’ methods, while certainly of value, rely on the assumption of temporal stasis in habitat preferences within a lineage over evolutionary time. They also require a robust estimate of phylogeny, as well as taxonomic identifications of specimens to the level of genus or species, which can limit sample sizes and introduce bias. The functional morphology approach requires little in the way of taxonomic or phylogenetic information, providing a good complement to ‘faunal list’ methods.

Phylogenetic relationships do play an indirect role in the functional morphology approach to paleoenvironmental reconstruction. The morphology of an organism is constrained and shaped by its evolutionary history, and is not engineered specifically and solely for its current habitat. As such, phylogeny represents a potentially confounding variable in attempting to infer habitat preference from functional morphology. For example, the one forest-dwelling species of an otherwise open-country subfamily is likely to retain some open-country locomotor adaptations due to its evolutionary history. Similarly, a lineage that shifts from the forest to the plains may retain, at least for some time, a few adaptations associated with closed habitat locomotion. So the use of functional morphology to infer paleohabitats is only ‘taxon-free’ in the limited sense that the method does not require taxonomic identification of the fossils used beyond family level (i.e. that they are bovids; cf. [13]; though knowing the number of species represented is helpful). In practice, however, the confounding effect of phylogenetic constraint can be identified and excluded from the analysis by identifying anatomical features that co-vary with locomotion/habitat, rather than phylogeny, as described below.

The practical implementation of a functional morphology approach to paleohabitat reconstruction focuses on morphological characters, usually metric in

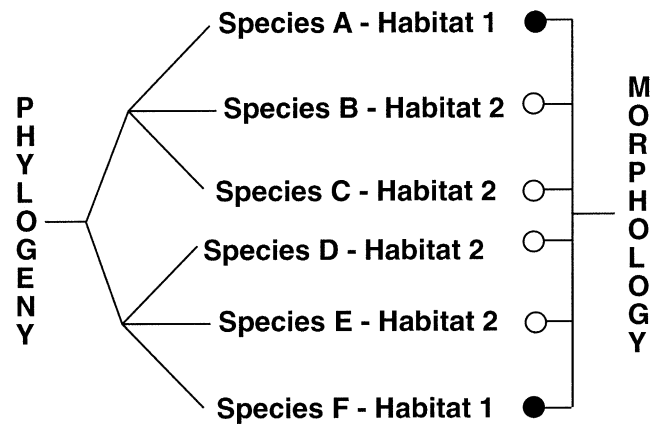


Fig. 1. The goal of ‘ecomorphology’ is to identify morphological characters that reflect habitat preference independent of phylogeny. In this figure, such characters would be those shared between species A and F to the exclusion of species B, C, D, and E.

nature (measurements) but sometimes non-metric (shape defined according to descriptive criteria), that are potentially related to locomotion. The goal is to locate characters which co-vary with habitat preference, but do not co-vary with phylogeny, as such characters permit the accurate prediction of habitat preference independent of phylogeny/taxonomy. Characters thought to be potentially indicative of habitat are tested using samples of modern taxa whose habitat preferences are known. The variation of those characters in modern taxa reveals whether they are correlated with habitat preference, and thus whether they are ‘good’ characters for habitat prediction. Specifically, statistical techniques are used to predict the habitat preference from the morphological characters alone. The predicted habitat preferences for the modern specimens are then compared to their known habitat preferences to quantify the character’s utility for habitat prediction. This empirically tests the link between the anatomical features and habitat preference.

This procedure identifies characters which are primarily influenced by habitat rather than phylogeny (Fig. 1). For example, characters of the locomotor skeleton that are shared between the bovids *Tragelaphus spekei* and *Kobus megaceros*, but which are not possessed by other species of the *Tragelaphus* or *Kobus* genera, are likely due to the shared habitat preference of *T. spekei* and *K. megaceros* (swampy ground) which differs from that of their co-genera. If the state of such characters were primarily determined by phylogeny (as discussed above), then *T. spekei* should resemble the general *Tragelaphus* condition, rather than that of the phylogenetically more distant *K. megaceros*.

The postcranial functional morphology approach to paleohabitat prediction has, to date, focused on bovids [4,10–13,16,19,25], though it has also been applied to suids [1] and cercopithecoids [3]. Bovid taxa are found in

a wide range of habitats, and are reasonably habitat specific, making them both broadly applicable and potentially reliable habitat indicators [7]. They are typically under selection by predation, and usually employ locomotion as a component of their escape strategy, so they are theoretically likely to have postcranial characters which are good habitat predictors. Extant bovids are taxonomically diverse, so modern samples can provide robust tests of the utility of particular characters for habitat prediction. Bovid remains are also relatively common in the archaeological and paleontological record, allowing such methods to be applied at many sites and on relatively large samples.

A variety of workers have identified various morphological characters of bovid postcrania as being indicative of habitat preference. Gentry [4] rather informally described approximately 40 non-metric characters covering a range of postcranial elements, and Köhler [16] described about 38 non-metric characters of the metapodials and phalanges. However, neither Gentry [4] nor Köhler [16] systematically tested their characters on modern bovid samples to quantify their utility for habitat prediction. As such, those characters are currently unverified, and should not be used for habitat reconstruction until such a test (which we have conducted) is published. Kappelman [10–12] identified and tested nine metric characters of the femur, which allow habitat prediction with an accuracy of 81–85% using a four-category habitat scheme (Plains, Light Cover, Heavy Cover, Forest; [13]). Plummer and Bishop [19] described and tested 19 metric characters of the metapodials, which allow habitat prediction with an accuracy of 62–89% using a three-category habitat grouping scheme (Open, Intermediate, Closed).

These methods are intended to reconstruct past habitats, as the habitats of extant bovids can be assessed via direct observation. As such, the utility of these methods must be evaluated in terms of their applicability to the fossil and archaeological records. In this regard, the Kappelman [10–12] method is often of limited utility due to taphonomic factors and collection bias, since it requires either a complete femur (for greatest accuracy) or a proximal femur. For example, Kappelman [12] used only five bovid femora to revise the paleohabitat of Fort Ternan. There are over 2000 identified bovid fossils from those deposits, representing five genera and four tribes [26], making it highly unlikely that the analyzed sample of five specimens is representative. In contrast, the metapodial method of Plummer and Bishop [19] is more widely applicable. Their method requires, ideally, a complete metapodial, but can be applied to either proximal articular ends or distal articular ends with enough shaft preserved to allow distal metatarsals and metacarpals to be distinguished. For the remains from Olduvai Gorge, Plummer and Bishop [19] were able to use 319 fossil metapodials from Bed I, while Kappelman

et al. [13] were able to use only 22 femora from the entire site.

