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**Species Diversity in the Hypertragulid (Mammalia: Artiodactyla) Population of the John
Day Basin, Oregon**

by

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An undergraduate honors thesis submitted in partial fulfillment of the

requirements for the degree of

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ABSTRACT

Members of the family Hypertragulidae (order Artiodactyla, class Mammalia) are the most abundant mammals in the Turtle Cove Member (Oligocene) of the John Day Formation, located in central and eastern Oregon, and make up about 40% of the preserved specimens of the John Day Basin. Three species and two separate genera are described in the area, but any preexisting research lacks statistical support for this level of variation. Species designation among extinct artiodactyls is predominantly based on morphological and morphometric examination of dentition, but studies conducted with extant artiodactyls have revealed that this may not be a reliable diagnostic technique. Other research introduces the possibility of postcranial morphology as indicative of species, but this is not successful in all artiodactyl families. Given these two possible metrics, I use coefficients of variation (V) on dental measurements and astragali measurements of hypertragulid specimens designated *Hypertragulus hesperius*, *Hypertragulus minutus*, and *Nanotragulus planiceps* as a metric for determining if there is more than one species present in the population. Both the asymptotic V equality test and the modified signed-likelihood ratio V equality test show that V values of anterior-posterior molar length (APL) and transverse molar width (TW) vary significantly when comparing single species of modern ecological analogs (*Muntiacus muntjak*, *Muntiacus reevesi*, and *Tragulus javanicus*) to groupings at the genus level. However, the V equality tests on dental and postcranial measurements yield almost no significant results when comparing variation in the extinct John Day hypertragulid population to an extant population comprised of a single species. The low level of variation in the hypertragulids statistically supports the hypothesis that there is only one species present in the population, which suggests over-splitting of the species in the John Day Basin.

INTRODUCTION

Members of the family Hypertragulidae (order Artiodactyla, class Mammalia) are the single most abundant mammals in the Turtle Cove Member of the John Day Formation of central and eastern Oregon and make up almost 1,500 of the preserved specimens of the John Day Basin—about 40% of the total collection (Famoso, 2014). While there have been three species of hypertragulids identified in the John Day Basin, there has been no prior statistical analysis of variation in the population to determine if this specific division is accurate. To conduct a

paleoecological analysis of hypertragulids within the John Day area, the number of verifiable species present must first be determined. This project aims to determine the species-level variation in hypertragulid specimens present in the John Day Basin and whether both dental and postcranial measurements reflect the same amount of variation in the population.

BACKGROUND

Figure 1. Localities of hypertragulid specimens (blue) in the John Day Basin, with units of the John Day Fossil Beds National Monument and nearby cities..

The extinct Family Hypertragulidae consisted of small basal ruminant artiodactyls known for their lack of horns and distinct tusklike canines (Métais & Vislobokova, 2007). The extant taxa most closely related to this family are the tragulids (*Tragulus* sp.), also known as chevrotains or mouse-deer, which can serve as a modern phylogenetic and ecological analog for hypertragulids. Hypertragulids likely lived in similar forested habitats and consumed mixed foraging and browsing diets (Métais & Vislobokova, 2007) similar to the tragulids, as well as the modern muntjac (*Muntiacus* sp.). Hypertragulids were widespread across North America from the late

middle Eocene to the early Miocene, which corresponds to the Duchnesean (40.5 Ma) to late Arikareean (21 Ma) North American Land Mammal Ages (Métais & Vislobokova, 2007). In the John Day region (Figure 1), there have been three species identified to date—*Hypertragulus hesperius* (Hay, 1902), *Nanotragulus* (= *Allomeryx*) *planiceps* (Sinclair, 1905), and *Hypertragulus minutus* (Lull, 1922).

Hypertragulid specimens are preserved in the Turtle Cove, Kimberly, and Haystack Valley members of the John Day Formation (Tedford et. al., 2004; Woodburne, 2004; Famoso, 2018). While there has been little research into the John Day hypertragulids, previous work done in the White River Group of Badlands National Park in South Dakota clarifies morphometric and phylogenetic distinctions among species (Gardner, 2015). While this work has found distinguishable characters between *H. minutus* and *N. planiceps*, there has been no confirmed discrepancy between *H. hesperius* and other species of Hypertragulidae. This uncertainty, amid other discussions of phylogenetics in Hypertragulidae (Webb & Taylor, 1980; Vislobokova, 2001; Métais & Vislobokova, 2007), provides sufficient reason to closely examine the population and the statistical variation between species. While a phylogenetic analysis is outside the scope of this project, this work will set a foundation for further inspection of specimens, potentially leading to more fossils with associated species-level designations.

