6-2018

Dental measurements do not diagnose modern artiodactyl species: Implications for the systematics of Merycoidodontoidea

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Palaeontologia Electronica
palaeo-electronica.org

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ABSTRACT

Though dental measurements are frequently used to diagnose the fossil species of Merycoidodontoidea and other extinct artiodactyls, the effective diagnosis of modern artiodactyl taxa via dental measurements has not been extensively tested. Our study finds that variation in artiodactyl dentition is generally higher than in primates, carnivores, rodents and even elephants, with molar coefficients of variation ranging up to 18% (*Camelus bactrianus*), and that dental measurements poorly diagnose modern artiodactyls via discriminant function analysis, adjusted *t*-tests on coefficients of variation, or finite mixture analysis. The higher-than-expected coefficients of variation for artiodactyls imply that some fossil taxa may be over-split, but the low utility of dental measurements in separating sympatric species of duikers also suggests that dental measurements are not effective for fully diagnosing certain artiodactyl groups. We advocate a systematic revision of Merycoidodontoidea and many other fossil artiodactyl groups with lower emphasis on dental measurements and better accounting for the ways selenodont dentition varies.

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Keywords: quantitative variation; dental morphology; Mammalia; Artiodactyla; Merycoidodontoidea; discriminant function analysis

Submission: 22 November 2016 Acceptance: 20 April 2018

Emery-Wetherell, Meaghan M. and Davis, Edward Byrd. 2018. Dental measurements do not diagnose modern artiodactyl species: Implications for the systematics of Merycoidodontoidea. *Palaeontologia Electronica* 21.2.23A 1-28. https://doi.org/10.26879/748
palaeo-electronica.org/content/2018/2202-dental-variation-of-artiodactyl

INTRODUCTION

Selenodont artiodactyls are a diverse group of mammals with a rather homogenous set of dentition: though family and even genus-level identifications can be made using dental morphology, species-level identifications of fossil artiodactyls are often made using only dental measurements (e.g., Phleger and Putnam, 1942; Gustafson, 1986; Stevens and Stevens, 2005). Measurements have some natural variance, and so defining a species requires identifying expected levels of intraspecific variation. Expected levels of dental variation in fossil artiodactyls should be guided by the variation of modern artiodactyls, but while qualitative or geographic studies of dental variation exist for a number of different artiodactyls (e.g., Robinette et al., 1957; Hewison et al., 1999; Veiberg et al., 2007; Anezaki et al., 2008; Cucchi et al., 2009; Evin et al., 2013), data or variation values are rarely reported in many of these studies. When reported, variation is often discussed in terms of geometric morphometrics, but paleosystematic revisions continue to rely heavily on simple linear measurements (e.g., Lander and Hanson, 2006; Emery et al., 2015). Therefore, fossil artiodactyl systematics may vary depending on the intraspecific variation cut-off each paleosystematist uses to define "a species."

Simpson and Roe (1939) suggested a 10% rule of thumb for distinguishing intraspecific from interspecific variation in mammals, but also rightly pointed out that it is impossible to convincingly diagnose vertebrate species in the fossil record when the extent of osteological variation in modern species is unknown. If intraspecific variation were constant across the animal kingdom, the lack of artiodactyl-specific studies should not matter. Recent papers have explored dental variation on several extant mammalian groups, with particular emphasis on carnivores (e.g., Pengilly, 1984; Polly, 1998; Szuma, 2002; Meiri et al., 2005), elephants (e.g., Roth, 1989, 1992), primates (e.g., Gingerich and Schoeninger, 1979; Cope, 1993), and rodents (e.g., Austin and Stangl, 1995; Polly, 2003; Carrasco, 2004; Polly and Head, 2004; Caumul and Polly, 2005; Cordeiro-Estrela et al., 2006; Calede and Glusman, 2017). The abundant research on variation has made it clear that there exists a wide range of variation in mammalia, both by morphology measured and by species – one size range does not fit all groups.

Without modern-derived parameters for normal intraspecific variation, the systematics literature for different fossil artiodactyl lineages contains many contradictions, a point exemplified by the extinct superfamily Merycoidodontoidea. Merycoidodontoidea has experienced four separate systematic revisions in the last century with results ranging from 88 to 219 diagnosable species, and up to 290 diagnosable taxa when subspecies are included (Thorpe, 1937; Schultz and Falkenbach, 1968; Lander, 1976, 1998; Ludtke, 2007; Stevens and Stevens, 2007). Such divergent systematics systems make it difficult to evaluate this group for any long-term ecological or evolutionary trend, as each system yields different estimates of diversity in different time periods (Figure 1).

To help address the differing species criteria, our study tests whether dental measurements of the kind typically used in Merycoidodontoidea systematics can diagnose between related, similarly-sized artiodactyls both with *a priori* knowledge of species (discriminant function analysis) and without (adjusted *t*-test on Coefficients of Variation and finite mixture analysis). We also compare our data to the CVs reported for oreodont species by Stevens and Stevens (2007), and test for increased CV values indicative of multiple species. Our study also tests how wear, sexual dimorphism and dental functionality influence variation in these dental measurements. We used linear regressions of wear against widths or lengths of teeth to test for the influence of wear on variation; three different distributional tests to determine whether sexual dimorphism might present a similar pattern to mixed species samples; and we evaluated the dental variation trends in these 14 species of artiodactyls with regards to trends of functional constraints in the tooth row.

ABBREVIATIONS

Museums

Museum of Comparative Zoology in Harvard (MCZ), Museum of Vertebrate Zoology at Berkeley (MVZ), Vertebrate Paleontology Laboratory at UT Austin (VPL), American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH).

Terminology

Length (L), Width (W), Height (H), Coefficient of Variation (CV). Caniniform teeth include I3, P2 and C1 of camelids.

Species

Camelus bactrianus (bact), *Camelus dromedarius* (drom), *Lama guanicoe* (guan), *Vicugna vicugna* (vicu), *Hylochoerus meinertzhageni* (hylo), *Muntia-*

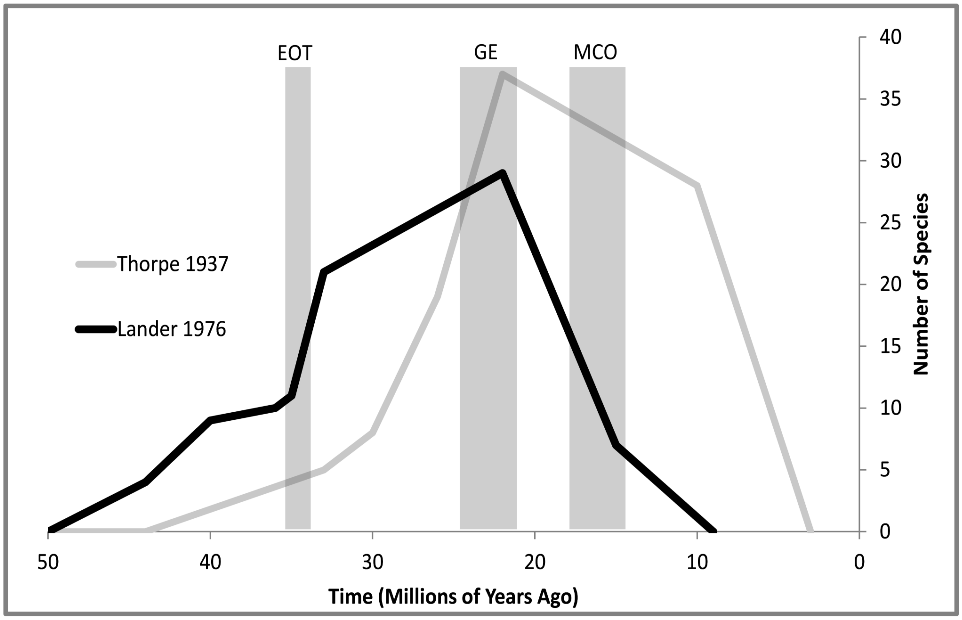

FIGURE 1. Oreodont diversity through time by worker (Thorpe 1937 vs Lander 1998). Time bins show important North American climatic and ecological turnover events, including Eocene-Oligocene Extinction (EOT), beginning of grassland expansions (GE), and the Miocene climactic optimum (MCT) (Zachos et al. 2001; Strömberg 2011).

cus reevesi (reev), *Muntiacus muntjak* (munt), *Philantomba monticola* (phil), *Cephalophus dorsalis* (dors), *Cephalophus weynsi* (weyn), *Cephalophus silvicultor* (silv), *Cephalophus nigrifrons* (nigi), *Cephalophus leucogaster* (leuc), *Ovis dalli* (ovis).

MATERIALS

We examined the skulls of 14 different species of artiodactyls in four different families, all selected as analogues for Merycoidodontoidea (Appendix 1). We included camelids as a phylogenetic analogue (*Camelus bactrianus, Camelus dromedarius, Lama guanicoe* and *Vicugna vicugna)*, several species with analogous morphological features (*Muntiacus muntjak, Muntiacus reevesi, Hylochoerus meinertzhagheni, Philantomba monticola, Cephalophus dorsalis, Cephalophus leucogaster, Cephalophus nigrifrons*, *Cephalophus silvicultor* and *Cephalophus weynsi)* and an additional ecological analogue (*Ovis dalli*). These species were also selected for maximal sample size (many species of interest had too few specimens in the museums visited to be included in a variation study). Our selection of species covers a range of body sizes with and without sexual dimorphism and includes grazers, browsers and mixed feeders. All six species of *Cephalophus* overlap in the central lowland forests of Africa (Turpie and Crowe, 1994) and so were also chosen as a sympatric comparative sample.

To our knowledge, paleosystemtically-applicable studies of dental variation have previously been conducted on only five different modern artiodactyl species (Vrba, 1970; Stevens and Stevens, 2005; Carranza and Pérez-Barbería, 2007; Natsume et al., 2008) and our dataset therefore quadruples the number of species with current published literature on quantitative dental variation.

METHODS

Measurements

The specimens discussed in this paper are housed at museums across the United States, and their examination was conducted over the course of the first author's dissertation (Emery, 2016). To expedite the 10+ weeks of museum work conducted over three years and maximize potential future research, we created 3D models of specimens in Agisoft Photoscan (Agisoft, 2013). Agisoft Photoscan combines photos taken of a specimen at different angles into a single, high-resolution 3D model. We used this unconventional but useful technique instead of digital caliper measurements as a form of permanent, re-collectable data. To ensure compatibility between Photoscan and digital caliper measurements, we checked for significant differences between identical dental measurements on three specimens of *Ovis aries* using an F test (Zar, 1999). We used three different sets of photos for our photogrammetric models, taken over the course of a year. This is a highly conservative methods test: between improvements in photographic technique by the lead author and improvements in the software, our more recent 3D models are far better than earlier models. Different models do have different levels of accuracy, and variation in accuracy may affect our measurements. To determine whether digital calipers and 3D models were comparable, we performed *t*-tests in R to compare different measurements between our subsets (R Core Team, 2016). We also tested our measurement variance for significant differences from small measurements on small species, to explore whether our measurement error overwhelmed intraspecific variation in small organisms.

Mahalanobis Test of Outliers

Our sample of *Camelus, Lama* and *Vicugna* included zoo, circus and other captive-raised specimens, and most of our specimens of *Camelus bactrianus* were raised in captivity. Because the nutrition and health of these organisms may differ from those in the wild, it is possible they do not represent an appropriate analogue for wild organisms. We evaluated whether zoo specimens were outliers in our wild-dominated datasets using Mahalanobis distance tests in R (Rasmussen, 1988). For our anomalously zoo-heavy grouping of *Camelus bactrianus,* we defined outliers as non-zoo specimens to see whether wild specimens lay outside the norm for zoo specimens.

Discriminant Function Analysis

Because tooth size is correlated with body size (Janis, 1990), and dental size is highly heritable (Bader, 1965; Alvesalo and Tigerstedt, 1974), teeth are presumed adequate for making size-based species diagnoses in fossil populations – but this hypothesis assumes that morphologically similar species have distinct enough size classes for dental measurements to diagnose them. We tested these assumptions using linear and quadratic discriminant function analysis (DFA).

We ran DFA on three groups combined by a family or subfamily group that would be easily distinguished by dental morphology: camelids, *Muntiacus* and Cephalophinae. We excluded *Hylochoerus* and *Ovis*, as our sample only had a single species per genus and so could not be "discriminated" from other species that might be morphologically confused for them. We ran our discriminant function analyses in R using jacknife verification, which is a more robust measure for evaluating DFA success (DeGusta and Vrba, 2003; Meloro, 2011). Quadratic DFA would not run on our complete dataset because of multicollinearity issues, so we subsampled for two sets of analyses by length vs. width measurements.

Finite Mixture Analysis

Though we tested the robustness of dental material for species separation with prior knowledge of species divisions, paleontologists work on samples of unknown numbers of species. To mimic an unknown sample, we created a combined species sample of four mid-size duikers, all sympatric and co-occurring in the lowland forests of the Congo (Johnston and Anthony, 2012): *Cephalophus dorsalis, C. nigrifrons, C. leucogaster* and *C. weynsi*. We tested our multi-species samples for diagnostically different distributions using multivariate Finite Mixture Analysis. Finite Mixture Analysis determines whether data is better fit by multiple overlapping distributions instead of being composed of a single distribution (McLachlan and Peel, 2004). We used the 'mixtools' package in R, running a bootstrapping function that determines whether a consecutively increased number of multivariate distributions is more likely than the previous number of distributions (i.e., whether two overlapping distributions is a better fit than one distribution) (Young et al., 2015).

t-test of the Coefficient of Variation

A common method for detecting multiple species in a population is to look for unusually high coefficients of variation (CV) (e.g., Cope and Lacy, 1992; Cope, 1993; Plavcan and Cope, 2001). We used adjusted *t* tests to test for significant differences in CV values between multi- and single-species samples (Sokal and Braumann, 1980). We also used a CV correction factor for data that had <8 measurements, as CV underestimates in small sample sizes (Sokal and Braumann, 1980; Sokal and Rohlf, 1995).