An informal survey of the bovid postcranial fossils recovered from several Ethiopian Plio-Pleistocene hominid sites revealed that sufficiently complete femora were only very rarely present, and sufficiently complete metapodials were fairly limited in number as well. By contrast, a large number of complete astragali were present, as well as considerable numbers of phalanges. For the Omo bovid collection, for example, there are very roughly 10 astragali for every metapodial, and about 100 astragali for every femur. While element proportions differ across sites, taphonomic considerations (e.g. [1,15,17]) suggest that relatively complete astragali are likely to almost always be better represented than relatively complete femora or metapodials. In addition, astragalus morphology is likely to be adapted for locomotion, given its anatomical position and function. This led us to develop and test a method for using metric characters of the bovid astragalus to predict habitat preference. We present this method here, and believe that it represents a useful addition to the current array of techniques for inferring past environments.

2. Materials

The method described here was developed and tested using a sample of modern African bovids from the American Museum of Natural History. The taxonomic composition of the sample is given in Table 1. One astragalus from each of 218 individuals was measured (no preference for side). Only adult individuals (as determined by complete fusion of postcranial epiphyses) that were documented as wild-caught (non-captive) were included in the sample. Specimens with skeletally evident postcranial pathological processes were excluded. The specimens were sampled without regard to sex, since this parameter cannot currently be determined for isolated postcranial fossils, but the sample includes 61 documented males and 39 documented females.

3. Methods

Eight measurements (Fig. 2) were taken on each astragalus as follows.

Medial length (LM): The maximum proximal–distal dimension of the medial surface taken parallel to the main proximal–distal axis of the astragalus (Fig. 2a).

Intermediate length (LI): The minimum proximal–distal dimension of the astragalus, taken parallel to the main proximal–distal axis of the bone (Fig. 2c).

Lateral length (LL): The maximum proximal–distal dimension of the lateral surface taken parallel to the main proximal–distal axis of the astragalus (Fig. 2b).

Table 1

Taxonomic composition and habitat assignments of the modern African bovid sample, using taxonomy of Gentry [5]

Subfamily	Tribe	Species	# Measured	Habitat group	
Alcelaphinae	Aepycerotini	<i>Aepyceros melampus</i>	10	Light Cover	
	Alcelaphini	<i>Alcelaphus buselaphus</i>	13	Open	
		<i>Connochaetes gnou</i>	1	Open	
		<i>Connochaetes taurinus</i>	7	Open	
		<i>Damaliscus dorcas</i>	6	Open	
		<i>Damaliscus hunteri</i>	2	Open	
		<i>Damaliscus lunatus</i>	5	Open	
Antilopinae	Antilopini	<i>Antidorcas marsupialis</i>	8	Open	
		<i>Gazella granti</i>	10	Open	
		<i>Gazella thomsoni</i>	5	Open	
		<i>Litocranius walleri</i>	4	Open	
	Neotragini	<i>Madoqua kirki</i>	2	Forest	
		<i>Neotragus batesi</i>	2	Forest	
		<i>Ourebia ourebia</i>	10	Light Cover	
		<i>Raphicerus campestris</i>	5	Light Cover	
Bovinae	Cephalophini	<i>Cephalophus monticola</i>	3	Forest	
		<i>Cephalophus natalensis</i>	3	Forest	
		<i>Cephalophus niger</i>	1	Forest	
		<i>Cephalophus nigrifrons</i>	3	Forest	
		<i>Cephalophus sylvicultor</i>	6	Forest	
		<i>Taurotragus oryx</i>	12	Open	
	Tragelaphini	<i>Tragelaphus angasi</i>	3	Forest	
		<i>Tragelaphus buxtoni</i>	7	Heavy Cover	
		<i>Tragelaphus euryceros</i>	9	Heavy Cover	
		<i>Tragelaphus imberbis</i>	4	Heavy Cover	
		<i>Tragelaphus scriptus</i>	12	Forest	
		<i>Tragelaphus spekei</i>	6	Heavy Cover	
		<i>Tragelaphus strepiceros</i>	10	Heavy Cover	
Hippotraginae	Hippotragini	<i>Addax nasamaculatus</i>	4	Open	
		<i>Hippotragus niger</i>	5	Open	
		<i>Oryx dammah</i>	3	Open	
		<i>Oryx gazella</i>	4	Open	
	Reduncini	<i>Kobus ellipsiprymnus</i>	6	Heavy Cover	
		<i>Kobus kob</i>	5	Light Cover	
		<i>Kobus megaceros</i>	5	Heavy Cover	
		<i>Kobus vardonii</i>	2	Light Cover	
		<i>Redunca arundinum</i>	4	Light Cover	
		<i>Redunca fulvorufula</i>	7	Light Cover	
		<i>Redunca redunca</i>	4	Light Cover	

Intermediate width (WI): The minimum medial–lateral dimension on the anterior surface in the area of the junction between the proximal and distal articular regions. Any projections or tubercles are included (Fig. 2c).

Distal width (WD): The medial–lateral dimension of the distal end at its distal-most point (Fig. 2c).

Proximal thickness (TP): The anterior–posterior dimension of the proximal end of the lateral surface (Fig. 2b).

Intermediate thickness (TI): The minimum anterior–posterior dimension of the lateral surface in the area of the junction between the proximal and distal articular regions (Fig. 2b).

Distal thickness (TD): The anterior–posterior dimension of the distal end of the lateral surface (Fig. 2b).

The measurements were taken with digital calipers and recorded to the tenth of a millimeter. All measurements were taken by one individual (D.D.), eliminating concerns of interobserver error. The intraobserver error for each measurement was determined by measuring six specimens twice, with a separation of at least 4 days between measurements, and the results are given in Table 2. The proximal width of the astragalus was initially included as one of the metrics, but during data-gathering it became apparent that this measurement was essentially unrepeatable due to the lack of landmarks in the region.

All 'ecomorphological' methods must utilize a habitat grouping scheme, in which the continuous range of possible habitats is partitioned into an arbitrary set of finite categories. Early work on bovids [10–12,19] used a