The most widely used method for determining species among extinct artiodactyls is examination of dental characters; both morphology and measurement. However, research conducted with modern artiodactyls has called into question the validity of dentition as a faultless diagnostic technique—populations of artiodactyls experience such uneven wear on their teeth that there is greater than average variation in dental measurements among same-species individuals (Emery-Wetherell & Davis, 2018). Recently, there has been increased interest in the possibility of postcranial characters as a diagnostic on fine taxonomic scales (DeGusta & Vrba, 2003; Davis & Calède, 2012; Davis & McHorse, 2013). While this has not yet been successful in all families, there is potential that astragali could function as a second diagnostic character to support the primary analysis of dentition in Hypertragulidae (Métais & Vislobokova, 2007).

HYPOTHESES

H₀: There is no variation in the dental and postcranial measurements to support separate taxa, and there is only one hypertragulid within the John Day Basin.

H₁: There is enough substantiated variation in both the dental and post-cranial measurements to support two separate hypertraguline taxa, but there is not enough support of either dental or postcranial measurements to classify three taxa.

H₂: Both the dental and post-cranial specimens show enough variation to substantiate the presence of three taxa in the John Day Basin, namely *Hypertragulus hesperius*, *H. minutus*, and *Nanotragulus planiceps*.

METHODS

Dentition

I examined the collection of hypertragulid material from John Day Fossil Beds National Monument (JODA), Kimberly, OR (Figure 1). The majority of the hypertragulid specimens in the JODA collection are teeth, but there is also a great deal of postcranial material. To determine species-level variation in dentition, I measured the anterior-posterior length (APL) and transverse width (TW) of both upper and lower molars, as shown in Figure 2. Specimens were only chosen when tooth position could be determined (i.e. if the molar is the first, second or third molar in the tooth row). This sample group included molars from maxillae, dentaries, and isolated teeth. All measurements were taken in millimeters using Mitutoyo 4" digital calipers (instrumental error is ± 0.02 mm). To maintain consistency, APL was measured along the buccal side of upper molars and along the lingual side of lower molars. I also took care to measure APL at the base of the tooth, at the enamel-dentine junction, to reduce variation from wear and wear-stage. TW was measured at widest width on each individual tooth. I am limiting my analysis to fossils found in the Turtle Cove Member of the John Day Formation, but one could also apply similar techniques to specimens found in the other members for a broader study.

All statistical analysis was conducted in R version 3.5.1 (R Core Team, 2018), with use of the packages dplyr (Version 0.7.8, Wickham et. al., 2016), ggfortify (Version 0.4.5, Tang, Horikoshi, & Li, 2016), and cvequality (Version 0.1.3; Marwick & Krishnamoorthy, 2019).

Figure 2. Anterior-posterior length (APL) and transverse width (TW) measurements, shown on a *Hypertragulus hesperius* skull (JODA 16548). Top image shows APL taken along the enamel-dentine junction from the right lateral view. Bottom image shows APL and TW from the ventral view.

Figure 3. Lateral view of *Hypertragulus hesperius* skull (JODA 16548) and right dentary with tooth positions labeled. The six tooth positions are the upper molars on the maxilla (M1-M3) and the lower molars on the dentary (m1-m3).

After measuring teeth in all six tooth positions (Fig. 3), I conducted an Analysis of Variance (ANOVA) and a post-hoc Tukey Test (Fisher, 1928; Tukey, 1949; Hammer & Harper, 2008; Famoso, 2018) on both the APL and TW data, to determine which specific molars differ significantly between individuals. I then calculated the coefficients of variation (V) for the entire population of hypertragulids as shown in Equation 1, where μ is the mean and σ is the standard deviation. The V gives a percentage of variation in the entire population for a linear measurement, which is a previously established metric of identifying populations with more than one species present (Pearson, 1896; Simpson & Roe, 1939; Cope & Lacy, 1992; Famoso, 2017). For groups with a sample size smaller than $n = 5$, I used a small-sample correction (Sokal & Braumann, 1980) shown in Equation 2 .