Relationship of CV and Size

Variation is inherently linked with size – large things vary more than small things, and this variation is assumed to be proportionally related with a predicted trend of about 10% variation within species (Simpson and Roe, 1939). The advantage of CVs is their status as a unit-less measure of variation that removes the effect of size (Carrasco, 1998; Lovie, 2005). Our dataset returned significantly higher single-species CV values than we expected, causing us to suspect that CV may not perform as uniformly across size classes as expected. We used linear and nonlinear regression models in R to compare standard deviation and means for measurements across our dataset, and the Akaike Information Criterion to discern which model best fit our data (Bozdogan, 1987). If CV truly removes the effect of size, the relationship between standard deviation and mean should be linear with an intercept not significantly different from 0 (proportional variation). If CV does not completely account for the influence of size on variation, either a nonlinear model (allometric variation), or a linear model with an intercept significantly different from 0 (anisometric variation) would best model the relationship between standard deviation and mean.

Additional Causes of Variation

Given that higher variation increases the likelihood that a paleosystematist may reject a single-species hypothesis, it is also important to test whether common factors like ontogeny, sexual dimorphism, and dental functionality affect quantitative dental variation. We found considerably higher variation than expected in many of our dental measurements, and tested for two possible causes: sexual dimorphism, and age-related dental wear.

1) Sexual Dimorphism. Sexual dimorphism is an oft-cited cause for high variation in caniniform teeth (e.g., Schultz and Falkenbach, 1949; Herring, 1972; Gittleman and Van Valkenburgh, 1997), but because body size is correlated with chewing area, size dimorphism can also affect chewing teeth (Carranza and Pérez-Barbería, 2007). Our possible size-dimorphic sample was limited to those specimens with identified sex (bovid and cervid species); of these, only *Ovis* and *Muntiacus* are size dimorphic. With too few females to test for size dimorphism in *Muntiacus*, we only tested for size dimorphism in *Ovis dalli* molars. We also evaluated the caniniform teeth of our suid and camelid samples. We tested for sexual dimorphism using *t*-tests, where sex is known *a priori*, and a series of sex-unknown distribution tests to replicate tools available to paleosystematists: 1) the Shapiro-Wilk test to detect deviation from normal distributions, 2) the Hartigan's Dip test for multimodality, and 3) Finite Mixture Analysis to determine whether our data were best described by more than one normal distribution (Shapiro and Wilk, 1965; Hartigan and Hartigan, 1985; McLachlan and Peel, 2004). We used the 'mvshapiro.Test', 'dip.test' and 'mixtools' packages in R, and conducted our *t*-tests in R (Hartigan and Hartigan, 1985; Villasenor Alva and Estrada, 2009; Young et al., 2015). Our suid and camelid teeth had too few specimens with identified sex, limiting their usage to only distribution tests.

2) Age-Related Dental Wear. Our measurements were taken on the maximal length and width of the tooth, which was typically larger at the occlusal surface than it was at the base (trapezoidal). Because artiodactyl teeth flare at the occlusal surface, progressive wear should yield progressively shorter measurements (Figure 2.2), which could add to measured variation. We used the crown height of the first molar to measure wear and compare to our other teeth because the early eruption of M1 captures the greatest potential time series of change in length and width.

Accounting for Type I Error

Most of our dataset involved large numbers of tests on different species divisions, increasing the likelihood of getting a significant *p* value without biological meaning (Type I error). To combat our possible Type I error rate we also report the cumulative binomial probabilities for each test, or likelihood of that number of significant tests occurring by random chance (Weintraub, 1962).

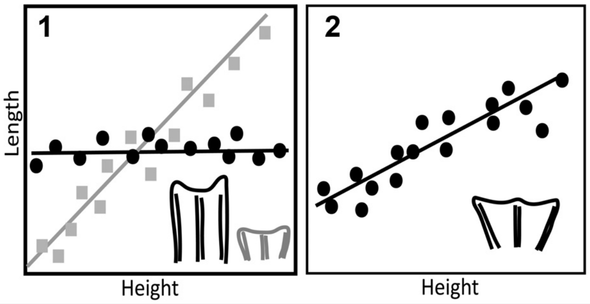

FIGURE 2. Representative data samples of the crown length and crown height in species where A. wear does not affect crown length, or B. wear does affect crown length. If wear does not occur, the relationship between length and width of teeth of multiple individuals should be tightly correlated, with an intercept of 0 (Gray, 1). If wear does occur, but the molar is uniform at length at all heights, there will be no linear relationship between length and height (Black, 1). If wear does influence length, there will be a linear relationship and a non-0 intercept (2).

RESULTS AND DISCUSSION

Model Uncertainty and Methodology

None of our species had zoo specimens that were outliers in multivariate space from the species mean. Our Mahalanobis distance test showed that outliers were more likely to be wild-caught specimens than zoo specimens, except for in the predominantly captive sample of *Camelus bactrianus*, where no wild specimens were outliers. Given that there was no trend for zoo specimens to be dental outliers (or vice versa in *Camelus bactrianus)*, we included zoo specimens with equal consideration in our study of dental traits.

The average 3D model uncertainty for skulls was 0.0155cm +/- 0.0182 cm (mean +/- standard deviation), not as low as the uncertainty reported by Mitutoyo digital calipers (.00254 cm) (Suzuki and Matsumoto 1986). Measurement variance was not significantly different between 3D model measurements and digital caliper measurements ($p = 0.24$), but the actual measurements were significantly different for two of 16 measurements ($p < 0.5$). Finding significance in two of 16 tests should happen by random chance about 19% of the time (cumulative binomial probability of 0.19), indicating that digital calipers and Photoscan measurements are comparable.

Though Photoscan measurements are comparable to digital caliper measurements, the methodological uncertainty of Photoscan measurements was sometimes larger than the measured uncertainty for several of the smaller characters of smaller duiker species. Specifically, 38 of 96 measurements had measured uncertainty that was significantly smaller ($p < 0.05$) than our Photoscan measurement uncertainty (cumulative binomial probability of <.001), while only 9 were less variable than our digital caliper measurement uncertainty (cumulative binomial probability of 0.05; Table 1). Small measurements were more susceptible to this phenomenon, supporting of the findings of Polly (1998), which found that the natural variation of small measurements are often overwhelmed by measurement uncertainty.

The measured variation of our small measurements is still incredibly small: the smallest premolars (*Cephalophus* and *Philantomba*) were less variable than the large premolars in our dataset (Table 1). The higher uncertainty of Agisoft Photoscan therefore does not eradicate the dental variation trends discussed in this paper, though our CV values should be considered maximum CVs for our smallest measurements.

Discriminant Function Analysis

The percentage of specimens correctly classified by dental measurements (Table 2) ranged from <15% (*Camelus bactrianus, Muntiacus reevesi* and *Cephalophus weynsi*) up to 100% (*Cephalophus silvicultor* and *Philantomba monticola).* Overall classification rates within family ranged from 52% to 82% accuracy (Table 2). Species with dramatic size differences had overall higher classification accuracy: for example, *Cephalophus silvicultor*, part of the lineage of giant duikers (50 kg), was easy to distinguish dentally from the dwarf duiker *Philantomba monticola* of around 5 kg (Prins and Reitsma, 1989).

t-Tests for Significant Differences in Coefficients of Variation

Given the high variation in our artiodactyl samples, how likely is it a paleontologist would reject a single-species hypothesis for a sample of similarly variable dental material using CVs? For the sample of combined *Cephalophus* species, only one measurement came up as significant when compared to a single species sample – the row length of the premolars, and only when compared to *Cephalophus weynsi* (Table 3). When compared to the CV size of the other three duiker species, or of the two peccary species, the premolar CV of the combined *Cephalophus* sample was not larger than expected from a single-species sample. In this case, the CVs of dental measurements alone were not adequate to detect the presence of a lumped sample of four species.

When the oreodont sample is compared to single species of *Cephalophus weynsi*, two measurements showed up as being statistically significant: the premolars, when compared to *Cephalophus weynsi*, and the full toothrow when compared to *Cephalophus weynsi* or *Cephalophus nigrifrons.* Neither *C. dorsalis* nor *C. leucogaster* had any significantly different CV values, and CVs for the two peccary species evaluated by Stevens and Stevens (2005) also are not statistically different. The statistical determination of a multispecies sample of *Miniochoerus* species therefore relies entirely upon the species it was compared to. Had Stevens and Stevens (2005) compared their samples to *Cephalophus weynsi* they would have had excellent reason to reject a single-species hypothesis with two of five measurements being statistically significant (cumulative binomial probability of .02); with the single significant result of *Cephalophus nigrifrons* (cumulative binomial probability of .23) they would have less reason to reject a sin-

TABLE 1. Individual species coefficients of variation, and coefficients of variation in genus-level mixtures (*Muntiacus, Camelus*, Mix 1: *Cephalophus* and *Philantomba*, Mix 2: Mid-sized *Cephalophus* species, Mix3: *Lama* and *Vicugna*). 'n' indicates sample size for measurement.

Measurement	bact	dors	drom	hylo	lama	leuc	mont	munt	nigi	ovis	reev	silv	vicu	weyn	*Camelus*	*Cephalophus/ Philantomba*	Medium *Cephalophus*	*Vicugna/ Lama*	*Muntiacus*
L C1	26.2 n=12		39.6 n=21	26.6 n=19	28.5 n=13			28.1 n=6			43.5 n=7		26.4 n=11		37.9 n=33			31.3 n=24	34.2 n=13
L I3					25.6 n=13								28 n=11					28.7 n=24	
L P2	33 n=15	7.6 n=13	28.3 n=19	32.9 n=3		8.5 n=22	5.5 n=15	11.6 n=12	5.5 n=16	15.7 n=12	4.7 n=7	8.5 n=9		6 n=11	32 n=34	26.3 n=86	9.4 n=62		13.2 n=19
L P3	9 n=13	10.9 n=17	13.1 n=21	15.5 n=13	26.2 n=11	8.9 n=22	8.5 n=16	11.4 n=11	6.6 n=16	9.1 n=14	4 n=7	8.5 n=9	20.9 n=7	10.2 n=12	11.9 n=34	25.4 n=92	10.1 n=67	30.2 n=18	12.9 n=18
L P4	7.5 n=13	7.3 n=16	9.3 n=21	14.5 n=11	9.3 n=13	8.5 n=21	8.1 n=16	16.8 n=12	8.1 n=16	9.3 n=13	8.6 n=7	8.6 n=9	10.6 n=10	6.8 n=12	8.7 n=34	24.5 n=90	8.9 n=65	16.9 n=23	18 n=19
L M1	18.1 n=15	11.7 n=17	17 n=23	10.8 n=19	11.7 n=14	10.4 n=25	9.9 n=20	12.5 n=15	11 n=17	12.2 n=20	10.9 n=10	11.7 n=9	18.2 n=19	13.1 n=13	18.7 n=38	25.6 n=101	11.8 n=72	17.1 n=33	14.1 n=25
L M2	13.9 n=14	10.2 n=17	14 n=21	11.9 n=19	14.4 n=14	7.4 n=25	8 n=19	14.4 n=15	8.5 n=17	8.8 n=19	8 n=8	9.5 n=9	14.2 n=15	10.4 n=13	14.6 n=35	24.7 n=100	9.5 n=72	17.1 n=29	14.5 n=23
L M3	8.3 n=12	8.9 n=17	6.3 n=20	4.8 n=12	11.9 n=13	5.5 n=25	7.4 n=16	10.7 n=13	7.5 n=17	7.9 n=14	5.4 n=7	9.1 n=9	4.8 n=10	6.5 n=13	8 n=32	25 n=97	8.1 n=72	16.2 n=23	12.9 n=20
W C1	37.1 n=11		41.8 n=21	34.7 n=12	35.6 n=13			19.4 n=6			49.3 n=7		23.1 n=11		45.9 n=32			37.7 n=24	34.8 n=13
W I3					29.6 n=13								25.3 n=11					34 n=24	
W P2	25.6 n=13	9.4 n=13	28.4 n=18	23.6 n=2		9 n=22	11.2 n=15	14.8 n=12	8.4 n=16	8.6 n=12	7 n=7	6.9 n=9		10.5 n=11	32.3 n=31	28.5 n=86	9.8 n=62		15.3 n=19
W P3	9.5 n=13	7.9 n=17	11.2 n=21	18.8 n=13	20.9 n=11	9.4 n=22	11.4 n=16	9.7 n=11	7.3 n=16	8.9 n=14	6.2 n=7	4.8 n=9	14.7 n=7	6.8 n=12	10.7 n=34	30.3 n=92	10.2 n=67	20.2 n=18	11.9 n=18
W P4	12.5 n=13	6.6 n=16	7.2 n=21	16.9 n=11	19 n=13	5.3 n=21	9.2 n=16	9.8 n=12	6.9 n=16	5.8 n=13	4.7 n=7	6.4 n=9	16.1 n=10	7 n=12	9.9 n=34	27.6 n=90	6.8 n=65	24.8 n=23	12.5 n=19
W M1	13.1 n=15	9 n=17	8 n=23	14 n=19	11.9 n=14	5.5 n=25	8.2 n=20	10.3 n=15	6.4 n=17	7.3 n=20	10.4 n=10	6.5 n=9	9.9 n=19	6 n=13	10.1 n=38	25.9 n=101	7.7 n=72	18 n=33	14.2 n=25
W M2	14.1 n=14	6.8 n=17	6.3 n=21	13.7 n=19	10.4 n=14	5 n=25	6.6 n=19	9.9 n=15	7 n=17	8 n=19	7.3 n=8	8.6 n=9	14.8 n=14	6.1 n=13	9.9 n=35	25.4 n=100	7.4 n=72	20.1 n=28	12.4 n=23
W M3	18.1 n=12	6.3 n=17	8.3 n=20	13.1 n=12	9.6 n=13	6.4 n=25	6.2 n=16	11.3 n=13	8 n=17	6.5 n=14	4.8 n=7	7.6 n=9	10.6 n=10	6.6 n=13	13.6 n=32	24.2 n=97	8.1 n=72	17.1 n=23	12 n=20
Premolars	6.3 n=13	6.8 n=15	8.1 n=21	27.9 n=14	13.7 n=12	7.4 n=22	6 n=16	12 n=11	5.3 n=16	11.8 n=14	14.6 n=7	7.6 n=9	15 n=10	3.4 n=11	7.4 n=34	25.7 n=89	7.8 n=64	21 n=22	14.7 n=18
Molars	13.8 n=12	6.8 n=17	7.8 n=20	11 n=12	10 n=13	5.5 n=25	5.2 n=16	10.4 n=12	5.7 n=17	5.5 n=14	5.6 n=7	5.6 n=9	10 n=10	6.1 n=13	11.1 n=32	23.7 n=97	6.6 n=72	16.3 n=23	12.8 n=19
Toothrow	7.9 n=12	5.2 n=15	5.9 n=20	7.6 n=13	11.2 n=13	5.5 n=22	4.9 n=16	9.7 n=11	3.9 n=16	6.1 n=14	5 n=7	5.4 n=9	12.7 n=10	3.1 n=12	7.3 n=32	24.8 n=90	5.3 n=65	17.1 n=23	13.1 n=18

TABLE 2. Results for Discriminant Function Analyses. Linear Discriminant Analysis (LDA), Quadratic Discriminant Analysis with Lengths (QDA L) and Widths (QDA W). Family summaries provided at the bottom.