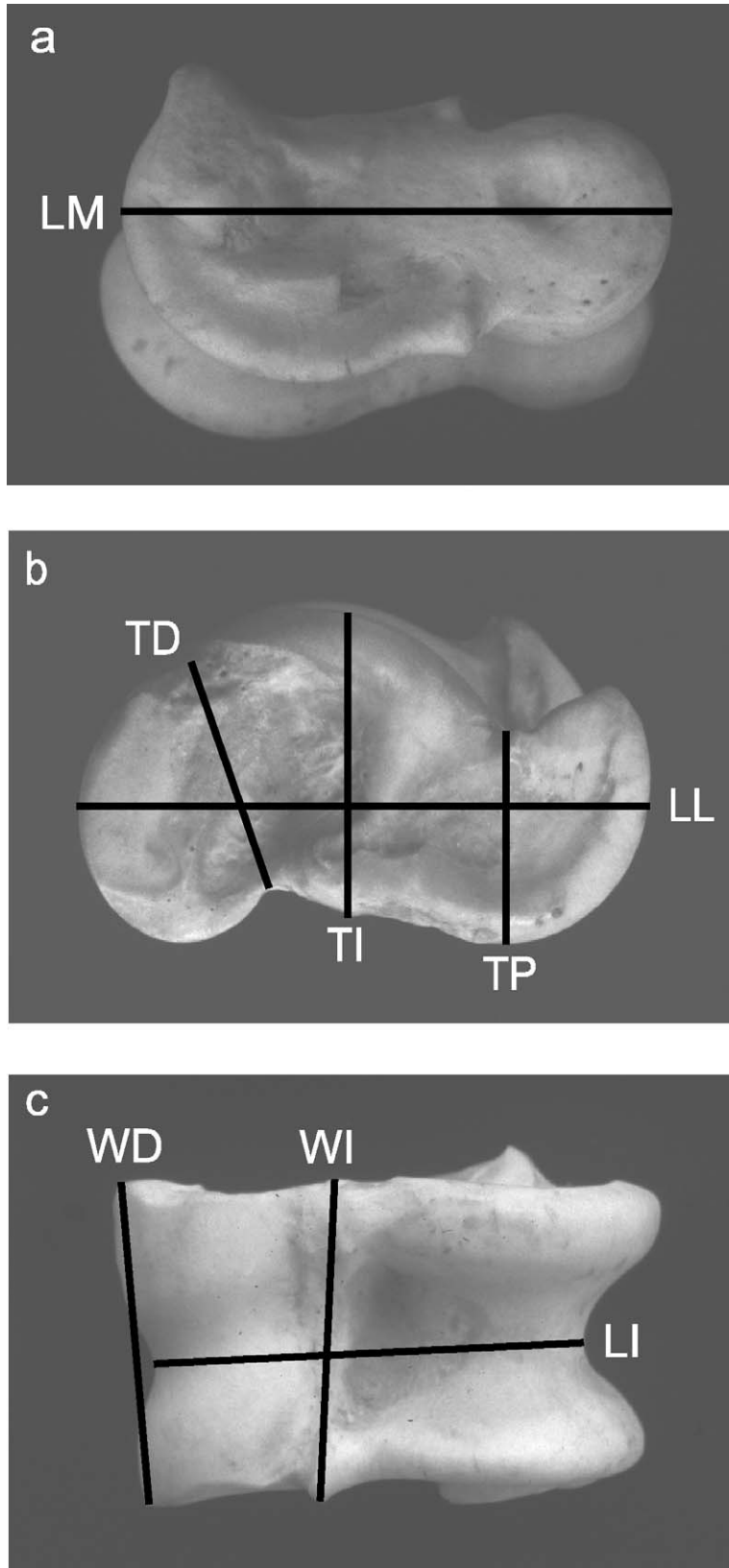


Fig. 2. (a) Medial view of bovid right astragalus with medial length (LM) measurement marked. (b) Lateral view of bovid right astragalus with distal thickness (TD), intermediate thickness (TI), proximal thickness (TP), and lateral length (LL) measurements marked. (c) Anterior view of bovid right astragalus with distal width (WD), intermediate width (WI), and intermediate length (LI) measurements marked.

Table 2
Intraobserver measurement error

Metric	Mean error (%)	Range (%)
LL	0.2	0–0.6
LI	0.6	0–1.2
LM	0.4	0–0.8
WI	0.8	0.4–1.5
WD	0.9	0–2.1
HP	1.0	0–2.1
HI	1.2	0–2.5
HD	0.6	0–1.4

three category system: open habitat, closed habitat, and ‘intermediate’ habitat. Subsequent work refined this into a four category scheme: Plains, Light Cover, Heavy Cover, and Forest [13]. We used the four categories of Kappelman [13], but performed our own assignment of bovid taxa to habitat categories. Our assignments are given in Table 1. The ‘Forest’ taxa are, naturally, forest-dwelling taxa. ‘Heavy Cover’ taxa are those which frequent bush, woodland, swamp, and near-water habitats [13]. ‘Light Cover’ taxa are those which frequent light bush, tall grass, and hilly areas [13]. ‘Open’ taxa (the ‘plains’ category of Kappelman et al. [13]) are those which frequent edge or ecotone, open country, and arid country [13]. The characterization of the habitat preferences of the modern bovid taxa was conducted independently of the statistical analysis described below. The assignments were based on extensive field observations by one of us (E.V.), as well as a large body of literature describing modern bovid habitat preferences (e.g. [1,14,18,28,29]). Even so, it should be emphasized that this habitat grouping scheme is an arbitrary division of a continuous range, as any such scheme must be (cf. Kappelman et al. [13]). Furthermore, many bovid taxa range over several habitat types, and so the assignment of a taxon to a particular category is a ‘best fit’ designation rather than an exclusive one. This habitat grouping scheme is thus a significant (albeit necessary) simplification of the complex range of bovid habitat utilization, as are all such schemes.

Having obtained astragalus measurements and habitat preference information for a large sample of modern bovinds, the remaining step was to determine the degree to which habitat could be predicted from the measurements. Using the statistics program JMP (versions 3.2.6 and 5.0 for the Macintosh, SAS Institute, Cary, NC) a discriminant function was constructed to predict the habitat preference from the astragalus measurements. Extensive experimentation with inclusion and exclusion of measurements and ratios revealed that optimal results were obtained using the eight ‘raw’ measurements and one ratio (LI/WI). We used this empirical method of variable selection, rather than the automated ‘stepwise’

procedure of variable selection employed in previous such analyses (e.g. Plummer and Bishop [19]), based on the cautions of Huberty and Barton [9]. The use of log-transformed measurements produced results effectively identical to that of the untransformed data, and so all subsequent discussion refers to the analysis of untransformed measurements.

Previous applications of discriminant function analysis to postcranial functional morphology have devoted substantial attention to avoiding correlated measurements (e.g. [3,19]). The addition of a correlated variable to a (hypothetically) otherwise uncorrelated set of variables does not increase the discriminating power of the function, but neither does it decrease it. In practice, this is demonstrable with a simple empirical experiment: one variable in the current analysis was duplicated, producing two perfectly correlated (identical) variables, with no resulting alteration of the discriminant function results. In theory, since the purpose of such discriminant functions is solely to predict habitat preference, rather than to provide a balanced representation of overall morphology, there is little need to be concerned with the independence (or lack thereof) of the measurements used. If habitat preference could be predicted with complete accuracy from several correlated measurements of, say, astragalus width, this would be completely acceptable for our purposes. Therefore, so long as a predictive discriminant function is sufficiently accurate, and the sample size sufficiently large [30], there is little need to be concerned with inter-correlations among the variables used, except perhaps to weed out redundant measures to speed data collection.