$$V = \frac{\sigma}{\mu} * 100 \quad (1)$$

$$V = \frac{\sigma}{\mu} * \left(1 + \frac{1}{4 * n}\right) * 100 \quad (2)$$

I compared measurements of upper molars of the fossil hypertragulids to the modern southern red muntjac, *Muntiacus muntjak*, using data from Emery-Wetherell & Davis (2018). I compared the lower molars to modern *M. muntjak*, *Muntjack. reevesi* (Reeve's muntjac), and *Tragulus javanicus* (Java mouse-deer) using data provided by C. Janis (Janis, 1990; Janis, personal communication, February 14th 2019). *M. muntjak* and *M. reevesi* have similar morphologies and dietary habits to the extinct hypertragulids making them excellent ecomorphs. *T. javanicus* is among the most closely related taxa to the Hypertragulidae, and therefore serves as a phylogenetic analog to the hypertragulids. I used both asymptotic (Feltz & Miller, 1996) and modified signed likelihood ratio tests (Krishnamoorthy & Lee, 2014) as part of the 'cvequality' R package to compare the *V* values of all analyzed populations. To determine how well the *V* equality tests can compare the ancient and modern populations of basal ruminants, I used these tests to compare lower molars of modern species amongst each other. I sorted the modern analogs into groups: one total 'population' comprised of all three species, another made up of the two species in the genus *Muntiacus*, and each of the single species populations. I compared these groups to each other, expecting to find the highest variation in the total population, followed by the *Muntiacus* group, and followed by the individual species having the lowest level of variation. The *V* values should vary significantly amongst these groups, with statistical significance denoted by a *p*-value ≤ 0.05 (Fisher, 1928). Given that the John Day Basin hypertragulid population is stated to have three separate species belonging to two genera, I expect the *V* values of the hypertragulid population to be similarly high to those of the combined extant population and significantly higher than that of a single extant species. The resulting *p*-values from each test will indicate if the variation within groups of hypertragulids is significantly different than what is expected for a single-species population, which would then substantiate the alternate hypotheses that there is more than one species present in the John Day Basin. If the *V* test value is not significantly different between the modern analog and the hypertragulids, then the null hypothesis of only one species will be supported.

Astragali

measured high-quality photographs of eight *T. javanicus* specimens from the Museum of Comparative Zoology (MCZ) Harvard Vertebrate Collection, located in Cambridge, Massachusetts, using ImageJ (Schneider,

To corroborate the analysis from the dental characters, I measured astragali of the hypertragulids. Astragali (ankle bones) are a postcranial element which are useful as a measure of body size (Davis & Calède, 2012; Davis & McHorse, 2013). Eight measurements of astragali are needed for analysis, as per DeGusta & Vrba (2003) and illustrated in Figure 4: medial length (LM), intermediate length (LI), lateral length (LL), distal thickness (TD), intermediate thickness (TI), proximal thickness (TP), distal width (WD), and intermediate width (WI). I then used a Principal Components Analysis (PCA) to determine which of these measurements covary, and which are significant for analysis (Davis & Calède, 2012; Davis & McHorse, 2013). While there are fewer postcranial specimens with species-level identification, I still calculated *V* values and performed *V* equality tests to compare the number of species inferred from the dental measurements. I compared measured astragali dimensions of hypertragulids to the same measurements of *T. javanicus* astragali. I

Figure 4. Photo of JODA 2920, hypertragulid astragalus, or ankle bone. Top image shows anterior view, with intermediate length (LI), intermediate width (WI), and distal width (WD) measurements. Middle image shows medial view with medial length (LM) measurement. Bottom image shows lateral view with lateral length (LL), proximal thickness (TP), intermediate thickness (TI), and distal thickness (TD) measurements.

Rasband, & Eliceiri, 2012). V values were calculated and compared as previously described for dentition, but given lack of data on other modern analogs and limited sample sizes of *H. minutus* and *N. planiceps* specimens, the primary analysis was conducted by comparison of the entire hypertragulid population to that of the modern *T. javanicus* specimens.