	LDA	QDA Length	QDA Width
Camelus bactrianus	0.42	0.5	0.08
Camelus dromedarius	0.8	0.8	0.6
Lama guanicoe	0.91	0.91	1
Vicugna vicugna	0.71	0.29	0.29
Muntiacus muntjak	0.8	0.9	0.8
Muntiacus reevesi	0.86	0.57	0.14
Cephalophus dorsalis	0.85	0.54	0.38
Cephalophus leucogaster	0.76	0.67	0.67
Cephalophus nigifirons	0.4	0.33	0.27
Cephalophus silvicultor	1	1	0.78
Cephalophus weynsi	0.4	0.1	0.1
Philantomba monticola	1	1	1
Overall Camelidae	0.72	0.52	0.68
Overall Cephalophinae	0.73	0.61	0.55
Overall *Muntiacus*	0.82	0.76	0.53

TABLE 3. *t* values for comparisons between two species mixtures (*Cephalophus* and *Miniochoerus)* and multiple single-species CVs. Significance is marked as follows: p<.05 *, p<.01 **, p<.001***.

Mixed Sample	Measurement	dors	leuc	nigi	weyn	dico	taya
Combined *Cephalophus*	H.M1	0.68	0.58	0.3	0.46		
Combined *Cephalophus*	L.M1	0.03	0.33	0.16	0.2		
Combined *Cephalophus*	L.M2	0.16	0.69	0.25	0.19		
Combined *Cephalophus*	L.M3	0.2	1.21	0.19	0.51	0.31	0.3
Combined *Cephalophus*	L.P2	0.51	0.27	1.52	1.11		
Combined *Cephalophus*	L.P3	0.18	0.33	1.17	0.02		
Combined *Cephalophus*	L.P4	0.52	0.13	0.23	0.65		
Combined *Cephalophus*	Molars	0.08	0.51	0.34	0.18	0.33	0.47
Combined *Cephalophus*	Premolars	0.31	0.11	0.99	2.4 **	0.33	0.34
Combined *Cephalophus*	Toothrow	0.04	0.1	0.81	1.45	0.44	0.44
Combined *Cephalophus*	W.M1	0.33	0.99	0.48	0.61		
Combined *Cephalophus*	W.M2	0.19	1.17	0.13	0.41		
Combined *Cephalophus*	W.M3	0.65	0.67	0.02	0.45	0.32	0.29
Combined *Cephalophus*	W.P2	0.1	0.23	0.39	0.12		
Combined *Cephalophus*	W.P3	0.68	0.2	0.89	1.01		
Combined *Cephalophus*	W.P4	0.04	0.63	0.04	0.07		
Miniochoerus affinis & gracilis	L.M3	0.5	1.58	0.86	1.11	0.31	0.3
Miniochoerus affinis & gracilis	Molars	0.83	1.37	1.21	1.04	0.33	0.46
Miniochoerus affinis & gracilis	Premolars	0.62	0.47	1.15	1.96 *	0.33	0.34
Miniochoerus affinis & gracilis	Toothrow	1.22	1.16	1.82 *	2.18 *	0.44	0.44
Miniochoerus affinis & gracilis	W.M3	1.3	1.32	0.81	1.15	0.31	0.29

gle-species hypothesis, and with *Cephalophus leucogaster, C. dorsalis* or either peccary species there would be no statistical reason to suspect a multi-species sample. Yet while choosing an appropriate analogue for comparison is important, our combined duiker sample was not signifcantly different from single-species samples. Therefore, multiple species of similar sizes are possible within a low-CV sample – simply having a non-significant variation difference does not guarantee that a sample does not contain multiple species.

Finite Mixture Analysis of Multi-Species Sample

We conducted a finite mixture analysis on the same multi-species sample used for the adjusted *t*-test on CVs conducted above. The finite mixture analysis also failed to reject the null hypothesis of a single distribution ($p>.05$). The failure of both the *t*-test and the mixture analysis to identify multiple species may relate to two different causes: 1) biological species are defined with such increased precision that paleontological species are not comparable, and 2) that species do not always diverge in size as well as morphology (or at least, not enough to test without a much larger sample size). Considering that only rarely do paleontological species samples contain in the tens of skulls with full dentition (oreodonts being a rare exception), it is likely that the distinction does not matter: dental measurements are not always sufficient to detect co-existing paleontological species.

Extent and Pattern of Variation

Coefficients of variation ranged from very low (3-4%) to very high (58%). The most variable were caniniform teeth (canines, and P2 and I3 in camelids), but molars were also more variable than the no-larger-than-10% intraspecies rule of thumb suggested by Simpson and Roe (1939) or the variation reported in primates and carnivores (Gingerich and Schoeninger, 1979; Gingerich and Winkler, 1979). In fact, many molar CV values were even higher than several dental measurements of elephants, which were previously presumed to be the uppermost limit of natural dental variation (Roth, 1992).

For primates, the least variable dental measurement is the length of M1 (Cope, 1993). Primate dental variation is higher in the premolars, and increases posteriorly in the molar row – possibly as a result of functional constraints, and possibly as a result of greater sexual dimorphism expressed in posterior teeth, which develop after the animal reaches puberty (Gingerich and Schoeninger, 1979; Plavcan and Cope, 2001). This pattern is similar in carnivores, with a greater emphasis on dental functionality minimizing variation: carnassial teeth, which must properly occlude, have the lowest variance in the tooth row (Gingerich and Winkler, 1979; Pengilly, 1984).

This pattern was starkly different in our sample, where the least variable dental measurements were the width of M1 and the length of M3 (Figure 3).

Variation was highest in the premolars, but decreased posteriorly in each functional unit. In artiodactyls, premolars are far anterior of the maximal force produced during chewing and may have fewer functional constraints (Greaves, 1978). This lowered functionality is also seen in qualitative variations: artiodactyl premolars are often subject to rotation, absence or replication in the tooth row (Miles and Grigson, 2003).

Duikers were an exception to the artiodactyl variation pattern. Duiker variation was overall much lower and unchanged throughout the toothrow: the premolars of duikers were no more variable than their molars (Figure 4). The low variation of duiker teeth runs contrary to the elevation effect expected by measurement error for teeth of this size; smaller measurements should have higher CVs, but the smallest teeth in our sample still had the smallest CVs, suggesting that the overall character stability of duiker dentition is a trait rather than a methodological artifact.

Influence of Age-Related Wear on Dental Variation

Though duiker variation was low, the variation in other species was much higher (Table 2). A possible explanation for such high variation in artiodactyl teeth is the influence of wear on tooth dimensions. Our sample had significant correlation between height and length of M1 for most species (Table 4). Eleven of 17 regressions had slopes significantly different from zero (each with $p < 0.05$), and all regressions had intercepts significantly different from zero (Table 4). The correlation between length of the molars and M1 height (our age proxy) was stronger in the anterior of the molar row than in the posterior (M1 H and M1 L were more correlated than M1 H and M3 L). This trend was reversed when compared to molar widths: there were more significant correlations between M1 H and M3 W than there were between M1 H and M1 W, and there were higher R^2 values for correlations in the posterior of the molar row (Table 4).

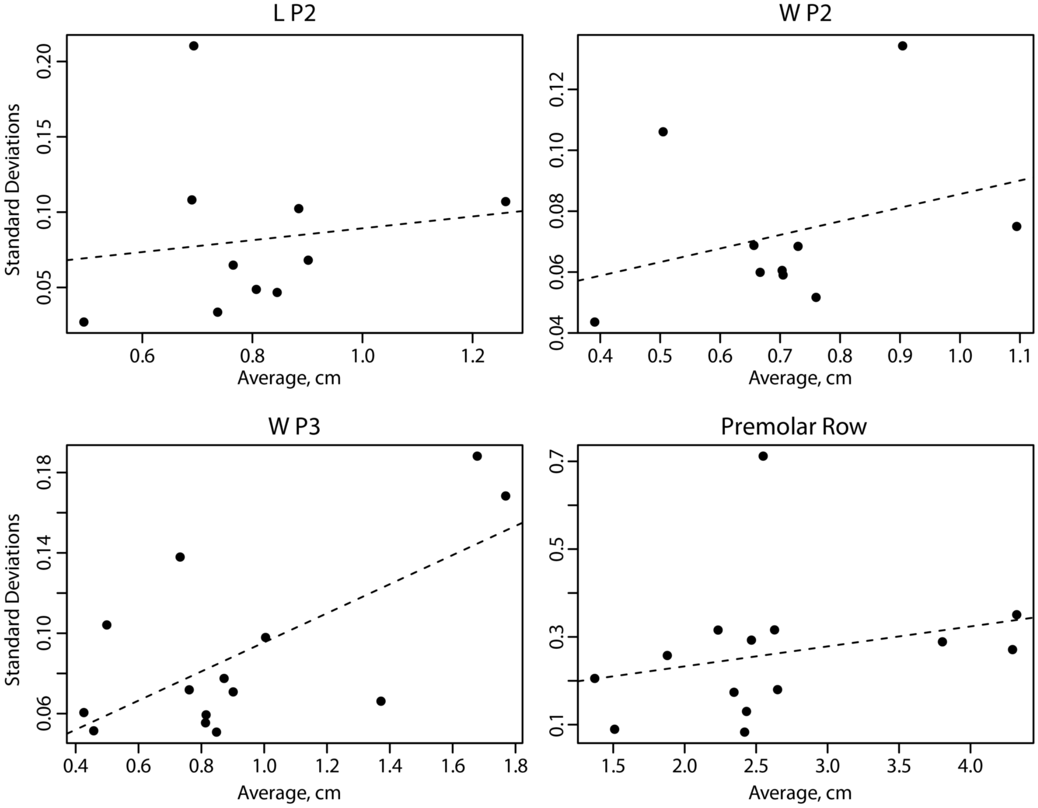

FIGURE 3. Nonsignificant linear regressions of standard deviation and average.

The relationship between height and length is particularly strong in M1, possibly because of the higher degree of size correlation when comparing the height of a tooth to the length of the same tooth, and possibly because of the longer preserved wear sequence across all individuals. The morphology of M1 is also a possible cause for correlation: M1 is visibly flared anteroposteriorally at the occlusal surface in many artiodactyl species, far more so than M2 or M3, and may lose more length through wear than the other teeth.

The reasons for this extreme flare of M1 are not clear. In *Camelus,* M1 bears the brunt of the chewing force (Greaves, 1978); as the first molar to erupt it also carries nearly the entirety of the chewing force for the first several years of the animal's life. *Camelus* may benefit from having a longer M1 before the rest of the tooth row erupts. The decreasing length of M1 through wear may be a spandrel, or perhaps creates accommodation space for the other teeth as they erupt. Tooth impaction can occur from a lack of accommodation space in the tooth row, and can lead to abscesses, displacement, and bone infection (Forsberg, 1988; Dixon, 2006); having a smaller M1 as the tooth wears could minimize risk of impaction of M2.

Width measurements tell a different story. The correlation between height of M1 and width of different molars is negative: older teeth are wider teeth. This may be a result of cryptic eruption: if a tooth appeared fully erupted but wasn't, we would have underestimated the width. It is possible that increased surface area through wear is of benefit in M3 as the tooth is retained into senescence, or that a smaller initial occlusal surface could help to avoid impaction. If so, it is likely that there is a pattern in artiodactyl teeth between eruption timing and morphology: teeth that erupt in rapid sequence early in an animal's lifespan would be straight rather than trapezoidal, while teeth that erupt more slowly should have trapezoidal lengths for accommodation space or reverse trapezoidal widths to retain occlusal area through tooth wear in the posterior of the tooth row.