We also carried out canonical variates and principal component analyses (again using JMP) to further investigate the structure of the data. Regressions (simple and multiple) of the measurements against mean body weight were done using StatView (version 4.5.1 for the Macintosh, SAS Institute).

4. Results

A discriminant function which allows the habitat preference category to be predicted from astragalus measurements of modern African bovinds is given in Appendix A, and summary statistics for the measurements used are given in Table 3. This discriminant function correctly predicted habitat group for 146 out of the 218 bovinds in the sample, for an overall accuracy of 67% (2.7 times than expected by chance, $p < 0.0001$ using Fisher’s exact chi-squared test). The specific mistakes made by the discriminant function are detailed by taxon in Table 4 and by habitat group in Table 5. We explored

Table 3
Summary statistics for the astragalus measurements by habitat group

Metric	Habitat group	Mean (mm)	SD	Range (mm)
LL	Forest	31.2	10.2	13.3–48.2
	Heavy Cover	55.5	8.6	40.0–70.4
	Light Cover	34.0	7.1	21.6–45.7
	Open	47.5	14.6	25.7–79.3
LI	Forest	25.3	8.1	10.6–37.8
	Heavy Cover	44.8	7.4	32.2–57.9
	Light Cover	27.0	5.7	17.0–37.6
	Open	37.8	12.3	19.5–65.1
LM	Forest	29.3	9.2	12.7–43.2
	Heavy Cover	51.2	8.3	33.7–64.5
	Light Cover	31.7	6.7	20.2–44.2
	Open	44.4	13.8	23.1–74.3
WI	Forest	17.8	6.3	7.4–20.8
	Heavy Cover	31.6	5.3	22.8–40.6
	Light Cover	19.7	4.3	12.0–26.5
	Open	28.8	8.4	14.7–47.1
WD	Forest	18.8	6.5	7.9–29.0
	Heavy Cover	33.8	5.7	23.3–44.2
	Light Cover	19.9	4.4	12.5–27.4
	Open	29.7	9.4	14.5–51.7
HP	Forest	11.6	4.2	4.5–18.1
	Heavy Cover	21.2	3.7	14.4–27.8
	Light Cover	12.3	2.7	7.7–17.0
	Open	18.8	6.1	9.1–32.7
HI	Forest	15.6	5.3	6.5–23.9
	Heavy Cover	27.3	4.6	19.3–37.8
	Light Cover	17.0	3.7	10.7–23.3
	Open	24.3	7.3	11.8–41.7
HD	Forest	13.1	4.5	5.2–20.6
	Heavy Cover	23.8	4.2	15.2–32.7
	Light Cover	14.6	3.2	9.2–20.7
	Open	21.7	6.8	10.8–36.7

the discriminant function and underlying data in a variety of ways, as discussed below, to establish the reliability of these results.

4.1. Accuracy

Previous efforts to predict habitat from bovid morphometrics have described the accuracy of their discriminant functions as the percentage of the modern sample that was correctly classified by the discriminant function (i.e. the ‘resubstitution’ accuracy, 67% in this case). However, this procedure tests the function on the same sample used to generate it, so the resulting estimate of accuracy is dubious, and likely a maxima [9]. To further investigate the accuracy of the astragalus discriminant function, we used a jackknifing procedure whereby one specimen was removed from the sample, the discriminant function derived from the ‘ $n-1$ ’ sample, and then applied to the held-out specimen. This

procedure was repeated 39 times, using one ‘held-out’ specimen per species. The ‘held-out’ specimens were correctly classified 26 out of 39 times, for an estimated accuracy of 66.7%. The misclassifications invariably involved specimens that had also been misclassified by the original discriminant function. To investigate the effects of withholding larger numbers of specimens simultaneously, we split the sample into a ‘generator’ subsample and a ‘test’ subsample, the latter composed of one individual from each species. We derived a discriminant function from the ‘generator’ subsample and then applied it to the ‘test’ subsample, with a resulting accuracy of 79.5% (31 out of 39 specimens correctly classified). We repeated the ‘generator-test’ procedure several times using completely random ‘test’ subsamples ($n=55$ specimens, 25% of total sample) and obtained accuracies ranging from 60 to 70%. Based on the results of multiple methods of estimating the accuracy of the astragalus discriminant function, we are confident that 67% is a representative estimate of its accuracy.

Even so, all predictions generated by a particular discriminant function are not equal: different specific predictions have different odds of being accurate. The discriminant function, in addition to a prediction of habitat group, also provides an associated percentage probability (confidence value) for that prediction. (More specifically, the discriminant function provides an estimate of the probability that a specimen belongs to each one of the habitat groups, and the group with the highest probability is the predicted group.) Imagine two astragali, both predicted by the function to belong to the Forest habitat preference group. The confidence value of one prediction might be 99%, while the confidence value of the other prediction might be only 50%. So even though both predictions are the ‘same’ (Forest), and were produced by the same discriminant function, it would be a mistake to assume that they are of equal reliability.

Instead, we use the associated confidence values to determine which individual predictions generated by our discriminant function are statistically significant. Specifically, we posed the question, “What confidence value would we have to use as the cutoff value to obtain a misclassification rate of less than 5%?” For our astragalus data set, the answer is 75%. In other words, if we consider habitat predictions with associated confidence values of less than 75% to be ‘indeterminate’, then the number of misclassifications is only 11 out of 218, or 5.0%. This is equivalent to a p -value of 0.05, and so such predictions can be thought of as statistically significant (assuming an alpha of 0.05). We do not suggest that specific predictions which fall short of statistical significance be ignored, just that they should be accorded less weight.

An overall accuracy of 67% is nominally 2.7 times greater than expected by chance with four habitat categories (25%). However, discriminant functions are