RESULTS

Extant Analog Dentition

V values calculated for lower first molars of the modern analogs are presented in Table 1. The V equality tests, the asymptotic test (AT) and the modified signed-likelihood ratio test (MSLRT), both show a significant level in variation of lower molars when comparing multiple species of ecologic analogs and related taxa together, as presented in Table 2. The difference in variation is significant for both the APL (AT $p = 0.000345$, MSLRT $p = 0.0000797$) and TW (AT $p = 0.0000105$, MSLRT $p = 0.00000107$) when distinguishing between the total population of modern analogs (two species of modern *Muntiacus* (*M. muntjak* and *M. reevesi*) and one species of *T. javanicus*), as compared to a population of the *Muntiacus* species and a population of only *Tragulus* specimens. The V equality tests varied between the APL and the TW when comparing two *Muntiacus* species together compared to only one of the tested *Muntiacus* species. There was no significantly different level of variation in the APL (AT $p = 0.154$, MSLRT $p = 0.125$), but the TW did show significant variation (AT $p = 0.025$, MSLRT $p = 0.019$). However, both tests did have significant p -values for the APL (AT $p = 0.027$, MSLRT $p = 0.024$) and the TW (AT $p = 0.025$, MSLRT $p = 0.014$) when comparing the two *Muntiacus* species to the single species of *Tragulus*.

Table 1. V values for lower first molars of modern analog taxa

	m1 APL	m1 TW
Combined modern analog V	28.346081	32.063406
<i>Muntiacus</i> sp. V	14.242417	12.444297
<i>M. muntjak</i> V	8.440777	5.065173
<i>M. reevesi</i> V	9.843680	10.543084
<i>T. javanicus</i> V	5.857791	5.059644

Table 2. *V* equality tests for different groupings of modern analogs, both asymptotic test and modified signed likelihood ratio test (SLRT). Bold *p*-value denotes significant difference in *V* values, where $p < 0.05$.

	m1 APL		m1 TW	
	Asymptotic <i>p</i> -value	Modified SLRT <i>p</i> -value	Asymptotic <i>p</i> -value	Modified SLRT <i>p</i> -value
Total pop + <i>Muntiacus</i> sp. + <i>T. javanicus</i>	0.0003449965	0.00005928526	0.00001048545	0.000001068119
<i>Muntiacus</i> sp. + <i>M. muntjak</i>	0.1543812368	0.1251785	0.02539143	0.01949895
<i>Muntiacus</i> sp. + <i>T. javanicus</i>	0.0271961171	0.02404749	0.02525581	0.01388957

	m2 APL		m2 TW	
	Asymptotic <i>p</i> -value	Modified SLRT <i>p</i> -value	Asymptotic <i>p</i> -value	Modified SLRT <i>p</i> -value
Total pop + <i>Muntiacus</i> sp. + <i>T. javanicus</i>	0.0005201665	0.00002394129	0.00001929317	0.000004147852
<i>Muntiacus</i> sp. + <i>M. muntjak</i>	0.6849871822	0.632067	0.04824467	0.03734388
<i>Muntiacus</i> sp. + <i>T. javanicus</i>	0.0084862230	0.002485922	0.1108129	0.09272634

	M2 APL		M2 TW	
	Asymptotic <i>p</i> -value	Modified SLRT <i>p</i> -value	Asymptotic <i>p</i> -value	Modified SLRT <i>p</i> -value
Total pop + <i>Muntiacus</i> sp. + <i>T. javanicus</i>	0.0004860584	0.0003491246	0.0003829668	0.0003154157
<i>Muntiacus</i> sp. + <i>M. muntjak</i>	0.6251837576	0.5547034290	0.5026901915	0.4375754255
<i>Muntiacus</i> sp. + <i>T. javanicus</i>	0.7792352902	0.7807018776	0.9643010143	1.0000000000

Hypertragulid Dentition

The ANOVA and post-hoc Tukey test showed a statistically significant difference in measurements of APL of the first and the third tooth position, as well as a difference in TW of

the upper and lower molars, as seen in Figures 5 and 6. Given this, I focused my analysis on the upper and lower molars in the first and third tooth positions.

V values of the upper and lower first molars for the combined Hypertragulidae population, *H. hesperius*, *H. minutus*, and *N. planiceps* are presented in Table 3 as well as the p -values from the V equality tests. The modified SLRT test showed significant variation between the total population and the three individual species in one case, the m3 APL, where the p -value was slightly below the designated threshold of 0.05 ($p = 0.041$). All other V equality tests (both asymptotic and modified SLRT) for upper and lower first molars were not significant when comparing variation from the species groups to the total hypertragulid population. Figure 7 shows V values for these taxa in addition to V values of the modern analogs presented in Table 1.