Sexual Dimorphism

Another possible reason for high variation in artiodactyl dentition is the presence of sexual size dimorphism. Our *t*-tests for sexual dimorphism in *Ovis dalli* were significant for M1 L, but not for any other measurement (Table 5). Our Shapiro-Wilk tests were not significant, indicating no deviation

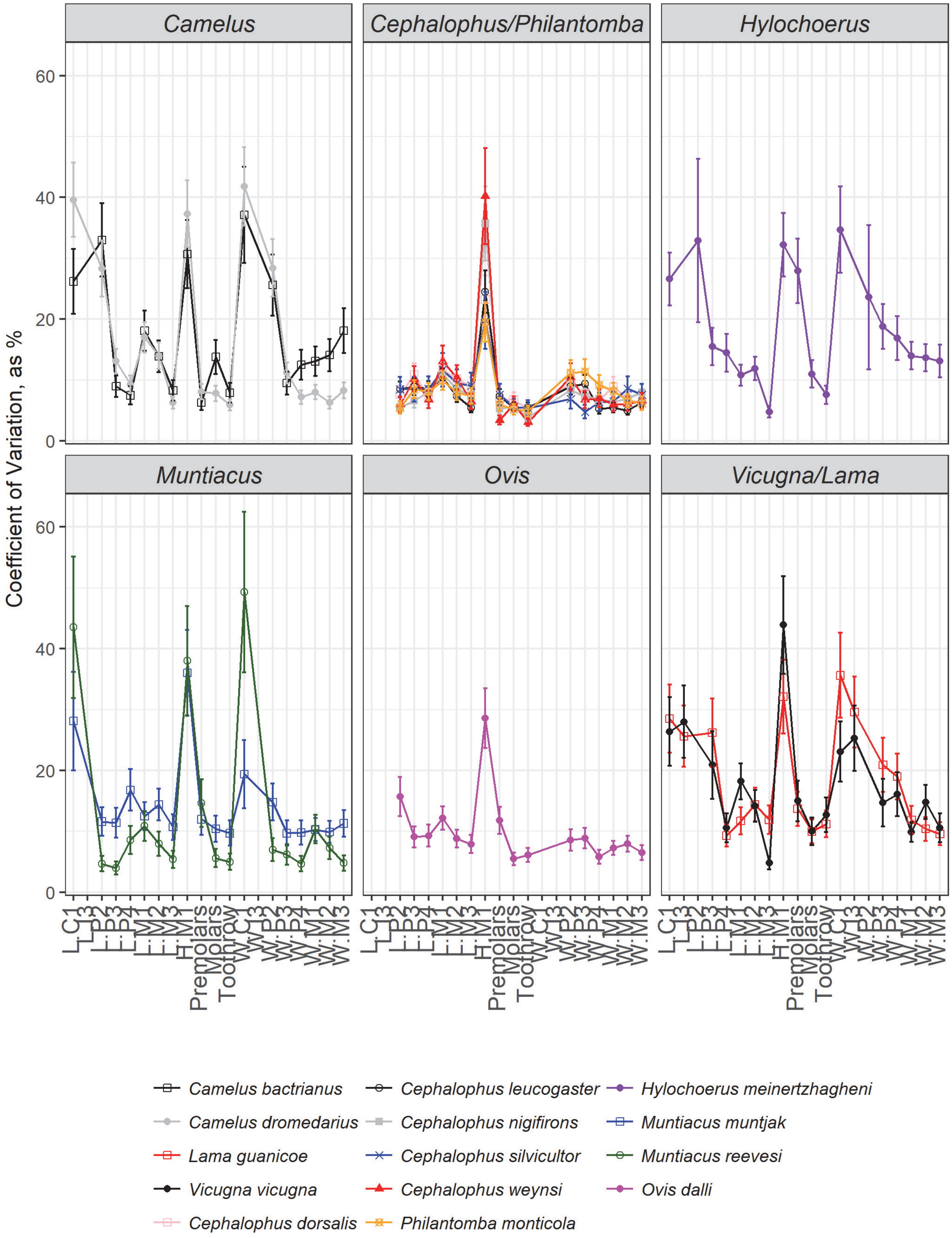

FIGURE 4. Variation line graphs of different species, including lengths and widths. Combined samples of *Camelus, Muntiacus, Lama* and *Vicugna,* and *Cephalophus leucogaster, nigrifrons, dorsalis* and *weynsi* are also included on their respective graphs.

TABLE 4. Regressions of M1H on tooth measurements (M1 L, M1 W, M2 L, M2 W, M3 L and M3 W). Significant *p* values are filled in grey. Adjusted R^2 values, slope, slope significance, standard error, intercept, and intercept significance are reported for each measurement.

		bact	drom	guan	vicu	hylo	dors	leuco	dilv	nigi	weyn	phil	munt	reev	ovis
M1 L	adjR2	0.31	0.29	0.22	0.19	0.18	0.64	0.54	0.96	0.85	0.66	0.55	0.74	0.15	-0.07
	Slope	0.62	0.47	0.40	0.40	0.48	0.78	0.62	1.03	0.61	0.52	0.76	0.80	0.31	0.02
	pSlope	0.02	<.01	0.05	0.06	0.04	<.01	<.01	<.01	<.01	<.01	<.01	<.01	0.17	0.89
	StEr	0.23	0.15	0.18	0.20	0.21	0.14	0.11	0.08	0.06	0.11	0.16	0.13	0.20	0.17
	Intercept	2.19	2.17	1.41	1.15	1.39	0.54	0.61	0.61	0.67	0.72	0.38	0.70	0.75	1.54
	pIntercep	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01
M2 L	adjR2	0.10	0.67	0.51	0.39	0.14	0.54	0.36	0.53	0.61	0.58	0.17	0.50	0.11	0.15
	Slope	0.36	0.66	0.79	0.54	0.70	0.77	0.47	0.78	0.51	0.49	0.47	0.85	0.30	0.22
	pSlope	0.15	<.01	<.01	0.01	0.07	<.01	<.01	0.02	<.01	<.01	0.05	<.01	0.22	0.08
	StEr	0.23	0.10	0.21	0.18	0.36	0.17	0.12	0.25	0.10	0.12	0.22	0.23	0.22	0.12
	Intercept	3.28	2.54	1.35	1.29	1.95	0.75	0.92	1.11	0.97	0.98	0.58	0.87	0.93	1.56
	pIntercep	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01
M3 L	adjR2	0.34	0.01	-0.08	0.15	-0.01	0.53	0.04	0.29	0.14	-0.00	-0.03	0.20	0.05	0.01
	Slope	0.41	0.10	0.08	0.18	0.30	0.67	0.16	0.65	0.25	0.11	0.19	0.46	0.36	0.14
	pSlope	0.03	0.29	0.80	0.14	0.36	<.01	0.16	0.08	0.08	0.35	0.45	0.08	0.31	0.32
	StEr	0.16	0.09	0.30	0.11	0.31	0.15	0.11	0.31	0.13	0.12	0.25	0.24	0.31	0.14
	Intercept	3.77	4.02	2.24	1.68	4.23	0.80	1.09	1.36	1.11	1.21	0.70	1.03	0.91	1.86
	pIntercep	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01
M1 W	adjR2	0.02	-0.03	-0.08	-0.07	0.14	-0.06	-0.04	-0.00	-0.06	0.01	0.01	0.02	0.14	0.25
	Slope	0.19	-0.05	-0.05	-0.04	0.51	0.08	0.01	-0.25	-0.02	-0.11	0.25	0.27	-0.41	0.13
	pSlope	0.28	0.60	0.83	0.74	0.07	0.77	0.95	0.36	0.87	0.31	0.28	0.28	0.18	0.02
	StEr	0.17	0.09	0.21	0.12	0.26	0.25	0.11	0.26	0.12	0.10	0.22	0.24	0.27	0.05
	Intercept	2.57	3.07	1.73	1.33	1.23	1.19	1.11	2.02	1.17	1.26	0.62	1.18	1.18	1.03
	pIntercep	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01
M2 W	adjR2	-0.07	0.18	0.22	0.10	0.13	-0.07	-0.04	-0.14	0.06	0.07	0.07	-0.02	0.66	0.09
	Slope	0.08	-0.15	-0.37	-0.26	0.62	0.03	-0.00	-0.01	-0.21	-0.16	0.32	0.21	-0.53	0.12
	pSlope	0.70	0.03	0.05	0.16	0.08	0.89	0.99	0.98	0.17	0.19	0.15	0.41	0.01	0.14
	StEr	0.20	0.06	0.17	0.17	0.33	0.22	0.12	0.41	0.15	0.12	0.21	0.25	0.14	0.08
	Intercept	2.97	3.41	2.12	1.51	1.54	1.38	1.28	2.07	1.48	1.49	0.70	1.31	1.32	1.05
	pIntercep	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01
M3 W	adjR2	-0.10	0.30	0.66	0.47	0.00	-0.05	0.28	-0.10	0.12	0.63	-0.07	0.09	-0.12	-0.09
	Slope	0.03	-0.22	-0.50	-0.42	0.42	-0.10	-0.37	-0.16	-0.27	-0.33	-0.02	0.42	-0.21	0.01
	pSlope	0.94	0.01	<.01	0.02	0.34	0.60	<.01	0.64	0.09	<.01	0.94	0.18	0.58	0.92
	StEr	0.31	0.07	0.10	0.14	0.41	0.19	0.12	0.33	0.15	0.07	0.21	0.29	0.35	0.07
	Intercept	3.05	3.20	2.16	1.57	1.83	1.36	1.35	2.05	1.41	1.44	0.78	1.18	1.21	1.07
	pIntercep	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01	<.01

TABLE 5. *p* values for different dimorphism tests in molars of *Ovis dalli,* including t-tests with equal variance, Hartigan's dip test, Shapiro-Wilk test for skew, and Finite Mixture analysis of more than 1 overlapping distribution. Significant *p* values are filled in grey. Samples without adequate sample size filled in with *na.*

Test	L M1	L M2	L M3	W M1	W M2	W M3
T-Test	0.01	0.23	0.99	0.35	0.58	0.64
Hartigan's Dip Test	0.76	0.45	0.68	0.63	0.69	0.59
Shapiro-Wilks	0.08	0.70	na	0.32	0.23	na
Finite Mixture Model >1	0.61	0.90	0.48	0.86	1.00	0.87

TABLE 6. Tests for sexual dimorphism in caniniform teeth of *Camelus bactrianus, Camelus dromedarius,* and *Hylochoerus meinertzhagheni. p* values reported for Shapiro-Wilk test, Hartigan's Dip test, and for Finite Mixture Models of >1 or >2 distributions. Significant *p* values filled in grey.

		Shapiro-Wilks	Hartigan's	>1	>2
C. dromedarius	L C1	0.01	0.99	0.05	0.38
	W C1	0.01	0.46	0.03	0.35
	L P2	0.95	0.91	0.98	
	W P2	0.01	0.71	0.41	
	Multivariate			0.78	
C. bactrianus	L C1	0.47	0.97	0.88	
	W C1		0.85	0.82	
	L P2	0.11	0.47	0.16	
	W P2	0.34	0.06	0.31	
	Multivariate			0.07	
Hylochoerus	L C1	0.40	0.45	0.76	
	W C1	0.47	0.40	0.45	
	C1 Height	0.01	0.89	0.40	
	Multivariate			0.61	

from normality in *Ovis dalli* molars, though the *p* value for M1 L did approach significance (*p* = 0.08, Table 5). Our Hartigan's Dip test was also not significant for any variable, indicating no significant deviation from unimodality in the molar measurements of *Ovis dalli* (Table 5). Finally, our mixture analysis could not reject the null, single distribution hypothesis for any of our univariate molar measurements in *Ovis dalli* (Table 5).

Similarly, several of our caniniform values had significant Shapiro-Wilk results, but none showed signs of multimodality according to Hartigan's Dip test (Table 6). Finite Mixture analysis rejected the null hypothesis of a single distribution for the lengths and widths of C1 for *Camelus dromedarius*, but did not reject the null hypothesis for any other caniniform measurements, including multivariate analyses of multiple measurements. None of our data were significantly likely to have more than a single distribution present.

These results do not rule out the presence of sexual dimorphism in these species, as sexual dimorphism in body size is not always isometrically correlated with tooth dimensions; male artiodactyl teeth can be smaller than anticipated given skull size (Carranza and Pérez-Barbería, 2007), which may increase the difficulty of separating groups by sex using only their teeth. Difference in lifespan is also a complicating factor: because female artiodactyls live longer than males, there may be a longer female tail to the distribution that could exacerbate non-detection of dimorphism (Carranza and Pérez-Barbería, 2007). In this case, there was no significant difference when male and female M1 heights were evaluated with a *t*-test (*p* = 0.15), but this difference in age distributions may be a problem in other samples. Sexual dimorphism should not be excluded as a possible source of variation for dental measurements, but it may be difficult to support the hypothesis of sexual dimorphism over a multispecies hypothesis when analysing dentition other than the canines.

TABLE 7. Regression Coefficients for Average and Standard deviations. Significant p values are italicized and highlighted in grey. Change in AIC reflects increase in model fitness from Linear to Non-Linear model, negative numbers indicate linear model is preferred. AIC likelihood reflects likelihood of that AIC change being statistically significant; <.05 is a statistically significant likelihood. Acronyms: NLS (non-linear least squares regression), AIC (Akaike Information Criterion).

Character	Intercept	p of intercept	Slope	p (slope of 0)	p (slope of .1)	R2	NLS intercept	NLS slope	change in AIC	AIC relative likelihood
All	-0.01	0.74	0.14	<.001	<.001	0.55	<.01	1.06	-0.05	0.98
L P2	0.05	0.55	0.04	0.69	0.54	-0.1	0.01	0.4	-0.02	0.99
L P3	<.01	0.95	0.11	<.001	0.69	0.45	<.01	0.96	-0.02	0.99
L P4	0.01	0.51	0.08	<.001	0.28	0.72	<.01	0.87	-0.37	0.83
L M1	-0.08	<.01	0.2	<.001	<.001	0.95	<.01	1.39	-3.74	0.15
L M2	-0.07	<.01	0.16	<.001	<.001	0.95	<.01	1.27	0.13	0.94
L M3	0.02	0.47	0.06	<.001	0.01	0.73	<.01	0.85	-0.31	0.85
W P2	0.04	0.27	0.04	0.37	0.28	-0.01	<.01	0.43	0.02	0.99
W P3	0.02	0.34	0.07	0.01	0.25	0.41	<.01	0.81	0.45	0.8
W P4	-0.01	0.83	0.1	<.001	0.91	0.51	<.01	1.06	0	1
W M1	-0.03	0.28	0.12	<.001	0.39	0.74	<.01	1.2	0.1	0.95
W M2	-0.04	0.39	0.12	<.001	0.51	0.62	<.01	1.19	0.17	0.92
W M3	-0.12	0.02	0.18	<.001	0.01	0.77	<.01	1.77	-1.26	0.53
Premolars	0.14	0.3	0.05	0.36	0.27	-0.01	0.08	0.47	-0.11	0.95
Molars	-0.22	0.03	0.13	<.001	0.07	0.85	0.03	1.49	-0.98	0.61
Tooth row	-0.04	0.73	0.08	<.001	0.14	0.65	0.07	1.04	0.08	0.96

Relationship Between Size and Coefficients of Variation

For most measurements, the relationship between standard deviation and mean was proportional and best described by a linear relationship with a zero intercept (Table 7). M1 L, M2 L, M3 T and length of the molar row all had intercepts that were significantly different from zero (Table 7). We also found that four of our characters had slopes that were significantly different from 0.10 (or, different from the rule-of thumb coefficient of variation of 10%), as did the slope of all our measurements combined and all caniniform teeth together. P2 L, P2 W and the length of the premolar row all had slopes that were not significant from zero, indicating no linear relationship between standard deviation and size (Figure 3). While the relationship between standard deviation and mean was explained well in several measurements by nonlinear relationships, there was not a significant improvement in fit (Table 7). Four of our measurements show non-proportional relationships between standard deviation and mean, and three show no relationship at all (slope not significantly different from 0), meaning that in 7 of 19 measurements CV does not evenly remove the effect of size on this distribution of variance. These results contain a higher number of significant values than would be expected by random chance (cumulative binomial probability of <0.001). When we excluded camels, we found that the anisometric relationship disappeared for M1 L and AP M2 (Table 8). Anisometry was still present in the molar row and width of M3 with or without camels.