Table 4
Discriminant function habitat classifications by taxon

Species	Habitat group	# Correctly classified	Misclassifications ^a
<i>Addax nasamaculatus</i>	Open	2	2L
<i>Aepyceros melampus</i>	Light Cover	10	
<i>Alcelaphus buselaphus</i>	Open	13	
<i>Antidorcas marsupialis</i>	Open	3	4L, 1F
<i>Cephalophus monticola</i>	Forest	3	
<i>Cephalophus natalensis</i>	Forest	3	
<i>Cephalophus niger</i>	Forest	1	
<i>Cephalophus nigrifrons</i>	Forest	2	1L
<i>Cephalophus sylvicultor</i>	Forest	0	4O, 1H, 1L
<i>Connochaetes gnou</i>	Open	1	
<i>Connochaetes taurinus</i>	Open	7	
<i>Damaliscus dorcas</i>	Open	6	
<i>Damaliscus hunteri</i>	Open	2	
<i>Damaliscus lunatus</i>	Open	5	
<i>Gazella granti</i>	Open	2	8L
<i>Gazella thomsoni</i>	Open	0	5L
<i>Hippotragus niger</i>	Open	4	1H
<i>Kobus ellipsiprymnus</i>	Heavy Cover	5	1O
<i>Kobus kob</i>	Light Cover	3	2H
<i>Kobus megaceros</i>	Heavy Cover	1	3L, 1F
<i>Kobus vardoni</i>	Light Cover	1	1O
<i>Litocranius walleri</i>	Open	1	2L, 1F
<i>Madoqua kirki</i>	Forest	2	
<i>Neotragus batesi</i>	Forest	2	
<i>Oryx dammah</i>	Open	1	1H, 1L
<i>Oryx gazella</i>	Open	3	1H
<i>Ourebia ourebia</i>	Light Cover	5	5F
<i>Raphicerus campestris</i>	Light Cover	2	3F
<i>Redunca arundinum</i>	Light Cover	4	
<i>Redunca fulvorufula</i>	Light Cover	6	1F
<i>Redunca redunca</i>	Light Cover	4	
<i>Taurotragus oryx</i>	Open	4	8H
<i>Tragelaphus angasi</i>	Forest	0	2O, 1H
<i>Tragelaphus buxtoni</i>	Heavy Cover	5	2O
<i>Tragelaphus euryceros</i>	Heavy Cover	9	
<i>Tragelaphus imberbis</i>	Heavy Cover	2	2L
<i>Tragelaphus scriptus</i>	Forest	8	4L
<i>Tragelaphus spekei</i>	Heavy Cover	5	1F
<i>Tragelaphus strepiceros</i>	Heavy Cover	9	1O

^aThis column lists the specimens of that taxon that were misclassified, broken down by the habitat group (abbreviated using the initial letter of the group) that they were mistakenly assigned to by the discriminant function.

designed to emphasize the differences between pre-determined categories [30], and so may be able to do better than chance even if the categories have no biological reality. As an experiment to establish an empirical baseline of accuracy, we used a variety of clearly incorrect habitat assignments for our sample, and generated discriminant functions to predict those 'wrong' habitats. Depending on how the 'wrong' habitats were assigned, the resulting discriminant functions had accuracies ranging from 40 to 50%, with a median near 45%. This suggests that, for this data set, a discriminant function can do two times better than chance, regardless of the 'reality' of the categories. Importantly, though, there are two characteristics of

these 'wrong' discriminant functions that distinguish them from our original function. First, their misclassifications are relatively randomly distributed relative to habitat types, whereas the misclassifications of the original function are concentrated in certain habitat types (Table 5). Second, the associated confidence values for specific classifications in 'wrong' functions appear to be, on average, much lower than the average for the original function. This provides additional support for the importance of considering the confidence values for specific predictions, as discussed above. These distinguishing features of the original function, combined with its greater accuracy, indicate that it does perform better than chance.

Table 5
Discriminant function habitat classifications by actual habitat type

Actual habitat	Classified as:				Accuracy (actual) ^a
	Forest	Heavy Cover	Light Cover	Open	
Forest	21	2	6	6	60.0%
Heavy Cover	2	36	5	4	76.6%
Light Cover	9	2	35	1	74.5%
Open	2	11	22	54	60.7%
Accuracy (pred) ^b	61.8%	70.6%	51.5%	83.1%	67%

^a‘Accuracy (actual)’ reports the accuracy of the classification by the actual habitat groups. In other words, of those specimens actually belonging to a particular habitat group, what percentage were properly classified?

^b‘Accuracy (pred)’ reports the accuracy of the classification by the predicted habitat groups. In other words, of those specimens predicted to belong to a particular habitat group, what percentage actually do?

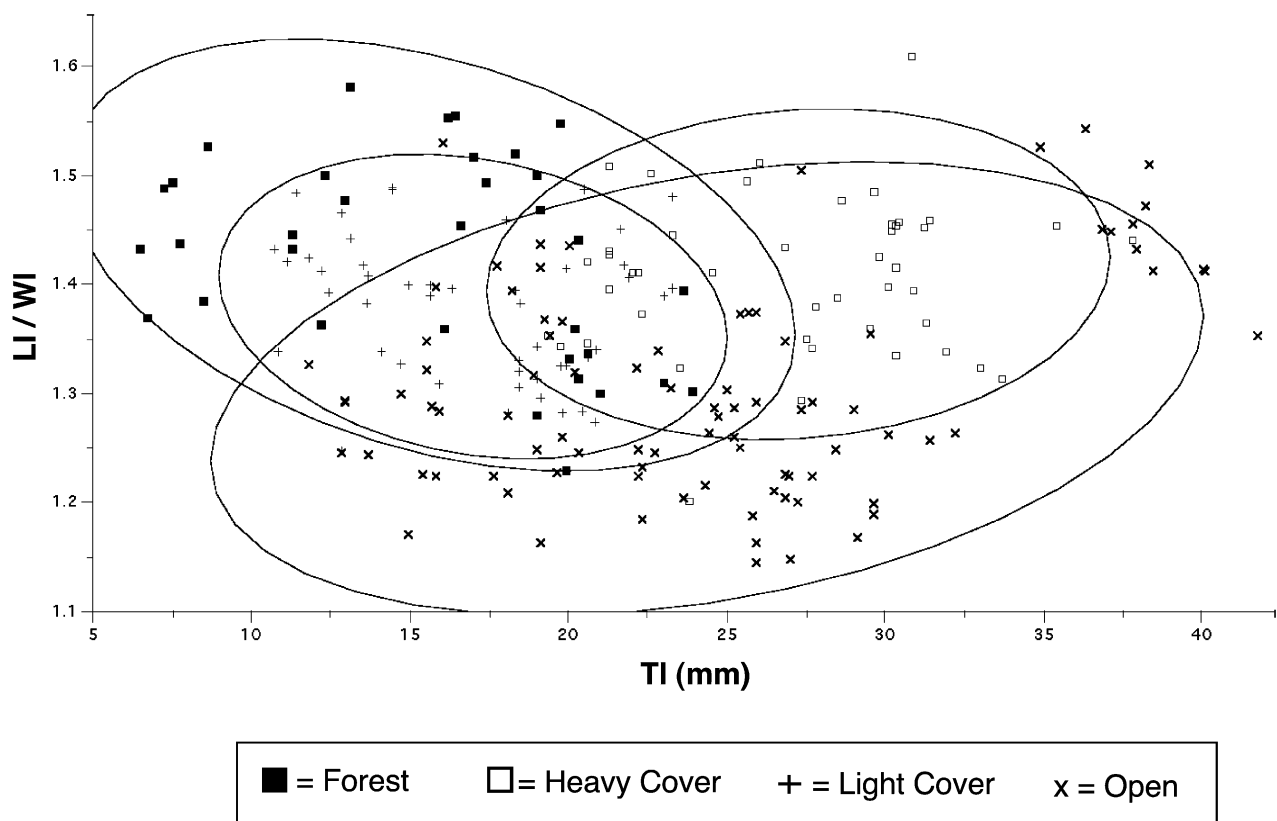


Fig. 3. A plot of intermediate thickness (TI) versus the ratio of intermediate length (LI) to intermediate width (WI) for all the bovid specimens in our modern sample. The actual habitat classifications for the specimens are denoted by symbols: closed boxes are Forest, open boxes are Heavy Cover, +’s are Light Cover, and ×’s are Open. The ellipses represent 90% of each habitat group’s distribution.