Table 4 contains V values for the upper and lower first and third molars of both the total hypertragulid population and the modern *M. muntjak* population, and the associated p -values for the V equality tests. For these eight total dimensions, only the m3 APL measurement is significantly different (AT $p = 0.022$, MSLRT $p = 0.008$) from the entire fossil population to the single modern species.

Table 3. V values and resulting V equality p -values for first molars of hypertragulids. Bold p -value denotes significant difference in V values, where $p < 0.05$.

	M1 APL	m1 APL	M1 TW	m1 TW
Hypertragulid population V	11.51817664	11.2226980	11.8304483	8.3699800
<i>H. hesperius</i> V	11.35982404	9.2223921	10.0620888	7.6646850
<i>H. minutus</i> V	8.89803094	16.5717275	10.9235310	9.4735571
<i>N. planiceps</i> V	2.28762388	16.6905915	6.2604599	1.2306002
Asymptotic p -value	0.25163408	0.5460764	0.4515642	0.5174573
Modified SLRT p -value	0.04110553	0.3924073	0.7124514	0.1914327

Figure 5. Boxplot of ANOVA results for APL of different tooth positions across all hypertragulids. APL is correlated by molar, with the upper and lower values for each molar overlapping significantly.

Figure 6. Boxplot of ANOVA results for TW of different tooth positions across all hypertragulids. TW is similar for all lower molars, which is significantly different from the upper molars.

7a. Coefficients of Variation--Lower First Molar

7b. Only Modern--Lower First Molar

7c. Only Fossil--Lower First Molar

Figure 7a. V values for lower first molar measurements of all modern analogs, all fossil hypertragulid species, as well as combined populations for comparison. Highest value is for the total modern analog population. 7b. V values for only modern analogs. 7c. V values for only extinct species.

Figure 8a. V values for upper and lower second molar measurements of all modern analogs, all fossil hypertragulid species, as well as combined populations for comparison. Highest value is for the total modern analog population. 8b. V values for only modern analogs. 8c. V values for only extinct species.

Table 4. *V* values and *V* equality *p*-values for all tooth position measurements of the total hypertragulid population as compared to the modern *Muntiacus muntjak* population. Bold *p*-value denotes significant difference in *V* values, where $p < 0.05$.

	M1 APL	m1 APL	M2 APL	m2 APL	M3 APL	m3 APL
Fossil Hypertragulid <i>V</i>	11.5181766	11.2226980	11.1426880	8.89243245	11.0692139	13.924553175
Modern <i>M. muntjak V</i>	12.5114072	8.4407769	8.8489405	14.96139669	10.7185901	5.358249526
Asymptotic <i>p</i> -value	0.7000734	0.8909070	0.4937135	0.02626072	0.3758709	0.021665986
Modified SLRT <i>p</i> -value	0.8553496	0.8716533	0.3737391	0.08548824	0.2912266	0.008271829

	M1 TW	m1 TW	M2 TW	m2 TW	M3 TW	m3 TW
Fossil Hypertragulid <i>V</i>	11.830448	8.3699800	12.7041264	8.89243245	13.6722155	13.1002201
Modern <i>M. muntjak V</i>	10.262837	5.0651729	9.3829699	5.29238168	11.3184878	8.0713118
Asymptotic <i>p</i> -value	0.532573	0.4412137	0.3840301	0.13751851	0.3758709	0.1645751
Modified SLRT <i>p</i> -value	0.483879	0.3690194	0.2995962	0.09456959	0.3078046	0.1127612

Astragali

The Principal Components Analysis was done on 35 undamaged hypertragulid astragali. The first principal component (PC1) accounts for 75.35% of the variation but when combined with the second principal component (PC2) brings the total variation explained up to 83.77%.

Figure 9. PCA and loading plot of whole astragali. Different individuals are labeled as points, with the first two principal components as axes. Correlated dimensions are grouped closest together, and unrelated dimensions are at right angles.