The non-proportional relationships between standard deviation and mean is contrary to the correlation predicted by Simpson and Roe (1939), who suggested that larger measurements and larger animals should have proportionally larger standard deviations. Polly (1998) found that measurement error caused inflated CVs for small measurements and suggested these may drive non-isometric relationships between standard deviation and mean. Indeed, smaller measurements in our data show little to no linear relationship between standard deviation and mean (Figure 4); possibly the influence of measurement error overwhelms any linear trend (Polly 1998). However, our results agree with the suggestion by Davis and Calède (2012) that large endmembers are responsible for some of the non-proportionality in CVs. Our measurements were, on the whole, much larger than

TABLE 8. Regression Coefficients for Average and Standard deviations, without *Camelus* species. Significant p values are italicized and highlighted in grey. Change in AIC reflects increase in model fitness from Linear to Non-Linear model, negative numbers indicate linear model is preferred. AIC likelihood reflects likelihood of that AIC change being statistically significant; <.05 is a statistically significant likelihood. Acronyms: NLS (non-linear least squares regression), AIC (Akaike Information Criterion).

Character	Intercept	p of intercept	Slope	p (slope of 0)	p (slope of .1)	R2	NLS intercept	NLS slope	change in AIC	AIC likelihood
All	0.01	0.38	0.11	<.001	0.3	0.56	0.11	0.98	0.02	0.99
L P2	0.05	0.55	0.04	0.69	0.54	-0.1	0.09	0.4	-0.02	0.99
L P3	-0.02	0.75	0.15	0.12	0.59	0.15	0.12	1.15	0.05	0.97
L P4	-0.03	0.29	0.14	<.01	0.29	0.59	0.1	1.41	-0.11	0.95
L M1	-0.02	0.49	0.14	<.001	0.12	0.75	0.12	1.12	0.16	0.93
L M2	-0.06	0.14	0.15	<.001	0.06	0.79	0.09	1.34	0.11	0.95
L M3	0.04	0.25	0.05	0.01	0.01	0.48	0.09	0.71	-0.77	0.68
W P2	0.04	0.27	0.04	0.37	0.28	-0.01	0.08	0.43	0.01	0.99
W P3	0.08	0.01	<.01	0.94	0.01	-0.1	0.08	0.01	0	1
W P4	-0.01	0.93	0.1	0.19	0.98	0.08	0.1	0.99	0.01	1
W M1	-0.04	0.47	0.12	0.01	0.63	0.44	0.08	1.3	0.06	0.97
W M2	-0.07	0.21	0.14	<.01	0.3	0.55	0.07	1.56	-0.03	0.98
W M3	-0.09	0.04	0.15	<.001	0.08	0.74	0.06	1.79	-0.67	0.72
Premolars	0.09	0.67	0.07	0.41	0.72	-0.03	0.15	0.63	-0.05	0.98
Molars	-0.19	0.03	0.12	<.001	0.21	0.82	0.03	1.59	-1.43	0.49
Tooth row	-0.22	0.35	0.11	0.01	0.85	0.42	0.03	1.45	0.14	0.93
Caniniform Teeth	-0.01	0.6	0.29	<.001	<.001	0.91	0.27	1.06	-0.2	0.91

those conducted by Polly (1998). It seems that CV poorly accounts for size in endmembers: for small measurements, CVs are larger than predicted because of measurement error; yet for large measurements, CVs are larger than anticipated by a purely isometric relationship between standard deviation and mean. In either case, the expectation of the 10% rule of thumb simply does not hold. In our dataset non-proportionality has manifested in linear relationships with non-zero intercepts, or no significant slopes; in larger datasets that showed inflation in both large and small measurements with significantly lower values in the middle, this should result in a nonlinear relationship between standard deviation and mean.

Importantly, when we subsampled our data to remove the two largest endmembers (*Camelus* species), our trends for the lengths of M1 and M2 became isometric again. Further research should be conducted with additional large ungulates to see whether our anisometric trend is truly size-bias in CV, or results from phylogenetic influence on morphology and variation in our particular sample.

Regardless of the cause for anisometry between standard deviation and mean, this pattern has strong implications for the use of the CV in systematics studies. CVs are simple statistics that are easily compared between species, but our data suggest that they should not be compared between measurements of considerably different size classes or phylogenetic groups.

CONCLUSION

Dental measurements in artiodactyls are not always sufficient for identification at the species level, whether species is known *a priori* or not. Artiodactyl dentition is more variable than that of carnivores, primates, rodents and in several cases even elephants. Artiodactyl dental variation follows a different variation pattern than in carnivores or primates, with the width of M3 and the length of M1 as the most variable molar measurements. Artiodactyl premolars are highly variable, which may result from a decrease in functional constraints in the anterior of the chewing battery. Premolars are also prone to rotation, replication and absence, which makes premolar rows more variable than either molar rows or overall tooth-row lengths.

With the exception of duikers, selenodont molars show measurement changes through wear, and this should be considered when selecting analogous taxa for comparisons to fossil populations. Canines and caniniform teeth often show signs of sexual dimorphism, but this signal may be difficult to detect without *a priori* knowledge of sex. Molariform teeth can also show signs of sexual dimorphism related to sexually dimorphic body sizes, but this signal may be less than expected and also may be undetectable because of the obscuring trend of female senescence. We found that distribution tests were unable to detect the presence of two sexes, and it is quite likely that sexually dimorphic traits will not be detectable using statistical techniques.

When selecting a modern analogue for a comparative sample for a paleontological study, it is important to select an analogue that is morphologically similar but also similar in size as our research shows that CV may not perfectly adjust for size differences between different taxa. Though variable within species, artiodactyl dental measurements are often conserved between species and do not always diagnose taxa via DFA or demonstrate multi-species groups via CV *t*-tests or mixture analysis. Dentition may be generally too conservative to oft-reveal multispecies samples of artiodactyls.

ACKNOWLEDGEMENTS

This work was funded by a Field Museum Research Grant from the Field Museum of Natural History in Chicago, a Theodore Roosevelt Grant from the American Museum of Natural History, an Ernst Mayer Grant from Harvard University and a Thomas Condon and a Smith Scholarship from the University of Oregon. B. McHorse (Harvard) took additional *Hylochoerus* pictures. M. Fonstad (UO) introduced us to Photoscan after J. Roering (UO) suggested it. Access to collections was given by J. Chupasko (MCZ), R. Banasiak (FMNH), E. Westwig (AMNH), C. Sagabiel (VPL) and C. Conroy (MVZ). D. Polly (Indiana) and an anonymous reviewer contributed valuable edits through peer review. B. McHorse (Harvard), I. Burke, M. Ball (UO), K. Burns, and David, Becky, Leo and Isaac Houts provided much-needed housing during museum travels. S. Hopkins (UO), D. Warrick (OSU), S. Frost (UO), and J. Roering (UO) gave important feedback on this research during the lead author's dissertation.

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APPENDIX 1.

Supplemental raw measurement data.

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
AMNH	14889	*Ovis dalli*						1.68	2.06											1.05	1.19		0.000098
AMNH	14517	*Ovis dalli*						1.82			0.8									1.04			0.000074
AMNH	128025	*Ovis dalli*						1.8	1.82											0.98	1		0.000185
MCZ	11508	*Ovis dalli*						1.81												1.02			0.0001
MCZ	34514	*Ovis dalli*						1.84	2.14		0.97									1.1	1.04		0.000185
AMNH	123038	*Ovis dalli*			0.89	1.02	1.18	1.63	1.75		1.06	3.03	5.5	8.26			0.75	0.87	1.06	1.11	1.19		0.000152
MCZ	16280	*Ovis dalli*			0.69	0.79	0.94	1.71	1.87		0.9	2.59					0.7	0.83	0.96	1.12	1.04		0.000125
AMNH	31403	*Ovis dalli*			0.63	0.88	0.84	1.33	1.8	2.19	1	2.33	5.24	7.36			0.62	0.85	1.04	1.16	1.17	1.1	0.000335
AMNH	123042	*Ovis dalli*							1.56	2.18											1.16	1.1	0.00026
AMNH	128026	*Ovis dalli*					0.96	1.69	1.7	2.13	1.26	2.59	5.53	7.93					1.08	1.16	1.37	1.2	0.000187
AMNH	129329	*Ovis dalli*			0.69	0.76		1.5	1.86	1.97	1.4	1.71	5.43	6.97			0.77	1.01		1.33	1.15	0.97	0.000026
MCZ	35940	*Ovis dalli*			0.53	0.74	1.07	1.7	1.66	1.84	0.95	2.52	5.23	7.6			0.66	0.91	0.96	1.11	1.19	1.04	0.000006
MCZ	37010	*Ovis dalli*			0.58	0.92	0.96	1.66	1.87	2.26	1.24	2.43	5.73	8.06			0.64	0.88	0.98	1.16	1.19	1.15	0.000181
MCZ	16279	*Ovis dalli*			0.74	0.9	0.92	1.66	1.75	1.94	0.89	2.56	5.53	7.82			0.76	0.91	1.01	1.18	1.09	1.04	0.000194
AMNH	16224	*Ovis dalli*			0.57	0.85	0.9	1.31	1.7	2.24	0.66	2.42	5.18	7.24			0.7	0.91	1.09	1.22	1.22	1.18	0.000056
AMNH	125579	*Ovis dalli*			0.71	0.86	0.99	1.49	1.78	1.87	0.82	2.47	5.05	7.39			0.6	0.86	0.93	1.16	1.12	1.06	0.000162
AMNH	19031	*Ovis dalli*			0.72	0.87	0.91	1.53	1.77	1.89	0.96	2.41	5.23	7.48			0.72	0.8	0.92	1.08	1.09	0.95	0.000091
MCZ	35941	*Ovis dalli*			0.67	0.88	1.02	1.69	1.77	2.01	1.18	2.67	5.61	8.08			0.75	0.88	0.98	1.18	1.14	1.09	0.000092
AMNH	123039	*Ovis dalli*			0.86	0.87	1.03	1.53	1.99	1.88	1.27	2.64	5.27	7.57			0.77	0.88	1.06	1.19	1.22	1.06	0.000647
AMNH	19032	*Ovis dalli*				0.75		1.24	1.82	2.09	1.7		4.97	6.73				0.95		1.26	1.34	1.11	0.000283
AMNH	14888	*Ovis dalli*				0.78	0.88	1.2	1.46	1.79	0.45	2.18	4.63	6.99				0.67	0.95	1.13	1.23	1.07	0.000098
MCZ	25862	*Muntiacus muntjak*	0.77		0.74	0.75	0.73	0.99	1.09	1.09	0.52	2.44	3.16	5.41	0.48		0.75	0.94	1.01	1.1	1.22	1.25	0.000057
MCZ	25863	*Muntiacus muntjak*			1.04		0.99	1.19	1.49	1.39	0.5	3.2	3.94	6.89			1.02		1.15	1.21	1.49	1.58	0.00003
MCZ	6034	*Muntiacus muntjak*						0.94	0.96											1.14	1.17		0.000052
MCZ	38633	*Muntiacus muntjak*	0.93					1.13	1.35		0.5				0.4					1.33	1.42		0.00012
MCZ	6962	*Muntiacus muntjak*						1.08	1.13											1.09	1.22		0.00009
MCZ	13682	*Muntiacus muntjak*						1.26	1.41	1.39	0.67		3.81							1.5	1.53	1.41	0.000083
MVZ	184217	*Muntiacus muntjak*			0.74	0.66	0.51	0.78	0.88	0.92	0.19	2.13	2.66	4.7			0.76	0.84	0.85	1.1	1.16	1.04	0.00146
MCZ	13163	*Muntiacus muntjak*	0.54		0.81	0.78	0.66	0.8	0.96	1.14	0.16	2.19	3.03	5.55	0.58		0.92	0.97	1.04	1.32	1.43	1.31	0.000108
MCZ	38111	*Muntiacus muntjak*			1	0.95	0.84	1.07	1.29	1.28	0.46	2.83	3.62	6.29			1.08	1.18	1.18	1.44	1.52	1.53	0.000082
MCZ	7955	*Muntiacus muntjak*			0.94	0.94	0.86	1.07	1.28	1.21	0.42	2.87	3.53	6.16			1.01	1.08	1.16	1.42	1.52	1.44	0.000013