4.2. Misclassifications

There are two notable concentrations of misclassifications. First, 22 Open specimens were misclassified as Light Cover. This corresponds with the results of the principal components and canonical variates’ analyses (results not shown), in which reasonable separation was seen between most groups with the greatest overlaps involving Light Cover (cf. Scott et al. [25]). Second, eight

of 12 *Taurotragus oryx* (eland) specimens were incorrectly classified as Heavy Cover rather than Open. This is likely a consequence of the great body weight of this taxon and/or associated allometric effects [22]. Other analyses have omitted *T. oryx* on these grounds [13,19], but this renders dubious the application of the resulting discriminant functions to large-bodied fossil forms. As such, we included *T. oryx*, though its exclusion does not notably alter the accuracy of our discriminant function.

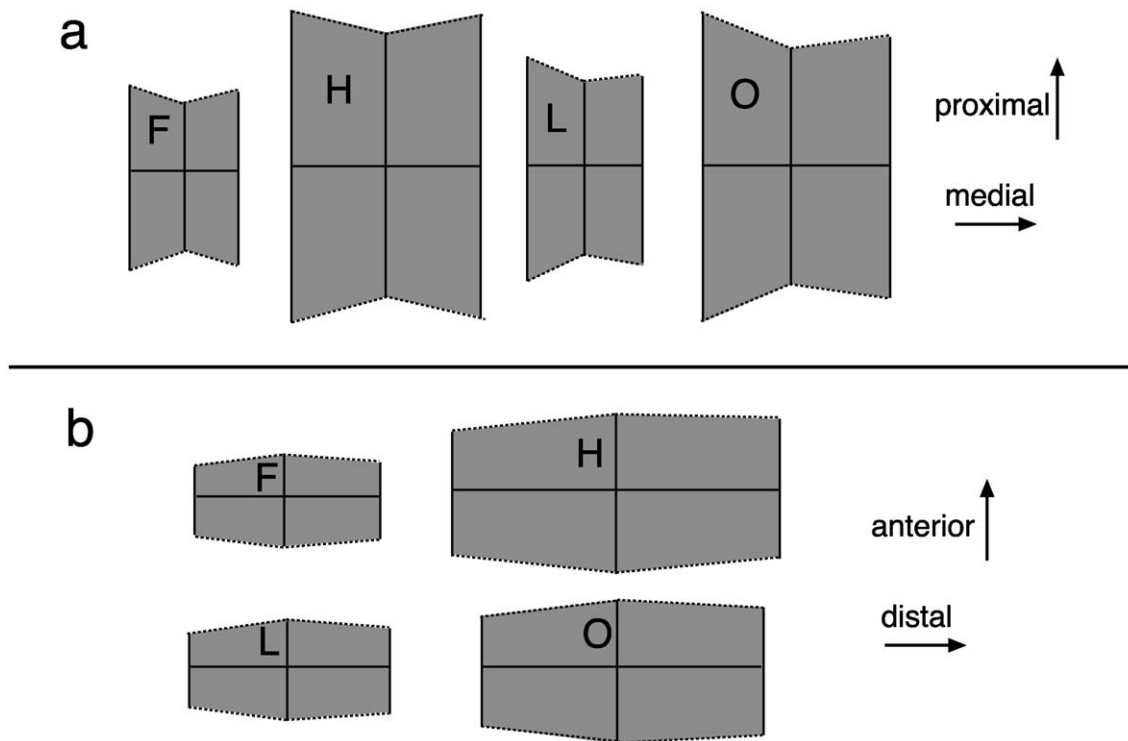


Fig. 4. Graphic representation of the relative mean dimensions of Forest (F), Heavy Cover (H), Light Cover (L), and Open (O) habitat astragali. The solid lines indicate the measured dimensions of the astragali (see text), while the dashed lines merely complete the polygons and are not indicative of actual dimensions. (a) Anterior views. (b) Lateral views.

4.3. Morphotypes

When using a discriminant function to differentiate between habitat groups, it might be argued that, as per the physicist Werner Heisenberg, “the equation knows best”, [6, p. 5]. But while the equations are certainly the preferred method for generating the predictions, it is also desirable to have a sense of the underlying morphological differences between habitat groups so as to begin to characterize the actual functional anatomy involved. The morphological differences between the astragali of different habitat groups are best illustrated by a comparison of their length (superior–inferior), width (medial–lateral), and thickness (anterior–posterior). Fig. 3 is a graph of the LI/WI ratio (intermediate length/intermediate width) against TI (intermediate thickness) for all the modern bovid specimens (different choices of length, width, and thickness measures yield similar graphs). This graph provides a general indication of the morphological differences between the habitat groups. It illustrates how the most extensive overlap involves Light Cover taxa, and demonstrates that *Taurotragus oryx* is an outlier (almost certainly due to its massive body weight). If Open taxa are taken as the basis of comparison, then Forest and Light Cover taxa have anterior–posteriorly compressed astragali, while Heavy Cover taxa have anterior–posteriorly expanded astragali. In addition, Open taxa tend to have superior–inferiorly

compressed astragali relative to the medial–lateral width (compared with other habitat types). The (hypothetical) mean morphotype of each habitat group is represented graphically in Fig. 4. It is tempting to assert specific functional correlates of these differences, but rigorous analysis of the biomechanics involved is preferable to such speculation.

4.4. Body weight

Body weight is a potential complicating factor in analyses of this type. A priori, it is likely that at least some dimensions of the astragalus are correlated with body weight (see below). This creates a risk that the discriminant function will really predict body weight, with its success at habitat classification only a secondary consequence. One solution to this problem is to use ratios to eliminate the effects of absolute size (cf. Plummer and Bishop [19]). However, for the current data set, various ‘all ratio’ discriminant functions had prediction accuracies of only about 60%, probably due to the correlation between body weight and habitat preference in bovids (e.g. Kingdon [14]). The weight–habitat correlation is statistically significant in our modern bovid sample, using mixed-sex body weight means calculated from the ranges given in Kingdon [14]. (We realize that the cautions of Smith and Jungers [27] regarding the source of body weight data apply here,

Table 6
Predicted body weight ranges for predicted habitat groups

Predicted habitat group	Range of predicted body weights (kg)	Mean (kg)	SD
Forest	9–73	26	16
Heavy Cover	59–733	266	187
Light Cover	17–111	49	21
Open	33–933	178	184

and that substantial sexual dimorphism in some taxa makes mixed-sex means broad approximations, but only a general indication of body weight is necessary for our purposes.) This suggests that the complete elimination of size is undesirable if habitat prediction is the goal. On the other hand, exploration of the relationship between the measurements and body weight is certainly merited to ensure that body weight is not driving the prediction.