The loading plot of astragali dimensions in Figure 9 shows a strong correlation between: distal width and intermediate length; medial length, lateral length, and intermediate width; proximal thickness and intermediate thickness; and distal thickness was unrelated to the other components.

I used this correlation of dimensions to select the four primary dimensions for analysis: intermediate length (LI), intermediate width (WI), intermediate thickness (TI), and distal thickness (TD). I then added partially damaged astragali where these four dimensions were intact to my dataset, bringing the total sample up to 53. This group contained 31 unidentified hypertragulid astragali, 19 *H. hesperius*, two *H. minutus*, and one identified *N. planiceps* astragali, the measurements of which are shown in Figure 10.

Figure 10. Boxplots of four chosen astragali measurements, with the y-axis showing millimeters and the x-axis sorted according to species designation. The single *N. planiceps* specimen is recorded as a line.

Table 5. *V* values and *V* equality *p*-values for selected astragali dimensions of fossil hypertragulids and the modern *T. javanicus* population

	LI	WI	TI	TD
Fossil Hypertragulid population <i>V</i>	9.540501	11.38828	10.14137	11.66088
Modern <i>T. javanicus</i> <i>V</i>	11.526675	14.34874	11.69205	16.73888
Asymptotic <i>p</i> -value	0.4796086	0.3821922	0.6016645	0.1518182
Modified SLRT <i>p</i> -value	0.6074324	0.5786480	0.2737831	0.2737831

Table 5 displays V values and p -values of V equality tests for each of the astragali dimensions examined. There is no significant difference in variation for any of the four principal dimensions between the extinct and extant species, with no p -value for either test below 0.05.

DISCUSSION

Among the eight dental measurements examined in this study, only one measurement (m3 APL) showed significant variation between the hypertragulid population of the John Day Basin and a single modern species. My examination of modern artiodactyl dentition illustrated that variation follows an expected progression of increasing V values as the taxonomic group broadened, seen in both Table 1 and Figures 7 & 8, but to confirm this pattern the analysis needs to be extended to cover as many tooth positions as possible. The variation of a single species being doubly accounted for in the total population likely explains the one exception of modern analogs not varying significantly. However, the hypertragulid population that was thought to contain three separate species of two different genera has a much lower V than expected—if the observed pattern in a modern group of three species of two genera holds true, the V value should be greater, and there should be a distinguishable variation between the total population, one genus, and individual species. Instead the predominantly non-significant variability between the total hypertragulid population and individual hypertragulid species supports the null hypothesis that only one species of hypertragulid was present in the John Day Basin, and rejects the alternate hypotheses.

The examination of the astragali, and the consequential statistical lack of variation between extinct and extant populations, seems to further confirm this hypothesis of a single species. This could simply reflect the limited sample size of identified *H. minutus* and *N. planiceps* astragalus specimens. The variance seen in the group of specimens unidentified at the species level (Figure 10) is potentially wide enough to be more representative of the population than I can confirm. Lack of associated craniodental material with these astragali means that no better designation can be reached at this point for these specimens, and further data would be required to strengthen the support for the single-species hypothesis. Additionally, a more thorough analysis of astragali in modern small ruminant taxa, similar to the one conducted with dentition in this study, is necessary to determine whether astragali variability is a reasonable premise to separate these species.

Taxonomic over-splitting is likely responsible for the the discrepancy between the levels of variation seen in this study and the initial description of three species. A normal distribution of variation in a single-species population can be split somewhat arbitrarily, and new species can be designated based on only a small subset of the actual total population. The work done in this study reveals a lack of statistical support for these designations, but there are many other ways to designate species besides dentition and postcranial characters, most notably qualitative cranial characters (Famoso, 2017)

While a preliminary study of the hypertragulids used a Shapiro-Wilks test on upper first molars to search for multiple means in the population, this step was omitted in this study given that only one mean was found (Famoso, 2018). However, modern mouse-deer, chevrotains, and muntjacs all exhibit sexual dimorphism—tragulid males are smaller, but possess larger canine tusks (Janis, 1984), while muntjak males are larger with a larger upper canine tusk than females (Janis, 1990). Since astragali dimensions are a known indicator of body size in artiodactyls (Martinez & Sudre, 1995; DeGusta & Vrba, 2003; Davis & McHorse, 2013) future research should account for the possibility of sexually dimorphic astragali dimensions and sort variation in these two separate populations accordingly.

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