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
MCZ	35917	*Muntiacus muntjak*	0.98		0.83	0.77	0.77	0.99	1.13	1.16	0.46	2.42	3.13	5.6	0.47		0.88	1	1.02	1.17	1.21	1.14	0.000185
MCZ	34245	*Muntiacus muntjak*			0.84	0.82	0.71			1.16							0.63	0.87	0.95			1.21	0.00011
MCZ	13164	*Muntiacus muntjak*	1.26		1.02	0.96	0.89	0.97	1.23	1.34	0.3	2.72	3.38	6.18	0.54		0.92	1.03	1.16	1.23	1.43	1.28	0.000105
MCZ	25989	*Muntiacus muntjak*			0.88	0.8	0.81	1.1	1.25	1.19	0.46	2.69	3.52	6.15			0.9	1.03	1.14	1.27	1.36	1.39	0.000064
MCZ	35918	*Muntiacus muntjak*	1.08		0.84	0.8	0.76	0.99	1.17	1.24	0.23	2.6	3.49	6.03	0.68		1.05	1.09	1.18	1.31	1.44	1.39	0.000068
MCZ	1839	*Muntiacus muntjak*			0.93	0.88	0.96	1.05	1.27	1.3	0.47	2.83	3.53	6.14			0.93	1.02	1.13	1.31	1.42	1.37	0.000044
MCZ	16485	*Muntiacus reevesi*						1.05												0.93			0.000009
MCZ	16024	*Muntiacus reevesi*						0.98			0.44									0.87			0.000082
MCZ	11544	*Muntiacus reevesi*						0.91	1.12		0.62									1.02	0.99		0.00005
MCZ	16484	*Muntiacus reevesi*	0.37		0.7	0.74	0.72	0.92	1.17	1.08	0.27	2.26	3.05	5.12	0.25		0.78	0.82	0.83	1.04	1.19	1.16	0.000176
MCZ	16483	*Muntiacus reevesi*	0.9		0.78	0.71	0.58	0.74	0.98	1.01	0.27	2.93	2.85	4.96	0.43		0.77	0.89	0.94	1.08	1.17	1.12	0.000137
MCZ	11543	*Muntiacus reevesi*	0.9		0.74	0.66	0.58	0.81	1.01	1.01	0.3	2.1	2.82	4.63	0.41		0.75	0.79	0.9	1.21	1.2	1.2	0.000072
MCZ	16494	*Muntiacus reevesi*	0.33		0.78	0.68	0.68	0.86	1.01	1.02	0.25	2.12	2.82	4.74	0.22		0.68	0.79	0.87	1.01	1.09	1.09	0.000112
MCZ	51183	*Muntiacus reevesi*	0.88		0.7	0.71	0.65	0.89	0.99	0.97	0.24	2.14	2.82	4.92	0.88		0.85	0.92	0.94	1.17	1.2	1.14	0.000082
MCZ	25858	*Muntiacus reevesi*	1.22		0.74	0.68	0.65	0.89	1.04	1.05	0.43	2.02	2.88	4.9	0.5		0.76	0.85	0.87	0.92	1.08	1.11	0.000123
MCZ	25860	*Muntiacus reevesi*	1.11		0.72	0.68	0.6	0.75	0.91	0.92	0.25	2.07	2.53	4.43	0.53		0.73	0.88	0.91	1.06	1.24	1.24	0.000112
AMNH	52874	*Cephalophus dorsalis*				0.99	0.71	1.04	1.27	1.31	0.62	2.83	3.38	5.95				1	1.09	1.18	1.44	1.33	0.000188
AMNH	52880	*Cephalophus dorsalis*				0.84		1.07	1.21	1.21	0.65		3.27					0.95		1.34	1.37	1.2	0.000028
AMNH	52881	*Cephalophus dorsalis*			0.93	0.97	0.8	1.03	1.19	1.13	0.57	2.8	3.19	5.79			0.73	0.91	0.98	1.17	1.34	1.28	0.000205
AMNH	52898	*Cephalophus dorsalis*			0.96	0.92	0.86	0.9	1.11	1.15	0.44	2.84	3.16	5.81			0.72	0.91	1.03	1.27	1.49	1.46	0.000223
AMNH	52900	*Cephalophus dorsalis*			0.92	0.92	0.73	0.94	1.2	1.17	0.5	2.74	3.13	5.74			0.75	0.89	0.94	1.21	1.41	1.3	0.000119
AMNH	52987	*Cephalophus dorsalis*			0.92	0.86	0.76	1	1.15	1.28	0.53	2.64	3.35	5.8			0.68	0.8	0.96	1.17	1.3	1.29	0.00015
AMNH	55391	*Cephalophus dorsalis*			0.86	0.96	0.82	1.01	1.2	1.17	0.5	2.61	3.35	5.78			0.8	0.95	0.96	1.39	1.48	1.33	0.00014
AMNH	55393	*Cephalophus dorsalis*			0.88	0.9	0.75	0.91	1.17	1.14	0.44	2.61	3.09	5.43			0.79	0.99	0.99	1.25	1.32	1.22	0.000111
AMNH	89617	*Cephalophus dorsalis*			0.75	0.75	0.7	0.8	0.99	1.01	0.4	2.2	2.84	4.92			0.65	0.82	0.87	0.97	1.22	1.11	0.000064
AMNH	89619	*Cephalophus dorsalis*			0.92	0.87	0.76	0.98	1.14	1.12	0.66	2.72	3.07	5.66			0.78	0.99	1.12	1.25	1.46	1.33	0.000133
AMNH	52883	*Cephalophus dorsalis*			0.92	0.89	0.79	0.95	1.17	1.13	0.54	2.56	3.24	5.53			0.71	0.83	0.94	1.22	1.37	1.31	0.000068
AMNH	52896	*Cephalophus dorsalis*			1.03	0.86	0.79	0.7	0.89	0.99	0.31	2.69	2.69	5.18			0.65	0.76	0.92	1.08	1.23	1.27	0.00017
AMNH	52903	*Cephalophus dorsalis*				0.83	0.84	0.92	1.24	1.15	0.48	2.82	3.17	5.75				0.92	0.99	1.14	1.32	1.35	0.000182
AMNH	52905	*Cephalophus dorsalis*			0.91	0.91	0.85	0.83	1.08	1.04	0.43	2.69	3.04	5.59			0.69	0.87	1.01	1.2	1.47	1.3	0.000192

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
AMNH	52916	*Cephalophus dorsalis*			0.81	0.75	0.69	0.76	1.03	1.04	0.48	2.33	2.88	5.16			0.66	0.86	0.96	1.34	1.5	1.39	0.000093
AMNH	100285	*Cephalophus dorsalis*				0.61	0.7	0.79	0.88	0.92	0.25		2.7					0.9	0.91	1.41	1.51	1.38	0.000132
AMNH	119821	*Cephalophus dorsalis*			0.91	0.81	0.81	0.9	1.17	1.11	0.38	2.68	3.13	5.58			0.88	0.97	1.04	1.21	1.49	1.4	0.000053
AMNH	52824	*Cephalophus leucogaster*						0.95	1.26	1.23	0.53		3.11							1.04	1.17	1.06	0.00007
AMNH	52827	*Cephalophus leucogaster*						0.92	1.21	1.1	0.49		3.12							1.02	1.22	1.15	0.000165
AMNH	52831	*Cephalophus leucogaster*						1.04	1.21	1.19	0.55		3.27							1.12	1.2	1.06	0.000053
AMNH	52834	*Cephalophus leucogaster*			0.83	0.88		0.87	1.27	1.31	0.62	2.86	3.45	5.89			0.77	0.84		1.14	1.3	1.1	0.000093
AMNH	52804	*Cephalophus leucogaster*			0.68	0.77	0.61	0.9	1.13	1.19	0.46	2.18	2.97	4.94			0.56	0.73	0.9	1.09	1.24	1.12	0.000113
AMNH	52835	*Cephalophus leucogaster*			0.79	0.78	0.69	0.94	1.16	1.18	0.51	2.39	3.09	5.25			0.71	0.77	0.91	1.24	1.27	1.24	0.000073
AMNH	52836	*Cephalophus leucogaster*			0.8	0.83	0.7	0.95	1.15	1.22	0.6	2.38	3.13	5.29			0.63	0.73	1	1.08	1.31	1.14	0.000186
AMNH	52840	*Cephalophus leucogaster*			0.7	0.67	0.6	0.9	1.02	1.06	0.54	2.21	2.76	4.79			0.66	0.77	0.97	1.1	1.26	1.05	0.000119
AMNH	52842	*Cephalophus leucogaster*			0.75	0.78	0.7	1.01	1.24	1.1	0.58	2.29	3.25	5.39			0.73	0.9	1	1.15	1.26	1.12	0.000099
AMNH	52849	*Cephalophus leucogaster*			0.7	0.7	0.7	0.97	1.17	1.19	0.5	2.36	3.13	5.25			0.68	0.72	0.91	1.09	1.28	1.18	0.000161
AMNH	52851	*Cephalophus leucogaster*			0.73	0.7	0.61	0.88	1.15	1.11	0.46	2.3	2.93	5.09			0.57	0.75	0.89	1.04	1.18	1.08	0.000071
AMNH	52852	*Cephalophus leucogaster*			0.75	0.75	0.64	0.99	1.18	1.15	0.54	2.39	3.14	5.36			0.75	0.78	0.91	1.11	1.31	1.18	0.000091
AMNH	52787	*Cephalophus leucogaster*			0.73	0.82	0.66	0.81	1.03	1.07	0.38	2.25	2.87	4.93			0.61	0.72	0.86	1.12	1.2	1.18	0.000111
AMNH	52789	*Cephalophus leucogaster*			0.8	0.8	0.7	0.83	1.05	1.15	0.41	2.29	2.91	5.17			0.68	0.81	0.88	1.1	1.32	1.12	0.000282
AMNH	52793	*Cephalophus leucogaster*			0.85	0.8	0.81	0.98	1.19	1.11	0.46	2.49	3.01	5.43			0.67	0.75	0.92	1.13	1.28	1.2	0.000104
AMNH	52797	*Cephalophus leucogaster*			0.82	0.86	0.77	0.86	1.14	1.19	0.37	2.17	3.01	5.06			0.77	0.83	0.96	1.04	1.24	1.24	0.000298
AMNH	52801	*Cephalophus leucogaster*			0.8	0.78	0.67	1.01	1.18	1.23	0.47	2.35	3.28	5.51			0.68	0.81	0.99	1.27	1.3	1.19	0.000117
AMNH	52802	*Cephalophus leucogaster*			0.84	0.88	0.8	0.84	1.11	1.2	0.25	2.55	3.18	5.52			0.63	0.82	0.99	1.12	1.29	1.33	0.000074
AMNH	52841	*Cephalophus leucogaster*			0.8	0.68	0.62	0.71	1.03	1.09	0.15	2.08	3.03	4.99			0.57	0.55	0.92	1.11	1.25	1.19	0.000259
AMNH	52844	*Cephalophus leucogaster*			0.72	0.74	0.7	0.79	1.04	1.13	0.41	2.31	3.14	5.23			0.64	0.71	0.91	1.02	1.26	1.24	0.000064
AMNH	52845	*Cephalophus leucogaster*			0.72	0.7	0.68	0.8	0.98	1.07	0.39	2.15	2.85	4.84			0.68	0.71	0.86	1.11	1.28	1.2	0.000079
AMNH	52853	*Cephalophus leucogaster*			0.59	0.68	0.67	0.7	1.01	1.18	0.38	2.26	3.05	5.18			0.65	0.7	0.85	1.17	1.34	1.24	0.000073
AMNH	52854	*Cephalophus leucogaster*			0.85	0.79	0.74	0.81	1.12	1.25	0.37	2.45	3.27	5.54			0.63	0.74	0.99	1.13	1.44	1.31	0.000162
AMNH	52861	*Cephalophus leucogaster*			0.77	0.73	0.73	0.84	1.18	1.14	0.37	2.25	3.09	5.1			0.7	0.76	0.89	1.2	1.34	1.24	0.000134

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
AMNH	89391	*Cephalophus leucogaster*			0.81	0.89	0.73	1	1.24	1.2	0.61	2.61	3.43	5.81			0.7	0.86	0.97	1.13	1.41	1.21	0.001729
MCZ	32598	*Cephalophus nigifirons*			0.81	0.75		1.02	1.23	1.22	0.57	2.55	3.23	5.5			0.67	0.77		1.08	1.26	1.15	0.000157
MCZ	8094	*Cephalophus nigifirons*			0.82	0.84	0.73	0.96	1.26	1.15	0.47	2.56	3.29	5.65			0.75	0.8	1.02	1.26	1.37	1.21	0.000106
MCZ	14735	*Cephalophus nigifirons*			0.81	0.82	0.83	0.98	1.24	1.29	0.43	2.5	3.24	5.47			0.72	0.82	0.9	1.11	1.28	1.26	0.000014
MCZ	31774	*Cephalophus nigifirons*			0.77	0.73	0.72	0.99	1.14	1.13	0.55	2.17	2.97	4.95			0.57	0.71	0.82	1.13	1.26	1.07	0.000849
MCZ	32430	*Cephalophus nigifirons*			0.83	0.81	0.74	0.95	1.18	1.18	0.57	2.36	3.12	5.33			0.64	0.77	0.94	1.05	1.32	1.23	0.000018
MCZ	32449	*Cephalophus nigifirons*			0.9	0.92	0.8	1.08	1.43	1.31	0.63	2.57	3.51	5.82			0.71	0.92	1.04	1.29	1.49	1.25	0.000084
MCZ	32596	*Cephalophus nigifirons*			0.89	0.8	0.75	1.14	1.27	1.3	0.69	2.48	3.52	5.75			0.75	0.8	1.03	1.18	1.32	1.38	0.000109
MCZ	32597	*Cephalophus nigifirons*			0.82	0.8	0.74	1.05	1.31	1.3	0.58	2.22	3.45	5.51			0.69	0.79	0.88	1.14	1.31	1.2	0.000088
MCZ	32599	*Cephalophus nigifirons*			0.84	0.87	0.76	0.95	1.18	1.28	0.46	2.44	3.27	5.52			0.7	0.77	1.03	1.2	1.47	1.3	0.000024
MCZ	32615	*Cephalophus nigifirons*			0.87	0.82	0.79	0.88	1.19	1.2	0.43	2.53	3.19	5.5			0.73	0.8	0.97	1.17	1.38	1.34	0.000016
MCZ	26841	*Cephalophus nigifirons*			0.84	0.82	0.84	0.82	1.13	1.19	0.37	2.43	3.18	5.51			0.73	0.81	0.99	1.09	1.39	1.33	0.000098
MCZ	31811	*Cephalophus nigifirons*					0.63	0.76	0.95	1	0.08		2.81						0.96	1.09	1.3	1.25	0.000004
MCZ	32429	*Cephalophus nigifirons*			0.96	0.91	0.88	0.91	1.23	1.37	0.45	2.52	3.42	5.69			0.77	0.85	1.03	1.13	1.47	1.35	0.000002
MCZ	32451	*Cephalophus nigifirons*			0.79	0.76	0.7	0.81	1.11	1.24	0.21	2.26	3.39	5.49			0.6	0.91	1.02	1.22	1.59	1.46	0.000107
MCZ	32453	*Cephalophus nigifirons*			0.85	0.81	0.79	0.85	1.16	1.27	0.28	2.5	3.21	5.39			0.77	0.92	1.06	1.22	1.46	1.33	0.000059
MCZ	32613	*Cephalophus nigifirons*			0.88	0.82	0.79	0.84	1.13	1.22	0.3	2.53	3.3	5.6			0.76	0.83	1.04	1.28	1.49	1.47	0.000187
MCZ	32614	*Cephalophus nigifirons*			0.84	0.75	0.7	0.9	1.15	1.1	0.45	2.3	3.1	5.18			0.72	0.77	0.99	1.1	1.41	1.27	0.000133
AMNH	53125	*Cephalophus silvicultor*			1.2	1.19	1.19	1.58	1.89	2.03	0.94	3.96	4.95	8.55			1.14	1.41	1.5	1.66	2.03	2.02	0.00012
AMNH	53129	*Cephalophus silvicultor*			1.16	1.15	1.01	1.52	1.81	1.96	0.85	3.85	4.93	8.65			0.99	1.27	1.44	1.7	1.94	1.82	0.00005
AMNH	53136	*Cephalophus silvicultor*			1.34	1.31	1.28	1.66	1.99	1.99	1.04	4.29	5.37	9.23			1.11	1.43	1.64	1.78	2.09	1.69	0.000226
AMNH	194296	*Cephalophus silvicultor*			1.17	1.3	1.29	1.53	1.58	1.8	0.92	3.89	4.77	8.49			0.96	1.31	1.65	1.68	1.84	1.87	0.000242
MCZ	8018	*Cephalophus silvicultor*			1.48	1.44	1.13	1.66	1.98	2.14	0.98	4.1	5.34	9.17			1.17	1.47	1.66	1.97	2.31	2.06	0.000201
MCZ	17723	*Cephalophus silvicultor*			1.25	1.33	1.16	1.45	1.73	1.72	0.83	3.64	4.79	8.24			1.08	1.31	1.5	1.84	1.87	1.84	0.00008
MCZ	32588	*Cephalophus silvicultor*			1.33	1.18	1.1	1.34	1.72	2.07	0.73	3.56	5.17	8.47			1.14	1.42	1.72	1.98	2.32	2.17	0.000131
AMNH	53132	*Cephalophus silvicultor*			1.16	1.1	1.04	1.13	1.59	1.69	0.53	3.48	4.57	7.8			1.17	1.37	1.46	1.87	1.98	1.86	0.000214
MCZ	18622	*Cephalophus silvicultor*			1.25	1.22	1.08	1.35	1.56	1.71	0.66	3.46	4.76	8.11			1.09	1.36	1.59	1.85	2.17	1.95	0.000171