Multiple regression (least squares) of the natural log of body weight against all eight measurements demonstrates a strong correlation between these variables and body weight (adjusted R^2 of 0.91). The regression equation is provided in Appendix A since it can be used to estimate the body weight of fossil bovids, which may be of interest (cf. Scott [24]). Independent regressions of the natural log of each measurement were carried out against the natural log of body weight to investigate allometric effects. All eight measurements exhibit significant ($p < 0.001$) negative allometry, with slopes ranging from 0.32 to 0.36. The astragalus thus seems to show somewhat less negative allometry (i.e. is closer to isometry) than long bone lengths in bovids, which have slopes from 0.18 to 0.27 when similarly regressed against body weight [23].

To evaluate whether body weight was driving the habitat predictions, the regression equation was used to predict the body weight for every specimen in our sample. The predicted body weights were then compared with the predicted habitat groups. If body weight were driving the habitat predictions, then each predicted habitat group should correspond to a fairly discrete range of predicted body weights—for example, specimens with a predicted habitat of Forest might encompass predicted body weights of 10–50 kg, Light Cover 40–120 kg, Heavy Cover 110–200 kg, and Open >190 kg. In fact, each predicted habitat type encompasses a wide range of predicted weights, and there is substantial overlap in those predicted weights across predicted habitat groups (Table 6). Thus, despite the link between body weight and measurements of the astragalus, the habitat predictions of the discriminant function are not primarily driven by body weight. Further confirmation of this is found in an examination of the discriminant function itself. The coefficients of the variables in the discriminant function clearly indicate that the most important variable for prediction is the

LI/WI ratio, which (as a ratio) is demonstrably not correlated with body weight.

We also used principal component analysis (PCA) to quantify the contribution of overall size and body weight to the predictive power of the discriminant function. PCA was used to generate nine independent principal components from the correlation matrix of the nine variables used in the original discriminant function (results using the covariance rather than correlation matrix were similar). The first principal component clearly reflects overall astragalus size (and size-linked shape) since it scales tightly with both astragalus length and the natural log of mean species body weight. We then constructed a new discriminant function to predict habitat group using the second through ninth principal components (rather than the measurements themselves). This ‘PCA’ discriminant function predicted habitat with an accuracy of about 54%, or about twice that expected by chance. Since the first principal component, which represents overall size, was omitted from this analysis, the ‘PCA’ discriminant function provides a measure of how well shape discriminates between the habitat groups when size is largely removed. Comparing that accuracy, 54%, with the accuracy of the original discriminant function (67%) suggests that approximately 13% of the discriminating power of the original discriminant function derives from overall size. This provides further evidence that size and body weight are not the primary determinants of the habitat predictions.

4.5. Taxonomic issues

The predictions of the discriminant function are inevitably a result of the modern sample used to generate it. As such, the discriminant function depends on the taxonomic composition of the modern sample (R. Klein, personal communication). For example, our sample contains 12 individuals of *Tragelaphus scriptus*, but only one of *Cephalophus niger*. Both are classified as Forest taxa, but the unequal sampling means that the composite Forest morphotype inferred from our sample is more dependent on *T. scriptus* morphology than *C. niger* morphology. This raises the question of how sensitive our discriminant function is to the sampling of taxa included in the modern sample. To investigate this question, we produced an altered version of the dataset with artificially equalized numbers of individuals per species (e.g. measurements of individual astragali were duplicated, or occasionally deleted, until all species within a habitat category were represented by an equal number of ‘individuals’). The ‘species-balanced’ discriminant function yielded results very similar to that of the original function, with habitat assignments changing for less than 10% of specimens and overall accuracy remaining approximately constant. The specimens whose habitat predictions shifted between the original

Table 7
Accuracy of habitat predictions from bovid postcranial elements

Element	Portion	Accuracy ^a	Source
Femur	Complete	3.4 ×	Kappelman et al. [13]
Femur	Proximal	3.2 ×	Kappelman et al. [13]
Astragalus	Complete	2.7 ×	This study
Metatarsal	Complete	2.7 ×	Plummer and Bishop [19]
Metacarpal	Complete	2.5 ×	Plummer and Bishop [19]
Metatarsal	Distal	2.1 ×	Plummer and Bishop [19]
Metacarpal	Distal	2.0 ×	Plummer and Bishop [19]
Metatarsal	Proximal	1.9 ×	Plummer and Bishop [19]
Metacarpal	Proximal	1.8 ×	Plummer and Bishop [19]

^aAccuracy expressed relative to chance (times better than random function).

and ‘species-balanced’ discriminant functions were uniformly those with low confidence values, supporting the use of such values to assess the reliability of specific predictions.

We also investigated the impact of removing individual species from the analysis in order to evaluate the sensitivity of the results to the inclusion/exclusion of taxa. When each species, in turn, was withheld from the analysis, the overall accuracy of the discriminant function varied from 63 to 70%. The omitted specimens were correctly classified 124 out of 218 times (57%). However, the misclassifications were heavily concentrated in a few taxa: *Antidorcas marsupialis* (8), *Cephalophus sylvicultor* (6), *Gazella* (14), and *Taurotragus oryx* (12). This suggests that the discriminant function is, as expected, sensitive to the inclusion of a few particular species, but is otherwise robust.

The dataset of modern bovid astragalus measurements can, in theory, also be used to predict taxonomic affiliations, though that is not the focus of the current study. Using the taxonomy of Gentry [5] and the same set of astragali measurements as described above, we were able to predict subfamily at 68% accuracy and tribe at 66% accuracy. These discriminant functions (available on request from D.D.) may provide some additional insight into the nature of a fossil bovid assemblage, particularly if combined with predictions of body weight and habitat preference. The ability to predict taxonomic affiliation does not contradict the use of these measurements to predict function/habitat, since different discriminant functions are used to disentangle the co-existing influences of phylogeny and function.

5. Discussion

The accuracy of a discriminant function needs to be considered relative to the number of groups it is attempting to discriminate between—a random function will, on average, be 33% accurate for a three habitat category scheme (e.g. Plummer and Bishop [19]), but only 25%

accurate for a four habitat scheme (e.g. Kappelman [13]). Discriminant function accuracy can be standardized by considering it relative to chance. This can be calculated by dividing the ‘raw’ accuracy by the accuracy expected by chance (e.g. a function that discriminates between four habitat groups with 75% accuracy is three times better than chance). The standardized accuracies of different discriminant functions for predicting habitat from bovid postcrania are given in Table 7.