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
AMNH	53067	*Cephalophus weynsi*			0.71	0.8		1.1	1.31	1.31	0.88	2.42	3.63	5.84			0.61	0.77		1.15	1.34	1.15	0.000102
AMNH	53030	*Cephalophus weynsi*			0.77	0.74	0.7	1.08	1.3	1.25	0.64	2.45	3.44	5.71			0.68	0.83	0.93	1.24	1.34	1.22	0.000017
AMNH	53037	*Cephalophus weynsi*			0.85	0.81	0.75	1.05	1.34	1.31	0.57	2.51	3.41	5.69			0.64	0.82	1.05	1.23	1.41	1.2	0.000188
AMNH	53041	*Cephalophus weynsi*			0.8	0.8	0.77	1.08	1.2	1.16	0.66	2.41	3.3	5.6			0.69	0.85	0.82	1.2	1.33	1.19	0.000008
AMNH	53055	*Cephalophus weynsi*			0.86	0.76	0.78	1.15	1.4	1.34	0.54	2.44	3.51	5.78			0.71	0.81	0.97	1.27	1.55	1.35	0.000183
AMNH	53058	*Cephalophus weynsi*			0.85	0.9	0.82	1.06	1.34	1.41	0.55	2.41	3.6	5.63			0.76	0.91	1.02	1.28	1.53	1.3	0.000064
AMNH	53070	*Cephalophus weynsi*			0.75	0.8	0.76	1	1.27	1.17	0.64	2.33	3.13	5.3			0.69	0.81	0.99	1.18	1.38	1.25	0.000037
AMNH	53026	*Cephalophus weynsi*			0.8	0.83	0.72	1.04	1.25	1.29	0.52	2.4	3.31	5.51			0.64	0.83	0.94	1.1	1.34	1.24	0.000162
AMNH	53048	*Cephalophus weynsi*			0.86	0.87	0.75	1.03	1.29	1.27	0.6	2.52	3.19	5.47			0.67	0.72	0.89	1.2	1.36	1.21	0.000265
AMNH	53049	*Cephalophus weynsi*			0.81	0.63	0.82	0.83	1.13	1.21	0.39	2.23	3.1	5.33			0.64	0.82	0.91	1.1	1.38	1.3	0.000242
AMNH	53062	*Cephalophus weynsi*					0.75	0.79	0.99	1.11	0.06		3.28	5.51					1.01	1.32	1.55	1.47	0.000126
AMNH	53066	*Cephalophus weynsi*			0.82	0.82	0.85	0.95	1.2	1.3	0.39	2.49	3.47	5.74			0.49	0.87	0.97	1.11	1.44	1.33	0.00001
AMNH	53073	*Cephalophus weynsi*				0.65	0.67	0.73	0.99	1.31	0.24		2.95					0.72	0.88	1.25	1.31	1.26	0.000019
MCZ	8091	*Philantomba monticola*						0.74			0.46									0.7			0.000084
MCZ	31610	*Philantomba monticola*						0.62	0.76		0.29									0.66	0.69		0.000051
MCZ	32490	*Philantomba monticola*						0.69	0.77											0.75	0.89		0.000017
MCZ	40956	*Philantomba monticola*						0.62	0.65											0.66	0.76		0.000014
AMNH	52739	*Philantomba monticola*			0.45	0.5	0.43	0.69	0.77	0.76	0.41	1.48	2.1	3.49			0.36	0.46	0.58	0.75	0.83	0.75	0.000075
AMNH	170437	*Philantomba monticola*			0.5	0.57	0.5	0.67	0.74	0.79	0.4	1.62	2.1	3.58			0.4	0.43	0.58	0.74	0.83	0.79	0.000084
MCZ	18618	*Philantomba monticola*			0.5	0.5	0.51	0.63	0.74	0.7	0.31	1.54	1.93	3.25			0.33	0.39	0.47	0.59	0.8	0.8	0.000121
MCZ	23021	*Philantomba monticola*			0.5	0.51	0.51	0.72	0.84	0.82	0.4	1.67	2.14	3.68			0.42	0.54	0.65	0.84	0.88	0.84	0.000051
MCZ	23079	*Philantomba monticola*			0.48	0.46	0.45	0.6	0.67	0.79	0.3	1.41	1.95	3.24			0.34	0.4	0.54	0.63	0.71	0.7	0.00007
MCZ	31818	*Philantomba monticola*			0.48	0.53	0.47	0.64	0.77	0.78	0.29	1.45	2.11	3.52			0.45	0.47	0.55	0.75	0.85	0.75	0.00009
MCZ	32196	*Philantomba monticola*			0.47	0.47	0.41	0.64	0.7	0.66	0.35	1.42	1.96	3.33			0.37	0.43	0.56	0.72	0.8	0.72	0.000152
MCZ	32480	*Philantomba monticola*			0.54	0.55	0.5	0.67	0.75	0.82	0.36	1.48	2.12	3.46			0.43	0.45	0.56	0.71	0.84	0.83	0.000061
MCZ	32602	*Philantomba monticola*			0.53	0.52	0.54	0.63	0.78	0.8	0.33	1.52	2.09	3.52			0.41	0.44	0.58	0.69	0.82	0.77	0.000076
MCZ	32605	*Philantomba monticola*			0.45	0.51	0.46	0.67	0.77	0.85	0.4	1.5	2.19	3.58			0.4	0.51	0.65	0.7	0.84	0.78	0.000131

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
MCZ	40957	*Philantomba monticola*			0.5	0.46	0.47	0.61	0.7	0.73	0.32	1.49	1.97	3.31			0.33	0.51	0.6	0.64	0.76	0.7	0.000018
AMNH	170420	*Philantomba monticola*				0.43	0.45	0.52	0.64	0.75	0.25	1.42	1.94	3.2				0.38	0.57	0.77	0.87	0.87	0.000094
AMNH	170430	*Philantomba monticola*			0.45	0.45	0.51	0.61	0.75	0.75	0.26	1.43	1.97	3.23			0.36	0.43	0.62	0.72	0.8	0.8	0.00007
AMNH	170431	*Philantomba monticola*			0.51	0.53	0.48	0.55	0.69	0.79	0.2	1.46	1.91	3.25			0.4	0.47	0.58	0.68	0.78	0.77	0.000193
MCZ	32603	*Philantomba monticola*			0.49	0.58	0.56	0.68	0.82	0.8	0.34	1.7	2.14	3.58			0.47	0.52	0.65	0.77	0.84	0.76	0.000097
MCZ	32604	*Philantomba monticola*			0.49	0.51	0.49	0.49	0.63	0.65	0.33	1.43	1.84	3.18			0.35	0.37	0.48	0.66	0.78	0.75	0.000027
MCZ	1135	*Lama guanicoe*	0.81					2.04	2.3		1.01				0.99					1.49	1.59		0.00058
MCZ	1050	*Lama guanicoe*	1.38	1.15		1.01	1.25	1.67	2.13	2.7	1.13	2.23	6.2	8.22	0.69	0.86		0.32	1.12	1.77	1.91	1.76	0.000105
MCZ	1744	*Lama guanicoe*	0.92	0.81		0.84	1.31	1.96	2.48	2.15	1.3	2.05	6.36	8.17	0.46	0.44		0.68	1.21	1.74	1.59	1.52	0.000072
MCZ	1745	*Lama guanicoe*	0.72	0.88		1.2	1.22	1.97	2.27	2.47	1.09	2.21	6.64	8.63	0.36	0.43		0.49	1.47	1.85	1.95	1.71	0.00014
MCZ	1746	*Lama guanicoe*	0.77	0.76		0.76	1.22	1.89	2.11	2.15	1.02	1.94	6.25	7.83	0.42	0.37		0.56	1.22	1.78	1.73	1.59	0.000566
MCZ	20972	*Lama guanicoe*		0.5		0.76	1.33	1.75	2.33	2.27	1.12	2.07	6.12	7.78		0.3		0.59	1.07	1.6	1.63	1.47	0.000133
MCZ	1134	*Lama guanicoe*	1.36	1.1			1.34	1.96	1.96	2.5	0.8	1.92	5.87	6.84	0.69	0.69			1.86	1.77	1.82	1.86	0.00027
MCZ	1882	*Lama guanicoe*	0.63	0.57		0.6	1.24	1.78	1.64	2.45	0.55	1.73	5.72	7.19	0.32	0.38		0.4	1.03	1.62	1.75	1.92	0.00018
MCZ	1884	*Lama guanicoe*	0.74	0.65		0.96	1.05	1.4	1.67	1.86	0.92	1.92	4.77	6.08	0.4	0.52		0.44	1.12	1.33	1.58	1.51	0.000133
MCZ	5399	*Lama guanicoe*	0.92	1.02		1.27	1.35	1.69	2.03	2.33	0.66	1.73	5.79	7.19	0.55	0.58		0.53	1.23	1.66	1.87	1.84	0.00031
MCZ	6171	*Lama guanicoe*	0.82	0.71		0.63	1.18	1.62	1.54	1.92	0.57	1.32	4.95	5.97	0.35	0.47		0.43	0.97	1.6	1.97	1.9	0.000025
MCZ	19108	*Lama guanicoe*	0.74	0.78			1.43	1.7	2.16	2.79	0.7		6.42	7.33	0.43	0.44			1.06	2	2.07	1.82	0.00016
MCZ	29878	*Lama guanicoe*	1.2	0.91		1.3	1.14	1.39	1.68	2.25	0.53	1.8	5.24	6.62	0.57	0.63		0.45	1.24	1.44	1.74	1.9	0.000096
MCZ	61749	*Lama guanicoe*	1.34	1.17		0.94	1.05	1.6	2	2.15	0.45	1.63	5.5	6.89	0.61	0.6		0.6	1.34	2.05	2.18	1.9	0.000147
MCZ	5243	*Vicugna vicugna*																					0.00006
MCZ	5244	*Vicugna vicugna*																					0.000068
MCZ	6170	*Vicugna vicugna*						1.95												1.29			0.000054
MCZ	7132	*Vicugna vicugna*						1.92												1.29			0.000055
MCZ	40983	*Vicugna vicugna*						1.79	1.85											1.06			0.000108
FMNH	49753	*Vicugna vicugna*						1.79			0.58									1.1			0.000054
AMNH	244136	*Vicugna vicugna*						1.73			0.47									1.09			0.000138
AMNH	15997	*Vicugna vicugna*	0.61	0.58				1.54	1.9		0.8				0.31	0.25				1.26	1.29		0.000121
MCZ	58030	*Vicugna vicugna*						1.58	1.86		0.58									1.18	0.96		0.000031
FMNH	92748	*Vicugna vicugna*						1.63	1.83		1.36									1.13	1.09		0.000026
AMNH	46	*Vicugna vicugna*	0.94	0.9		0.79	1.03	1.63	1.97	1.97	0.84	1.84	5.44	7.17	0.47	0.47		0.54	1.08	1.46	1.33	1.27	0.000146
MCZ	7877	*Vicugna vicugna*						1.49	1.85											1.16	1.09		0.000067
FMNH	36047	*Vicugna vicugna*	0.76	0.71		0.52	0.95	1.32	1.76	1.73	0.84	1.41	4.72	6.04	0.42	0.41		0.44	0.81	1.31	1.17	1.09	0.000047
FMNH	121665	*Vicugna vicugna*	0.78	0.75		0.7	0.79	1.37	1.62	1.81	0.66	1.31	4.52	5.77	0.39	0.39		0.36	1.06	1.32	1.33	1.2	0.000286
MCZ	1883	*Vicugna vicugna*	0.64	0.6		0.66	0.98	1.33	1.77	1.82	0.58	1.51	4.72	6.17	0.31	0.29		0.42	0.91	1.41	1.63	1.36	0.000091
MCZ	6167	*Vicugna vicugna*	0.73	0.71		0.81	1.06	1.21	1.61	1.82	0.42	1.47	4.38	5.55	0.31	0.31		0.45	0.91	1.35	1.48	1.37	0.000053
MCZ	6168	*Vicugna vicugna*	0.46	0.37			0.99	1.22	1.68	1.82	0.62	1.36	4.44	5.58	0.29	0.26			0.69	1.41	1.64	1.5	0.000101

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
MCZ	6169	*Vicugna vicugna*	0.91	0.87			0.87	1.12	1.26	1.69	0.51	1.12	3.92	4.96	0.44	0.44			0.71	1.34	1.39	1.43	0.000103
FMNH	21505	*Vicugna vicugna*	0.96	0.9			1.02	1.04	1.24	1.71	0.19	1.2	3.99	4.96	0.47	0.49			0.72	1.27	1.4	1.46	0.000126
MCZ	42785	*Vicugna vicugna*	0.54	0.56		0.58	0.89	1.46	1.61	1.78	0.93	1.25	4.7	5.68	0.28	0.3		0.37	0.84	1.45	1.32	1.13	0.000248
MCZ	42923	*Vicugna vicugna*	0.43	0.39		0.47	0.78	1.21	1.29	1.69	0.31	1.24	4.08	4.68	0.24	0.27		0.4	0.96	1.42	1.32	1.35	0.000098
AMNH	2911	*Camelus bactrianus*			0.89																		0.000034
AMNH	14109	*Camelus bactrianus*	2.35		2.24	1.64	2.18	2.96	4.27	4.48	1.39	4.11	11.31	15.07	1.65		1.49	1.71	2.14	2.7	2.62	3.87	0.000237
AMNH	14110	*Camelus bactrianus*	1.66		1.17	1.73	2.32	3.19	4.01	4.47	2.28	3.9	11.26	14.76	1.14		1.02	1.69	2.44	2.52	2.72	2.84	0.000208
AMNH	14113	*Camelus bactrianus*	3.2		2.03	2.11	2.62	3.33	4.15	4.81	2.66	4.65	12	16.13	2.27		1.37	1.8	2.83	3.32	3.45	2.97	0.000093
AMNH	80232	*Camelus bactrianus*	2.43		1.27	2.07	2.35	3.38	3.66	4.01	1.96	4.39	10.57	14.78	0.97		0.69	1.55	2.27	2.77	3.03	2.12	0.000066
AMNH	80233	*Camelus bactrianus*	2.55		1.46	1.9	2.16	2.64	2.96	3.95	1.39	4.03	6.88	13.26	1.47		1.46	1.9	2.16	2.33	2.85	2.76	0.000203
AMNH	90117	*Camelus bactrianus*	3.73		2.33	1.98	2.25	3.2	4.33	4.02	0.53	4.19	11.31	14.86	2.71		1.56	1.48	2.93	2.93	3.23	3.04	0.00016
AMNH	90380	*Camelus bactrianus*			1.24			4.33			2.06						0.86			2.72			0.000198
AMNH	139842	*Camelus bactrianus*	3.09		2.08	2.12	2.16	3.12	3.98	4.76	1.89	4.68	11.84	17.06	2.2		1.45	2.09	3.08	3.41	3.07	3.07	0.000346
FMNH	18847	*Camelus bactrianus*	2.74		1.43	1.85	2.15	2.73	3.4	4.46	2.01	3.95	10.36	14.02	1.77		0.95	1.7	2.44	2.71	2.72	2.51	0.0004
FMNH	18848	*Camelus bactrianus*						4.25	5.02		2.55									2.66	2.63		0.000002
FMNH	21708	*Camelus bactrianus*	2.58		1.2	1.8	2.4	2.9	3.51	4.61	1.57	4.3	10.7	14.57	1.46		0.97	1.67	2.5	3.31	3.44	2.93	0.000126
FMNH	60503	*Camelus bactrianus*	2.2		1.37	2.06	2.56	3.41	3.97	4.99	2.33	4.45	12.14	15.96			1.36	1.72	3.08	3.49	3.6	3.6	0.000107
FMNH	64438	*Camelus bactrianus*	2.27		1.92	1.79	2.35	2.79	3.45	4.64	1.52	4.06	10.64	14.14	1.32		1.04	1.99	2.56	2.68	3.16	3.36	0.000072
VPL M	8822	*Camelus bactrianus*	4.31		2.61	1.67	2.24	4.07	4.23	5.08	2.28	4.55	13.06	17.15	3.14		1.69	1.85	2.86	3.53	4.2	4.1	0.000179
MVZ	74673	*Camelus bactrianus*			1.03	2.06	2.65	4.5	4.76		2.85	4.55						1.84	2.65	3.18	3.06		0.000233
AMNH	14107	*Camelus dromedarius*	2.05		1.36	2.19	1.99	2.25	2.96	4.07	0.83	3.98	9.5	13.45	0.98		0.72	1.45	2.55	3.04	3.17	2.97	0.000234
AMNH	14108	*Camelus dromedarius*	1.31					4.23			1.9				0.53					2.6			0.00017
AMNH	14111	*Camelus dromedarius*	3.02		1.78	1.94	2.41	2.83	3.45	4.5	1.8	4.35	10.45	14.82	1.64		1.05	1.77	2.57	3.31	3.35	3.02	0.000197
AMNH	14112	*Camelus dromedarius*	1.51		1.06	1.59	1.86	2.34	3.49	3.96	1.06	3.98	9.91	13.42	1.04		0.74	1.66	2.31	3.16	3.2	2.74	0.000016
AMNH	80198	*Camelus dromedarius*	2.82		1.85	2.14	2.34	2.48	3.17	4.24	1.59	4.45	10.02	14.24	1.65		0.93	1.64	2.46	2.73	2.94	2.57	0.000757
AMNH	201157	*Camelus dromedarius*				2.06	2.53	3.05	3.76	4.72	2.28	4.43	11.93	15.06				1.82	2.83	2.91	3.05	2.8	0.000583
FMNH	42446	*Camelus dromedarius*	1.44		0.92	1.62	1.95	2.55	3.43	4.18	1.72	3.79	10.21	13.87	0.85		0.69	1.64	2.28	3.05	3.09	2.66	0.000181
FMNH	42447	*Camelus dromedarius*	1.56		1.25	2.05	2.33	2.83	3.14	4.16	0.97	4.37	9.82	13.87	0.92		0.58	1.76	2.49	3	3.35	3.02	0.000094

Specimen	ID Number	Species	L C1	L I3	L P2	L P3	L P4	L M1	L M2	L M3	H M1	Premolars	Molars	Toothrow	W C1	W I3	W P2	W P3	W P4	W M1	W M2	W M3	Uncertainty (m)
FMNH	42448	*Camelus dromedarius*	1.54		0.9	1.65	2.19	2.63	3.38	4.24	1.45	4.27	10.02	13.78	0.93		0.67	1.44	2.23	2.63	3.38	2.64	0
FMNH	42449	*Camelus dromedarius*	0.9					3.76			1.74				0.5					2.71			0.00033
FMNH	42451	*Camelus dromedarius*	1.38		1.1	2.16	2.42	2.68	3.33	4.02	1.99	4.17	10.28	14.19	0.88		0.7	1.34	2.4	3.26	3.29	2.79	0.000112
FMNH	129800	*Camelus dromedarius*	1.83		1.35	2.16	2.4	3.51	4.43	4.33	2.3	4.52	8.98	15.59	1		0.77	1.63	2.6	3.4	3.42	2.76	0.000382
VPL M	4170	*Camelus dromedarius*	3.16		1.71	2.47	2.18	3.38	4.14	3.48	2.12	4.9	10.53	15.05	1.92		1.09	1.82	2.63	3.33	3.14	2.83	0.000074
MCZ	1049	*Camelus dromedarius*	2.51		1.56	1.91	2.44	2.89	4.03	4.29	2.25	4.35	10.87	14.87	1.64		1.02	1.61	2.46	2.93	3.1	2.82	0.00005
MCZ	8058	*Camelus dromedarius*	2.46		1.6	1.88	2.4	3	3.72	4.37	1.49	4.53	10.6	14.81	1.82		1.06	1.65	2.46	2.95	3.12	2.83	0.000058
MCZ	10787	*Camelus dromedarius*				2.16	2.55	3.12	4.32	4.27	2.47	4.64	11.02	15.33				1.73	2.37	2.82	2.92	2.57	0.000276
MCZ	16891	*Camelus dromedarius*	1.18		0.63	1.94	2.44	3.11	4.5		2.36	4.35			0.78			1.77	2.23	2.8	2.76		0.000097
MCZ	42152	*Camelus dromedarius*	1.34		1.1	1.58	2.3	2.39	2.95	3.91	1.1	3.88	8.95	12.55	0.83		0.6	1.6	2.28	2.63	3.05	3.06	0.000148
MCZ	47405	*Camelus dromedarius*	1.48		1.15	2.07	1.89	2.49	3.03	3.88	0.45	3.87	9.13	12.83	0.97		0.76	1.84	2.31	3.29	3.25	2.81	0.00006
MCZ	51314	*Camelus dromedarius*	1.52		1.27	2.31	2.16	2.89	3.74	4.08	2.2	4.37	10.39	14.4	0.93		0.74	1.44	2.32	2.96	3.29	2.79	0.000076
MCZ	57837	*Camelus dromedarius*	1.57		1.41	2.1	2.08	2.92	3.6	4.38	1.09	4.18	10.73	14.4	0.91		0.86	1.78	2.73	3.17	3.36	3.21	0.000017
MCZ	60131	*Camelus dromedarius*	3.81		2.21	2.49	2.1	2.51	2.96	4.24	0.49	5.27	9.23	13.48	2.32		1.6	2.23	2.76	3.11	3.56	3.54	0.000182
MVZ	101026	*Camelus dromedarius*	1.89		1.25	1.8	2.32	3.62	4.22	4.36	2.05	4.12	11.39	15.17	1.19		0.88	1.62	2.57	3.02	2.87	2.57	0.000548
AMNH	53670	*Hylochoerus meinertzhagheni*	2.97		0.68	1.13	1.43	1.65	2.3	4.29	0.56	4.6	6.75	11.3	3.34		0.58	0.78	1.13	1.68	1.91	1.99	0.000288
AMNH	Unlabeled Female	*Hylochoerus meinertzhagheni*	3.06			1.12	1.18	1.66	2.07	4.43	0.32	1.97	7.97	9.89				0.89	1.18	1.6	2.07	2.29	0.000209
MCZ	21202	*Hylochoerus meinertzhagheni*	2.96				1.42	1.68	2.22	4.08	0.34	2.49	7.96	10.43	2.75				0.95	1.65	2.01	1.622	0.00013
AMNH	36431	*Hylochoerus meinertzhagheni*	3.1844			0.91		1.71	2.29	4.21	0.78	2.29	8.15	10.58	4.39			0.73		1.49	2	1.76	0.000535
AMNH	36438	*Hylochoerus meinertzhagheni*	3.19					1.81	2.42	4.46	0.87	2.26	8.5	10.73						1.69	2.15	2.25	0.000186
AMNH	89456	*Hylochoerus meinertzhagheni*	2.94			0.79	1.16	1.17	1.7	4.22	0.21	1.86	7.08	8.88	3.36			0.52	0.94	1.24	1.59	1.8	0.000114
AMNH	Unlabeled Male	*Hylochoerus meinertzhagheni*	4.5			0.87	1.12	1.84	2.35	4.41	0.62	1.99	8.82	10.07				1.08	1.34	1.91	2.41	2.4	0.000214
MCZ	27851	*Hylochoerus meinertzhagheni*	3.93			1.32	1.65	1.81	2.19	4.78	0.68	3.32	8.74	11.78	3.78			0.66	1.26	1.81	2.17	2.43	0.000312
MCZ	38011	*Hylochoerus meinertzhagheni*	3.18			1.08	1.1	1.79	2.46	4.53	0.76	2.22	8.75	10.08	3.02			0.65	0.922	1.66	2.14	2.17	0.000419
AMNH	53665	*Hylochoerus meinertzhagheni*	2.43			1.08		1.57	2.52	4.26	0.61	2.32	8.34	10.62	2.59			0.69		1.56	1.91	1.83	0.0002
AMNH	81803	*Hylochoerus meinertzhagheni*	3.22					1.58	2.39	4.66	0.43		8.47	10.28						1.41	2.02	2.15	0.00022
MCZ	12410	*Hylochoerus meinertzhagheni*	2.14		0.91	1.05		1.42	1.71		0.52	3.06	6.07	9.07	1.9		0.43	0.733		1.33	1.55		0.00001

Specimen	**ID Number**	**Species**	**L C1**	**L I3**	**L P2**	**L P3**	**L P4**	**L M1**	**L M2**	**L M3**	**H M1**	**Premolars**	**Molars**	**Toothrow**	**W C1**	**W I3**	**W P2**	**W P3**	**W P4**	**W M1**	**W M2**	**W M3**	**Uncertainty (m)**
AMNH	36430	*Hylochoerus meinertzhageni*	2.5					1.61	2.71		0.58				1.63					1.54	1.52		0.0004
AMNH	36432	*Hylochoerus meinertzhageni*	2.23			1.28	1.25	1.62	2.56		0.77	2.49						0.68	0.95	1.38	1.82		0.000129
AMNH	36433	*Hylochoerus meinertzhageni*	2.03			1.24	1.37	1.62	2.56		0.55	2.26						0.71	1.08	1.4	1.79		0.000321
AMNH	81802	*Hylochoerus meinertzhageni*	3.59						2.49	4.15				10.08							2.09	2.3	0.000335
AMNH	81804	*Hylochoerus meinertzhageni*	1.91			1.26	1.05	1.66	2.53		0.6				1.88			0.79	0.91	1.33	1.8		0.000064
AMNH	89401	*Hylochoerus meinertzhageni*	1.77		0.49	0.94	1.15	1.48	2.44		0.35	2.57			1.94			0.61	0.75	1.01	1.4		0.000143
MCZ	39428	*Hylochoerus meinertzhageni*						2.01			0.41									1.44			0.000553
MCZ	39429	*Hylochoerus meinertzhageni*	1.74					1.66	2.68		0.5				1.5					1.52	1.75		0.000092