Habitat classifications based on astragali measurements are 2.7 times better than chance, which is better than that of the various metapodial methods [19]. The astragalus method is not quite as accurate as Kappelman et al.’s [13] femur-based methods, but the frequent preservation of the astragalus is a redeeming feature. In addition, the use of the confidence values to identify specific predictions which are statistically significant (as discussed above) results in effective 95% accuracy for astragalus-based predictions, which is much greater than that currently obtainable for femora or metapodials. We suggest that the raw data for the metapodial [19] and femora [13] studies be examined to establish equivalent cutoff points for confidence values to permit the identification of statistically significant predictions generated by those discriminant functions. Furthermore, the sensitivity of those functions to the taxonomic composition of their modern samples should be investigated, and their accuracy estimated by means other than resubstitution, as done here. For the astragalus discriminant function, however, extensive manipulation and exploration of the data indicate that the results are robust.

The accuracy and broad applicability of habitat predictions based on measurements of bovid astragali make it a useful addition to similar methods which use other bovid elements. Even so, every method has its limitations, which include both the inherent limits of the approach and the limits of the particular implementation of that approach. Bovid ‘ecomorphology’ is no exception in this regard. The inherent limitations include the difficulty of constructing a habitat grouping scheme

that is both sufficiently precise and sufficiently accurate, especially since some bovid species use a range of habitat types. This approach also assumes that characters found to be indicative of habitat in modern bovids are similarly indicative of habitat in fossil bovids. This is likely to be a reasonable assumption, because modern bovids are taxonomically and geographically diverse, and because the mechanical principles which condition functional morphology do not change over time, but this is still an assumption. As with any method, the less-than-100% accuracy is a limitation, though at least the accuracy of specific predictions is quantifiable in this approach. Finally, these methods represent only one approach to inferring paleohabitats. The most robust reconstructions of paleoenvironments are those which draw on multiple lines of evidence (geological, geochemical, paleobotanical, archaeological, 'faunal list' approaches, etc.), so the results of 'ecomorphological' studies should not be viewed in isolation.

In addition to these inherent limits, a more refined understanding of the functional anatomy of the bovid astragalus, as it relates to the biomechanics of locomotion, would likely provide deeper insight into the current results. Biomechanical data would provide a direct test of the link between astragalus morphology and locomotion, strengthening the inferences made here. Unfortunately, such data are not currently available in the literature. In addition, while the statistical manipulation of taxa and specimens suggests that these results will be stable as the sample is expanded, the incorporation of additional specimens and species is needed in order to establish this conclusively.

6. Conclusion

The use of the functional morphology of bovid postcrania to infer paleohabitats has been shown to be a useful method (e.g. [13,19]). The extension of this method to the oft-recovered astragalus, with a 'raw' habitat classification accuracy of 67% and a 'filtered' accuracy of 95%, should increase the value of this approach. This in turn should improve our understanding of past environments, and the technological and biological evolution that occurred in them.

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Appendix A

A.1. Discriminant function for habitat prediction

The following equations are the discriminant function generated from the modern African bovid data using JMP (version 5.0 for the Macintosh, SAS Institute). All calculations use the measurements reported in millimeters. For measurement abbreviations, see Section 3.

$$\text{Probability of Forest Habitat} = [\exp^{(-0.5 \times \text{DIST}[F])}] / \text{DIST}[Z]$$

$$\text{Probability of Heavy Cover Habitat} = [\exp^{(-0.5 \times \text{DIST}[H])}] / \text{DIST}[Z]$$

$$\text{Probability of Light Cover Habitat} = [\exp^{(-0.5 \times \text{DIST}[L])}] / \text{DIST}[Z]$$

$$\text{Probability of Open Habitat} = [\exp^{(-0.5 \times \text{DIST}[O])}] / \text{DIST}[Z]$$

where

$$\begin{aligned} \text{DIST}[F] = & \text{DIST}[Z] + (-39.2 \times \text{LL}) + (186.0 \times \text{LI}) + (-21.5 \\ & \times \text{LM}) + (-173.8 \times \text{WI}) + (-16.5 \times \text{WD}) + (24.2 \\ & \times \text{TP}) + (8.4 \times \text{TI}) + (10.5 \times \text{TD}) + [-3826.9 \\ & \times (\text{LI}/\text{WI})] + 2754.5 \end{aligned}$$

$$\begin{aligned} \text{DIST}[H] = & \text{DIST}[Z] + (-41.7 \times \text{LL}) + (184.2 \times \text{LI}) + \\ & (-20.4 \times \text{LM}) + (-172.3 \times \text{WI}) + (-14.9 \times \text{WD}) + \\ & (-24.0 \times \text{TP}) + (10.1 \times \text{TI}) + (10.2 \times \text{TD}) + \\ & [-3769.8 \times (\text{LI}/\text{WI})] + 2692.2 \end{aligned}$$

$$\begin{aligned} \text{DIST}[L] = & \text{DIST}[Z] + (-40.6 \times \text{LL}) + (183.4 \times \text{LI}) + (-20.7 \\ & \times \text{LM}) + (-171.7 \times \text{WI}) + (-14.2 \times \text{WD}) + (24.6 \\ & \times \text{TP}) + (8.6 \times \text{TI}) + (9.8 \times \text{TD}) + [-3756.9 \\ & \times (\text{LI}/\text{WI})] + 2660.7 \end{aligned}$$

$$\begin{aligned} \text{DIST}[O] = & \text{DIST}[Z] + (-39.6 \times \text{LL}) + (184.0 \times \text{LI}) + (-20.7 \\ & \times \text{LM}) + (-171.2 \times \text{WI}) + (-15.9 \times \text{WD}) + (23.3 \\ & \times \text{TP}) + (8.8 \times \text{TI}) + (9.1 \times \text{TD}) + [-3744.0 \\ & \times (\text{LI}/\text{WI})] + 2649.1 \end{aligned}$$

$$\text{DIST}[Z] = \exp^{(-0.5 \times \text{DIST}[F])} + \exp^{(-0.5 \times \text{DIST}[H])} \\ + \exp^{(-0.5 \times \text{DIST}[L])} + \exp^{(-0.5 \times \text{DIST}[O])}$$

A.2. Regression equation for body weight prediction

All calculations use the measurements reported in millimeters. For measurement abbreviations, see Section 3.

$$\text{In Body Weight (kg)} = 1.343 + 0.060\text{LL} - 0.068\text{LI} \\ - 0.007\text{LM} + 0.047\text{WI} + 0.025\text{WD} \\ + 0.015\text{TP} + 0.044\text{TI} - 0.001\text{TD}$$

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